Monograph of Cimicidae

(Hemiptera - Heteroptera)

By

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With Sections on

THE PARAGENITAL SYSTEM AND SCENT GLANDS
by JACQUES CARAYON
Muséum National d'Histoire Naturelle, Paris

REPRODUCTIVE PHYSIOLOGY *by* NORMAN T. DAVIS
University of Connecticut, Storrs

CYTOLOGY AND CYTOGENETICS *by* NORIHIRO UESHIMA
University of California, Berkeley

and

INHERITANCE OF X CHROMOSOMES *by* HARLLEY E. MC KEAN
Purdue University, Lafayette, Indiana

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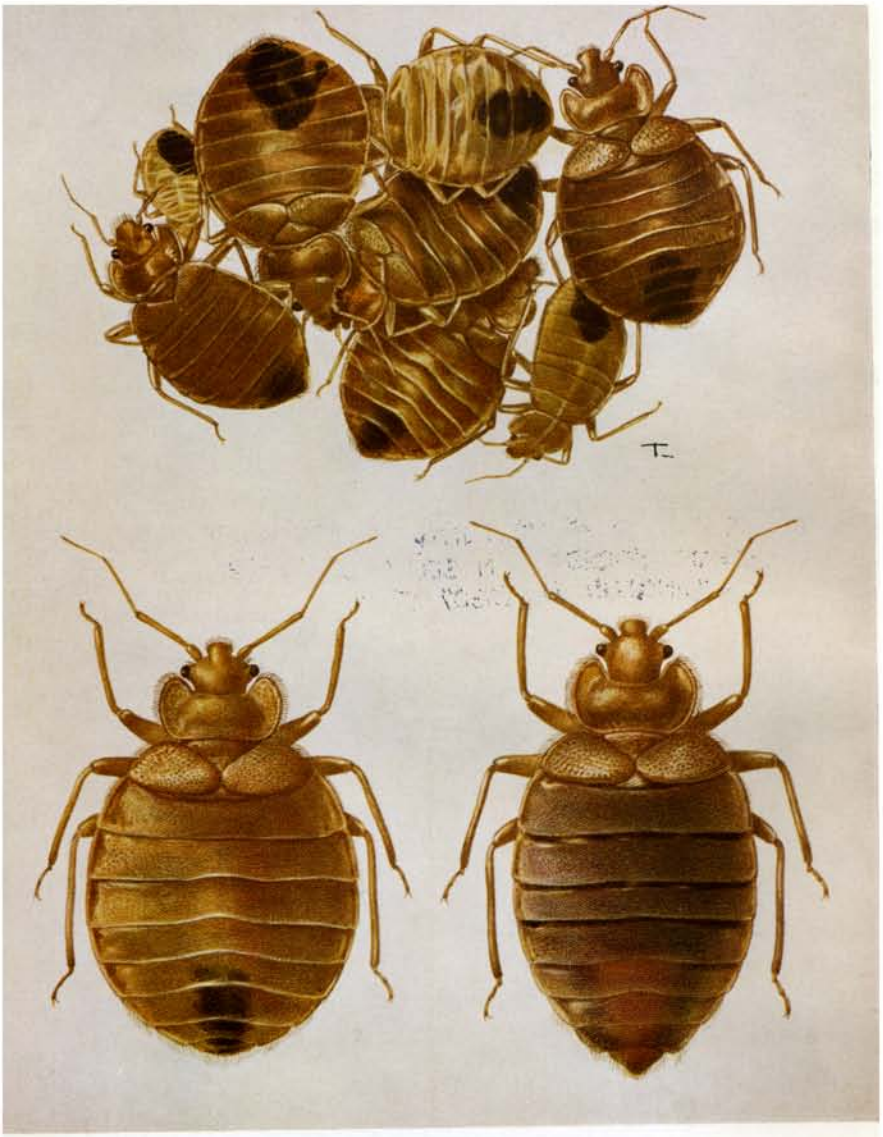

FRONTISPIECE

Cimex lectularius Linnaeus. Left, female; right, male; above, cluster of nymphs and adults (Terzi).

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Preface

Before World War II the leading centers of bed bug research were in Germany and England. Taxonomic work on Cimicidae, based on the early collections of Rothschild and Jordan, was centered at the British Museum (Natural History) in London. The curator of Hemiptera there, W. E. China, was consulted by those engaged in studies of genetics, ecology, and taxonomy. The present study began in London in 1948 when Dr. China indicated that his plans for a world monograph had to be abandoned due to the pressure of other work.

The first step in taking up this project was to enlist the aid of the late G. F. Ferris of Stanford University, with whom I had worked on an earlier study of bat bugs of the family Polyctenidae. With great enthusiasm Professor Ferris set out to illustrate every species in characteristic dorsal/ventral view and to study the external morphology of *Cimex lectularius*. A preliminary report, with descriptions of new species, was published in Microentomology (Ferris and Usinger 1957), and several shorter papers appeared before Ferris' death in 1958.

In 1957 the work broadened and took a somewhat different turn. Emphasis shifted to a study of host selection (supported by grants from the U. S. Public Health Service) and the highly specialized internal reproductive structures (in collaboration with Dr. Jacques Carayon at the Museum d'Histoire Naturelle in Paris). Old and new species were studied in all the leading museums of the world, and colonies of live bugs were established in Berkeley from specimens collected on expeditions to South America in 1957, 1962, and 1964; to Africa in 1959; and to the Orient in 1957 and 1959. The availability of live bugs enlarged the scope of the work. Comparative studies of behavior, as well as experimental taxonomy, cytology, and genetics, became possible. Dr. Norihiro Ueshima collaborated in these studies and has prepared a summary of cytogenetics that is included in this book.

In many ways, this project has been a unique adventure. From museum taxonomy it has led to experimental studies of the nature of species and the processes of speciation. Field studies have led to bat roosts in hollow trees in Patagonia, to ancient tunnels of grave robbers in the pyramids of Egypt, and to hundreds of caves throughout the world. Field assistants

included wood cutters to fell huge trees harboring fish-eating bats in mangrove swamps in Trinidad, quarry workers to blast open bat roosts in cliffs in the Western Desert near Cairo, and mountaineers to rope down vertical cliffs to the nests of white-throated swifts in California. Literary pursuits included studies of bed bugs in relation to man from earliest times as revealed by folk-lore and comparative linguistics. The use of bed bugs to relieve human suffering is a fascinating story as told in pharmacopoeas of ancient times. Early methods of control are amusing, compared with present-day techniques employing residual insecticides.

And so the present work has grown until now a "final" report is long overdue. Every page contains questions or points that need further study. This is especially true of the taxonomic treatment of isolated populations of bat bugs in Europe and North America and of the infinite array of bugs that inhabit the nests of cave swiftlets on the thousands of islands of Southeast Asia. Thus the work is finished but not complete—it points the way to further studies of these fascinating insects.

Acknowledgments

The main support for this work came from the University of California Agricultural Experiment Station, the Miller Institute for Basic Research in Science on the Berkeley campus of the University, and the U. S. Public Health Service (Research grants E-1496A to F). Dr. W. E. China of the British Museum (Natural History) and Dr. Jacques Carayon of the Museum National d'Histoire Naturelle in Paris were close collaborators over the years, and the late Professor G. F. Ferris co-authored all the work until his untimely death in 1958. Dr. Norman T. Davis of the University of Connecticut (under Public Health Service grant E-3862) worked for a year at Berkeley on reproductive physiology and contributed much to the final manuscript. Dr. T. R. E. Southwood of Imperial College Field Station, Silwood Park, England, helped in many ways during his year at Berkeley.

Students and research assistants carried out a great deal of the laboratory work on the project. Of these, Norihiro Ueshima is solely responsible for the all-important work on cytogenetics and many of the experimental crosses; R. E. Ryckman did the original work on *Hesperocimex;* R. D. Lee, that on *Haematosiphon;* Jon Herring and Barbara Wilson, bibliography; Mrs. Valerie Williams Linsdale, much of the work on host selection and the biology of *Leptocimex duplicatus;* Alan Berryman, most of the behavior studies; P. D. Ashlock, preliminary work on computer analysis; Woodbridge H. Foster, experimental crosses in *Oeciacus;* and Barbara Wilson, descriptions of immature stages of *Oeciacus, Bucimex,* and *Leptocimex,* experimental crosses, and general assistance with illustrations. The original work of each assistant is acknowledged in the text.

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1 Introduction

The family Cimicidae includes the human bed bugs, the bat bugs, chicken bugs, swallow bugs, pigeon bugs, and others for which no common names have been proposed. Seventy-four species are recognized and arranged in 22 genera and 6 subfamilies. Half of the species have been discovered in the past 10 years during the course of this project.

The Cimicidae are related to the Anthocoridae, which prey on insects and mites and may occasionally bite warmblooded animals, and to the Polyctenidae, which are permanent ectoparasites of bats. Cimicidae are only temporary ectoparasites, usually remaining in the nests or in cracks in rooms or roosts of their hosts between blood meals. They are not well adapted to cling to the fur or feathers of their hosts in flight but do so on rare occasions and are distributed in this way at least for short distances.

Twelve of the genera are associated exclusively with bats and 9 with birds. Only the genus *Cimex* has some species that are attached to bats and others that occur on birds. There are 3 human bed bugs: *Leptocimex boueti* Brumpt on bats and man locally in West Africa; *Cimex hemipterus* (F.) attacking man, chickens, and rarely bats throughout the Old and New World tropics; and *Cimex lectularius* L. associated with man, bats, chickens, and occasionally other domesticated animals over most of the world. The 2 last-named species of *Cimex* have followed man since the dawn of recorded history and contributed not only to his misery but also to his folklore, pharmacopoeia, and literature.

Scientifically, bed bugs are fascinating to study. Because they are easy to rear they are ideal subjects for classroom demonstrations and laboratory research.

ORIGIN OF HUMAN BED BUGS

It has been assumed by Sailer (1952) and others that *C. lectularius* was associated with man and bats when all three lived together in caves somewhere in the Middle East. The bugs later adapted to man-made dwellings and spread throughout the world as civilization advanced. Kiritshenko (1951) even thought that Vlassov (1929) had located an

original "biotope," a huge cave in Turkmenia where bats and bugs lived far removed from man. These bugs proved not to be *C. lectularius* and I describe them farther on as a new species of bat bug. According to Horvath (1914b) *C. hemipterus* also became associated with man in the Old World—being more of a tropical species, it was thought to have originated either in southern Asia or in tropical Africa. Such theories, while probably true, were based on scanty evidence.

Fortunately new types of evidence are now available. First, morphological evidence shows that all Old World species of *Cimex* have a narrowly cleft paragenital sinus. In contrast, the American bat bugs have a rounded notch. Both *C. lectularius* and *C. hemipterus* have the narrowly cleft sinus and therefore belong with the Old World species. Second, linguistic evidence shows that there is no word for bed bug in any native American language, whereas many names are known in Old World languages (Table 1–1). Third, the geographical distribution of the species of *Cimex* that are associated exclusively with bats is Holarctic and does not even include North Africa. Hence it is unlikely that the human bed bugs originated in Africa, even though there are names for the bed bug in many African languages.

Within the area of Europe, the Middle East, and India the question of the origin of *C. lectularius* becomes highly speculative. According to Oakley (1956) man did not regularly occupy caves or rock shelters before he had domesticated fire as a protective weapon against carnivores, approximately 250,000 years ago in Europe. About 100,000 years ago Neanderthal man lived in caves in the Middle East with *Myotis* and *Rhinolophus* and perhaps other bats, and Cromagnon man lived under similar conditions through the last Ice Age (12,000 B.C.) (Bodenheimer 1960). Still later (8000 to 5000 B.C.) man began the practice of agriculture and the domestication of animals around the "fertile crescent" in southwestern Asia (Braidwood 1960). The move from cave to village was gradual—some people still live in caves in Europe and the Middle East today. However, there was a steady trend toward congregating in large cities like the Sumerian city-state between the Tigris and Euphrates rivers with tens of thousands of inhabitants by 4000 B.C. (Adams 1960). As civilization advanced, deforestation and soil erosion altered the total ecology of the Middle East. Man and presumably also bats and bugs were profoundly affected by the change. It is of course possible that the bed bug was associated with man throughout his early evolution in the Pleistocene and on through the Paleolithic and Neolithic periods. However, it seems more likely that it became permanently associated with man during the period of movement from cave to village to city. As an alternative hypothesis, the bugs may have turned to man on many occasions while their bat hosts roosted in his houses. *C. lectularius* occurs in Europe today in bat roosts in churches and other manmade structures and in tree holes, and a colony has recently been discovered by

Povolný in a bat cave near Kabul, Afghanistan (Usinger and Povolný 1966).

The spread of *C. lectularius* is not easy to document, but it was certainly present in Greece by 400 B.C., in Italy by 77 A.D., and in China by 600 A.D. According to Kemper (1936), the first record for Germany was at Strassburg in the 11th century, for France the 13th century and for England, 1583. There is an oft-repeated story that the bed bug "did not exist in England previous to the fire of London in 1666 and that it was transported thither in timber from America" (Latreille 1829), but Mouffet (1634) records that Thomas Penny, in 1583 (misprinted 1503, Matheson 1941) was called by 2 noble ladies of Mortlake who were troubled by *Cimex*.

Man's use of fire definitely made him a more suitable host for the bed bug, especially in temperate regions in the winter. Johnson (1942) has shown that the tremendous increase in infestations in northern European cities in the early 20th century was favored by the increased use of central heating.

The pigeon bug, *Cimex columbarius* Jenyns, probably followed a similar route northward from the Mediterranean, although I mention alternative hypotheses later. As for the tropical bed bug, evidence is lacking except for collections on bats in southern India and Java.

LINGUISTICS

Language and folklore provide valuable evidence of bed bugs in prehistoric times. Table 1–1 lists the names that I have been able to find applied to bed bugs in various languages. Many more undoubtedly exist. Kemper (1959) gives additional variants, nicknames, and slang expressions. I am indebted to Murray B. Emeneau, William E. Welmers, Jean Rageau, and other colleagues and students for assistance in tracing names in various languages.

Generalizations are probably unjustified with such a small sample but I should mention a few points. First, all Indo-European, African, and Oriental languages that we investigated had names for the bed bug. Many of the names are obviously distinct and unrelated, but it is interesting to note the groups of related names in the Romance languages based on *Cimex*, in the Germanic languages based on *Wandlaus* (wall louse), and in the Slavic languages based on *pluskwa*, meaning "flat" (an unfed bug that hides in cracks?). Other groups of names not listed center around the Czech *štěnice*, meaning "wall," and the Sanskrit words *uddamsa* and *matkunah*. The latter (Emeneau)[1] has variant derivatives in Kashmiri (*mȏkun*), Gujarati (*mākan*), Hindi (*makhūn*), Singhalese

[1] Authors in parentheses without dates indicate unpublished work, principally of colleagues or assistants.

Table 1–1.—Native names for the bed bug.

Name	Language	Meaning	Source
Coris	Greek	to bite	Kemper
Cimex	Latin	(Gray?)	"
Cimice	Italian	from *Cimex*	"
Chinche	Spanish about 1400	from Castilian *cisme* or *Chisme* (*L. Cimex*)	"
Chinga	Gallic	from *Cimex*	"
Wanze	German (Bavaria) about 1200	Abbreviation of wall louse	"
Wandluis	Old High German and Dutch	Wall louse	"
Wandlaus	German	Wall louse	"
Wegluis	Old High German	Wall louse	"
Wägglus	Swedish	Wall louse	"
Vaeggelus	Danish	Wall louse	"
Wäntele	Switzerland	Little *Wanze*	"
Nachtkrabbler	German (Eifel region)	Night crawler	"
Venerschen	German (Fehrmarn)	Little venereal	"
Tüchwanze	German (Schleswig-Holstein)	Clothbug	"
Tapetenflunder	German (Ruhr)	Wallpaper flounder	"
Kammerflunder	German (Dresden)	Chamber flounder	"
Punaise	French	*Puer* (to stink)	Kemper
Pute	French dialect		"
Perceveja	Portuguese	Pursuer	"
Lude	Finnish		Hackman
Lutikka	Finnish		"
Kotilude	Finnish	House louse	"
Stěnice	Czechoslovakia	Wall	Povolný
Plostice	Czechoslovakia	Flat	"
Pluskwa	Polish	Flat	Halperin
Poloska	Hungarian	Flat	Novikoff
Klop	Russian		Povolny
Wall louse	English		Kemper
Miol-fhioda	Scottish Gaelic		Kirkaldy
Bug	English–Celtic	Spirit, ghost, goblin	Kemper
Buk	Arabic—widely used		Husseiny
Fusfus	Syria—in villages		Hoogstraal
Akalan	Egyptian villages	Itching	"
Katman	Arabic—Bagdad		
Pishpesh	Hebrew		Halperin
Sass	Persian		Voidjani
Tuhan	Amharic—Ethiopia		
Chuar	Shilluk—Sudan		Hoogstraal
Thuar	Dinka—Sudan		"
Baan	Nuer—Sudan		"
Kpilikpili	Kpelle—Liberia		Welmers
Ototon	Ewondo (Boulou)—Bantu		Rageau
Ket i nan	Bassa—Bantu		Rageau
Ekukulan	Douala—Bantu		"
Mandere	Baya (Gbaya)—Ubangi-Chari		"
Burmudi	Peul-Fula		"
Kunguni	Swahili		Natives Tanganyika
Yele	Kirega—Uvira		"

Table 1–1.– (continued)

Name	Language	Meaning	Source
Limosa	Lonkundo–Bantu		Welmers
Uddamsa	Sanskrit	Biter	Emeneau
Matkunah	Sanskrit		Emeneau
Tua Ruad	Thai		Chakratong
Rep	Vietnamese		
Piq-seq	Chinese–Shanghai	Wall louse	Chou
Nankinmusi	Japanese	Nanking bug	Carr
Tokozirami	Japanese	Bed louse	Carr

(*makunā*), and Panjabi (*mãgnū*), and the former in Prakrit (*uddamsa*), Assamese (*urah*), Hindi (*uras*), and Nepali (*urus*).

Kemper (1959) gives nicknames in several languages, including the following in English: "mahagony-flat" (Baltimore), "heavy dragoons" (Oxford), and "red coats" (New York).

The origin of the word "bug" is of special interest. The Oxford "New English Dictionary" (Murray, J. A. H., 1888, Vol. I, part II, p. 1159–60) says of "bug" as applied to *Cimex*, "etymology unknown." The English word "bug" (possibly from the Welsh *bwg*) meant a goblin or ghost (like the English "bugbear") and this is the sense in which it was used by Shakespeare in 1603: "With, ho! such bugs and goblins in my life" (Hamlet, Act V, Scene 2).

Apparently the word was first applied to *C. lectularius* in England in the 17th century: "*Spungius.* We have bugs, Sir!" (Massinger, P., and T. Decker, 1622, The Virgin Martyr, Act III, Scene 2). Prior to that time the name "wall louse" was used. The choice of name could have been fortuitous, or it might have been used because the bugs contributed to the terror of the night. Another possibility is derivation from the Arabic word *buk* (pronounced quite like the English "bug"). *Buk* is an old and widespread name for *C. lectularius* throughout the Arab world and could have been picked up by travelers and brought back to England.

There is a tendency in modern times for the name "bug" to be used as a collective term for all Hemiptera or as a combining form: plant bug, stink bug, etc. Also the order Hemiptera is referred to as the "true" bugs in contrast to beetles, flies, etc. All insects and other small arthropods are commonly called "bugs," and even bacteria are included in colloquial usage. The names *punaise, Wanze, pluskwa, buk,* and perhaps others have likewise been applied to the Hemiptera as a whole.

Like anything small, the new "compact" automobiles often are referred to as "bugs." An American newspaper of recent date refers to "Volkswagen's bug-free bugs," meaning a small car free of mysterious defects. Other common usages are: "bughouse," or insane asylum; "to bug," meaning to bother or cast a spell (or hide a microphone in a room); "bug-eyed," with protruding eyes; "buggy," a horse-drawn car-

riage; "big bug," an important person; "tennis bug," a tennis enthusiast (applied to any other sport or hobby). Liquor of inferior quality is sometimes referred to as "bug juice."

FOLKLORE

Because of its long and intimate association with man the bed bug has entered into the legends and lore of many peoples. The German language is especially rich in such references (Kemper 1959). In the United States there are references of unknown origin that are obviously fallacious. For example: "bed bugs are a warning of a fight" (1948, New York Folklore Quart., 4: 163) or "a bedbug that has first seen the light of day between August 15 and September 8 is strong enough to penetrate seven walls" (1946, J. Amer. Folklore 61: 278).

Also, there are sayings, such as "snug as a bug in a rug" or "crazy as a bed bug," that have proved difficult to analyze or explain (Taylor, A., 1956, Folklore Studies 3: 29) (Kentucky Folklore Record 2: 2).

An oft-quoted rhyme states:

"The June bug has a gaudy wing,
The lightning bug a flame,
The bed bug has no wings at all
But he gets there just the same."

Of more zoological interest are the sayings that swallows bring bed bugs (Hand, W. D., 1956, Western Folklore 15: 290), that "chimney swifts bring bed bugs if they can get into a room" (Rupp, W. J., 1946, Proc. Penn. German Soc. 52: 266), and that "bats flying into the house are sure to bring bed-bugs with them; you can see such vermin under the bat's wings." (Archibald, R., 1959, unpubl., Kentucky). The first of these refers to the swallow bug (*Oeciacus*), the second to the chimney swift bug (*Cimexopsis*), and the third to a bat bug (*Cimex adjunctus* Barber).

EARLY RECORDED HISTORY

Bed bugs are mentioned frequently in early literature (Bodenheimer 1928–1929). Aristophanes in 423 B.C. (The Clouds) refers to bed bugs as follows:

"Socrates: Where is Strepsiades? Come forth with your couch.
Strepsiades (from within): The bugs do not permit me to bring it forth."

In *Historia Animalium* (Book V: 31), Aristotle (384–322 B.C.) says that, "Bugs are generated from the moisture of living animals, as it dries up outside their bodies." Medicinal uses were given by Dioscorides of

Cilicia, a Greek army surgeon of the time of Nero (54–68 A.D.). He refers to "Cimices lectorum" as neutralizers of the venom of serpents and, in an early translation by Goodyer (see Gunther 1933) says, "Cimices of ye bed [being taken] to the number of seven of them and put in meate with beanes, and swallowed downe before the fitt, doe help such as have ye quartaine ague. And being swallowed downe without beanes [they help such as are] bitten by an Aspick. Being smellt unto, they call back such againe as are fallen into a swoune by the strangulation of the vulva. Being dranck with wine or vinegar, they expell horse leeches. Being beaten small and put into the Urinaria Fistula they cure the Dysuria."

Matthioli (1568), in his commentary on Dioscorides, gives a fuller treatment with a large figure of a bed infested with bugs (Fig. 1–1). Pliny in 77 A.D. (Bostock and Riley translation, Book XXIX, Chap. 17) quotes freely from Dioscorides and other early sources, giving remedies that seem worse than the diseases that they were intended to cure. Perhaps the best known are the verses quoted by Mouffet (Topsel transl. 1658) from Quintus Serenus on a remedy for "Tertian agues" (malaria?):

> "Shame not to drink three Wall-lice mixt with wine,
> And Garlick bruised together at noon-day.
> Moreover a bruis'd Wall-louse with an egge, repine
> Not for to take, 'tis loathsome, yet full good I say."

And another remedy:

> "Some men prescribe seven Wall-lice for to drink,
> Mingled with water, and one cup they think
> Is better than with drowsy death to sink."

The bed bug is mentioned in the Talmud (Bodenheimer 1929) but, curiously, it is not mentioned in the Bible. Nevertheless, in the "Acts of John" (Leucius, 2nd century A.D.) (from James 1924, *The Apocryphal New Testament*), we read:

"Now on the first day we arrived at a deserted inn, and when we were at a loss for a bed for John, we saw a droll matter. There was one bedstead lying somewhere there without coverings, whereon we spread the cloaks which we were wearing, and we prayed him to lie down upon it and rest, while the rest of us all slept upon the floor. But he when he lay down was troubled by the bugs, and as they continued to become yet more troublesome to him, when it was now about the middle of the night, in the hearing of us all he said to them: I say unto you, O bugs, behave yourselves, one and all, and leave your abode for this night and remain quiet in one place, and keep your distance from the servants of God. And as we laughed, and went on talking for some time, John ad-

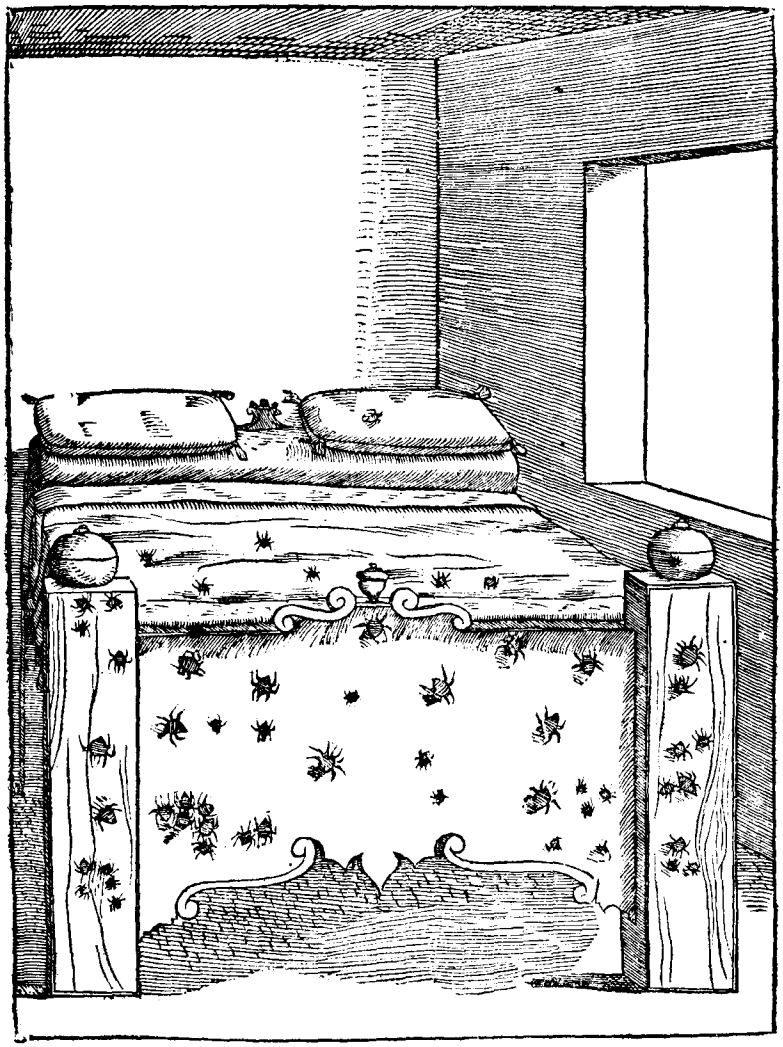

FIG. 1–1.—Early woodcut showing infestation of bedbugs (from Matthioli 1568).

dressed himself to sleep; and we, talking low, gave him no disturbance (or, thanks to him we were not disturbed).

"But when the day was now dawning I arose first, and with me Verus and Andronicus, and we saw at the door of the house which we had taken a great number of bugs standing, and while we wondered at the great sight of them, and all the brethren were roused up because of them, John continued sleeping. And when he was awaked we declared to him what we had seen. And he sat up on the bed and looked at them and said: Since ye have well behaved yourselves in hearkening to my rebuke, come unto your place. And when he had said this, and risen from the bed, the bugs running from the door hasted to the bed and climbed up by the legs thereof and disappeared into the joints. And John said again: This creature hearkened unto the voice of a man, and abode by itself and was quiet and trespassed not; but we which hear the voice and commandments of God disobey and are light-minded: and for how long?"

2 Ecology

Many studies have been made of the environmental factors that influence development and behavior of the human bed bugs. Several publications are so extensive (Hase 1917, Kemper 1936, Omori 1941, Johnson 1942) that they amount to small books. Quantitative studies of natural populations have been conducted by Mellanby (1939b) and Johnson (1942). For purposes of this work, I have tried to select the most significant material bearing on temperature, humidity, nutrition, reproduction, etc. The original publications should be consulted for further details.

No detailed investigations have been carried out on the microclimates where the bugs actually live in the nests of birds, or in hollow trees or caves where bats roost. Nidicolous bugs are certainly in close contact with their hosts during the period when the birds are in the nests. Cave-dwelling species stay on the walls and ceilings where the bats are roosting. Eggs are seen in cracks in the rocks and the bugs are commonly found running over the surface. Some cave dwellers like *Cimex cavernicola* Usinger, n. sp., show no obvious adaptations for cave life, but others like *Afrocimex, Stricticimex,* and especially *Leptocimex,* seem to be typical troglobionts with relatively long legs and antennae and pale color. The reduction of wings is a characteristic feature of cave insects, but it is also typical of parasites, so the small wing pads of cimicids are not necessarily connected with cave life. Unlike many cave insects, cimicids have well-developed eyes.

TEMPERATURE

Like other organisms, bed bugs are part of a complex ecosystem and are affected by diverse elements in their environment. Of the various factors, temperature is by far the most important, since it influences all aspects of the bugs' activities. Only in species that inhabit warm caves is temperature likely to be so uniform that it does not affect the rate of development or such vital activities as searching for food or mates.

The threshold for hatching, nymphal development, and adult activity in *C. lectularius* is between 13° and 15°C (Hase 1930, Mellanby 1935,

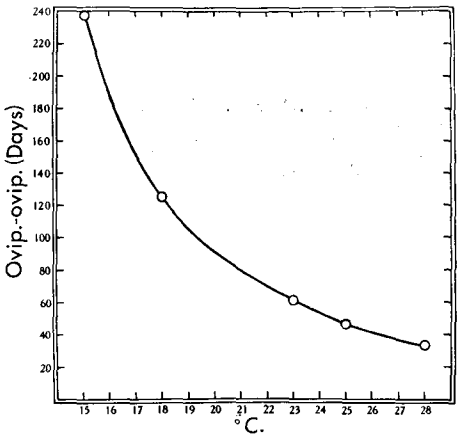

FIG. 2–1.—Mean period from oviposition to oviposition for *Cimex lectularius* at various temperatures (Johnson 1942).

Kemper 1936, Johnson 1942), although that insect can tolerate extremes as low as −15°C for brief periods. The thermal death point is between 44° and 45°C, but Omori (1941) found that development ceased, especially with *C. lectularius,* at 36° or 37°C. The total period of development ranges from 36.6 days at 33°C to 127.9 days at 18°C (Table 2–1) (Johnson 1942, Fig. 2–1).

C. hemipterus has a somewhat higher threshold of development [15°C (Mellanby 1935), 18°C (Omori 1941), 19°C (Geisthardt 1937)]. Curiously, the rate of development (Table 2–1) in the tropical bed bug is

Table 2–1.—Total period of development of *C. lectularius* and *C. hemipterus* females at various constant temperatures (Omori 1941).

°C	Egg stage	Nymphal stage					Preoviposition period	Total days
		1st	2nd	3rd	4th	5th		
				Cimex lectularius				
18	20.9	19	18	17	19	26	8	127.9
22	12.1	8.8	7.2	7	6.8	10.4	6	58.3
27	5.3	4	4	4	4	6	4	31.3
30	4.4	4.4	2.8	2.4	3.2	4	3	24.2
33	4.1	3.6	4.4	5.7	8	7.8	3	36.6
				Cimex hemipterus				
18	25	17.0	21	119	54	21	8	265.0
22	13.2	10.1	7.6	8.0	10.3	11.7	6	66.9
27	5.9	4.5	4.2	3.2	4.3	5.7	3	30.8
30	4.6	5.5	2.7	3.3	3.2	4.0	2	25.3
33	4	3.3	3.8	7.5	16.0	32.8	2	69.4

slower than in *C. lectularius* (except at 27°C) and this is most striking at the lowest and highest temperatures (18° and 33°C). On a temperature gradient plate, Omori (1941) found that *C. hemipterus* clustered in the range from 32° to 33°C, while *C. lectularius* clustered between 28° and 29°C.

In limited tests, *Hesperocimex sonorensis* Ryckman was active within approximately the same range of temperatures as the 2 species of *Cimex* (Berryman).

In nature, fluctuating temperatures are usually encountered, even in the tropics. Johnson (1942) found that the egg stage of *C. lectularius* was 1 week shorter (14 days vs. 21 days) with a diurnal fluctuation between 23° and 13.1°C, than with a constant temperature of 17.9°C. Also he found a difference of 1 day (8.45 vs. 9.70) with a fluctuation between 27.8° and 17.5°C as compared with a constant temperature of 22.7°C. Omori (1941) found that summer temperatures varying about a mean of 30°C at Taihoku, Taiwan, were less favorable for *C. lectularius* (fewer eggs, less hatching, and smaller percent emerging as adults) than rearing at a constant temperature of 30°C. In this case, the highest daytime temperatures were unfavorable to this normally temperate-zone species. In contrast, *C. hemipterus* was less resistant to extremes of cold temperature than *C. lectularius,* 10°C being its lower limit, whereas *C. lectularius* could stand short exposures as low as 6°C. It is doubtless this susceptibility to low temperatures that limits the geographic distribution of *C. hemipterus* to the tropics. However, extremes of temperature must be less severe in the protected microhabitats where the bugs spend most of their time.

The longevity of fasting adults of *C. lectularius* and *C. hemipterus* (after having once fed) is greatest at low temperatures and least at high temperatures (Omori 1941, Table 2–2). This is an important point in survival of the species over the winter in unheated rooms in northern Europe.

Developmental periods are given for representatives of several other genera and subfamilies in Table 2–3. It is interesting to note that *Haematosiphon* and *Caminicimex* have only 4 nymphal instars whereas *Ornithocoris,* in the same subfamily, has 5.

Under "field" conditions in a tropical climate like Puerto la Cruz, Venezuela (Hase 1931) with a mean temperature of 27.5°C, either of the human bed bugs theoretically could develop at the rate of 1 generation per month. On the other hand, for *C. lectularius* in an unheated bedroom in London, Johnson (1942) calculated that temperatures would permit only 1 full generation and an uncompleted second generation in a year. Development would be limited to the period between the second week of May, when the temperature rose to 16°C (68°F), to the second or third week in October, when it dropped again to that level. Only between the second week of June and the first week of September did

Table 2-2.—Longevity (mean days) of once-fed *C. lectularius* and *C. hemipterus* at various temperatures and 70–75% RH (Omori 1941).

Stage	10°C		18°C		27°C		37°C	
	Lect.	*Hemipt.*	*Lect.*	*Hemipt.*	*Lect.*	*Hemipt.*	*Lect.*	*Hemipt.*
1	274.6	115.0	113.6	67.8	27.8	23.8	16.8	10.5
2	398.9	197.3	171.1	124.8	45.6	41.4	30.4	19.7
3	412.7	248.5	214.4	213.2	71.2	75.9	35.3	23.6
4	432.5	295.1	234.5	263.8	73.3	86.7	37.2	26.4
5	484.9	265.5	161.4	156.3	39.5	40.2	32.6	14.9
♀	425.0	187.3	277.1	153.9	86.7	54.2	31.9	23.3
♂	401.9	184.5	175.6	134.2	43.4	36.9	28.6	17.4

the mean temperature exceed 20°C; a peak of 24°C occurred in the second week of August.

Conditions would, of course, be totally different in a bat roost in a cave or tree hole. In the cave habitats of *Afrocimex leleupi* Schouteden in the Congo (Ancíaux de Faveaux 1959) the temperature was practically constant at 22° to 24°C. Allen (1939) says that the caves in which northern bats hibernate (habitat of members of the *Cimex pilosellus* complex) show a more or less constant winter temperature at about 6°C.

HUMIDITY

It is generally stated that human bed bugs are but little, if at all, affected by the different degrees of humidity that are normally encountered in human dwellings (Kemper 1936). Relative humidities ranging from 10 to 70% were tested and found to have a negligible effect on the rate of development of nymphs of *C. lectularius* (Rivnay 1932b).

Table 2-3.—Mean developmental period in days for eggs and nymphs of various species of Cimicidae.

Species	Reference	Egg	Nymphal stages					Total	Temp. °C
			1st	2nd	3rd	4th	5th		
Hesperocimex sonorensis	Ryckman 1958	6.0	8.1	7.1	5.4	5.5	8.0	40.1	27
Ornithocoris toledoi	Snipes et al. 1940	7.5	6.5	6.5	7.9	7.9	7.0	41.5	20.5
Haematosiphon inodorus	Lee 1955b	5.1	8.5	7.8	7.4	8.3	—	37.1	25–29
Caminicimex furnarii	Orig.	8.6	7.2	6.4	8.6	9.4	—	40.2	24
Bucimex chilensis	Orig.	6.0	15.5	15.2	30.6	37.1	18.8	123.2	28
Leptocimex duplicatus	Orig.	9.7	7.6	7.7	8.7	8.6	14.1	56.4	24

On the other hand, Kemper (1936) noted that nymphs kept under extremely dry atmospheric conditions (0 to 20% RH) often died during molting. Jones (1930) and Mellanby (1935) found that unfed first-instar nymphs survived for different periods, depending on the humidity. According to Mellanby, in air at 90% RH and a temperature of 30°C, they survived 26.3 days. At lower humidities (60, 30, and 0%) survival time dropped progressively to 5.68 days and desiccation was the principal cause of death. Careful analysis of results revealed that the water was probably lost at a rate proportional to the saturation deficiency. Because in all cases survival time was increased if the bugs were fed, it was concluded that the blood must have provided a supply of water.

Working with eggs of *C. lectularius,* Johnson (1942) noted that, "Humidity appears to have a very slight but noticeable effect on mortality within the greater part of the optimum range of temperatures." He adds that, "At 12°C the longest survival time occurs in the dampest air (i.e. that with the lowest saturation deficit)." Extensive tests of eggs, nymphs, and adults at 33, 64, and 98% RH led Omori (1941) to the conclusion "that the moisture content of the air has little effect on *Cimex hemipterus* . . . but extreme wet conditions are not suitable for *C. lectularius.*"

As noted by Kemper (1936), high humidities frequently cause death in laboratory cultures by encouraging fungus growth.

Under cave conditions the various bat bugs are exposed to humidities ranging from saturation (wet caves) to extreme desiccation (dry, dusty caves). Unfortunately, data are lacking on the range of tolerance of particular species to cave moisture, but I collected *Afrocimex leleupi* in moist caves and *Leptocimex duplicatus* Usinger under dry conditions. In California *Cimex pilosellus* (Horvath) sometimes occurs in old mine tunnels where the air approaches complete saturation.

NUTRITION

In *C. lectularius* the frequency of food intake is closely correlated with egg-laying, molting, longevity, and temperature, which affects all other processes including rate of digestion. Johnson (1942) found that at 23°C and 75% RH, the weight of unfed females (mean, 4.98 mg) and the weight of the first blood meal as an adult (mean, 7.60 mg) determined the number of eggs (mean, 8.87). Larger bugs took larger blood meals and produced more eggs. In the simplest case, a mated female will feed once to repletion in about 5 to 10 minutes and then retreat to a harborage and remain quiescent while digesting the blood and developing eggs. At 23°C, the time after feeding until the first eggs were laid (latent period) was 5 or 6 days, and oviposition lasted for 6 days, producing 6 to 10 eggs. Thus the graph for egg production was a series of peaks and troughs with about a 12-day cycle. However, if given the opportunity, the female does not wait this long to feed again. At room

temperatures of 18° to 20°C, Kemper (1936) found that young adults are stimulated to search for another blood meal at approximately weekly intervals, while at 27°C the time is reduced to about 3 days. Johnson (1942) found that at 23°C and 90° RH feeding at 7-day intervals reduced the latent period to 1 to 3 days and that with semiweekly feeds it was obliterated completely. Thus, egg production was continuous and at a rate ranging from a 2.76 mean weekly egg output during the first week to 8.29 in the fourth week and remaining above 5 eggs per week for 18 weeks. The percentage of sterile eggs ("imperfect," "malformed," or "taub") increased from 0 to 1% during the fertile period (Titschack 1930). A few eggs may be laid before the first feeding, but in such cases the eggs develop from food reserves left over from the last nymphal instar. Hase (1917) gives 12 as the maximum number of eggs laid in a day, and Titschack (1930) gives 541 as the greatest number produced by a single female in her lifetime.

Nymphs can feed within 24 hours after molting, having slightly shorter feeding intervals than adults. Average weights of blood ingested in the several stages, together with the proportionate increases in body weight, are given in Table 2–4 (Titschack 1930). The largest quantities taken were by a fifth-instar nymph (10.7 mg) and an adult female (13.9 mg). The efficiency with which the food is used to increase body weight was studied by Johnson (1960). He reported that, "The increase in body-weight before feeding of successive instars of *Cimex lectularius* is of the order of 30% of the weight of the blood ingested at each instar, except in the 1st–2nd instars where it is approximately 40%."

The proportionately larger blood meals of nymphs, as compared with adults, in relation to size and body weight, are due to a different capacity for expansion of the integument (Hase 1917). Recently engorged nymphs look like round red berries. The expansion takes place due to the membranous areas on the entire ventral surface and at the first, second, and part of the third abdominal terga. In the sclerotized adults the situation is quite different. Midventrally the abdomen has a flexible "hunger fold." Also the abdominal segments are telescoped and the

Table 2–4.—Average weights of blood ingested and proportionate increase in body weight at various stages for *C. lectularius* (Titschack 1930).

Stage	Weight of blood, mg	Proportionate increase, times
1st instar	0.34	3.4–4.3
2nd "	0.96	3.9–5.2
3rd "	2.08	3.8–5.1
4th "	4.11	3.7–5.3
5th "	7.09	2.4–6.1
♂	2.37	1.46
♀	7.81	2.19

flexible intersegmental membranes can stretch to increase the total length.

Digestion of the blood meal (probably with the aid of symbiotes) is accompanied by a darkening and a concentration of the blood. Several water-clear drops are eliminated through the anus and liquid fecal matter is excreted soon after feeding. Omori (1941) found that half of the entire blood meal (by weight) is lost in this way in the first 5 hours after feeding. The fecal spots (Hase 1917) are conspicuous signs of bed bug infestation, and range in color from white to yellow, reddish brown, or dark brown to black.

Laboratory studies that permit regular and even forced feeding are of interest to show maximum rates of development. However, such figures are seldom if ever attained in nature because of the influence of fluctuating temperatures on behavior and because of the element of chance in searching for a host and in completing the piercing-sucking act. Also, of course, man's efforts at control reduce the chances of bugs' obtaining regular and full blood meals. Therefore, bed bugs do not always feed to repletion and frequently must survive short or long periods of fasting. This is especially true of *C. lectularius* in the winter, and of the swallow bugs (*Oeciacus*) during the many months of each year when the swallows leave their nests and migrate to the south. Development is delayed if only partial meals are taken and halted under conditions of starvation (Kemper 1936).

The effect of starvation on survival is so intimately connected with temperature and humidity that it is difficult to assess the effect of starvation alone. At 22°C and 40 to 45% RH, Kemper (1930) found mean survival times for *C. lectularius* without food to be 83.7 days in first and second instars, 130.6 days in adult females, and 142.6 days in males. In a practical test of survival, Bacot (1914) fed bugs of various stages once and then kept them fasting in an outhouse for 18 months. Several fed at the end of this period. Johnson (1942) concludes that "if a house has remained unoccupied for a long time, fifth instars, unmated adult females or mated adult males would be most likely to predominate in the surviving population."

Kemper (1936) called attention to the "hunger bubbles" that, during fasting, may fill the entire midgut.

Johnson (1937) investigated the effect of the blood of different hosts on egg production of *C. lectularius,* using man, mouse, and fowl as hosts. Females bred on mouse laid the greatest number of eggs and those on man the least. In my experiments bugs from a rabbit colony were reared on rabbit, chicken, man, and pigeon and laid eggs in decreasing order as listed above, the average number of eggs on pigeon being only one-third that on rabbit. Rates of development from first nymphs to adults were tested and were shortest for chicken, approximately equal for pigeon, bat, and rabbit, and longest for man.

BEHAVIOR

The behavior of Cimicidae, like other animals, is largely directed to the search for food, shelter, and mates. The species living on birds and bats react more or less like those on man, but the present discussion is based on the large amount of information available on *C. lectularius* and includes only comparative notes on other species.

The bed bug is not evenly distributed over its environment. Instead, the bugs are concentrated in harborages often at some distance from the host animal upon which they are dependent for food. Hence, much of their activity is concerned with searching, and their behavior tends to facilitate this search.

Shelter

C. lectularius finds shelter in cracks and crevices in houses of man as well as in roosts of chickens and tree-holes and caves of its original hosts—bats. The bugs are thigmotactic, seeking places where the body surface can make contact with a rough substrate. This often leads to a cluster or heap of bugs, each in contact with others, in "brood centers" where much fecal matter, egg shells, and exuviae accumulate. Bugs return to such harborages after each meal (Kemper 1936) and remain there in a quiescent state while digestion takes place. Such clusters are formed where the substrate is dry, rough, and offers at least partial darkness (Hase 1917). Wood and paper surfaces are preferred to stone, plaster, or metal, and even to textiles (Kemper 1936).

Bed bugs generally react negatively to light but will feed in daylight when hungry. In a test (Berryman) involving 20 bugs held in an arena (petri dish) at 29°C with one half darkened, there were never less than 18 bugs in the dark side after 1 hour. *Oeciacus vicarius* Horvath was slower in its reaction to light, with half the bugs on each side after 10 minutes; at the end of 45 minutes all specimens were grouped on the dark side. Lee (1954a) showed that another bird bug, *Haematosiphon inodorus* (Dugès), was indifferent to light.

Kemper (1936) reports an aversion of *C. lectularius* to drafts, causing the bugs to cling to the surface on which they are walking or to seek to escape.

The stimulus to leave the harborage is not fully understood, but hunger seems to be critical and, of course, both the rate of digestion and the actual movement of the bugs depend upon temperature. In an experimental room fitted with harborages and traps to indicate the movement of bugs, Johnson (1942) found that activity started at 10°C, Mellanby (1939b) gave 11°C as the threshold, and Kemper (1936) 15°C. Mellanby (1939b), using a natural infestation in an animal colony, showed that bugs are most active just before dawn (Fig. 2–2). He used both "Demon" cockroach traps into which the bugs fell and could not

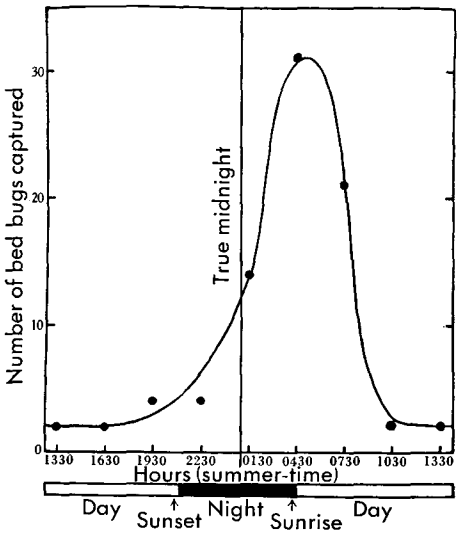

FIG. 2-2.—Activity of *Cimex lectularius* during a 24-hour period. Bugs were trapped at 3-hour intervals throughout the day and night. True midnight is indicated on an English "summer-time" scale (Mellanby 1939b).

escape, and corrugated paper harborage traps. He found the bugs most active after 3 AM (standard time). A light burning all night reduced the activity but did not stop it. A period of total darkness maintained for 45 hours did not upset the rhythm of activity.

Searching

The means of finding a host is the most controversial subject in the study of bed bug behavior. Rivnay (1932a) claimed that the bugs searched entirely randomly until they were 3 or 4 cm from the host, when they recognized a temperature differential of 2°C or more (1°C according to Sioli 1937). At this point the biting reflexes described hereafter were initiated and the bug moved directly to the host. This is in agreement with earlier works of Hase (1917) and Kemper (1929a). On the other hand, Marx (1955) found that bugs can perceive man from a distance of 150 cm and can find the host by means other than chance. Rivnay tested various odors such as blood and perspiration, as did Marx, and both agreed that odor does not play a part in attracting the bugs to their hosts. Marx attributes host attraction mainly to warmth plus CO_2. Hase (1917) had long ago noted that warm breath was exciting to bed bugs.

In numerous tests using T-tube olfactometers (Fig. 2-3) and offering various choices of rabbit, chicken, man, and glass tubes heated to the temperatures of the various hosts, I found an overall preference (χ^2 significance at 1% level) for rabbit (3480 individuals tested). However,

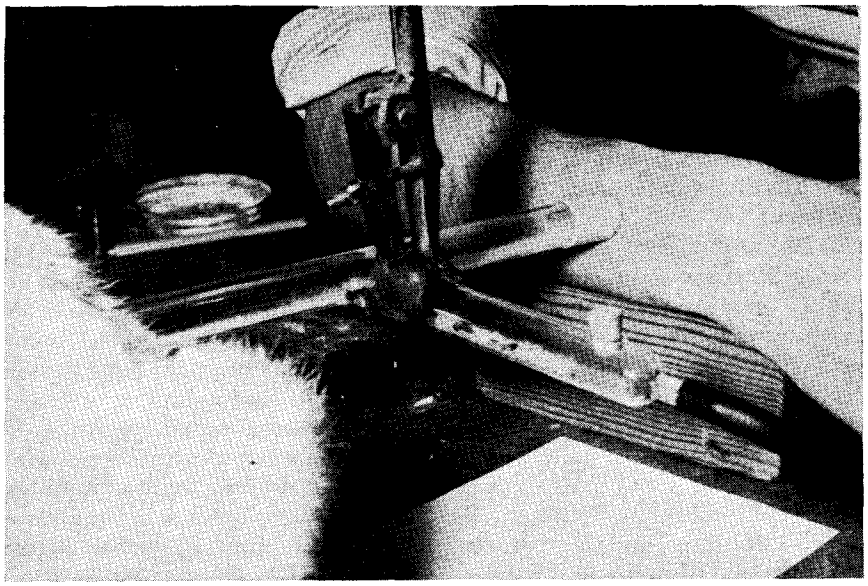

FIG. 2–3.—T-tube host-selection olfactometer. Ten bugs are dropped into the corked opening and make a choice between man and rabbit at the top of the T. The rubber tube aspirator creates a movement of air in the tube. The inner surface of the tube is roughened to provide traction for the bugs.

many of the tests were made with a small T-tube (3.5-cm arms), where the temperature gradient between rabbit (39.6°C) and man (37°C) might have been detected by the bugs. Tests with a large T-tube (12-cm arms) using rabbit and a blank tube heated to the temperature of the rabbit, showed choice for the rabbit (5 and 1% level of significance). However, when the blank was heated 10° and 20°C above the temperature of the rabbit, the bugs chose the high-temperature blanks (1% level of significance).

Bugs bred originally on man but changed for one or many generations to a new host failed to show changes in host preference. Within a single generation, when nymphs were fed on a host different from the parent colony, successive instars or the adult did not show preference for the new host (olfactory conditioning).

Only 1 case of cannibalism has been reported in bed bugs (Rivnay 1930). He advanced the theory that recently fed bugs might be attacked because they were still warm with the host's blood.

Chatton and Blanc (1918) found that bed bugs fed on a cold-blooded gecko, a chameleon, and frog (*Rana temporaria*), and suggested that this phenomenon disproved the theory of heat as the primary attraction in biting. However, Rivnay (1930) was unable to induce feeding on 2 species of snakes and on the lizard *Eumeces fasciatus,* except when the

latter was enclosed in a vial (as was the case in the Chatton and Blanc experiments). Rivnay found that enclosing the space raised the temperature—the bugs then reacted as expected.

Obviously, more work is needed on the complicated subject of searching and host selection, but it is clear that the bed bug cannot detect a host beyond 5 feet and probably not beyond a few inches. It is also clear that heat is of prime importance, at least in the final approach to the host.

Whether searching at greater distances is entirely at random is a moot point. The possibility of scent trails has not been ruled out and Hase (1917) described fecal spots and tracks (foot prints and a trail made by dragging the engorged abdomen) made in dust. Kemper (1936) found that bugs traveling 20 m to a host followed paths involving considerable detour from a direct line. Hase (1917) reported that nymphs can travel at a speed of 13 to 28 cm per minute, while adults attained speeds up to 126 cm per minute. Activity ceased when the temperature dropped to 12°C (Kemper 1936). Movement of *Haematosiphon inodorus* is much more rapid than that of *Cimex* (Lee 1955b). Davis observed that *Leptocimex duplicatus* and *Hesperocimex sonorensis* jump frequently when contained in cultures.

Movement is very erratic in *C. lectularius,* with much aimless wandering and long pauses, even when a host or other bugs are nearby. In walking, the antennae are held forward and outward and somewhat raised. Wet surfaces are avoided, or, if necessary, traversed by stretching the legs, holding the abdomen horizontally, and moving in a "stilted" fashion (Hase 1917). Bugs usually climb upward and even walk on a ceiling, but of the species raised in my laboratory only *C. pilosellus* and its allies were able to climb vertical glass surfaces.

The often-repeated story that bed bugs will crawl to the ceiling and drop on the bed to reach their host goes back at least to Latreille (1829). Kemper (1936) denies that bed bugs do this purposely but points out that they often drop when alarmed. Righting movements have been described in great detail by Hase (1917). In general *Cimex* arches its body and moves until it reaches an edge or corner, then seizes whatever object is within reach and pulls itself over.

Hesperocimex and other bird bugs, when disturbed, are more inclined than bat bugs to remain immobile, possibly because their bird hosts are accustomed to feed in daylight and the bugs would be less conspicuous when motionless. *Caminicimex furnarii* (Cordero and Vogelsang), *Hesperocimex sonorensis,* and *Oeciacus vicarius,* when shaken, prodded, or dropped, freeze into immobility, remaining as if dead for periods from 30 seconds to several minutes, even when violently disturbed. The reaction is especially noticeable when the bug falls on its back (Fig. 2–4). After they are again prodded into activity, the bugs move forward rapidly for a short distance and then freeze again.

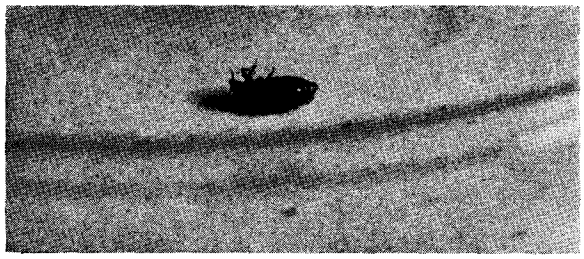

FIG. 2-4.—*Hesperocimex sonorensis* "frozen" into immobility when dropped on its back.

How bugs find each other and return to harborages is not understood. Marx (1955) attributes the gregarious habit to the scent gland odor, finding that bugs detected "nest odor" at a distance of 75 cm. To test the attractiveness of bug odors (scent gland secretions and feces), an arena was floored with blotting paper, one half of which was exposed to a large number of bugs for 1 week. The other half was clean. In a ½-hour exposure of 10 new bugs to the whole arena, wandering was completely random with equal numbers on the clean and soiled sides most of the time (Berryman).

The odor in *C. lectularius* has been described by Kemper (1936) as an "obnoxious sweetness." The odors are distinctive. Among my colonies Ueshima was able to distinguish 3 species in the *C. pilosellus* complex. He could detect no odor from *C. hemipterus,* and I have never been able to smell *Leptocimex duplicatus.*

Schildknecht (1964) was able to study fractions of the scent gland secretions of *C. lectularius* by chromatographic techniques. He found 70% Δ^2-*n*-hexenal and 30% Δ^2-*n*-octenal. There was no Δ^2-*n*-decenal or any unknown carbonyl compound such as are found in "stink bugs" of the family Pentatomidae.

Kemper (1936) believed that the odor is of value in laying trails, as an attractant to harborages and clusters, and for protection against being eaten by the hosts. Unfortunately, he gave no conclusive evidence on any of these points. Mellanby (1939b) reported that bugs in his infested animal colonies were eaten by the rats. In my laboratory 70 bed bugs (fifth instars and adults) were confined in an escape-proof plastic cage with a white mouse. The mouse ate no bugs during the first 4 hours (7:00 PM to 1:00 AM) but all bugs were eaten during the next 10 hours. Many cuticle fragments were found later in the mouse's stomach (Barbara Wilson).

To test a more natural host, the bat *Antrozous pallidus* was used for feeding experiments. Two captive bats had been conditioned for several months to eat meal worms. Then live specimens of *Oeciacus vicarius, Cimex adjunctus* Barber, *Cimex pipistrelli* Jenyns, *Cimex pilosellus,* and

C. lectularius were placed in the bats' mouths. In every case, the bats vigorously rejected the bugs but accepted meal worms immediately thereafter. Three mealworms smeared with the scent secretion of *Cimex pilosellus* were likewise rejected, although clean worms were readily accepted (Barbara Wilson).

Dispersal

While a certain amount of dispersal is incidental to active search for a host, especially with bed bugs in apartments and hotels, most dispersal is passive. I was bitten on the back of the hand by *C. lectularius* while riding a city bus in Atlanta, Georgia, and I saw a thriving colony of *C. hemipterus* on a bunk of one of the large ocean liners sailing from Hong Kong to San Francisco. Airplanes (Whitfield 1939), trains, moving vans, and all manner of vehicles carry bed bugs. On native hosts the situation is somewhat different. The areas between bat roosts or between groups of swallows' nests, for example, are completely uninhabitable for cimicids. Because every cliff swallow nest I have examined in North America and Europe has been infested, it is obvious that *Oeciacus* can be carried readily to new nesting sites by the birds. The exact means by which this is accomplished is not known. Possibly eggs or nymphs adhere to the birds, although eggs are normally laid on the outside of the mud nests and, unlike Mallophaga and fleas, live bugs have no special adaptations for clinging to the feathers or body of a bird while in flight. Djonic (1937) claimed that house martins transport bed bugs over long distances. It is clear, however, that *Oeciacus* cannot manage long flights because it has never been found in swallows' nests in the tropics or in the southern hemisphere where the birds migrate annually. To check the negative evidence, I examined mud nests of swallows in southern India, Peru, and Ecuador and found no bugs.

The dispersal of bat bugs from 1 roosting place to another presents similar problems. Here, there is more evidence. Kühnelt found *Aphrania barys* Jordan and Rothschild attached to the wings of bats in South Africa (Fig. 11–15), and members of the *Cimex pilosellus* complex are found on bats fairly frequently in North America. In the latter case, bugs are dispersed often enough to establish new colonies but not often enough to prevent the development of reproductive isolation.

Biting

Here we are concerned with behavior before and during biting; the action of stylets after they are inserted in the host has been described elsewhere. The bug approaches its host with antennae outstretched and, at close range, with its beak raised and pointed. The antennae are used to test the surface; smooth surfaces and wet areas are rejected. The front legs are advanced to grasp the skin of the host. If the forelegs are amputated, no feeding occurs. Hase (1917) describes the ensuing events as

they occur under normal conditions: "The bug secures itself with its claws on the skin, with the forelegs reaching quite far forward, in order to have leverage when introducing the stylets. In starved bugs there may be an intense vibrating movement before piercing. First the beak is touched vertically to the surface and the skin is tested repeatedly with its tip . . . The antennae are no longer pointed forward, but rather backward on a line level with the eyes. At this point—while the insect makes rather energetic pushing movements with the head and the entire body may be brought into sway with the abdomen moving up and down—the introduction of the stylets begins." Engorgement (Fig. 2–5) (Girault 1905) required 3 minutes for first-instar nymphs but 10 to 15 minutes for adults. When the bug is satiated it withdraws the stylets and ensheaths them in the labium, which is then returned to the resting position ventrally between the legs. The bugs are wary at the beginning and end of the feeding act, but while engorging they can be touched or even turned around on the axis of the stylets without interrupting them (Hase 1917). After feeding, the bugs leave the vicinity of the host

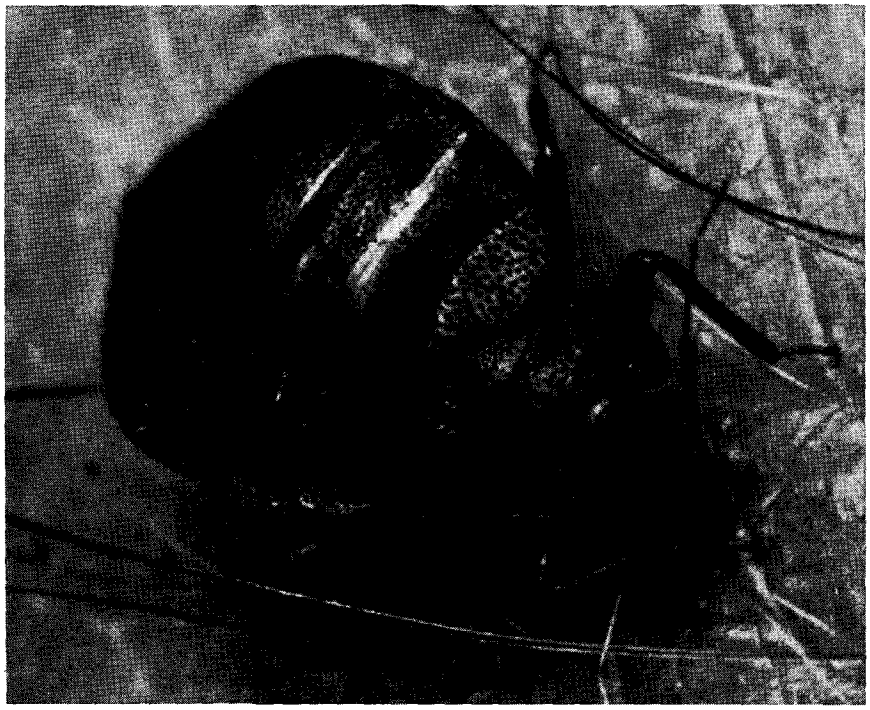

FIG. 2–5.—*Cimex lectularius* biting the arm of a man. The stylets are inserted and the abdominal segments are beginning to spread as the stomach becomes engorged (E. S. Ross, original).

quickly and return to their harborage where, if undisturbed, they remain motionless for several days.

Mating

Because of the different positions of the spermalege in the various genera, mating behavior is quite varied in the Cimicidae. A single male may mate with the same or different females more than once in a day. Hase (1917) found a sex ratio of 110 males:100 females in his laboratory colonies and 128:100 in wild populations. The disproportionate number of males is partly explained by their longer survival time. Another factor in my culture tubes might have been trauma due to repeated matings in such close quarters. Males always predominated in my cultures and thriving colonies of *Caminicimex, Ornithocoris,* and *Haematosiphon* were eventually lost because they were reduced to males only.

Because of temperatures below the mating threshold, Johnson (1942) found that in a sample of bugs taken in London from Jan. 24 to May 1, 1939, "the mean values for proportion of fertile females out of the total of females in the sample . . . was only 18.4%."

Working with *C. lectularius,* Rivnay (1933) found that males failed to recognize females (or other males) at a distance greater than 15 mm. The males did not differentiate between sexes and repeatedly attempted to mate with other males, dead females, and even with a piece of cork carved in the shape of a bug. Rivnay termed this "morphotaxis" or reaction by sign to a particular form rather than reaction to scent, which is so common in other insects such as the cecropia moth, *Hyalophora cecropia* (L.), and others.

In *Afrocimex,* Ferris and Usinger (1957a) first noticed that the male has a well-developed ectospermalege at the base of the abdomen on the left side like that of the female. Carayon (1959) found sperm in the hemocoel, confirming that the structure is functional and that homosexual mating actually occurs. Hinton (1964) explained the evolution of such a structure on the basis of survival value of the injected sperm as nutriment for the male that receives and absorbs them by phagocytosis. The idea of nutritive value of sperm or "hypergamesis" had already been considered in females by Berlese (1898) and had been rejected by Mellanby (1939a). It is rejected as an explanation for the situation in *Afrocimex* by Davis elsewhere in the present work. However, no other suggestions have been made to account for the evolution of this extraordinary structure and behavior.

In *C. lectularius,* Mellanby (1935) found that not one of 300 males copulated if it had starved longer than 2 weeks, and that teneral females, and females that had not fed recently, were not ready for mating. Mating behavior was first observed by Patton and Cragg (1913) and later described in detail by Rivnay (1933). The male mounts the female obliquely in such a manner that his head falls over the left side of the

pronotum of the female (Fig. 2–6a); his left legs grasp the posterior part of her abdominal margins and his posterior abdominal segments are bent so that the tip reaches the right side of the ventral segments of the female where the paragenital sinus is located (Fig. 12–6). Pairing lasts from one to several minutes, sometimes for half an hour. Mellanby (1935) and Titschack (1930) noticed female demand movements consisting of upward movements of the abdomen.

In *Hesperocimex sonorensis* (Fig. 2–6b), Ryckman (1958) likewise found that males "seem to be capable of recognizing a female only at a relatively short distance. It would seem that the male is approximately the length of his antennae from the female before he reacts in a definite manner. Once the female has been detected, the male climbs upon her back with a very swift almost jumping motion . . . the male's legs are

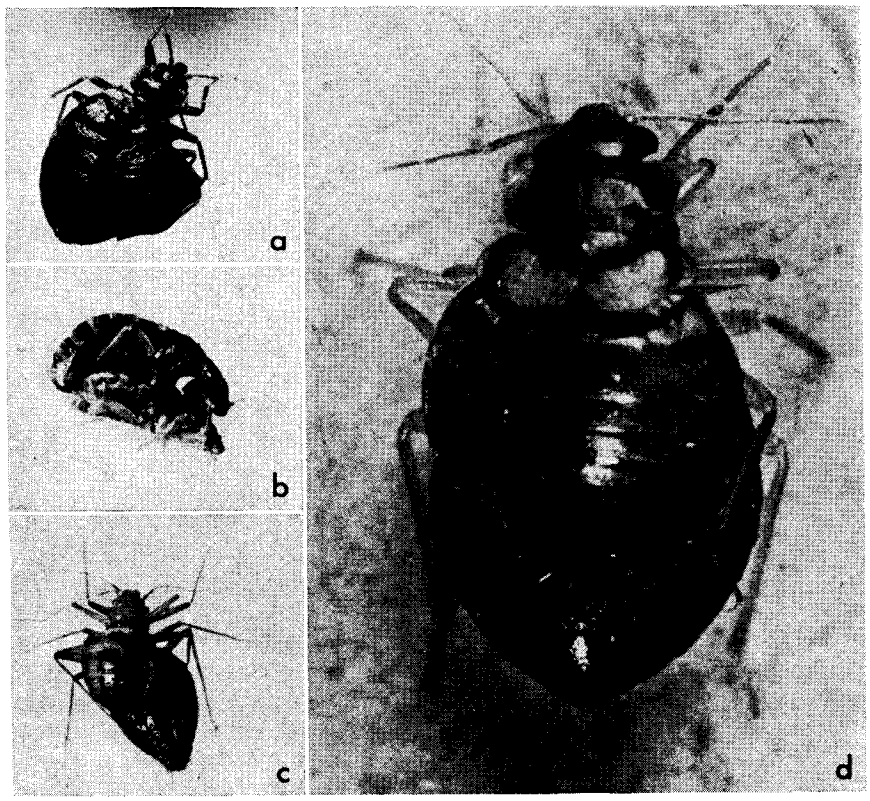

FIG. 2–6.—Mating behavior: a, *Cimex lectularius,* female spermalege right ventral on fifth segment; b, *Hesperocimex sonorensis,* spermalege ventral at right edge behind sixth segment; c, *Leptocimex duplicatus,* spermalege dorsal and double, with 2 openings behind fifth segment (N. T. Davis, original); d, *Haematosiphon inodorus,* spermalege dorsal between fifth and sixth segments (Carayon, original).

flexed at the femora-tibial joint, thus forming an acute angle which fits over the lateral margins of the female's thorax or the anterior abdominal segments if the female is engorged. In the typical copulatory pattern the male . . . directs the terminal position of his abdomen over the right side of the female's abdomen" (the ectospermalege is located ventrolaterally on the sixth abdominal segment). With probing motions, the curved part of the paramere is inserted in the small hat-shaped ectospermalege. Mating lasted for 12 and 23 minutes in 2 typical cases and for 122 minutes in another case involving a teneral female.

Mating in *Leptocimex duplicatus* (Fig. 2–6c) is of special interest because: 1) the spermalege is double, with 2 separate openings, and 2) the openings are dorsal between the fifth and sixth abdominal segments. The male mounted the female with the front legs grasping the sides of her prothorax behind, the middle legs holding at the hind coxae, and the hind legs resting on the posterior part of the female abdomen. The male was oriented almost on a longitudinal axis with the female but during copulation moved the tip of the abdomen slightly to the side to insert the long, slender, coiled paramere. This seemingly difficult act required no twisting or turning, there being enough flexibility in the abdomens and in the tubular ectospermalege to accommodate the paramere with ease. The female did not resist at first but later shook violently for several seconds. Copulation was accompanied by a rhythmic but very slight up-and-down movement of the male, which must have had considerable effect where the sharp paramere was probing. The point of contact between the tip of the male abdomen and the female ectospermalege was enveloped in a clear fluid which remained around the opening after separation. The first copulation was interrupted several times over a period of about 5 minutes. Then the paramere was withdrawn and inserted in the second tube for over 5 minutes. According to Davis, "mating always occurs on the right side first" and mating on one side only resulted in normal egg production.

Lee (1955b), working with *Haematosiphon inodorus* (Fig. 2–6d), also found that males mounted other males and attempted to copulate. In this species, which has the ectospermalege opening middorsally at the fifth segment, the male climbs on the dorsal surface of the female, lining up with her on a parallel axis. He inserts the paramere into the ectospermalege and they shake vigorously from side to side much of the time while mating; the female may even run about with the male still in position.

Oviposition, Hatching, and Molting

C. lectularius and *C. hemipterus* (Fig. 2–7) lay eggs mostly in and around harborages. When offered a choice of substrates in a petri dish (Berryman), females laid all eggs on corrugated rough paper, none on plain or corrugated smooth paper, and none on plain rough paper. The

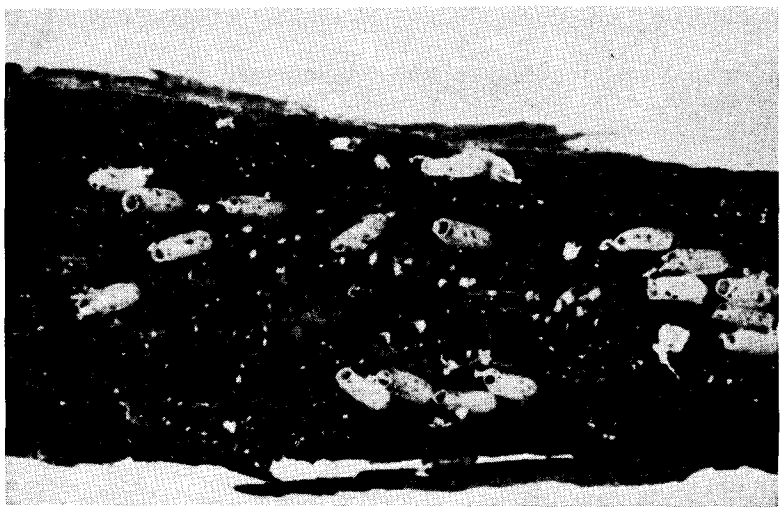

FIG. 2–7 (above).—*Cimex hemipterus* eggs, cast skins, and fecal drops on a rough surface; Viet Nam (Robin Leech, original). FIG. 2–8 (below).—*Bucimex chilensis* eggs laid on under surface of loose bark of *Nothofagus* tree; Chiloe Island, Chile (R. L. Usinger, original).

eggs are laid individually, and, because they are coated with a transparent cement, they quickly adhere to the substrate. There is no regular arrangement although suitable places are usually limited so the eggs are often touching. They are laid with the long convex side (dorsal surface

of embryo) down or at the side. *Bucimex chilensis* Usinger (Fig. 2–8) lays its eggs on the rough surface of loose bark of *Nothofagus* trees. The eggs are laid in a more or less linear arrangement. *Oeciacus vicarius* (Fig. 2–9) lays its eggs on the outside of the mud nests of cliff swallows in such large numbers that the pale egg shells impart a gray color to the nests when seen from a distance. In his colonies of *Hesperocimex sonorensis,* Ryckman (1958) scribed lines on blotter paper with a blunt instrument. The bugs laid their eggs in the small grooves, thus facilitating the counting of eggs which, otherwise, were laid in irregular masses of 50 or 75. In my colonies, *Hesperocimex* laid eggs on cast skins and on dead bugs as well as the blotter paper.

Sikes and Wigglesworth (1931) have described the hatching process as follows:

"The larva of the bed-bug shows very little activity before hatching, and the sculpturing of the shell precludes any detailed observations upon it. But during the twenty-four hours before emergence the body of the insect comes to fill the egg more completely, the eyes moving forward to the cap; the yolky contents of the gut become more apparent, the globules of fat becoming larger; and occasional pumping movements are visible in the head. It is probable, therefore, that the larva is swallowing the amniotic fluid during this period, like the other insects studied.

FIG. 2–9.—*Oeciacus vicarius,* eggs laid on the outside of mud nests of cliff swallows (R. E. Ryckman, original).

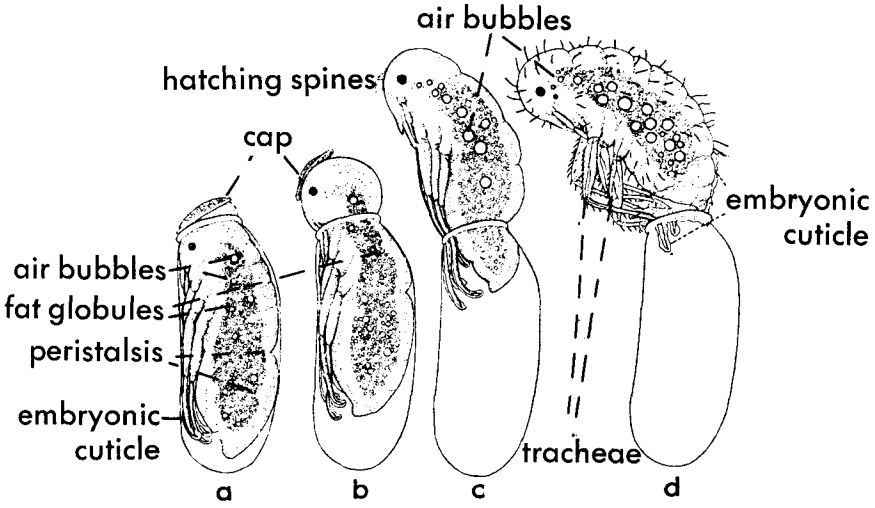

FIG. 2–10.—Hatching of egg of *Cimex lectularius*: a, cap is being forced off; b, active peristalsis continues and the head is distended and bulges from the egg; c, air is swallowed, hatching spines are visible on front of head; d, embryonic cuticle has split and slipped backward, allowing bristles to stand erect, tracheae have filled with air (Sikes and Wigglesworth 1931).

"At the time of hatching, peristaltic, or rather anti-peristaltic movements of the gut, and similar movements of the abdominal wall, become very active, and drive the fluid contents of the insect into the region of the head. It is almost certainly this force which serves to dislodge the cap of the egg [Fig. 2–10a]; and the process is aided by the larva swallowing a certain amount of air, which increases the distension of the gut. As the cap is raised a small vesicle bulges through the orifice. This is composed of the escaping head and thorax, which are blown up like a bladder with the body-fluids. This bladder slowly enlarges as the larva squeezes its way through the constricted neck of the egg [Fig. 2–10b], and the process continues until only the tip of the abdomen remains inside [Fig. 2–10c].

"The insect, however, is still enclosed within its pre-larval skin or embryonic cuticle. It now begins once more to swallow large quantities of air [Fig. 2–10c], distending the body more and more until the cuticle splits. The split appears over the top of the head and as the cuticle slips backwards, the bristles on the larva stand erect and the limbs and antennae become free [Fig. 2–10d]. During this process a layer of fluid can be seen between the larva and the cast skin; but on exposure, the surface of the larva dries at once, and air enters the tracheal system for the first time. The air can be seen passing rapidly down the larger trunks, but more slowly along the finer branches, for example, in the distal portions of the legs.

"When it has extricated itself from this first moult, the larva begins, for the third time, to swallow air most vigorously, until the entire gut is enormously distended. Meanwhile it alternately flexes and extends its body, assuming its characteristic flattened form and increasing in size until it far exceeds that of the egg from which it came. Within an hour or so, all this air has disappeared.

"There is another feature of the hatching mechanism which has not been mentioned so far. Between the embryonic cuticle or 'inner egg-membrane' and the chorion or 'outer egg-membrane' is a third layer, presumably the vitelline membrane, conveniently called by Speyer the 'middle egg-membrane'. Before it can escape from the egg, the larva must rupture this membrane, and to this end it has a series of hatching spines. These arise from the embryonic cuticle, and take the form of a file-like margin to the prominent labrum and, more particularly, a series of small teeth which are arranged in two divergent tracts running downwards and backwards from the vertex of the head [Fig. 2–11]. This hatching mechanism could not be observed in action; but judging by its structure it is probably actuated by slight flexion of the head. It is possible that it may play a part in the separation of the cap, but we have no evidence on this point. On the other hand, it is possible that these small, backwardly directed spines play no part in rupturing the membranes, but serve merely to prevent the head from slipping back into the egg as the cap is lifted."

Molting of the nymphal cuticle takes place as follows: The nymph clings tightly to the substrate. By pressure from the gut contents, includ-

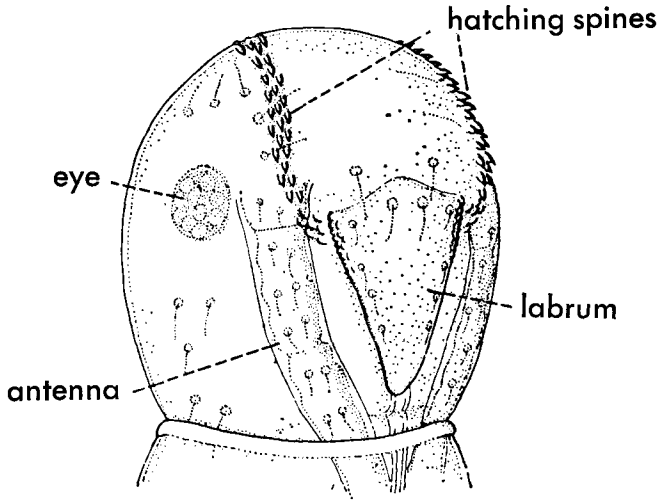

FIG. 2–11.—*Cimex lectularius,* head extruded from egg but enclosed in embryonic cuticle (Sikes and Wigglesworth 1931).

ing air swallowed for the purpose, the region of the last thoracic and first abdominal segment is split longitudinally along the molting suture. Then, as the sides of the old cuticle are spread and the anterior part of the head (in front of the ecdysial sutures) is split forward, the bug begins to emerge, thorax first, then the abdomen and head, and finally the appendages. The process requires only a few minutes under favorable conditions of temperature and humidity but may be delayed because of previous injury of a part or because of excessive dryness. Since the new cuticle, after quickly expanding, starts to harden, a delay of 2 hours results in death. The cast-off exuviae are persistent signs of the presence, or former presence, of bed bugs.

NATURAL ENEMIES

A good deal of interest has always been shown in the insect predators of bed bugs. *Reduvius personatus* (L.) has long been known as the "masked bed bug hunter" because of its predacious habits and because the young stages pick up lint that conceals them effectively. Linnaeus (1758) called attention to this species as a predator on bed bugs and Klein-Krautheim (1932) reports more fully on it. Johnson (1952) lists the thread-legged bug, *Ploiaria domestica* Scott, as an enemy of bed bugs. According to Howard and Marlatt (1896) the Pharaoh ant, *Monomorium pharaonis* (L.), abated a bed bug nuisance in a single day in Meridian, Mississippi during the Civil War (reported by Theo. Pergande). Mallis (1960) says, "The Argentine ant [*Iridomyrmex humilis* (Mayr)] has likewise given short shrift to the bedbug" and Negi (1933) reports that the small red ant, *Solenopsis geminata rufa* Jerdon, feeds on bed bugs in India. Linnaeus (1767) mentions *Formica* (now *Myrmica*) *rubra* L. as a predator. The pseudoscorpion *Chelifer cancroides* (L.) is often mentioned (Kemper 1936); the centipede *Scutigera forceps* Rafinesque was cited as a "natural enemy" by Howard and Marlatt (1896); Cloudsley-Thompson (1958) reports *Eremobates pallipes* (Solfugae); and Kemper (1936) reports that the straw itch mite, *Pediculoides* (now *Pyemotes*) *ventricosus* (Newport), completely destroyed bed bug colonies in 3 weeks. Newman (1855) reported that cockroaches feed on bed bugs and cited an extract from Webster's (1834) "Narrative of Foster's Voyage" of 1828–30 to St. Helena as corroboration. However, Johnson and Mellanby (1939) tested the American cockroach, *Periplaneta americana* (L.), and concluded that cockroaches exercised no control over bed bugs.

Various spiders have been reported feeding on bed bugs. Povolný found that a colony of *C. lectularius* on bats in a castle at Austerlitz was destroyed by *Steaboda bipunctata* (L.). Another interesting case is the claim of Lorando (1929) that a spider, *Thanatos flavidus* Simon, de-

stroyed all the bed bugs in refugee camps near Athens between 1923 and 1925. Hase (1934) confirmed the effectiveness of this spider in laboratory tests but warned that predators were not a practical solution to bed bug control under ordinary conditions.

Mr. Robin Leech found a reduviid bug preying on bed bugs in Viet Nam, where two young nymphs were fed exclusively on bed bugs. Also, a little-known predator, *Joppeicus paradoxus* Puton, found in the nests of mammals in Egypt, was reared through several generations in bed bug colonies (Ueshima and Davis). E. A. Steinhaus reported on a disease in one of my cultures of *Paracimex* received from Malaya. The specimens were infected with *Aspergillus flavus* Link, a fungus that is widespread and is known to infect other insects.

POPULATION DENSITY

Most economically important insects, such as the codling moth, *Carpocapsa pomonella* (L.), and the alfalfa weevil, *Hypera postica* (Gyllenhal), are known to increase in a predictable manner under prescribed conditions. In the case of *C. lectularius* a vast amount of ecological data is available, but predictions are difficult because chance plays such a large part in its development. Quantitative data in infested houses are lacking as well. Nevertheless, Johnson (1942), by making certain assumptions, attempted "to synthesize the separate factors studied in the laboratory . . . into a general account of possible happenings to a population under natural (domestic) conditions." He chose rooms in 2 dwellings in London, one at Oakworth Road which was unheated in the winter, and one in Sutton Dwellings which was heated. Thermographs and thermometers were kept in these and some other rooms for 12 consecutive months. For the unheated room he started with a small theoretical population of 40 adult bugs and 2 fourth- and 5 fifth-instar nymphs and assumed that 5 of the 20 adult females were fertilized and capable of producing eggs soon after feeding without having to mate (assumptions were based largely on laboratory experiments). The first feeding would take place when the temperature rose to 16°C in the second week of May. From then on a feed would be taken once every 2 weeks until August when the temperature would range from 21° to 24°C and feeding would become a weekly event. Later the 2-week feeding interval would be resumed and feeding would cease after October.

By assuming that a host would always be found on schedule, by ignoring mortality, and by applying known periods at given temperatures for all the developmental stages, a total progeny by Nov. 2 of 1665 was computed. Of these, 951 were blood-sucking bugs and the rest were eggs destined never to hatch because of the cold winter. Many of the nymphs and adults would also die from old age and from inability to feed at low temperatures. Thus, even with a theoretical increase from 47 to

951 bugs (more than 20 times) it is probable that a population of about the same small size might be all that would survive the winter. In contrast, the same calculations made for heated rooms in Sutton Dwellings resulted in 5905 total progeny, of which 3282 were in blood-sucking stages. That a high reproductive potential is realized in heated rooms throughout northern Europe is well known. In the tropics, of course, quite a different pattern is to be seen. This is discussed but not calculated as to totals in an annual cycle by Omori (1941) for both *C. lectularius* and *C. hemipterus.*

Some other species have still a different pattern of development. *Oeciacus vicarius,* for example, is subjected to freezing temperatures in the north in winter; the swallows are gone for over half the year and rear brood for only a few weeks. Yet Myers (1928) counted 1333 bugs ranging from the second instar to adults (first instars were very numerous but too difficult to count) on June 4, 1926, barely 2 months after the first eggs were noted. "By the end of the summer the nests were literally swarming with the bugs and the outsides were gray with the egg shells." Ryckman (1958) discusses the possibility of other species of birds utilizing the swallows' nests, thus providing temporary food. However, the occurrence of such numbers of *Oeciacus* in all nests of cliff swallows that have been examined suggests that the cycle is adjusted to the long period of fasting. Ryckman (1958) took 77 second- to fifth-instar nymphs, 22 females, and 34 males from 4 old cliff swallow nests on the campus of the University of California in Berkeley on March 19, 1957 before the swallows had returned. Foster brought specimens into the laboratory in January and found that they fed and laid eggs well before the return of the swallows in the spring.

Haematosiphon inodorus builds up to even greater numbers according to Lee (1955b). He found 1425 bugs in one nest and 1778 bugs in another of the barn owl, *Tyto alba pratincola* (Bonaparte), on a steep bank of the Santa Ana River near Norco, Riverside County, California.

3 Bites

The act of biting involves the bed bug in a complicated series of reflexes, a definite behavior pattern, and an intimate reaction between parasite and host. Searching and biting behavior are discussed in Chapter 2. The mechanics of biting and the reactions of the host are treated here.

FEEDING

Dickerson and Lavoipierre (1959) devised an ear-chamber apparatus with which they could observe and photograph through the microscope the movements of the mouthparts of *C. lectularius* in the transparent tissues of the ear of a mouse. They also studied histological sections of mouthparts and host tissue by cutting off the proboscis during the act of biting. Their description of the feeding method follows:

"*The attitude of the bug on the skin of the host.* Before feeding . . . the bug swings its proboscis forward to an angle of 90° so that it comes to rest with the tip against the surface of the . . . skin. As probing commences, the insect grips the skin of the host with its tarsal claws and flexes its body, with the result that a 'hump' is produced at the thorax. The fascicle is then thrust in and out of the tissues while the bug describes a rocking motion; all the legs are used in the purchase for the forward thrust, the first pair being used mainly to enable the fascicle to be withdrawn from the tissues.

"Though the fascicle is driven into the skin, the labium does not enter the tissues, although it plays an important part in the act of feeding, its lip-like tips grasping the fascicle in a pincer-like grip and helping to steady it as it is thrust into the tissues. The mechanism whereby the fascicle is able to probe deeply into the host's tissues involves the shortening of the labium by a bending action at the more distal joints and by a slight telescoping of the proximal parts (Hase 1917, Kemper 1932). The shortening of the distance between the proximal and distal ends of the labium by this bending action enables the mandibles and maxillae to probe more deeply into the host's tissues, the bend in the labium governing the depth to which the fascicle can enter.

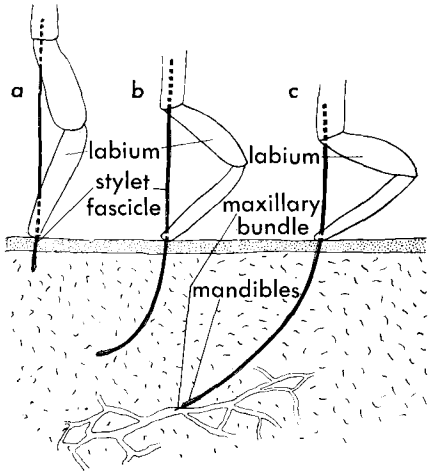

FIG. 3–1.—Diagram showing successive stages (a, b, c) in penetration of stylet fascicle through the skin and into a blood vessel (Dickerson and Lavoipierre 1959).

"Feeding in the host's tissues. Entry of the fascicle into the skin of the host is rapid, the mandibles and maxillae together piercing the skin surface as a compact bundle [Fig. 3–1a]. During the act of piercing the skin, the mandibles (the tips of which are toothed) move in rapid alternating movements and project slightly in front of the maxillae, forging a path for them in the tissues.

"Having entered the tissues, the fascicle which is extremely flexible [Fig. 3–1b], readily probes in various directions, moving forwards and backwards and at times bending well over 90°. Whilst probing, the fascicle often pierces, cuts across, and sometimes enters, minute capillaries and larger vessels, without ceasing its restless movements. This active probing results in the formation of small and large haemorrhages in the tissues, but we have seldom observed the bug to feed upon them. The fascicle continues its active movements in the tissues until it encounters and enters a vessel of suitable calibre, from which the blood meal is then taken up. We believe that the uptake of blood by the bug is governed by the size of the lumen of the vessel (among other factors), and it is our impression that, if the fascicle encounters a very small capillary or a large vessel, it is ignored by the insect, the mouth-parts continuing their restless movements in the tissues.

"In the fascicles search for a suitable blood-vessel, the tips of the mandibles appear to guide the direction of movement of the maxillae. On entering a suitable vessel, the fascicle ceases its probing movements whilst blood rushes up the food canal formed by the apposition of the two maxillae. At times, when the fascicle is in the lumen of a capillary, the vessel can be seen partially to empty of blood and then to refill with an

accompanying pulsating movement . . . It appeared to us that although both the mandibles and the maxillae abutted on the wall of the vessel, only the maxillae (probably only the right maxilla) entered the lumen of the vessel [Fig. 3–1c].

"Once the fascicle has encountered and entered a suitable vessel, the bug rapidly becomes engorged with blood, its shape changing from the typical flat squat form of the unfed bug to the distended rounded form of the replete insect. When engorgement is complete, the bug withdraws its fascicle, the blood pours out of the lacerated vessel, and a withdrawal haemorrhage is produced. If the fascicle has penetrated deeply into the tissues of the host the insect may have some difficulty in withdrawing it, owing to the small backwardly directed teeth on the tips of the mandibles, which fix them firmly in the tissue [Fig. 3–2]. As the mandibles and maxillae are withdrawn, the bent labium is slowly straightened out to accommodate the emerging fascicle. When the fascicle is completely freed from the tissues, the labium is swung back through a right angle and is accommodated in the resting position on the undersurface of the head and thorax."

In a previous paper, Lavoipierre et al. (1959) showed that triatomine bugs also feed in capillary vessels but that "the mandibles penetrate only into the superficial tissues, where they then cease all movement and act as anchors to the fascicle while the maxillae penetrate deeply into the tissue as a single bundle, which is highly flexible and capable of being thrust in all directions." Formerly, it was thought by Gorden and Crewe (1948) that the bed bug is a pool feeder, taking up blood that results from hemorrhage produced by the rupture of a vessel.

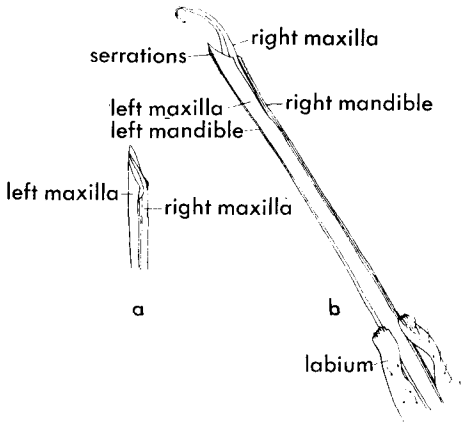

FIG. 3–2.—Tips of maxillae of *Cimex lectularius*: a, locked together in non-feeding position; b, feeding position, right maxilla J-shaped and extruding beyond spear-shaped left maxilla. The functional mouth is at the end of the left maxilla (Dickerson and Lavoipierre 1959).

REACTION OF THE HOST

According to Rothschild and Clay (1952), "Professor J. B. S. Haldane once demonstrated at a Royal Society Conversazione that he is immune to the bite of bed bugs. So was his father." Kemper (1936) says that no one is refractory to the bite, but nearly one-fifth of the persons he tested showed no reaction. During the present study I have observed persons with all degrees of sensitivity, from a colleague whose eyes were swollen shut after an unfortunate encounter with bed bugs to a dermatologist who believed that bed bugs would not bite her but submitted to the bites of laboratory bugs and showed no reaction at all. My own reactions fall between these extremes and follow the typical pattern described for fleas by Benjamini et al. (1960a, 1960b). The actual bite (like that of other well-adapted parasites such as fleas, mosquitoes, and ticks) is painless. Only the merest tickling sensation is felt, probably during the period of probing. Reddish spots due to hemorrhage are observed only when large numbers of bugs feed in a small area, and then only after the edematous swelling has disappeared. An itching sensation usually is felt for several hours after a bite. Hase (1917) described and figured the typical wheal (Fig. 3–3). It is simply a lump or swelling, with no red spot or other distinguishing characteristics like the bites of black flies and some other insects. The reaction is an allergic one (Hecht 1930) stimulated by the saliva that is injected during the bite. Even brief probes without blood sucking produce typical reactions, so the saliva must be injected early in the biting. Cornwall and Patton (1914)

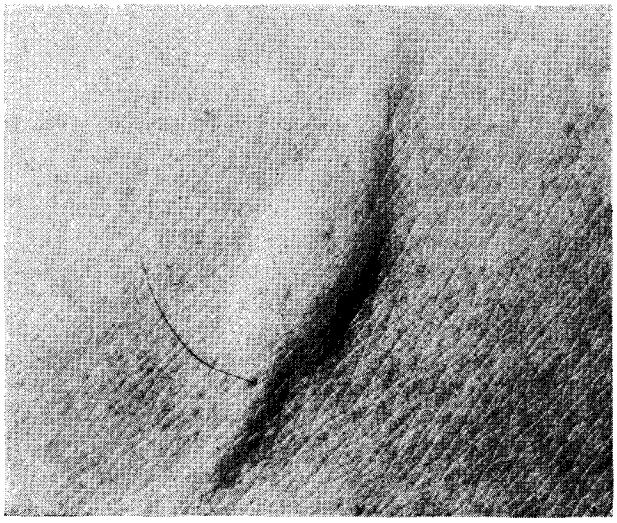

FIG. 3–3.—Lump or wheal resulting from the bite of *Cimex lectularius*.

found no evidence of an anticoagulin in the saliva of *C. hemipterus,* but Puri (1924) tested the secretion from the accessory glands (colorless and watery) and from the salivary glands (deep yellow and slightly thicker) of *C. lectularius* by mixing them with fresh human blood. Secretion from the salivary glands prevented coagulation for 24 hours and that from the accessory glands for 20 to 30 minutes, whereas blood mixed with normal saline coagulated in 10 to 15 minutes. According to Benjamini et al. (1960b) "The substance in the oral secretion [of fleas] responsible for the induction of hypersensitivity shows characteristics of a hapten."

I am indebted to B. F. Feingold and E. Benjamini for permission to cite the unpublished results of their experimental induction of sensitivity to bed bug bites in guinea pigs. The pattern is exactly like that seen in flea bites, but the authors found no cross-reactions between bug bites and flea bites. In the experiments 5 bed bugs were fed on the shaved skin of each of 10 guinea pigs each day. At first, there was no reaction of any kind (latent period), but on the seventh day (5 days in fleas) the animals became sensitized and a delayed (24 hours) reaction was observed in the form of a papular lesion at the site of the bites. After a week with no exposure to bites the animals were again challenged. This time there was an immediate (20 minutes) reaction, followed the next day by a delayed reaction. Four days later the same pattern was observed. One month after the initial exposure a change began to occur. The reactions were mostly immediate with only a few delayed. This continued when the animals were challenged after 2, 3, and 6 weeks. At the end of the experiment all reactions were immediate except one. Theoretically, continued exposure would have resulted in complete desensitization with no reactions at all, but this stage was not reached in the experiments with bed bugs.

My own reactions, after 7 years of feeding a colony at weekly intervals, progressed from delayed to immediate and showed no evidence of desensitization. Kemper (1936), who claimed to have received over 100,000 bites while engaged in experiments over many years, likewise never reached the stage of complete immunity. On the other hand, Hase achieved immunity to the bites after permitting himself to be bitten by 2500 bugs over a 9-month period (Hartnack 1939).

For comparative purposes, I observed the effects of the bites of 3 other species of Cimicidae in 1960, after feeding *C. lectularius* on myself for 3 years. The first of these bugs, *Cimex pilosellus,* caused only an immediate reaction precisely like its congener, *C. lectularius.* The second, *Hesperocimex sonorensis,* caused an immediate reaction but of a quite different appearance—red swellings about 5 mm in diameter. The third species, *Leptocimex duplicatus,* caused no reaction at all by its first bite and almost none by its second feeding a week later. Then 2 weeks after the first bite there was a strong delayed reaction, with a red swelling 2 to 3 inches in diameter appearing after 24 hours and lasting for several days.

Thus the 2 species of *Cimex* caused complete cross reactivity, the distantly related *Hesperocimex* caused cross reactivity with a difference in the type of swelling, and *Leptocimex* caused no cross reaction at all, following an independent and, as far as it was carried, typical pattern of development of sensitivity. It is interesting to note that these reactions correspond in a general way to the taxonomic relationships of the bugs.

Claims that swallow bugs (Myers 1928), bat bugs, and chicken bugs (Lee 1955b) bite man have been confirmed in the course of field collecting and laboratory rearing. At various times bugs of several genera and species have been fed on man and on chickens, rabbits, bats, etc. However, there is no record of swallow bugs or bat bugs becoming established on man as a regular host, and reports of *Haematosiphon* infesting houses (Lee 1955b) are rare.

4 Disease Transmission

Because of their blood-sucking habits and intimate association with man, often under conditions of filth and disease, the bed bugs have long been suspect in the transmission of human diseases. According to Girault (1906a), who reviewed the early literature on pathogenic relations of the bed bug, Elias Metschnikoff (1887) was the first to suggest that the bed bug might be an agent in the transmission of human diseases. Nuttall (1900), on the basis of his own experiments and a critical review, concluded that there was no positive evidence to incriminate the bed bug. Zumpt (1940) in a later study and Burton (1963), reviewing more than half a century of work, came to the same conclusion. Burton's survey of 93 publications showed that laboratory experiments had led certain investigators to the conclusion that bed bugs transmit leprosy, oriental sore, kala-azar, Q fever, relapsing fever, and brucellosis. Transmission, however, was not scientifically proved. Burton reports that bed bugs have been found infected in nature with *Wuchereria bancrofti, Brugia malayi, Trypanosoma cruzi, Brucella melitensis, Coxiella burnetii,* and rickettsiae causing exanthematous typhus, but that proof of transmission of the associated diseases was lacking. Table 4–1 summarizes the maximum survival time in bed bugs of the causative organisms of diseases suspected of being transmitted by bed bugs.

Cimicidae also have been suspected of transmitting trypanosomes between bats. Bowhill (1906) first observed blood parasites in South African bats and suggested, but did not prove, that *"Acanthia pipistrelli* Jenyns" (probably *C. lectularius*) was the vector. Pringault (1914) in Tunis likewise suggested that *"Cimex pipistrelli" (Cacodmus?)* was the transmitting agent of trypanosomiasis between bats. Chatton and Blanc (1918) cultured the trypanosome of a gecko in the bed bug. More recently Berghe et al. (1960) found trypanosomes in the blood of the horseshoe bat, *Hipposideros caffer* (Sundevall), living in a cave on the shores of Lake Tanganyika near Nyanza-Lac. Metacyclic forms of the trypanosome were found in the rectum of the cimicid *Stricticimex brevispinosus* Usinger, which I described from that cave. The authors regard this mode of transmission as identical to that of species of *Triatoma* in the transmission of Chagas disease. Unfortunately, the short note gives no details as to the technique or experimental methods used.

Table 4–1.—Survival time of various disease organisms in *C. lectularius* and *C. hemipterus* (Burton 1963).

Disease	Disease organism	Location of organism in body	Maximum survival time, days
	C. lectularius		
Filariasis	*Wuchereria bancrofti*	Throughout body	8
Mansonelliasis	*Mansonella ozzardi*	Gut	14+
Kala-azar	*Leishmania donovani*	Gut	35
Oriental sore	*Leishmania tropica*	Gut	35
Espundia	*Leishmania braziliensis*	Gut	35
Leprosy	*Mycobacterium lepros*	Head, proboscis, and hemocoel	16
Septicemia	*Staphylococcus aureus*	Salivary glands	14–15
Anthrax	*Bacillus anthracis*	Body and feces	4
Pneumonia, type 2	*Diplococcus pneumoniae*	Gut and malpighian tubules	30–85
Tularemia	*Pasteurella tularensis*	Feces	250+
Brucellosis	*Brucella abortus, melitensis, suis*	Gut	90+
Paratyphoid fever	*Salmonella paratyphi*	Gut and feces	21
Plague	*Pasteurella pestis*	Gut	147
Rocky Mountain spotted fever	*Rickettsia rickettsii*	Gut	7–27
Epidemic typhus	*Rickettsia prowazekii*	Gut	30
Murine typhus	*Rickettsia typhi*	Gut	6
Q fever	*Coxiella burnetii*	Feces	285
Relapsing fever	*Borrelia recurrentis*	Not specified	1+
Relapsing fever	*Borrelia duttoni*	Not specified	150+
Relapsing fever	*Spirochaeta merionesi*	Not specified	200
Infectious jaundice of Brazzaville	*Leptospira icterohaemorrhagiae*	Not specified	38
Poliomyelitis	Poliomyelitis virus	Not specified	7
Yellow fever	Yellow fever virus	Feces	15
Smallpox	Smallpox virus	Salivary glands and hemolymph	12
Lymphocytic choriomeningitis	Lymphocytic choriomeningitis virus	Feces	85+
	C. hemipterus		
Filariasis	*Wuchereria bancrofti*	Throughout body	1–20+
Oriental sore	*Leishmania tropica*	Alimentary tract	
Kala-azar	*Leishmania donovani*	Midgut (after 6 uninfected blood meals)	41
Relapsing fever	*Borrelia recurrentis*	Gut, coelomic fluid, and legs	28+
Yellow fever	Yellow fever virus	Feces	1–2

Mazzotti (1941) was able to experimentally infect the "Mexican chicken bug," *Haematosiphon inodorus,* with *Trypanosoma cruzi* and after 21 days, to infect 2 white mice by inoculating them intraperitoneally with the saline-diluted intestinal contents of the bugs. *Cimex stadleri* Horvath, *Oeciacus hirundinis* (Lamarck), and *Leptocimex boueti* (Brumpt) were listed by Lent (1939) in addition to *C. lectularius* and *C. hemipterus* as natural or experimental hosts of *T. cruzi.*

Cases of iron deficiency caused by excessive feeding of bed bugs on infants were reported in India by Venkatachalam and Belavadi (1962). During my 7 years of feeding bugs, my haemoglobin decreased from a normal 14.5 g per 10 cc of blood in 1958 to 11.5 in 1963 and 1964. It remained low even with supplemental iron taken orally and by injection, but rose to 13.2 g in 1965 several months after I discontinued feeding the bugs.

In summary, Cimicidae have been suspected in the transmission of many diseases or disease organisms of man and bats, but in most cases conclusive evidence is lacking.

5 Control

Control of bed bugs has tested man's ingenuity for centuries. Democritus' recommendation—hang the feet of a hare or of a stag at the foot of the bed—was typical of ancient remedies (Cowan 1865). Linnaeus (1750) gave the name *Actaea cimicifuga* to a plant, the bugbane, that has recently been confirmed as having insecticidal properties (Heal et al. 1950). In 18th-century England, professional exterminators concocted secret formulas guaranteed to destroy bugs. The best-known company for over 100 years was the Messrs. Tiffin and Son, "Bug-destroyers to Her Majesty and the Royal Family." With a sword at his side and a cocked-hat and bag-wig on his head, the elder Tiffin went about his work, catering, as he says, "only to the upper classes" (Cowan 1865).

Another exterminator, John Southall (1730), with the approval of Sir Hans Sloane and the Royal Society, published the first scientific treatise on the bed bug (Fig. 5–1), a work that was often quoted and seldom improved upon for 150 years. Southall learned the formula for his "Nonpareil Liquor" from a native while on a trip to the island of Jamaica. One hundred years later in an anonymous work (1828) entitled "Moyens surs et facile de détruire les punaises," 2 secret formulas were divulged and the subject of bed bug control was reviewed in great detail.

Early in the 20th century, with the continued growth of large cities and the war-time movement of people, bed bug infestations became a major problem. It was estimated that one-third of the dwellings in Stockholm were infested and 4 million people were affected in Greater London. In Germany 700 exterminators plied their trade. Albrecht Hase (1917), Heinrich Kemper (1936), and others at the Preussische Landesanstalt für Wasser-, Boden-, und Lufthygiene in Berlin-Dahlem carried out extensive work on control during this period. Traps were devised and rooms were heated to above 45°C to kill bugs. Oil sprays with or without pyrethrum were only partially effective because of the difficulty of reaching the bugs in their hiding places. Fumigation was recommended as the best means of control but only if done thoroughly by the individual using sulfur dioxide, or if done by licensed exterminators using ethylene oxide or cyanide. In Great Britain heavy naphtha was tested and found to be the most practical fumigant. Unfortunately, all

A

TREATISE

OF

BUGGS:

SHEWING

When and How they were firſt brought into *England.* How they are brought into and infect Houſes.

Their Nature, ſeveral Foods, Times and Manner of Spawning and Propagating in this Climate.

Their great INCREASE accounted for, by Proof of the Numbers each Pair produce in a Seaſon.

REASONS given why all Attempts hitherto made for their Deſtruction have proved ineffectual.

VULGAR ERRORS concerning them refuted.

That from *September* to *March* is the beſt Seaſon for their total Deſtruction, demonſtrated by Reaſon, and proved by Facts.

Concluding with

DIRECTIONS for ſuch as have them not already, how to avoid them; and for thoſe that have them, how to deſtroy them.

By *JOHN SOUTHALL,*

Maker of the Nonpareil Liquor for deſtroying *Buggs* and *Nits,* living at the *Green Poſts* in the *Green Walk* near *Faulcon-ſtairs, Southwark.*

LONDON: Printed for J. ROBERTS, near the *Oxford-Arms* in *Warwick-Lane.* M.DCC.XXX.

(Price One Shilling.)

FIG. 5–1.—Title page from the earliest book on the bed bug (Southall 1730).

methods of control at that time were ineffective or expensive and at best only temporary because of reinfestations. Therefore bed bug control became a community problem like that of rats, house flies, and mosquitoes. Prevention was stressed, moving vans and railroad cars were fumigated regularly, building codes sought to eliminate bed bug harborages, and legal questions arose as to the responsibilities of landlords and tenants for freeing premises of bugs.

In houses, bugs hide in crevices and corners of wooden bedboards, behind loose wallpaper, in nail holes and cracks in the walls, behind pictures, conduits, light switches, wall panels, baseboards, door and window frames, floor crevices, and in furniture and mattresses.

Bed bugs gain entrance to a house in old furniture that has been stored or brought in from infested premises, in luggage of travelers, in laundry baskets, and on clothes of people exposed to bugs in their own homes, places of work, or in theaters and other public places. Apartments may be infested by bugs wandering in from neighboring rooms.

Bed bug annoyance in homes arises from bites and allergic effects, from the odor and spotting of walls (Fig. 5–2) and furniture, and es-

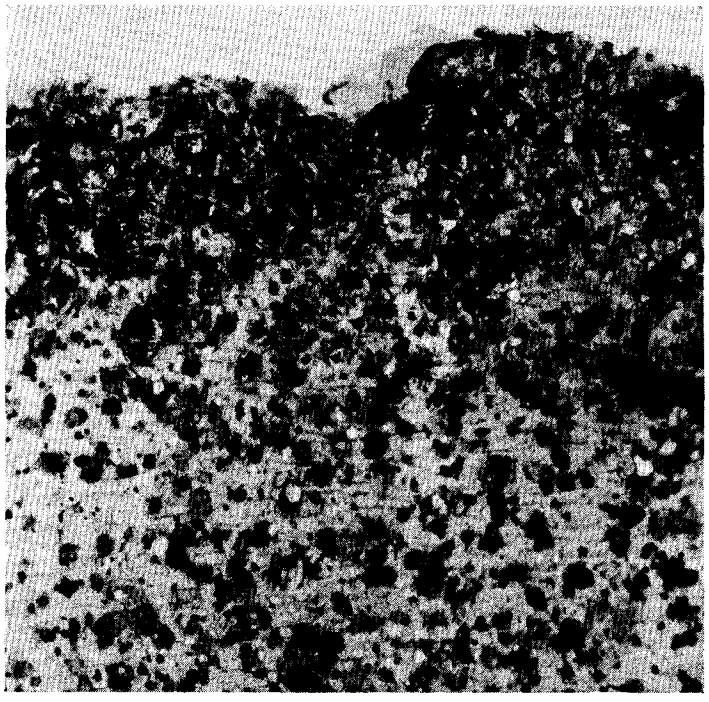

FIG. 5–2.—Bed bug harborage with accumulated cast skins and fecal spots.

pecially from loss of sleep caused by apprehension that the bugs are present ("entomophobia"). The bed bug has been called "the bug that nobody knows"—a common reaction of people whose houses are infested. The very word "bug" is still avoided in polite conversation, and an infestation is regarded as shameful. This situation makes attempts at community control difficult.

Soon after the beginning of World War II, DDT became available and was used extensively for control of mosquitoes and, incidentally, other pests. Because of its residual action when sprayed on surfaces frequented by bed bugs, DDT seemed the perfect answer to man's age-old problem (Fig. 5–3). Complete control was attained and sprayed surfaces remained toxic for months. But success was short-lived. By 1947 Johnson and Hill (1948) found that bed bugs in barracks at Pearl Harbor had

FIG. 5–3.—Spraying to leave a deposit of residual insecticide on walls of bedroom.

Table 5–1.—Resistant and nonresistant strains of bed bugs exposed to filter paper treated with DDT at the rate of 200 mg DDT/ft² (Mallis and Miller 1964).

Bed bug strain	Test date	Average % dead and moribund			
		24 hr	48 hr	72 hr	144 hr
Nonresistant	January 1959	35	85	95	100
Resistant	January 1959	0	0	0	0
Nonresistant	September 1962	60	100	100	100
Resistant	September 1962	0	0	0	5
Nonresistant	October 1963	30	70	100	100
Resistant	October 1963	0	0	0	5

developed resistance to DDT. Since that time resistance has been noted for both *C. lectularius* and *C. hemipterus* in many parts of the world (Rao and Halgeri 1956, Lofgren et al. 1958, Busvine 1959). Mallis and Miller (1964) tested bugs that had been proved resistant to DDT 5 years earlier and found that, although not exposed in the interim, they had maintained their resistance (Table 5–1). Strains showing the highest resistance to DDT were almost completely immune, particularly after feeding. Busvine (1959), in a world-wide survey of bed bug resistance for the World Health Organization, showed that 2 kinds of resistance developed, either independently or in combination. One involves DDT, methoxychlor, and their analogs. This type of resistance cannot be overcome by the addition of the DDT synergist DMC. The other kind of resistance involves benzene hexachloride, dieldrin, and various other chlorinated cyclodiene insecticides. Within each group, resistance to one insecticide involves resistance to all. There were "definite indications of resistance to pyrethrins in strains resistant to DDT, reaching about 10 times normal" in one strain.

Undoubtedly, resistance is a serious threat to the future of bed bug control. However, in spite of resistance, Lofgren et al. (1958) were able to achieve complete control in from 1 to 8 days in homes and apartments in Denver, Colorado, using several of the leading insecticides (Table 5–2). With a compressed air sprayer, each of the materials was applied as a solution in 1 to 2 pints of odorless kerosene to bed frames, mattresses, woodwork, etc. When malathion, of special interest because it has induced no resistance, was applied in a series of tests in Orlando, Florida, using the technique just described, 1 live bug was found after 2 days; thereafter the sprayed homes were free of bugs during a 9-month inspection period.

An entirely different approach to bed bug control was suggested in the experiments of Lindquist et al. (1944), who fed sublethal doses of DDT and pyrethrum to rabbits and found that bed bugs died after a few hours when fed on them.

Table 5–2.—Control of natural populations of bed bugs in substandard hotels in Denver, Colorado, with several insecticides (Lofgren et al. 1958).

Insecticide and concentration, %	Number of rooms	Number of live bed bugs found after indicated days							
		1	2	3–5	7–8	9–10	11	12	14
Diazinon									
0.5	4	0	0	0	–	0	0	–	–
.1	5	1	1	1	–	0	0	–	–
Ronnel (as Dow ET-57)									
1.0	4	6	0	1	0	0	0	1	0
0.5	4	1	3	1	0	0	0	0	0
Trichlorfon (as Dipterex)									
1.0	5	13	6	0	0	0	0	0	0
0.5	4	23	14	0	8	–	0	0	0
Chlorthion®[a]									
1.0	4	2	5	0	0	–	0	0	0
0.5	4	1	0	11	1	–	0	0	0
Malathion									
1.0	5	3	1	3	0	0	0	0	0
0.5	6	1	0	0	1	0	0	0	0
Dieldrin									
0.5	3	5	7	5	–	0	0	0	–
DDT									
5.0	3	41	4	4	1	0	1	0	–
Pyrethrins plus piperonyl butoxide									
0.1 + 1.0	3	11	0	0	[b]	[b]	–	–	–

[a] *O*-(3-chloro-4-nitrophenyl) *O,O*-dimethyl phosphorothioate.
[b] Newly hatched nymphs in all treated rooms.

At present, DDT and malathion are recommended for the control of bed bugs. Pyrethrum (with a synergist) kills bugs more quickly than DDT but does not have a residual effect. Therefore, the two are combined in most household sprays. Sprays may be in the form of emulsions in water or kerosene solutions. In either case, the object is to leave an invisible deposit of insecticide on all surfaces where bed bugs are likely to walk or hide. Therefore, a wet spray rather than an aerosol space spray that fills the air in a room is needed. Preferably, a garden-type compressed-air sprayer should be used with a nozzle that makes a flat, fan-shaped spray. One quart of 5% DDT will cover 250 to 500 ft^2. In cases of DDT resistance, malathion is recommended in a 2% spray for general use and in a weaker solution (½%) for upholstery and mattresses. The latter should not be soaked with spray and must be dried completely before use. Premium-grade malathion should be used to avoid offensive odor. Diazinon (0.5%) may be used if bed bugs are resistant to

both DDT and malathion. The precautions given on the label should always be followed.

Travelers who are troubled with bed bugs for a single night and are not concerned with long-term eradication need to use a somewhat different type of control. The bed should be moved away from the walls, preferably to another part of the room, the bedding shaken out, and the mattress, springs, slats, and beadstead sprayed thoroughly at close range with a "bug bomb." In tests using HEP (pyrethrins 0.2%, *N*-octyl bicycloheptene dicarboximide 0.4%, technical piperonyl butoxide 0.72%, petroleum distillate 1.34%) as an aerosol, nymphs and adults of both resistant and nonresistant strains were rendered quiescent in 4 minutes—mortality was 100% in 16 hours (Barbara Wilson). Because bed bugs wander extensively and take a long time to find a host, the treatment should be sufficient to permit a night of undisturbed sleep. Laboratory tests indicate that DDT will not repel bed bugs that approach the bed from elsewhere in the room. All the common insect repellents were tested (Berryman), and none prevented bugs from crossing a treated ring on a post simulating the leg of a bed. In many skin tests only Off® (15% deet), applied as an aerosol spray, gave complete protection up to 5 hours and fair protection for 7 hours. However, the use of a repellent against bed bugs requires spraying the entire body and is not recommended.

In animal cages, roosts, and nests, all surfaces and cracks should be sprayed with the same materials recommended for human dwellings. Poultry houses should be sprayed with 0.5% lindane, 1% malathion, or 0.2% pyrethrins. Since conspicuous residues are not objectionable under such circumstances, coarse sprays may be applied to the point of run-off. In laboratories where animals or birds are kept for experimental purposes and insecticide contamination is to be avoided, pyrethrum may be used on cages, or residual insecticides can be applied carefully to cracks and other hiding places without contaminating caged animals.

6 | Morphology

The classic work on the anatomy of *C. lectularius* is that of Landois (1868–1869). More recent works include the general treatment of *C. hemipterus* by Patton and Cragg (1913) and specialized studies by Davis (1956) and many others. The most recent work on external morphology of *C. lectularius* is by Ferris in Ferris and Usinger (1957a). The description of *C. lectularius,* presented herein with comparative notes, is modified from Ferris with suggestions by Matsuda. Except for details of head structure and male and female genitalia, the illustrations are the Ferris originals.

EXTERNAL MORPHOLOGY

THE LAST NYMPHAL INSTAR
(Fig. 6–1, 6–2)

Head

The labrum appears as a free sclerite at the extreme anterior margin of the head. It is somewhat semicircular or semielliptical in form and marked by a definite labral suture. Ordinarily, it is deflexed beneath the head and covers the base of the rostrum. In *Primicimex* it is long and narrow.

The clypeus is only partially delimited by lateral sutures, which extend a short distance into the dorsal aspect of the head and then disappear, thus not defining the clypeus posteriorly. On either side of the clypeus are paraclypeal lobes or juga and surrounding the base of the rostrum are the maxillary lobes.

The ecdysial lines are defined in the head of the nymph, where they connect with the middorsal line of the thorax and split during molting. On the head they form a broad V, the base of which rests near the posterior margin of the head capsule. From this point the arms pass to the anterior margin of the head between the eyes and the bases of the antennae. There are no ocelli. The eyes are small knobs projecting from the side of the head and are composed of several facets. They arise from the lateral margins of the sclerotized head capsule. The ventral wall is membranous except for 2 ventral plates separated along the median line.

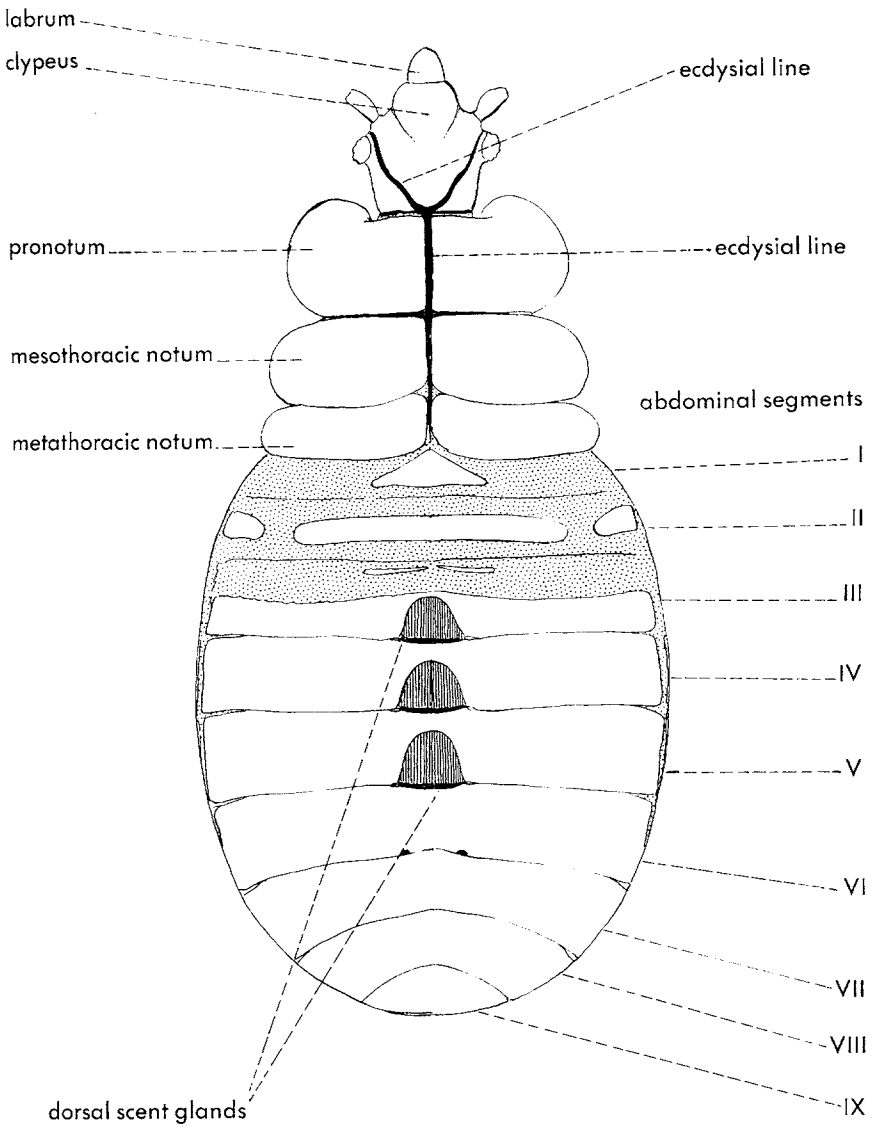

FIG. 6–1.—Last-stage nymph, *Cimex lectularius*, dorsal view (Ferris 1957a).

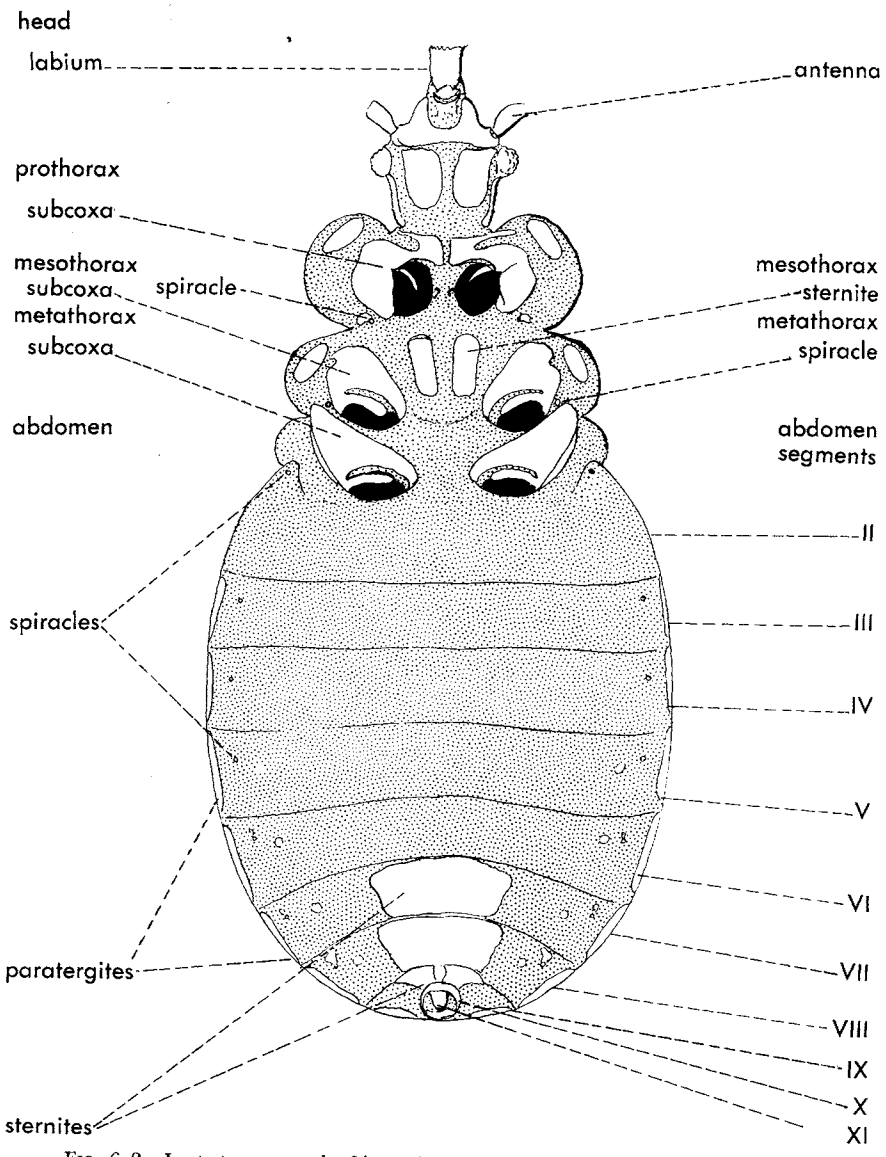

FIG. 6–2.—Last-stage nymph, *Cimex lectularius*, ventral view (Ferris 1957a).

The labium arises from just within the anterior margin of the head beneath the labrum. A very small sclerite at its base may be a vestige of a fourth segment but for practical purposes the labium may be regarded as 3-segmented. On the anterior or (at rest) ventral surface is a longitudinal groove which contains the fascicle of stylets. The tip of the labium consists of 2 lobes bearing minute sensory papillae. According to Snodgrass (1944), "The mandibular stylets are much slenderer than the maxillary stylets and lie against the posterior surface of the former. Between the maxillary stylets is the relatively large food canal and a minute salivary canal. At the base of the beak the stylets turn backward into the head pouches and on their enlarged bases are inserted the protractor and retractor muscles, there being no lever arm connected with either the mandibular or maxillary stylet in the bed bug" (Fig. 6–3). The mandibular stylets are minutely serrate apically and the right maxilla is hooked at the tip (Dickerson and Lavoipierre 1959).

The antennae are always 4-segmented. The first segment is inserted on a small protuberance between the eye and the clypeus. It is stout and widened apically. The second segment is long and subcylindrical and, in cleared specimens, has a pale ring subbasally. The third and fourth segments are thinner, the latter shorter and slightly fusiform. There is a minute intercalary segment at the base of each of these segments that is visible only in expanded, slide-mounted specimens.

Thorax

The prothorax is broad, receiving the head in its concave anterior margin, with the sides extending winglike laterally. Dorsally, the pronotum consists of a single plate. The mesothorax and metathorax are each composed dorsally of a single transverse plate which differs from the pronotum essentially only in length.

On the ventral side (Fig. 6–2) the prothorax is largely membranous. It is occupied by the subcoxae (=pleural plates) which extend in an irregular arch about the outer side of the coxae. These plates are separated by a distinct suture at the median line. They bear the coxal condyle and extending from it a suturelike line which indicates the pleural suture or phragma. Between the somewhat separated coxal foramina lie the 2 prosternal apophyses. The trochantins are pieces detached from the subcoxae, lying in the anterior part of the coxal foramina. Just laterad of the coxa lies on each side a small sclerotized plate, perhaps a detached portion of the notum. The notum, except for this plate, terminates at the margin of the thorax. Posterior to each coxa is the mesothoracic spiracle lying in a small surrounding sclerite.

The ventral side of the mesothorax is likewise largely membranous. The subcoxae (=pleurites) are rather oval pieces, broadly separated mesally and bearing the trochantins, which are attached to them close to the subcoxal condyle. Between the subcoxae lie 2 rather large longitu-

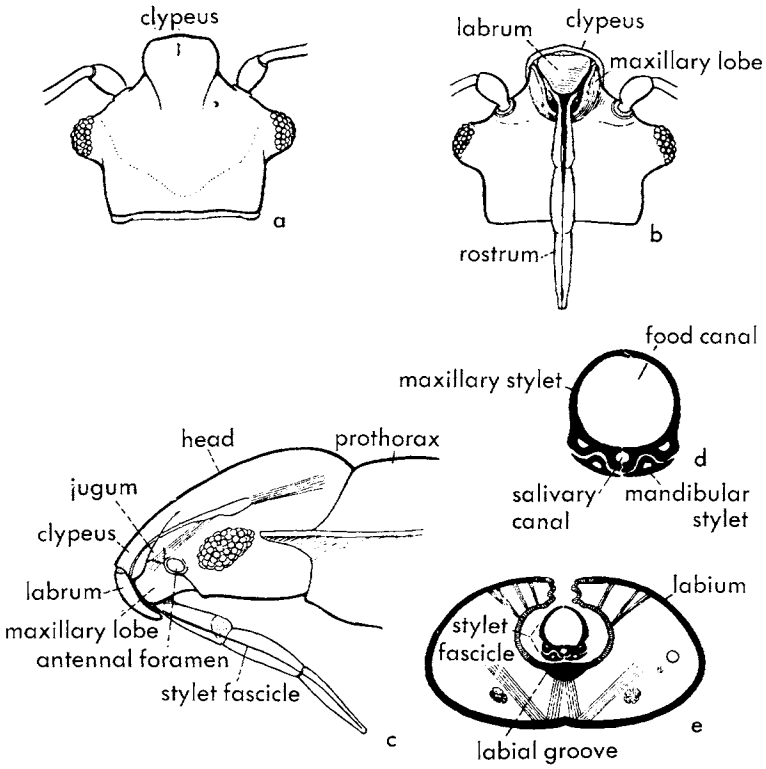

FIG. 6–3.—Details of head and rostrum, *Cimex lectularius* (Snodgrass 1944).

dinal plates which may represent the sternites. Laterad of each subcoxa lies a small oval piece possibly representing a portion of the notum, which otherwise ends at the margin of the body. There seem to be no sternal apophyses. The metathoracic spiracle lies in a small plate just behind the subcoxae.

The ventral side of the metathorax bears only the sclerotized subcoxae, which are shaped like the subcoxae of the mesothorax but are slightly larger and show a distinct division into episternum and epimeron. There is no evidence of sternal plates and none of the sternal apophyses.

Abdomen

The dorsal side of the abdomen is sclerotized except for a partial membranization of the first to third segments. The first segment presents medially a small, triangular plate. The second segment bears a broad, short plate with a small plate at each end. Near its middle anteriorly, the third segment bears a pair of very small plates; its posterior half bears a short, broad plate extending from one margin to the other.

The 3 largely unsclerotized basal segments, light in color, are conspicuous features which serve to distinguish the nymph from the adult even without a microscope. The degree and pattern of sclerotization differ in the various genera.

The fourth to ninth segments are sclerotized throughout, and the third to fifth have, along the median line, an almost semicircular dark area; the base of this area rests upon the posterior margin of the segment. These are the dorsal scent glands. The sixth segment has merely a pair of dark spots in this position. The ninth segment terminates the dorsal aspect of the body; the tenth and eleventh segments are concealed beneath it except when protruded. Laterad of the termination of the sclerotization of the dorsum, each of the third to eighth segments bears a small paratergite.

The ventral side of the abdomen is almost entirely membranous. The sixth to eighth segments each bear a small circular sclerotization just mesad of the spiracle. The seventh and eighth segments each bear a small trapezoidal sclerite, occupying about the median third of the segment, and the ninth segment has a small sclerotization medially. The tenth segment is much reduced in size and bears a complete or nearly complete sclerotized ring within which is presumably situated the very small eleventh segment bearing the anus.

THE ADULT

(Fig. 6–4, 6–5)

Head

The head is entirely similar to that of the nymph except for the complete fusion of the ecdysial lines and the sclerotization of the ventral side.

Thorax

The dorsum of the prothorax remains the same as in the nymph but the ventral side is considerably altered. The ventral side is for the most part sclerotized, all sutures are closed, and the evidence of the individual sclerites is much obscured. However, there are certain points of reference that remain in place and are visible. The first of these are the openings of the pleural apophyseal pits, which lie just laterad of the coxal condyles. They define some portion of the area in which they lie as subcoxal (= pleural) but do not indicate the pleural limits, which, because of the closing of the sutures, are indicated only in general. The widely separated sternal apophyseal pits lie between and are concealed by the coxae. The sclerotized area between the pits and partially surrounding them is certainly sternal. Bearing in mind the arrangement of the parts in the nymph and the conditions to be seen in more generalized forms, it may be assumed that the remainder of the sclerotized ventral side is composed of the subcoxae, which now occupy most, if not all, of the

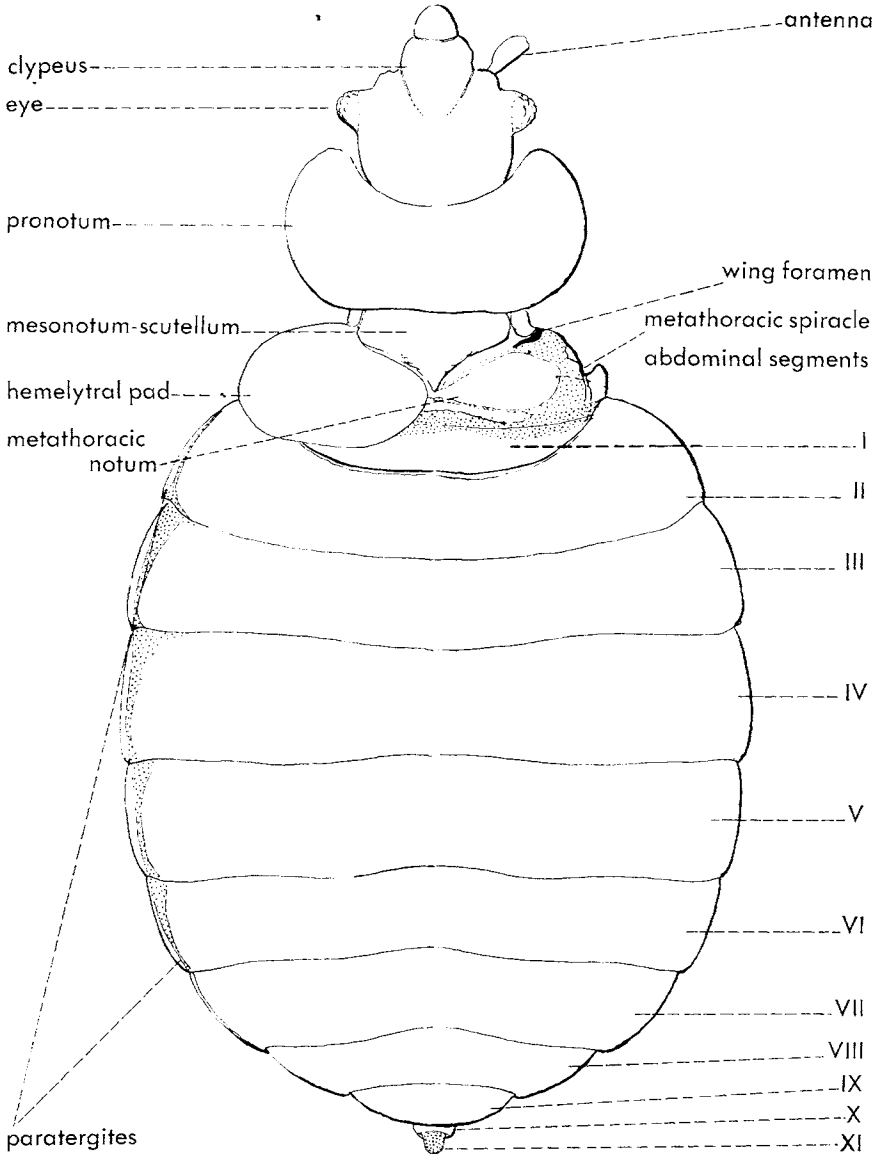

FIG. 6–4.—Adult female, *Cimex lectularius*, dorsal view (Ferris 1957a).

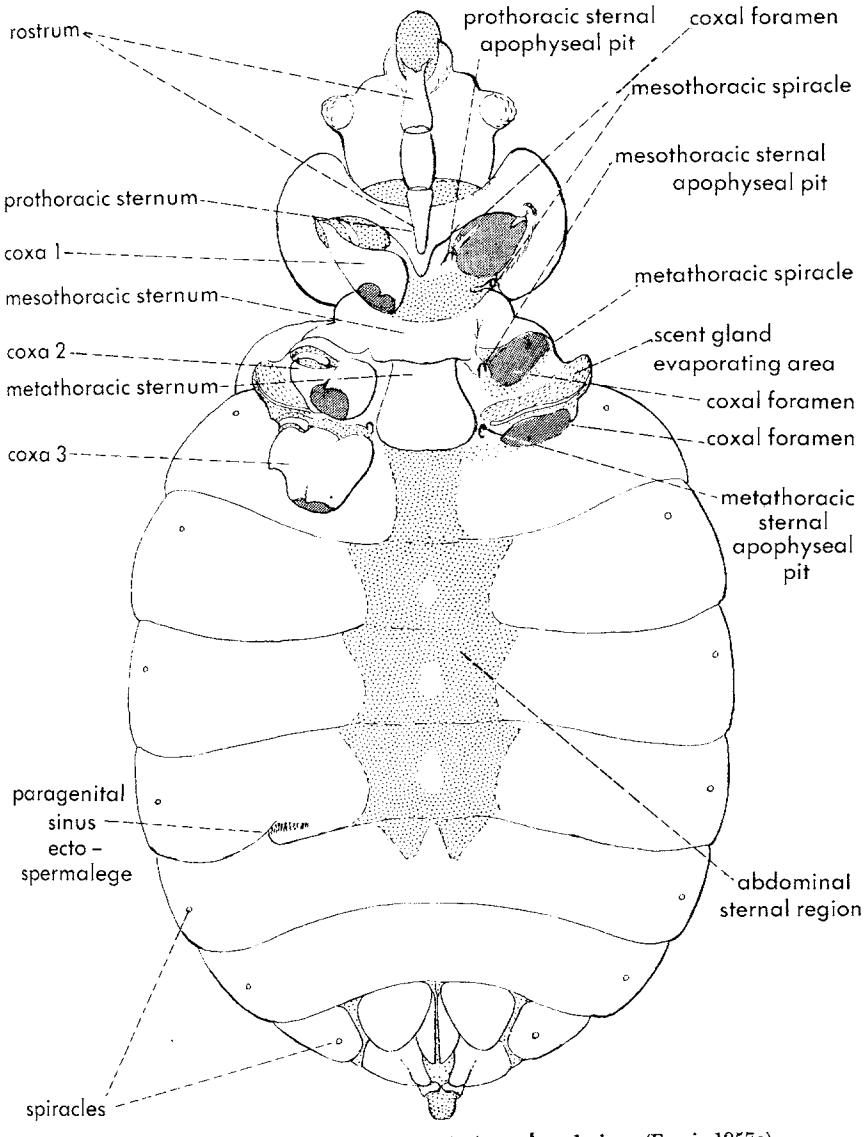

FIG. 6–5.—Adult female, *Cimex lectularius*, ventral view (Ferris 1957a).

area laterad and cephalad of the coxae. These subcoxal areas are completely fused across the median line and here form the prominent, projecting median point lying between the coxae. The trochantin appears as a small, detached sclerite in the membrane anterior to the coxae. The mesothoracic spiracle lies in a small plate just posterior to the coxae. A membrane lies between these elements and the mesothorax.

Dorsally and at its lateral extremity the mesothorax now bears the reduced forewings or hemelytral pads, attached by a narrow base. At this point a bit of the subcoxa (=pleurite) extends slightly to the dorsal side, and a distinct, short longitudinal suture appears, separating the subcoxa from the notum. The median portion of the dorsum between the bases of the wing pads is occupied by a broad sclerite, the mesothoracic notum or scutellum, which terminates in an acute point posteriorly. Behind the scutellum and underlying the wings is an ill-defined transverse plate that may belong either to the mesothorax or to the metathorax; posterior to this is a narrow transverse plate that appears certainly to belong to the metathorax. Following this plate is another that may conceivably belong to the metathorax but is here regarded as belonging to the first abdominal segment.

The hemelytral pads are always reduced and vary in form and extent throughout the group, but at their greatest development never reach much beyond the second abdominal segment. In form they vary from the nearly circular pads of *Primicimex* to the almost bladelike transverse organs of *Bertilia valdiviana* (Philippi) and to a scarcely perceptible ridgelike elevation of the notum in *Leptocimex*. There is no trace of the posterior wings.

On the ventral side (Fig. 6–6) the mesothorax is almost completely sclerotized, only slight areas about the coxal foramina remaining membranous. The landmarks of the coxal condyles and the sternal apophyses may be taken as the starting points for an interpretation of the structures. At the margin of the body a narrow, sclerotized isthmus connects the sclerotization of the mesothorax and metathorax; in this isthmus the spiracles of the metathorax lie close to the coxal condyle of the mesothorax. From almost the same point arise the trochantins of the mesothorax. Widely separated between the coxae are the sternal apophyseal pits, which are borne within narrow sclerotized arms branching from the median sclerotized area. The subcoxae (=pleurites) are separated from the sternum by a slight partial suture. The mesothoracic sternum shows no evidence of the median longitudinal suture seen in Anthocoridae and many other Hemiptera.

The metathorax is in general similar to the mesothorax in the arrangement of its ventral sclerotization, but the encroachment of the coxae of

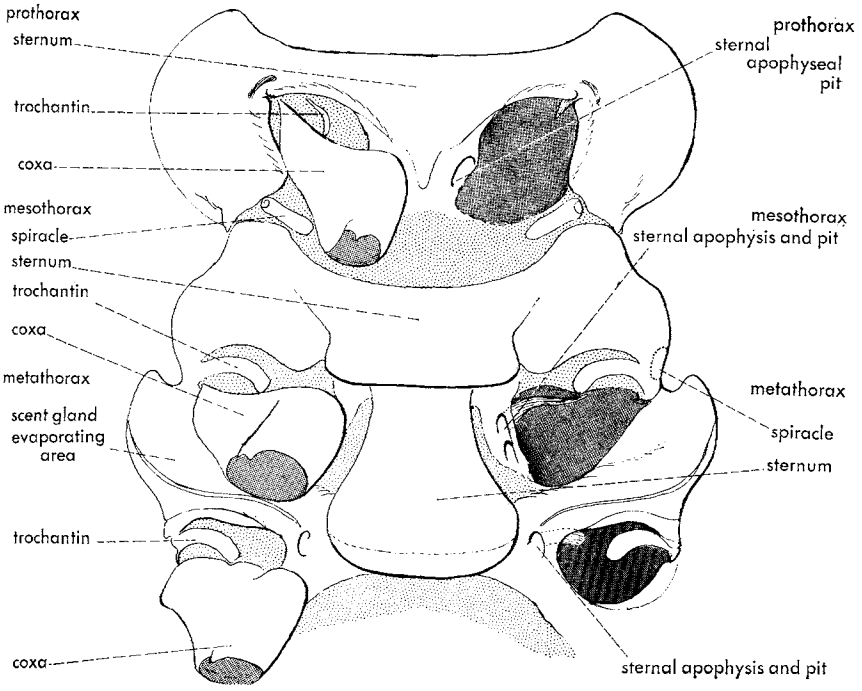

FIG. 6–6.—Adult *Cimex lectularius*, ventral aspect of thorax (Ferris 1957a).

the mesothoracic legs has somewhat narrowed its lateral portions (Fig. 6–7). The coxal condyle and the trochantin are in a position corresponding to that on the mesothorax. The area of the subcoxae anterior and laterad to the coxal condyle bears the slitlike opening of the scent gland, and the adjacent evaporating areas extend inward to meet the sternum. The sternal apophyseal pits are widely separated from each other and are placed close to the median margin of the coxae in sclerotized plates which arch about the coxal condyle and fade out or merge with the first abdominal sternite. Apparently continuous with these plates is a median raised plate of varying form and size (but always present) which may be regarded as the metasternum. In *Cimex* this plate is broad and apically spatulate, but in other forms it varies from this shape and size.

Legs

The normal parts are always present except for the pulvilli and arolia. The tarsus is always 3-segmented (2-segmented in nymphs), the terminal

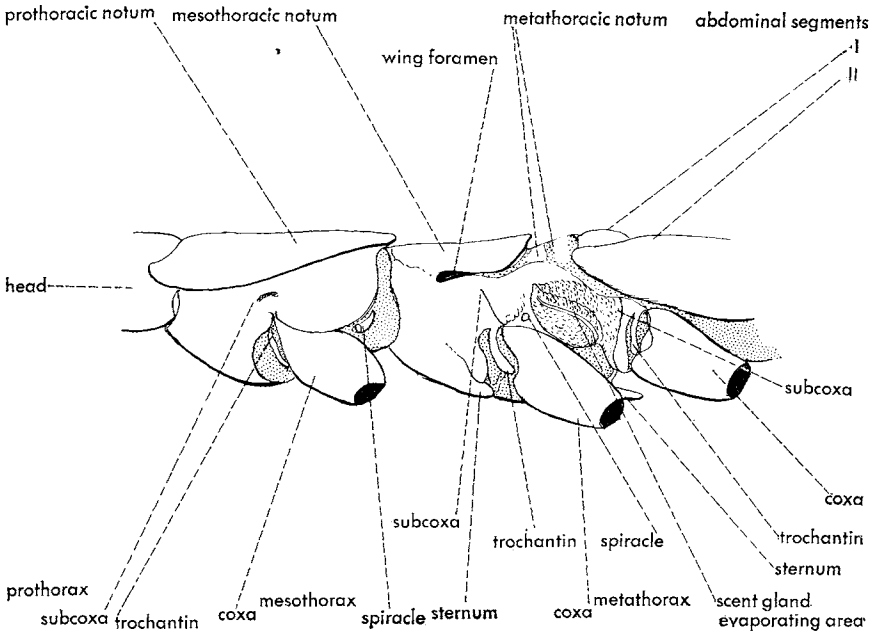

FIG. 6–7.—Adult *Cimex lectularius*, lateral aspect of thoracic region (Ferris 1957a).

segment about as long as the other 2 together, and there are always 2 simple claws.

In *Primicimex* and *Leptocimex* the legs are long and slender, the posterior legs almost as long as the body itself. In *Cacodmus* these legs are scarcely half as long as the body and there is every variation between these extremes in other genera.

In the genus *Paracimex* the morphologically posterior side of the femur is beset, toward the apex, with a row of stout spines, and in *Afrocimex* the prothoracic femora alone are thus armed. In *Leptocimex* a row of short, stout setae extend from the apex almost to the base of the femur of the prothoracic legs. The stout setae, interspersed with slender setae, on the tibiae of the middle and posterior legs of the Haematosiphoninae are a distinctive feature of that group.

On the morphologically posterior side at the apex of the tibiae of *C. lectularius* there occurs a brush of short, soft bristles or hairs. In some species they are merely a slight and scarcely recognizable tuft of fine hairs but in others they are a quite conspicuous group of similar struc-

tures borne upon a slightly raised, distinct sclerite. In some genera, such as *Leptocimex,* they seem to be entirely lacking on all the legs. In *Cacodmus* they are highly developed on all the legs; every variation between these two extremes exists.

In some Cacodminae a slight transverse break in the continuity of the sclerotization occurs subapically in the tibiae, giving the appearance of a pseudosegmentation.

Abdomen

The abdomen is much the same in its general features in all Cimicidae. There are always 11 more-or-less recognizable segments, and 7 pairs of spiracles which are borne on the second to eighth segments. In the adult, sexual differences involve mainly the genitalic structures and the form and position of the spermalege in the female. The nymph differs in the disposition of sclerotization and in the entire absence of any of the structures associated with reproduction.

The abdomen is capable of enormous expansion at the time of engorgement. In the nymphs, elasticity is achieved by the membranous areas at the base of the abdomen. In the adult the intersegmental membranes are wide and the second to fifth abdominal segments are membranous at the middle of the ventral surface, forming the so-called "hunger folds."

The primary genitalic structures of the female (Fig. 6–8) form a recognizable homologue of the ovipositor and occupy the ventral aspects of the eighth and ninth segments. Laterally, the paratergites of the eighth segment bear the last spiracles. The gonocoxae consist of a pair of broad, flat plates which occupy the median two-thirds of the ventral aspect of the eighth segment. From each there arises a narrow, apically rounded gonapophysis. The lateral plates of the ninth segment are the fused paratergite +2nd gonocoxa. The second gonapophyses are reduced to thin membranous lobes concealed beneath the first gonapophyses with their bases forming the sclerotized rami.

In *Primicimex* the ninth paratergites and second gonocoxae are completely separate and the second gonapophyses are well developed. A small sclerotized strut (gonangulum) is concealed beneath each first gonapophysis.

In the male (Fig. 6–8) the abdomen narrows toward the posterior extremity and the ninth segment is longer and asymmetrical. The paramere arises close to its apex on the ventral side. The paramere is always strongly curved to the left (viewed from the dorsal side), its external

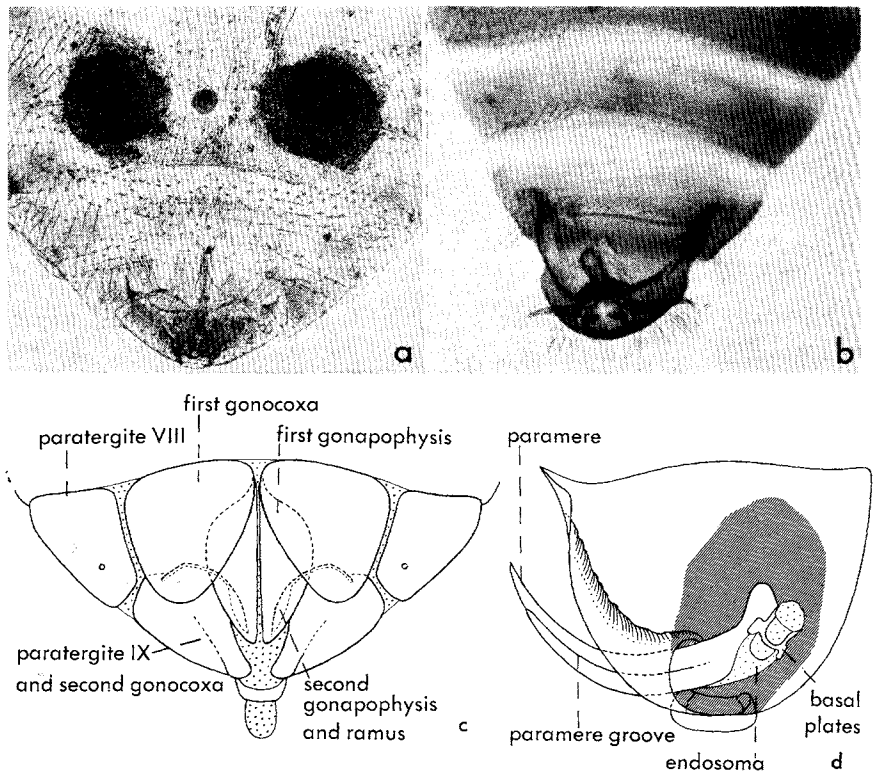

FIG. 6–8.—a, *Oeciacus hirundinis,* female with two spermaleges (Carayon); b, *Cimex hemipterus,* male with two parameres; c, *Cimex lectularius,* female genitalia, ventral view; d, *Cimex lectularius,* male genitalia, dorsal view.

portion lying in a furrow in the side of the ninth segment. Christophers and Cragg's (1922) conclusion that this is the left paramere has been generally accepted by later workers. The right paramere is entirely lacking except in teratological specimens.

The base of the paramere is retracted into the body for a short distance. The paramere is grooved on the outer or convex side, except apically where it is folded to form a tube. The aedeagus lies just above the base of the paramere. The basal plates are asymmetrical with connections which are inconspicuous except in cleared and stained preparations. There is a membranous phallosoma and beyond this, an endosoma which, during mating, everts to form a long membranous tube that fits in the groove of the paramere. In *Primicimex* the basal plates form a stout ringlike structure.

The paramere varies in length and breadth in the various genera, being very short in *Paracimex* where it does not attain the anterior margin of the ninth segment, and very long and slender in some *Cacodmus,* where it extends to the eighth or seventh segments.

On the morphologically right half of the ventral side of the female there appears a notch or paragenital sinus in the posterior margin of the fifth segment. The sclerotized organ or ectospermalege into which this slit opens may belong either to the fifth or the sixth segment of the body, occurring at the point of union of these 2 segments. Carayon details the position and structure of the spermalege in various genera in Chapter 7.

Cragg (1920) first observed that the spermalege and paragenital sinus may be double in rare cases. A paired spermalege is here recorded in *Oeciacus hirundinis* and double parameres in a male of *C. hemipterus* (Fig. 6–8a, b).

Setae

All Cimicidae are more or less clothed with setae. Rothschild (1912b) was the first to show that these are of different types, the simple bristles with pointed tips occurring on the middle of the abdominal venter, on the inner sides of the tibiae, and elsewhere. The second type tapers from base to apex and is cleft at the tip. This type is found on the basal abdominal terga and is longer in the males than in the females. It also occurs on other parts of the body. The third type is thickened toward the apex, bears ridges, and is dentate at the tip and often on the convex side. This type is found mainly at the sides of the body and is best seen on the lateral margins of the pronotum. Most of the dorsal setae are set in prominent pits. In addition to these characteristic types, various sensory hairs are interspersed, especially on the antennae, and in other genera very long, erect bristles (*Afrocimex*) or short, stout spines (Haematosiphoninae) occur on the tibiae. Rows of spines forming a comb are seen on the femora of *Paracimex*. Jordan and Rothschild (1912) used the type of bristles as an important character in their subfamily classification.

INTERNAL ANATOMY

The internal anatomy of *C. lectularius* was treated by Landois (1868–1869) but Dufour (1833) did pioneer work. Details have been added in recent years by Andre (1912), Patton and Cragg (1913), Murray (1914), Cornwall (1923), Büchner (1923), and Hutchinson (1925);

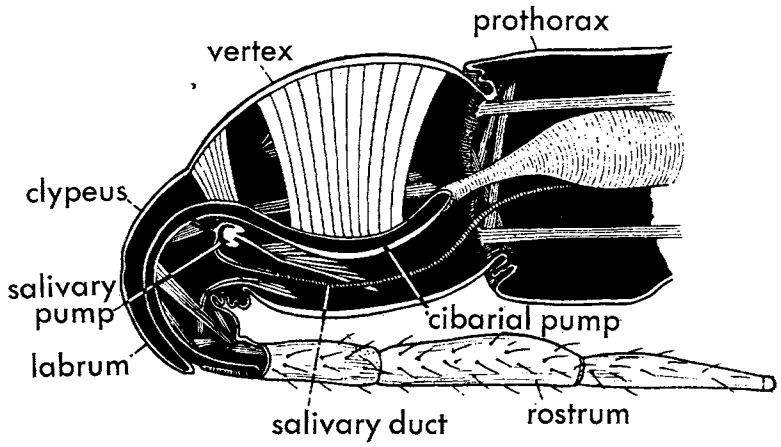

FIG. 6–9.—Diagram of internal anatomy of head of *Cimex lectularius,* side view (Snodgrass 1944).

especially on mouthparts by Puri (1924), Snodgrass (1944), and Dickerson and Lavoipierre (1959); on scent glands by Puri (1924) and Kemper (1929b); and on reproductive organs by Davis (1956). Carayon (1959) gave a comparative account of reproductive organs in other genera. In the present work, separate sections have been prepared by Carayon on the types of scent glands and reproductive systems in Cimicidae.

ALIMENTARY TRACT

In the head (Fig. 6–9) the food channel of the stylet fascicle connects with the cibarial pump. The pearshaped salivary gland and smaller round accessory gland are actually in the thorax but their long ducts join and extend into the head. The salivary pump forces saliva down the salivary channel. The cibarial pump has dorsal and lateral muscles to pump blood from the host. It is connected by a thin-walled esophagus to the first ventriculus or stomach, which is large and bulbous. The stomach narrows abruptly at a sphincter and connects with the second ventriculus and thence by a tubular region with the third ventriculus and the top-shaped rectum. At the junction of the third ventriculus and rectum, 4 long convoluted malpighian tubules arise (Fig. 6–10).

TRACHEAL SYSTEM

There are 2 main longitudinal tracheal trunks (Fig. 6–10) with numerous branches to all the organs. Near each spiracle a branch arises which connects across to the corresponding branch on the other side (shown only at the sides in Fig. 6–10). There are 2 pairs of spiracles on the thorax and 7 on the abdomen.

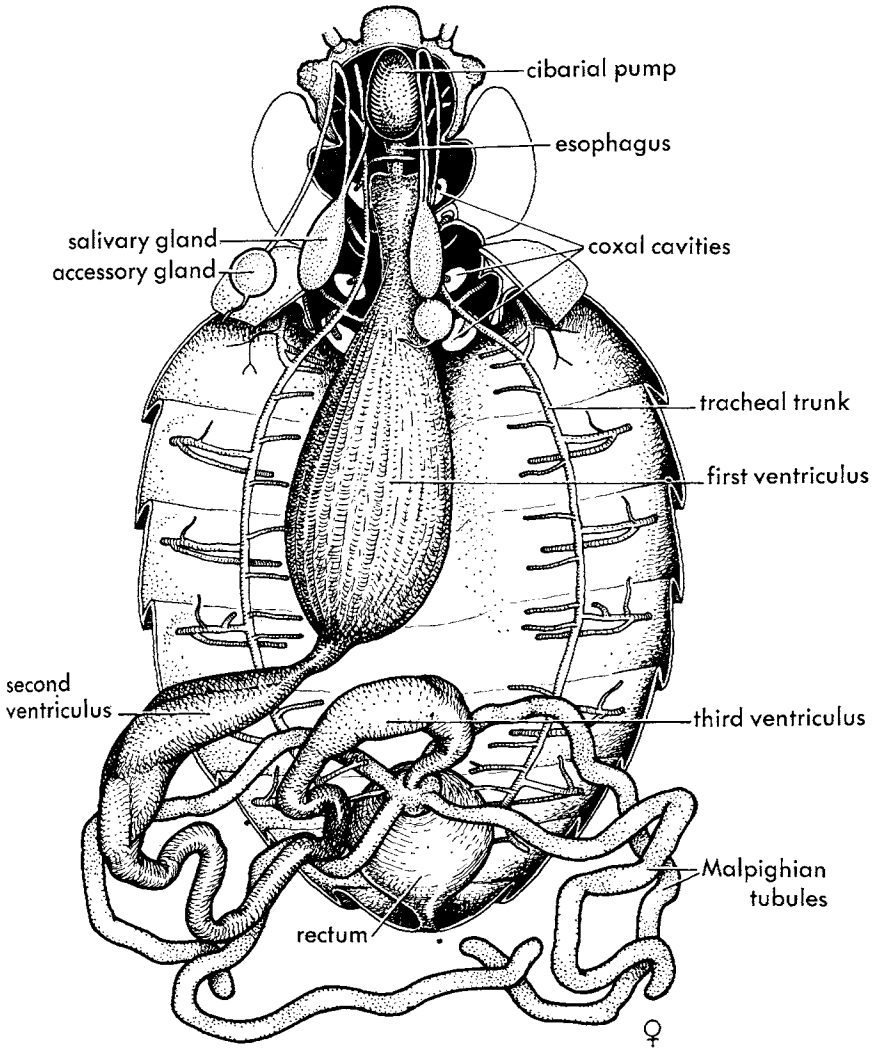

FIG. 6-10.—Internal anatomy of *Cimex lectularius*. Alimentary tract and parts of tracheal system (Catts, original).

CIRCULATORY SYSTEM

The dorsal vessel is a simple tube extending from the posterior part of the abdomen forward to the cerebral ganglion (brain). It is thicker posteriorly than anteriorly. The opening is directed ventrally and has 3 rounded lobes. Nephrocytes occur along the dorsal vessel. The small clumps of periesophageal cells are connected at the anterior end. The parietal nephrocytes and the pericardial nephrocytes are much more numerous and are attached to the sides of the dorsal vessel along most of its length (Puri 1924).

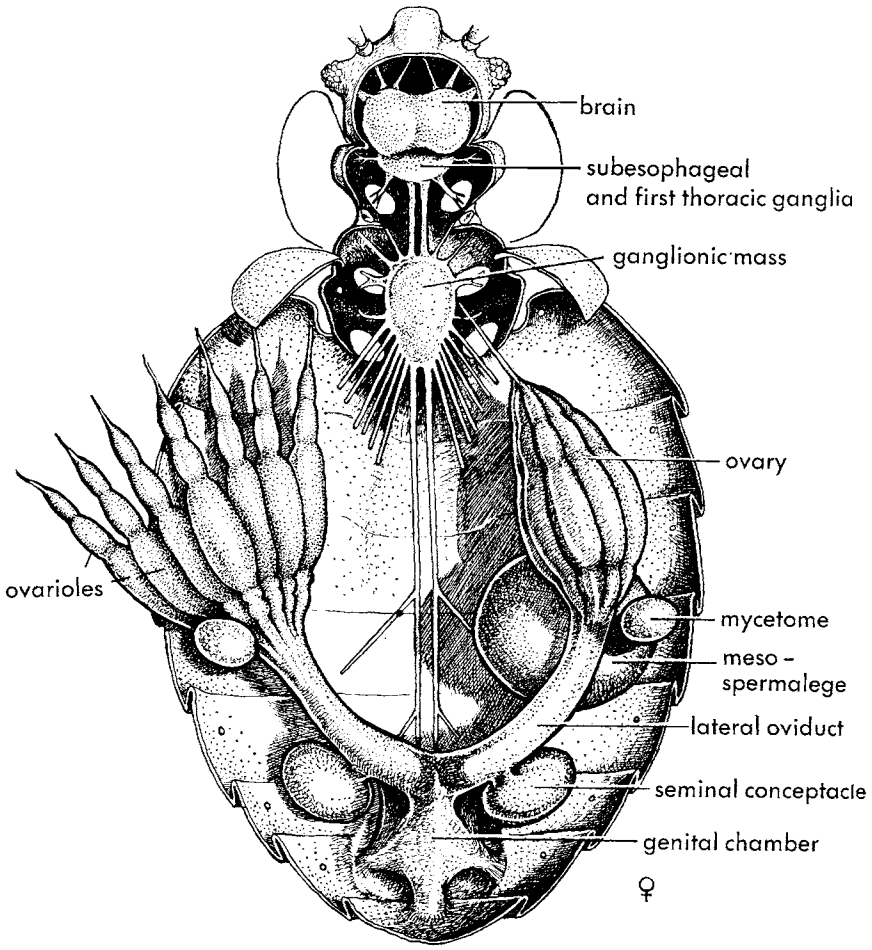

FIG. 6-11.—Internal anatomy of *Cimex lectularius*. Female reproductive organs, mycetomes, and parts of nervous system (Catts, original).

NERVOUS SYSTEM

(Fig. 6-11)

The cerebral ganglion or brain is a relatively large bilobed structure just behind and above the cibarial pump. The subesophageal ganglion lies below and a little behind the brain and is connected to it by commissures forming the ring through which the esophagus and tracheal trunks pass. Behind this ring the ventral nerve cords extend to the region of the metathorax, where the thoracic ganglion is located. This ganglion represents a fusion of thoracic and abdominal ganglia into a large ganglionic mass from which segmental nerves extend to most organs of the body.

REPRODUCTIVE SYSTEM

The male reproductive organs (Fig. 6–12) consist of the testes, vasa deferentia, seminal vesicles, mesadenia and reservoir, ejaculatory duct, and aedeagus. Each testis is made up of 7 large white follicles that open into the vas deferens. The latter enlarges to form the seminal vesicle. Posteriorly the slender mesadenia join to empty into a reservoir which supplies the sperm fluid when the sperm are discharged through the ejaculatory pump and aedeagus.

In the female (Fig. 6–11), each ovary consists of 7 ovarioles with 2 small swellings anteriorly, and a large swelling in which the eggs mature. There are 2 smaller swellings at the base of each ovariole just beyond the point where the pedicels join the large oviduct. Laterad of the bases of the oviducts are the prominent, oval seminal conceptacles which function to receive the migrating sperm mass as described elsewhere. The oviducts open into a large genital chamber. On the right side beneath the ovary in the region of the fourth and fifth abdominal segments is the large, round, whitish mesospermalege.

MYCETOMES

On each side between the fourth and fifth abdominal segments are the mycetomes (Büchner 1921, 1923; Pfeiffer 1931). These are oval, flattened, whitish structures about 0.5 mm long and 0.3 mm wide (Fig. 6–11, 6–12), somewhat obscured by cells of the fat body. In the male each mycetome is attached to the vas deferens on the concave side at the base of the testis. In the female the mycetomes are in the same general region but are not attached to the ovaries or oviducts. Mycetomes have been found in many Cimicidae (Fig. 6–13a) and probably occur in all genera except *Primicimex* (Carayon 1959). The mycetomes contain obligate symbiotic bacteria discovered by Büchner (1921) and figured by Pfeiffer (1931). These may be the organisms named *Corynebacterium pauro-metabolum* by Steinhaus (1941).

A rickettsialike organism, *Rickettsia lectularia,* was described by Arkwright et al. (1921) from the gut and malpighian tubules. Hertig and

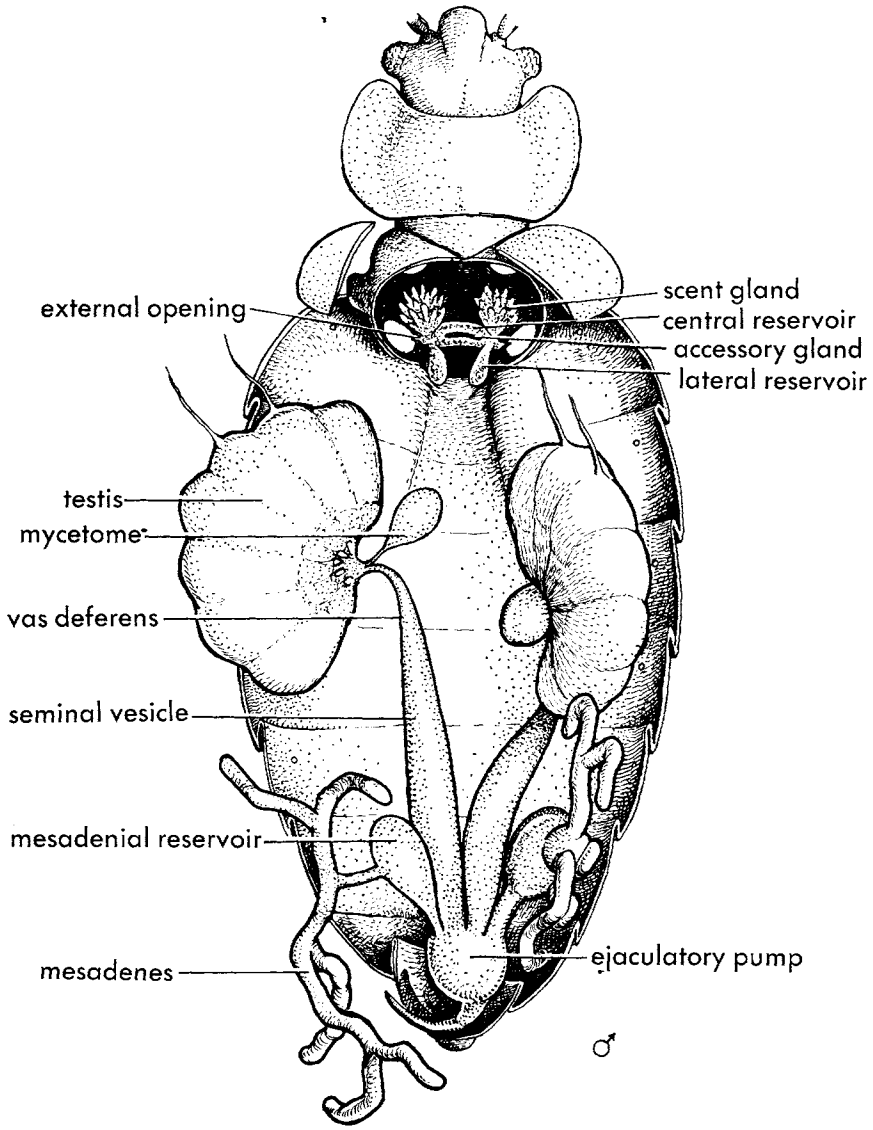

FIG. 6–12.—Internal anatomy of *Cimex lectularius*. Male reproductive system, mycetomes, and scent glands (Catts, original).

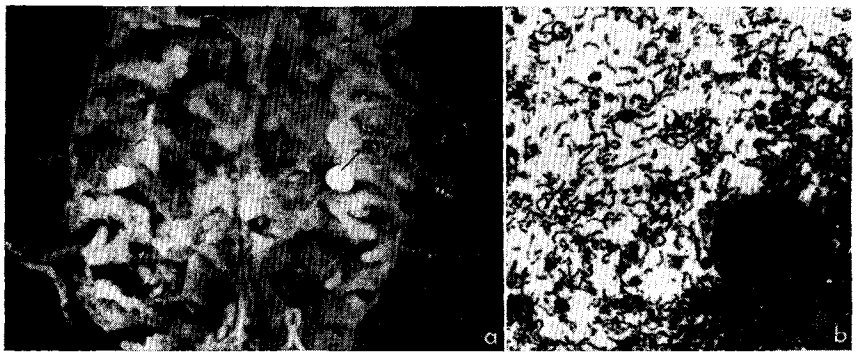

FIG. 6–13.—a, *Bucimex chilensis,* my = mycetomes (Carayon, original); b, *Cimex lectularius,* mycetome bacteria (Martignoni, original).

Wolbach (1924) suggested the species might be identical with the mycetome symbiote, but Pfeiffer (1931) believed that the two are different. Philip (1956) proposed the generic name *Symbiotes* for *Rickettsia lectularia,* but Krieg (1961) rejected the name on the grounds that "the rickettsiae of *Cimex* may not be identical with the inhabitants of the mycetomes" (Krieg 1963). Krieg placed *lectularia* in the genus *Wolbachia.*

Martignoni prepared slides of the microorganisms shown in Fig. 6–13b, taken from the mycetomes of male *C. lectularius* supplied from my colonies. No microorganisms were found in the gut or malpighian tubules.

Steinhaus (1941) found other bacteria in *C. lectularius,* including a new species, *Bacterium tegumenticola,* isolated from the integument.

Arkwright et al. (1921) also reported a bacillary organism in *Oeciacus hirundinis,* and Cowdry (1923) referred to it as *Rickettsia hirundinis.* Pfeiffer (1931) figured microorganisms from the mycetomes of *Oeciacus hirundinis.*

Büchner (1921, 1923) first demonstrated the transmission of mycetome symbiotes to the next generation via the egg. Ray and Dasgupta (1955) and Dasgupta and Ray (1956) reported that "*Wolbachia lectularia* induces the formation of vacuole-like inclusions, especially in testes and ovarian follicular cells . . ." These NR bodies must be the sites in which the rickettsiae multiply (Krieg 1963).

METATHORACIC SCENT APPARATUS

by Jacques Carayon

The metathoracic scent apparatus has been known only in *C. lectularius* (Fig. 6–12). It has been described in a more or less exact and complete way by almost all authors who have studied the anatomy of the species, notably Landois (1868–1869), Murray (1914), and Puri (1924),

but the detailed work by Kemper (1929b) is still the best publication on the subject.

Situated in the metathorax and the base of the abdomen against the inner face of the ventral wall, the scent apparatus of the bed bug consists, as in all the other Heteroptera Geocorisae, of 2 principal elements, the glands and the reservoir.

The first element, paired and laterally arranged, is the branching tubular glands, the structure of which has been described with precision by Kemper (1929b) and Henrici (1940). Each gland is an oblong, whitish translucent mass formed by the coalescence of the secretory tubules which join at the base in a common, short efferent canal. The canals of the 2 glands empty into the lateral extremities of the reservoir almost at the point where the extremities open to the outside. The reservoir opens by 2 orifices situated on the inner margins of the metacoxal cavities near the bases of the apophyseal pits. An odoriferous channel, impressed in the integument, leads from each orifice and is directed toward the side of the thorax away from the episternum; around the channel there extends an evaporating area characterized by the wrinkled structure of the cuticle.

The reservoir is a rather large pocket with orange-red pigment. It consists of an unpaired median anterior part, extending transversely between the orifices, and 2 lateral lobes which extend into the abdomen in a posterior direction. The surface of this pocket, thin and folded, consists of a simple flat epithelium covered by a cuticular intima. It is of uniform structure, except for an organ at the middle of the posterior surface, most often designated as the "kidney-shaped organ"; the term "accessory gland" proposed by Brindley (1930) is much more suitable, however. Here the parietal epithelium is very thick and modified and in *Cimex* forms a plain or feebly incurved oval disk (Fig. 6–14c, longitudinal section). Arranged in a single row but without visible lateral limits, the tall epithelial cells of the disk have dense, rather basophil cytoplasm containing several irregular vacuoles, more numerous and larger in the apical region; their voluminous and subspherical nuclei are near the basal pole. The cuticular intima covering these cells appears to be rather modified, being even thicker and differently colored than in the wall of the reservoir. The intima forms invaginations that are tubular and a little less inflated toward the apex; each invagination is buried deeply in the cytoplasm of one of the nearby epithelial cells. In a microscopic preparation of the entire reservoir, with the disk seen in front or in profile, these regularly distributed invaginations appear as a group of equidistant punctures or as a series of small parallel tubes.

The function of the "accessory gland" is still unknown; even its nature has been the object of controversy. Landois (1868–1869), who never saw the odoriferous glands, believed that this parietal organ produced all the secretion filling the reservoir. Murray (1914), following erroneous his-

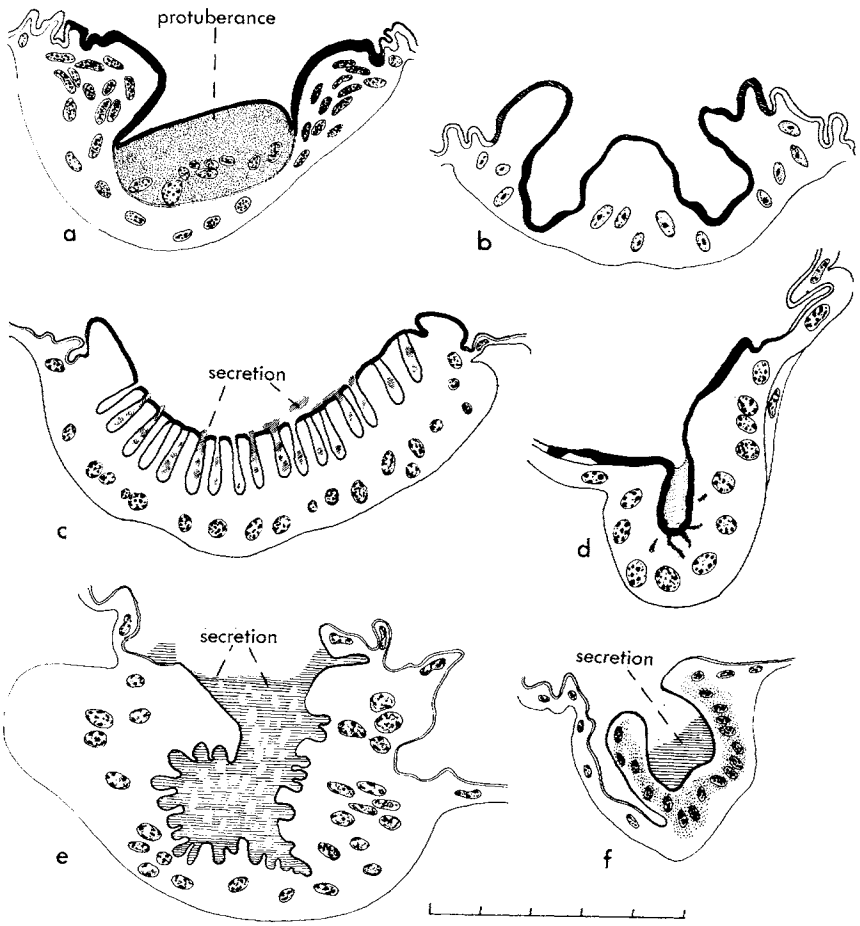

FIG. 6–14.—Accessory glands of the scent reservoir in sagittal section: a, *Afrocimex constrictus,* male; b, *Hesperocimex coloradensis,* female; c, *Cimex lectularius,* female; d, *Haematosiphon inodorus,* female; e, *Aphrania orientalis,* male; f, *Caminicimex furnarii,* female (Carayon, original). Scale equals 50 microns.

tological interpretations, thought that it was sensory in nature and attributed to it an olfactory function. His errors were partially corrected by Puri (1924), who recognized the secreting activity of the structure without, however, excluding the possibility of a sensory role. Kemper (1929b) gave some decisive arguments in favor of the unique glandular nature of the reniform organ; since that time they have been generally accepted (Brindley 1930, Henrici 1940, etc.). This organ, which in most cases bears no resemblance to a kidney, is better designated by the term "accessory gland."

The secretion, apparently always lipo-protein, produced by the accessory gland is very different from that issuing from the odoriferous glands. Strongly osmiophil and coagulated by histological fixatives, it is not abundant in *Cimex*. It appears in histological sections in the form of unequal globules more or less completely filling the tubular invaginations and flowing down a projecting passage outside of the orifices before passing into the cavity of the reservoir (Fig. 6–14c).

The preceding information, obtained by a study of *C. lectularius* alone, is applicable to other species of *Cimex* and related genera, but not to all Cimicidae. We have examined most of the known genera of Cimicidae, and have found that the metathoracic scent apparatus varies much more than in any other family of Heteroptera. Such diversity in a group with a small number of species probably derives from its ethological peculiarities. We may suppose an interaction between the scent apparatus of the Cimicidae and the relations of these ectoparasitic insects with their diverse hosts.

A general discussion of the variability of each element of the metathoracic scent apparatus in the Cimicidae follows.

Scent Channel and Evaporating Area

These are the only external parts of the apparatus. They are the most accessible for study but parts must be specially prepared for precise and comparative examination. Their dimensions, form, and contour vary, sometimes remarkably, from one species to another. The structure of the evaporating areas especially appears to furnish characters useful for specific differentiation. I have confirmed the opinion of Sailer (cited by Ferris and Usinger 1957a, p. 4) on the systematic value of this structure.

Scent Glands

To study the scent glands it is necessary to dissect living specimens or to fix specimens for histological examination. In dried specimens, treatment with potassium hydroxide followed by staining of the cuticle permits one to see the connecting canals and the efferent tube of the glands, and gives some indication of their relative dimensions and structure. Unfortunately, the difficulties in preparing and observing precisely these fragile structures have hindered us in analyzing their variation and evaluating their systematic importance.

The scent glands are present and apparently functional in all the Cimicidae studied. They never show any indication of regression in the family. The number, length, and ramification of their collecting branches, as well as the form and arrangement of the secretory channels, appear to be quite variable.

Reservoir

This structure is a membranous and extensible sac. It presents rather

important individual variations as to volume and details of form; its contour and the relative dimensions of its parts remain constant within a single species but are very diverse in the family as a whole (Fig. 6–15 to 6–17).

In the majority of Cimicidae the reservoir is bilobed like that described for *Cimex* and like that in 2 nearly related groups of Heteroptera, the Anthocoridae and the Nabidae-Prostemmatinae. Thus, all the Cimicinae we studied, the Haematosiphoninae with the exception of *Hesperocimex,* the aberrant genera *Latrocimex* and *Afrocimex,* and the Cacodminae of the "first group" (*Cacodmus, Loxaspis,* and *Aphrania*) possess a reservoir provided with well-differentiated lateral lobes. The relative dimensions of these lobes vary; they are large in *Latrocimex* (Fig. 6–17), in which the metathoracic apparatus is particularly well-developed, in the Cacodminae of the first group, and in the Cimicinae. All of these groups have lateral lobes more voluminous than the transverse reservoir.

Among the Haematosiphoninae, one finds several intermediates between the great development of the lateral lobes in *Ornithocoris pallidus* Usinger and their absence (or at least their vestigial state) in *Hesperocimex.* In *Cimexopsis nyctalis* List, the lobes are less well differentiated than usual in the subfamily and relatively small with respect to the transverse reservoir (Fig. 6–16a). An analogous structure is seen outside of the Haematosiphoninae in the genus *Afrocimex.*

Certain lines of Cimicidae tend toward the reduction or complete absence of lateral lobes. In the genera *Primicimex, Hesperocimex, Crassicimex,* and *Stricticimex,* only the last two of which are closely related, the reservoirs are devoid of lateral lobes, and the transverse portion retains almost the same diameter throughout its width or, at most, appears as a slight swelling near its 2 extremities.

Differing from all the other known Cimicidae, the representatives of the genus *Leptocimex* have a reservoir completely divided into 2 lateral parts broadly separated from each other; each is a small sac which, with the scent gland of the same side, constitutes an autonomous organ independent of its counterpart (Fig. 6–15c). This peculiarity of the scent apparatus of *Leptocimex* is of systematic interest but not of fundamental importance. In fact, many families of Heteroptera-Geocorisae are now known in which the scent reservoir is completely divided in certain species and united in others, with intermediary states between these 2 extremes. There is reason to think that the scent apparatus in these quite different groups underwent a more or less rapid parallel evolution, in which the dividing of the reservoir constitutes the final phase (Carayon 1962).

Among the Cimicidae, however, we have not found the intermediate stages in which the median thinning of the reservoir is a prelude to its division. In no other member of the family does the degree of evolu-

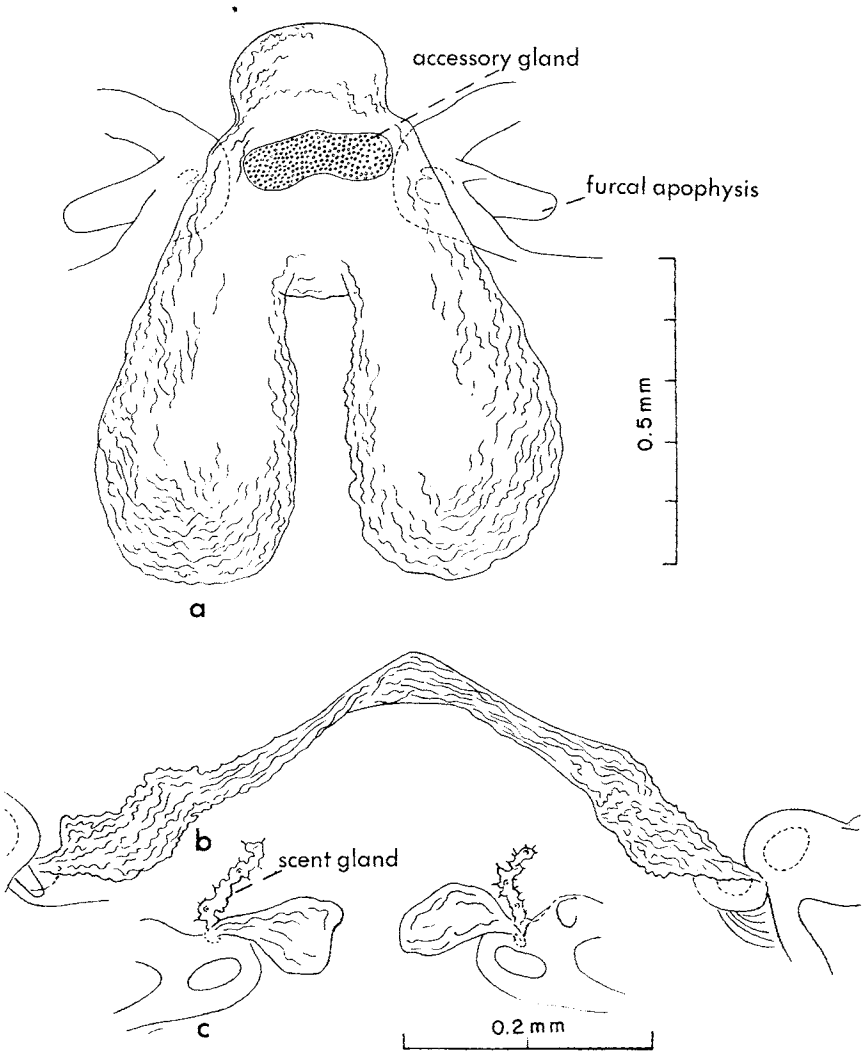

FIG. 6–15.—Metathoracic scent apparatus, cleared, in dorsal view: a, *Loxaspis seminitens*, female; b, *Primicimex cavernis*, male; c, *Leptocimex duplicatus*, female. Efferent conduits shown only in c (Carayon, original).

tion of the scent apparatus equal or even approach that attained in *Leptocimex*. Hence, on the basis of the scent apparatus, *Leptocimex* appears to represent a completely divergent phyletic branch.

According to present observations, the general conformation of the scent reservoir is similar or nearly so among all species of any one genus. Also it remains quite comparable among the representatives of definitely related genera. It appears much more varied within, and at the present stage of our knowledge of little help in the definition of, subfamilies. Within the Cimicidae, its diversity (cf. Fig. 6–16 to 6–17) is greater than

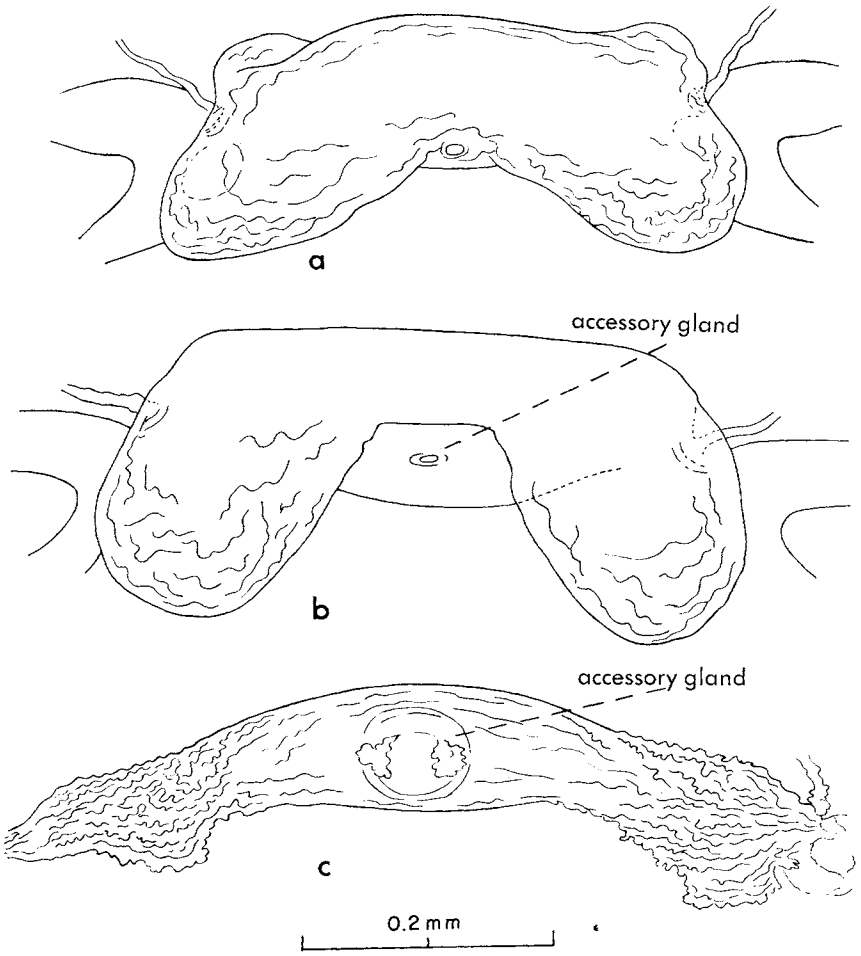

FIG. 6–16.—Metathoracic scent apparatus, cleared, in dorsal view: a, *Cimexopsis nyctalis*, female; b, *Haematosiphon inodorus*, female; c, *Hesperocimex coloradensis*, female. Efferent conduits shown only in a and b (Carayon, original).

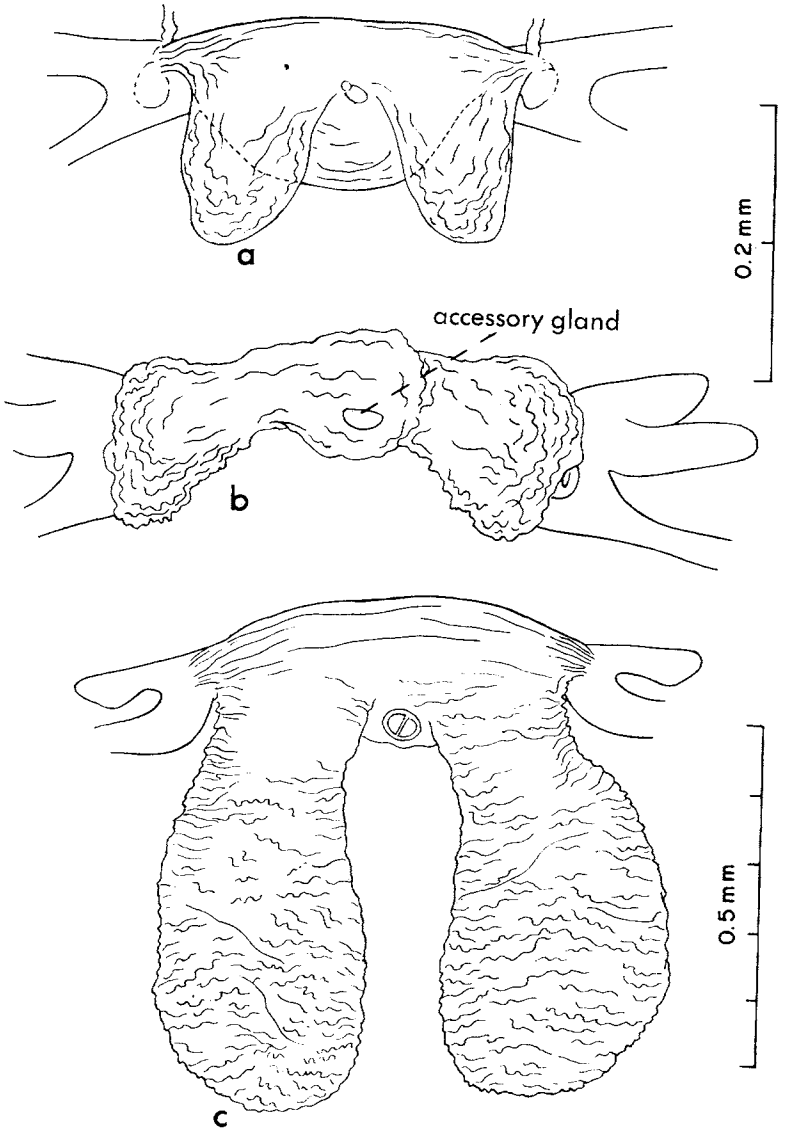

FIG. 6–17.—Metathoracic scent apparatus, cleared, in dorsal view: a, *Caminicimex furnarii,* male; b, *Afrocimex constrictus,* male; c, *Latrocimex spectans,* male. Efferent conduits shown only in a (Carayon, original).

that observed in the very closely related, yet much larger, family Anthocoridae.

Accessory Gland

Although part of the reservoir, the accessory gland deserves separate study because of its systematic interest, which is greater than that of other elements of the scent apparatus. With the exception of the genera *Primicimex* and *Leptocimex*,[1] where its absence appears to be the result of a secondary regression, the accessory gland occurs in all Cimicidae. It shows a very remarkable diversity without any known equivalent elsewhere in the order Heteroptera. Its dimensions, its form, and its structure, in all other respects consistent in the same species, vary greatly within the family and in such a manner that the differences it exhibits in any 2 Cimicidae in many cases are proportional to the degree of relationship of the species.

The accessory gland thus may furnish characters useful for the determination of groups at various systematic levels and for the evaluation of affinities. It should be studied in special microscopic preparations, or even in histological sections, which are often indispensable for the precise observation of its structure.

According to our findings, the differences in this structure are important for higher systematics. Three principal types of accessory glands can be distinguished among the Cimicidae:

1) The *Cimex* type is the only one known previously and has been described most precisely in *C. lectularius*. All the accessory glands of this type have the form of a flat or slightly incurved disk, within which are sunken regular tubular invaginations of the cuticular intima (Fig. 6–14c). The *Cimex* type is easy to recognize in a simple preparation. It is probably primitive since it is the only type found also in the related families of Cimicomorpha (Nabidae and Anthocoridae). Among the Cimicidae it is encountered in the Cimicinae, except *Propicimex,* and in the Cacodminae of the first group except *Aphrania*. In the last-named genus, the accessory gland presents a structure intermediate between the *Cimex* type and the *Haematosiphon* type described subsequently (Fig. 6–14e). It resembles the *Cimex* type in its cuticular invagination, although less deep and irregular; and the *Haematosiphon* type by its cupulate form. In *Propicimex* the accessory gland, known only by the study of a cleared specimen, departs again from that in *Aphrania* of the *Cimex* type, and its structure recalls slightly that observed in the genus *Hesperocimex*.

In the genus *Bucimex* we have studied the scent apparatus only in a series of sections from a single individual. The accessory gland is apparently divided into very small elements and appears so aberrant that

[1] In the genus *Paracimex,* most species possess a well-developed accessory gland, but in *Paracimex caledoniae* Ferris and Usinger it is totally lacking.

it must—if the first observations are confirmed—constitute a very different type from the others.

2) The *Haematosiphon* type is characterized by the general tubular (Fig. 6–14d) or cuplike (Fig. 6–14f) form of the accessory gland and by the absence of intracellular invaginations of the intima. Examined as preparations of the entire reservoir, the accessory glands of this type have a smooth surface rather than a regularly punctate one. They appear limited by an oval or semicircular line which represents the demarcation between the parietal cuticle of the reservoir and that modified by the gland. A more or less distinct contour, generally at the interior of this border but occasionally merging with it, corresponds to the orifice of the cup. The glands of the *Haematosiphon* type have various contours, often less distinct than those of the *Cimex* type, and frequently less apparent upon direct examination. The details of their form and structure, observable only in histological sections, may present marked differences from one genus to another (compare Figs. 6–14e and 6–14d).

In spite of these variations, the *Haematosiphon* type is generally constant in character and, with the exception of 1 or 2 unrelated genera (*Afrocimex*, etc.), is easy to distinguish. This type is observed among all Haematosiphoninae and among Cacodminae of the second group, except in the aberrant genus *Leptocimex*.

Judging by the accessory gland, the genus *Hesperocimex* may be placed in the Haematosiphoninae, but in a rather distant position. The accessory gland of *Hesperocimex* has the form of a large, oval, transverse cup much shallower at the center than at the sides, where 2 irregularly mamilliform diverticula of the cuticular intima push into the subjacent epithelium (Fig. 6–14b). The gland is larger in the male than in the female. Its general form is of the *Haemotosiphon* type but it is more broadly bell-mouthed and lacks tubular invaginations of the cuticle. On the other hand, it resembles the glands of the following type in several features.

3) The *Afrocimex* type, which, perhaps, represents only a subdivision of the *Haematosiphon* type, is characterized by a strong crest or prominent protuberance in the middle of the large cup which forms the gland. This protuberance has a rather complex appearance; a histological study of the material available has not permitted complete analysis. According to the sections (Fig. 6–14a), it appears to consist of a very thin layer of endocuticle, because it joins laterally with the intima which lines the rest of the gland; however, this layer is provided with rather voluminous and irregular nuclei so it is difficult to consider it as cuticular; it most likely represents a group of modified and secondarily isolated epithelial cells of the subjacent layer. Lacking visible lateral limits, as is the case throughout the organ, these cells have a dense basophilic cytoplasm, giving the impression that they are no more than a coagulated mass of secretion.

Just as in the other types of accessory glands, neither canaliculi nor pores which permit the outflow of the secretion are visible in the intima with the light microscope. Moreover, the secretions are generally produced in greater abundance than in *Cimex* and fill the cup to overflowing, as do those observed in most of the glands of the *Haematosiphon* type. When overflowing they spill out at the bottom of folds of the reservoir.

The *Afrocimex* type also appears in *Latrocimex,* in which the accessory glands, despite differences in detail, are sufficiently similar to indicate a rather close relationship.

Summary of Principal Characters of the Metathoracic Scent Apparatus in Various Groups of Cimicidae

Subfamily PRIMICIMICINAE.—

Primicimex.—Reservoir narrow, transverse, and V-shaped with the broad opening toward the posterior; its lateral portions slightly swollen and more strongly folded than in the central part. No accessory gland.

Bucimex.—Transverse reservoir broad and short with lateral lobes moderately developed; accessory glands apparently divided into small elements of a quite aberrant type.

Subfamily CIMICINAE.—Reservoir always bilobed; accessory gland very rarely absent, most frequently of the *Cimex* type.

Cimex and *Oeciacus.*—Lateral lobes of the reservoir always well developed; transverse reservoir rather narrow, bearing an accessory gland of the *Cimex* type, flat or weakly concave toward the anterior.

Paracimex.—Lateral lobes wide and much folded; accessory gland of the *Cimex* type, convex toward the anterior, present in most species but absent in *Paracimex caledoniae.*

Bertilia.—Lateral lobes large; accessory gland of the *Cimex* type but perhaps with peculiarities which can be determined only by histological study.

Propicimex.—Transverse reservoir broad but short; lateral lobes slightly developed; a relatively large reservoir forming a cupula projecting over the posterior wall of the transverse reservoir. This gland, not studied histologically, does not belong to the *Cimex* type but vaguely recalls the gland of *Hesperocimex.*

Subfamily HAEMATOSIPHONINAE.—Transverse reservoir broad, often swollen in its median part; lateral lobes present but variously developed. Accessory gland never absent, always of the *Haematosiphon* type and not deviating at all from that type within the genus *Hesperocimex.*

Haematosiphon.—Transverse reservoir drawn out with lateral lobes moderately developed; accessory gland in the form of a narrow and rather deep tube, small and barely visible in a preparation of the entire reservoir.

Ornithocoris.—Large reservoir with spacious lateral lobes; accessory gland in the form of a little pouch.

Psitticimex.—Like *Ornithocoris.*

Caminicimex.—Rather narrow transverse reservoir; lateral lobes well developed; accessory gland in the form of an urn.

Cimexopsis.—Reservoir drawn out; weakly bilobed; accessory gland in the form of a little pouch.

Synxenodorus.—The scent apparatus could not be studied in this genus.

Hesperocimex.—Transverse reservoir with lateral lobes, vestigial or absent; accessory gland in the form of a large, oval, transverse cup.

Subfamilies AFROCIMICINAE AND LATROCIMICINAE.—

Afrocimex.—Reservoir drawn out; swollen in the middle and weakly bilobed; attached gland of the *Afrocimex* type.

Latrocimex.—Reservoir voluminous; well-developed lateral lobes; attached gland of the *Afrocimex* type.

Subfamily CACODMINAE.—Very heterogenous group; characters of the scent apparatus suggest 3 different types.

First type

Cacodmus and *Loxaspis*.—Voluminous reservoir with large, much-folded lateral lobes; large accessory gland, distinctly related to the *Cimex* type.

Aphrania.—Reservoir bilobed; accessory gland apparently intermediate between the *Cimex* type and the *Haematosiphon* type.

Second type

Crassicimex.—Reservoir drawn out, not bilobed, with attached gland of the *Haematosiphon* type, conical in form.

Stricticimex.—Reservoir drawn out, not bilobed, attached gland of the *Haematosiphon* type, mushroom shaped.

Third type

Leptocimex.—Reservoir divided into 2 completely separate lateral parts; no attached gland.

7 Traumatic Insemination and the Paragenital System

by JACQUES CARAYON

Among the Cimicidae, insemination is never effected by the usual genital route. At the time of mating, the male punctures the body wall of the female with his copulatory organ and injects an abundance of sperm into her abdomen but outside of the usual reproductive tract. Insemination is thus "extragenital" and "traumatic," because it always begins with an integumental wound.

In direct correlation with this singular process, the female system possesses various more or less complex structural differentiations which together constitute the "paragenital system," which is absent among insects exhibiting normal insemination.

HISTORICAL ACCOUNT

The original studies were carried out at the end of the last century in the Laboratorio di Zoologia Generale e Agraria at Portici, Italy. Published in the "Rivista di Patologia Vegetale," a periodical one would scarcely expect to contain a subject of this kind, they remained unnoticed for many years. As a result, a number of researchers were unable to consult them directly.

The initial observations were made at the suggestion of Berlese by Ribaga who, by means of histological sections of *C. lectularius,* discovered a curious formation, peculiar to the female, situated on the right side of the abdomen between the fourth and fifth visible sterna.

In a note, Ribaga (1897) gave a detailed and precisely illustrated description of the entire structure. He indicated that it is composed of 2 connected organs, one external and integumentary, the other internal and composed of a "pocket of amoebocytes." But he did not understand the relationships of these organs and interpreted the cuticular part as a stridulating apparatus with which the females attracted the males.

In 2 reports published the following year, Berlese (1898) studied only

the internal portion of the structure discussed by Ribaga and did not rectify or mention elsewhere the hypothesis that the role of the external portion, which he designated as "the organ of Ribaga," was stridulatory. He revealed that the "pocket of amoebocytes," although lacking any connection with the reproductive apparatus, is one of the places in the female bed bug where, after copulation, one finds very abundant and singularly distributed spermatozoa. In inseminated females, the numerous spermatozoa are in fact observed not only in the 2 "spermathecae," the walls of the genital ducts, and the bases of the ovarioles, but also at certain times in the blood and in the pocket of amoebocytes. Observing that the latter contained the spermatozoa in different stages of degradation, Berlese called them "spermatophages" and thought that, like certain elements of the "spermathecae" of the oviducts and of the ovarioles, they resorbed a large portion of the sperm, which is introduced by the male in quantities much greater than necessary for fecundation. According to Berlese, such a superabundance or "hypergamesis" has a double function—on the one hand it constitutes a useful nutritive contribution to the female in preparing for oviposition and on the other, it stimulates ovarian development.

Granting first importance to the resorption of excess male gametes and ignoring the peculiarities of copulation, Berlese inexactly reconstructed the pattern followed by spermatozoa in the female organ. According to him, the sperm is deposited directly during copulation into 1 of 2 "spermathecae," always the one on the right in accordance with the asymmetry and orientation of the male copulatory organ. Then, in turn, numerous spermatozoa invade the left "spermatheca" as well as the walls of the genital ducts and the bases of the ovarioles, where most of them are gradually resorbed for the most part. Many others leave the right spermatheca in a column, freely cross the hemocoel, penetrate the pocket of amoebocytes, and reach the spermatophage cells. The latter, while destroying the spermatozoa, are filled with inclusions which are finally transformed into homogeneous droplets. Berlese believed that these later pass into the envelope of the pocket, then are assimilated by the organism. He compares the entire process to one of digestion where the waste, excreted, he says, by the integumental epithelium covering the pocket of amoebocytes exteriorly, is discharged in the form of a blackish-brown mass which Ribaga had already seen in the cuticular thickening of the organ bearing his name.

Carazzi (1902), after studying Berlese's original preparations at the same time as his own, presented a note on the "pouch of Berlese," called "pocket of amoebocytes" by previous authors. He granted that the spermatozoa penetrate this structure in abundance and are destroyed, but he sharply criticized Berlese's interpretation of the mechanism of this destruction. According to Carazzi, the alleged spermatophage cells contain

spermatozoa only rarely and never resorb them. By means of a special transformation of the cytoplasm approaching complete lysis, these cells produce a substance that crosses their membrane, accumulates outside in finely granulated masses, and by a sort of extra-cellular digestion reduces the spermatozoa packets to the state of an anhistic mass. Carazzi denied that the products of this digestion would be absorbed by the envelope of the "pouch of Berlese," the exact role of which remained unknown.

In his general text on insects, Berlese (1903) devoted a short chapter to hypergamesis, summarizing his 1898 observations on *Cimex* and discounting Carazzi's criticisms on the basis of inadequate study of the preparations. However, Berlese modified his original remarks about the manner in which the spermatozoa leave the spermatheca to return to the "pouch of Berlese." He then theorized that they passed in a column through a small aperture situated in the anterior angle of the insertion of the spermatheca on the genital ducts. His publication on this subject includes, as did the earlier ones, exact facts mixed with errors of interpretation. The most serious error—serious because it delayed the comprehension of the actual phenomenon—concerned the migration of spermatozoa between the "pouch of Berlese" and the "spermatheca," a migration that takes place exactly opposite to Berlese's belief.

We are indebted to Patton and Cragg (1913) for the discovery of the remarkable peculiarities of copulation and insemination in *C. lectularius* and *C. hemipterus*. Their observations showed for the first time that, unlike other Heteroptera, *Cimex* males never introduce their copulatory organs into the vagina of the females. The male straddles the back of the female obliquely, his abdomen strongly incurved against the right side of his partner's abdomen so that his extremity reaches not the orifice of the genital duct but that of the "organ of Berlese," where the "penis" penetrates and injects the sperm. That which Patton and Cragg called the organ of Berlese is the composite organ. Its integumentary portion, situated in the membrane connecting the fifth and sixth sternites, appears in *C. hemipterus* as a small, oval plaque at the center of which, according to Patton and Cragg, there is a "minute aperture guarded by extremely fine spines. From this aperture a chitinous duct leads into the interior of the organ." Patton and Cragg assumed that the sperm is injected through this tube into the pouch of Berlese, which is the only location where spermatozoa are observed immediately after copulation in females inseminated the first time. They showed that the spermatozoa, after leaving the organ of Berlese, pass into the abdominal cavity, where they form the characteristic mass; then they accumulate at the base of the genital duct, which constitutes without doubt their route to the oocytes.

The observations of Patton and Cragg, doubted in the inadequate work by Murray (1914), have been confirmed in all subsequent works, particularly those from 1915 to 1924.

In a preliminary note, Cragg (1914) described for the first time the different phases of spermatozoan activity starting with the organ of Berlese and extending to the "spermathecae." The latter he recognized as not homologous with the spermathecae of other insects. He pointed out the irregularities that complicate the study of the process—frequent absence of insemination after apparently effective copulation, significant variation in the quantity of sperm injected by the male, and the delay in migration of the sperm from the first copulation to the commencement of egg-laying. Cragg emphasized the relatively enormous volume of sperm which repeated copulations introduced into the female organism but could find no explanations for the superabundance and fate of the excess spermatozoa; he believed neither the theory of hypergamesis nor the idea of resorption of spermatozoa in the organ of Berlese or in any other part of the genital apparatus.

In a short paper, completely unnoticed, Wiltberger (1916) presented the organ of Berlese in *C. lectularius* as formed solely by 1 ectodermal invagination and gave a very different idea of the transverse section than the figure published by Patton and Cragg (1913) for the same section in *C. hemipterus.* This note is of interest principally because it contains the first mention of a fact the significance of which was not to be understood until very much later—the deterioration, after copulation, of the integumental epithelium at the point where the male introduces his copulatory organ. Wiltberger believed that this cytolysis was caused by the passage of the spermatozoa through the wall of the body, and he compared the mode of insemination of *Cimex* to that observed in certain worms.

Hase, in 1918, published his complete observations on copulation in bed bugs. He described the peculiarities of copulation exactly but left the reader unaware that Patton and Cragg had discovered them before him. He confirmed the role of the pouch of the "organ of Berlese" but called it the "organ of Ribaga" to emphasize that Ribaga had priority in its discovery.

Cragg's 1920 report constitutes the basis of our understanding of insemination in *Cimex* and, in certain respects, remains today the most detailed account ever published on this subject. In the report, Cragg analyzed all previous works except those of Wiltberger and Hase. Describing the female copulatory structure, he called its integumental part the "organ of Ribaga" and recognized, contrary to the remarks of Patton and Cragg, that it has no orifice. According to Cragg, the long cuticular processes of the organ of Ribaga should be hollow from end to end and constitute the passage used by the spermatozoa to reach the subjacent pocket, designated the "organ of Berlese." Although Cragg was completely mistaken about the initial phenomenon of insemination, thanks to the study of females sacrificed at increasing periods of time after their

first copulation, he reconstituted exactly the principal phases of the migration of spermatozoa to the ovaries. He described minutely the important cyclic modifications of cells of the organ of Berlese after the arrival of the sperm—the formation of large vacuoles at the center of which voluminous inclusions appear, are modified, and then gradually disappear; and the return of the cells to their former state after occasionally dividing amitotically. Cragg considered these modifications to be proof that the organ of Berlese is a gland of a very unusual type, the secretion of which is discharged into the blood in direct correlation with the migration of spermatozoa. He traced the progress of this migration outside of the organ of Berlese. The spermatozoa begin to leave in packets approximately 4 hours after copulation, and pass into the hemocoel where they make up the spherical masses which gradually reassemble about the "spermathecae." After having studied their structure and development, Cragg correctly affirmed that these "spermathecae," which are mesodermal in nature and lack communication with the lumen of the genital ducts, are not homologs of the spermathecae of other insects. Cragg said that the spermatozoa penetrate into the spermathecae, crossing the parietal epithelium by a process which remains to be explained, and accumulate there. Next, they proceed into the walls of the oviducts, then the walls of the pedicels, until they reach a special structure situated at the base of each ovariole behind the posterior oocytes of the vitellarium. Cragg called this "a mass of nucleated protoplasm" and described in detail the structure which had already been demonstrated by Berlese. He erroneously attributed to it a role in the growth of the follicle which it precedes, but notes that it contains, in reserve, numerous spermatozoa that are living and mobile and ready to complete their migration. When the oocyte, which directly surmounts the structure under consideration, completes its vitellogenesis, some of the spermatozoa go directly into the thick part of the follicle to another "mass of nucleated protoplasm" situated against the anterior pole of the oocyte. Then they undoubtedly penetrate into the mass of nucleated protoplasm before the formation of the chorion. Fecundation was not directly observed but is certainly intra-ovarian. Cragg denied any phagocytosis or destruction of spermatozoa during their passage to the ovaries. He supposed that in the ovaries, the vast excess of spermatozoa is resorbed and used for the development of oocytes.

After his report of 1921, Cragg presented 3 less extensive notes augmenting his previous observations, without important modifications. In the first, in collaboration with Christophers (Christophers and Cragg 1922), he showed that the curved, sclerotized structure of the male, until then considered to be the penis, is actually the left element of a pair of genital appendages today called "parameres." The true penis, small

and membranous, is situated at the base of a channel that extends nearly the entire length of the paramere.

In the second note, Cragg (1923) reported studies primarily on the influence of insemination and nutrition in both male and female on the number of eggs deposited. He presented evidence that a single copulation, regardless of the quantity of sperm deposited, is not sufficient to enable the female to oviposit during her lifetime, but permits her to produce only about 170 eggs. Having observed that "the spermatozoa are not retained intact by the female during periods of starvation at a temperature suitable for oviposition," Cragg conceded the possibility that the sperm might be utilized for complementary nutrition of the female during oviposition and in the preoviposition period.

Cragg's (1925) last publication on *Cimex,* rarely cited, concerns the mechanisms of copulation and the passage of spermatozoa from the male copulatory organ to the organ of Berlese. Cragg, undoubtedly dissatisfied with his previous explanation of this process, resumed his original study. He fixed 22 females during copulation and examined them histologically. Only one permitted an observation pertinent to the problem—the spermatozoa already filled the organ of Berlese but several, gathered in bundles, were still found in the thickened part of the organ of Ribaga, the epithelium of which was damaged at this level. Cragg concluded that the spermatozoa of *Cimex,* given the remarkable power of penetration and doubtless channeled by cuticular spines grouped in bundles, actively penetrate the integument to reach the organ of Berlese.

All the works just mentioned relate exclusively to *C. lectularius* and *C. hemipterus.* Jordan's short note (1922) was the first to demonstrate the presence in other Cimicidae of integumental structures corresponding to the organ of Berlese. Quite comparable among members of the genus *Cimex,* these structures in other genera and species were found to vary greatly in their form and placement in the abdomen; several Cimicidae appeared to lack them.

Abraham's memoir (1934), in which *C. lectularius* is again the only species studied, concerns the migration of spermatozoa and the fate of excess sperm in the female. Abraham confirmed Cragg's observations of the process of insemination and added several new ones, the most important of which concerns the entrance of the spermatozoa into what he calls the "organ of Ribaga" (according to him the entire female copulatory structure). Abraham verified that the integument appears as a darkening depression with local deterioration immediately after copulation. He implied that the point of the "penis" (actually the paramere) penetrates between the chitinous processes existing at this place so that the spermatozoa directly attain the internal pocket of the structure. The external portion of the organ of Ribaga recovers very rapidly, without further signs of alteration 20 minutes after copulation, and constitutes

an occluding organ that prevents the sperm from flowing out. Abraham considered the internal part of the organ to be a gland the secretion of which at first activates the spermatozoa and then flows into the hemocoel, carrying the sperm away with it almost mechanically. Because of the function which he attributed to them, Abraham named the oviduct structures (called sphermathecae by preceding authors), the "organs of resorption." According to Abraham, they are simple diverticula the lumen of which communicates with that of the median oviduct and encloses the free cells issuing from the parietal epithelium. The spermatozoa do not penetrate over the whole surface but cross the membrane at the anterior angle formed by the union of the diverticulum with the oviduct where the tissue appears to be favorable for penetration. Berlese (1903) had already noted that the spermatozoa pass through this spot across a small orifice. Abraham indicated that the median oviduct is another route taken by the spermatozoa in reaching the "organs of resorption," and that the spermatozoa penetrate here and cross the wall to enter the lumen in large numbers and proceed to the organs in question.

Contrary to Cragg, Abraham believed that a large number of spermatozoa were destroyed and resorbed at nearly all points in their passage through the female. This is most commonly effected by the spermatophage cells beginning in the organ of Ribaga where it involves only the few spermatozoa left behind after the others have passed on. Resorption continues in the hemocoel in the posterior region of the abdomen. Near the organs of resorption the process, according to Abraham, is different—the spermatozoa enter the organs and lose their motility 2 hours later but remain otherwise unaltered for 1 or 2 weeks, then degenerate by fragmentation, lysis, etc., and are transformed into granular debris which is finally evacuated into the genital ducts. According to Abraham, the majority of spermatozoa are destroyed by this process, whereas others are phagocytized by the spermatophage cells in the "lumen" of the paired oviducts. However, a certain number of spermatozoa survive, arrive intact in the walls of the oviducts, and migrate in bundles to the base of each ovariole. Here, behind the last oocyte of the vitellarium, Abraham recognized 2 distinct, successive zones of structure and function. One of these is posterior with irregular nuclei (Cragg's mass of nucleated protoplasm). It resorbs most of the spermatozoa but allows several to pass into the anterior zone, where the nuclei are arranged irregularly and transversely and where spermatozoa are preserved for the greater part of 3 weeks, not only intact but very motile. Abraham only confirmed Cragg's observations of the final phase of migration and the fecundation of the oocytes. At the end of his memoir Abraham reported the results of artificially injecting sperm—experiments which led him to conclude that the spermatozoa must cross the organ of Ribaga

to be able to pass to the ovaries. He also mentioned having studied Anthocoridae, close relatives of the Cimicidae, and failed to find a structure analogous to the organ of Ribaga. Although, like Berlese, Abraham insisted on the importance of the phenomenon of resorption of spermatozoa among *Cimex* females, he expressed no opinion on the theory of hypergamesis and made no reference to a possible function of the sperm resorbed in this manner.

Precise information is found in the work of Mellanby (1939a) concerning the influence of insemination and of nutrition on the production of fertilized and unfertilized eggs by *C. lectularius*. It appears from the convincing experiments of this author that insemination, by greatly augmenting the metabolism of the female, shortens her life; it induces ovarian development but afterwards has little or no influence on egg production, which depends primarily on nutrition. A female, separated from males after insemination, can produce fertile eggs only for a limited time. Its reserve of spermatozoa is conserved in the "spermathecae" and is not destroyed, as Abraham contended; the supply is exhausted after a delay that, at a given temperature, remains the same regardless of the number of eggs laid and the initial quantity of sperm, provided that this quantity at least equals that furnished by a normally nourished male in a single copulation. The females receiving a large number of spermatozoa by multiple copulation with many males do not lay more eggs during their "period of fertility" than do those nourished in the same fashion but inseminated only once. Moreover, too frequent inseminations, such as occur when more than 6 males are placed with 1 female, may kill the females. In all of his observations, Mellanby concluded that the excess of sperm is in any case without nutritive value.

In 1937 there appeared 2 interesting but little known reports on the copulatory apparatus and its anomalies. The first (Ludwig 1937) shows the existence of males with 2 symmetrical parameres and females with the organ of Ribaga reversed, i.e., placed on the left side. In the second report, Ludwig and Zwanzig (1937) describe the male genital structures. The relationships of the phallus and the paramere are shown and a description is given of their role at the time of transfer of the sperm. Ludwig and Zwanzig studied principally the anomalies of the female copulatory apparatus, for which they adopted the terminology of Cragg (integumentary organ of Ribaga and internal organ of Berlese). Their observations, today the most complete that we possess, are reported below in the discussion of the spermalege.

During the last 2 decades, the paragenital system and insemination of Cimicidae have been the subjects of a number of works the analysis of which would unduly prolong this historical record; these are given and cited in detail in other parts of the present chapter. These works are divided roughly into 3 categories—those of systematic interest by Ferris

and Usinger, Usinger, Ryckman, Wygodzinsky, and Lent; those by Davis on *C. lectularius,* which have augmented and deepened our knowledge of insemination in this species, principally the physiological aspects; and my works, which deal with the majority of Cimicidae and a number of other Cimicoidea, revealing the existence of traumatic insemination accompanied by structural differentiation in very diverse degrees of complexity. I have shown that these degrees correspond to stages of evolution and have reconstructed their general outlines, permitting a glimpse of the origin and probable significance of the phenomenon of traumatic insemination.

The following generalities are based not only on published works but also on my unpublished observations. Although they concern essentially the Cimicidae, they utilize some of the data obtained by the study of related families.

THE *CIMEX* TYPE

The diversity in the process of traumatic insemination and the structural differentiations which are associated with it necessitate a preliminary description of a moderately specialized type, including definitions and explanation of basic ideas. *Cimex* represents such a type and has been well studied. Therefore, the first portion of these generalities is devoted primarily to *Cimex;* the structural differentiations are discussed first; then the process of insemination.

THE PARAGENITAL SYSTEM

We propose to designate as the "paragenital system" all of the morphological, anatomical, and histological differentiations of the female organism related to the processes of traumatic insemination. The principal elements of this system are shown schematically in Fig. 7–1; they may be divided into 2 categories. One of these includes structures associated with the abdominal integument and is found in the region where the male introduces his copulatory organ and injects the sperm; these structures are principally represented by the *spermalege.* The other element, associated with the reproductive apparatus itself, includes the structures associated with the walls of the genital ducts; the most apparent are the seminal conceptacles.

The Spermalege

The terms "organ of Ribaga" or "organ of Berlese," used previously to designate all or part of the spermalege, are inconvenient because they lack precision, do not specify the role of the organ, and are used in different senses by various authors. In 1959 I suggested a new term, "spermalege," defined as follows: "Among certain Hemiptera Cimicoidea, the

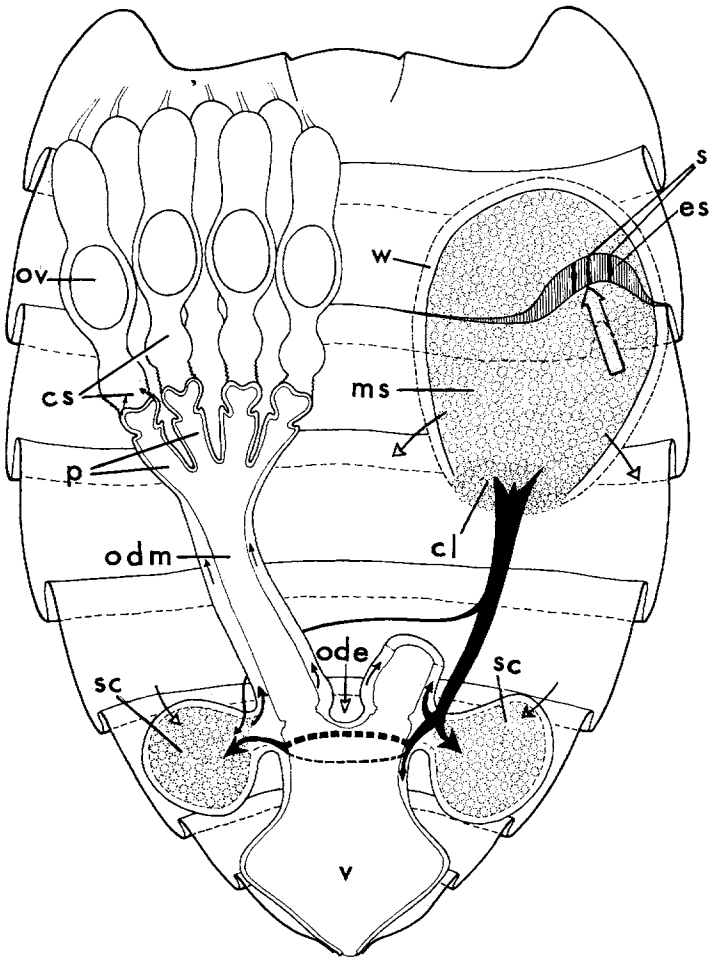

FIG. 7–1.—Diagram of paragenital system and process of insemination in Cimicidae, based principally on *Cimex* "type." Right ovary and nearly all of corresponding lateral oviduct omitted, and spermalege shown farther forward than actually the case in *Cimex*. Short, broad white arrow shows course followed by paramere of ♂ in reaching ectospermalege (hatched and crossed by 3 black bands representing scars of copulation). Black arrows indicate normal routes of migration of spermatozoa from mesospermalege to bases of ovarioles. Small arrows with white points correspond to migratory routes never or rarely used in *Cimex* but seen in other Cimicidae. Cl, conductor lobe; cs, syncitial body; es, ectospermalege; ms, mesospermalege; od e, paired ectodermal oviduct; od m, paired mesodermal oviduct; ov, oocyte; p, pedicel; s, scars or traces of copulation; sc, seminal conceptacle; v, vagina; w, wall of mesospermalege.

structure receiving the sperm during copulation but lacking a direct communication with the genital apparatus itself and not having the same origin." The spermalege is confined to the female sex, except in the exceptional case of the male of *Afrocimex*. It is connected to the abdominal integument in various positions, according to the species. Typically it is composed of 2 closely related parts, an ectodermal one called the "ectospermalege" and a mesodermal one called the "mesospermalege."[1]

The Ectospermalege.—The ectospermalege (organ of Ribaga in the sense of Berlese and of Cragg) is generally situated in an intersegmental fold which is modified and occasionally obliterated. It is sometimes part of the intersegmental membrane and sometimes included in the area of a segment covered by the posterior margin of the preceding segment. To observe this previously unknown difference, one may compare the ectospermalege of *C. lectularius* (Fig. 7–20a) with that of *C. hemipterus* (Fig. 7–20b); that of the former occupies the membrane between segments V and VI, while that of the latter is found in a channel formed by sternite VI slightly behind its anterior margin.

This channel is an example of the diverse modifications surrounding the ectospermalege itself seen in various species. The essential characteristic of the spermalege is a histological differentiation of the integument. However, it is often difficult to distinguish the ectospermalege itself from these modifications, and it is convenient to speak of a single structure, provided that all the parts belong to the same segment or intersegment.

On the other hand, in many Cimicidae the depression or fissure existing in the posterior border of the segment preceding the ectospermalege, although linked to the presence of the latter, is a very distinct modification. We propose that this be designated as the paragenital sinus.

The structural differentiation of the integument at the level of the ectospermalege is essentially a hypertrophy, consisting of a swelling projecting on the inner side. Upon examination of the abdomen of a cleared specimen by transmitted light, this swelling appears in *Cimex* as an oblong transverse mass on the right side under the posterior margin of sternite V. It may differ in dimensions and aspect from one species to another. Thus in *C. lectularius* (Fig. 7–22c), it is about 45 μ long and 60 μ in maximum width and has a hazy, irregular contour barely distinguishable from the surrounding cuticle except for its greater thickness and the presence of small spiniform projections covering its external surface. In *C. hemipterus* (Fig. 7–22d) it is much more clearly visible, thanks to the greater contrast in coloration from that of the adjacent integument, and to its distinct, regularly oval (approximately 280 μ long by 110 μ wide) shape.

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[1] Composed of parts of 2 Greek words: $\sigma\pi\epsilon\rho\mu\alpha$, seed; and $\lambda\epsilon\gamma\omega$, to gather.

The complex histological structure of the ectospermalege of *Cimex* has not been analyzed in detail since Ribaga (1897), whose thorough descriptions contain several inaccuracies and errors of interpretation. In sections, the ectospermalege appears to be formed by the same elements as the integumental area from which it is differentiated. But these elements are hypertrophied and modified in their structure, especially at the cuticular level. The ectospermalege of *C. lectularius,* from exterior to interior, is composed of the following layers (Fig. 7–20a):

a) A tight row of erect spatulate processes projecting into the lumen of the intersegmental fold. These processes are longer at the center, where they reach 25 μ, then at the margins of the mass; they result from a superficial differentiation of the subjacent layer and are of the same nature.

b) An exocuticle of intersegmental type which is eosinophilic and has closely packed internal fibers or longitudinal bundles. Some of the latter are inner prolongations of the superficial processes.

c) An endocuticle, always colored differently and much thicker than the preceding layer. It consists of a vaguely cylindrical central mass having a very irregular, filamentous structure, with dark granular inclusions abundant in places and present but less apparent in the exocuticle. This mass is surrounded laterally by a layer of less modified, homogeneous cuticle, especially developed on the dorsal side where it stops before reaching the bottom of the integumental swelling.

The epithelium of the ectospermalege has denser and taller cells in comparison with the adjoining epidermis. Usually forming a unique layer in *C. lectularius,* but occasionally irregular or folded, these cells have a spongy cytoplasm which is poorly delimited from the endocuticle; they are separated from the adjacent mesospermalege by a usually distinct basement membrane.

During perforation of the ectospermalege at copulation, the male paramere causes local damage which I (1953a) called "traces of copulation." They are rather quickly repaired but leave permanent scars. Irregular in form and dimensions, they cross the cuticle of the ectospermalege more or less obliquely. In the hours following traumatic copulation, the scars are characterized by the presence of an amber brown to black substance which is generally observed in the integumental scars of insects. Proteinaceous and containing no chitin, it is usually considered as an epidermal product or as blood clotting the wound, but I consider it to be a result of the alteration of the cuticle because it is also formed following a trauma that does not reach the epidermis.

The dark, oblong masses of this "scarring substance" were observed by Ribaga and Berlese, who assumed that they were products secreted or excreted by the "glandular" epithelium of the organ of Ribaga. They provide an easily recognizable marking of the traces of copulation in

histological sections and in preparations of the entire integument (Fig. 7-21b). Treatment in KOH, however, dissolves the masses of scar substance, leaving only a little puncture made in the cuticle by the paramere of the male.

There are rather important differences in structure between the ectospermalege of *C. lectularius* and that of *C. hemipterus;* at least part of one is originally from a different integumentary region than the other. In *C. hemipterus* the superficial exocuticle of the ectospermalege, naturally brownish-yellow, is segmental; it usually constitutes the spiniform processes which are more numerous, slender, and differently grouped than those of *C. lectularius.* Beneath it a layer of eosinophilic exocuticle with a distinctly "palisade" structure occurs, then the endocuticle, much thinner than that of *C. lectularius,* is found. The epidermal cells, on the other hand, are generally taller and, in places, laid out in several rows.

The Mesospermalege.—The mesospermalege in the bed bug appears as a whitish, almost hemispherical, pocket about 1 mm in diameter, touching the integument at the inner face of the ectospermalege. Its appearance varies considerably upon dissection, and histological sections show that it varies according to the phases of physiological activity, but 2 parts are always recognized. One of these is an external membrane; the other consists of internal, densely clustered free cells in more or less separated temporary masses that occasionally simulate compact tissue.

Earlier descriptions of the mesospermalege of *Cimex* do not completely elucidate the nature of its components. In the most recent work, Davis (1956) indicated, like Berlese and others, that the internal cells in the pocket resemble hemocytes, therefore are named "hemocytoid cells." The wall is formed by a thin "peritoneal sheath" which, according to Davis, is ensheathed externally by a layer of adipocytes.

Some unpublished observations bearing upon the development of the spermalege in *Cimex* led to a slight modification and a more precise description of this structure. In the female nymph, the outline of the mesospermalege appears, at about the middle of the fifth instar, in the form of a simple blood cavity broadly extended against the internal surface of the integument at the level of sternites V and VI (Fig. 7–2). This cavity is limited ventrally by the epidermis which produces the imaginal cuticle, and dorsally by a continuous cover of adipose tissue. It encloses numerous free, spherical, and identical hemocytes which at times can extend pseudopodia, an ability recognized by Ribaga and Berlese but denied incorrectly or unrecognized by authors who followed. Capable also of phagocytosis and rich in PAS-positive inclusions, they belong to the broad category of blood cells that Wigglesworth (1955) in *Rhodnius* named "amoebocytes," a term which will be used here.

In the Cimicoidea with traumatic insemination, it is these amoebocytes which constitute the most important part of the paragenital system; en-

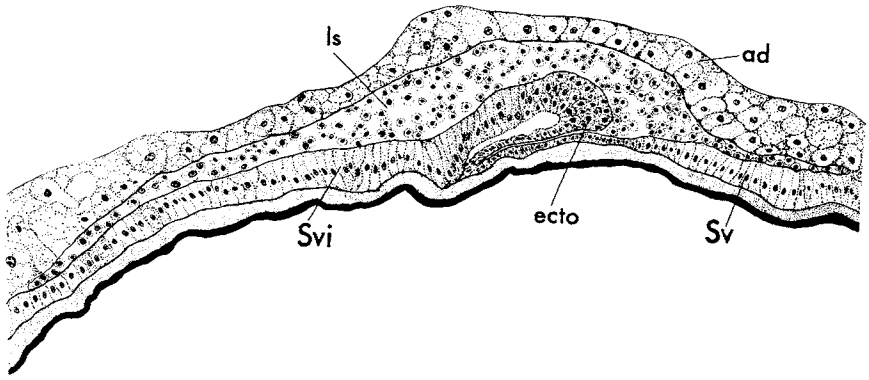

FIG. 7-2.—*Cimex lectularius*. Sagittal section of ventral abdominal integument at level of spermalege, fifth instar ♀. ad, layer of adipocytes; ecto, ectospermalege; ls, blood cavity adjacent to mesospermalege; Sv, Svi, sternites V and VI, respectively.

dowed with extensive potentialities, they undergo many, varied, and often reversible differentiations.

In inseminated females of Cimicidae, the amoebocytes of the mesospermalege show cyclical or noncyclical changes in structure and have a double function. One of these is microphagocytosis of the sperm "plasma," a proteinaceous secretion of the male mesadenia, the molecules of which are absorbed and degraded by the amoebocytes of the spermalege. This also occurs in the closely related pericardial cells which they resemble (Carayon 1953a). The other function is macrophagocytosis of a portion of the spermatozoa which are resorbed and destroyed. In the bed bug this activity, exaggerated by Berlese and doubted by Cragg and others, is usually more discrete than the preceding phenomenon. According to the Cimicidae considered, its intensity varies considerably and may be quite great.

Since in every case, the amoebocytes of the spermalege resorb at least the sperm plasma, they deserve the name of spermatophage given to them by Berlese in 1898. Among *Cimex* and other Cimicidae, the spermatophages are present not only in the spermalege; they are found also in fewer numbers dispersed in the hemocoel of the posterior portion of the abdomen.

Toward the end of the last larval stage the adipocytes which surround the spermalege begin to undergo modification. Losing a large part of their contents, they become flat, acquire rather dense basophilic cytoplasm, and finally form a thin envelope, the inner face of which is enclosed in an anhistic PAS-positive thin film, which is a true basement membrane. Some unmodified adipocytes, variably placed in 1 or more rows, ordinarily cover the external face of this envelope.

In all the Cimicoidea provided with a delimited mesospermalege, the

outer wall seems to be formed of adipose layers, the innermost of which may present varying degrees of differentiation and produce a basement membrane which is remarkably thick in some species.

The covering of the mesospermalege has a posterior and slightly lateral cavity, not previously recognized, across which the internal mass of the organ projects more or less into the hemocoel, constituting a thick "conductor lobe" (cl, Fig. 7–1). This lobe is more apparent in *C. hemipterus* than in *C. lectularius* and is much better developed in *Paracimex* and *Cacodmus.* Its position and orientation are such that the spermatozoa passing across it in leaving the mesospermalege are oriented toward the seminal conceptacles and the bases of the genital ducts.

Anomalies of the Spermalege.—Known only in *Cimex* and *Oeciacus,* the anomalies of the spermalege have been studied most thoroughly by Ludwig and Zwanzig (1937). Usually they are characterized by the production of 2 symmetrical organs placed at the sides of the abdomen. Already pointed out by Cragg (1920) and Abraham (1934), this doubling was found by Ludwig and Zwanzig in 0.5 to 40% of the females examined in the populations studied. They considered the doubling to be purely phenotypic. In general, the left supernumerary organ resembles the other but does not receive sperm during copulation. Less often, the left ectospermalege shows various degrees of reduction, whereas the corresponding mesospermalege retains normal or nearly normal dimensions. It has been observed, although rarely, that the mesospermaleges are rudimentary or absent in females having either 2 ectospermaleges or only the normal 1; such females remain sterile.

Inversion of the spermalege, in which that organ is found on the left rather than on the right, is about 30 times as rare as doubling. Of 3 "inverted" females which were observed alive and placed with males, one died in a short time; another, although possessing a complete spermalege, was never inseminated. The third female produced normal progeny.

Ludwig and Zwanzig point out again the very interesting case of 2 males that had a purely masculine internal reproductive apparatus and yet were provided with a well-developed "organ of Ribaga." Their account did not specify whether this organ was the ectospermalege itself or only the indentation in the posterior border of sternite V (paragenital sinus). One of the males in question had 2 abnormal copulatory organs and showed signs of oogenesis in a part of the testes.

"Paragenital" Differentiations of the Reproductive System

The elements of the paragenital system belonging to or directly attached to the original reproductive system are ordinarily formed by a more or less distinct differentiation of certain normal constituents of that

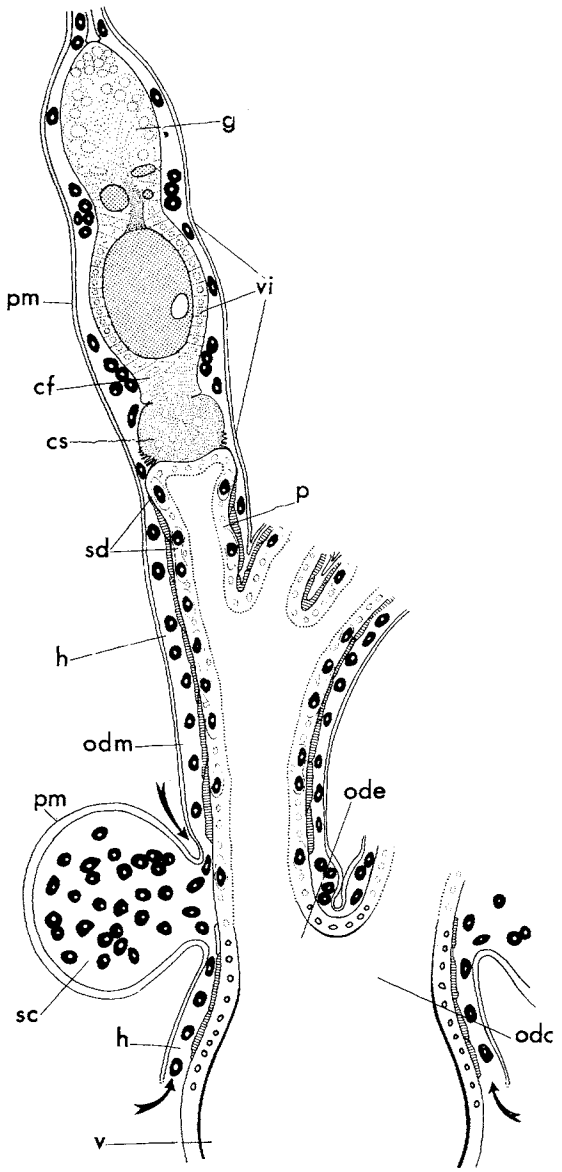

FIG. 7–3.—Diagram of ♀ genital apparatus of cimicid (type *Cimex*), showing connections of seminal conceptacles with perigenital envelopes. Only left portion of paired ectodermal oviducts and 1 ovariole shown. Amoebocytes are conventionally represented in black and white nucleus. cf, follicular body; cs, syncitial body; g, germarium; h, hemochrism; od c, common oviduct; od e, paired ectodermal oviduct; od m, paired mesodermal oviduct; p, pedicel; pm, peritoneal membrane; sd, spermodes; v, vagina; vi, vitellarium.

system. Some are observed at the level of the genital ducts; these are "seminal conceptacles" (Carayon 1954a) and the "spermodes." Others occur partly at the bases of the ovarioles; these are the "syncitial bodies."

The Seminal Conceptacles.—By reason of their role in the storage of spermatozoa, the seminal conceptacles have long been called "spermathecae" in *Cimex,* although the majority of authors must have suspected or recognized that they are not homologs of true spermathecae. They consist entirely of mesodermal formations annexed to the paired oviducts.

The seminal conceptacles in dissected virgin females of *Cimex* appear as 2 whitish translucent sacs symmetrically placed against the lateral faces of the paired oviducts, a little anterior to the junction of the latter. Narrowed basally but rarely pediculate in *Cimex,* they have variable dimensions and an ill-defined form somewhat resembling an ear. Like the mesospermalege, they are composed of an external membrane and an internal mass of free or temporarily agglomerated cells.

The membrane, which Cragg (1920) and Abraham (1934) decided was formed by a simple evagination of the membrane of the genital ducts, has been described by Davis (1956) as composed of unstratified epithelium. However, its true nature appears not to have been recognized by any of these authors. It is schematically represented in Fig. 7–3.

In reality the normal sheaths of the genital system, distended locally and more or less modified, form the seminal conceptacles in Cimicidae. These sheaths have been little studied and only at the level of the ovarioles, where, except for the tunica propria, 2 such sheaths are recognized in Hemiptera (Bonhag 1958).

One sheath is external and always very apparent; it is generally termed the "peritoneal membrane" (a rather unsuitable name but sanctioned by usage and more convenient than "outer epithelial sheath" proposed by Bonhag). Of variable appearance and complex structure, this external covering is not a simple epithelium. It seems to consist of a continuous layer of *adipocytes* (Fig. 7–4), usually slightly, if at all, charged with inclusions. To this layer are attached numerous tracheae and tracheal cells. The adipose nature of the peritoneal membrane was described in *Periplaneta* by Bonhag and Arnold (1961) from histochemical studies. I discovered it in Cimicidae and proved that this external sheath can, by degrees and with many transitions, become a typical adipose cover.

Under the external covering, between it and the tunica propria that covers the ovariole itself, free cells are found, sometimes aligned or layered and forming what Bonhag (1958) called the "inner envelope." According to my observations, first made in the Nabidae with hemocoelic insemination (Carayon 1952b) and extended to a number of other Heteroptera, these cells are hemocytes and the subperitoneal spaces they occupy are filled with blood. The internal, peri-ovarian envelope thus

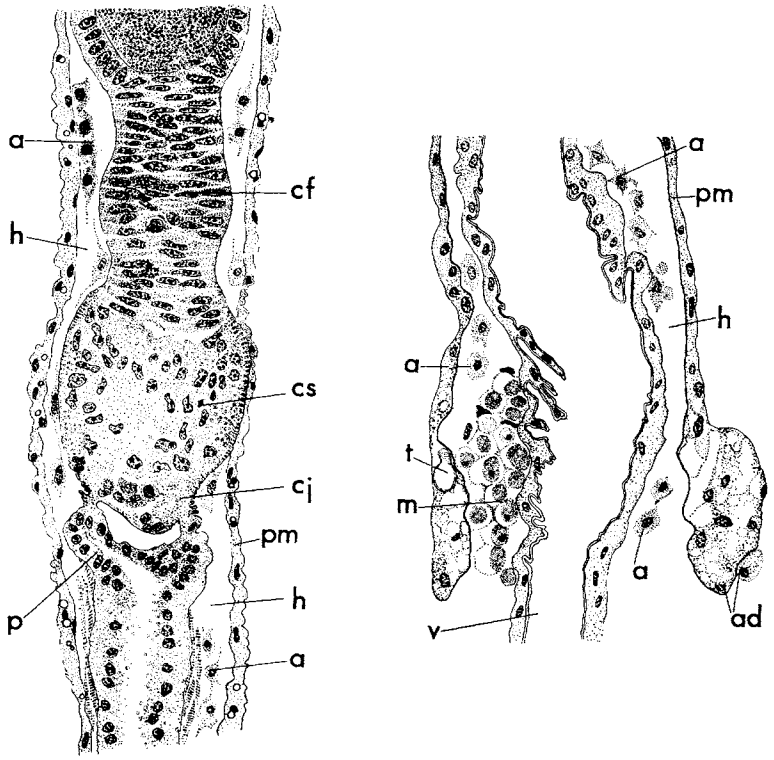

FIG. 7–4 (left) .—*Cimex lectularius*. Base of ovariole and pedicel in longitudinal section, virgin ♀. a, amoebocytes; cf, follicular body; cj, yellow body; cs, syncitial body; h, hemochrism; p, pedicel; pm, peritoneal membrane.

FIG. 7–5 (right) .—*Cimex lectularius*. Portion of sagittal section at level of vagina, showing posterior extremity of peritoneal membrane and hemochrism. a, amoebocytes; ad, adipocytes; h, hemochrism; m, muscular fibers; pm, peritoneal membrane; t, trachea; v, vagina.

actually appears as a blood layer for which I am proposing the name "hemochrism."[2]

The published findings on the ovariole sheaths generally have not mentioned the important fact that these envelopes also cover a large part of the genital ducts. In Cimicidae and many related families, they extend posteriorly to and cover the anterior half of the vagina.

In *Cimex,* the peritoneal membrane is altered in structure at the level of a small mass of transverse muscle fibers on the dorsal surface of the vagina a little before its posterior termination, where it appears as a rather thin, apparently epithelial layer. Where it thickens irregularly,

[2] From αιμα, blood; and χρισμα, layer.

its cells have the appearance of typical adipocytes, rich in inclusions. The adipose muff thus terminating the peritoneal envelope of the female reproductive apparatus remains largely free and is attached to the wall of the vagina only in places. The result is that the hemochrism is neither closed nor limited posteriorly and communicates at its base with the hemocoel (Fig. 7–5).

It is at the junction of the very short ectodermal and mesodermal portions of the paired oviducts that the peritoneal envelope and the locally swollen hemochrism form the seminal conceptacles. In most of the Cimicidae, this swelling, much more pronounced on one surface than on the others, produces a sessile or pediculate pocket; thus the fundamental annular conformation of the seminal conceptacle does not appear.

The seminal conceptacles are always connected without abrupt change in structure at the unmodified perigenital envelopes from which they arise. Also, they lack anatomical and histological limits. This, together with their location, explains why they have been considered by authors as evaginations either of the median ectodermal oviduct or of the lateral mesodermal oviducts.

The wall of the seminal conceptacles is formed by the peritoneal envelope itself, usually without a great change in structure. At the conceptacles, the peritoneal envelope becomes thicker, and its appearance may vary not only between but within species according to age and physiological condition. Nevertheless, 2 elements are generally distinguished (Fig. 7–6). One of these, the wall itself, is composed of a unique layer of flat cells; its lateral limits are usually invisible and its nuclei, ovoid and irregularly spaced, show only small grains of rather dense chromatin. In *Cimex*, these cells contain several PAS-positive inclusions which disappear at the end of larval development. The other element comprises the "inner processes," which are formed by a localized proliferation of parietal cells and are connected in places to the inner face of the wall. Often grouped in irregular and occasionally very long clusters, they form protrusions into the lumen of the conceptacles; the extremities of some appear isolated in histological sections. Preceding authors have failed to recognize these processes or have not understood their exact nature—Cragg (1920) considered them to be deep folds in the wall, and Abraham (1934) saw the free cells in the interior of the conceptacles as they formed and detached from the wall.

In fact, these free cells are hemocytes (more precisely amoebocytes) and the inner portions of the conceptacles correspond to the locally dilated hemochrism. Dispersed at the end of development, and in the very young females, the spherical amoebocytes next tend to congregate with themselves and with the cells of the internal processes. They are distinguished from the latter by their smaller nuclei, grains of dense chromatin, a large nucleolus, and especially by the abundance of PAS-

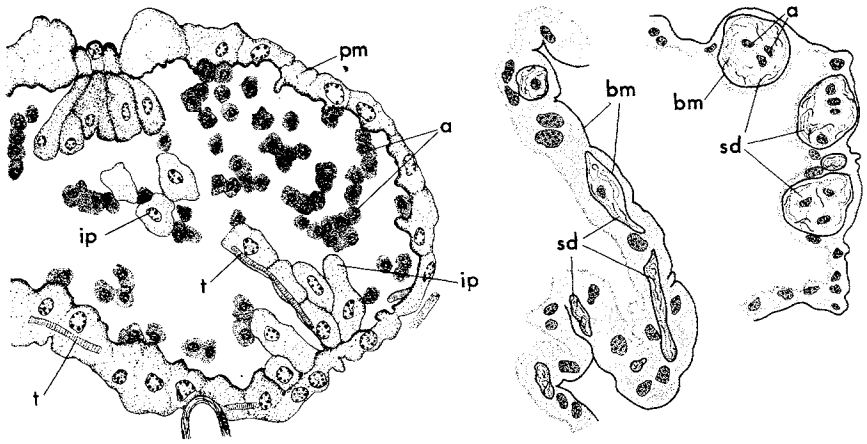

FIG. 7–6 (left).—*C. lectularius*. Portion of sagittal section of seminal conceptacle stained with PAS-hemalum, virgin ♀. a, amoebocytes (cytoplasm with PAS-positive granules); ip, internal processes; pm, peritoneal membrane; t, tracheae.

FIG. 7–7 (middle and right).—*C. lectularius*. Parietal epithelium of mesodermal oviduct, inseminated ♀. Middle, longitudinal section of anterior region of oviduct; right, transverse section of posterior region of oviduct slightly anterior to conceptacle, stained with PAS-hemalum. Spermodes (sd) included in epithelium have a wall identical to basement membrane (bm) and strongly PAS-positive. They enclose typical amoebocytes (a), often many in a single section, and numerous spermatozoa.

positive inclusions. In virgin females, at least, these amoebocytes do not differ from those observed in the remainder of the hemochrism.

Abundant tracheae and tracheoles pass through the wall, just as in the inner processes of the conceptacles. The bottom of the fold forming the anterior bases of these conceptacles where they connect to the oviduct is occupied by a poorly defined mass of spongy parenchymous tissue. Numerous, dense tracheae with their tracheal cells constitute the essence of this mass, which anastomoses posteriorly with the wall of the seminal conceptacles which is strongly fenestrated and thicker at this point of attachment than elsewhere.

The "Spermodes."—The seminal conceptacles are not the only differentiations of the genital ducts associated with the processes of traumatic insemination. In *Cimex* and in a number of other Cimicidae, the walls of the pedicels and of the paired oviducts anterior to the conceptacles have a continuous network of canals called "spermodes,"[3] as they are used by the spermatozoa in migrating to the ovarioles.

Most authors who have studied the female reproductive system of Cimicidae have indicated only that the spermatozoa proceed in fascicular

[3] From σπερμα, seed; and οδος, track.

clusters from the conceptacles in the wall of the anterior genital ducts. According to Berlese and others, this progression is made across the cells of the parietal epithelium, where histological sections of inseminated females seem to show the existence of numerous spermatozoa.

Davis (1956) discovered that the spermatozoa in *C. lectularius* do not actually progress through the epithelial tissues but through a special net-like formation, the special cells of which he called the "sperm tract cells." These cells, undescribed by Davis, are long and ramified and connect with each other at their extremities. After a study of several Cimicidae, especially of *C. lectularius,* I concluded that the intra-epithelial network through which the spermatozoa pass consists of tubular canals, for which I propose the name "spermodes."

Extending from the bases of the seminal conceptacles to the anterior extremities of the pedicels, the spermodes are best seen in preparations of the entire wall of the genital tracts of inseminated females (Fig. 7–20b). Somewhat rectilinear, most often longitudinal, and extremely variable in diameter, they are joined by short transverse or oblique branches; the entire appearance is that of an irregular network. The often numerous spermatozoa present make the contours and route very clear but more or less mask the structure. The combined use of various stains and microdissection, however, show that the spermodes are tubes with thin anhistic walls, connected to each other without visible discontinuity and containing dispersed free cells, more abundant toward the base and at the intersections of the network.

These free amoebocytes are more easily studied in virgin than in inseminated females, because spermatozoa have not closely surrounded them. They are rich in PAS-positive inclusions, resembling those of the hemochrism, but infiltrate the epithelium of the anterior genital tract. The walls of the spermodes, which have all the characteristics of basement membranes, are no doubt secreted by them. Strongly PAS-positive, the wall appears vivid red with McManus stain, which also causes the spermodes, often difficult to see with the usual histological stains, to become quite distinct upon sectioning. In *Cimex,* the spermodes appear as shown in Fig. 7–7. The average diameter increases toward the bases of the mesodermal oviducts and numerous amoebocytes, often several in the same transverse section of each spermode, may be seen in the lumen.

At their posterior extremities near the bases of the conceptacles, all the spermodes are flared out and open broadly into the hemochrism. Here, the muscular tunic of the genital ducts is interrupted for a short distance and there is a junction with different parts of the hemochrism, especially the interior of the conceptacles and the spermodes. The presence of numerous tracheae and tracheal cells mixed with many amoebocytes gives a rather complex alveolar structure to this junction.

Anteriorly, most of the spermodes thicken and become varicose, at least in inseminated females; they terminate at the distal extremity of the pedicels near what is called here the "syncitial body"—a special structure of the ovariole bases.

The "Syncitial Bodies."—These bodies form part of the entire complex designated as the "epithelial plug" or corpus luteum (sensu lato), which blocks each ovariole posteriorly. In adult females of nearly all Cimicidae, 3 successive zones with different structure and undoubtedly different functions may be distinguished in this complex:

a) The anterior zone, situated behind the more mature oocytes in the vitellarium, is composed of unmodified interfollicular tissue and is called the "follicular body." The flat cells, often incurved and regularly stacked, have transversely elongated nuclei and clearly distinct limits. The tunica propria is not folded and remains thin. Such more or less developed follicular bodies are observed in the bases of the ovarioles of most insects.

b) The middle zone, more swollen than the preceding, is partially separated by a transverse annular fold of the tunica propria. It has bizarre nuclei of irregular form and dimensions arranged without order in a rather homogeneous cytoplasmic mass that lacks visible cellular limits. These nuclei appear to be dispersed or variously grouped at the center or toward the base of the mass. The peripheral tunica propria remains unfolded, but some short fibers are arranged perpendicularly on its internal face; these fibers are indistinct or invisible anteriorly.

When the oldest oocyte of the vitellarium has matured, the posterior part of the interfollicular tissue surmounting it is differentiated and constitutes the middle zone. After ovulation, it is found inside the base of the ovariole; in contrast to the anterior zone, it is characteristic only of some Cimicoidea having traumatic insemination.

The middle zone has attracted the attention of all authors who have studied the detailed structure of the ovarioles of *Cimex lectularius*, where the zone is clearly differentiated. Berlese (1898) defined and illustrated it and showed that abundant spermatozoa are found assembled in it after insemination. Cragg (1920) described it in detail and called it a "mass of nucleated protoplasm." Abraham (1934) designated it as a "zone of irregularly disposed nuclei" and believed that it destroys and resorbs a large part of the spermatozoa which penetrate into the ovariole. On the contrary, Davis (1964) believed that it permits fecundation of the oocyte just before the secretion of the chorion and termed it the "corpus seminalis." My own observations agree with the hypothesis of Abraham, and I prefer to apply to this structure the term "scyncitial body" or "corpus scyncitiale," which are terms based on clearly structural rather than disputed functional characteristics.

The scyncitial bodies seem to be the only elements of the ovarioles the differentiation of which would be in keeping with traumatic insemina-

tion. Their presence has been verified in all the Cimicidae studied except in *Crassicimex* and *Stricticimex* where the paragenital systems are much more complex and highly evolved than any others known in the family. The probable significance of these remarkable exceptions will be examined later with respect to the process of insemination.

c) The posterior zone corresponds to the corpus luteum or "residual body," in which, after ovulation or degeneration of the posterior oocyte, the follicle of the vitellarium and the follicular formations behind it subside, then undergo a partial resorption. Subject to incessant alterations, the corpus luteum shows an extremely variable, complex structure within an individual and often from one ovariole to another. Nevertheless, it always remains very distinct from the preceding zone, at least in the character of the tunica propria; the latter shows the transverse folds which, already visible in the moulting female, afterwards become more numerous and closer together.

THE PROCESS OF INSEMINATION

The essential phenomena of the process of insemination (Fig. 7–1) are the introduction of the sperm into the female and the successive migration of the spermatozoa to the oocytes. These phenomena are accompanied by secondary ones more or less directly connected with the traumatic extragenital character of the insemination—integumental puncturing and resorption of sperm plasma and a part of the spermatozoa.

These phenomena show modalities nearly constant within a species but variable within the family. The following generalities on this subject are based on the moderately specialized case in *C. lectularius*.

The process of insemination generally includes 3 successive phases, each named according to the part of the female organism where it occurs—the spermalege phase, the hemocoel phase or "spermathemie," and the intragenital phase. The duration of each of these phases can be stated only in approximate terms, as it varies within a species because of temperature, age, physiological condition of the female, quantity of sperm injected, etc.

Spermalege Phase

During copulation, which in *C. lectularius* usually lasts from 1 to 5 minutes, the male paramere perforates the ectospermalege and injects sperm in a single, compact mass into the adjacent part of the mesospermalege (ejs, Fig. 7–20d). This part, which is not exactly central, appears prior to copulation as a cavity where the amoebocytes are much less numerous than elsewhere or lacking (l, Fig. 7–20c).

In the injected mass of sperm, the spermatozoa are at first immobile and mixed with sperm plasma; the latter, as shown by Davis (1964), is

a secretion of the male mesadenia which activates the spermatozoa. The viscosity of the sperm plasma is sufficient to maintain contact with the spermatozoa during the time required for their activation; however, activation of sperm is effected equally well in the Cimicoidea which lack a mesospermalege. Contrary to Davis, I believe that the spermalege does not permit the sperm plasma to activate the spermatozoa.

The spermatozoa become very mobile in about 30 minutes, according to Abraham (1934), and gradually leave the mass of ejaculated sperm. Grouped for the most part in irregular bundles and dispersing the amoebocytes in passage, they progress toward the periphery of the mesospermalege, where the first arrive 1 to 2 hours later. They collect there under the wall in an irregular layer (sz, Fig. 7–20d). Often they collect into "balls" under the influence of the seminal plasma, according to Davis. However, this aggregation, which can be caused by a number of other factors, is far from being constant in the spermalege of Cimicidae, as aggregations are frequently seen in the hemocoel and seminal conceptacles.

In *Cimex,* the spermatozoa do not distribute themselves equally all over the periphery of the mesospermalege in the course of their centrifugal migration; they appear more numerous in its posterior region where the "conductor lobe" is found. It is principally if not exclusively in crossing this lobe that they leave the mesospermalege and pass into the hemocoel. Their exit, which begins ordinarily 3 to 4 hours after copulation, usually takes place by groups, but only after partial separation of the bundles or dense masses formed to that time (Fig. 7–20e).

In *C. lectularius,* according to Abraham (1934), the exit of the spermatozoa takes place elsewhere, especially through the anterior region of the mesospermalege. Such an occurrence, which I have not verified in the bed bug, is frequent in other Cimicidae with a less well-differentiated spermalege.

The changes in the structure of the spermalege caused by copulation and insemination have already been mentioned in the description of this structure. It is important to re-examine them briefly here from the point of view of their functional significance.

On the right side of the female, where the male paramere perforates the integument, a winding fissure in the cuticle is observed immediately after copulation. The fissure is often filled with a trail of sperm and a local break-through of the epidermis, the shattered cells of which have pycnotic nuclei. The ectospermalege, thanks to the great thickness of its soft endocuticle, no doubt facilitates the rapid occlusion of the wound and hinders the loss of fluids or subjacent tissues in spite of pressure of the injected sperm. This possible role, however, cannot be considered as either very important or general, as a number of Cimicoidea having traumatic insemination lack an ectospermalege; moreover, that organ

tends to become very thin in the more highly differentiated paragenital systems.

The arrival of the sperm in the mesospermalege triggers important cyclic modifications of the internal cells. Complex and still insufficiently analyzed in spite of the detailed description by Cragg (1920), these modifications can be outlined here only schematically. They start with a swelling and a strong vacuolization in most of the amoebocytes, in each of which the development of a voluminous vacuole (in which the nucleus often seems to float) reduces the cytoplasm to a thin peripheral layer and several very thin central fibers. At the center of this vacuole a large mass of granular inclusions soon appears; it gradually condenses to form a homogeneous, somewhat spherical globule (Fig. 7–20g), and disappears by progressive thinning during the 24 hours or so which follow copulation. A further reduction of the vacuoles returns the amoebocytes to their initial condition.

The intravacuolar inclusions change in form and structure and in chemical composition, as shown by a change in their staining affinities. These inclusions are colored initially as a mesadenic secretion injected with spermatozoa, and all the modifications observed show evidence of activity identical to that of the pericardial cells. I (Carayon 1953a) concluded from this observation that the elements of the mesospermalege have as their essential role the resorption of the sperm plasma; Davis (1956) arrived at the same conclusion.

The resorption of part of the spermatozoa by the mesospermalege, of variable importance in the Cimicidae, has been disputed by some authors who have studied *Cimex*. It is, however, rather clear in the representatives of that genus. In the mesospermalege of the bed bug, one can see spermatozoa within some of the amoebocytes 1 or 2 hours after copulation. Then, as these intracellular spermatozoa become more numerous, they show many signs of progressive disintegration—alteration in form, diminution of colorability, fragmentation, then total lysis. Part of the amoebocytes which have resorbed sperm plasma or spermatozoa or even both are altered and lysed. According to Cragg, they are replaced by amitotic division of the existing amoebocytes. Several days after a single mating, the spermalege of *Cimex* no longer contains spermatozoa because those which remained there after the others continued their migration have been resorbed.

Hemocoel Phase or "Spermathemie"

As soon as the spermatozoa leaving the spermalege reach the hemocoel, they clearly appear to be attracted by the basal region of the genital apparatus and the nearby seminal conceptacles, particularly the one on the right. The first of the spermatozoa do not delay in penetrating here after only a short stop and a short passage in the hemocoel. However,

the spermatozoa which follow remain in the hemocoel for a longer time. Doubtless unable to enter the conceptacles in such great numbers at the time that they leave the mesospermalege, the spermatozoa accumulate gradually in the hemocoel of the posterior portion of the abdomen. They are often found here in large numbers when copulation is repeated at frequent intervals. Always highly motile, they may be distributed more or less widely among the various abdominal organs, but most of them congregate in balls visible to the naked eye; they then surround and completely conceal the conceptacles and the bases of the genital ducts.

The penetration of the conceptacles by the spermatozoa continues, their number thus increasing in the hemocoel. After attaining their maximum within 6 to 12 hours, their numbers begin to diminish provided that a new copulation has not occurred. In this case the spermatozoa always disappear from the hemocoel 1 to 2 days later, or a small portion of them are resorbed by amoebocytes identical to those of the mesospermalege.

Intragenital Phase

Except for the work of Abraham (1934), nothing has been published on the route followed by the spermatozoa in penetrating the so-called genital apparatus and Abraham's work was incomplete and not entirely accurate. Therefore a brief description and diagram of the intragenital phase of insemination are given here based on recent publications and the results of personal investigations.

The principal route of penetration of the spermatozoa, as described by Abraham, is along the latero-external side of the right oviduct to the base of the conceptacle. Here, where there is no true orifice, the spermatozoa, often in fascicular clusters, cross the peritoneal envelope. The latter consists of partly dissociated elements mixed with numerous tracheae and forms the lacunar parenchyma mentioned above. The spermatozoa migrate not, as assumed by Abraham, through the median oviduct but in the hemochrism zone which surrounds the connection between the paired oviducts and the median oviduct. This zone provides them with a base from which they emigrate in different ways.

Many of the spermatozoa penetrate the right conceptacle while others immediately pass through the wall of the oviduct and thence are conveyed to the ovarioles. Still others make their way back and overrun the postero-ventral region of the hemochrism under the median oviduct and accumulate there. The left conceptacle is filled soon after the right one, especially with spermatozoa coming from the hemochrism, but it also receives spermatozoa from the hemocoel which penetrate into its base through the peritoneal envelope at the junction of the ectodermal and mesodermal parts of the left oviduct.

The posterior and indirect path is restricted to that portion of the hemochrism between its base and the conceptacles. Not recognizing the exact relationships of the conceptacles which he thought open into the lumen of the oviducts, Abraham misinterpreted his own observations (also incomplete in other respects) on the passage of spermatozoa in the posterior genital ducts. According to him, the spermatozoa enter the lumen of the median oviduct after crossing the wall and move anteriorly to the conceptacles. Actually, the spermatozoa are found about the posterior genital ducts during spermathemie and enter the hemochrism in great numbers. The base of the hemochrism joins broadly with the hemocoel, and here the spermatozoa proceed anteriorly to enter the conceptacles. Contrary to the opinion of Abraham, who confused the hemochrism with the lumen of the oviduct, the latter never contains either spermatozoa or blood cells.

The spermatozoa greatly and often irregularly distend the walls of the conceptacles. They accumulate here in great numbers in the form of a dense mass of flexible bundles, or when they are less abundant, in the form of separate spherical aggregates. Most of them momentarily lose their motility because of their great concentration and remain in place, conserving their viability during several weeks or months after copulation (Mellanby 1939a, Davis 1956).

As all of the investigators except Abraham (1934) recognized, the basic role of the seminal conceptacles is to maintain a reserve of spermatozoa. A small portion of the spermatozoa are resorbed here; nevertheless, this resorption, the importance of which Abraham exaggerated, affects only the isolated spermatozoa. It occurs in the same fashion as in the mesospermalege, but to a lesser degree, by the intra- and extra-cellular lysing action of the amoebocytes. After the spermatozoa arrive in the conceptacles, they change slightly in appearance or display modifications different than those observed in the mesospermalege. These cells have been insufficiently studied. Their cytoplasm is often swollen and spongy.

The clusters of spermatozoa have hardly formed in the conceptacles when a partial and progressive dissociation commences, liberating newly mobile spermatozoa which continue their course toward the ovarioles. Once having left the conceptacles, the spermatozoa disperse in the hemochrism zone surrounding the oviduct at the same level, constituting the intersection designated previously. At first dispersed without order in this intersection, they soon converge toward the posterior orifices of the spermodes where they congregate and proceed to the distal region of each pedicel. There they leave the spermodes, the anterior extremities of which are difficult to see but appear to be open. They then enter the base close to the ovariole without passing anteriorly to the syncitial bodies, where they disperse in large numbers.

It is only when vitellogenesis occurs in the posterior oocyte of the

vitellarium that the final step in the migration of the spermatozoa is accomplished. Some of the sperm congregate in the syncitial body at the base of the ovariole, cross the follicular body, and then proceed into the thickness of the follicle to attain the syncitial body. The latter is newly differentiated against the anterior pole of the oocyte. Although fecundation has not yet been observed directly, everything indicates that it occurs at this moment, just before chorion formation.

The syncitial body has a special relationship with traumatic insemination, but contrary to Davis's suggestion (1964), quite probably does not represent a means for the spermatozoa to enter the oocyte just before the chorion forms. In the opinion of Abraham (1934), confirmed by my observations on many different Cimicoidea, the principal or only function of the syncitial body is the resorption of spermatozoa flowing in excess into the ovarioles.

My observations indicate that the spermatozoa penetrating the syncitial body remain motile and alive for only a short time. Soon they show signs of a rapid alteration, but even before resorption is achieved, they are replaced by other spermatozoa coming from the spermodes. These are destroyed in their turn except for those which have completed the last step in their migration, the fertilization of an oocyte.

Because of this almost continuous reprovisioning, the syncitial body seems to provide a reserve of spermatozoa, whereas actually it destroys nearly all of them and contributes largely to depletion of the stock. Very conclusive in this regard is the great reduction or complete absence of the syncitial bodies in all Cimicoidea with traumatic insemination, in which the presence of a highly differentiated spermalege greatly reduces the number of spermatozoa entering the ovarioles.

Is it possible that the newly-formed syncitial body plays a secondary role in fecundation? I think not, because intra-ovarial fecundation similar to that in *Cimex* is achieved in the complete absence of syncitial bodies among a great many Cimicoidea with or without traumatic insemination.

Determinism of the Process of Traumatic Insemination

Once the spermatozoa have been activated by the seminal plasma, it is only because of their own mobility that they complete all the complicated stages of their migration in the female. The attractive agent or agents which guide them remain unknown in spite of the research on the physiology of insemination in *C. lectularius* (see the contribution of Davis in this work). The many experiments performed by Abraham (1934), Mellanby (1939a), and Davis (1956, 1964, 1965a), by injecting sperm or by implanting spermaleges and conceptacles of inseminated females into virgin females, have produced no results of interest on this subject. The same is true for most of the in vitro observations on the behavior

of active spermatozoa in the presence of various substances or parts of organs. While lacking confirmation, Abraham's observations show that isolated seminal conceptacles, fragments of their wall, or fragments of the median oviduct placed in a drop of Ringer's solution attract spermatozoa if they are no farther than 1 mm away. On the other hand, no attraction is produced by bits of lateral oviducts, by ovarioles, or by the vagina.

Davis (1956) discovered that in the bed bug, feeding greatly increases the migration of spermatozoa from the conceptacles and their subsequent entrance into the spermodes. The quantity of spermatozoa contained in the latter, very great after a meal, decreases progressively as a starvation period continues. Such an influence, perhaps due to simple mechanical compression of the conceptacles, is evidently only indirect. It increases the intensity of or completes the action of migration, but does not reveal its nature.

Observations on all Cimicoidea with traumatic insemination have led me to believe that among these Hemiptera, the movements of spermatozoa in the female are guided above all by differences in oxygen tension. Several of the criteria on which this hypothesis is based are reported herewith.

In the case of intense and prolonged spermathemie, seen only in several species of the nabid genus *Alloeorhynchus,* there is a strong tendency for the spermatozoa to gather about the tracheae in locations well provided with oxygen (Carayon 1952b). As the period of sexual maturity begins, a probable rapid increase in the respiratory intensity of the ovaries attracts the spermatozoa.

It is noteworthy that the tracheae and tracheoles are particularly plentiful in those parts of the paragenital system where the stream of spermatozoa indicates the existence of a strong attraction. In *Cimex,* for example, the great abundance of tracheae in the wall of the mesospermalege, which explains the centrifugal migration of spermatozoa, is even greater in the "conductor lobe" through which the spermatozoa pass in order to reach the hemocoel. The seminal conceptacles and the walls of the genital ducts contain even more tracheae, but their abundance is not so significant because most of the elements of the female reproductive system are normally provided with a very dense tracheal network. It does appear significant, however, that the penetration of spermatozoa into the conceptacles occurs precisely at the spot where a compact mass of tracheae also penetrates.

The idea that a gradient in oxygen tension in the female guides the spermatozoa does not, of course, exclude the possibility of the intervention of other factors, such as variations in pH or chemotactic effects, for example.

EVOLUTION OF THE PARAGENITAL SYSTEM AND THE PROCESS OF INSEMINATION

As just indicated, the paragenital system of Cimicidae consists of structures which commonly occur in female insects but which have undergone a special differentiation for traumatic insemination. This differentiation is quite variable, according to the Cimicidae considered, being absent or nearly so in some and strongly developed in others, with nearly all intermediates. These variations (Carayon 1959), correspond to stages of evolution, the general direction and principal levels of which may be reconstructed by arranging a series of Cimicidae in order of increasing complexity of paragenital system.

PARAGENITAL SYSTEM

Primicimex cavernis Barber, which seems in many respects to be the most "primitive" of the known Cimicidae, has the simplest paragenital system (Fig. 7–9), without a spermalege (Carayon 1954b). Histological study of inseminated females reveals the presence of scars, usually of multiple copulations, in an unmodified area of the dorsal abdominal integument. Nevertheless, a dark brown, externally visible band (Fig. 7–21a) extends more or less broadly into the left portion of the fold between segments V and VI, indicating the place where copulation scars are most numerous. This region differs from the adjacent integument only by its pigmentation and by a very slight hypertrophy. Were it to exist in virgin females, it might be considered as an incipient spermalege. Scars are also seen in other places, especially in the fold between segments IV and V and less often tergite VI (Fig. 7–8, 7–23h). Thus, copulation may take place over a rather large area of the abdomen wherever the male in copulatory position may conveniently reach with his paramere.

There is no mesospermalege, and the hemocytes, which are numerous in the hemocoel, show no tendency to congregate beneath the area of copulation. The seminal conceptacles represent almost all of the paragenital system. They are shaped like 2 large, oblong sacs, without pedicles, but become gradually more slender toward their apparent dorsal attachment on the oviducts. To date their walls, distended by a quantity of spermatozoa, have been studied only in inseminated females; they are thin but quite irregular with slender ramified internal processes. Many spaces, filled with spermatozoa, give them a spongy or tortuous appearance and render their contours difficult to distinguish. The cytoplasm of the cells, lacking visible limits, often seems transformed into unequal masses of coagulated secretion. Relatively few amoebocytes are found in the conceptacles; they are small, spherical, and resemble those of the hemochrism.

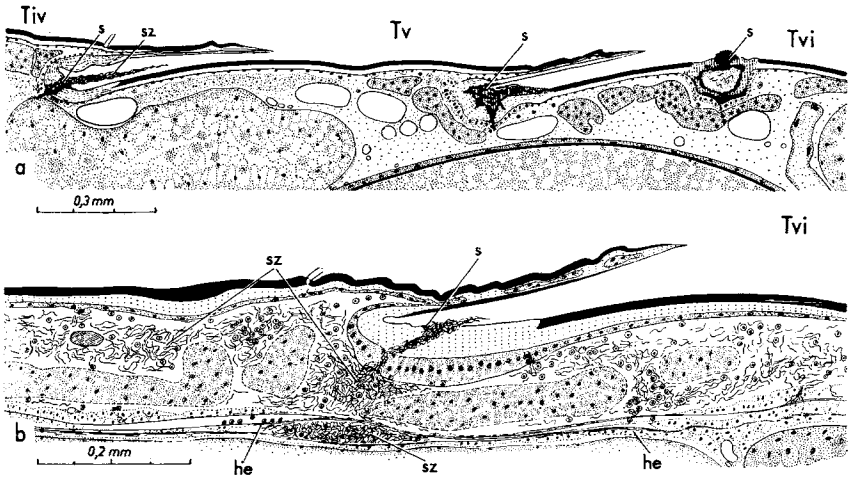

FIG. 7–8.—*Primicimex cavernis*. Sagittal sections in dorso-abdominal region of inseminated ♀. a, scars or traces of copulation (s), variously situated, one of these in the middle of tergite VI. b, recently inseminated female, medio-sagittal section. Numerous spermatozoa (sz) are seen in trace of copulation (s) in adjacent hemocoel and lumen of cardiac tube (he); T, tergite.

The spermodes are not differentiated, at least not as well as in *Cimex*. However, large syncitial bodies exist at the bases of the ovarioles. The evolution of the paragenital system in *Primicimex cavernis* is still in an early stage. The next stage is characterized by the appearance of a *mesospermalege,* the phyletic differentiation of which always seems to precede that of the ectospermalege except for the special case, discussed later, of males of *Afrocimex*. Examples of this stage, numerous among the Anthocoridae: Lyctocorinae, are absent among most Cimicidae where the ecto- and mesospermalege coexist.

The most primitive type of spermalege known in the family Cimicidae is found in the females of *Afrocimex* (Fig. 7–9). It is greatly extended but poorly delimited. Its mesodermal portion appears as a diffuse mass of cells free or joined in rows occupying a large part of the anterior region of the abdomen and not enclosed within an envelope. The ectospermalege, situated on the ventral integument in the same region, consists of 2 swellings with irregular contours lying on the left side of the folds between segments II and III and III and IV (Fig. 7–21g). The posterior borders of segments III and IV are broadly indented paragenital sinuses. The swellings are formed by a local thickening of the intersegmental membrane. Its cuticle, principally the endocuticle, appears to be scarcely modified in structure, but is 2 or 3 times as thick as elsewhere. The ectospermalege, formed previous to the imaginal molt, is the only location on the integument of the abdomen of inseminated females where

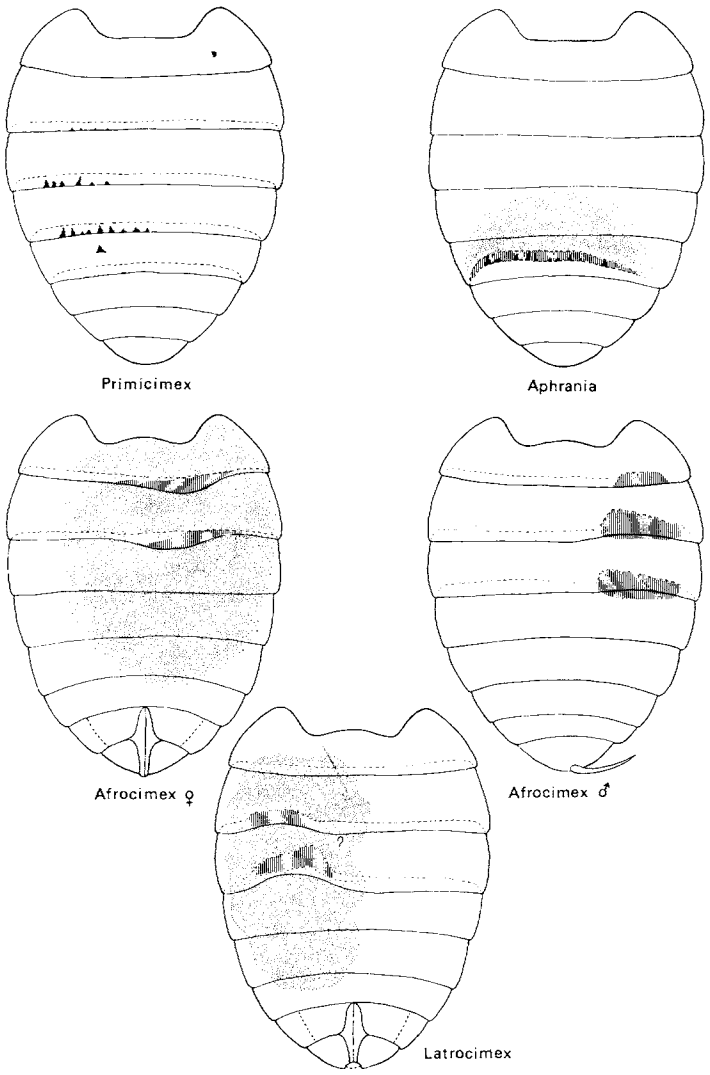

FIG. 7–9.—Structure and position of spermalege in *Primicimex, Aphrania, Afrocimex,* and *Latrocimex*. Scars of copulation shown as black spots only in first 2 genera, ectospermalege indicated by parallel lines, mesospermalege by stippling with double dotted lines when a wall is present. Ventral views recognizable by ♂ paramere or ♀ genital plates.

copulation scars are found; they are usually quite apparent, often numerous within the same individual, and are dispersed over the length of each swelling.

Afrocimex females have large seminal conceptacles resembling those of *Primicimex cavernis,* but with a wall that is less spongy and more clearly delimited. As seen in histological sections of inseminated females, there are differentiated spermodes which appear to be larger and more swollen by the spermatozoa than are those of *Cimex*. Large syncitial bodies are also present.

Unlike all other known Cimicoidea having traumatic insemination, the *Afrocimex* male has a spermalege (Fig. 7–9) used for inseminating other males, although neither hermaphrodites nor intersexes occur (Carayon 1959). Equally exceptionally, only an ectospermalege is present. Its position and histological constitution are as in females, yet it is quite differently shaped and better developed, consisting of 3 successive swellings in the membranes between segments II to V, with a large "sinus" in each (Fig. 7–21e,f). These swellings are not as broad as, but much thicker than, those of the female; they increase in size from anterior to posterior, and those of inseminated males are traversed here and there by prominent copulation scars (Fig. 7–23b).

Afrocimex males are of great interest in connection with problems posed by the evolution of the paragenital system, especially those concerning the significance of the ectospermalege and the mechanism, still conjectural, of its phyletic differentiation. *Afrocimex* shows that the ectospermalege can be formed in the absence of the mesospermalege without being, at least directly, of any use whatsoever in reproduction. It is stressed that this male ectospermalege, doubtlessly related to the high frequency of attempted homosexual couplings among Cimicidae, has developed only in *Afrocimex,* the spermalege of which is of a less differentiated type.

Only in the primitive stages seen in *Primicimex* and *Afrocimex* can the general tendencies of evolution of the spermalege be traced. In the following discussion, evolutionary trends will be treated under separate headings corresponding to the principal parts of the paragenital system.

The Ectospermalege

From the point of view of evolution, the size, form, and structure are the most significant; the position of the ectospermalege, although quite variable, is of less interest. Primitively greatly extended on the abdomen, it tends to become more localized in phyletically higher forms.

Double ectospermaleges having 2 consecutive swellings tend to become simple and then joined in a single integumental fold following the reduction of the anterior swelling. All degrees in this sequence are found among the Haematosiphoninae (Fig. 7–10). The anterior swelling is

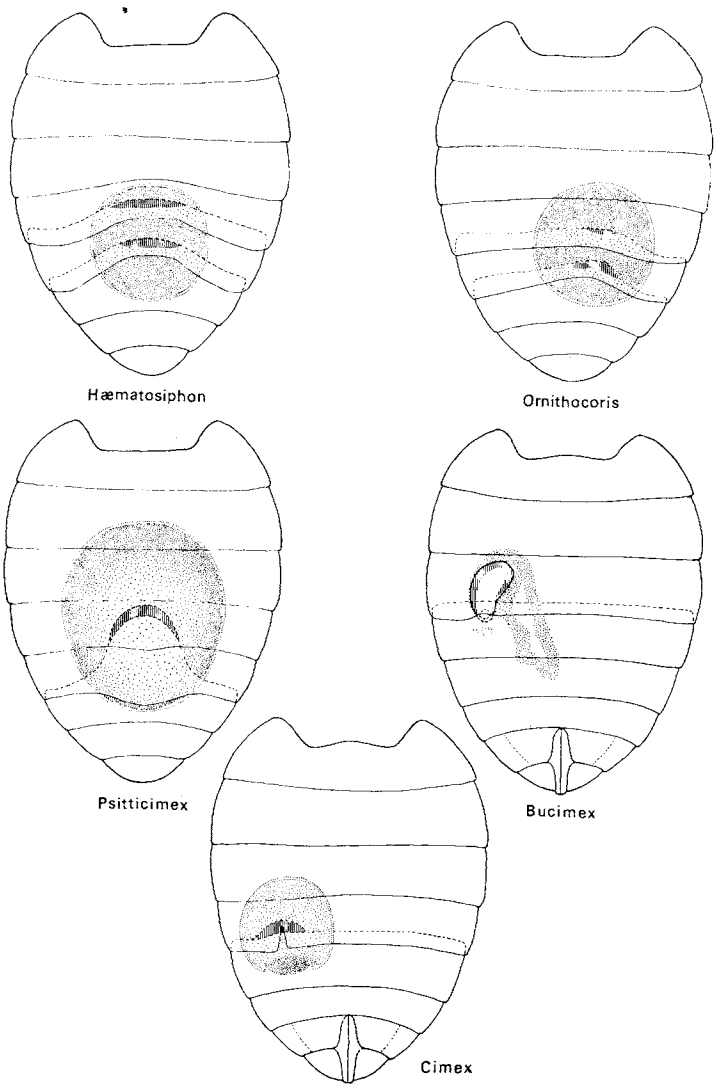

FIG. 7–10.—Structure and position of spermalege in *Haematosiphon, Ornithocoris, Psitticimex, Bucimex,* and *Cimex.*

rather well developed in *Haematosiphon inodorus,* decidedly smaller than the posterior swelling in *Ornithocoris toledoi* Pinto, vestigial and nonfunctional in *Caminicimex furnarii,* and is completely lacking in *Psitticimex uritui* (Lent and Abalos).

The localization likewise continues in the integumentary fold by reduction in breadth of the area occupied by the ectospermalege. The different widths of the latter in *Cimex* species, for instance, appear to correspond to more or less advanced stages in evolution.

At the time it becomes localized, the ectospermalege changes in structure and form. Originally it is formed by a simple hypertrophy of the endocuticle and of the integumentary epithelium, producing a swelling which is most often irregular as in *Afrocimex,* though occasionally regular and not very apparent as in *Aphrania vishnou* Mathur. In the course of the first stages of evolution, hypertrophy is accentuated and spreads to the exocuticle. It is accompanied by histological modifications which, before the first copulation, give to the structure of the endocuticle and the epidermis an irregular and vaguely pathological appearance, resembling the alteration of the integument in the proximity of a wound. The exocuticle becomes thick while remaining nearly unchanged in structure and forms an apparatus which seems to facilitate the intromission of the paramere. The serrate rows of spiniform processes arranged on the surface of the ectospermalege in *Cimex* and *Oeciacus* no doubt help to guide the male copulatory apparatus to the place where the integument is to be punctured.

In the highly localized ectospermalege of *Hesperocimex,* the exocuticle is very thick and forms a dark, globular, compact mass (Fig. 7–25d), at the center of which is found a slight funnel-shaped depression which is prolonged anteriorly in *Hesperocimex coloradensis* List by a slender canal. This exocuticular structure, quite comparable to the "omphalus" described in certain Anthocoridae (Carayon 1957), appears to represent the phyletic beginnings of the highly differentiated ectospermaleges of the type with "copulatory tubes." Like the latter, but with less efficiency, it assures the guidance of the paramere during copulation, thanks to the small cavity which the paramere at least partly traverses.

The copulatory tubes, which I described in the Anthocoridae: Anthocorinae (Carayon 1953b) and in certain Cimicidae (Carayon 1959), represent the highest evolutionary stages of the ectospermalege. In the final stages it is completely transformed into a conduit. Its distal extremity, blind in virgin females, leads into the mesospermalege, whereas its proximal end connects with a "vestibule"[4] communicating with the exterior. In simple copulatory tubes such as those of *Paracimex* (Fig. 7–11), the

[4] The vestibule, the most distinct of the diverse, purely morphological modifications in the vicinity of the ectospermalege, has the same origin as the latter, but its structure differs little, if any, from that of normal integument.

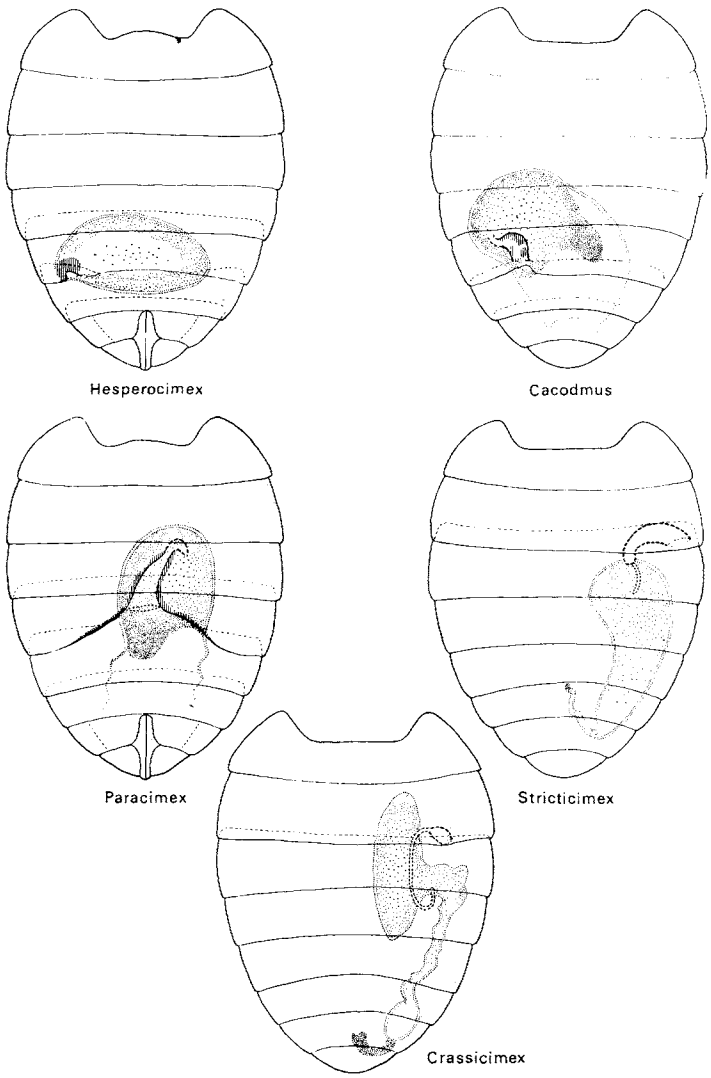

FIG. 7–11.—Structure and position of spermalege in *Hesperocimex, Cacodmus, Paracimex, Stricticimex,* and *Crassicimex.* In *Cacodmus* and *Paracimex,* dotted line extending wall of mesospermalege posteriorly represents "velum."

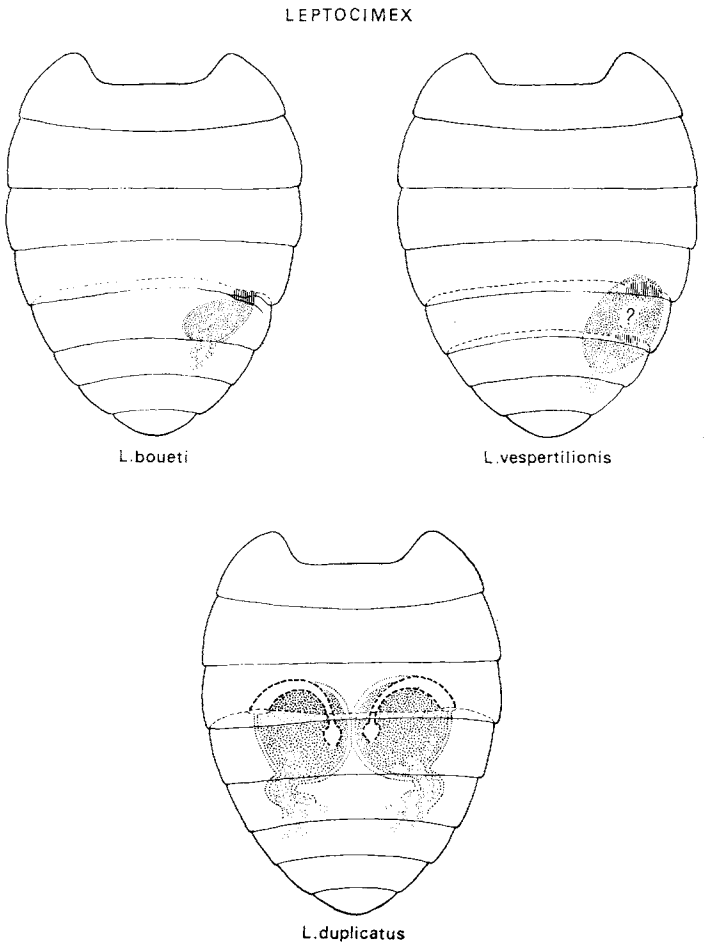

FIG. 7–12.—Structure and position of the spermalege in *Leptocimex*. Mesospermalege has not been observed in *L. vespertilionis*.

vestibule and the tubular ectospermalege are not distinctly separated. The complex copulatory tube of *Stricticimex* and *Crassicimex* (Fig. 7–11), on the other hand, is composed of 2 very distinct parts. One of these is basal and has a large lumen and a thick parietal cuticle comparable to that of the integument corresponding to the vestibule.[5] The other, called "diverticulum" by Carayon 1959, is apical and consists of a very slender tube and a thin, villous cuticular wall, no doubt corre-

[5] Designated as the "copulatory tube" in *Stricticimex brevispinosus* by Carayon (1959).

sponding to the ectospermalege. The structure of the latter seems to be considerably modified, regular, and lacking the almost pathologically bloated appearance found in the primitive types of ectospermalege. The initial tendency to hypertrophy seems to be reversed, so that the wall of the deep portion of the copulatory tube becomes much thinner than the integument from which it is derived.

When the ectospermalege has attained the evolutionary stage of the "copulatory tube," it may undergo duplication comparable to the anomalous case already described in *Cimex,* but it is constant in a given species. All the females in such a species thus possess 2 identical copulatory tubes placed symmetrically within the same intersegmental fold. Although I have seen many cases of such a duplication among Anthocoridae, only 1 has been encountered in Cimicidae—that of *Leptocimex duplicatus,* representing a genus in which the evolution of the spermalege seems aberrant and at times very rapid (Fig. 7–12).

The Mesospermalege

Primitively, as in females of *Afrocimex,* this formation consists of a vast, diffuse mass of amoebocytes, all alike and free or joined in rows. Situated beneath the integument where copulation occurs, this mass is much more extended than the corresponding ectospermalege. The next

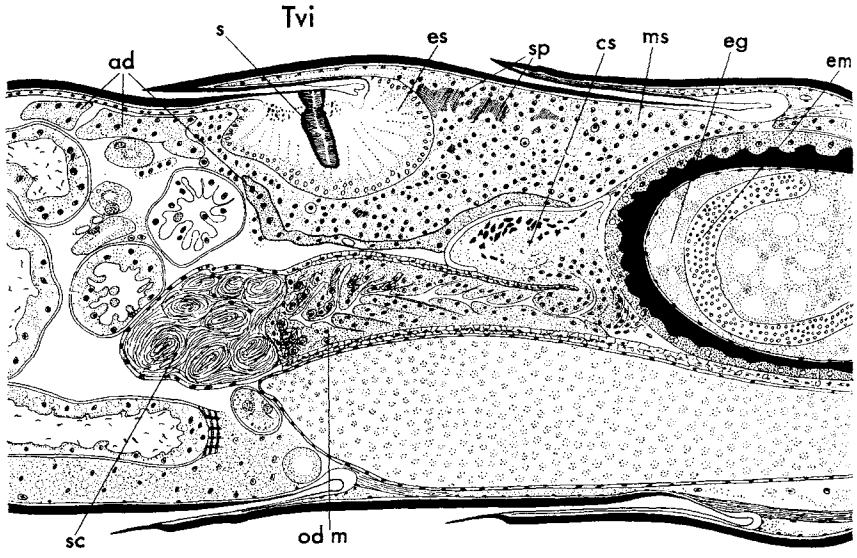

FIG. 7–13.—*Aphrania vishnou.* Portion of whole sagittal section of inseminated, gravid ♀. ad, adipose tissue; cs, seminal body; eg, egg containing embryo (em); es, ectospermalege; ms, mesospermalege; od m, mesodermal oviduct; s, trace of copulation; sc, seminal conceptacle; sp, masses of seminal plasma in mesospermalege; T vi, tergite VI.

evolutionary stage begins with a condensation and a progressive delimitation, of which *Aphrania vishnou* shows the first indications. In that species, the mesospermalege appears almost as primitive as in *Afrocimex* females, but its cells form a smaller mass and are much more strongly condensed in the vicinity of the ectospermalege. The ectospermalege is a simple swelling occupying almost all of the intersegmental membrane between tergites VI and VII (Fig. 7–23e). The periphery of the mesospermalege, however, remains diffuse and poorly delimited, although it is bordered here and there by a discontinuous adipose sheet (ad, Fig. 7–13).

A comparative study of the mesospermaleges of more highly evolved types indicates that this adipose sheet plays an increasing role in their organization and progressively acquires the characteristics of a dense envelope without lacunae. The adipose sheet surrounds the central cellular mass almost completely, evolves in structure little by little, covers the inner face of a basement membrane of increasing thickness, and terminates by merging completely with and forming the wall of the mesospermalege. Still poorly developed in *Cimex* and *Oeciacus,* for example, and somewhat more marked in the Haematosiphoninae, the differentiation of this wall almost completely masks its adipose nature; it becomes more pronounced in *Paracimex* and attains maximum development in the genera *Crassicimex* and *Stricticimex*.

In many cases, whatever its degree of differentiation, the wall does not circumscribe all of the central mass of mesospermalege, but leaves a portion of its posterior region free. This region is in direct contact with the hemocoel and projects more or less to form that which we have called the "conductor lobe" in *Cimex*.

The conductor lobe of the mesospermalege, where the amoebocytes are differently grouped and generally denser than elsewhere, appears only at an advanced evolutionary stage, thereafter tending to become more and more distinct. It is barely distinguishable in *Cimex* but is more developed in *Oeciacus* (Fig. 7–24b), and especially in *Paracimex* and *Cacodmus* (Fig. 7–11). In the latter 2 genera, the region of the hemocoel between the mesospermalege and the base of the genital ducts where the conductor lobe guides the spermatozoa is completely surrounded, or nearly so, by a membrane which I call the "velum." It is rather thick in certain places and has the structure of an adipose sheet; elsewhere it is tenuous and often difficult to see. The velum is nothing but the wall of the mesospermalege, detached posteriorly from the latter and extended posteriorly. It consists of a large enclosure where spermatozoa accumulate in large numbers over a long period of time before entering the conceptacles.

With the progressive differentiation of its wall, more clearly delimited in *Cacodmus* than in *Paracimex,* this enclosure comes to form most of

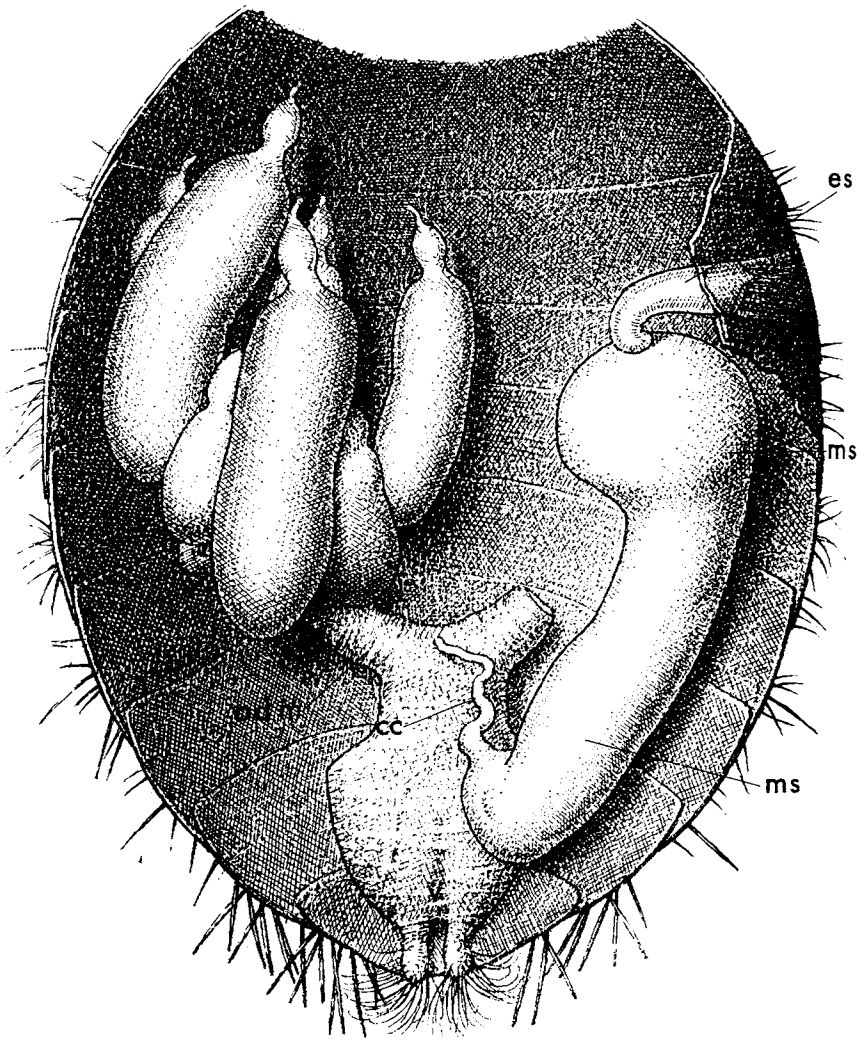

FIG. 7–14.—*Stricticimex brevispinosus*. Genital apparatus and spermalege in immature inseminated ♀. Other organs of abdominal cavity, including right ovary, have been removed, and only a fragment of dorsal abdominal wall remains, surrounding opening of ectospermalege. cc, conductor cord of spermatozoa; es, ectospermalege; ms, mesospermalege; od m, mesodermal oviduct; v, vagina.

the "reservoir" and "conductor cord," elements characteristic of the mesospermalege at the most advanced stage of its evolution.

The mesospermalege of *Stricticimex brevispinosus,* where such a stage is attained (Carayon 1959), appears as a highly individualized organ; it is oblong and lies in the right side of the abdomen from segments IV to VIII (Fig. 7–14). Anatomically, 3 successive portions may be distinguished from anterior to posterior:

a) a more or less swollen "bulb" near the dorsal surface of the abdomen. The distal extremity of the copulatory tube enters the anterior portion of the bulb, which opens posteriorly on the right side of the abdomen between tergites III and IV.

b) a subcylindrical "body" variably swollen in places but always smaller than the bulb. It extends posteriorly far into the abdomen while gradually approaching the ventral surface. It terminates above the right side of the vagina in a sharp bend directed anteriorly to the left.

c) the "conductor cord," an extension of the body of the mesospermalege, is clearly distinguished from the latter by its much smaller diameter. It looks like a slightly sinuous vermiform appendix the distal extremity of which is joined to the dorsal wall of the genital ducts midway between the bases of the paired oviducts.

Histologically the mesospermalege of *Stricticimex brevispinosus* occupies the entire length of a central region of variable diameter, completely surrounded by a parietal layer of regular thickness. This layer, the originally adipose nature of which is in no way recognizable, has a rather complex structure. It is covered interiorly from one end of the organ to the other by a thick basement membrane. The central region sometimes appears to be occupied by amoebocytes, most abundant and densely arranged in the "bulb." Posteriorly, these amoebocytes become less and less numerous and are entirely absent in the posterior portion of the "body" of the mesospermalege, a large, blindly ending cavity which serves as a reservoir for the spermatozoa. Behind it the parietal layer contracts abruptly, forming the basal portion of the conductor cord, in the center of which an axial filament of PAS-positive substance replaces the lumen. In the apical region of the conductor cord this filament is replaced by a series of closely joined amoebocytes which may be likened to a "conductor lobe."

In spite of its very different and more complicated form, the mesospermalege of *Crassicimex* (Fig. 7–15) is composed of the same elements as that of *Stricticimex* and, like it, undoubtedly represents a terminal evolutionary stage.

The peculiarities of the spermalege in certain Cimicidae lead one to think that they represent divergent evolutionary branches, especially in the genus *Leptocimex,* in which the ectospermalege is still quite simple (*Leptocimex boueti*) and must have undergone a rapid and unique

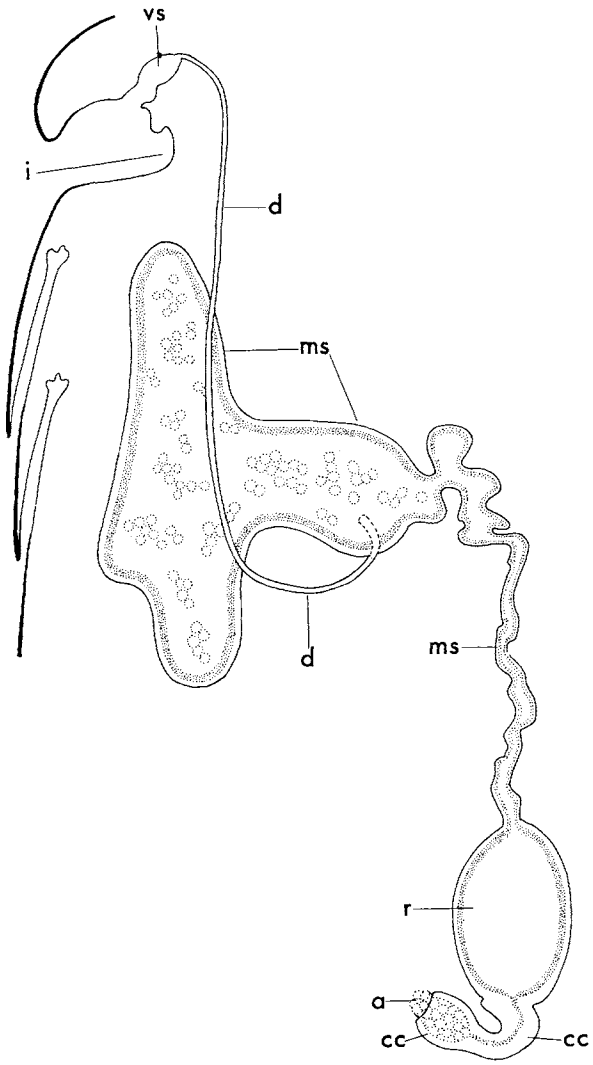

FIG. 7–15.—*Crassicimex sexualis*. Diagram of spermalege reconstructed from series of sagittal sections of abdomen. a, amoebocytes joined in mass extending outside distal bulb of conductor cord; cc, conductor cord; d, diverticulum of copulatory tube; i, intersegment (III–IV modified); ms, mesospermalege; r, reservoir of mesospermalege; vs, vestibule of ectospermalege; i, intersegment.

phyletic differentiation in forming double copulatory tubes (*Leptocimex duplicatus*). Except for its duplication in the latter case, the mesospermalege remains rather similar in the 2 species and is characterized by a special type of "conductor lobe." This is composed of amoebocytes joined in strands extending from the posterior region of the mesospermalege, passing through a lacuna of the wall (Fig. 7–25h), and dispersed into the hemocoel. In *Leptocimex duplicatus,* the rows of amoebocytes are confined for a long distance by a tubular prolongation of the wall which forms a sort of "conductor cord."

The species of the genus *Hesperocimex* also seem to represent an aberrant branch, as the structure of the mesospermalege is not comparable to that of any known in other Cimicidae. Some of the amoebocytes of the mesospermalege, joined in a regular layer, form a pocket which doubles the normal wall interiorly and is inserted on the periphery of the ectospermalege (Fig. 7–11, 7–18). The amoebocytes grouped in this manner differ from others (dispersed in the rest of the mesospermalege) in certain of their cytological characteristics and in their function, as they resorb only the sperm plasma.

As these examples indicate, the evolution of the spermalege in Cimicidae follows the same general tendency (localization, condensation, and delimitation, then formation of a lobe or conductor cord) but progresses along separate lines and at different speeds.

Although the ecto- and mesospermalege are not alike and may be present independently of each other, their evolution unfolds nearly correlatively; never, for example, does one observe a copulatory tube associated with a diffuse type of mesospermalege.

Paragenital Differentiations of the Reproductive System

The evolution of parts of the original reproductive system is correlated with that of the spermalege, but begins prior to it, since seminal conceptacles and syncitial bodies exist at least in *Primicimex cavernis,* where a differentiated spermalege does not yet occur.

In all probability the most primitive of the seminal conceptacles among Cimicidae are those of *Primicimex cavernis.* They are sacciform, voluminous, and have an irregular wall which, at least in inseminated females, appears spongy and is no doubt penetrable by spermatozoa at many points. The rather small number of amoebocytes present resemble those of the hemochrism and are modified only slightly after the arrival of the spermatozoa.

By an evolution already begun in *Afrocimex,* the walls of the conceptacles tend to become more regular and less lacunar. Usually the spermatozoa may cross only at a single location having a peculiar structure and situated, as in *Cimex,* usually in the anterior basal region.

Hesperocimex species are set apart by the fact that the mesospermalege

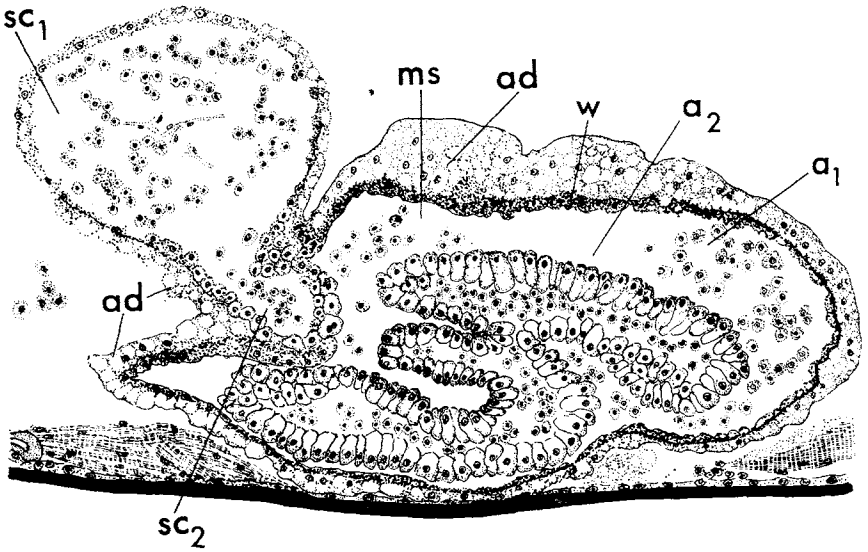

FIG. 7–16.—*Hesperocimex coloradensis,* virgin ♀. Sagittal section of mesospermalege (ms) where it enters ventral lobe (sc_2) of a seminal conceptacle (sc_1). Wall (w) of mesospermalege, surrounded by adipocytes (ad), is deeply depressed by ventral lobe of conceptacle. Note amoebocytes of mesospermalege—some not differentiated and dispersed (a_1) the others altered into large elements grouped to constitute an internal sack (a_2).

extends transversely on the inner ventral surface of the abdomen and joins the conceptacles (Fig. 7–16). There is no direct communication between the lobes and the mesospermalege, but there is a structural modification of their touching walls, across which the spermatozoa pass.

In the majority of other Cimicidae, the seminal conceptacles, like the spermodes (first appearing in *Afrocimex*) and the syncitial bodies, vary relatively little, at least in structure, which remains similar to that observed in *Cimex*. Moreover, some Cimicidae never have, at the base of the paired oviducts, sacciform diverticula in which the spermatozoa accumulate. These Cimicidae may be divided into 2 distinct categories.

In one, there is no formation of the wall of the genital ducts to replace the seminal conceptacles; the absence of the latter doubtlessly results from a secondary regression which is apparently related to the last stages of evolution of the mesospermalege and begins when the latter acquires the function of keeping spermatozoa in reserve over a long period of time. Thus, the seminal conceptacles show varying degrees of reduction in *Paracimex* and *Cacodmus,* in which the spermatozoa accumulate for a long time in the large enclosure which forms the "velum" behind the mesospermalege. The regression of the conceptacles is complete in *Stricticimex* and *Crassicimex,* in which the mesospermalege retains the sperma-

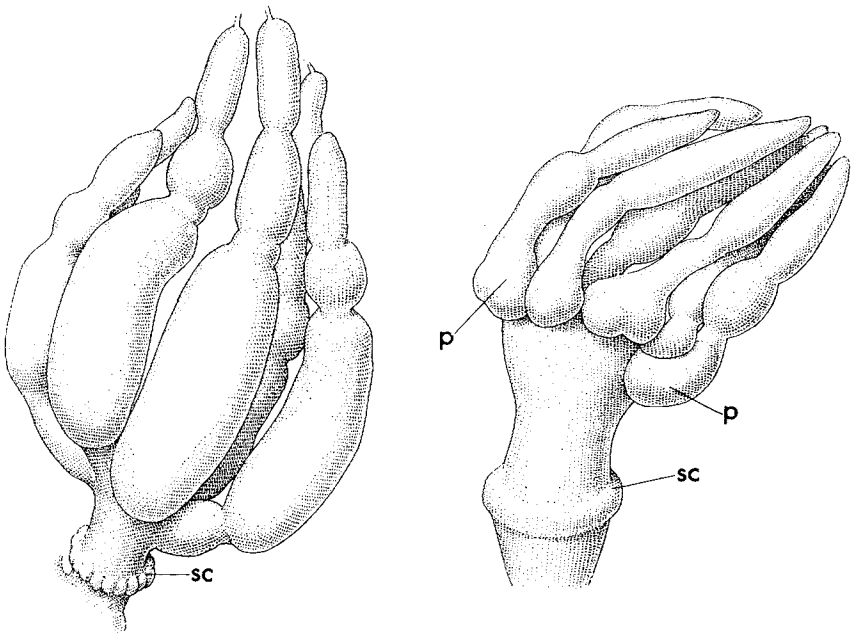

FIG. 7–17 (left).—*Haematosiphon inodorus*. Oviduct and right ovary of gravid inseminated ♀, showing annular "conceptacles" (sc).

FIG. 7–18 (right).—*Psitticimex uritui*. Oviduct and right ovary of immature inseminated ♀ of *Haematosiphon* group showing annular "conceptacles" (sc), different in conformation and structure from seminal conceptacles of other Cimicidae. Note pedicels (p) distended by masses of spermatozoa.

tozoa in reserve and liberates them a small amount at a time. This process is accompanied by a regression of the syncitial bodies and probably also of the spermodes.[6]

A completely different case is presented by members of the subfamily Haematosiphoninae, members of which also lack seminal conceptacles comparable to those of other Cimicidae. However, structures in which spermatozoa accumulate in abundance are present in the wall of the anterior genital ducts in that subfamily. In dissections, the paired oviducts appear surrounded by a clearly visible annular swelling having small, ovoid, regularly aligned protuberances in *Haematosiphon* (Fig. 7–17) and smooth and less distinct ones in *Psitticimex* (Fig. 7–18). These swellings may be considered to be reduced or slightly developed seminal conceptacles, but their structure is very peculiar and their volume, after insemination, changes little or not at all. On the other hand, the pedicels

[6] Spermodes cannot be considered to be certainly absent except by examination of the entire oviduct wall or of specially stained histological sections.

near the base of the ovarioles are transformed in inseminated females into whitish masses which are voluminous and dented, since they are distended by large quantities of spermatozoa (Fig. 7–18).

Histological sections of *Haematosiphon* reveal that the spermatozoa accumulate abundantly all along the walls of the anterior genital ducts from the annular swelling to the distal extremity of the pedicels, where they are especially numerous (Fig. 7–25e). Between the epithelium and the muscular tunic of the wall, they occur in a thick layer of special tissue, where their presence masks its complex structure. The tissue appears to be formed by cells without clearly distinct limits, forming a relatively wide, sinuous, anastomosed cord. The cells are enveloped by a thin membrane. This is almost certainly a case of highly developed spermodes which hypertrophy strongly toward the apex of the pedicels and toward their base around the paired oviducts, where they comprise the annular swellings. In section, their interior appears as a rather compact parenchyma, rich in lacunae and irregularly partitioned by abundant membranes; the entire formation recalls that observed in other Cimicidae, not in the conceptacles themselves, but a little deeper in the region of the wall where the spermodes start.

THE PROCESS OF INSEMINATION

Although the process of insemination is basically the same in all Cimicidae, its details vary mostly as a function of the progress of phyletic differentiation of the spermalege; the most primitive characters are seen in *Primicimex cavernis,* where differentiation has not begun, and also among other Cimicoidea with a nonexistent or poorly developed paragenital system.

During copulation, the *Primicimex cavernis* male injects a great quantity of sperm directly into the hemocoel of the female, where the spermatozoa disperse widely, some of them reaching the head and the extremities of the legs (Carayon 1954b). The remarkably intense and prolonged spermathemie seems to be permanent. It is seen during repeated copulations and the long period when the spermatozoa are in the blood. However, most of the spermatozoa disappear from the blood by congregating about the base of the genital system, then penetrating into the conceptacles through the ducts, which are undoubtedly of the multiple access type. One of the indirect but important routes or means of access is the posterior portion of the hemochrism, which joins broadly with the hemocoel. The other points of entry seem to be the lacunae in the conceptacle wall. After congregating in the conceptacles in large quantities, the spermatozoa continue their massive migration toward the ovarioles. They are very numerous all along the walls of the mesodermal genital ducts and occupy nearly all of the layers of the walls—the hemochrism, the muscular tunic, and an adjacent layer of amoebocytes mixed

with tracheae but not organized into spermodes. Finally, there are certain epithelial cells which the spermatozoa cross in reaching the lumen of the oviducts and the pedicels. The invasion of the syncitial bodies and the end of the migration in the ovarioles is no doubt accomplished as in *Cimex* and other Cimicidae.

Despite the absence of a mesospermalege in *Primicimex cavernis,* the numerous hemocytes in the blood lacunae resorb part of the spermatozoa and probably the seminal plasma as well. This resorption, however, seems minor considering the extent and duration of spermathemie. It certainly increases in intensity and efficiency with the grouping of the amoebocytes in primitive mesospermaleges like those in *Afrocimex* and *Aphrania.*

These primitive mesospermaleges, located to receive the sperm injected by the males, play the role of a filter. They retain and completely resorb the seminal plasma but allow all or nearly all of the spermatozoa to cross rapidly. The spermatozoa then disperse in the hemocoel but less widely and for a shorter length of time than in *Primicimex cavernis.*

The appearance of the mesospermalege and the progress of its phyletic organization leads to a progressive reduction and finally to the disappearance of spermathemie. The destruction of some of the spermatozoa by the amoebocytes of the mesospermalege seems to be an important factor in such a reduction. It is minor or lacking in *Afrocimex* and *Aphrania* but more apparent in *Cimex,* and it tends to increase throughout the evolution of the process of insemination, becoming very intense in *Stricticimex.*

The second, more important factor in the reduction of spermathemie is the "guiding effect" of the mesospermalege. When the mesospermalege is not or only slightly delimited, the spermatozoa leave at any point where the surface touches the hemocoel; this means of exit favors their dispersal. In the final stages of evolution, the wall surrounding the spermalege forms a barrier which allows the spermatozoa to leave only through the area nearest the posterior genital ducts, as shown for the *"Cimex"* type. It is only in the region of the ducts, often differentiated into a conductor lobe, that the wall forms either a lacuna or a structural modification permitting the passage of spermatozoa.

The spermatozoa are thus liberated as close as possible to the bases of the genital ducts. Nevertheless, the course which they take in the hemocoel always depends upon the position of the mesospermalege in the posterior extremity of the abdomen. In *Hesperocimex* the mesospermalege is transversely spread beneath the conceptacles and is in close contact with the ventral lobes into which the spermatozoa penetrate directly (Fig. 7–19). Such an arrangement suppresses spermathemie considerably before the components of the paragenital system have reached their maximum phyletic differentiation.

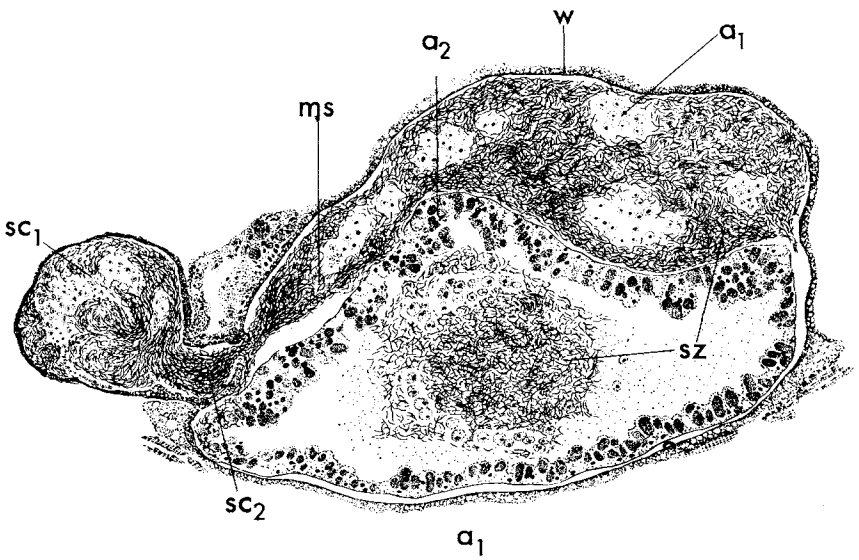

FIG. 7–19.—*Hesperocimex coloradensis,* recently inseminated ♀ (somewhat less enlarged than Figure 7–16). Sagittal section of mesospermalege (ms) where it enters ventral lobe (sc_2) of a seminal conceptacle (sc_1). Spermatozoa (sz) mixed with amoebocytes (a_1) are again seen at center of internal sack. Amoebocytes, with large inclusions, have resorbed seminal plasma; spermatozoa, lodged in greatest quantity between internal sack and wall (w) of mesospermalege, enter into ventral lobe (sc_2) of seminal conceptacle.

On the other hand, when the mesospermalege occupies a median or anterior position, its evolution continues; it tends to extend more and more posteriorly until it reaches the median oviduct. This elongation is mostly of the wall which first forms the velum of *Paracimex* and *Cacodmus.* The velum encloses most of the spermatozoa leaving the mesospermalege, maintaining them in groups. But it has more or less important lacunae across which a small quantity of spermatozoa pass into the neighboring hemocoel.

In *Stricticimex* and *Crassicimex,* not only is spermathemie suppressed, but the spermatozoa enter the walls of the genital ducts only in small numbers at a time. The process of traumatic insemination seems to have reached the end of its evolution, as it has resulted in the mesospermalege becoming a long and complex organ connecting the ectospermalege directly with the reproductive apparatus and has assumed multiple functions. In its anterior region, this organ resorbs the sperm plasma and a large proportion of the spermatozoa, whereas in its middle portion it retains the remaining unaltered spermatozoa in reserve. Finally, it conducts the spermatozoa to the wall of the median oviduct, slowing them

down considerably; their passage can be made only through the axis of the conductor cord. But this axis has at its base a filament of soft material forming a narrow inlet and distally a row of amoebocytes which resorb another portion of the spermatozoa. Only a few spermatozoa leave the conductor cord intact; they are found either in the immediate vicinity of the median oviduct (*Crassicimex*) or beneath its external envelope (*Stricticimex*).

ORIGIN AND SIGNIFICANCE OF TRAUMATIC INSEMINATION

On this very interesting subject I have restricted myself to several brief remarks inspired by observations made in Cimicidae and in many other Cimicoidea.

Numerous indications, especially the accidental injection of sperm into the hemocoel among various Cimicoidea having normal insemination, lead one to believe that traumatic insemination very likely had its origin in individual aberrations of the sexual behavior of males (Carayon 1964). Unfortunately, it is impossible to explain why and how such aberrations, pathological in themselves and in their consequences, have become the rule in species and in entire groups.

On the other hand, the course of the evolution of traumatic insemination, from the time it is first apparent in an evolutionary line, is made clear by the presently known facts. This evolution tends to bring about adaptations in the female which largely resemble defense reactions such as local integumentary hypertrophies, concentrations of amoebocytes, secretions of PAS-positive membranes, etc.

Up to a certain evolutionary stage, the spermaleges in the zone of copulation serve only to minimize the inconvenience of extra-genital insemination in the female. They thicken and restrict the integumentary area where the male copulatory organ penetrates, confine the sperm, and resorb the seminal plasma. As they become much more efficient in their function of "protection," the highly differentiated spermaleges also come to play a very important role in keeping in reserve and guiding the spermatozoa to the genital organs.

THE PARAGENITAL SYSTEM AND CLASSIFICATION

In Cimicidae, as in other Cimicoidea in which it exists, the paragenital system exhibits great diversity. Generally, it is constant within a species, is comparable among related species, and is rich in characters because of its often complex form. Therefore it appears to be of great taxonomic interest.

Yet, from what we know of its nature and its rapid evolution, caution should be exercised in drawing systematic conclusions based on its comparative study. Similarities in this system do not necessarily indicate

related forms but may result from the same evolutionary stage having been attained by different lines. For example, a double copulatory tube occurs in 1 species of Cimicidae, several Anthocoridae, and 1 Plokiophilidae[7]; its presence does not signify that these diverse Heteroptera are closely related. On the other hand, closely related forms may possess quite different types of paragenital systems if they belong to a line in which the evolution of this system is especially rapid. Such is the case in representatives of the genus *Leptocimex*.

Nevertheless, the characters of the paragenital system, provided they are studied closely and compared with other parts of the organism, are often valuable and reliable in the systematics of Cimicidae. Without going into detail, we shall examine several examples of information which these characters can furnish at various levels on the taxonomic scale.

AFFINITIES OF CIMICIDAE WITH RELATED FAMILIES

Traumatic insemination by "integumentary" copulation exists in 4 related families of Cimicoidea—Anthocoridae, Cimicidae, Polyctenidae, and Plokiophilidae, the first 3 of which are incontestably the most closely related.

Although possessing close affinities, Cimicidae and Polyctenidae are distinct families, having numerous morphological characters sufficient to separate them clearly. The manner of traumatic insemination serves only to confirm this separation. In Polyctenidae, according to my unpublished observations, the type of insemination is uniform and more primitive than in any known Cimicidae. Copulation takes place in an abdominal region lacking a spermalege or even its beginning. The spermatozoa are distributed widely and in great abundance in the hemocoel, where they remain for a long time before penetrating the walls of the genital ducts and without having accumulated in the seminal conceptacles or in analagous structures, which are completely lacking. The syncitial bodies are highly developed at the bases of the ovarioles and appear to represent the entire paragenital system. It is remarkable that in Cimicoidea as highly evolved in external form as these, traumatic insemination should remain at such a primitive stage.

The systematic position of Cimicidae in relation to the Anthocoridae is less clear. These 2 families, very unequal in the number and the diversity of representatives, appear so close that some authors have united them, claiming that there is greater difference between certain of the subfamilies of Anthocoridae than between the latter and the Cimicidae.

The general characters and evolution of the paragenital system in these

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[7] A double copulatory tube occurs in an undescribed African species representing a new genus of this family near *Embiophila* China.

2 groups do not argue in favor of such a union. It is true that in certain Anthocoridae the first stages of this evolution are comparable to those of Cimicidae, but a divergence soon appears and becomes accentuated in the final stage.

When it is phyletically well-differentiated, the mesospermalege of Anthocoridae is peculiar in being organized about an anterior diverticulum of the ectodermal genital ducts (Carayon 1954a, 1957). This diverticulum is part of the vaginal opening. It is detached toward the end of nymphal development after becoming narrow at the base. The important mesodermal elements which represent the spermalege, envelope it and form with it the "sperm pocket," into which an ectospermalege of either the "omphalus" or the "copulatory tube" type penetrates.

A sperm pocket is found in several different subfamilies of Anthocoridae but is completely lacking in Cimicidae. The paragenital system in Anthocoridae is more varied than that of Cimicidae but does not have mesospermaleges comparable with those of *Stricticimex, Crassicimex,* or *Leptocimex duplicatus.*

Because they are generally associated with a sperm pocket, the omphalus and the copulatory tubes of Anthocoridae are situated midventrally near the posterior extremity of the abdomen. On the other hand, the copulatory tubes of Cimicidae occur laterally in the middle or anterior region of the abdomen. These differences lead one to conclude that the Cimicidae and the Anthocoridae are no doubt derived from the same ancestral group but over the years have evolved separately so that today they represent 2 distinct families.

According to the characters of the spermaleges, the lyctocorine Anthocoridae of the genus *Xylocoris* resemble the Cimicidae most closely, but the different nature of their seminal conceptacles prevents considering them as very closely related.

CLASSIFICATION OF THE CIMICIDAE

Suprageneric Groupings

Many of the elements of the paragenital system provide evidence of affinities between genera. Thus they help to define groups having the value of subfamilies.

The seminal conceptacles in Haematosiphoninae are absent or greatly modified with respect to the special development of the spermodes. The latter play the role of a reservoir for the spermatozoa and probably constitute the annular swelling surrounding each paired oviduct. This is the only case in which the paragenital structures of the main reproductive system are of systematic interest, but lessened because the structures can be examined only with live or fixed specimens. Another group is also distinguished by the complete absence of conceptacles, but this is due to

secondary reduction (*Stricticimex, Crassicimex*) and thus is without great taxonomic value.

The spermalege, especially the ectospermalege, which usually may be studied in dry specimens in collections, furnishes more useful characters in the classification of Cimicidae. Often the cuticular modifications associated with the presence of the ectospermalege are easy to observe by the usual morphological methods, such as mounting in Canada balsam after treatment in KOH, but in such preparations the ectospermalege tends to disappear. To bring it completely into view, I stain the endocuticular structures with black chlorazol. With the abdomen still in KOH the dorsal wall is separated from the ventral wall and its internal surface is wet with a fine jet of an alcohol solution of black chlorazol. The ectospermalege then is blue, whereas the rest of the integument retains its natural color or remains uncolored. Most of the photographs reproduced here have been made from such preparations. Where the ectospermalege consists of a weak and regular endocuticular thickening (*Aphrania* and several Haematosiphoninae), the black chlorazol process should be followed by a histological examination.

The absence of a spermalege, verified by sections, is one of the peculiarities which sets *Primicimex cavernis* apart from all other Cimicidae. However, this does not, in itself, constitute a distinctive subfamily character, nor even a generic character judging by the situation in the Anthocoridae. In many genera of Anthocoridae, especially in *Xylocoris* and *Cardiastethus,* some otherwise related species possess an ectospermalege and others do not.

In contrast, the position of the ectospermalege is of greater and more reliable systematic significance. It is always either dorsal or ventral in groups of definitely related genera and may aid in defining subfamilies; the ectospermalege is dorsal in all the Haematosiphoninae (except the aberrant *Hesperocimex*) and ventral in all the Cimicinae.

Genera

In the family Cimicidae, the rather closely related species considered as being members of a single genus generally have similar spermalege occupying almost the same place in the abdomen. Thus the spermalege, and especially its cuticular portion with integumentary deformations accompanying it, usually provides interesting generic characters. It is stressed that these characters are proportionally more distinct as seen in the more highly differentiated ectospermalege. Also, in almost all Cimicidae in which they exist, the copulatory tubes allow precise generic discrimination. In fact, their placement as well as their general conformation is ordinarily similar in all representatives of a given genus, and quite different among different genera.

A remarkable, apparently unique exception in the Cimicidae occurs in

the genus *Leptocimex,* in which 2 species, *boueti* and *duplicatus,* have quite dissimilar ectospermaleges, though the 2 are closely related in other respects. The mesospermaleges of these 2 species have some common structural peculiarities, but that of *Leptocimex boueti* is less differentiated than *Leptocimex duplicatus* and no doubt represents the phyletic origin of the more complicated structure. The case of *Leptocimex* and analogous cases observed mostly among the Anthocoridae indicate that the spermalege undergoes an especially rapid evolution in certain closely related groups and in such cases loses much of its systematic interest at the generic level.

Species

The special conformation of the integument at the site of the ectospermalege varies within certain limits in representatives of the same genus. Generally, it is sufficiently constant in a given species and sufficiently different in related species to be of great value in specific diagnoses, as shown in the systematic portion of this work. Photographic illustrations are restricted to several examples, particularly those of *C. lectularius* and *C. hemipterus.* Their ectospermaleges are very clearly distinguished by their form (Fig. 7–22b, c) and structure (Fig. 7–20a, b).

In certain Cimicidae the value of the ectospermalege for specific determination may be limited by individual, or at least infraspecific, variability. The photographs of 3 females of *Caminicimex furnarii,* collected on the same date and from the same locality, provide an example of this variability (Fig. 7–21l, m, n).

The fissures or sinuosities of the hind margins of the abdominal segments adjacent to the ectospermalege vary less from one individual to another and are not secondarily altered by traumatic copulation. In many Cimicidae they also furnish specific characters which are more constant and likewise more apparent. In many cases, they and they alone have been described and figured by systematists as the "organ of Ribaga" or the "organ of Berlese."

DESCRIPTION OF THE PARAGENITAL SYSTEM IN VARIOUS GENERA

I have been able to examine the paragenital system in representatives of nearly all the genera of Cimicidae; the descriptions are arranged in the systematic order adopted in the present work. Available material and its state of preservation are shown in appropriate footnotes.

Primicimex[8]

The ecto- and mesospermalege are absent (Fig. 7–8). The area of

[8] Ten females of *Primicimex cavernis* fixed or preserved in alcohol; studied only in serial histological sections.

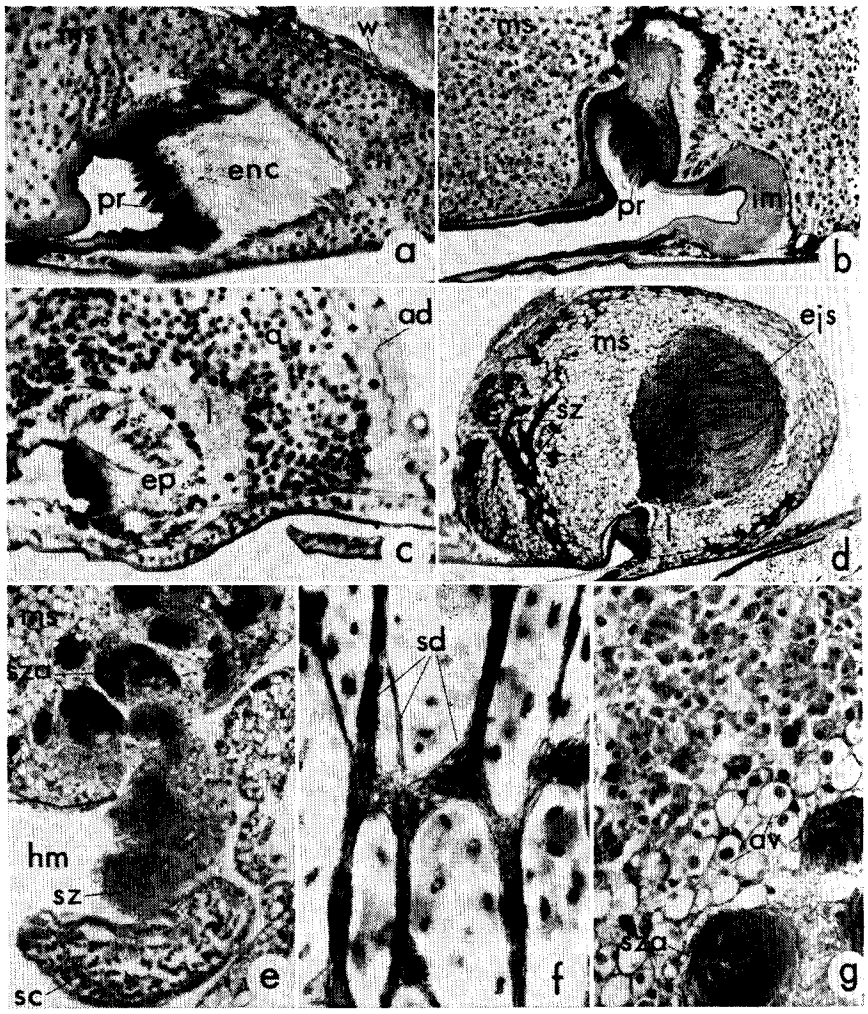

FIG. 7–20.—All photographs except f represent sagittal sections stained with hematoxylin-eosin-fast green. The first 4 are oriented with ventral surface at bottom and anterior to right. a, Ectospermalege and adjacent portions of mesospermalege (ms) in virgin adult ♀ of *C. lectularius:* pr, cuticular processes of the ectospermalege; enc, endocuticle of ectospermalege; w, wall of mesospermalege. b, *C. hemipterus,* same: im, intersegmental membrane. c–g, *C. lectularius,* spermalege. c, at imaginal molt; mesospermalege composed of spherical and moderately agglomerated amoebocytes (a), wall appearing as envelope of adipocytes (ad); ep, epidermis of ectospermalege; l, cavity of mesospermalege. d, spermalege 4 hours after copulation; a mass of ejaculated sperm (ejs) is shown at center of mesospermalege; dark trails (sz) represent bundles of spermatozoa moving toward periphery. e, posterior region of mesospermalege 5 hours after copulation; massive entrance of spermatozoa (sz) into hemocoel (hm); seminal

copulation is rather extensive, ill-defined, situated on the left of tergites IV to VI, and does not differ histologically from the neighboring integument. A band of dark brown pigment extends more or less the length of intersegment V–VI at the point where copulation is most frequent (Fig. 7–24a) but apparently is not structurally modified prior to copulation. Scars of copulation are very marked in histological sections (Fig. 7–8, 7–23h) but are much less distinct on direct examination of the abdomen.

A pair of spacious sacciform seminal conceptacles are inserted lateroventrally at the base of the paired oviducts; their walls are rather irregular, spongy, and penetrable by spermatozoa over a large area. The spermodes are very probably absent. Syncitial bodies are well developed.

Spermathemie is intense and prolonged, with extensive diffusion of spermatozoa within the female.

Bucimex[9]

The ectospermalege (Fig. 7–10) is situated in the right ventral side of the abdomen at sternites IV and V but is invisible or nearly so upon direct examination of the ventral face. After treatment in KOH and staining, it appears (Fig. 7–22g) in the form of a vast pocket longer than wide, oriented toward the front, and open at its base in the anterior border of sternite V. Just posterior to its orifice, which resembles a fish's mouth, a diffuse spot of dark brown pigment is found.

Histological sections (Fig. 7–24c) show that at the base of the ectospermalege the sternal integument is deeply invaginated and modified. In the dorsal portion of the pocket, the epidermis and the cuticle remain rather thin, except for a narrow but prominent dorsal protuberance of the exocuticle (visible as a black mass in Fig. 7–3). Anteriorly, the epidermal cells become especially long and compressed (Fig. 7–24d), whereas the cuticle is transformed into a thick, soft layer composed solely of endocuticle.

The mesospermalege, as observed by dissection, is a whitish, relatively voluminous, oblong organ with irregular contours, but it is distinct once the adjacent adipose masses have been cleared away. Histological examination shows it to be composed of dense tissue, made of polymorphic cells tending to become fibrous toward the periphery of the organ, where they separate incompletely and form a loose cortical parenchyma con-

[9] Four females of *Bucimex chilensis;* studied by dissection and a series of histological sections.

conceptacle (sc) still empty; sza, aggregates of spermatozoa. f, entire wall of exposed, stained (black chlorazol) mesodermal oviduct, showing spermodes (sd) filled with spermatozoa in inseminated ♀. g, diverse views of amoebocytes of mesospermalege in inseminated ♀; above, elements of dense cytoplasm; below, strongly vacuolated amoebocytes (av) containing a large inclusion and aggregates of spermatozoa (sza).

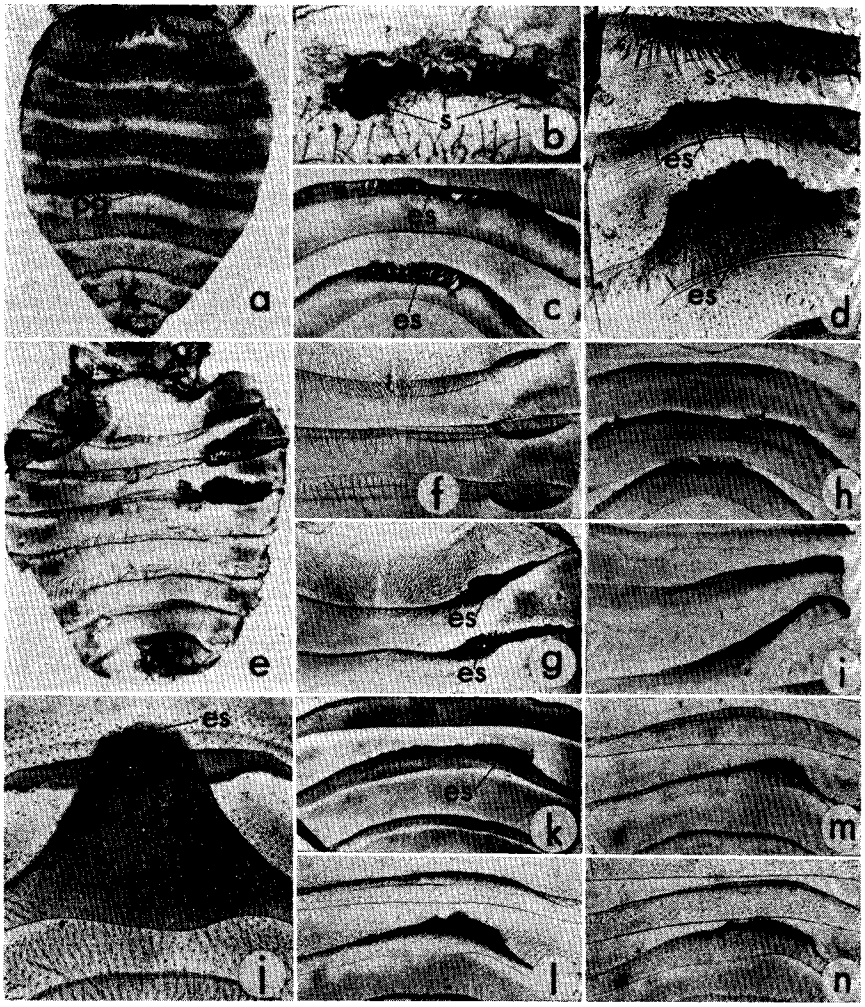

FIG. 7–21.—Ectospermaleges of various Cimicidae; external view of cleared abdominal wall treated with potassium hydroxide-black chlorazol, except a and b, in which integument was cleared in lactophenol. a, *Primicimex cavernis* ♀, dorsal wall of abdomen; no ectospermalege, but a band of dark pigment (pg) in portion of integument where copulations are most frequent. b, *Aphrania vishnou* ♀, many scars of copulation (s) marking location of ectospermalege in dorsal region of intersegment VI–VII. c, *Haematosiphon inodorus* ♀, medio-dorsal region of intersegments V–VI and VI–VII. d, *Latrocimex spectans* ♀, right side of abdominal sternites II to V showing the 2 unequal pads of ectospermalege and trace of copulation (s) in intersegmental fold II–III. e, *Afrocimex constrictus* ♂, ventral wall of abdomen with the 3 pads of ectospermalege. f, *Afrocimex leleupi* ♂. g, *Afrocimex leleupi* ♀, the 2 pads of ectospermalege. h, *Cimexopsis nyctalis* ♀, mediodorsal region of urites IV to VIII; ectospermalege of "Haematosiphon" type. i, *Synxenoderus comosus* ♀, right side of tergites IV to VII showing deformation

taining numerous infiltrated hemocytes (Fig. 7–24e). The mesospermalege lacks a wall or a well-defined covering. Topographically it is possible to distinguish 2 parts in the mesospermalege. One is ventral, encompassing a thick layer of ectospermalege, and the other, covering the preceding dorsally and extending farther toward the apex of the abdomen, is a pocket with a shallow central depression. This pocket is divided at its posterior extremity into 2 unequal lobes (Fig. 7–24c).

The seminal conceptacles are not very voluminous and are almost regularly spherical in inseminated females. Very thin through their base, they are attached to the latero-external face of the paired oviducts. The spermodes are almost certainly absent, judging from a study of histological sections and a preparation of the entire wall of the mesodermal oviducts.

The process of insemination can be reconstructed in large part. At the time of copulation, the paramere perforates the ectospermalege in the region where the cuticle is soft and thick. The traces of copulation, most frequent at the bottom and along the length of the dorsal surface of the pocket, appear as tortuous fissures without the usual deposit of brown substance, at least in the females examined. Some spermatozoa are dispersed in the cuticle, but most of them occupy the cavity of the dorsal portion of the mesospermalege. They quickly migrate in large numbers toward the periphery, where they fill the lacunae of the cortical parenchyma. Next they leave the mesospermalege, not through a fixed region, but through all points of its surface in contact with the hemocoel (Fig. 7–24f). There is a great abundance of tracheae in the hemocoel near the mesospermalege.

In spite of their initial dispersion, the spermatozoa are not widely distributed in the hemocoel and without doubt do not remain there very long. They move toward the apex of the abdomen and then penetrate the conceptacles, first on the right very near the posterior extremity of the mesospermalege. They have 2 routes of access. One is in each conceptacle wall, which, thin and continuous elsewhere, near the oviduct appears thick and pitted with lacunae through which the spermatozoa enter. The structure closely resembles that of *Primicimex* conceptacles. The other, indirect access route is the wall of the median oviduct, through which the spermatozoa penetrate and traverse the lateral lacunae of the external envelope. In *Bucimex,* the posterior extremity of this envelope seems to be joined to the wall of the genital tract, so that the hemochrism does not open into the base of the hemocoel as in *Cimex.*

The paragenital system of *Bucimex* does not resemble any of those

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of intersegmental folds. j, *Psitticimex uritui* ♀, ectospermalege (es) at bottom of vast mediodorsal pocket of intersegment VI–VII. k, *Ornithocoris toledoi* ♀, ectospermalege of intersegment VI–VII (es). l, m, n, *Caminicimex furnarii,* various views of ectospermalege in 3 ♀ from same collection.

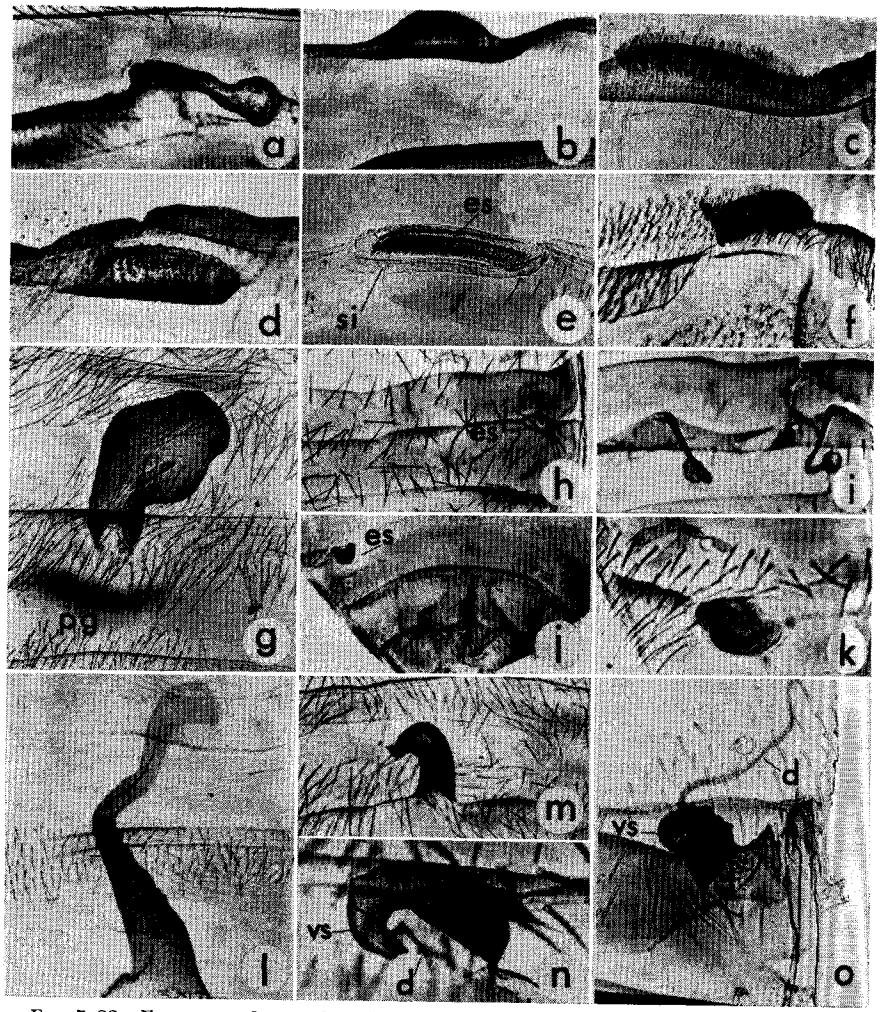

FIG. 7–22.—Ectospermaleges of various Cimicidae. KOH-black chlorazol preparations of abdominal walls of ♀. a, *Loxaspis seminitens,* medio-dorsal region of intersegment V–VI. b, *Oeciacus hirundinis,* right ventral side of intersegment V–VI. c, *C. lectularius,* same. d, *Cimex hemipterus,* same (♀ from equatorial Africa). e, *Cimex pipistrelli,* same; si, sinus and es, ectospermalege. f, *Bertilia valdiviania,* medio-ventral region of intersegment VI–VII. g, *Bucimex chilensis,* right side of sternites IV and V (note spot of dark pigment (pg) just posterior to orifice of ectospermalege). h, *Leptocimex boueti,* right side of tergites V and VI with ectospermalege (es). i, *Leptocimex duplicatus,* double ectospermalege formed of 2 symmetrical copulating tubes opening into dorsal region of intersegment V–VI. j, *Hesperocimex coloradensis,* posterior ventral wall of abdomen, showing position of ectospermalege (es). k, *Hesperocimex cochimiensis,* ectospermalege at greater magnification. l, *Paracimex setosus,* copulatory tube seen through cleared wall across sternites IV and V. m, *Cacodmus vicinus,* copulatory tube

found in other Cimicidae. It presents a peculiar mixture of primitive and evolved characters. In regard to its complex and well-defined form, the ectospermalege appears to belong to the "copulatory tube" type, although its structure is not highly differentiated. The mesospermalege appears to have attained a high degree of organization but, deprived of a conductor lobe and a well delimited wall, it allows the spermatozoa to diffuse into the hemocoel throughout its surface as in primitive mesospermaleges.

Two peculiarities, observed only in *Bucimex* and *Primicimex,* relate to the presence of a spot of dark pigment in the integument where copulation is accomplished, and the probably primitive absence of spermodes. Despite differences which are important in other respects, the characters of the paragenital system do not preclude the idea of a possible close relationship between these 2 genera.

Bertilia[10]

The ectospermalege, ventrally situated at the bottom of intersegment VI–VIII, is situated on the right side but very close to the median axis of the body. Examined after treatment in KOH and staining, it appears as a short transverse pocket, open somewhat obliquely toward the rear and, in its reverse loop, resembling a ship (Fig. 7–22f). At the level of this pocket, the strongly indented posterior border of sternite VI clearly shows a broad sinus.

In frontal histological section, the ectospermalege has the form of a half-open mouth (Fig. 7–24i); its upper lip, which corresponds to the anterior face of the pocket, is by far the thicker. It comprises 3 successive layers:

a) a modified exocuticle at the border of the cavity made of a row of tall, slender, brown lamellae tightly squeezed against each other. At places this layer is crossed by irregular masses the color of which varies from yellow-amber to black; these are the traces of copulation.

b) a clear endocuticle, thicker than the exocuticle, with an indistinct fibrous structure. The rather slender extensions of traces of copulation and of numerous scattered spermatozoa are evident here.

c) the epidermis, in which the cells, laid out over several rows, are embedded in the endocuticle adjacent to the long filiform processes.

The same layers are seen on the posterior face of the pocket but they

[10] A single female of *Bertilia valdiviana;* studied in an incomplete series of histological sections.

under left side of tergite VI. n, *Stricticimex brevispinosus,* copulatory tube under right dorsal region of intersegment III–IV; d, diverticulum; vs, vestibule. o, *Crassicimex pilosus,* copulatory tube, situated as in *Stricticimex;* diverticulum (d), displaced during preparation, is normally incurved posteriorly; vs, vestibule.

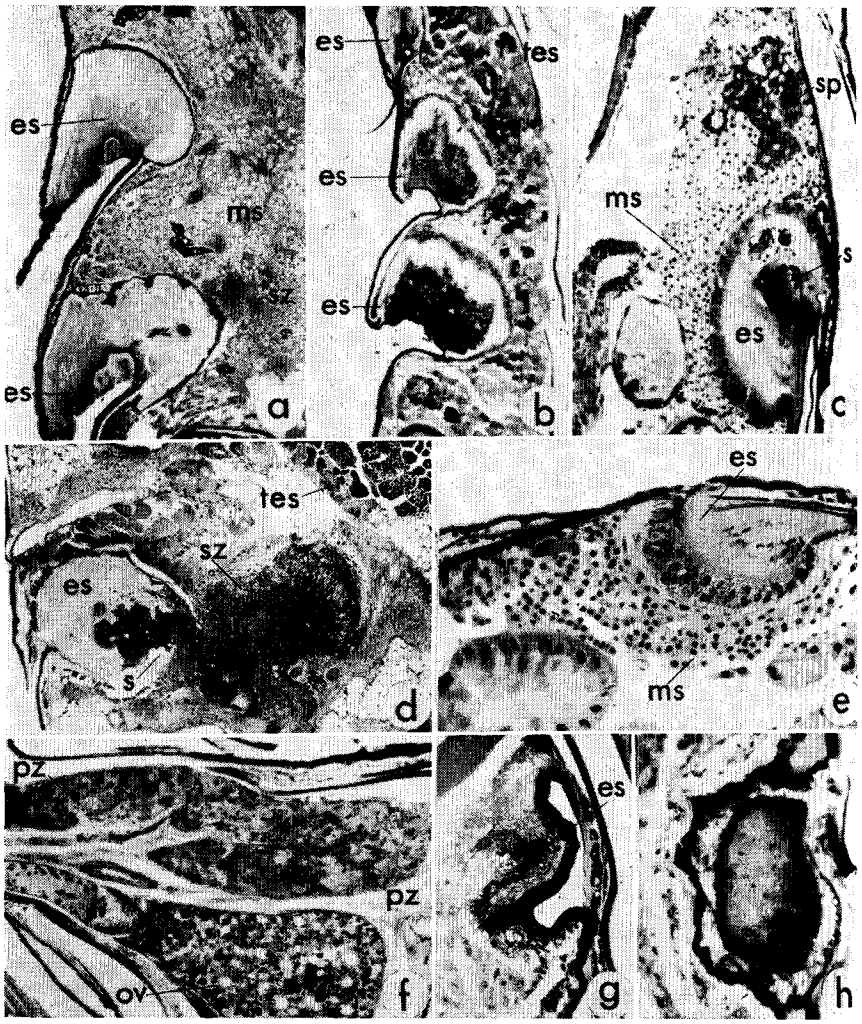

FIG. 7–23.—a, *Afrocimex constrictus,* sagittal section at level of spermalege in inseminated ♀; in mesospermalege (ms), black spots are adipocptes and gray spots are masses of spermatozoa (sz); es, ectospermalege. b, *Afrocimex constrictus,* ♂; significant traces of copulation in posterior pad of ectospermalege (es); tes, testis. c, *Aphrania vishnou,* recently inseminated ♀; distinct trace of copulation (s) and inclusions of seminal plasma in ectospermalege; seminal plasma (sp) abundant in mesospermalege (ms). d, *Afrocimex constrictus,* frontal section at level of ectospermalege in recently inseminated ♂; significant trace of copulation (s) in ectospermalege with voluminous mass of spermatozoa (sz) diffusing into hemocoel. e, sagittal section of spermalege in virgin ♀; mesospermalege (ms) lacking a wall. f, *Latrocimex spectans,* portion of sagittal section in inseminated ♀, showing one of the masses (pz) forming wall of anterior genital ducts; ducts filled with many spermatozoa; ov, oocyte. g, *Leptocimex boueti,*

are very much thinner and more modified in relation to the normal integument.

In spite of its well-defined and rather complicated form, the ectospermalege of *Bertilia* has a structure clearly related to the *Cimex* type, especially as shown by its exocuticle, the lamellae of which are undoubtedly homologous to the spiniform processes seen in *Cimex*.

The same relationship is indicated by other elements of the paragenital system. The mesospermalege of *Bertilia valdiviana* surrounds the ectospermalege in an apparently globular and rather compact mass, well delimited by a thin wall. Its structure resembles that in *Cimex*, but the abundant spermatozoa in the female examined are aggregated without being accumulated into balls or bundles. Seminal conceptacles and spermodes are present, but the syncitial bodies appear to be poorly developed.

Propicimex[11]

The ectospermalege is ventral and median, forming an irregular pad traversed by traces of copulation in the fold between segments V and VI. A broad sinus at the level of this pad is seen in the posterior margin of sternite V.

The following intersegment (VI–VII), although highly modified, should not be confused with the ectospermalege itself. Ventrally it forms a large, bellshaped curve opening posteriorly and apically nearly reaching the sinus. Along the distal and median part of this curve, the intersegmental fold disappears completely. There is an extensive, smooth surface at the posterior part of the ectospermalege on which the paramere probably slides without encountering any obstacle.

The integument of *Propicimex* may be strongly modified in form in the region of a weakly differentiated ectospermalege.

Cimex[12]

The paragenital system of representatives of this genus has already been described in detail; it will suffice here to summarize the principal characters. See schematic Fig. 7–1 and 7–10.

The ectospermalege is ventral and is situated on the right side, always between segments V and VI, and belonging to either the anterior margin of sternite VI or the intersegmental membrane. KOH preparations of the ventral wall of the abdomen show a transverse pad, finely striated or

[11] One female of *Propicimex tucmatiani* (Wygodzinsky): not in condition to be studied histologically but used for the examination of the cuticular portion of the ectospermalege.

[12] *C. lectularius* and *C. hemipterus;* studied both anatomically and histologically with an abundance of living material.

sagittal section at level of ectospermalege. h, *Primicimex cavernis* female, scar of copulation in center of tergite VI.

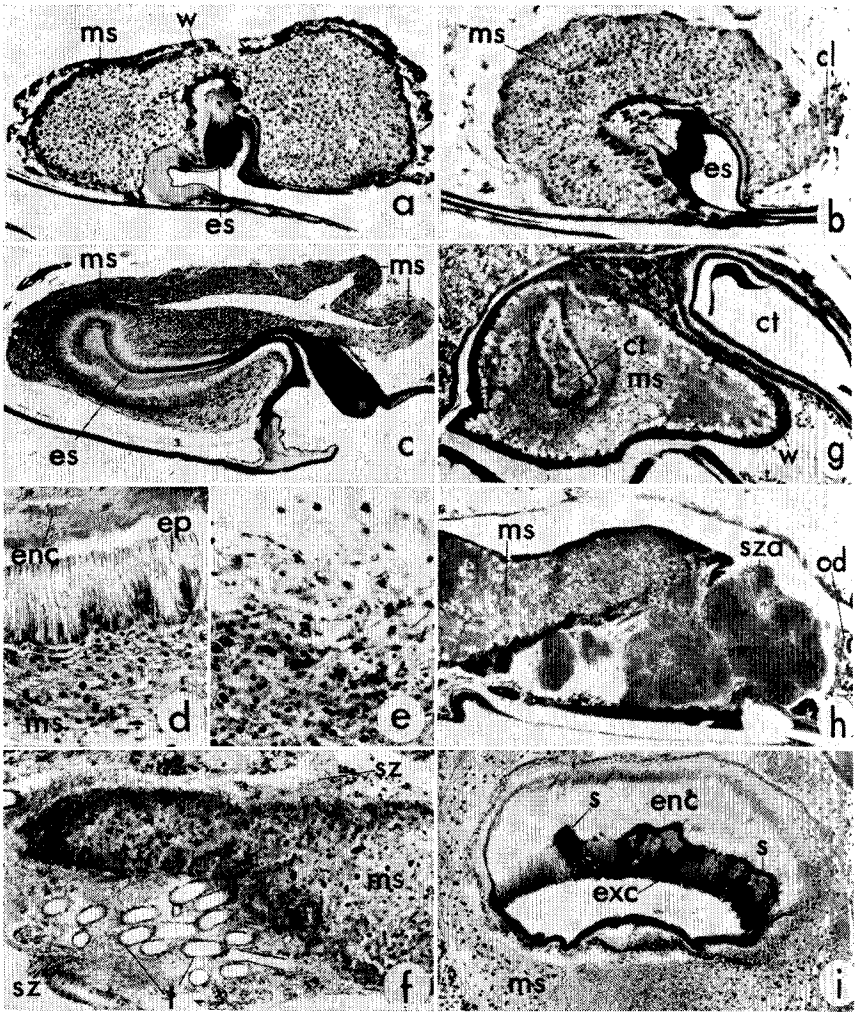

FIG. 7–24.—All figures except i represent sagittal sections of spermalege, with ventral surface at bottom and anterior to left. a, *Cimex hemipterus,* entire spermalege of virgin ♀; es, ectospermalege; ms, mesospermalege; w, wall of mesospermalege. b, *Oeciacus hirundinis,* as above; note well-developed conductor lobe (cl). c, *Bucimex chilensis,* as above. d, *Bucimex chilensis,* detail of wall of ectospermalege and adjacent part of mesospermalege (ms); note height of epithelial cells (ep) slightly detached from corresponding endocuticle (enc). e, *Bucimex chilensis,* detail of mesospermalege showing increasingly diffuse structure toward exterior (top of photograph). f, *Bucimex chilensis,* inseminated ♀, anterior lobe of mesospermalege surrounded by a cloud of spermatozoa (sz) diffusing into hemocoel where numerous, large tracheae (t) are seen. g, *Paracimex caledoniae,* inseminated ♀, anterior region of mesospermalege (ms), into which distal portion of copulatory tube (ct) penetrates; w, wall of mesospermalege.

bristling with little protuberances; its form, dimensions, and clarity of contour differ among species (Fig. 7–22c, d, e). A narrow sinus notches the posterior margin of sternite V adjacent to this pad. Structurally, the ectospermalege is characterized by exocuticular spiniform or spatulate processes; comparable processes seem to occur only in the related genus *Oeciacus.*

The mesospermalege is oblong and rather compact when not filled with spermatozoa (Fig. 7–24a). Its amoebocytes are not arranged in rows and often leave a free space in the vicinity of the ectospermalege. In the posterior part of the mesospermalege, closest to the right conceptacle, the structure and grouping of the amoebocytes change. There they are irregularly drawn out and each is surrounded by a slightly thickened membrane and interspersed with fine tracheae. Together, they constitute the "conductor lobe," which projects more or less to the exterior. The wall of the mesospermalege is absent or dissociated opposite this lobe, but is distinct and continuous elsewhere. It is composed of a thin layer, the originally adipose nature of which is hardly recognizable; on its scalloped internal surface a basal membrane is observed. Externally it is sheathed by an envelope of adipocytes which are slightly, if at all, modified.

The seminal conceptacles are sacciform and inserted lateroventrally near the base of the paired oviducts; their dimensions frequently differ from one side to the other after insemination. Spermodes and syncitial bodies are present.

Oeciacus[13]

The paragenital system in this genus is very closely related to that of *Cimex.* The differences observed between these 2 genera hardly seem more important than those existing between species of *Cimex.*

The ectospermalege is situated as in *Cimex,* but is in a widened part of the wall between segments V and VI, where it forms a short, slightly arcuate pad (Fig. 7–22b). Histological sections show that the exocuticle bears on its surface a central tuft of squamiform processes which are clearly tapered at the apex.

The mesospermalege is compact and more globular than in *Cimex,* even when void of spermatozoa. Its conductor lobe is quite apparent and often long (Fig. 7–24b), and is rather variable from one individual to

[13] Twelve females of *Oeciacus hirundinis* collected at the beginning of the hibernation period and studied from serial histological sections.

h, *Paracimex caledoniae,* inseminated ♀, posterior region of mesospermalege; a mass of spermatozoa (sza) have entered hemocoel across hole in its wall; od, oviduct. i, *Bertilia valdiviana,* ectospermalege and adjacent portion of mesospermalege (ms) in frontal section of inseminated ♀; exocuticle (exc) with scars of copulation (s).

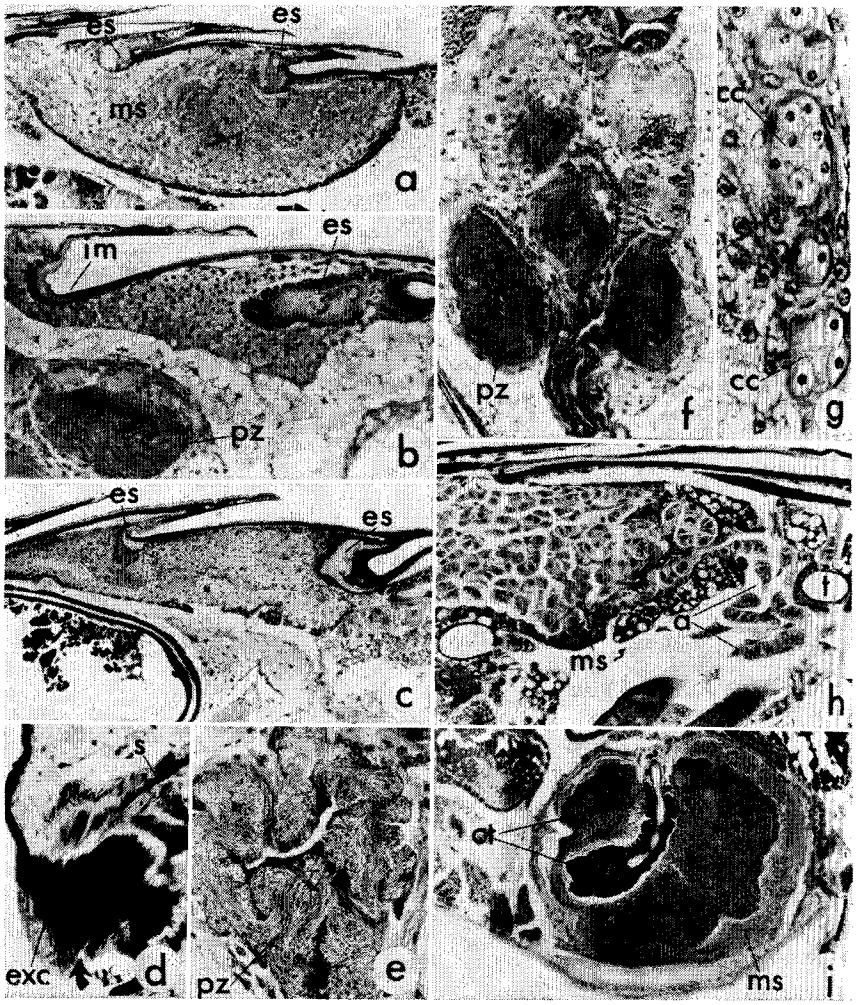

FIG. 7–25.—Fig. a, b, c, and h are sagittal sections; ventral surface is at bottom and anterior to left. Fig. e, f, g, and i are frontal sections, anterior at top. a, *Haematosiphon inodorus,* entire spermalege in inseminated ♀; anterior and posterior ectospermaleges (es) equally developed; ms, mesospermalege. b, *Caminicimex furnarii;* ectospermalege highly differentiated in intersegment VI–VII (es); membrane of preceding intersegment (im) only slightly thickened; pz, wall of genital duct filled with spermatozoa. c, *Ornithocoris toledoi,* same; anterior ectospermalege (es) functional but less well developed than posterior. d, *Hesperocimex coloradensis,* sagittal section (anterior at top) at level of ectospermalege; arrow indicates position of small canal in thick mass of exocuticle (exc); s, scar of copulation. e, *Haematosiphon inodorus,* many spermatozoa in wall of pedicel. f, *Caminicimex furnarii,* base of ovarioles and pedicels, the latter containing masses of spermatozoa (pz) more highly localized and otherwise distributed than in *Haematosiphon.* g, *Haematosiphon inodorus,* portion of a conductor cord (cc)

another. Its wall is provided with very voluminous nuclei identical to those of neighboring adipocytes.

The seminal conceptacles are nearly reniform and each is attached to a large portion of the circumference of a paired oviduct, leaving only the internal margin free.

All the females examined were collected in October and had undeveloped ovaries. Only one was inseminated, doubtless from a recent copulation, since spermathemie still persisted. Study of this female showed that spermatozoa were present in significant numbers in the antero-external region of the right conceptacle, having crossed the locally modified wall. The point of direct entry is quite different from that observed in *Cimex*. It is very near the posterior extremity of the conductor lobe. The right conceptacle contains a large quantity of spermatozoa whereas the left is nearly empty.

Paracimex[14]

The ectospermalege (Fig. 7–11) is ventral, situated on the right side near the center of intersegment V–VI. Although its dimensions are variable from species to species, its form is always that of a tube. The flared base of the tube opens at the apex of a curve described by the intersegment; the entire structure has the appearance of an inverted funnel. The tube is directed anteriorly on an incline or is incurved dorsally and toward the left (Fig. 7–22l). Its structure changes from the base to the apex. The pigmented and rather thick cuticle of the proximal portion has a layer of amber exocuticle; the epithelial cells are cubical. Distally the exocuticle is modified, then disappears so that only a thin layer of colorless endocuticle remains; the epithelial cells are tall and narrow.

The apical part of the tube penetrates the mesospermalege (Fig. 7–24g); it is blind in virgin females, but in inseminated females it has at its extremity an orifice which appears never to close again. It contains, as a portion of the lumen of the tube, cells (probably deriving from the mesospermalege) mixed with the rest of the sperm. The orifice results from a trauma occurring at the time of the first copulation, but not caused by the paramere.

In *Paracimex*, as in certain other Cimicidae, the length and the distorted form of the copulatory tube prevent the paramere, even when completely erected, from reaching the bottom. The pressure of the ejacu-

[14] Numerous females of *Paracimex borneensis* Usinger, *P. caledoniae*, and *P. setosus* Ferris and Usinger; studied by dissection and histological sections.

in virgin ♀. h, *Leptocimex boueti*, posterior region of mesospermalege (ms), showing cavity in its wall across which amoebocytes (a) are arranged in rows entering hemocoel; t, trachea. i, *Leptocimex duplicatus*, entire left spermalege in inseminated ♀; copulatory tube (ct), mesospermalege (ms).

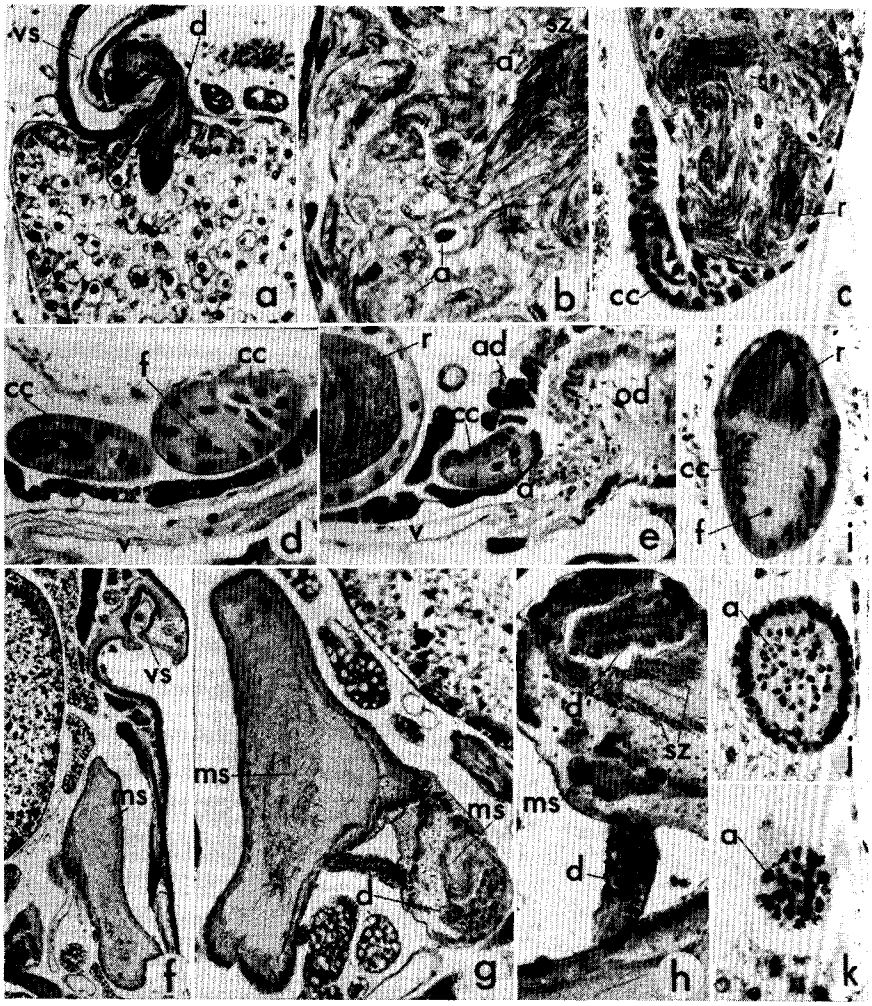

FIG. 7–26.—Sagittal sections; anterior at right in fig. d and e, at top in others. a–e, *Stricticimex brevispinosus:* a, vestibule (vs), diverticulum (d), and anterior region of mesospermalege. b, central region of mesospermalege showing spermatozoa (sz) mixed with variously modified amoebocytes (a). c, posterior region of mesospermalege serving as reservoir (r) and conductor cord (cc). d, 2 sections of conductor cord, the right one showing PAS-positive axial filament (f). e, distal extremity of conductor cord inserted in adipose tissue (ad) covering median oviduct (d); several amoebocytes (a) in axial region of cord; r, reservoir of mesospermalege; v, vagina. f–k, *Crassicimex sexualis:* f, inseminated ♀; vestibule (vs) in modified intersegmental membrane III–IV; ms, mesospermalege. g, anterior region of mesospermalege (ms), where it penetrates diverticulum (d) of copulatory tube. h, diverticulum under higher magnification; below, a section of its free portion; above, a section of its extremity plunging into mesospermalege; i, j, k, sections of conductor cord at different levels. i, its bent basal region

lated sperm probably ruptures the wall at the apex of the tube where resistance is least.

The mesospermalege is oblong and variable but distinct in contour. It is situated in the center or a little to the left against the internal face of the ventral wall and extends parallel to the axis of the body from urite III–VI.

In sections, a central mass and a wall are very clearly distinguished. The central mass is composed of more or less agglomerated cells all of which are spherical and similar in the developing organ but which become polymorphic at the imaginal moult. The posterior third or quarter of the central mass, which differs from the rest by its densely grouped cells, constitutes the conductor lobe. Its wall varies in thickness, probably within the same individual, and is composed of 2 cellular strata in close juxtaposition. One of these directly surrounds the central mass; its scalloped internal face bears a rather important layer of PAS-positive substance which represents a hypertrophied basal membrane. The external cellular stratum, often thicker and less regular than the preceding, has almost the same structure in the anterior region of the mesospermalege, but posteriorly it gradually assumes the original thickness and appearance of an adipose envelope. At the conductor lobe where these elements appear as typical adipocytes charged with enclosures, it tends to deviate more or less from the mesospermalege and initiates the formation of the "velum," a posterior expansion of the external adipose envelope of the mesospermalege. The internal or parietal layer has a distinct lacuna on the ventral surface near the posterior extremity of the conductor lobe. This is in direct contact with the hemocoel, as its external adipose envelope is broadly opened or interrupted. The anterior region of the mesospermalege receives the sperm during copulation, where some of the spermatozoa are resorbed by the amoebocytes. The other spermatozoa migrate in a posterior direction and temporarily form large masses in the central region. Infiltrating among the cells of the conductor lobe, they cross it, then leave by the lacuna described above and, in the hemocoel, form subspherical aggregations grouped in an often voluminous mass (Fig. 7–24h).

Extending posteriorly to the bifurcation of the oviducts, this mass is partially circumscribed, especially laterally, by the velum. With the velum, the walls of other abdominal organs such as the digestive tract contribute to the delimitation of a nearly closed area where the accumulated spermatozoa remain for a long time.

As a consequence of the role this formation plays as a reservoir, the seminal conceptacles tend to be reduced in the genus *Paracimex*. They

is continuation of reservoir of mesospermalege (r) and has PAS-positive axial filaments (f). j, its middle region bears a central mass of amoebocytes (a). k, mass of amoebocytes is no longer surrounded by wall in distal extremity.

remain well-developed in *Paracimex setosus,* in which they are composed of 2 globular sacs broadly attached to the latero-external faces of the paired oviducts, but in *Paracimex borneensis* and *Paracimex caledoniae* they are represented solely by 2 slight dilations of the hemochrism.

The spermatozoa penetrate the walls of the oviducts by following the same route as in *Cimex,* but some appear to infiltrate through other places also, notably at the bifurcation of the paired oviducts. The spermodes of inseminated females contain a great number of spermatozoa, which are sometimes also observed in the hemochrism of the anterior genital tracts.

Cacodmus[15]

The ectospermalege is dorsal, appearing as a tube that opens basally on the right side in the intersegment VI–VII. This tube, the form and pigmentation of which vary according to the species considered, is generally short, broad, and subcylindrical in its proximal portion. Directed anteriorly, it narrows and curves abruptly inward distally, appearing as a hook turned toward the exterior (Fig. 7–22m).

From sagittal sections it has been determined that the ectospermalege bends in a ventral direction and almost immediately penetrates the mesospermalege joined to the internal face of the dorsal wall of the abdomen. The structure of the tube does not differ greatly from that of the integument and changes little from one end to the other. There are, however, several inequalities in the thickness of the cuticle and epidermis. The cuticle bears very small oblique microtrichia and the epidermis is composed of cells which are generally taller than broad. Among the inseminated females examined, the distal extremity of the tube is open and several cells or the remainder of the sperm occupy its lumen.

The mesospermalege is organized as in *Paracimex,* from which it differs in form, position, and details of structure. Its central mass is composed of 2 morphologically and histologically distinct parts. One of these, much the more voluminous, is situated in the abdomen to the left at tergites IV–VIII; the ectospermalege is embedded there almost to the center. There is a group of polymorphic cells, dispersed for the most part and not grouped except at the periphery. On the right side of this group is found the other and more compact portion of the mesospermalege, the conductor lobe. It has the form of a thick cord, longer than broad, which is directed obliquely toward the right posterior ventral region of the abdomen.

Two cellular envelopes, similar to those in *Paracimex,* enclose the principal mass of the mesospermalege, except for its right side where the internal envelope stops; the external envelope swerves widely from

[15] Eight females of *Cacodmus vicinus* Horvath preserved in alcohol without previous fixation and difficult to study histologically; only 2 specimens have furnished the complete series of sections. The scheme of the entire spermalege is shown in Fig. 7–11.

the mesospermalege and extends approximately in the same direction as the conductor lobe to form the velum.

Better developed and apparently less lacunous than that of *Paracimex,* the velum of *Cacodmus* delimits a large portion of the enclosure where the spermatozoa leave the spermalege and accumulate in abundance in the form of subspherical aggregates. More completely closed than in *Paracimex,* this enclosure appears to extend to the conceptacles and to have an outlet into each of them, although the available histological sections do not permit confirmation of this observation. Nevertheless, it is certain that the spermatozoa contained in the enclosure enter directly and massively into the conceptacles which exist in *Cacodmus vicinus* but are little developed there and serve for passage rather than a reservoir for the spermatozoa. On the other hand, the spermatozoa occupy the spermodes in great numbers.

Aphrania[16]

The ectospermalege (Fig. 7–9) extends into the bottom of the fold between segments VI and VII on nearly the entire width of the dorsal abdominal surface, but it is very difficult to see either by direct examination or in cleared preparations of the abdominal wall. Its presence is indicated in inseminated females by numerous irregular, blackish-brown spots aligned under tergite VI. They are the traces of copulation (Fig. 7–21b), which disappear under treatment with KOH and appear as holes in the integumentary cuticle.

Histological study reveals that the ectospermalege, normally hardly visible, is a regular, nonpigmented pad resulting from a simple thickening of the intersegmental membrane, of which only the endocuticle and the epidermis are hypertrophied and without other significant structural modification (Fig. 7–13, 7–23c). The traces of copulation, distributed along the pad, are more numerous and marked on the left side; in histological sections they appear as sinuous fissures or cavities crossing the endocuticle obliquely; a yellow-amber to black substance fills them and the rest of the sperm is often observed there (Fig. 7–13, 7–23c).

The mesospermalege is represented by a delicate mass situated beneath tergite VI along the ectospermalege. It is best developed anterior to the latter, especially on the left side where it extends to intersegment V–VI (ms, Fig. 7–13). Its cells are densely grouped against the integument and in the center of the mass; they are less cohesive at the periphery where some, aligned in rows, extend to rather distant parts of the surrounding hemocoel. No actual wall, except for a very discontinuous adipose envelope (ad, Fig. 7–13), encompasses them completely.

After copulation the spermatozoa cross the mesospermalege rapidly,

[16] *Aphrania vishnou* studied histologically thanks to an abundance of fixed material.

as usually so few are found. On the other hand, significant masses of seminal plasma are observed there (sp, Fig. 7–13, 7–23c). The mesospermalege cells, quite comparable to pericardial cells, resorb the seminal plasma little by little.

The seminal conceptacles, located just beneath the mesospermalege, are voluminous, unequal, and usually dorsal, with a pedicle attaching each to the lateral wall of the oviducts. The spermatozoa leaving the mesospermalege have thus only a short trip in the hemocoel in order to reach the conceptacles. Some of them fill the conceptacles, which they penetrate massively, not as in *Cimex* but apparently across a large dorsal lacuna in the wall. Their entrance inhibits the penetration of some others, which accumulate exteriorly around the conceptacles in an agglomerated globular mass.

In *Aphrania,* the spermatozoa do not seem to use the access route at the base of the hemochrism; nevertheless, they are numerous anterior to the latter, sometimes as far as the pedicels. They are always plentiful in the spermodes.

Loxaspis[17]

The ectospermalege is dorsal and appears as a transverse pad, irregular and sinuous, situated at or near the middle of intersegment V–VI. Its form is variable and more or less elongated on the right side depending upon the species considered. In *Loxaspis malayensis* it appears as indicated in Fig. 7–22a. The intersegmental membrane is slightly hypertrophied and modified chiefly by the presence in the cuticle of a pigmented layer which becomes thicker from left to right. This layer, very irregular in form and varying in color from yellow-amber to black, very closely resembles a great "trace of copulation"; it is traversed at many points by tortuous fissures filled with spermatozoa. Its exact nature can be determined precisely only by examination of a virgin female, but it probably represents a layer of exocuticle altered secondarily by the partially confluent traces of copulation.

The mesospermalege is very voluminous, extending from urite IV nearly to VII or VIII and occupying almost the entire width of the abdomen. It is composed of a great quantity of identical cells, densely grouped in some places and separated in others, and surrounded by a nearly continuous envelope of unmodified adipocytes. In the females studied, numerous globular aggregates of spermatozoa are dispersed in the midst of the mesospermalege, which likely serves as a reservoir.

The seminal conceptacles are small and contain relatively few spermatozoa. It has not been possible to study their structure, which seems

[17] Two females of *Loxaspis malayensis* Usinger in alcohol; only one well preserved histologically; complete series of sections, but damaged in places.

rather peculiar, nor the mode of entry of the spermatozoa, which leave in packets close to the mesospermalege.

The wall of the mesodermal genital ducts in *Loxaspis* is remarkable for the copious secretion which produces its epithelium. The wall contains many spermatozoa, some of which filter into the muscular tunics and some occupy the hemochrism and the spermodes.

Stricticimex[18]

The ectospermalege is of the "copulatory tube" type, occupying a dorsolateral position at the junction of tergites III and IV not far from the right margin of the abdomen. It consists of 2 successive parts, morphologically and histologically quite distinct. One of these, the "vestibule," is a deep, broad, tubular, transverse pocket open on the right side in the intersegmental fold and progressively narrowed and incurved like a hook on the opposite side (Fig. 7–22n). The vestibule wall has a cuticle of nearly the same structure and the same thickness as that of the neighboring integument, but its epithelial stratum, clearly hypertrophied in relation to normal epidermis, has subcylindrical cells where, after insemination, vacuoles and eosinophilic inclusions are seen.

The other part of the copulatory tube, the "diverticulum," is a slender, subcylindrical conduit. It originates at the distal region of the vestibule, describes a curve in the shape of a shepherd's crook, proceeds posteriorly, and penetrates deeply into the mesospermalege (Fig. 7–26a). The diverticulum, the lumen of which is not more than several microns in diameter, has a very thin cuticular intima. It is clearly visible in KOH preparations only after staining (Fig. 7–22n). Under sufficient magnification, the cuticle exhibits a covering of slender processes exteriorly. In histological sections, the epithelium of the diverticulum appears to consist of a layer of tall, narrow cells with basal nuclei. Following inseminations, large vacuoles with eosinophilic inclusions and several spermatozoa are observed. The first insemination produces an opening in the posterior extremity of the diverticulum, which is blind in virgin females.

The mesospermalege is complex, presenting upon dissection the appearance indicated in Fig. 7–14. Its general characters have already been described. It is composed of 3 successive regions which are morphologically, histologically, and physiologically distinct: a) an anterior one corresponding roughly to a bulb, into which the sperm is injected and where resorption of the seminal plasma takes place at the same time as the destruction of some of the spermatozoa (Fig. 7–26b); b) a central region serving as a reservoir for the spermatozoa which have not been destroyed (r, Fig. 7–26c); and c) a "conductor cord" extending from

[18] *Stricticimex brevispinosus* studied by dissection and serial histological sections from numerous fixed specimens. Paragenital system as in Fig. 7–14 and schematically as in Fig. 7–11.

the central region and introducing the spermatozoa little by little into the wall of the median oviduct (cc, Fig. 7–14, 7–26d, e).

Seminal conceptacles and probably the spermodes are absent. Syncitial bodies are not differentiated.

Leptocimex[19]

The spermaleges of the species studied, schematically represented in Fig. 7–12, are so different that they are described separately.

Leptocimex boueti.—The ectospermalege is dorsal and situated very close to the right side of the abdomen in the wall between segments V and VI. Its small size and slight differentiation render it barely apparent. In KOH preparations of the dorsal wall it appears as a vaguely quadrangular or oval mark (Fig. 7–22h). Histological sections show that the integument is hypertrophied and slightly deformed and that it consists of a very short pad projecting to the center of a depression (Fig. 7–23g). The exocuticle, irregular and distinctly thicker than that adjacent to it, has small, scattered protuberances.

The mesospermalege, not very voluminous, is an oblong sac attached below the integument at the periphery of the ectospermalege and oriented obliquely toward the apex of the abdomen. Its regular and continuous wall, except for a small opening at the posterior extremity, is formed from a thin layer of flat cells covered internally by a fine basal membrane and surrounded externally by an envelope of adipocytes having several lacunae. Inside the sac in virgin females a rather dense mass of cells is observed. Nearly all of them are aligned in more or less tortuous rows, several of which leave by the posterior orifice (Fig. 7–25h), and are abundant posterior to the mesospermalege and found dispersed far from it in various places in the dorsal region of the abdomen. They possess all the characters of pericardial cells, including the ability to absorb Trypan blue.

Thus the mesospermalege of *Leptocimex boueti* results from a local concentration of pericardial cells. This is neither an exception nor a contradiction to the idea that the essential components of the mesospermalege are amoebocytes, as the latter are capable of a variety of secondary differentiations and are related to pericardial cells. It is common elsewhere that the elements of dorsal mesospermaleges are arranged in rows and resemble pericardial cells.

After copulation, the mesospermalege of *Leptocimex boueti* contains masses of spermatozoa which are never aggregated in spheres. These masses disperse the rows of cells, and for a short time form voluminous vacuoles with large central inclusions. The resorption of seminal plasma appears to be intense and brief. Some of the cells, the contours of which

[19] Anatomical and histological study of many specimens of *Leptocimex boueti* and of 8 ♀ of *Leptocimex duplicatus*.

become obscure, probably destroy some of the spermatozoa also. However, many spermatozoa leave the mesospermalege by the posterior orifice and form sheets and streams and pass to the conceptacles without being widely distributed in the hemocoel.

The relatively small, ovoid seminal conceptacles of *Leptocimex boueti* have, on the interior face, a pedicle connecting them to the oviducts. The stream of spermatozoa penetrates into the conceptacles across lacunae in the anterior wall of the pedicle, where they also enter the hemochrism surrounding each paired oviduct. The duct of the posterior hemochrism surrounding the median oviduct does not seem to be used.

Leptocimex duplicatus.—The spermalege is completely divided into 2 symmetrical parts with respect to the median plane of the body without any connection between them.

The ectospermalege is dorsal, annexed to intersegment V–VI, and formed by a pair of symmetrical copulatory tubes of a special type. KOH preparations of the dorsal wall of the abdomen (Fig. 7–22i), show each of these tubes to be rather slender, nearly cylindrical, and originating in a shallow triangular recess in the intersegmental membrane. The tube bends toward the ventral surface, then curves toward the center of the body, and ends apically in a small ovoid ampule which is always open at the extremity.

Histological sections (Fig. 7–25i) show that the distal half around the ectospermalege is buried in the mesospermalege and that all its subcylindrical portion has a simple structure. It is composed of a) a regular layer of cuticle, principally amber exocuticle, bordering a usually empty lumen, and b) an external foundation of cubical cells grouped in two's and three's. At the base of the ampule the exocuticular layer is modified and constitutes a rather thick, bulging septum completely plugging the lumen of the tube. The wall of the ampule shows the same modified exocuticle, and its external face and all its internal cavity are lined with epithelial cells, resulting in a fingerlike invagination of the distal region of the copulatory tube which is found to be plugged well before its extremity. This explains why the ampule is open in the mesospermalege of virgin females.

Insemination induces significant changes in the structure of the ectospermalege. The transverse septum closing the ectospermalege is without a permanent opening; it is doubtless crossed by the very long paramere of the male and probably prevents the back flow of injected sperm. The epithelium of the portion of the copulatory tube that penetrates the mesospermalege undergoes a peculiar modification. Its cells, colored by a red-brown substance, are hypertrophied and profoundly altered in sections; they end by forming a dark crest, scalloped and nearly anhistic, around the tube and the ampule. Other less significant changes are produced among the epithelial cells lining the cavity of the ampule.

The mesospermalege is composed of 2 separate organs placed symmetrically under tergites V and VI. Each of these disklike organs becomes subspherical when it is filled with sperm; the corresponding copulatory tube penetrates to the middle of its dorsal face. Its wall is thick and made of indistinct cells having nuclei arranged in 1 or 2 rows and is covered interiorly by a well-developed basement membrane bearing intracytoplasmic sticks of uniformly PAS-positive substance. At the postero-external border of each organ, the wall thins and extends outward, forming a tortuous "conductor tube." The diameter of this tube decreases progressively and its distal bellshaped extremity opens into the hemocoel in a posterior direction. The internal cells of the mesospermalege are densely grouped but not aligned with the principal mass. They join together in rows in the conductor tube and exit in this manner through the posterior orifice, behind which they are dispersed. Although much better organized, this is the arrangement observed in *Leptocimex boueti.*

The 2 organs of the mesospermalege are filled equally with sperm and function simultaneously, judging by the identical appearance in each of the females studied. I have observed that, at the time of copulation in *Leptocimex duplicatus,* the male plunges its paramere successively into one and then the other copulatory tube. The sperm, directly injected into the ampule, afterward fill the entire interior of the organ, subdividing and separating the mass of cells. The spermatozoa deposited during a copulation appear to group themselves in a vast ensemble without forming globular aggregates. They concentrate in the region of the organ where the conductor tube opens, penetrating massively into it and following it to enter the hemocoel. The spermatozoa have only a short trip to make, as the external orifices of the conductor tubes are near the seminal conceptacles. Their entrance into the conceptacles could not be observed in the specimens available.

Leptocimex duplicatus has seminal conceptacles that are not very voluminous and resemble those of *Leptocimex boueti* by their regular ovoid form and their mode of attachment to the paired oviducts, in the wall of which are spermodes which never appear to contain many spermatozoa.

Crassicimex[20]

The paragenital system of *Crassicimex,* schematically represented in Fig. 7–11, 7–15, is organized like that of *Stricticimex,* and in many details the structure is the same. It differs only in its form, which is very intricate and which differs in the two species.

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[20] One female of *Crassicimex sexualis* Ferris and Usinger and 7 ♀ of *C. pilosus* Ferris and Usinger; studied in serial histological sections.

The ectospermalege is of the "copulatory tube" type, opening dorsally near the right border of the abdomen in intersegment III–IV. With little or no natural pigment, the cuticular lining of the ectospermalege is seen with difficulty in the abdomen when treated with KOH; staining shows it to consist of a short, broad "vestibule" followed by a very long, slender diverticulum (Fig. 7–22o).

In *Crassicimex sexualis,* the relatively small vestibule opens into the anterior lamina of the modified intersegmentary fold (i, Fig. 7–15). It is extended at the apex by an extremely long diverticulum which, after following the course indicated in Fig. 7–15, penetrates the posterior wall of the second pocket of the mesospermalege.

In *Crassicimex pilosus,* the large vestibule has a folded wall which opens into the posterior leaf of the intersegmental fold, almost at the side of tergite VI. The diverticulum, much shorter than in the preceding species, in part follows a much less complicated course; it curves inward posteriorly and penetrates the anterior region of the mesospermalege.

The mesospermalege is very long and complicated in form but always has 3 successive parts which are distinct, at least in structure and function: a) an anterior part, rich in amoebocytes which resorb the seminal plasma and some of the spermatozoa; b) a reservoir where the intact spermatozoa accumulate; and c) a conductor cord, which guides the spermatozoa against the wall of the median oviduct.

In *Crassicimex sexualis* the anterior part of the mesospermalege consists of a series of pockets and tubes, the complicated contours of which are individually variable and are roughly represented in Fig. 7–15. A first pocket, oblong and dorsal, is followed by a smaller pocket which is directed rather obliquely toward the ventral face and into which the diverticulum penetrates. There follows next a tube which is at first large and tortuous and then narrow and sinuous; after a rather long course, this tube abuts against the reservoir, which is large and ovoid (r, Fig. 7–15) and is situated in the posterior region of the abdomen on the right side.

The conductor cord (cc, Fig. 7–15), which extends from the reservoir, bends to the left so that its distal extremity touches the wall of the median oviduct. As in *Stricticimex,* it consists of 2 successive regions, one basal and subcylindrical with a syncitial filament at the center (cc, Fig. 7–26i), the other apical and shaped like a deep cup. A dense mass of modified amoebocytes fills its cavity (a, Fig. 7–26j) and forms a protuberance at the exterior of the cup orifice (Fig. 7–26k). In traversing this mass, the spermatozoa proceed from the mesospermalege to the immediate vicinity of the wall of the oviduct, or even against the muscular tunic of this wall.

In *Crassicimex pilosus,* the form of the mesospermalege is much simpler and recalls that of *Stricticimex.*

Afrocimex[21]

In this genus, both the male and female possess a spermalege, but it is different in the two sexes (Fig. 7–9).

Female.—The ectospermalege is ventral, consisting of 2 successive, rather thin pads that extend broadly into the left portion of intersegments II–III and III–IV. Because their pigmentation is dark, these pads are clearly visible in preparations of the ventral wall of the abdomen (Fig. 7–21g). The sides are very thin but the median portion has a thickening which the intersegmental fold obliterates at the left side of the abdomen.

The 2 pads do not have exactly the same form or dimensions, and they differ from species to species. They result from a hypertrophy of the intersegmental membrane. Here, the very thick exocuticle has an opening in 1 part of its superficial layer, a large cord of amber exocuticle (Fig. 7–23a). It is to this cord, which is absent in the rest of the intersegment, that the pads owe their particular pigmentation. In inseminated females, the brownish-yellow to blackish traces of copulation, frequently long and narrow, traverse the cuticle of the ectospermalege.

The mesospermalege is very voluminous but has neither a wall nor a clear contour; it is formed by an enormous, diffuse mass of amoebocytes extending from the left side of the dorsal integument to behind urite VI. In the center of this mass are muscles, tracheae, shreds of adipose tissue, and, in inseminated females, a great quantity of spermatozoa scattered or amassed without order.

The amoebocytes of the mesospermalege are rather densely but irregularly grouped at points, particularly in the region near the ectospermalege where they present the appearance of a rather lacunous parenchyma (ms, Fig. 7–23a). Toward the periphery of the mass, the amoebocytes are more and more broadly dispersed and have a spherical form, the structure varying greatly according to the diverse phases of their activity. After insemination, the majority have large vacuoles in their cytoplasm and the others, lacking vacuoles, contain spermatozoa in the process of being resorbed.

Leaving from all sides of the diffuse periphery of the mesospermalege, spermatozoa in large numbers disperse into the abdominal hemocoel, where apparently they are able to remain for a rather long time. They next penetrate the oblong and very voluminous seminal conceptacles, the walls of which show a structure like that in *Primicimex* but are much less spongy. The spermatozoa appear to be able to cross the walls only through several lacunae situated on the anterior basal region near the insertion on the paired oviducts. The route of access by way of the

[21] Two females and 9 ♂ of *Afrocimex constrictus* Ferris and Usinger, 3 ♀ and 8 ♂ of *Afrocimex leleupi;* studied in serial histological sections.

posterior hemochrism is used, and the wall of the median oviduct is invaded by spermatozoa. The latter are especially numerous in the spermodes.

Male.—The spermalege consists uniquely of a ventral ectospermalege represented by 3 consecutive pads situated on the left side in intersegments II–III, III–IV, and IV–V. These pads, increasing in size from first to third, are better delimited and are narrower and thicker than those of the female. Their form changes in the two species as shown in Fig. 7–21e, f.

The pads of the ectospermalege are not the same in structure in the 2 sexes. In the male, the cord of amber exocuticle is lacking. Inclusions of a yellow-brown or blackish substance emanate from the surface at places in the endocuticle; they are variable, irregular in form, and represent traces of copulation (Fig. 7–23b).

Among these unformed and pigmented masses, as in females, one observes spermatozoa which are sometimes dispersed in the neighboring endocuticle. Most of the traces of copulation found in the ectospermalege of the males result from attempted homosexual couplings, the frequency of which is known in the Cimicidae. Effective copulations do occur in *Afrocimex* to the extent of ejaculation of the sperm into the hemocoel.

Among the males of *Afrocimex constrictus* studied, four showed obvious signs of copulation upon histological examination. In 1 specimen, fixed after homosexual coupling, a deep, broad hole with significant deterioration in the epithelium was seen in one of the pads (Fig. 7–23d). This hole and the neighboring hemocoel were filled with abundant spermatozoa, the orientation and distribution of which permitted the reconstruction of their course. The spermatozoa were injected through the hole into the hemocoel where they formed dense masses from which they were widely dispersed by the blood. Some invaded entire lobes of adipose tissue, and others penetrated into the metathoracic scent glands, probably attracted to them since spermatozoa were present there in 3 inseminated males; in 1 case they were clearly localized there. These "foreign" spermatozoa were never introduced into other organs of the abdominal cavity, certainly not into the male reproductive apparatus, which was otherwise normal and intact.[22] Most of them remained in the hemocoel, grouped here and there in disordered masses, where they were infiltrated by amoebocytes, some of which contained spermatozoa, in the process of resorbtion. But the phenomenon appears less intense than in the female mesospermalege, which is much richer in amoebocytes.

In *Afrocimex constrictus,* in which all the males studied frequently bear numerous traces of copulation, homosexual copulation appears sufficiently often (4 of 9 cases) so that it cannot be considered "accidental."

[22] It has been carefully verified that the observed spermathemie in males did not result from the rupture of the wall of the genital tract at the moment of fixation.

In *Afrocimex leleupi,* the traces of copulation are less numerous and are lacking completely in 2 of 8 males examined; furthermore, none of the latter showed signs of effective insemination. The frequency of attempted or realized homosexual copulation thus differs in the species of *Afrocimex;* a very important consideration in comprehending the significance of the differentiation of an ectospermalege in males.[23]

Latrocimex[24]

Female.—The ectospermalege is ventral, bearing 2 consecutive, unequal pads situated on the right side in intersegments III–IV and IV–V. In KOH preparations of the abdominal wall (Fig. 7–21d), these pads show a distinct resemblance in form to those of the male of *Afrocimex constrictus;* similarly ribbed, they are slightly broader and less well-delimited. Near the pads, the hind margin of the sternite covering each of them is weakly notched. The posterior pad and the smaller preceding one, in the female examined, bear clear traces of copulation. Several identical traces are also observed in the part corresponding to intersegment II–III, where no visible integumental differentiation exists.

The structure of the pads is probably comparable to that described in *Afrocimex,* but they could not be studied as sections of the right side of the abdomen were damaged in the only histological series available.

The mesospermalege is represented by a diffuse aggregation of subspherical amoebocytes, juxtaposed or separated, recalling those of the peripheral region of the mesospermalege in *Afrocimex.* Its contours, doubtless soft, were impossible to locate in the female studied because of the extent and the extraordinary intensity of spermathemie. An immense number of free spermatozoa are found in the hemocoel of almost the entire body, including the extremities of the legs. Many others fill the central lacunae and the interstices of cellular elements grouped in oblong masses which occupy a large part of the abdomen and part of the thorax (Fig. 7–23f). Most of these masses have a continuous external envelope that represents the singularly thick walls of the anterior genital ducts. Some masses which are slightly different in appearance, but which lack distinct limits and allow the spermatozoa to diffuse into the hemocoel, probably correspond to the lobes of the mesospermalege. This situation is difficult to analyze in sections since the mature eggs compress and deform the abdominal organs. It seems certain, however, that the spermalege of *Latrocimex* belongs to a primitive type and in many ways resembles that of *Afrocimex.*

Male.—Males of *Latrocimex* have no spermalege but do mate and in-

[23] The hypothesis proposed by Hinton (1964) regarding this, based only on my brief remarks (Carayon 1959), is not considered plausible and will not be examined here.

[24] One female and 2 ♂ of *Latrocimex spectans* Lent; studied in serial histological sections. Schematic presentation of the spermalege in Fig. 7–9.

seminate each other as do males of *Afrocimex*. A detailed morphological study has been made of the ventral wall of the abdomen in a male. This study has shown the existence in intersegment II–III on the right side, but absent on the opposite side, of a slight deformation bearing 3 or 4 small holes. These are probably traces of copulation, as shown by an histological examination of 2 other males, in one of which, especially, the signs of a recent traumatic insemination are extremely clear. A characteristic trace of copulation with deposits of brownish-yellow substance is found in the region of intersegment II–III. It leaves a dense trail of spermatozoa which extends deeply in the hemocoel in sheets and streams, indicating a rather wide dispersion, principally in the anterior region and along the dorsal wall of the abdomen. In many other places, the spermatozoa are accumulated under the integument, and a certain number of them become incorporated in the endocuticle.

It should be noted that the region of intersegment II–III that is utilized in both sexes for traumatic insemination lacks an ectospermalege in the female.

Ornithocoris, Caminicimex, Psitticimex, Haematosiphon, Cimexopsis, and Synxenoderus[25]

The general characters of the paragenital system are nearly the same in this group of 6 closely related genera; similar systems are not encountered in any of the other Cimicidae. Therefore, it suffices to treat the group as a whole and indicate the important peculiarities appropriate to each of the genera considered.

The dorsal ectospermalege is situated at the center or in the right half of intersegment VI–VII and frequently in the preceding intersegment. It is poorly differentiated and results from a slight hypertrophy of the intersegmental membrane which forms a thin pad along which, in inseminated females, the traces of copulation are seen. Depending upon the condition of the preparation,[26] these traces appear as holes (Fig. 7–21c) or as irregular, blackish stains (Fig. 7–21j, k); in many cases they are the only means of locating the exact position of the ectospermalege.

The ectospermalege can be studied precisely only by histological sections; they reveal the following characteristics.

In *Haematosiphon* (Fig. 7–25a) there is no appreciable difference in thickness and constitution of the 2 pads of the ectospermalege, but the anterior pad is used less than the posterior one at the time of copulation.

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[25] Material studied by dissection and serial histological sections: Numerous females of *Ornithocoris toledoi, Caminicimex furnarii, Psitticimex uritui, Haematosiphon inodorus,* and 2 ♀ and 1 ♂ of *Synxenoderus comosus* List; only a morphological examination of the ectospermalege has been possible in *Cimexopsis nyctalis.*

[26] The brown substance plugging the holes made in the cuticle by the male paramere sometimes persists and sometimes dissolves in KOH preparations. Its solubility appears irregular and depends upon the conditions of the treatment.

The posterior pad of *Ornithocoris* (Fig. 7–25c) appears much more developed and bears almost all the traces of copulation; however, some are also observed in the anterior pad. The intersegmental membrane V–VI in *Caminicimex* (Fig. 7–25b) is barely hypertrophied and copulation doubtless never causes it; the following intersegment on the other hand shows a more highly differentiated ectospermalege than in the other genera of the group; its very thick endocuticle constitutes a lamina which penetrates deeply into the mesospermalege anteriorly; the breadth and form of this lamina varies from individual to individual (Fig. 7–21l, m, n). In *Psitticimex,* the ectospermalege occupies only the apex of the curve described toward the front of intersegment VI–VII (Fig. 7–21j); there is no hypertrophy in the preceding intersegment. In *Synxenoderus,* the true ectospermalege, situated on the right wall of the abdomen in intersegmental membrane VI–VII, is represented by a very slight and not very extensive thickening; it would easily pass unobserved, even in histological examination, without the traces of copulation to mark its presence.

Although the ectospermalege in the Cimicidae discussed in the preceding paragraph shows only a weak structural differentiation of the integument, it is often accompanied by significant modifications in the form of the adjacent intersegments.

It is principally the intersegmental fold VI–VII which appears modified. This fold describes a curve forward, sometimes median and symmetrical (*Haematosiphon, Cimexopsis, Psitticimex*), sometimes asymmetrical, with the apex bearing more or less to the right (*Ornithocoris, Caminicimex, Synxenoderus*). Its depth may be either diminished or increased, so that, for example in *Psitticimex,* it constitutes (Fig. 7–21j) a very broad median pocket.

Although the ectospermalege itself is almost nonexistent in the genus *Synxenoderus,* the intersegment VI–VII and, to a lesser degree, the 2 preceding, appear greatly deformed near the right wall of the abdomen (Fig. 7–21i). A comparable deformation exists in the male. Histological examination of the male leads one to suppose that the region where the deformity is found serves in effect for homosexual copulations. However, the structure of this region is difficult to analyze in the sections obtained. It is found that, at the level of the intersegmental fold where a dense exterior trail of sperm is found, the integument is hypertrophied and contains spermatozoa. However, the testes of *Synxenoderus* are developed to the extent of extending into a portion of the thorax and up to the bases of the legs. It is possible that a testicular hernia and rupture of the intersegmental membrane occurred at the time of fixation.

The mesospermalege in all the Cimicidae of this group appears to be a unique and well-delimited mass connected to the internal face of the dorsal integument of the abdomen, where it rarely extends posteriorly toward the posterior margin of tergite VII and anteriorly toward the an-

terior margin of tergite V. Its form is regular, semi-ovoid, and globular, with a lateral lobe directed toward the left in *Synxenoderus* only.

The structure of the mesospermalege resembles in many ways that of *Cimex*. However, the amoebocytes of the internal mass, although not densely grouped, are often arranged in branching rows; some, even in virgin females, already contain not only vacuoles but large inclusions. At the moment of arrival of the sperm, the amoebocytes are dispersed more than in *Cimex,* then undergo the same modifications which indicate the resorption of seminal plasma and of a part of the spermatozoa. Those spermatozoa which are not destroyed apparently never group in subspherical aggregates but migrate toward the periphery of the internal mass. The wall of the mesospermalege is well-differentiated, relatively thin, covered internally by a distinct basement membrane and surrounded externally by an envelope of adipocytes which are sometimes reduced to several fragments.

The spermatozoa do not leave the mesospermalege in the same manner among the various representatives of the group; however, their departure is never massive nor in all directions.[27] It is followed by a limited spermathemie, most frequently in the area of the ovariole pedicels and of the paired oviducts.

In *Ornithocoris* and *Psitticimex,* the spermatozoa leave the spermalege by a lacuna situated in the anterior third near the dorsal surface; they occupy the narrow space between this surface and the integument, then migrate, in the case of *Ornithocoris,* toward the pedicels. In *Psitticimex* they spread in greater abundance and over a greater distance along the mesodermal genital ducts.

In *Caminicimex,* the spermatozoa appear capable of passing through the wall of the mesospermalege into the anterior region at several points where the wall protrudes into the hemocoel in rather discontinuous rows of cells. It is especially by progressing along these cells that the spermatozoa arrive in the proximity of the pedicels.

In *Haematosiphon,* the route followed by the spermatozoa is much clearer, as the mesospermalege possesses 2 true "conductor cords" of a special type. These cords are arranged symmetrically and branch from the lateroventral region of the mesospermalege. They are directed obliquely anteriorly and toward the sides of the abdomen until they reach the pedicels of the external ovarioles of each ovary. They are sinuous and irregular in thickness and made up of rows of amoebocytes, leaving the mesospermalege and enveloped by a fibrous membrane (Fig. 7–25g). In inseminated females, the spermatozoa leaving the internal mass of the mesospermalege enter the cords, where they fill the spaces

[27] Except perhaps in *Synxenoderus.*

between the rows of cells and their envelope. This leaves the distal extremity of each cord open, and the spermatozoa enter the hemocoel through it close to the pedicels of the ovarioles.

In *Haematosiphon* and its relatives, the intrahemocoelic migration of spermatozoa carries them to the extreme anterior area of the genital ducts and not into the basal region of the oviducts as in other Cimicidae. Thus, the retention of reserve spermatozoa is accomplished almost exclusively in the pedicels of the ovarioles.

Dissection of an inseminated female shows the ovarioles to appear irregularly swollen by silky white, globular, or ovoid masses resulting from the aggregation of a large number of spermatozoa (Fig. 7–17). Histological study shows that the spermatozoa grouped in this way are found uniquely in the walls of the pedicels, the central layer of which they often greatly distend. This layer is situated between the epithelium and a rather thin external layer, and its structure varies in members of the group.

In *Haematosiphon,* and doubtless also in *Psitticimex,* the pedicels of virgin females do not present significant peculiarities; it is only after insemination that the central layer becomes quite visible. It is filled with spermatozoa and comprises nearly all the thickness of a considerably distended wall (Fig. 7–25e). The spermatozoa accumulate not only in the pedicels but also in smaller numbers all along the walls of the paired oviducts, where they occupy principally the spermodes. It is almost certain that the distal portions of the spermodes, swollen and perhaps confluent, form the reservoir of spermatozoa in the pedicels.

In *Caminicimex,* a thick central layer is present and is quite visible in the walls of the pedicels of virgin females. This layer is developed only on the external side of each pedicel and is found between the epithelium and the very thin muscular tunic. It consists of tall cells without visible limits; the nuclei are voluminous here and are arranged near the external margin; the cytoplasm seems to be completely transformed into a heterogeneous mass of sticky secretion. During insemination, the spermatozoa, after having directly crossed the external parietal layer of the pedicels, accumulate there in great abundance and for the most part consist of globular aggregates (Fig. 7–25f). One rarely or never observes them elsewhere in the genital ducts. The formation which contains them appears very peculiar and its exact nature remains uncertain; they may result from a localization and a profound modification of the spermodes, or at least of their basic elements, the amoebocytes. The as yet imperfectly known case of *Ornithocoris,* which is in certain respects intermediate between that of *Haematosiphon* and *Caminicimex,* perhaps will allow final clarification of this question.

Another problem posed by the Cimicidae related to *Haematosiphon*

concerns their "seminal conceptacles." Probably because of the accumulation of spermatozoa in the pedicels, the seminal conceptacles either are absent or do not serve for the accumulation of spermatozoa; they are never sacciform in appearance as in the other Cimicidae. This is the only general conclusion which can be made, as nearly every genus examined in detail appears to constitute a special case. A summary of the rather disparate and often fragmentary observations on this subject follows.

Caminicimex and *Ornithocoris* lack conceptacles completely. In *Psitticimex,* the conceptacles form an annular and regular pad around each paired oviduct (Fig. 7–18). This pad results from a simple dilation of the hemochrism with a local accumulation of amoebocytes. Its thin wall has many lacunae permitting the spermatozoa to enter. The spermatozoa do not accumulate here, but rather, all along the anterior genital ducts. The spermatozoa also penetrate directly into the walls of the pedicels, where they are always especially numerous. In *Haematosiphon,* an annular pad, made up of small aligned protuberances, also surrounds each paired oviduct (Fig. 7–17). This pad, lacking the characteristic structure, may not be considered to be a true conceptacle. It is situated under the muscular tunic of the oviduct and represents the dilated base of the highly developed spermode, which is always more swollen by spermatozoa in its anterior than in its posterior portion. The annular pads contain few spermatozoa and do not serve as a place of entry, which is located more anteriorly across the peritoneal membrane surrounding the oviducts. In histological sections, this membrane appears locally distended with several lacunae which permit the passage of spermatozoa into a region near the distal extremity of the paired oviducts. The genus *Synxenoderus* differs distinctly from the other members of the group in many characteristics of its paragenital system. Toward the center of their dorsal surfaces, the paired oviducts bear a thick asymmetrical crest, the structure of which, observed only in 1 virgin female, recalls that of the annular pad of *Haematosiphon.* The manner in which the spermatozoa penetrate and accumulate in the walls of the genital ducts has been studied only very incompletely, the only inseminated female available being rather poorly preserved histologically and furnishing only a few satisfactory sections. However, it appears certain that the pedicels of the ovarioles not only lack a thick central layer, but they no longer contain aggregates of spermatozoa. These spermatozoa, leaving from the left side of the mesospermalege, appear to enter in large numbers across the peritoneal membrane all along the paired oviducts. The hemochrism here is very large, on 1 side at least, and perhaps serves as a reservoir for the spermatozoa.

These peculiarities, which must be confirmed, are not sufficient to exclude *Synxenoderus* from the *Haematosiphon* group.

Hesperocimex[28]

The ectospermalege is ventral, situated near the right side of the abdomen in intersegment VI–VII. Examined in KOH preparations of the abdominal wall, it appears (Fig. 7–22j) as a small, more or less dark brown mass, the form and orientation of which differ slightly from species to species (Fig. 7–22j, k). This mass consists of an external and an internal portion. The external part is rather regular and smooth, conical or truncate, and forms a protuberance at the surface of the integument which is slightly depressed around it[29]; the internal part, which is an extension of the external part beneath the integument, is differently pigmented, rather irregular in form, and striated. In preparations made by utilizing a clearing agent other than KOH, extremely variable blackish tracks may be observed. These cross the cuticle of the ectospermalege and penetrate more or less deeply into the abdomen—they are the traces of copulation.

Although the ectospermalege is strongly localized, the entire fold between segments V and VI appears modified; it is obliterated in the median region where the margins of the sternites not only face one another but are joined without histologically visible structural discontinuity. Only the lateral parts of the fold remain unmodified, the left part being slightly larger than the right, leaving the external protuberance of the ectospermalege open.

Histological study reveals that the ectospermalege results from a very marked hypertrophy which is quite localized in the integument. The integument here is more greatly modified in form than in structure. The exocuticle of the ectospermalege, composed of a yellow amber layer surmounting a brown layer with a fibrous appearance, constitutes the external protuberance (Fig. 7–25d). In the center and near the apex of this protuberance, a fine, rather short canal in the form of an inverted comma is seen, but only in histological sections; it is here that the male inserts his paramere.

The endocuticle of the ectospermalege is unpigmented, thick and fibrous, as is the epidermis, which is composed of tall cells arranged in several rows. It often appears disrupted in the vicinity of the traces of copulation, which cross it in inseminated females. The structure of the ectospermalege is not exactly the same in the 2 species studied; it differs in the appearance of the exocuticle and in the position and form of the small canal of the external protuberance.

[28] Studied from dissections and serial sections of many specimens of *Hesperocimex coloradensis* and of 5 ♀ of *H. cochimiensis* Ryckman and Ueshima. The entire spermalege is represented schematically in Fig. 7–11.

[29] Ryckman (1958) has called this depression a "sclerotized ring" and has illustrated it rather schematically, exaggerating its limits. In fact, it has neither a discontinuity nor a groove between the cuticular mass of the ectospermalege and the adjacent integument.

The mesospermalege consists of a slightly pyriform sac inserted in the right side on the periphery of the ectospermalege and elongated transversely in the abdomen against the internal face of sternite VI almost at the right side. Its true wall, most frequently very thin and covered internally by a thin basement membrane, is surrounded exteriorly by an irregular but continuous envelope of adipocytes. Inside the mesospermalege, 2 categories of cells are found which differ in structure and arrangement (a1, a2, Fig. 7–16). The first, relatively small, spherical, and dispersed, are recognizably amoebocytes. The others, distinctly larger and oblong with large basal nuclei, are also amoebocytes, but they are strongly modified and are united in a continuous layer by their lateral surfaces. This layer forms a second sac which is also inserted at its extremity on the circumference of the ectospermalege. The mesospermalege thus appears as a sac having a double wall. The external layer is the true wall, and the internal one comprises modified and normal amoebocytes; the latter are also present between the 2 walls.

To this remarkable structural peculiarity, one may add another concerning the relationships between the mesospermalege and the seminal conceptacles. The latter, attached to the latero-external surfaces of the paired oviducts, are composed principally of a dorsal subspherical and rather voluminous pocket containing many amoebocytes identical to those dispersed within the mesospermalege. This pocket, the wall of which consists of a simple layer of slightly modified adipocytes with long "internal processes," has a ventral lobe which penetrates into the posterior and dorsal region of the mesospermalege (Fig. 7–16). There is no direct communication between the 2 structures, but the wall of one deeply depresses the wall of the other and the 2 walls are modified throughout the region where they are in contact. That of the mesospermalege is swollen and its components, elsewhere only slightly distinct, appear here as rather large juxtaposed cells. Analogous modifications are observed in the opposite wall of the ventral lobe, which is composed of cells identical to those of the internal processes but layered and more voluminous.

The adipose envelope of the mesospermalege is attached directly to the adipose wall of the dorsal pocket of the conceptacles, assuring the permanent adherence of the latter to the mesospermalege.

During copulation, the sperm is injected into the internal sac of the mesospermalege. The modified amoebocytes constituting the wall of this sac resorb the seminal plasma. They increase in volume and are filled with large, oblong inclusions (a2, Fig. 7–19), whereas the spermatozoa infiltrate between them, leave the internal sac, and arrive in the cavity which surrounds the true wall of the mesospermalege. In this cavity, just as elsewhere in the internal sac, small, unmodified amoebocytes resorb some of the spermatozoa. In *Hesperocimex* the 2 categories

of internal cells of the mesospermalege thus differ not only in form, structure, and arrangement, but also in function. The large amoebocytes are grouped in the most efficient manner for the formation of a filter which resorbs the seminal plasma and allows the spermatozoa to pass. The spermatozoa leave the mesospermalege at only 2 places where its wall is joined to that of the ventral lobes of the conceptacles. En mass, they pass over these modified and lacunous double walls, thus arriving directly in the conceptacles without ever having crossed the hemocoel. Next, they migrate to the syncitial bodies through the spermodes.

The paragenital system of *Hesperocimex* is of great interest in several respects, especially since it allows better comprehension of the nature and functions of the system in general. It has so many peculiarities that it cannot be compared with any of the other paragenital systems known in the Cimicidae.

8 Reproductive Physiology

by NORMAN T. DAVIS[1]

The reproductive processes of cimicids have been studied extensively in *C. lectularius* (Cragg 1920, 1923; Abraham 1934; Mellanby 1939a; Davis 1956, 1964, 1965a, 1965b); therefore, the details given here will be concerned primarily with that species. Jordan (1922) and Carayon (1959) have shown that differences in the reproductive system occur in other cimicids, particularly with regard to the location and structure of the spermalege. To a certain extent these differences appear to represent various levels in the evolution of the unique mode of insemination found in this group. *C. lectularius* may be considered to represent an intermediate level, and its reproductive biology is probably reasonably typical of that found in most cimicids.

INSEMINATION

The details of insemination have already been discussed in Chapter 7, so only a few additional matters, particularly the timed sequence of events, need be mentioned here. As will be seen subsequently, the time that certain events occur has an important bearing on the control of egg maturation. To obtain consistent results, I (1964) have made observations on insemination and subsequent sperm migration, using controlled conditions and specimens of a known uniform nutritive and reproductive state and age. I have traced the migration of the spermatozoa to the sperm storage organs (seminal conceptacles) by direct observation through the cuticle, by dissections, and by histological sections made at various intervals after mating. Immediately after copulation the sperm mass may be seen in the living insect as an opaque area near the center of the more translucent mesospermalege. Gradually the mass becomes more diffuse and spreads outward, reaching the periphery of the spermalege about 2 hours after insemination. Within an hour thereafter the

[1]The work reported in this chapter was supported in part by Grant AI 03862 of the Public Health Service, National Institutes of Health.

sperm mass passes through the limiting membrane of the spermalege and into the hemocoel.

In the hemocoel most of the spermatozoa remain concentrated in a mass or masses which gradually move to the bases of the lateral oviducts where the seminal conceptacles are located. Here the sperm masses begin to lose their form, and in about 4 hours the spermatozoa form a fuzzy layer around the conceptacula and bases of the lateral oviducts.

In dissected specimens most of the spermatozoa are found to have entered the conceptacula in 12 hours, and by 24 hours they have become realigned with one another to form several compact C-shaped or circular bundles in the conceptacles.

SPERM ACTIVATION AND AGGREGATION

Although the foregoing events in insemination are easily observable, much is yet to be learned concerning the means by which they occur. Some information has been obtained by experiments using artificial insemination (Fig. 8–7) and in vitro studies of the activity of the spermatozoa (Davis 1965a). By injecting the spermatozoa and seminal fluid into the spermalege with a microinjector it has been possible to inseminate females and obtain normal production of fertilized eggs. If the insemination is made without the seminal fluid, the spermatozoa are unable to migrate and remain in the spermalege. Thus the seminal fluid plays an essential role in insemination.

In vitro the spermatozoa are immobile unless seminal fluid is present. They then form into dense masses from which the actively moving tails extend. These masses, washed free of seminal fluid, may be successfully used in artificial insemination. Therefore it appears that the primary function of the seminal fluid is to activate and aggregate the spermatozoa; once the spermatozoa are aggregated, the fluid is no longer essential.

The importance of sperm aggregation may be seen in experiments in which artificial insemination was made directly into the body cavity. Injection of spermatozoa alone results in very high mortality; the mortality is lower if seminal fluid is included, and very low if aggregated sperm masses are used. Injection of seminal fluid alone into the hemocoel has no harmful effect. Thus it is clear that entrance of non-aggregated spermatozoa into the hemocoel is harmful to the female, possibly because the spermatozoa, dispersed in the body cavity, interfere with various vital processes.

The sperm aggregates formed in vitro are very similar to those found in the hemolymph of recently inseminated females. In vitro, spermatozoa are unable to swim individually but can only gather into masses. It appears that, in vivo, the sperm mass draws itself through the spermalege and hemocoel to the conceptacles, since the wave patterns of the extended tails originate at the end of the tail and move toward the mass.

It is not known with certainty why the mass moves in the direction of the seminal conceptacles rather than in another direction. Abraham (1934) suggests a chemotactic response, but as yet chemotaxis has not been demonstrated conclusively for the sperm cells of any animal.

Apparently one of the important functions of the mesospermalege is to hold the spermatozoa so they may be acted upon by the seminal fluid before entering the hemocoel. Sperm aggregation induced by the seminal fluid was observed in several species of *Cimex* as well as in species of *Leptocimex* and *Hesperocimex*; it is probably of general occurrence, at least in those cimicids in which the spermatozoa pass through the hemocoel.

In *Stricticimex* the spermatozoa do not enter the hemocoel but reach the genital tract by way of a tissue bridge; the spermatozoa form into a mass in the posterior lobe of the mesospermalege where they are stored (Carayon 1959). It remains to be seen whether their condition in this case is the same as the activated sperm aggregates, or is more comparable to the inactive sperm masses observed in the seminal conceptacles of *Cimex*.

Carayon (1954b) has shown in *Primicimex* that the spermatozoa are introduced directly into the hemocoel and many become dispersed throughout the body. Apparently in this case sperm aggregation is not important and an abundance of free sperm cells in the body cavity is not harmful. This fact, however, in no way negates the importance of the mesospermalege in facilitating sperm aggregation in other cimicids.

Carayon (1959) has given an excellent account of the evolution of the spermalege and the insemination process in cimicids. He shows that the general evolutionary trend is from sperm introduced directly into the hemocoel, as in *Primicimex*, to sperm confined entirely to the mesospermalege and conducting tissues, as in *Stricticimex*. Therefore, one may deduce from his account that the exclusion of the sperm from the hemocoel is biologically advantageous. The phenomenon of sperm aggregation may be viewed in many species as a means of at least confining the sperm while they are in the hemocoel.

SPERM VIABILITY

Females of *C. lectularius* are able to produce viable eggs for 5 to 7 weeks ("fertile period") after a single mating (Abraham 1934, Mellanby 1939a, Khalifa 1952, Davis 1964). Similar periods have been observed in *Hesperocimex sonorensis* (Ryckman 1958) and *Leptocimex duplicatus* (Davis unpubl.). In *C. lectularius* the period is the same, even for females that have received larger than normal amounts of spermatozoa, and is independent of the number of eggs produced (Mellanby 1939a). However, the period is influenced by temperature, and these facts have led

to the conclusion that the period represents the time that the spermatozoa remain potent in the female.

Starvation of the male does not cause infertility of *C. lectularius* (Cragg 1923, Titshack 1930, Khalifa 1952).

HYPERGAMESIS

The amount of spermatozoa that the female bed bug receives, even in a single mating, is conspicuous. Multiple matings are not uncommon, and, no doubt, far more spermatozoa are received than can be used in egg fertilization. Berlese (1898) termed this condition "hypergamesis." As noted in the historical review in Chapter 7, several investigators have described the phagocytic removal of the seminal fluid and excess spermatozoa. In particular, Abraham (1934) described in detail the extensive phagocytosis of sperm cells in the mesospermalege, hemocoel, seminal conceptacles, and lateral oviducts. Indeed, the resorption he believed occurred in the conceptacles led him to conclude erroneously that the sole function of these organs is sperm resorption.

Berlese (1898) suggested that the excess sperm serves a nutritive function as well as a stimulation to the development of the ovaries. Similar ideas have since been proposed by several authors. Cragg (1923) found that spermatozoa do not remain intact in the female during periods of prolonged starvation, leading him to observe that "If the spermatozoa can serve as additional nourishment for the female during the oviposition period, it is not a great step to suppose that they can be so utilized during periods of starvation." On the other hand, Abraham (1934) proposed that sperm resorption provides some factor essential for egg production. Most recently Hinton (1964) has suggested that the selective value in the evolution of hypodermal insemination lies in providing nutrition by the resorption of excess spermatozoa. He pointed out that in parasitic animals the risk of starvation is particularly great, but that parasitic Hemiptera have acquired a high capacity to resist starvation.

In support of this thesis, Hinton noted an unusual phenomenon in the genus *Afrocimex* in that the males have an ectospermalege and apparently mate with one another (Carayon 1959). Hinton suggested that in this case the supposed value of sperm resorption is extended to the male. He believed that if some of the males in a population had been inseminated, they would be able to resist starvation better than those which had not. Therefore, such insemination would have a survival value.

Mellanby (1939a) and Davis (1956) have questioned the hypothesis that hypergamesis serves a nutritive function. The ratio of spermatozoa: egg production of an animal generally reflects the risks involved in fertilization. Sperm production by marine animals with external fertilization is characteristically high compared with animals with internal

fertilization. In *Drosophila* the utilization of spermatozoa is very efficient and the amount of sperm transferred is relatively small (Lefevre and Jonsson 1962). The large amount of sperm transferred in the cimicids may simply reflect inefficiency of sperm maintenance and utilization, requiring much resorption. Moreover, study of laboratory colonies may be misleading as to the extent of hypergamesis. Mellanby (1939b) has found considerably less sperm in females from natural populations than in those from laboratory colonies.

So little is yet known about the reproductive biology of *Afrocimex* that any speculation at this time is very risky. However, from what is known of other cimicids it seems unlikely that homosexual mating would increase the potential to survive of certain males within a population. *Cimex* males are known to mate most readily just after feeding and to avoid mating when starved. If this is also the case in *Afrocimex,* and if insemination of males has nutritive function, the net effect would be for the best-nourished males to expend themselves on other members of the population, resulting in an equalization of the population and eliminating the variation necessary for natural selection to be effective.

The essential question is whether or not phagocytic activity results in a net gain or loss in energy and productive capacity. If sperm resorption contributes to the productivity or survival of cimicids, such should be clearly demonstrable. In *C. lectularius* such has not been found to be the case. With regard to the value of hypergamesis to fecundity, Mellanby (1939a) found that the total number of eggs produced by females mated several times is not significantly greater than that of females mated only once. As for the value of hypergamesis in resisting starvation, Mellanby found that virgin females survived much longer (an average of 134 days) than mated females (82 days). This difference is presumably the consequence of the utilization of food reserves for egg production. Davis (unpubl.) has found that twice-mated females do not survive as long as females mated a single time, but the difference is not very great. Females artificially inseminated with unactivated sperm (thus producing no eggs) do not survive as long as uninjected or saline-injected virgins. Thus, if anything, hypergamesis appears to result in a net loss rather than gain for *C. lectularius.*

Finally it should be noted that starved females exhibit a distinct avoidance of mating, thus appearing to avoid hypergamesis.

FECUNDITY

The egg-laying of *C. lectularius* has been studied under various environmental conditions (Hase 1930, Titshack 1930, Omori 1941, Johnson 1942). As mentioned elsewhere in this work, the egg-laying pattern is fixed: At about 27°C, recently emerged adults when fed and mated will start ovipositing about 3 days later (Fig. 8–1). Oviposition ceases after

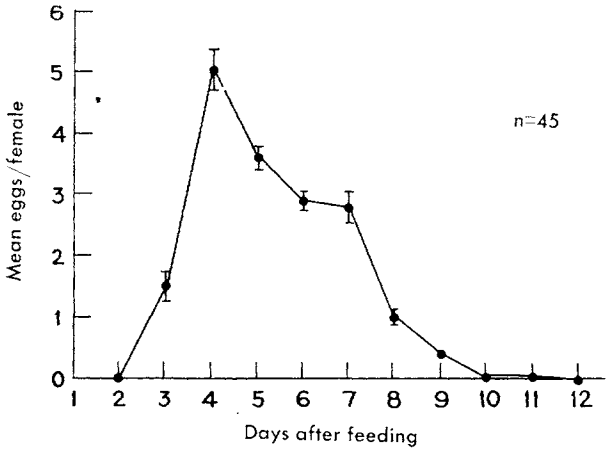

FIG. 8–1.—Daily egg production of 45 females given a single blood meal. Mean and standard error for each day (Davis 1964).

11 days if the insects are not fed again. During this period an average of about 3 eggs per female per day is produced. If the insects are fed weekly but not mated again, this level of production will continue for about 5 weeks; beyond this period, increasing numbers of non-viable eggs are produced, and within 2 to 3 weeks egg production stops entirely (Fig. 8–2). Females that are kept, fed, and mated regularly remain fertile during their adult life span (Titshack 1930), but become less fertile with age (see Chapter 2).

The oviposition potential of *Hematosiphon inodorus* has been studied by Lee (1954b), who used once-mated females fed every fourth day. These females produced an average of 4.43 viable eggs per day and viable eggs for as long as 30 days. In a similar study of *Hesperocimex sonorensis*, Ryckman (1958) determined the productivity of females given frequent opportunities to feed and mate. During a period of 28 weeks a mean of 371 eggs per female were produced. During the weeks of maximum productivity, females produced a mean of 4.31 eggs per female per day. *Ornithocoris toledoi* was found to produce about 4.5 eggs per female per day (Snipes et al. 1940).

Mated females of *C. lectularius* can produce a few eggs despite having not fed after becoming adults (Titshack 1930, Johnson 1942, Davis 1964). The number of eggs produced is probably related to the food reserves acquired in the previous instar (Jones 1930). Similar instances of autogeny have been found in *Hesperocimex sonorensis* (Ryckman 1958), *Hematosiphon inodorus* (Lee 1954b), and *Leptocimex duplicatus* (Davis unpubl). Autogeny is probably a general characteristic of the family.

Virtually no eggs are produced by *C. lectularius* unless mating has occurred (Cragg 1923). In unmated females the oocytes fail to grow be-

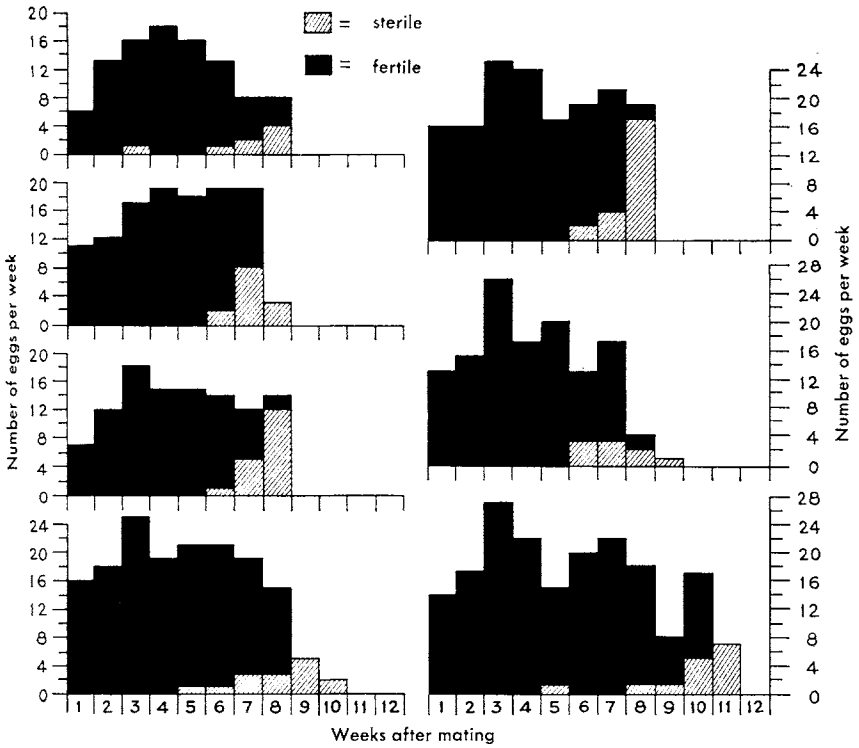

FIG. 8–2.—Weekly production of fertile and sterile eggs by 7 females mated a single time (Davis 1964).

yond a certain point and the fat body becomes enlarged (Mellanby 1939a). However, a few nonviable eggs are laid by older, well-fed females (Davis 1964). A similar dependency on mating for development of eggs has been found in *Hesperocimex* (Ryckman 1958), *Hematosiphon* (Lee 1954b), and *Leptocimex* (Davis unpubl.), and it probably occurs in other cimicids. Although this phenomenon is found in many insects, others produce eggs regardless of mating.

VITELLOGENESIS

In the Cimicidae, each ovary consists of 7 ovarioles. As in other Heteroptera the ovarioles are telotrophic, that is, comprised of an end chamber of nurse cells followed by a germarium, then by an egg in some stage of maturation (Fig. 8–3a). The following sequence of events may be observed in dissections and histological sections of *C. lectularius* females that have been fed and mated (Davis 1964). In the earliest stages an oocyte in the germarium enlarges and becomes surrounded by a clear

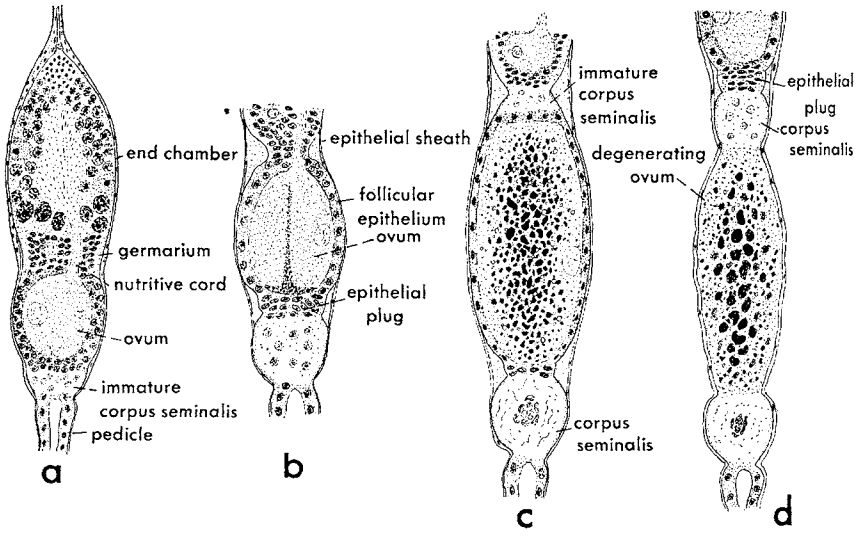

FIG. 8–3.—Histological sections of ovarioles representing stages of development of the corpus seminalis and of oocyte maturation and resorption: a, ovariole with very early oocyte; b, oocyte with axial core of granular material at the start of yolk deposition; c, oocyte in an early stage of yolk deposition, the corpus seminalis containing spermatozoa; d, oocyte in an early stage of resorption (Davis 1964).

homogeneous cytoplasm. As the growth continues, the cytoplasm is joined to the core of the end chamber by a nutritive cord, and as the egg passes posteriorly out of the germarium it is surrounded by a layer of follicular epithelium (Fig. 8–3a). The basal end of the follicular epithelium becomes differentiated into 2 distinct structures. One is the epithelial plug, a mass of tissue adjacent to the end of the egg. The second is the corpus seminalis, an almost spherical mass of tissue between the epithelial plug and pedicle of the ovariole (Fig. 8–3b).

In its initial growth the egg becomes more elongate and finely granular. When it reaches a length of about 0.3 mm, yolk granules and large vacuoles begin to be conspicuous (Fig. 8–3c). At this stage the nutritive cord is lost and the follicular epithelium completely covers the top of the egg, assuming the template form of the operculum. As the egg enlarges, the follicular epithelium becomes drawn out into a thinner layer, and when the egg is about 0.9 mm long it begins to form the chorion around the egg. As noted previously, by this time the egg has been fertilized and cleavage nuclei are seen in the yolk.

The foregoing events in maturation are dependent upon feeding and insemination (Fig. 8–4). In females that have fed but not mated, the egg grows to the stage at which the nutritive cord is broken and yolk granules have appeared; at this stage the egg is then resorbed (Fig.

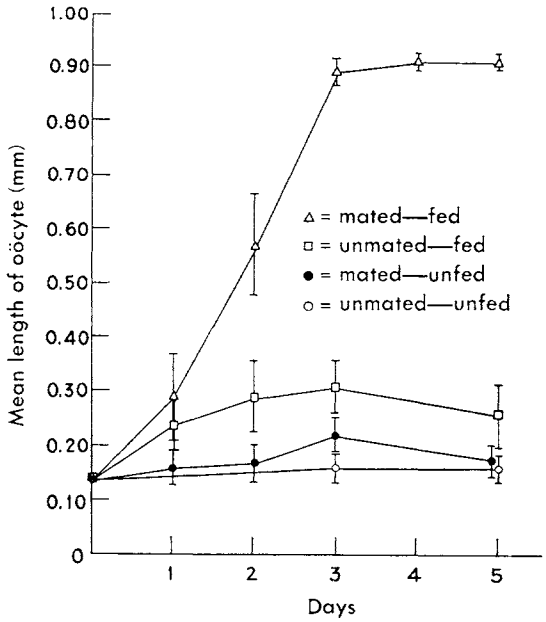

FIG. 8-4.—Lengths of 20 oocytes of groups of mated-fed, unmated-fed, mated-unfed, and unmated-unfed females measured on successive days. Mean and standard deviation for each (Davis 1964).

8-3d). In females that are mated but starved, virtually no maturation occurs (Davis 1964).

Büchner (1921) has described a pair of mycetomes alongside the gonads in *Cimex*; these bodies contain symbiotes which also invade other tissues, particularly the fat body and ovary. In the ovary they are very abundant in certain of the nurse cells of the end chamber, from where they pass through the nutritive cord into the yolk of the developing oöcyte. Thus the symbiotes are transmitted transovarially from one generation to the next.

The secretion of the corpus allatum has been shown to be essential for egg maturation in many but not in all insects. Its role in *C. lectularius* has been studied by Wigglesworth (1936), Mellanby (1939a), and Davis (1964). Ligatures (Fig. 8–5) were applied behind the head capsule at various stages in the reproductive process to deprive the remainder of the body of the corpus allatum hormone. Also, active corpora allata were implanted into ligatured bugs or into those in which the corpus allatum apparently was inactive. By these techniques it has been shown that the effects on egg production of both feeding and insemination are mediated by the corpus allatum.

In experiments on the role of feeding in corpus allatum activation,

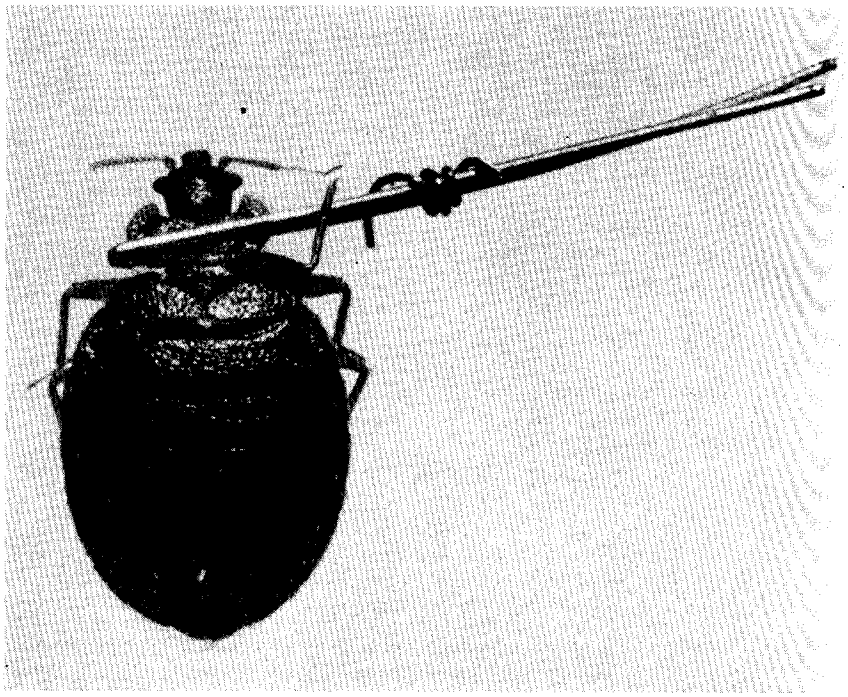

FIG. 8–5.—*Cimex lectularius* ligatured to control corpus allatum hormone (Davis, original).

mated females were ligatured at various intervals after feeding (Davis 1964). It was found that no eggs were produced by females ligatured within 10 hours after feeding, while after this period egg production increased directly with the time of ligation (Fig. 8–6). Females ligatured in the 10-hour period and receiving a corpus allatum implant can produce eggs. This critical period apparently represents the time required after feeding for the corpus allatum to become active and release hormone sufficient for egg production.

The failure of fed virgin females to produce eggs has been shown to be due to the inactivity of their corpus allatum (Davis 1964). Implantation of active corpora allata into such females results in the production of nonviable eggs, and at a rate only a little below that of mated females. Farnesol, a substance known to have an activity like the corpus allatum hormone, when applied to virgin females also results in egg production.

SEMINAL STIMULUS

The effect of insemination in activating the corpus allatum of *C. lectularius* has been studied by Davis (1965b) (Fig. 8–7). The mechanical

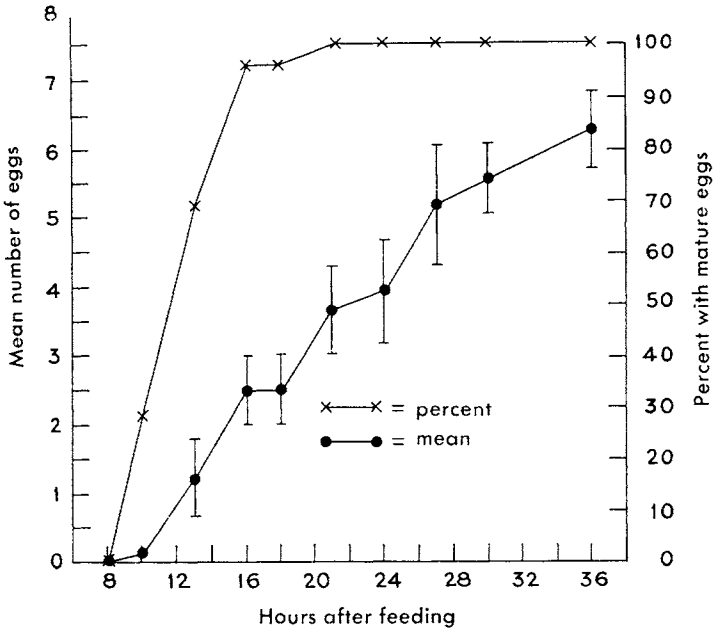

FIG. 8–6.—Egg production by mated females, allatectomized by ligation at various intervals after feeding (Davis 1964).

aspects of insemination play no role in this activation; neither a puncture of the ectospermalege nor the distention of the mesospermalege, produced by injecting physiological saline, results in egg production. Also, injection of seminal fluid or of unactivated spermatozoa does not result in the initiation of egg production. Surgical removal of the seminal conceptacles of mated females results first in the production of a batch of nonviable eggs and then in the stopping of egg production entirely. It is, therefore, concluded that the stimulus comes from the presence of spermatozoa in the conceptacula or lateral oviducts.

The time required for the seminal stimulus to become effective has been determined as follows (Davis 1965b). Females are mated 24 hours after feeding, and at various intervals after mating a ligature is applied behind the head. If the ligature is applied within 3 hours after mating, almost no eggs are produced, but the number increases abruptly after this time. Implantation of an active corpus allatum into females ligatured in the 3-hour period results in egg production. Therefore, 3 to 4 hours are required for the seminal stimulus to become effective. This period corresponds with the time required for the spermatozoa to reach the genital tract after insemination.

The length of time required for the seminal stimulus to become effective suggests that the stimulus is neural rather than humoral. This view

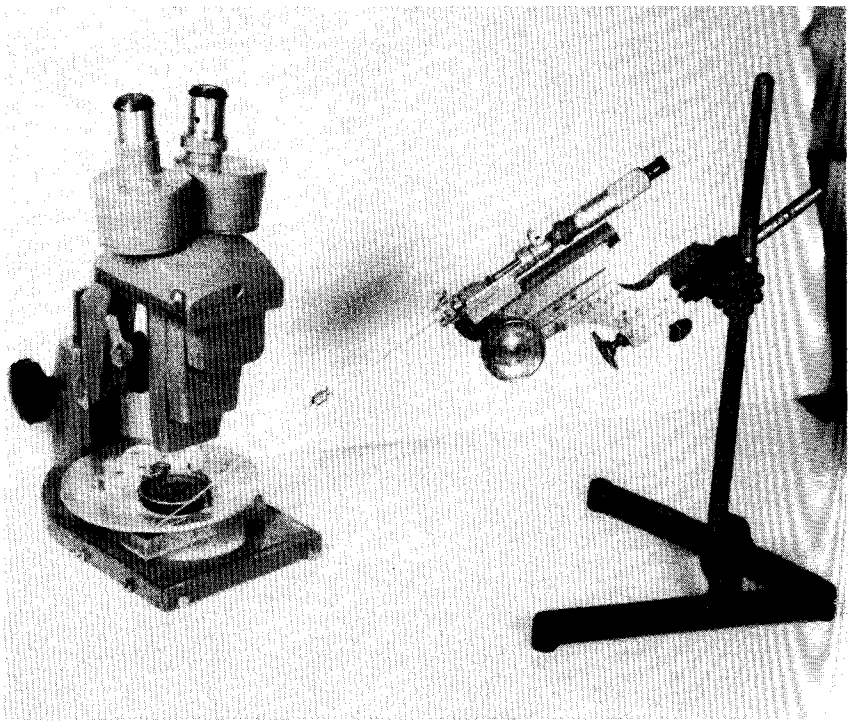

FIG. 8–7.—Apparatus for artificial insemination of Cimicidae (Davis, original).

has been partially confirmed by neurosurgical techniques (Davis 1965b). The nerves innervating the abdominal organs come from a metathoracic ganglionic mass which consists of the fused abdominal, meta-, and mesothoracic ganglia. If the nerve cord anterior to this ganglion is severed within 3 hours after mating, the stimulus is blocked. Implantation of an active corpus allatum into such females results in egg production.

Attempts to block the stimulus by cutting various abdominal nerves have been less successful (Davis 1965b). Cutting any 1 pair of abdominal nerves does not block the stimulus; cutting all of the abdominal nerves results in egg production regardless of mating and thus has the same effect as the stimulus. Cutting the abdominal nerves innervating the genital tract results in egg production by about 50% of both mated and unmated females. Since in this case the percentage is not higher in the mated females, the insemination apparently has no effect. These results suggest that the seminal stimulus results from summation of stimuli of many individual receptors on the genital tract.

9 Embryology

No detailed study on the embryology of Cimicidae has been published.[1] Hase (1917) described the gross appearance of the embryo in the egg of *C. lectularius* and recognized 5 stages in development.

Cobben studied living material of the Berkeley strain of *Cimex lectularius.* Parts of his manuscript are quoted here, with permission, prior to publication in a forthcoming general work on embryology of Hemiptera.

"*Chorion.* The chorion starts to be secreted about the time that the blastoderm of the embryo is formed (Davis, 1956). It is completely formed with a thickness of 15 μ in the neck region and about 10 μ elsewhere, when the germ-band invaginates. The inner air-filled layer is distinct in the anterior region. There it is 2.5 μ thick and the struts form large, irregular cells when seen in surface view. Posteriad, the struts are finer, shorter and more closely spaced. The short collar of the rim is margined externally with a thick, solid bar. The aeropyles do not reach this upper margin. They measure scarcely one micron in diameter and their number averages 150. Micropyles are absent, fertilization occurring just before the initiation of the chorion secretion.

"*Early embryogenesis.* About one-third of embryogenesis takes place within the ovary. The development of the embryo is roughly similar to that in other Cimicoidea having no lateral invagination: the germ-band is immersed with only the serosal contact at the cephalic site and blastokinesis is combined with a 180° rotation. In *Cimex,* the chorionic deposition starts much earlier than in *Anthocoris,* and only one egg at a time is formed in each ovariole. Moreover, at any one time there is not more than one fully formed egg in each ovary. In *Anthocoris,* the shell material starts to be laid down about the time that the germ-band invaginates and all ovarioles are producing more eggs at the same time. The shape-transformation of the band is different. In *Cimex,* the embryo invaginates in a straight line up to the subopercular part of the egg.

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[1] Heymons, R. (1899, Nova Acta, Abh. K. Leop.-Carol. Deutsch. Akad. Naturforsch. 74: 386) studied *Cimex dissimilis* (Fabricius) (not Horvath). This belongs in the family Pentatomidae.

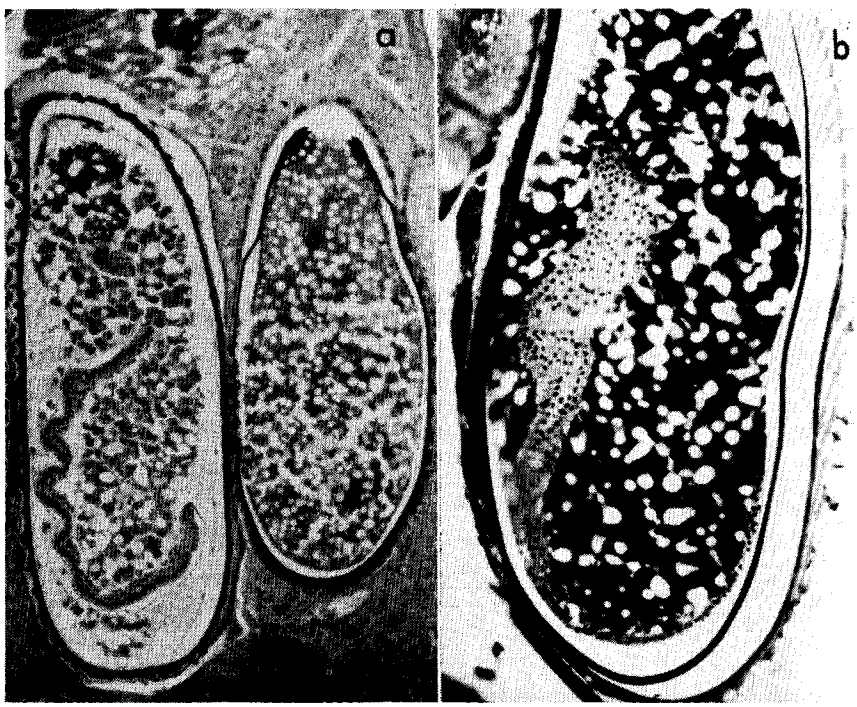

FIG. 9–1. a) *Aphrania vishnou*. Two eggs in the abdomen of a gravid female (top ends toward the head). At right, stage with peripheral blastoderm cells; left, invaginated germ band stage. b) *Crassicimex pilosus*. Egg in a gravid female in invaginated germ-band stage (Carayon).

Then, it shortens to make a ∫ in the posterior half of the egg. Again, a stretching-out is achieved, the maximum extent of which is reached at the time that the egg is dropped. In *Anthocoris* the blastopore is located somewhat higher up in the basal pole. The caudal and gnathal flexures are very distinct and have already arisen when the band has not yet surpassed the egg's middle. The later lengthening of the embryo before revolution never reaches the upper pole and "accordion-folding" is typical of the *Anthocoris* embryo at the time of the egg's release. It remains to be seen whether all these differences are constant enough to discriminate between the two families."

Several stages in embryonic development within a gravid female are shown for *Aphrania vishnou* Mathur in Figs. 9–1a and 9–2, and for *Crassicimex pilosus* Ferris and Usinger in Fig. 9–1b (Carayon, unpubl.).

Büchner (1923) described the method of symbiote transmission in *Cimex lectularius*. Infection takes place in the ovarioles via the nurse cells and the nutritive cords. Entering at the upper egg pole, the sym-

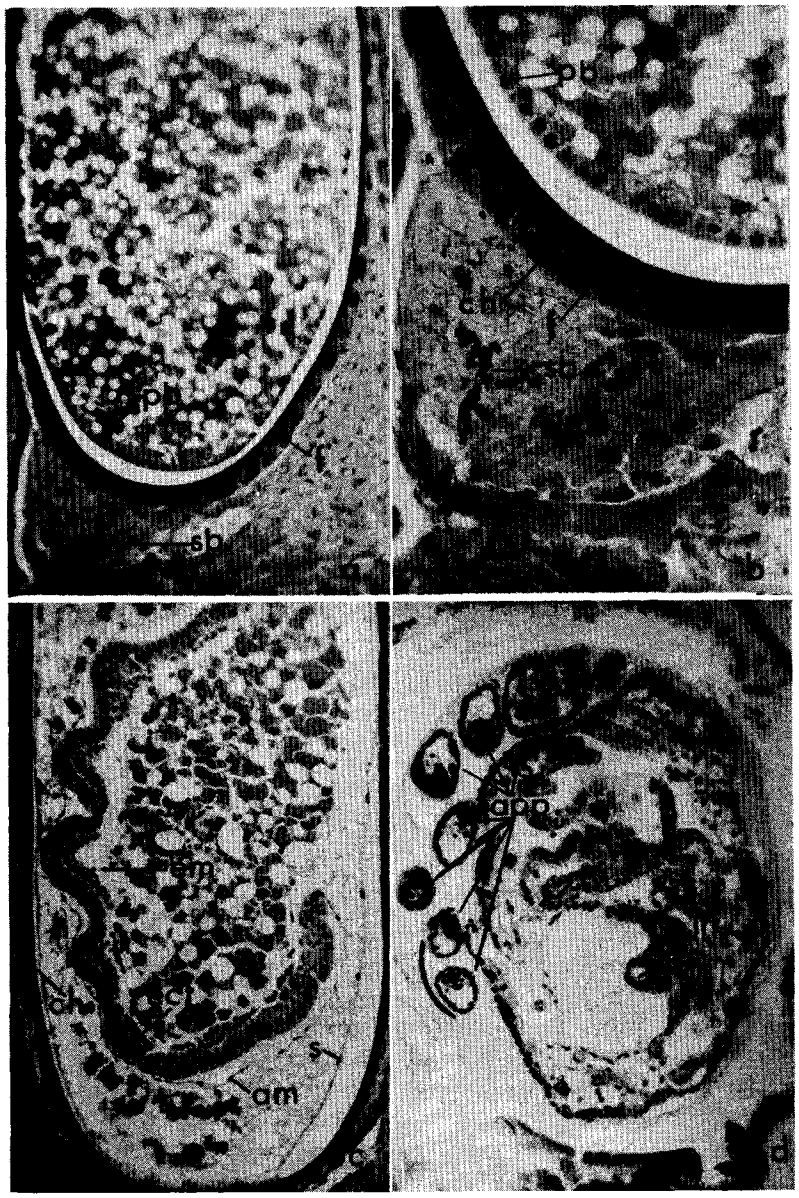

FIG. 9-2.—*Aphrania vishnou.* a) Egg in stage with peripheral blastoderm cells; b) same, further enlarged; c) egg in invaginated germ band stage; d) egg with embryo near the end of development (cross section) in genital tract of gravid female. pb= peripheral cells of blastoderm; ch=chorion, f=follicle; sb=syncitial body; em=endomesoderm; ect=ectoderm; am=amnion; s=serosa; in=intestine; app=appendages (Carayon).

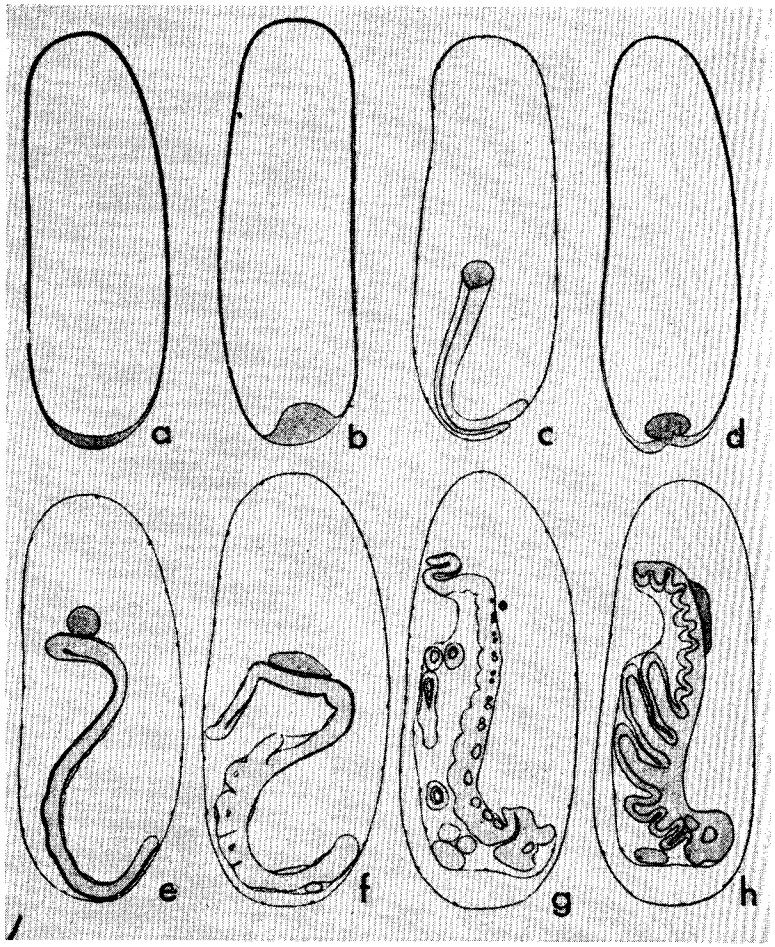

FIG. 9–3.—Transmission of symbiotes (dark mass) during embryonic development (Büchner 1923).

biotes are generally distributed, and later, when the yolk has formed, they are concentrated at the posterior pole. Eggs are fertilized at that time, and as the blastoderm forms, the chorion is laid down. As the germ band invaginates it carries the mass of mycetocytes into the yolk. When the appendages begin to form, the cell mass flattens and, before the development of the midgut and involution, it divides, each part going to its respective side of the abdomen where it develops into the mycetome of the adult. Thus the symbiotes are already in the developing oocytes and enter the egg via the nutritive strand. They take a place at the posterior pole and grow with the embryo through its invagination and later development (Fig. 9–3).

10 Cytology and Cytogenetics

by NORIHIRO UESHIMA
With a discussion of the inheritance of X chromosomes
by H. E. McKean

Chromosome cytology in the Cimicidae was first described by Slack (1938); shortly thereafter Darlington (1939) discussed the unique aspects of chromosome behavior in *Cimex columbarius* and *C. lectularius.* Further work with bed bug chromosomes has not been reported until quite recently. Ueshima (1963a) and Ryckman and Ueshima (1964) studied the *Cimex pilosellus* complex and the genus *Hesperocimex* and found a remarkable diversity of chromosome complements and development of supernumerary sex chromosomes. In the *Cimex pilosellus* complex, characteristics of the meiotic sequence were clearly demonstrated by the behavior of hetermorphic bivalents and trivalents in hybrids (Ueshima 1963a).

The Cimicidae, like most Hemiptera, have holokinetic chromosomes, i.e., chromosomes with diffuse kinetic activity having unique cytological features distinguishing them from those with kinetic activity localized in a single centromere. There is thus no centromere for aid in identifying mitotic chromosomes; in spermatogonial divisions in bed bugs, the chromosomes increase gradually in size, and all are similar in shape. Chromosome fragments maintain kinetic activity and may undergo normal maneuvers during division (Schrader 1947). In several distinct examples of holokinetic chromosomes the meiotic sequence is inverted. In the bed bug, the autosomes show typical behavior—they co-orient and separate reductionally at first anaphase, but the sex chromosomes auto-orient and separate equationally at the first metaphase and do not undergo reduction until the second division (Ueshima 1963a). Another unique feature is that sex chromosomes undergo "touch and go" pairing at the second division.

In all the species described, testes and ovaries were fixed in Carnoy or in an isopropyl-Carnoy solution (Ueshima 1963b). Most observations were made with fresh acetocarmine squashes, but some preparations were made by sectioning and staining with Feulgen. A camera lucida was used

for the drawings, and photographs of spermatogenesis were taken with a 35-mm camera and a Zeiss photomicroscope. Magnifications are indicated by the 10-μ lines. Sex chromosomes were identified by comparison of male and female complements. Species and sources of materials are listed in Table 10–1.

In all species the course of meiosis proved to be the same as in *C. lectularius* and other Heteroptera studied. Therefore, in the following descriptions, details of meiosis are given only when unique features not seen in *C. lectularius* have been observed.

DESCRIPTION OF CHROMOSOMES AND MEIOSIS

GENUS CIMEX

Cimex lectularius L.

Specimens from Berkeley, California; Monterrey and La Piedad, Mexico; Nagasaki, Japan; and Durtal, France.—The diploid chromosome numbers are 29 in the male and 30 in the female; there are 26 autosomes (13 pairs) in both sexes, and X_1X_2Y in the male (Fig. 10–1a, b) and $X_1X_1X_2X_2$ in the female (Fig. 10–1c).

It is almost impossible to analyze the early prophase of meiosis in these specimens. In the confused stage, the sex chromosomes (X_1, X_2, and Y) are revealed as heteropycnotic elements lying close together. In diakinesis the chromosomes become evident; the 2 members of each bivalent lie parallel or with their ends diverging and have 1 chiasma each as is usual in Heteroptera. In late diakinensis the sex chromosomes separate from each other and there are 16 chromosomal entities (Fig. 10–1g). Terminalization of the chiasmata is completed as condensation continues during prometaphase.

In the first metaphase, 13 autosomal tetrads and 3 sex-chromosome dyads (X_1, X_2, and Y) arrange themselves on the equatorial plate (Fig. 10–1h). The sex chromosomes are usually distinguishable from the autosomes not only because they are composed of 2 chromatids (4 in autosomes), but also because they usually stain less intensely. At the first division the autosomes divide reductionally while the sex chromosomes divide equationally.

The second metaphase, as usual in Heteroptera, directly follows the first without any resting stage; the sex chromosomes undergo "touch and go" pairing, the 2 X's lying on one side of the equatorial plate and the Y on the other, both always in the center of a ring formed by the 13 autosomes (Fig. 10–1i, j). At the second division the 2 X's move to one pole and the Y to the other (Fig. 10–1k), resulting in 2 kinds of spermatids, $13A + X_1X_2$ and $13A + Y$.

Specimens from Cairo, Egypt, and Moravia, Czechoslovakia.—The diploid chromosome numbers are 33 in the male and 38 in the female; there are 26 autosomes (13 pairs) in both sexes, plus $X_1X_2X_3X_4X_5X_6Y$

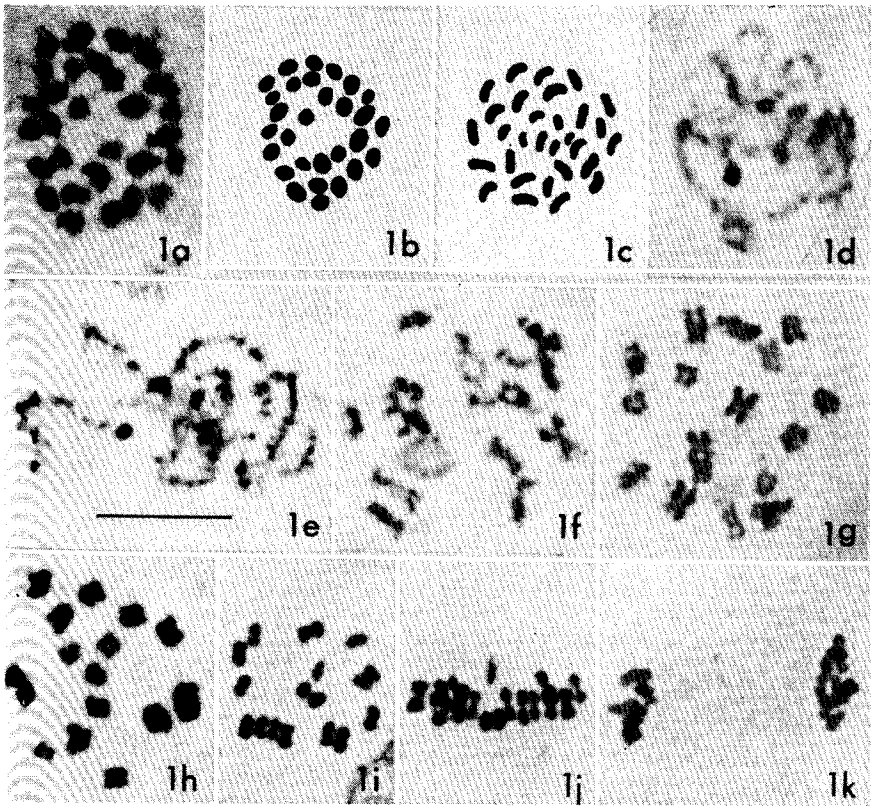

FIG. 10–1.—*C. lectularius* from Berkeley, California. a and d to k, photographs; b and c, camera lucida drawings. a and b, spermatogonial metaphase with 29 chromosomes; c, female somatic metaphase with 30 chromosomes; d, pachytene stage with heteropycnotic elements; e, late pachytene stage; f, diplotene stage; g, diakinesis with 13 bivalents and X_1X_2Y; h, prometaphase, terminalization of chiasma completed; i, second metaphase, sex chromosomes lie in center of ring formed by 13 autosomes; j, second metaphase (side view), X_1 and X_2 face one pole, Y faces the other; k, second telophase.

in the male (Fig. 10–2a, b) and 2 ($X_1X_2X_3X_4X_5X_6$) in the female (Fig. 10–2c).

The essential features of meiosis are the same as previously described, but there are 4 small and fully condensed heteropycnotic chromosomes during the diplotene stage (Fig. 10–2d). At the prometaphase, 13 autosomal tetrads and 7 sex-chromosome dyads are easily distinguishable. Twenty chromosomes arrange themselves on the plate (Fig. 10–2e). In the first division, 7 sex chromosomes divide equationally. At the second metaphase the 13 autosomes form a ring toward the periphery and the 7 sex chromosomes lie in its center (Fig. 10–2f); the 6 X's are removed

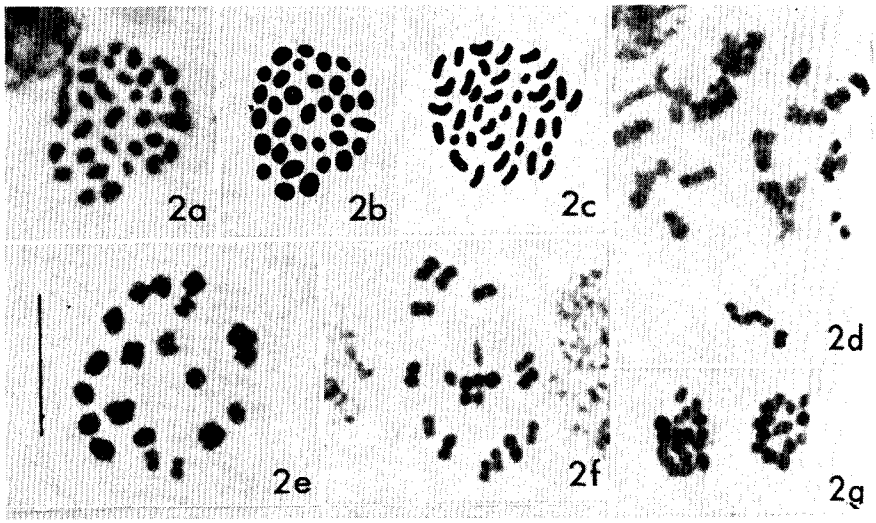

FIG. 10–2.—*C. lectularius* from Cairo, Egypt. a and d to g, photographs; b and c, camera lucida drawings. a and b, spermatogonial metaphase with 33 chromosomes; c, female somatic metaphase with 38 chromosomes; d, diplotene stage; e, prometaphase with 13 bivalents, 6X's and Y; f, second metaphase, sex chromosomes lie in center of ring formed by the autosomes, Y chromosome stained less intensely; g, second anaphase, 6X's segregate to one pole and Y to the other.

slightly from the equatorial plate toward one pole and the single Y toward the other. In the second anaphase the 6 X's go to one pole and the Y moves to the other (Fig. 10–2g).

Specimens from Columbus, Ohio.—The diploid chromosome number varies from 34 to 36 in different males (Fig. 10–3a to c) and from 39 to 42 in females (Fig. 10–3d to g). This variation is due to different numbers of X chromosomes—the complement of an individual with 34 chromosomes contains 13 pairs of autosomes, 7 X's, and a single Y; while complement of an individual with 36 consists of 13 pairs of autosomes, 9 X's, and a Y.

The meiotic processes are the same as in the other types previously described. At the prometaphase, 13 autosomal tetrads and 8 to 10 sex-chromosome dyads are encountered. In the first metaphase, 21 to 23 chromosomes arrange themselves on the equatorial plate (Fig. 10–3h to j). At the second metaphase the sex chromosomes are displaced, as previously described, slightly toward opposite poles but always in the center of a ring formed by the autosomes. The results are summarized in Table 10–2.

Specimens of a DDT-Resistant Strain from Pittsburgh, Penn.—The diploid chromosomes number 35 in the male (Fig. 10–4a) and 40 in the female (Fig. 10–4b). At the first metaphase the 21 chromosomes arrange

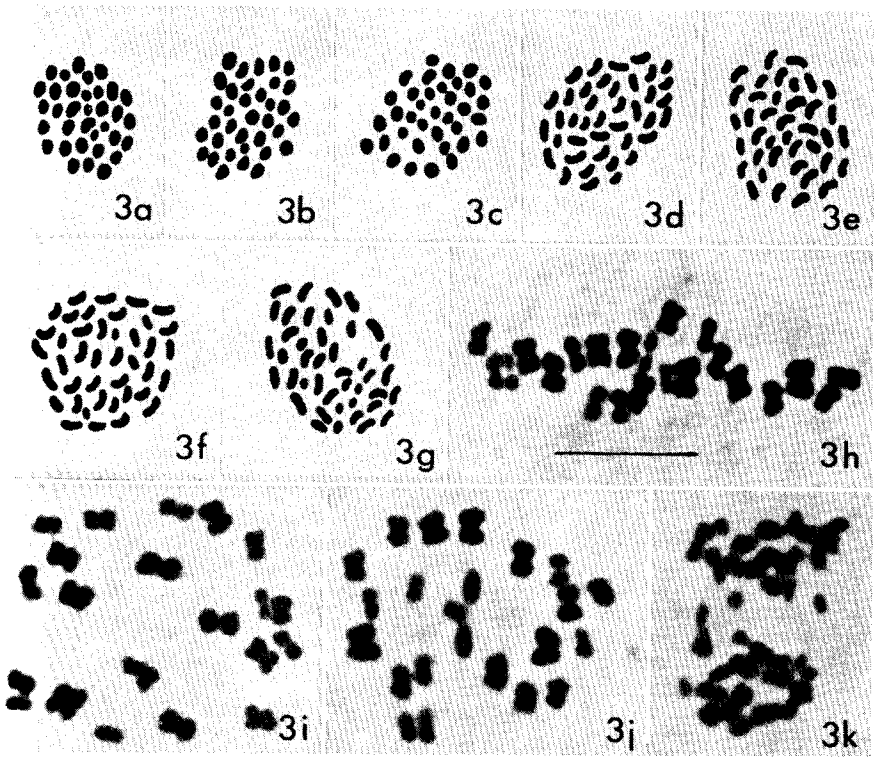

FIG. 10–3.—*C. lectularius* from Columbus, Ohio. a to g, camera lucida drawings; h to k, photographs. a, spermatogonial metaphase with 34 chromosomes; b, spermatogonial metaphase with 35 chromosomes; c, spermatogonial metaphase with 36 chromosomes; d, female somatic metaphase with 39 chromosomes; e, female somatic metaphase with 40 chromosomes; f, female somatic metaphase with 41 chromosomes; g, female somatic metaphase with 42 chromosomes; h, first metaphase with 22 chromosomes; i, first metaphase with 21 chromosomes; j, first metaphase with 23 chromosomes; k, first anaphase with lagging chromosomes.

themselves on the equatorial plate (Fig. 10–4c); in the second, 6 X's and Y lie in the center of a ring formed by the autosomes, and one of the dyads lies separately between the ring formed by the 13 autosomes and the centrally located sex chromosomes (Fig. 10–4d, e). Because no lagging of chromosomes is found in the second anaphase, it is presumed that the constituent chromatids separate normally. Although this separate entity behaves differently from both autosomes and sex chromosomes in the secondary spermatocyte, its behavior is more like that of the autosomes. It appears, therefore, that there are 14 autosomes; the origin of the extra pair of homologues is not known.

Hybrid: Specimens from Berkeley (♀) × *Specimens from Cairo* (♂) *and the Reciprocal.*—As described above, Berkeley specimens have 29 chromo-

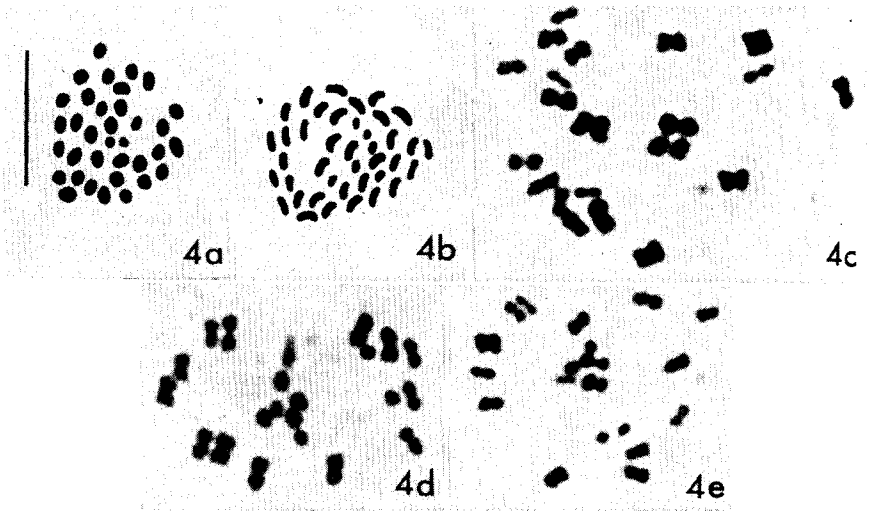

FIG. 10–4.—DDT-resistant strain of *C. lectularius* from Pittsburgh. a and b, camera lucida drawings; c to e, photographs. a, spermatogonial metaphase with 34 chromosomes; b, female somatic metaphase with 40 chromosomes; c, first metaphase with 21 chromosomes; d and e, second metaphase, 6X's and Y lie in center of ring formed by the autosomes and 2 monads lie near ring separately.

somes, the males with 13 pairs of autosomes and X_1X_2Y, while the Cairo specimens have 33 chromosomes, the males with 13 pairs of autosomes and $X_1X_2X_3X_4X_5X_6Y$. In order to obtain information on the possible origin and transmission of supernumerary X chromosomes, specimens of the 2 chromosomal types were hybridized.

To obtain the first progeny (F_1), last-instar nymphs were isolated individually in small vials in each parental colony. Ten single-pair matings were made and the chromosome complement and meiotic behavior of the F_1 males were observed. In nearly all crosses, 15 males were studied cytologically, but in some, only 10 were available. In the F_1, the vast majority of individuals had the complement $26A + X_1X_2Y$, expected if they received a Y from the Cairo fathers and 2 X chromosomes from the Berkeley mothers (Table 10–3). In single-pair matings no. 4, 6, and 9, the number of X chromosomes was greater than expected. In the first progeny of the reciprocal cross of *C. lectularius* (Cairo ♀ × Berkeley ♂), 15 males from each of 10 vials of single-pair matings, or a total of 150 specimens, were used for cytological study (Table 10–4). The chromosome complement in the first progeny of this cross was more variable than the previous one. Ten of 150 specimens observed cytologically were $26A + X_1X_2X_3Y$, 10 were $26A + X_1X_2X_3X_4Y$, 84 were $26A + X_1X_2X_3X_4X_5Y$, and 22 were $26A + X_1X_2X_3X_4X_5X_6Y$. The data from the recipro-

cal crosses indicate that transmission of supernumerary X chromosomes is mainly maternal.

The meiotic processes in these crosses are quite normal without any special irregularity, although lagging X chromosomes were very rarely observed in the first anaphase, indicating a possible non-disjunction.

The second progeny of these crosses were obtained by the interbreeding of the F_1, 10 males and 10 females per vial selected at random, and successive progenies were obtained by the same procedure.

The results of the fifth and successive progenies are not given in the tables. The chromosome complement in these *C. lectularius* crosses was fixed in the sixth progeny—usually at 26A + X_1X_2Y for Berkeley ♀ × Cairo ♂, and most often at 26A + $X_1X_2X_3X_4X_5Y$ for Cairo ♀ × Berkeley ♂.

Cimex columbarius Jenyns

The diploid chromosome numbers are 29, consisting of 13 pairs of autosomes and X_1X_2Y in the male (Fig. 10–5a), and 30, consisting of 13 pairs of autosomes and $X_1X_1X_2X_2$ in the female (Fig. 10–5b). At the first spermatocyte metaphase the 13 autosomes and 3 sex chromosomes arrange themselves on the equatorial plate (Fig. 10–5d). At the second metaphase the X_1, X_2, and Y lie in the center of a ring formed by the 13 autosomes; they undergo "touch and go" pairing and separate to opposite poles (Fig. 10–5e).

Hybrids of *C. lectularius* × *Cimex columbarius*

The methods of obtaining the progeny and observing the chromosome complement and meiotic behavior were the same as in the *C. lectularius* cross of Berkeley × Cairo. The first progeny of the hybrids were obtained by single-pair matings, and further progenies were obtained by interbreeding of the first progeny.

C. lectularius (Berkeley ♀) × Cimex columbarius (♂) and the Reciprocal.—As just described, both *C. lectularius* from Berkeley and *Cimex columbarius* have 29 chromosomes, 13 pairs of autosomes and X_1X_2Y in the male, and 30, 13 pairs of autosomes and $X_1X_1X_2X_2$ in the female. The chromosome complement and meiotic behavior were observed in the hybrids, no progeny of which were obtained in the no. 8 cross of *C. lectularius* (♀) × *Cimex columbarius* (♂) and in the no. 3 and 6 crosses of *Cimex columbarius* (♀) × *C. lectularius* (♂) (Tables 10–5, 10–6). In the hybrid *C. lectularius* (♀) × *Cimex columbarius* (♂), 107 first-generation specimens were studied cytologically—of these, 57 were 26A + X_1X_2Y, 37 were 26A + $X_1X_2X_3Y$, 5 were 26A + $X_1X_2X_3X_4Y$, and 8 were 26A + $X_1X_2X_3X_4X_5Y$. In the fourth generation of the hybrids, 119 of 135 specimens observed were 26A + X_1X_2Y and the remaining 16 were 26A + $X_1X_2X_3Y$. No other chromosome complements were observed. In the 10th generation of the hybrids the chromosome number of

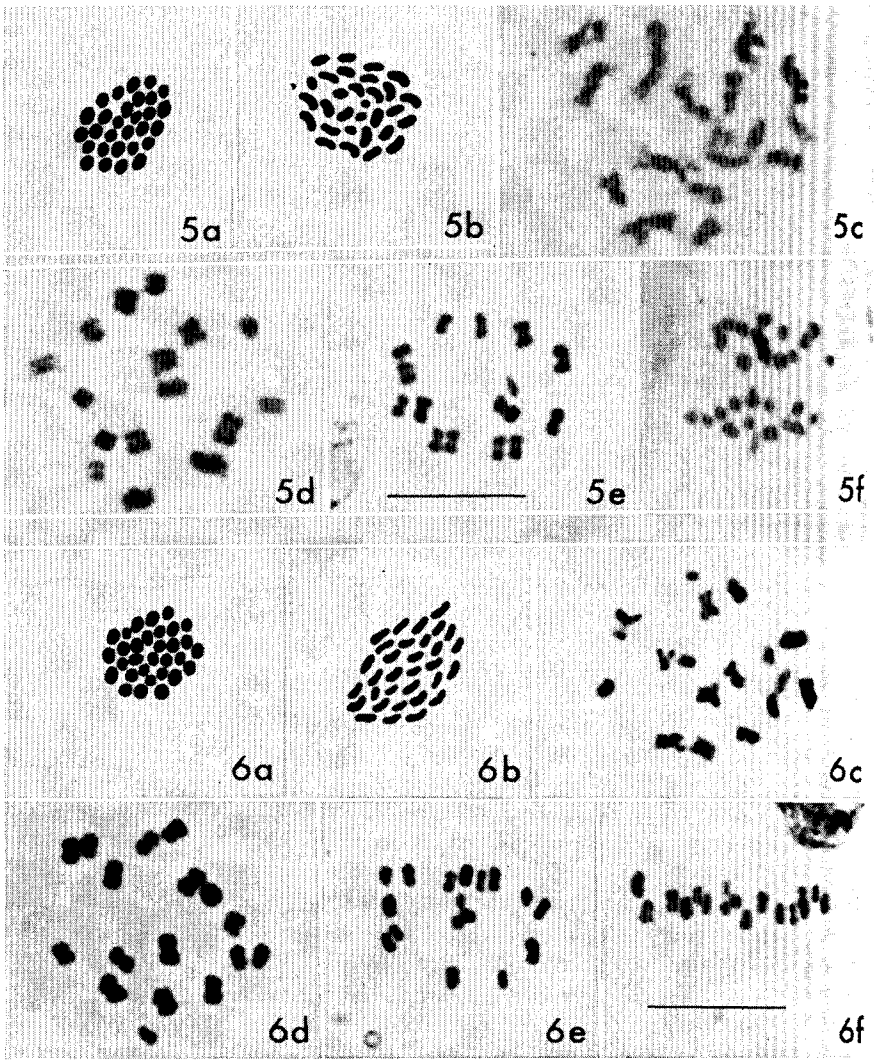

FIG. 10–5.—*Cimex columbarius*. a and b, camera lucida drawings; c to f, photographs. a, spermatogonial metaphase with 29 chromosomes; b, female somatic metaphase with 30 chromosomes; c, late diplotene stage; d, prometaphase with 13 bivalents and X_1X_2Y; e, second metaphase; f, second anaphase.

FIG. 10–6.—*Cimex hemipterus*. a and b, camera lucida drawings; c to f, photographs. a, spermatogonial metaphase with 31 chromosomes; b, female somatic metaphase with 32 chromosomes; c, early diakinesis; d, first metaphase with 14 bivalents and X_1X_2Y; e, second metaphase, X_1X_2Y lie in center of ring formed by the 14 autosomes; f, second metaphase, side view.

all specimens observed was completely stabilized at 26 + X_1X_2Y. As shown in Table 10–6, the reciprocal cross *Cimex columbarius* (♀) × *C. lectularius* (♂) was constant at 26A + X_1X_2Y, even in the first generation.

The meiotic processes in the hybrids were quite normal, although lagging X chromosomes were rarely observed, indicating a possible nondisjunction. There seemed to be no serious difficulty in pairing of autosomes between these 2 species, although genetic isolation is obvious (Ueshima 1964).

C. lectularius (Cairo ♀) × Cimex columbarius (♂) and the Reciprocal.—As just described, *C. lectularius* from Cairo has 33 chromosomes consisting of 13 pairs of autosomes and $X_1X_2X_3X_4X_5X_6Y$ in the male, while *Cimex columbarius* has 29 chromosomes consisting of 13 pairs of autosomes and X_1X_2Y in the male. In the first generation of the hybrids of *C. lectularius* × *Cimex columbarius,* a total of 105 specimens were used for cytological observations (Table 10–7)—12 were 26A + $X_1X_2X_3Y$, 11 were 26A + $X_1X_2X_3X_4Y$, 73 were 26A + $X_1X_2X_3X_4X_5Y$, and 9 were 26A + $X_1X_2X_3X_4X_5X_6Y$. Of 135 fourth-generation specimens analyzed cytologically, 42 were 26A + $X_1X_2X_3Y$, 3 were 26A + $X_1X_2X_3X_4Y$, 75 were 26A + $X_1X_2X_3X_4X_5Y$, and 15 were 26A + $X_1X_2X_3X_4X_5X_6Y$. In the 10th generation (not given in Table 10–7), all 90 specimens observed cytologically were 26A + $X_1X_2X_3X_4X_5Y$.

In the reciprocal cross *Cimex columbarius* (♀) × *C. lectularius* (♂), the chromosome number was very stable (Table 10–8). In the first generation, 4 of 68 specimens observed were 26A + $X_1X_2X_3Y$ and 64 were 26A + X_1X_2Y. In the 3rd and 10th generations, no deviation from 26A + X_1X_2Y was observed.

The meiotic process in the hybrids was quite normal and no peculiar pairing or irregularity was observed, although very rarely there was some lagging of chromosomes in the first anaphase, indicating a possible nondisjunction of sex chromosomes.

Cimex hemipterus F.

The chromosome complement of this species is 31, consisting of 14 pairs of autosomes and X_1X_2Y in the male (Fig. 10–6a), and 32, consisting of 14 pairs of autosomes and $X_1X_1X_2X_2$ in the female (Fig. 10–6b). Seventeen chromosomes arrange themselves on the equator at the first spermatocyte metaphase (Fig. 10–6d). In the second metaphase 14 autosomes form a ring, while the X_1X_2Y chromosomes lie in its center (Fig. 10–6e, f).

Cimex pipistrelli Jenyns, *Cimex stadleri* Horvath, *Cimex japonicus* Usinger

The diploid complement of these species consists of 31 chromosomes, 14 pairs of autosomes and X_1X_2Y in the male (Fig. 10–7a, 10–8a, 10–9a),

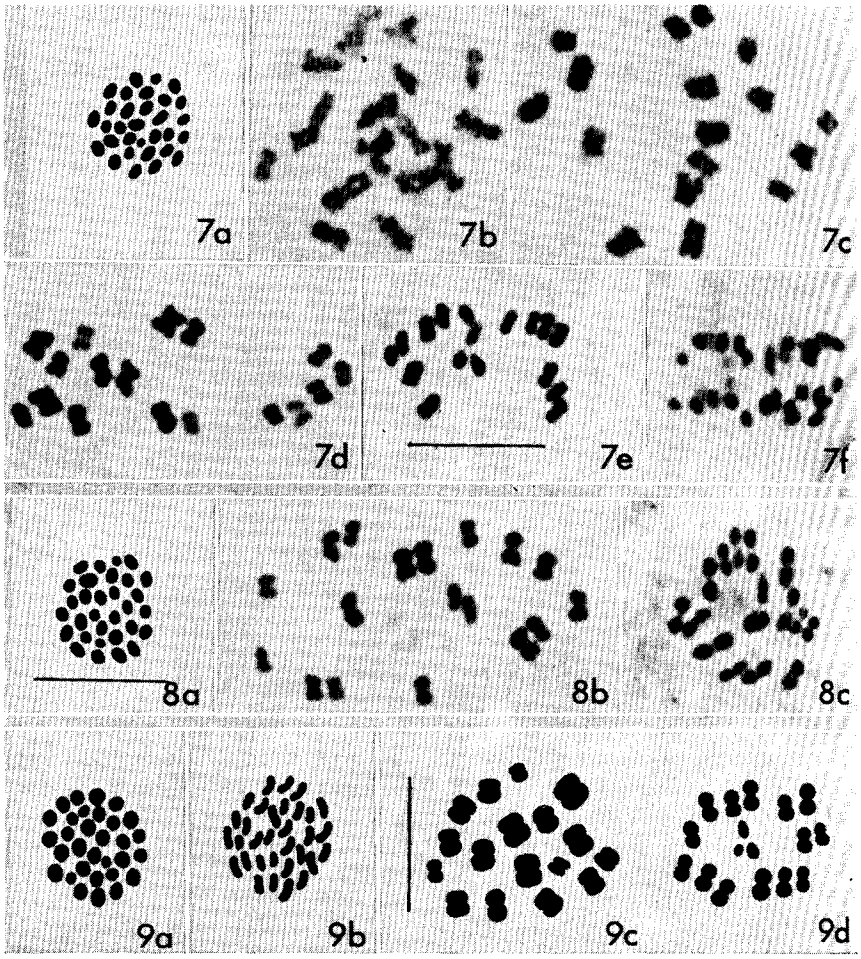

FIG. 10-7.—*Cimex pipistrelli*. a, camera lucida drawing; b to f, photographs. a, spermatogonial metaphase with 31 chromosomes; b, diplotene stage; c, diakinesis; d, first metaphase with 17 chromosomes; e, second metaphase, sex chromosomes lie in center of ring formed by the autosomes; f, second anaphase.

FIG. 10-8.—*Cimex stadleri*. a, camera lucida drawing; b and c, photographs. a, spermatogonial metaphase with 31 chromosomes; b, first metaphase with 17 chromosomes; c, second metaphase, X_1X_2Y lie in center of ring formed by the autosomes.

FIG. 10-9.—*Cimex japonicus*. a to d, camera lucida drawings. a, spermatogonial metaphase with 31 chromosomes; b, female somatic metaphase with 32 chromosomes; c, first metaphase with 17 chromosomes; d, second metaphase, X_1X_2Y lie in center of ring formed by the 14 autosomes.

and 32 chromosomes, 14 pairs of autosomes and $X_1X_1X_2X_2$ in the female (Fig. 10–9b). The first spermatocyte metaphase shows 17 chromosomes arranged on the equator (Fig. 10–7d, 10–8b, 10–9c). At second metaphase, 3 sex chromosomes, X_1, X_2, and Y, always lie in the center of a ring formed by the autosomes; X_1 and X_2 segregate from Y (Fig. 10–7e, 10–8c, 10–9d).

Cimex latipennis Usinger and Ueshima

The diploid chromosome complement of this species is 30—14 pairs of autosomes with XY in the male (Fig. 10–10a) and XX in the female (Fig. 10–10b). The X chromosome is the largest component of the chromosome set and is easily distinguished from the others. There are 2 heteropycnotic elements, the X and Y, lying close together in the confused stage; this situation may persist into diakinesis. At the first metaphase, 14 autosomal tetrads and the X and Y arrange themselves on the equator of the spindle (Fig. 10–10d). As the second spermatocyte metaphase plate is formed, the X and Y move to the center of a ring formed by the autosomes and undergo "touch and go" pairing (Fig. 10–10e, f). The X chromosome is distinctly larger than the Y. In the second anaphase, 14 autosomes and the X move to one pole; 14 autosomes and the Y go to the other.

Cimex pilosellus Horvath

The chromosome numbers of this species in the diploid are 31 in the male and 32 in the female. The spermatogonial metaphase reveals 14 pairs of autosomes and X_1X_2Y (Fig. 10–11a) and the female somatic metaphase 32 chromosomes (Fig. 10–11b). Seventeen chromosomes, 14 autosomes, and 3 sex chromosomes arrange themselves in the first spermatocyte metaphase plate (Fig. 10–11d, e). In the second metaphase the X_1X_2Y always lie in the center of a ring formed by 14 autosomes (Fig. 10–11f); the X_1 and X_2 are almost equal in size and the Y is smaller than either X_1 or X_2.

Cimex brevis Usinger and Ueshima, *Cimex adjunctus* Barber

The diploid chromosome numbers of these species are 33, consisting of 14 pairs of autosomes and $X_1X_2X_3X_4Y$ in the male (Fig. 10–12a, 10–13a), and 36, consisting of 14 pairs of autosomes and $2(X_1X_2X_3X_4)$ in the female (Fig. 10–12b). In the spermatogonial metaphase the 4 X chromosomes are distinguishable because of their smaller size; the Y chromosome is not distinguishable from the autosomes in the gonial metaphase plate. Five heteropycnotic elements lie close together in the confused stage. Fourteen autosomal tetrads and 5 sex-chromosomal dyads are easily recognized during the prometaphase. The first spermatocyte metaphase reveals 19 chromosomes (Fig. 10–12e to g, 10–13c). At the second metaphase the 14 autosomes form a ring at the periphery of the plate

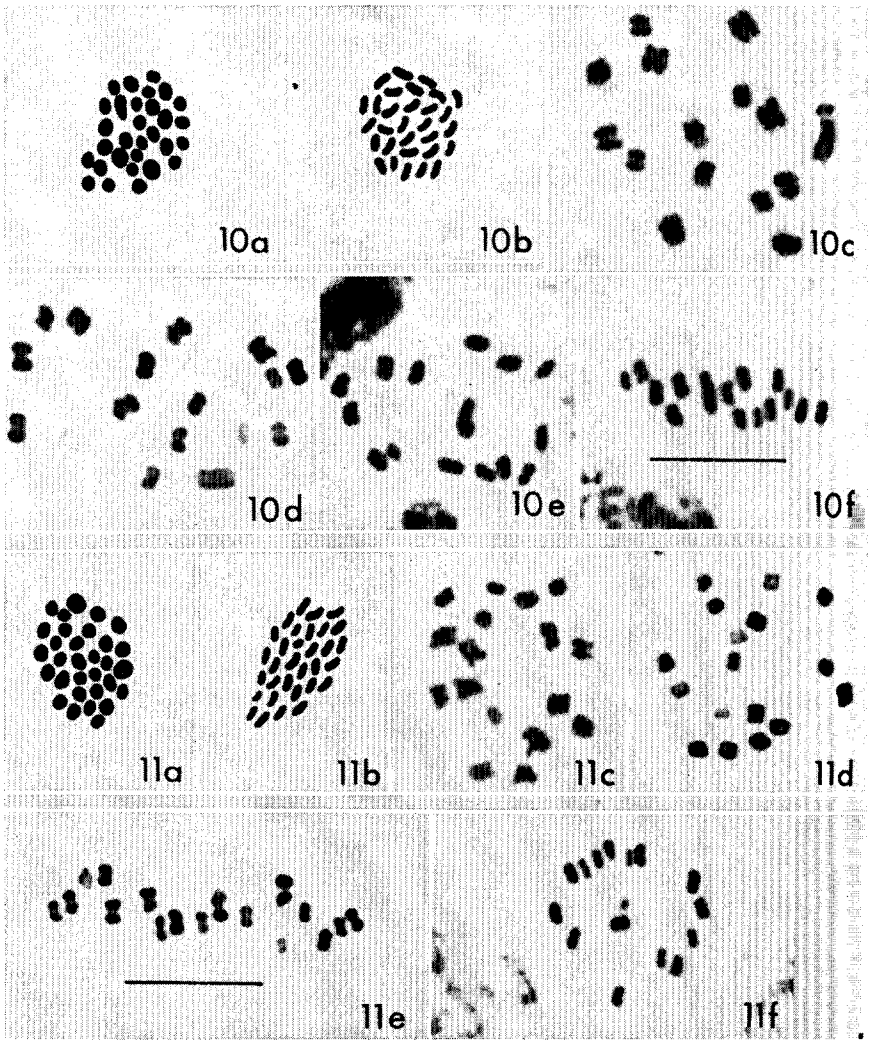

FIG. 10–10.—*Cimex latipennis*. a and b, camera lucida drawings; c to f, photographs. a, spermatogonial metaphase with 30 chromosomes; b, female somatic metaphase with 30 chromosomes; c, prometaphase with 14 tetrads and X and Y dyads; d, first spermatocyte metaphase with 16 chromosomes; e, second spermatocyte metaphase, X and Y lie in center of ring formed by 14 autosomes; f, second metaphase, side view.

FIG. 10–11.—*Cimex pilosellus*. a and b, camera lucida drawings; c to f, photographs. a, spermatogonial metaphase with 31 chromosomes; b, female somatic metaphase with 32 chromosomes; c, prometaphase with 14 autosomes and X_1X_2Y; d, first spermatocyte metaphase with 17 chromosomes; e, first spermatocyte metaphase, side view; f, second spermatocyte metaphase, X_1X_2Y lie in center of ring formed by the autosomes.

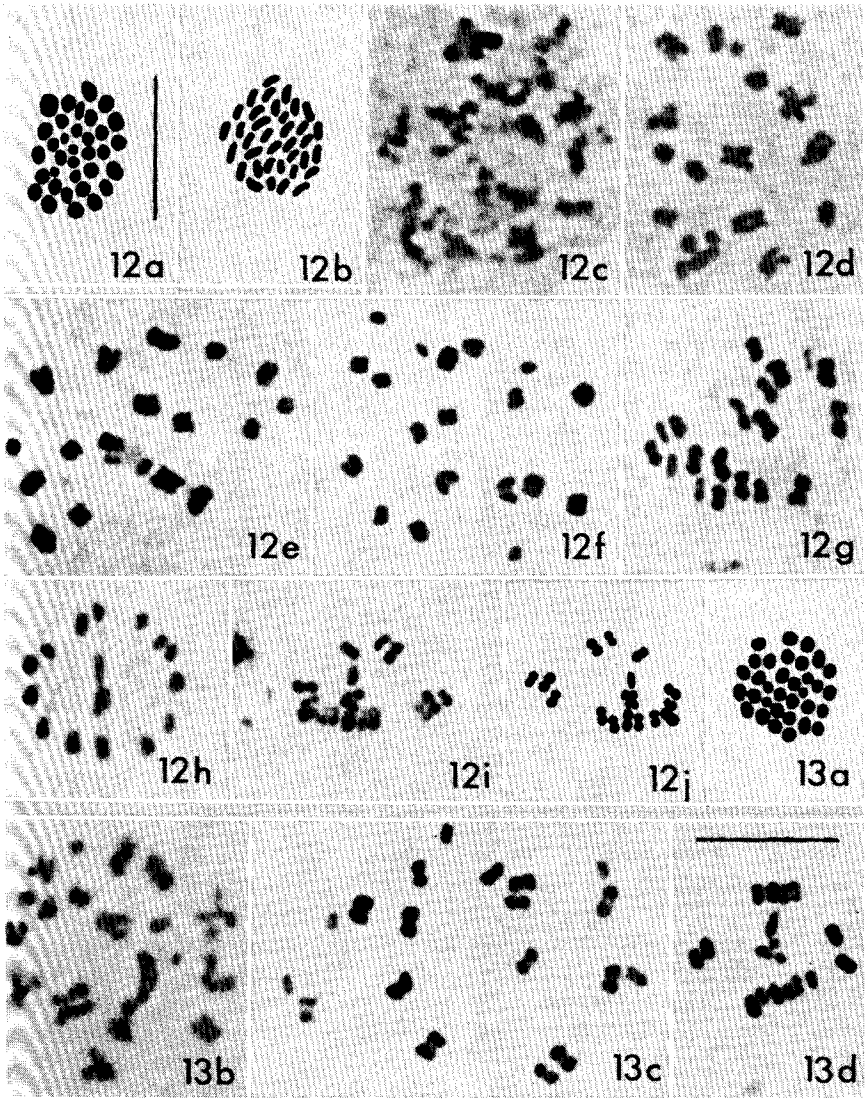

FIG. 10–12.—*Cimex brevis*. a, b, and j, camera lucida drawings; c to i, photographs. a, spermatogonial metaphase with 33 chromosomes; b, female somatic metaphase with 36 chromosomes; c, early diplotene stage, sex chromosomes are heteropycnotic; d, early diakinesis; e, late diakinesis with 14 autosomal tetrads and $X_1X_2X_3X_4Y$ dyads; f, prometaphase with 19 chromosomes; g, first metaphase; h to j,, second metaphase, 14 autosomes form ring and sex chromosomes take a central position.

FIG. 10–13.—*Cimex adjunctus*. a, camera lucida drawing; b to d, photographs. a, spermatogonial metaphase with 33 chromosomes; b, pachytene stage; c, first spermatocyte metaphase with 19 chromosomes; d, second spermatocyte metaphase, sex chromosomes lie in center of ring formed by 14 autosomes.

with the sex chromosomes in the center (Fig. 10–12h to j, 10–13d). In the second anaphase the 4 X chromosomes move to one pole and the Y to the other. The second division results in 2 kinds of spermatids—14A + $X_1X_2X_3X_4$ and 14A + Y.

Cimex antennatus Usinger and Ueshima

The diploid chromosome number of this species is 24—11 pairs of autosomes with XY in the male (Fig. 10–14a) and 2X in the female (Fig. 10–14b). In the spermatogonial metaphase, 2 pairs of autosomes are larger than the others, while the remaining 9 pairs gradually decrease in size. The X chromosome is the largest component in the chromosome set and the Y the smallest. At the first metaphase the 11 autosomal tetrads and the X and Y dyads are arranged at the equator of the spindle (Fig. 10–14d). At second metaphase the 11 autosomes form a ring toward the periphery, and the X and Y lie in the center (Fig. 10–14e).

Cimex incrassatus Usinger and Ueshima

The chrosome complement of this species is 22—10 pairs of autosomes plus XY in the male (Fig. 10–15a) and XX in the female. Although the X chromosome is the largest component in the spermatogonial metaphase plate and is easily recognized, the Y is a medium-sized chromosome and is not distinguishable from the autosomes. In the first spermatocyte metaphase, 10 autosomal bivalents and the X and Y are present (Fig. 10–15b). At the second metaphase the X and Y lie in the center of a ring formed by the 10 autosomes (Fig. 10–15c) and pass to the opposite poles on separation.

Hybrid of *Cimex antennatus* (♀) × *Cimex incrassatus* (♂)

All spermatogonial metaphase plates have 23 chromosomes (Fig. 10–16a) as expected from the combination of a *Cimex antennatus* egg (11A + X) and a *Cimex incrassatus* sperm (10A + Y). Evidence of abnormality or irregularity in the spermatogonial cells is not observed until the confused stage, in which there are heteropycnotic elements in addition to the sex chromosomes (Fig. 10–16b). Heteropycnotic segments appear in the diplotene stage (Fig. 10–16c). In early diakinesis there are 12 chromosome configurations—9 bivalents, 1 trivalent, and the X and Y univalents (Fig. 10–16d to f). Although the 2 chromosomes of each bivalent lie parallel or with their ends diverging, 8 of the 9 bivalents are heteromorphic and all usually have 1 chiasma (more than 1 chiasma in bivalents had never been observed). Although the chiasma is usually terminal, some are interstitial. Eighteen of 100 diakinesis cells have 1 unterminalized chiasma (Fig. 10–16f) and 3 cells have 2 (Fig. 10–16e). The trivalent always has 2 chiasmata (Fig. 10–16e, f) and is undoubtedly composed of 3 chromosomes, 2 maternal and 1 paternal.

The first metaphase again clearly shows 9 bivalents, of which 8 are

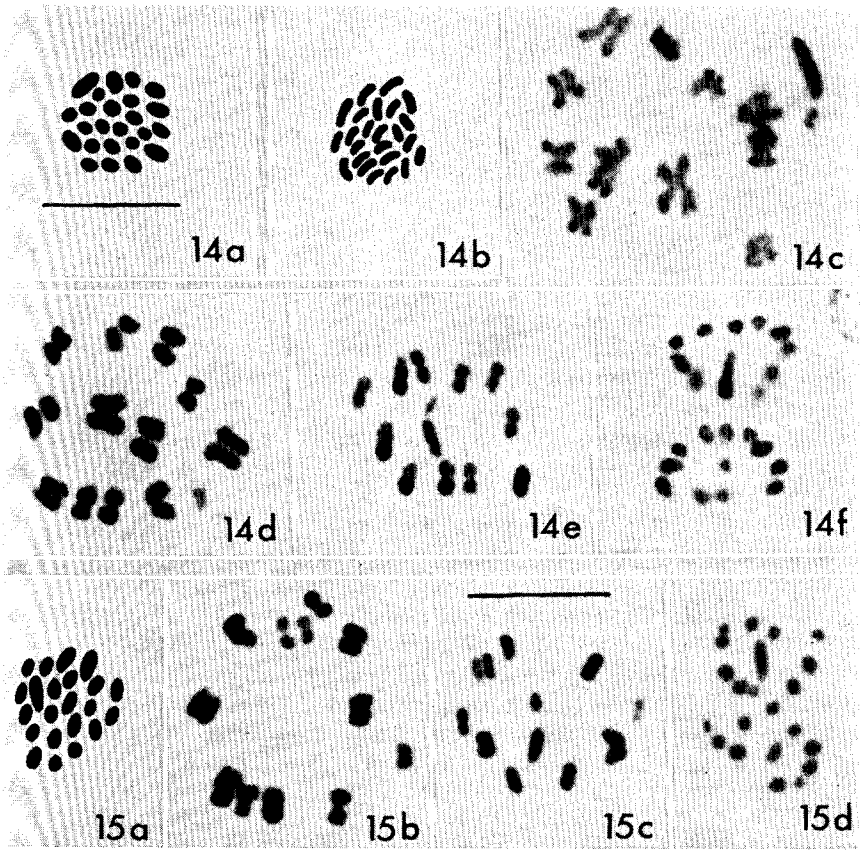

FIG. 10–14.—*Cimex antennatus*. a and b, camera lucida drawings; c to f, photographs. a, spermatogonial metaphase with 24 chromosomes; b, female somatic metaphase with 24 chromosomes; c, early diakinesis, X and Y lie close together; d, first spermatocyte metaphase, Y stains less intensely; e, second spermatocyte metaphase, the 11 autosomes form a ring toward the periphery, and X and Y lie in center; f, second anaphase, X and Y segregate to opposite poles.

FIG. 10–15.—*Cimex incrassatus*. a, camera lucida drawing; b to d, photographs. a, spermatogonial metaphase with 22 chromosomes; b, first spermatocyte metaphase with 10 tetrads and the X and Y dyads; c, second spermatocyte metaphase, sex chromosomes lie in center of ring formed by 10 autosomes, X chromosome distinctly larger than Y; d, second anaphase.

heteromorphic, 1 trivalent, and the X and Y (Fig. 10–16h, i). No particular arrangement of chromosomes in the first metaphase plate is evident. In the heteromorphic bivalents the 2 smaller chromatids are always oriented toward 1 pole and 2 larger ones toward the other (Fig. 10–16i), thus demonstrating co-orientation at the first metaphase. In the trivalent, 2 of the 6 chromatids are oriented toward one pole and 4 toward the other. On the other hand, the X and Y dyads are showing auto-orientation—at first anaphase, 29 of 120 such anaphase figures revealed a lagging dyad on the spindle (Fig. 10–16j), and one had a chromatid bridge (Fig. 10–16k); the others seemed to have no difficulties or irregularities in dividing.

As a result of the first division, 2 kinds of second metaphases appear as expected from a 1:2 separation of the trivalent—these are 10A + XY and 11A + XY (Fig. 10–16l, m). In both kinds of second metaphase the autosomes form a ring toward the periphery and the X and Y lie in the center. All autosomes in the second metaphase are uniform and no heteromorphic autosome dyads have been observed. In the second anaphase very little irregularity is seen (Fig. 10–16r); the X and Y move to opposite poles. As a result of the second division there are 4 types of spermatids: 11A + X, 11A + Y, 10A + X, and 10A + Y.

Hybrid of *Cimex incrassatus* (♀) × *Cimex antennatus* (♂)

The reciprocal cross is the same in every aspect of chromosome cytology as that just described. All spermatogonial metaphase plates have 23 chromosomes as expected from the combination of a *Cimex incrassatus* egg (10A + X) and a *Cimex antennatus* sperm (11A + Y). At the first spermatocyte metaphase there are 9 bivalents, of which 8 are heteromorphic and 1 is trivalent, and the X and Y. In the first anaphase some difficulties and irregularities in dividing are observed. At the second metaphase the same 2 kinds of chromosome complements are again observed.

Hybrid of *Cimex antennatus* (♀) × *Cimex brevis* (♂)

All spermatogonial metaphase plates have 27 chromosomes (Fig. 10–17a) as expected from the combination of a *Cimex antennatus* egg (11A + X) and a *Cimex brevis* sperm (14A + Y). In the spermatogonial metaphase and up to the confused stage of spermatogenesis, no abnormality or irregularity is observed. In the confused stage, heteropycnotic elements in addition to the sex chromosomes appear (Fig. 10–17b). Heterochromatic segments are visible at diplotene (Fig. 10–7d), although no heterochromatic segments are seen in the spermatogenesis of either parental species. In diakinesis, 8 bivalents, 3 trivalents, and X and Y (Fig. 10–17e) are usual, but in some cases 1 or 2 trivalents and 1 or 2 univalents are present instead. All bivalents appear to be heteromorphic, thus demonstrating the hybrid nature of these insects.

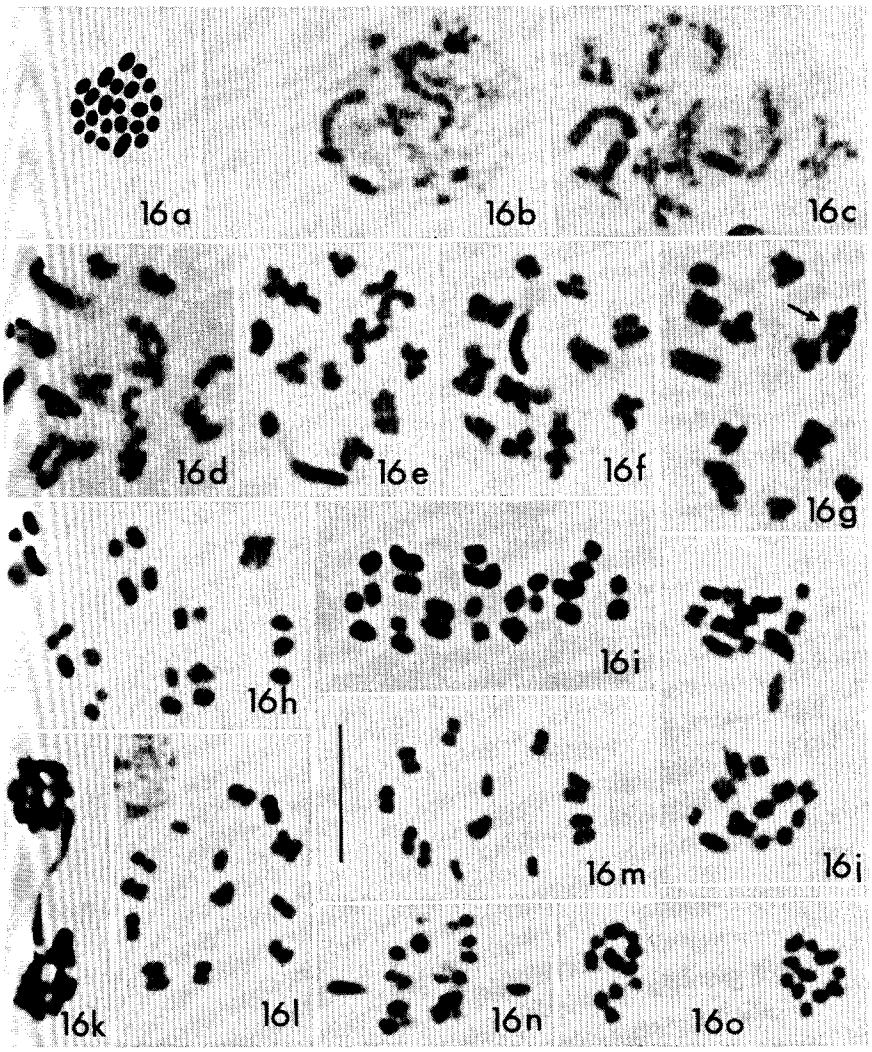

FIG. 10–16.—Hybrid of *Cimex antennatus* (♀) × *Cimex incrassatus* (♂). a, camera lucida drawing; b to o, photographs. a, spermatogonial metaphase with 23 chromosomes; b, confused stage, with heteropycnotic elements and X and Y; c, early diplotene stage; d, late diplotene stage; e and f, early diakinesis, with 9 bivalents, 1 trivalent, and X and Y; g, late diakinesis, with terminalization of chiasma completed and 1 trivalent (arrow); h and i, first spermatocyte metaphase, with 9 bivalents (8 of which are heteromorphic), 1 trivalent, and X and Y; j, first anaphase with a lagging chromosome; k, first anaphase with a chromatid bridge; l, second spermatocyte metaphase with 11 autosomes, the X and Y in center of ring formed by the autosomes; m, second metaphase with 10 autosomes and XY; n, second anaphase, X and Y show precocious movement; o, second telophase.

In the first spermatocyte metaphase, 3 kinds of chromosome complement are observed: 1) 8 bivalents, 3 trivalents, and the X and Y (Fig. 10–17f); 2) 9 bivalents, 2 trivalents, 1 univalent, and the X and Y (Fig. 10–17g, h); 3) 10 bivalents, 1 trivalent, 2 univalents, and the X and Y (Fig. 10–17i). No other kind of chromosome complement is observed, although there is the possibility of a chromosome complement of 11 bivalents, 3 univalents, and the X and Y. In 100 first-metaphase cells, 68 belonged to type 1, 18 to type 2, and 14 to type 3. Each bivalent in all 3 types is always heteromorphic. No particular chromosome arrangement is observed in the first metaphase. In the heteromorphic bivalents the 2 small chromatids always face toward one pole and the 2 larger chromatids toward the other, indicating co-orientation at the first metaphase in autosomes. In the trivalent, 2 of the 6 chromatids are oriented toward one pole and 4 chromatids toward the other. At first anaphase there are lagging dyads and chromatid bridges (Fig. 10–17j to p). The univalents that appear in the first metaphase fail to orient at metaphase and move to 1 pole at random. Despite these meiotic disturbances, a successful division finally occurs (Fig. 10–17q).

As a result of the first division, 5 kinds of second metaphase are observed: 1) 14A + XY (Fig. 10–17t, u); 2) 13A + XY (Fig. 10–17x); 3) 12A + XY (Fig. 10–17s, v); 4) 11A + XY (Fig. 10–17w); and 5) 10A + XY (Fig. 10–17r). In all of them the autosomes form a ring with the X and Y in the center. All autosomes in the second metaphase are uniform and no heteromorphic autosome dyads are observed. In the second anaphase of all types very little irregularity is observed. No further generations of hybrids were obtained.

Hybrid of *Cimex brevis* (♀) × *Cimex antennatus* (♂)

In essential features of chromosome cytology, the reciprocal cross is the same as that just described, except for the sex chromosomes and the formation of trivalents and bivalents at the first metaphase. All spermatogonial metaphase plates have 30 chromosomes (Fig. 10–18a) as expected from the combination of a *Cimex brevis* egg ($14A + X_1X_2X_3X_4$) and a *Cimex antennatus* sperm ($11A + Y$). At the first metaphase there are several types of chromosome complements: 1) 8 bivalents (heteromorphic), 3 trivalents, and the $X_1X_2X_3X_4Y$ (Fig. 10–18k); 2) 8 bivalents, 3 trivalents, 2 univalents, and $X_1X_2X_3X_4Y$ (Fig. 10–18g); 3) 8 bivalents, 2 trivalents, 1 univalent, and $X_1X_2X_3X_4Y$ (Fig. 10–18h); 4) 7 bivalents, 3 trivalents, 2 univalents, and $X_1X_2X_3X_4Y$ (Fig. 10–18i); and others (Fig. 10–18j, l). There are difficulties and irregularities in the division of the first spermatocyte, such as lagging chromosomes and chromatid bridges at the first anaphase (Fig. 10–18m to q). At second metaphase, 4 types of chromosome complement are observed: 1) $11A + X_1X_2X_3X_4Y$ (Fig. 10–18r); 2) $12A + X_1X_2X_3X_4Y$ (Fig. 10–18s); 3) 13A

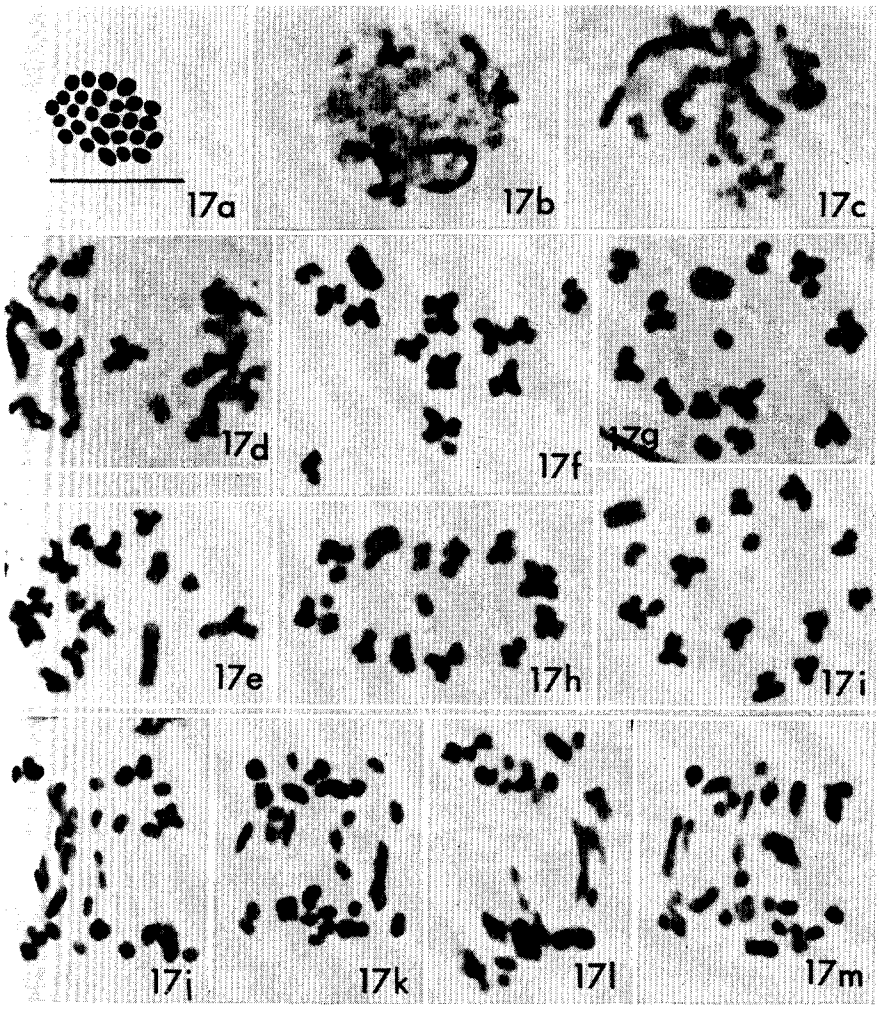

FIG. 10–17.—Hybrid of *Cimex antennatus* (♀) × *Cimex brevis* (♂). a, camera lucida drawing; b to m, photographs. a, spermatogonial metaphase with 27 chromosomes; b, confused stage with heteropycnotic elements and sex chromosomes; c, early diplotene stage; d, late diplotene stage; e, diakinesis; f, first spermatocyte metaphase with 3 trivalents, 8 heteromorphic bivalents, and X and Y; g and h, first spermatocyte metaphase with 2 trivalents, 9 heteromorphic bivalents, 1 univalent, and X and Y; i, first spermatocyte metaphase with 1 trivalent, 10 heteromorphic bivalents, 2 univalents, and X and Y; j to m, first anaphase with lagging chromosomes and chromatid bridges.

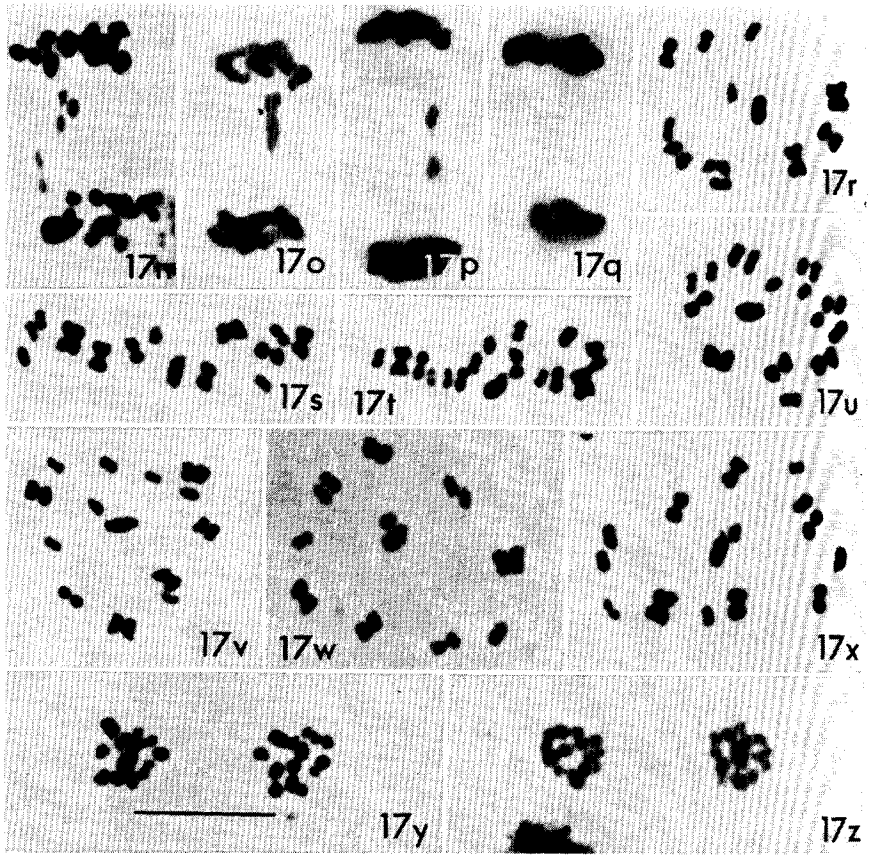

FIG. 10–17 (Cont'd).—Hybrid of *Cimex antennatus* (♀) × *Cimex brevis* (♂). n to p, first telophase with lagging chromosomes and (or) chromatid bridge; q, first telophase without any irregularity; r, second spermatocyte metaphase with 10 autosomes and X and Y; s, second metaphase with 12 autosomes and X and Y; t, second metaphase with 14 autosomes and X and Y; u, second metaphase with 15 autosomes and X and Y; v, second metaphase with 12 autosomes and X and Y; w, second metaphase with 11 autosomes and X and Y; second metaphase with 13 autosomes and X and Y; y and z, second anaphase.

+ $X_1X_2X_3X_4Y$ (Fig. 10–18t); and 4) 14A + $X_1X_2X_3X_4Y$ (Fig. 10–18u, v, w).

PRIMICIMICINAE

Primicimex cavernis Barber*[1]

No diploid chromosome complement was observed. In the first meta-

[1] Species marked with an asterisk (*) had been in ethyl alcohol for several months or years and were studied by means of the technique (Ueshima 1963b) described on p. 289.

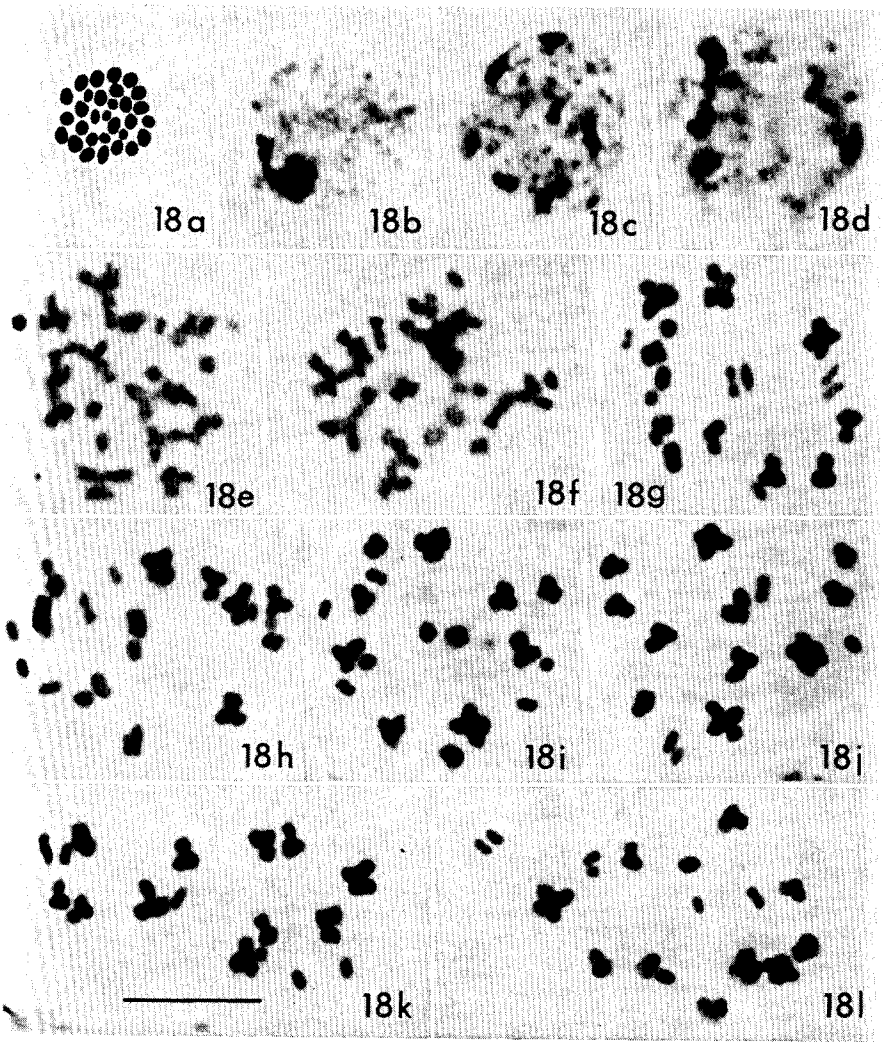

FIG. 10–18.—Hybrid of *Cimex brevis* (♀) × *C. antennatus* (♂). a, camera lucida drawing; b to l, photographs. a, spermatogonial metaphase with 30 chromosomes; b to d, confused stage with heteropycnotic elements and sex chromosomes; e and f, diakinesis; g, first spermatocyte metaphase with 3 trivalents, 8 bivalents, 2 univalents, and sex chromosomes; h, first metaphase with 2 trivalents, 8 bivalents, 1 univalent, and sex chromosomes; i, first metaphase with 3 trivalents, 7 bivalents, 2 univalents, and sex chromosomes; j, 3 trivalents, 8 bivalents, and sex chromosomes (one of X's missing); k, first metaphase with 3 trivalents, 8 bivalents, and sex chromosomes; l, first metaphase with 3 trivalents, 7 bivalents, 2 univalents, and sex chromosomes.

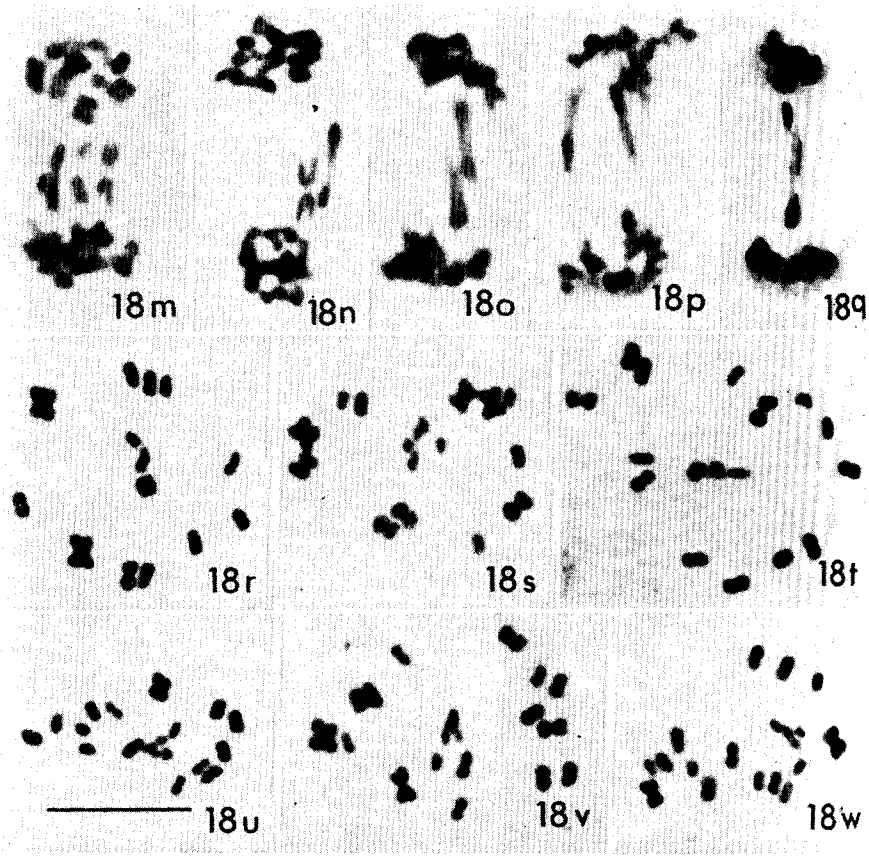

FIG. 10–18 (Cont'd.).—*Cimex brevis* (♀) × *Cimex antennatus* (♂). m to q, first spermatocyte anaphase with lagging chromosomes and (or) chromatid bridges; r, second spermatocyte metaphase with 11 autosomes and sex chromosomes; s, second metaphase with 12 autosomes and sex chromosomes; t, second metaphase with 13 autosomes and sex chromosomes; u, second metaphase with 14 autosomes and sex chromosomes; v, second metaphase with 14 autosomes and sex chromosomes; w, second metaphase with 15 autosomes and sex chromosomes.

phase the 6 chromosomes consist of 4 autosomal tetrads and the X and Y dyads (Fig. 10–46a). At the second metaphase, 4 autosomes take a peripheral position on the equatorial plate and the X and Y lie in the center of the ring (Fig. 10–46b). It may be safely assumed that the chromosome complement of this species is 10—4 pairs of autosomes with XY in the male and XX in the female.

Bucimex chilensis Usinger

The diploid chromosome number of this species is 28—13 pairs of

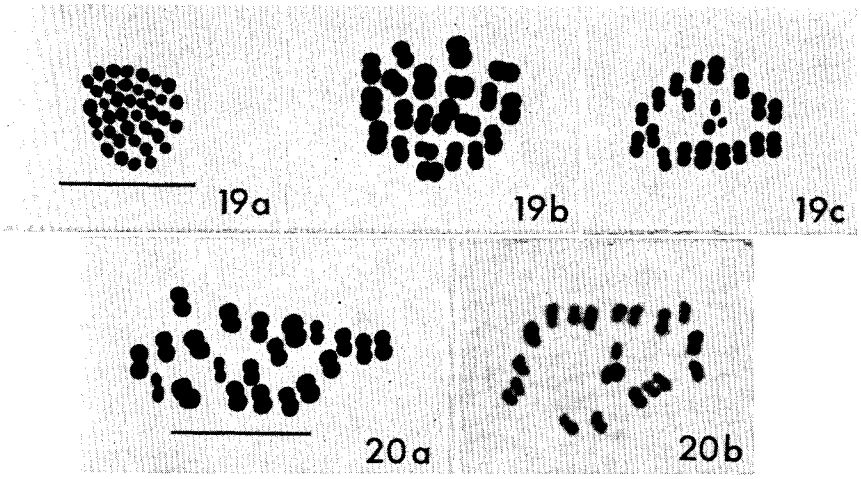

FIG. 10–19.—*Paracimex caledoniae*. a to c, camera lucida drawings. a, spermatogonial metaphase with 39 chromosomes; b, first spermatocyte metaphase with 18 autosomal tetrads and X_1X_2Y dyads; c, second spermatocyte metaphase, 18 autosomes form ring toward periphery, and sex chromosomes lie in center.

FIG. 10–20.—*Paracimex borneensis*. a, camera lucida drawing; b, photograph. a, first spermatocyte metaphase with 21 chromosomes; b, second spermatocyte metaphase, X_1X_2Y lie in center of ring formed by 18 autosomes.

autosomes plus XY in the male (Fig. 10–27a) or XX in the female (Fig. 10–27b). In the spermatogonial metaphase, 2 pairs of autosomes are somewhat larger than the others. The X chromosome is a little larger than the largest autosomes, but the Y is not easily distinguished from the autosomes, as it belongs to the medium-sized group in the chromosome set. In the confused stage there are 2 heteropycnotic elements, the X and Y. The first spermatocyte metaphase reveals 15 chromosomes—13 autosomal tetrads and the X and Y dyads (Fig. 10–27f). In the second metaphase the X and Y always lie in the middle of a ring formed by the 13 autosomes, undergo "touch and go" pairing, and pass to the opposite poles (Fig. 10–27g).

CIMICINAE

Oeciacus hirundinis Lamarck, *Oeciacus vicarius* Horvath

The diploid chromosome numbers of these 2 species are 31, consisting of 14 pairs of autosomes and X_1X_2Y in the male (Fig. 10–25a, 10–26a), and 32, consisting of 14 pairs of autosomes and $X_1X_1X_2X_2$ in the female. The first spermatocyte metaphase consists of 17 chromosomes—14 autosomes and X_1X_2Y (Fig. 10–25b, 10–26b). No particular arrangement of chromosomes in the first metaphase was noted. At the second metaphase, the sex chromosomes (X_1X_2Y) lie in the center of a ring formed by 14 autosomes (Fig. 10–25c, 10–26c).

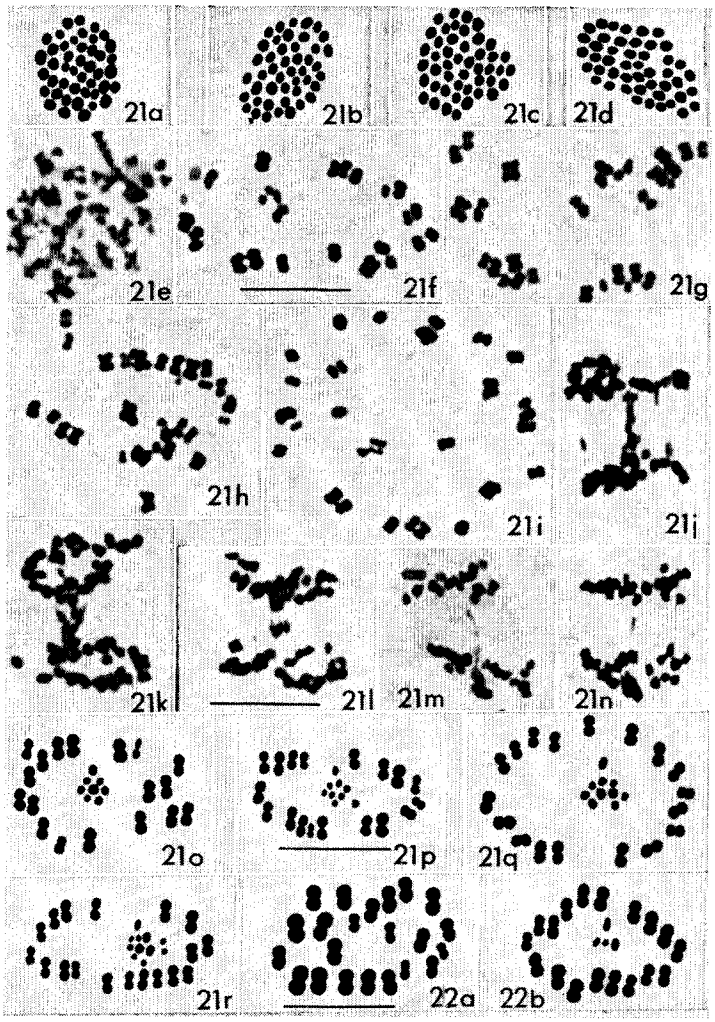

FIG. 10–21.—*Paracimex borneensis* from Malaya. a to d, o to r, camera lucida drawings; e to n, photographs. a, spermatogonial metaphase with 44 chromosomes; b, spermatogonial metaphase with 45 chromosomes; c, spermatogonial metaphase with 46 chromosomes; d, spermatogonial metaphase with 47 chromosomes; e, early diakinesis; f, first spermatocyte metaphase with 26 chromosomes; g, first metaphase with 27 chromosomes; h, first metaphase with 28 chromosomes; i, first metaphase with 29 chromosomes; j to n, first anaphase with lagging chromosomes and (or) chromatid bridges; o, second spermatocyte metaphase with 18 autosomes and $X_1X_2X_3X_4X_5X_6X_7Y$; p, second metaphase with 18 autosomes, 8X's, and Y; q, second metaphase with 18 autosomes, 9X's, and Y; r, second metaphase with 18 autosomes, 10X's, and Y.

FIG. 10–22.—*Paracimex capitatus* from Netherlands, New Guinea. a and b, camera lucida drawings. a, first spermatocyte metaphase with 22 chromosomes; b, second spermatocyte metaphase, $X_1X_2X_3Y$ lie in center of ring formed by 18 autosomes.

Paracimex borneensis Usinger* from Sarawak

The diploid chromosome complement was not observed, but it may be assumed safely, from observations of the chromosome configuration in the first and second spermatocyte metaphases, that this species has 39 chromosomes in the male and 40 in the female. At the first spermatocyte metaphase, 21 chromosomes are arranged on the equatorial plate (Fig. 10–20a). In the second metaphase 18 autosomes form a ring toward the periphery of the plate, while the X_1X_2Y lie in the center (Fig. 10–20b).

Paracimex borneensis Usinger from Malaya

The diploid chromosome complement in the male varies from 44 to 47 in different individuals (Figs. 10–21a to d), due to the number of sex chromosomes as judged from observations of meiotic figures. The complement of the individual with 44 chromosomes consists of 18 pairs of autosomes, 7 X's, and a Y, and that of the individual with 46 consists of 18 pairs of autosomes, 9 X's, and a Y.

At the first spermatocyte metaphase there are 18 autosomal tetrads and 8 to 10 sex-chromosomal dyads (Fig. 10–21e to h). In the first anaphase, lagging chromosomes and chromatid bridges (Fig. 10–21i to k) are seen. As the second metaphase is formed, 7 to 10 sex chromosomes usually lie in the center of a ring formed by the autosomes (Fig. 10–21l to o). The number of sex chromosomes in the second metaphase differs among individuals and within a single individual; the difference in number within an individual may be due to irregularity and abnormality at first anaphase. The total number of individuals observed was 18.

Paracimex capitatus Usinger* from New Britain

Although no diploid chromosome complement was observed, it may be safely assumed from observations at first and second metaphase that this species has 39 chromosomes in the male. At the first metaphase, 21 chromosomes are present on the equatorial plate (Fig. 10–24a); at second metaphase, 18 autosomes form a peripheral ring while the sex chromosomes, X_1X_2 and Y, take a central position (Fig. 10–24b).

*Paracimex capitatus** from Netherlands New Guinea

Although the diploid chromosome complement of this species was not observed, it may be safely assumed from the observations during meiosis that it has 40 chromosomes—18 pairs of autosomes with $X_1X_2X_3Y$ in the male. There are 22 chromosomes in the first spermatocyte metaphase (Fig. 10–22a); at second metaphase the sex chromosomes, $X_1X_2X_3$ and Y, lie in the center of a ring formed by the 18 autosomes (Fig. 10–22b).

Paracimex capitatus from Wau, New Guinea

The diploid chromosome number in the male varies from 41 to 42 in different individuals (Fig. 10–23a, b). The complement of the indi-

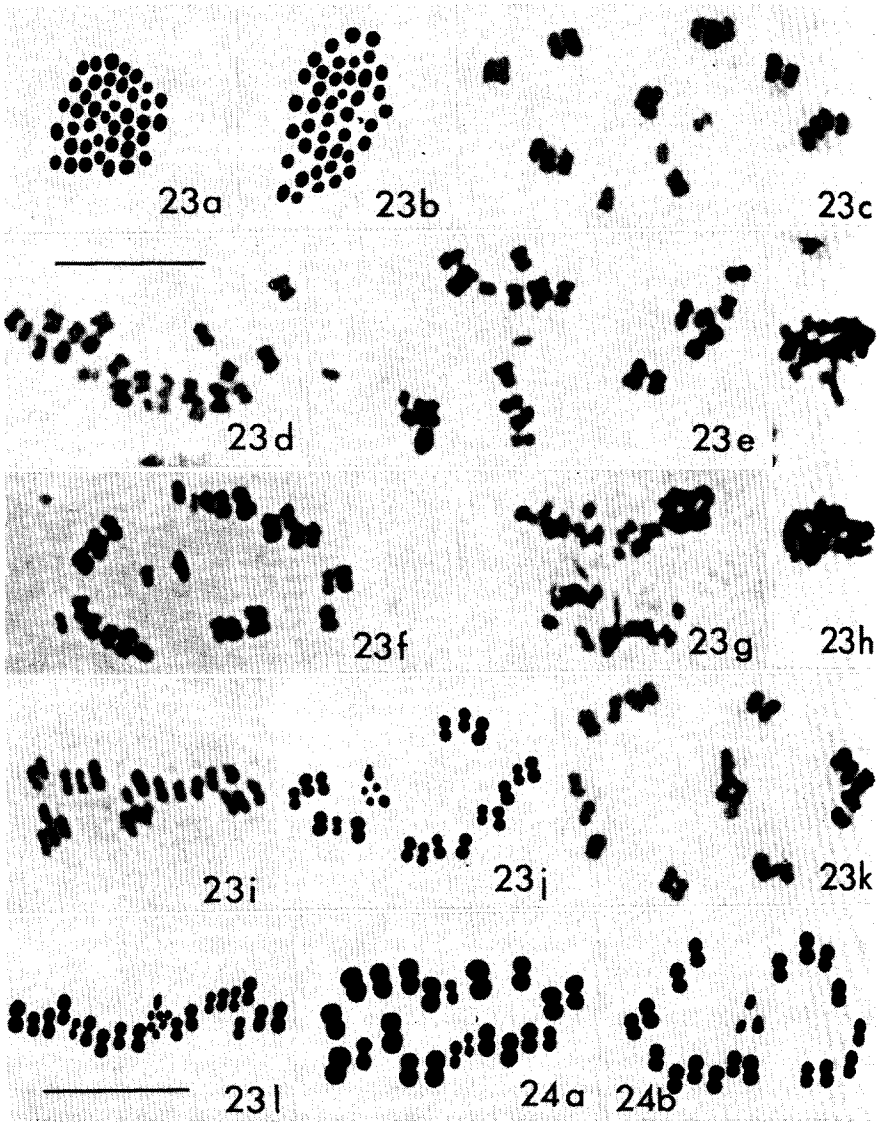

FIG. 10–23.—*Paracimex capitatus* from Wau, New Guinea. a, b, and j, camera lucida drawings; c to i and k, photographs. a, spermatogonial metaphase with 41 chromosomes; b, spermatogonial metaphase with 42 chromosomes; c, first spermatocyte metaphase with 22 chromosomes; d, first spermatocyte metaphase with 23 chromosomes; e, first metaphase with 24 chromosomes; f, first metaphase with 25 chromosomes; g, first anaphase with lagging chromosomes and chromatid bridges; h, first telophase with lagging chromosomes; i and j, second spermatocyte metaphase with 18 autosomes, 4X's, and Y; k, second metaphase with 18 autosomes, 5X's and Y; l, second metaphase with 18 autosomes, 6X's, and Y.

vidual having 41 chromosomes consists of 18 pairs of autosomes, 4 X's, and a Y, and that of the individual having 42 chromosomes, of 18 pairs of autosomes, 5 X's, and a Y. In the first metaphase, 18 autosomal tetrads, 3 to 6 X's, and a Y are observed. The first metaphase configurations show that some individuals must also have a complement of only 40 chromosomes; however, spermatogonial metaphases were not observed in individuals with 22 chromosomes at the first metaphase (Fig. 10–23c to f). Irregularities and abnormalities are seen in the first spermatocyte anaphase (Fig. 10–23g, h). At second metaphase the 18 autosomes form a ring while the sex chromosomes always lie in the center (Fig. 10–23i to l). A summary of the results observed in 15 individuals follows:

Spermatogonial metaphase	First metaphase	Second metaphase
(40) [2]	22	18A + $X_1X_2X_3Y$
41	23	18A + $X_1X_2X_3X_4Y$
42	24	18A + $X_1X_2X_3X_4X_5Y$
43	25	18A + $X_1X_2X_3X_4X_5X_6Y$

Paracimex caledoniae Ferris and Usinger*

The diploid chromosome number of this species is 39—18 pairs of autosomes and X_1X_2Y in the male (Fig 10–19a). The sex chromosomes, X_1X_2Y, lie close to each other in the confused stage. At the first metaphase, 21 chromosomes arrange themselves on the equator of the spindle (Fig. 10–19b), and in the second, X_1X_2Y locate in the center of a ring formed by the 18 autosomes (Fig. 10–19c).

CACODMINAE

Cacodmus vicinus Horvath

The diploid chromosome number of 10 consists of 4 pairs of autosomes and XY in the male (Fig. 10–38a, d). No female chromosome complement was observed. At first metaphase, 4 autosomal tetrads and the X and Y dyads appear (Fig. 10–38b, e); in the second metaphase, 4 autosomes form a ring toward the periphery, while the X and Y chromosomes lie in the center (Fig. 10–38c, f, g).

Aphrania vishnou Mathur*

No diploid chromosome complement was observed, but the number may be assumed as 10. In the first spermatocyte metaphase the 6 chromo-

[2] No spermatogonial metaphases were observed. The diploid chromosome number is based on observations at first and second metaphase.

FIG. 10-24.—*Paracimex capitatus* from New Britain. a and b, camera lucida drawings. a, first spermatocyte metaphase with 21 chromosomes; b, second spermatocyte metaphase with 18 autosomes and X_1X_2Y.

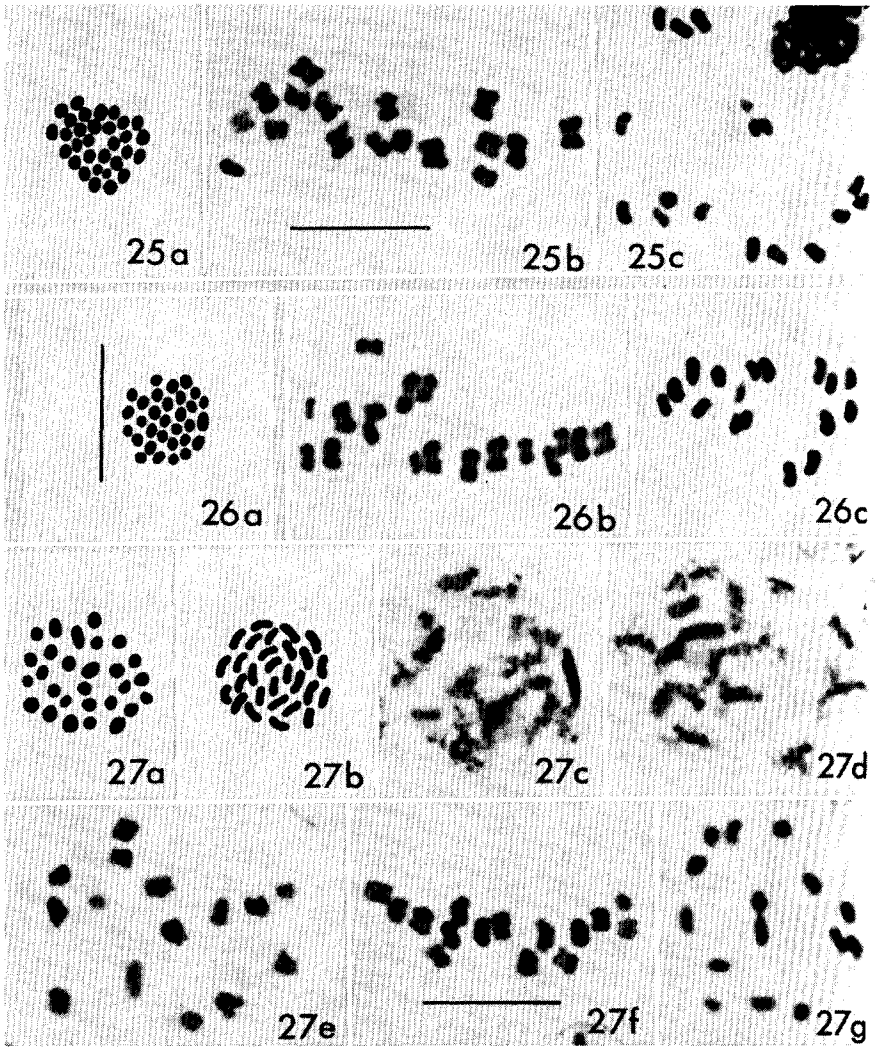

FIG. 10–25.—*Oeciacus hirundinis*. a, camera lucida drawing; b, c, photographs. a, spermatogonial metaphase with 31 chromosomes; b, first spermatocyte metaphase with 14 autosomal tetrads and 3 sex chromosomal dyads; c, second metaphase, X_1X_2Y lie in center of ring formed by 14 autosomes.

FIG. 10–26.—*Oeciacus vicarius*. a, camera lucida drawing; b, c, photographs. a, spermatogonial metaphase with 31 chromosomes; b, first spermatocyte metaphase, with 14 autosomes and X_1X_2Y chromosomes; c, second metaphase, X_1X_2Y lie in center of ring formed by 14 autosomes.

FIG. 10–27.—*Bucimex chilensis*. a, b, camera lucida drawings; c to g, photographs. a, spermatogonial metaphase with 28 chromosomes; b, female somatic metaphase with 28 chromosomes; c and d, diplotene stage; e, prometaphase; f, first spermatocyte metaphase with 13 autosomes (on periphery) and XY (in center).

somes consist of 4 autosomal tetrads and the X and Y dyads (Fig. 10–40a); in the second metaphase, 4 autosomes form a ring toward the periphery and the X and Y chromosomes lie in the center (Fig. 10–40b).

Loxaspis malayensis Usinger

The diploid chromosome complement of 10 consists of 4 pairs of autosomes, plus XY (Fig. 10–39a) in the male or XX in the female. In the spermatogonial metaphase there is 1 pair of large autosomes, 1 medium-sized pair, and 2 small pairs. The X chromosome is similar in size to the smaller autosomes; the Y chromosome is the smallest component of the chromosome set. In the first spermatocyte metaphase, 4 autosomal tetrads and the X and Y dyads arrange themselves on the equatorial plate (Fig. 10–39c). At the second metaphase the X and Y lie in the center of a ring formed by the 4 autosomes (Fig. 10–39d).

Stricticimex antennatus Ferris and Usinger*

No diploid chromosome complement was observed, but the number may be assumed as 24. In the first spermatocyte metaphase the 13 chromosomes consist of 11 autosomes and the X and Y (Fig. 10–42a). At the second metaphase 11 autosomes take a peripheral position, forming a ring, while the X and Y lie in the center (Fig. 10–42b).

Leptocimex duplicatus Usinger

The diploid chromosome complement is 24, consisting of 11 pairs of autosomes, with XY in the male (Fig. 10–41a) and XX in the female (Fig. 10–41b). At the first metaphase the autosomes and the sex chromosomes arrange themselves on the equator of the spindle (Fig. 10–41c). As the second metaphase is formed, the X and Y lie in the center of a ring formed by 11 autosomes, undergo "touch and go" pairing, and pass to the opposite poles in the following anaphase (Fig. 10–41d).

Crassicimex pilosus Ferris and Usinger*

No diploid chromosome complement was observed. The 21 chromosomes consist of 18 autosomal tetrads and 3 sex-chromosomal dyads, presumably X_1X_2Y, in the first spermatocyte metaphase (Fig. 10–44a). In the second metaphase 18 autosomes form a ring toward the periphery, while the 3 sex chromosomes lie in the center (Fig. 10–44b). It may be safely assumed that the diploid chromosome number of this species is 39, consisting of 18 pairs of autosomes and X_1X_2Y in the male, and 40, 18 pairs of autosomes and $X_1X_1X_2X_2$ in the female.

AFROCIMICINAE

Afrocimex leleupi Schouteden*

No diploid chromosome complement was observed. In the first spermatocyte metaphase there are 14 chromosomes—11 autosomal tetrads and 3

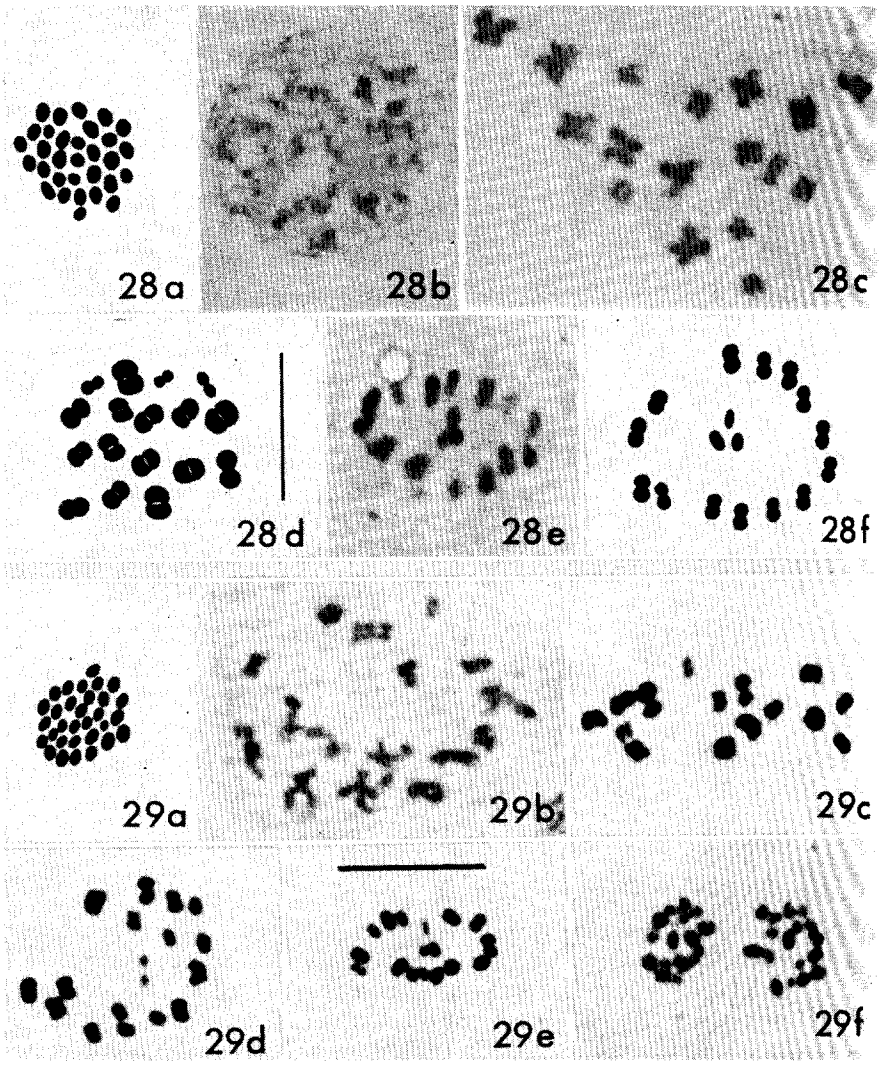

FIG. 10–28.—*Haematosiphon inodorus*. a, d, f, camera lucida drawings; b, c, e, photographs. a, spermatogonial metaphase with 31 chromosomes; b, confused stage; c, diakinesis; d, first spermatocyte metaphase with 17 chromosomes; e and f, second spermatocyte metaphase, X_1X_2Y lie in center of ring formed by 14 autosomes.

FIG. 10–29.—*Synxenoderus comosus*. a, camera lucida drawings; b to f, photographs. a, spermatogonial metaphase with 31 chromosomes; b, diplotene stage; c and d, first spermatocyte metaphase, X_1X_2Y chromosomes stain less intensely (sometimes these sex chromosomes take a central position, (Fig. d)); e, second metaphase, X_1X_2Y lie in center of ring formed by 14 autosomes; f, second anaphase.

sex-chromosome dyads (Fig. 10–43a). In the second metaphase, 11 autosomes form a ring toward the periphery while the 3 sex chromosomes, presumably X_1X_2Y, lie in the center (Fig. 10–43b). From the general features of cimicid chromosome cytology, it may be safely assumed that the diploid chromosome complement of this species is 25, consisting of 11 pairs of autosomes and X_1X_2Y in the male, and 26, including 11 pairs of autosomes and $X_1X_2X_3X_4$ in the female.

LATROCIMICINAE

Latrocimex spectans Lent*

No diploid chromosome complement was observed, but the number may be assumed as 24. The first spermatocyte metaphase reveals 13 chromosomes—11 autosomal tetrads and X and Y dyads (Fig. 10–45a). In the second metaphase the X and Y lie in the center of the ring formed by the 11 autosomes and pass to opposite poles with the autosomes at anaphase (Fig. 10–45b).

HAEMATOSIPHONINAE

Ornithocoris toledoi Pinto*

The diploid chromosome complement was not observed. The first spermatocyte metaphase reveals 6 chromosomes—4 autosomal tetrads and the X and Y dyads (Fig. 10–36a). In the second metaphase, as is usual in cimicids, the 4 autosomes form a ring toward the periphery of the plate, and the X and Y are in the center (Fig. 10–36b). From the chromosome configuration in the first and second metaphase, it may be safely assumed that the diploid chromosome number is 10 in both male and female.

Ornithocoris pallidus Usinger

The diploid chromosome number is 10—4 pairs of autosomes, plus the XY in the male (Fig. 10–35a) or the XX in the female (Fig. 10–35b). In the spermatogonial metaphase, 2 pairs of autosomes are large and 2 pairs are small. The X chromosome is smaller than the large autosomes and larger than the small ones; the Y is like the small autosomes.

The behavior of sex chromosomes in the meiotic process of this species is a little different than in the cimicids previously described. In the confused stage, the sex chromosomes usually tend to come close together, as usual in cimicids, but in late diakinesis the sex chromosomes (X and Y) lose their staining intensity; this persists into the first metaphase, where 4 autosomal tetrads and the X and Y dyads appear (Fig. 10–35d, e). At the second metaphase the X and Y always lie in the center of a ring formed by the 4 autosomes (Fig. 10–35f).

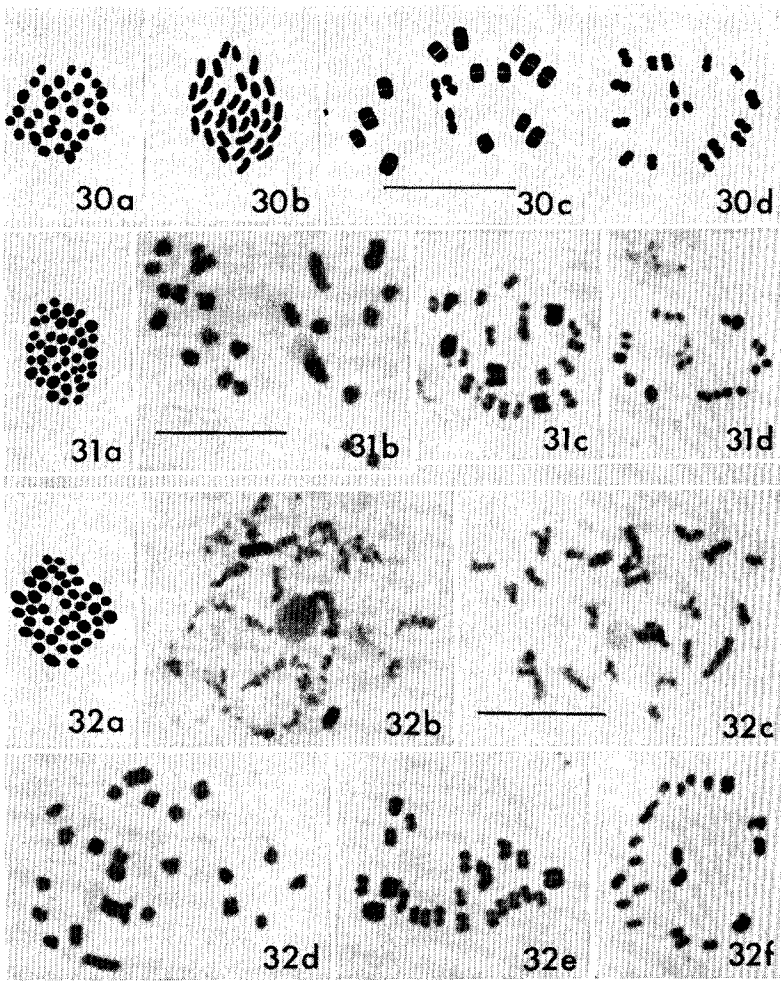

FIG. 10–30.—*Psitticimex uritui*. a to d, camera lucida drawings. a, spermatogonial metaphase with 31 chromosomes; b, female somatic metaphase with 32 chromosomes; c, first spermatocyte metaphase with 14 autosomal tetrads and X_1X_2Y dyads; d, second spermatocyte metaphase, X_1X_2Y lie in center of ring formed by 14 autosomes.

FIG. 10–31.—*Hesperocimex coloradensis*. a, camera lucida drawing; b to d, photographs. a, spermatogonial metaphase with 42 chromosomes; b, late diakinesis; c, first spermatocyte metaphase with 23 chromosomes; d, second spermatocyte metaphase, $X_1X_2X_3$ and Y lie in center of ring formed by 19 autosomes.

FIG. 10–32.—*Hesperocimex sonorensis*. a, camera lucida drawing; b to f, photographs. a, spermatogonial metaphase with 42 chromosomes; b and c, diplotene stage, X and Y are positively heteropycnotic and lie separately; d, prometaphase with 20 autosomal tetrads and X and Y dyads; e, first spermatocyte metaphase; f, second metaphase, 20 autosomes lie toward periphery of plate and form a ring, X and Y in middle of ring.

Caminicimex furnarii (Cordero and Vogelsang)

The diploid chromosome number is 34—16 pairs of autosomes and XY in the male (Fig. 10–37a). Although not observed, the female may be assumed to have 34 chromosomes in the diploid. The first spermatocyte metaphase plate reveals 18 chromosomes—16 autosomes and the X and Y (Fig. 10–37b). In the second metaphase the X and Y take a central position in a ring formed by the 16 autosomes and pass to opposite poles in the following anaphase (Fig. 10–37c).

Psitticimex uritui (Lent and Abalos)

The diploid chromosome numbers of this species are 31, 14 pairs of autosomes and X_1X_2Y in the male (Fig. 10–30a), and 32, 14 pairs of autosomes and $X_1X_1X_2X_2$ in the female (Fig. 10–30b).

The meiotic process of this species differs a little from that in *Haematosiphon;* it is similar to that in *Synxenoderus* until diakinesis. In the first spermatocyte metaphase the 14 autosomes tend to move toward the periphery of the plate and the sex chromosomes to take a central position, although not consistently (Fig. 10–30c). In the second metaphase, 14 autosomes form a ring toward the periphery of the plate, while the sex chromosomes lie in the center (Fig. 10–30d). In the second metaphase the Y chromosome is somewhat larger than X_1 and X_2.

Haematosiphon inodorus Duges

The diploid chromosome numbers are 31, 14 pairs of autosomes with X_1X_2Y in the male (Fig. 10–28a), and 32, 14 pairs of autosomes with $X_1X_1X_2X_2$ in the female. The course of meiosis is the same as in most other Cimicidae. There are 3 heteropycnotic elements in the confused stage. At the first metaphase, 14 autosomal tetrads and 3 sex-chromosome dyads arrange themselves on the equator of the spindle (Fig. 10–28d). At the second metaphase the sex chromosomes, X_1X_2Y, take a central position in a ring formed by the 14 autosomes (Fig. 10–28e, f).

Synxenoderus comosus List

The diploid chromosome number of this species is 31—14 pairs of autosomes and X_1X_2Y in the male (Fig. 10–29a). Although none was observed, the female may be assumed to have 32 chromosomes.

The process of meiosis in this species differs a little from that in *Haematosiphon.* Although, as usual in Cimicidae, there are 3 heteropycnotic elements in the confused stage, one of them stains less intensely and sometimes is very difficult to see. In late diakinesis the autosomes appear to be deeply stained during condensation, while the sex chromosomes tend to lose their staining intensity (Fig. 10–29c); this state of the sex chromosome persists into the first spermatocyte metaphase (Fig. 10–29d) and is unusual in Cimicids. One of the sex chromosomes sepa-

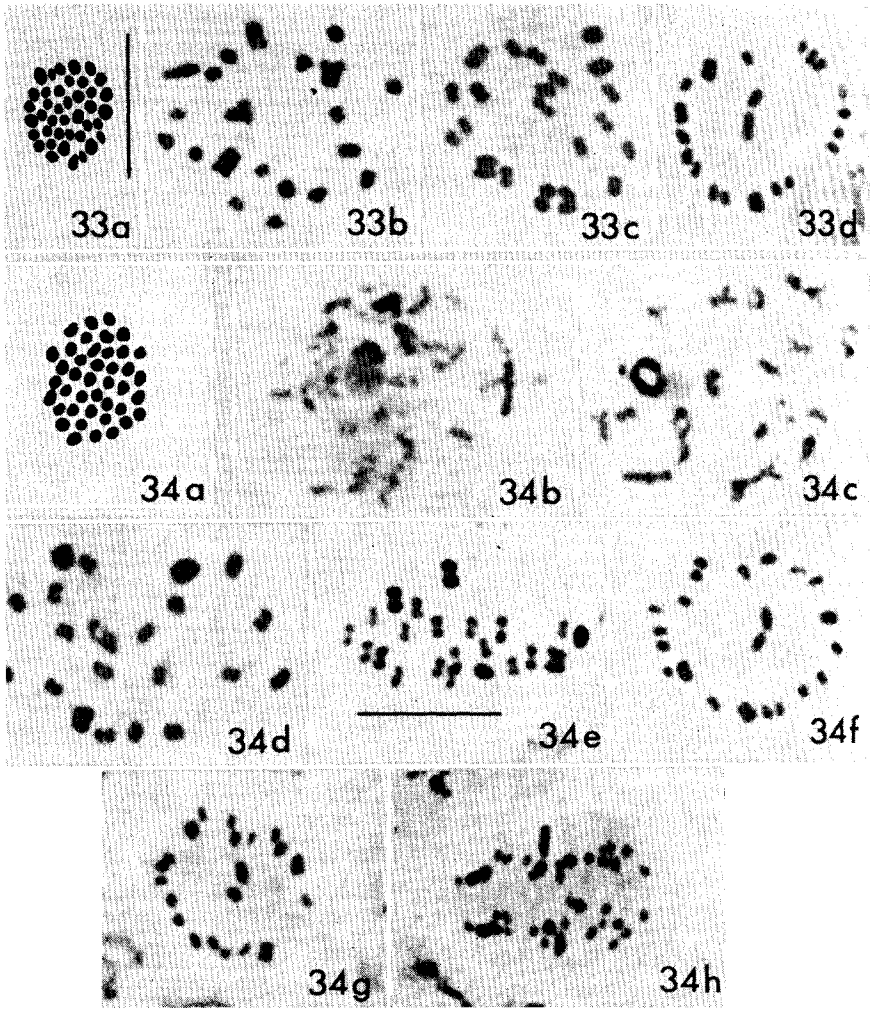

FIG. 10–33.—*Hesperocimex cochimiensis*. a, camera lucida drawing; b to d, photographs. a, spermatogonial metaphase with 40 chromosomes; b, prometaphase with 19 autosomes and XY; c, first spermatocyte metaphase; d, second spermatocyte metaphase, X and Y lie in middle of ring formed by 19 autosomes.

FIG. 10–34.—Hybrid of *Hesperocimex sonorensis* (♀) × *Hesperocimex cochimiensis* (♂). a, camera lucida drawing; b to h, photographs. a, spermatogonial metaphase with 41 chromosomes; b, early diplotene stage; c, late diplotene stage, a heteropycnotic element showing chromosomal ring comprising 4 subunits; d, prometaphase with 22 chromosome complements, one of which is a heteromorphic bivalent; e, first spermatocyte metaphase with 22 chromosomes; f, second metaphase with 20 autosomes and XY (in the center); g, second metaphase with 19 autosomes and XY (in the center); h, second anaphase, X and Y segregate to opposite poles.

rates in late diakinesis (Fig. 10–29d). At first metaphase there are 14 autosomal tetrads and 3 sex-chromosome dyads; the sex chromosomes stain less intensely and tend to take a central position on the equatorial plate. As the second spermatocyte metaphase figure is formed, 2 of the 3 sex chromosomes lose their negatively heteropycnotic character and stain with the same intensity as the autosomes, but one more or less retains its light staining. At the second metaphase the 14 autosomes lie toward the periphery of the plate and form a ring, while the sex chromosomes take a central position (Fig. 10–29e).

Hesperocimex coloradensis List

The diploid chromosome numbers of this species are 42, 19 pairs of autosomes plus $X_1X_2X_3Y$ in the male (Fig. 10–31a), and 44, 19 pairs of autosomes and 2 ($X_1X_2X_3$) in the female. There are 4 heteropycnotic elements, the sex chromosomes, in early diplotene stage. In the first spermatocyte metaphase 23 chromosomes—19 autosomes and $X_1X_2X_3Y$—are observed (Fig. 10–31c). In the second metaphase, 19 autosomes lie toward the periphery of the plate and form a ring, while the 3 X's and Y lie in the center (Fig. 10–31d).

Hesperocimex sonorensis Ryckman

The diploid complement of 42 chromosomes consists of 20 pairs of autosomes, with XY in the male (Fig. 10–32a) and XX in the female. In the spermatogonial metaphase, 3 pairs of autosomes and the X are somewhat larger than the others. There are 2 heteropycnotic elements, the X and Y, in the confused stage. The first spermatocyte metaphase reveals 20 autosomal tetrads and X and Y dyads (Fig. 10–32e). At the second metaphase the X and Y lie in the center of a ring formed by the 20 autosomes (Fig. 10–32f).

Hesperocimex cochimiensis Ryckman and Ueshima

The diploid complement of 40 chromosomes consists of 19 pairs of autosomes, with XY in the male (Fig. 10–33a) and XX in the female. At the first metaphase, 19 autosomal tetrads and the X and Y dyads appear (Fig. 10–33c). As the metaphase of the second division is formed, the X and Y always take a central position in the ring formed by the 19 autosomes and segregate to opposite poles (Fig. 10–33d).

Hybrid of *Hesperocimex sonorensis* (♀) × *H. cochimiensis* (♂)

The spermatogonial cells in the hybrid give no evidence of abnormality. All spermatogonial metaphase plates clearly have 41 chromosomes (Fig. 10–34a), as expected from the combination of an *Hesperocimex sonorensis* egg (20A + X) and an *Hesperocimex cochimiensis* sperm (19A + Y).

In the meiotic processes of the hybrid, no abnormality or irregularity

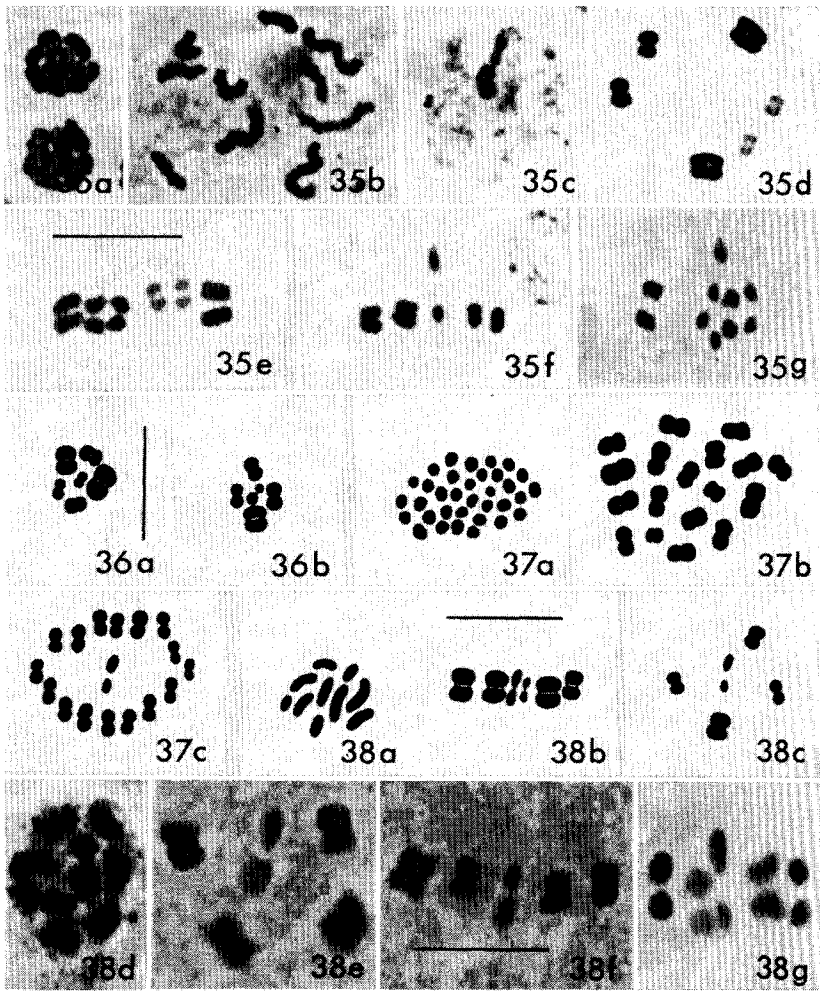

FIG. 10–35.—*Ornithocoris pallidus*. a to g, photographs. a, spermatogonial metaphase with 10 chromosomes; b, female somatic metaphase with 10 chromosomes; c, confused stage; d and e, first spermatocyte metaphase, sex chromosomes stain less intensely; f and g, second metaphase.

FIG. 10–36.—*Ornithocoris toledoi*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 6 chromosomes; b, second metaphase, X and Y lie in center of ring formed by 4 autosomes.

FIG. 10–37.—*Caminicimex furnarii*. a to c, camera lucida drawings. a, spermatogonial metaphase with 34 chromosomes; b, first spermatocyte metaphase with 18 chromosomes; c, second spermatocyte metaphase, X and Y lie in center of ring formed by 16 autosomes.

FIG. 10–38.—*Cacodmus vicinus*. a to c, camera lucida drawings; d to g, photographs. a and d, spermatogonial metaphase with 10 chromosomes; b and e, first spermatocyte metaphase with 6 chromosomes; c, f, g, second spermatocyte metaphase, X and Y lie in center of ring formed by 4 autosomes.

appears during the confused stage, but occurs very soon afterwards. In the early diplotene, in addition to the X and Y chromosomes (Fig. 10–34b), there appears a somewhat elongated heteropycnotic element which, in the late diplotene, forms a ring of chromosomes (Fig. 10–34c). This ring is composed of 4 subunits, two of which are much smaller than the others. The prometaphase and first metaphase possess 22 chromosomes—19 bivalents (one of which is heteromorphic), a univalent, and the X and Y (Fig. 10–34d). The heteromorphic bivalent in the first metaphase undoubtedly came from the ring of chromosomes in the late diplotene and indicates chromosomes of different species origin. In the heteromorphic bivalent, 2 smaller chromatids always face one pole and two larger ones the other (Fig. 10–34e), indicating co-orientation at first metaphase and reductional separation at first anaphase. In the first anaphase, 2 or 3 bivalents, including the heteromorphic one, have difficulty in dividing and lag on the spindle. In addition, 1 univalent lies in the center of the spindle, fails to orient at the first metaphase, and loses kinetic activity; no lagging has been observed, but disjunction of the chromatids of the univalent fails to occur. Despite this meiotic disturbance, division is finally completed successfully and 2 types of second metaphase occur as a result of the first division. One type contains 19 autosomes with X and Y, the other 20 autosomes (one a result of nondisjunction of the univalent in the first anaphase) and the X and Y.

In the second metaphase of both types, the X and Y always lie in the center of a ring formed by the autosomes (Fig. 10–34f, g). The second spermatocyte divisions of these 2 types are almost normal, although a few abnormalities such as lagging chromosomes on the spindle (Fig. 10–34h) are observed. Four kinds of spermatids are formed by the second division: 20A + X, 20A + Y, 19A + X, and 19A + Y.

The reciprocal cross of *Hesperocimex cochimiensis* (♀) × *Hesperocimex sonorensis* (♂) is very similar to that just described.

DISCUSSION OF CHROMOSOMES AND MEIOSIS

CHROMOSOME NUMBERS AND THEIR EVOLUTION

The chromosome number (2n ♂) of the cimicids ranges from 10 to 47 (Table 10–1), with some numbers lacking between the extremes. Usually Heteroptera have the same chromosome number within a genus, or, in many cases, within a tribe (see Makino 1951, White 1954). In cimicids, this tendency is seen in some cases but not in others, possibly in part because many genera are monotypic or have few species and each genus is very distinct morphologically. Yet, in some groups of very closely related species, there is a diversity in chromosome number. Therefore, the cytology of each genus is treated separately below.

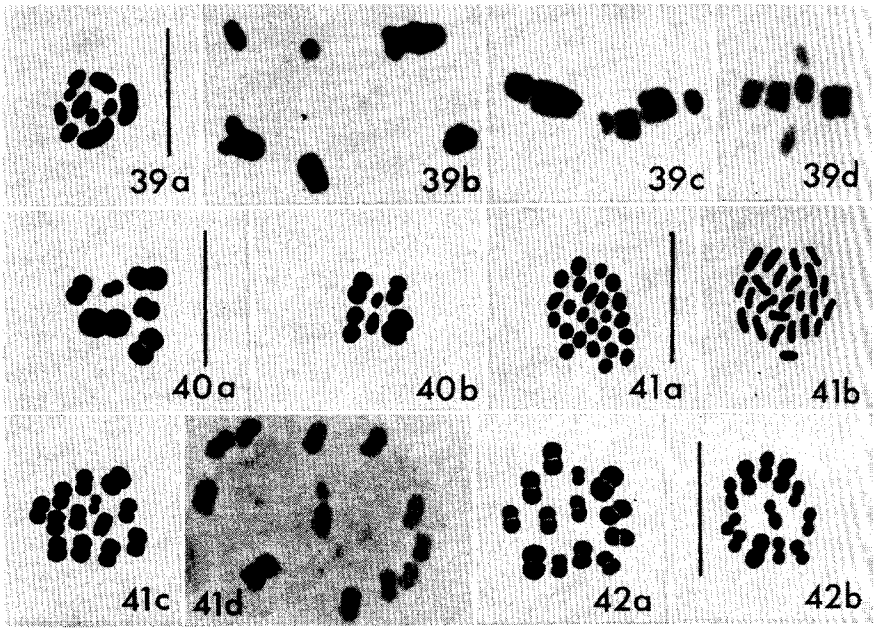

FIG. 10–39.—*Loxaspis malayensis* from Malaya. a, camera lucida drawing; b to d, photographs. a, spermatogonial metaphase with 10 chromosomes; b, late diakinesis; c, first spermatocyte metaphase (side view) with 6 chromsomes; d, second metaphase (side view) with 6 chromsomes; d, second metaphase (side view), X and Y lie in center and move precociously.

FIG. 10–40.—*Aphrania vishnou*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 4 autosomal tetrads, X and Y dyads; b, second spermatocyte metaphase, X and Y lie in center of ring formed by 4 autosomes.

FIG. 10–41.—*Leptocimex duplicatus*. a to c, camera lucida drawings; d, photograph. a, spermatogonial metaphase with 24 chromosomes; b, female somatic metaphase with 24 chromosomes; c, first spermatocyte metaphase with 13 chromosomes, consisting of 11 autosomal tetrads, X and Y dyads; d, second metaphase, X and Y lie in center of ring formed by 11 autosomes.

FIG. 10–42.—*Stricticimex antennatus*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 13 chromosomes; b, second spermatocyte metaphase, X and Y lie in center of ring formed by 11 autosomes.

Primicimicinae

This subfamily contains 2 very diverse types. *Primicimex* has a low (10) chromosome number with 4 pairs of autosomes, and *Bucimex* has a diploid number of 28, with 13 autosomes.

Cimicinae

The genus *Cimex* actually consists of 4 species groups: the *lectularius* complex, the *pipistrelli* complex, the *pilosellus* complex, and the monotypic *C. hemipterus* with several different chromosome numbers. In the

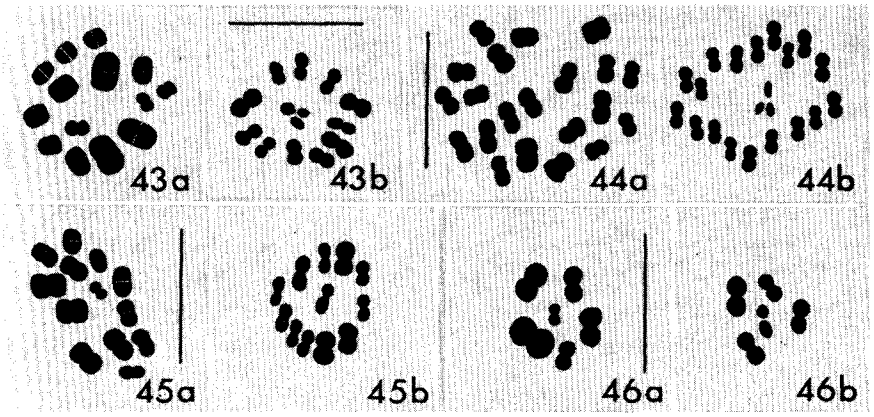

FIG. 10–43.—*Afrocimex leleupi*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 14 chromosomes; b, second spermatocyte metaphase, X_1, X_2, and Y lie in center of ring formed by 11 autosomes.

FIG. 10–44.—*Crassicimex pilosus*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 21 chromosomes; b, second spermatocyte metaphase, X_1 X_2, and Y lie in center of ring formed by 18 autosomes.

FIG. 10–45.—*Latrocimex spectans*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 13 chromosomes; b, second spermatocyte metaphase, X and Y lie in center of ring formed by 11 autosomes.

FIG. 10–46.—*Primicimex cavernis*. a and b, camera lucida drawings. a, first spermatocyte metaphase with 6 chromosomes; b, second metaphase, X and Y take a central position.

C. lectularius complex, chromosome numbers (2n ♂) range from 29 to 36, the diversity due principally to differences in the number of X chromosomes; the basic chromosome number is 29 (13 pairs of autosomes and X_1X_2Y). In *C. hemipterus* and in the *Cimex pipistrelli* complex, the chromosome number is consistently 31 (14 pairs of autosomes and X_1X_2Y). In the *Cimex pilosellus* complex, the chromosome number ranges from 22 (10 pairs of autosomes and XY) to 33 (14 pairs of autosomes and $X_1X_2X_3X_4Y$), the diversity due to differences in the number of autosome pairs (10, 11 or 14) and in X chromosomes.

Two courses of evolution seem possible on the basis of chromosome evidence. One of these is a decrease in number as a result of the fusion of autosomes and the other, an increase in number as a result of fragmentation of autosomes.

It is generally considered that an increase in number by fragmentation takes place more frequently in organisms having holokinetic chromosomes (Schrader 1947, Schrader and Hughes-Schrader 1956, Brown 1961, Nordenskiöld 1961). Hughes-Schrader and Schrader (1961) induced breakage of chromosomes by X-rays in 4 species of Pentatomidae and found that the fragments behaved quite normally and perpetuated themselves during the meiotic cycle.

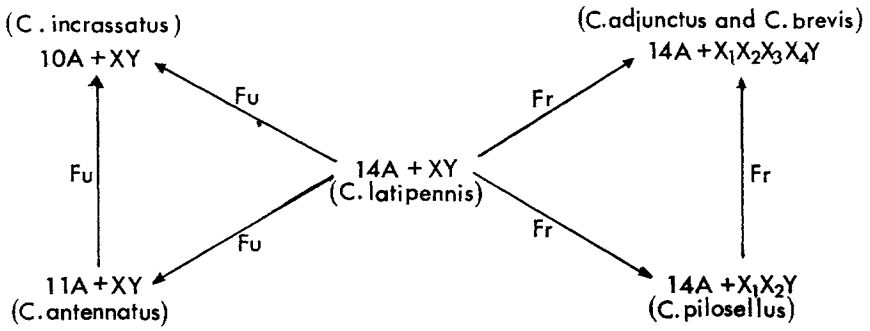

FIG. 10–47.—Possible chromosome evolution in the *Cimex pilosellus* Group. Fr, fragmentation; Fu, fusion.

On the other hand, a decrease in chromosome number may occur by fusion. Fusion of 2 chromosomes will reduce the chromosome number by one. The possibility of fusion has also been discussed in organisms with holokinetic chromosomes, but it takes place rarely compared with fragmentation. That relatively fewer fusions than fragmentations establish themselves in Heteroptera may be explained in part by the fact that there is seldom more than a single chiasma per bivalent; however, trivalents were frequently observed in the hybrids described in this report. In the Pentatomidae the overwhelming majority of the species investigated cytologically have 14 chromosomes. Many authors (Schrader 1940, Wilson 1913, Manna 1951, and Parshad 1957) have suggested that numbers below 14 may be the result of fusion. Decrease in chromosome number by fusion may have taken place in the Belostomatidae (Chickering and Bacorn 1933), and spontaneous fusions have been reported in several coccid species in the Homoptera (Brown 1961).

In the *Cimex pilosellus* complex, it seems most likely that 14 pairs of autosomes is the type number, and 10 and 11 pairs are derived by simple spontaneous fusion, thus numbers decreased from 14 may be more recent in origin than the type number. This assumption is confirmed by a study of hybrids during meiosis. In the hybrid between *Cimex antennatus* (11 pairs of autosomes) and *Cimex brevis* (14 pairs), the first metaphase reveals trivalents. Apparently the trivalent is formed by 1 large chromosome (undoubtedly from *Cimex antennatus*) and 2 small ones (from *Cimex brevis*). This evidence suggests 2 possibilities in chromosome evolution: That 1 large chromosome was formed from 2 small ones by fusion, or that 2 small chromosomes were formed from 1 large one by fragmentation. Of these 2 possibilities I prefer to assume that fusion rather than fragmentation took place—fragmentation would have caused the numbers to vary upward from 14. Instead, the great majority of species in the genus *Cimex* have 14 pairs of autosomes and the num-

bers decrease to 13, 11, or 10. The possible autosome evolution in the *Cimex pilosellus* complex is shown in Fig. 10–47.

The genus *Paracimex* has chromosome numbers that vary from 39 to 47. There are consistently 18 pairs of autosomes—the diversity in chromosome numbers is apparently due to differences in the number of X chromosomes (discussed subsequently).

Cacodminae

In this subfamily the cytological evidence suggests 3 groups. One of these includes *Cacodmus, Aphrania,* and *Loxaspis,* each with 4 pairs of autosomes; one includes *Leptocimex* and *Stricticimex,* each with 11 pairs; and the third comprises *Crassicimex,* which has 18.

Afrocimicinae

Afrocimex has unique external characters but the same number of autosomes as *Leptocimex, Stricticimex,* and the following subfamily.

Latrocimicinae

Latrocimex is unique morphologically, but the male has a diploid chromosome number of 24 with 11 autosomes, precisely as in *Leptocimex* and *Stricticimex.*

Haematosiphoninae

It is possible to divide this subfamily into 3 groups—one having fairly high (40–44) chromosome numbers (*Hesperocimex*); one having 31 to 34 chromosomes (*Haematosiphon, Caminicimex, Synxenoderus, Psitticimex*); and a third having low (10) chromosome numbers (*Ornithocoris*).

In the genus *Hesperocimex, coloradensis* and *cochimiensis* have 19 pairs of autosomes, but *sonorensis* has 20 pairs. In the hybrid between *Hesperocimex sonorensis* and *Hesperocimex cochimiensis,* there are 19 pairs (one of them distinctly heteromorphic) and a univalent with XY at the first metaphase. Were there a trivalent in the hybrid, doubtless 2 chromosomes in *Hesperocimex sonorensis* would be derived from 1 large chromosome in *Hesperocimex cochimiensis* by fragmentation, or 1 chromosome in *Hesperocimex cochimiensis* would be formed by fusion of 2 chromosomes in *Hesperocimex sonorensis.* Actually, no trivalent was observed in meiosis of the hybrid, hence it is difficult to reach a conclusion as to possible chromosome evolution in the genus. However, the cytological data suggest that 19 pairs of autosomes is the type number in *Hesperocimex* and that an increase in number is of more recent origin and hence is derived from fragmentation.

THE SEX-CHROMOSOME MECHANISM

The sex-chromosome mechanism is rather complex. About half of the species investigated have the XX-XY mechanism, the remainder a com-

pound mechanism. Moreover, some of the species with a compound sex-chromosome mechanism, particularly in Cimicinae, have so-called supernumerary sex chromosomes (Table 10–1).

XX-XY Sex-Chromosome Mechanism

There is little doubt that an XX-XY mechanism is more primitive than a compound mechanism (White 1954). This may be safely assumed in the Cimicidae, since an XX-XY mechanism is found in the Primicimicinae and has persisted unchanged in the more primitive genera throughout the family. When both XY and the compound mechanism appear in the same genus, such as in *Cimex* and *Hesperocimex,* the X chromosome in the XY mechanism tends to be a larger component, while the X chromosomes in the compound mechanism are rather small, suggesting that the compound sex chromosomes are derived by simple fragmentation from an originally single X (discussed subsequently).

Compound Sex-Chromosome Mechanism

Compound sex-chromosome mechanisms are very common in the Cimicidae, as in other Heteroptera. In the Cimicidae, the X_1X_2Y (♂) – $X_1X_1X_2X_2$ (♀) mechanism is more common than the other compound mechanisms (Table 10–1). In the X_1X_2Y mechanism, X_1, X_2, and Y tend to be almost the same size, or Y to be a little larger than the X. A compound mechanism in which the X is represented by more than 3 chromosomes is found in the genera *Cimex, Paracimex,* and *Hesperocimex.* In spermatogenesis each of these X chromosomes divides equationally at the first division without any particular arrangement on the equatorial plate, and in the second division the compound X chromosomes and a single Y always lie in the center of a ring formed by the autosomes. In the separation immediately following, the compound X chromosomes move to one pole and the single Y goes to the other. In the genus *Hesperocimex* and in the *Cimex pilosellus* complex, there is clear evidence that compound X chromosomes are derived by simple fragmentation of an originally large X. This evidence is supported by the fact that the total length of compound X chromosomes in the male meiotic metaphase is almost equal to that of a single X chromosome in closely related species. The features of compound X chromosomes found in the *C. lectularius* complex and in the genus *Paracimex* are quite different from others and consist of supernumerary X chromosomes (discussed subsequently).

Evolution of the Sex-Chromosome Mechanism Through Fragmentation

When compound sex-chromosome mechanisms occur in other insects such as Orthoptera and Diptera, the number of autosomes usually decreases as the number of sex chromosomes increases (White 1954), but in the Heteroptera, there is no such relationship. In the *Cimex pilosellus*

complex the number of autosomes ranges from 20 to 28 and of sex chromosomes from 2 to 5, but no correlation between the two is ever found. Troedsson (1944) suggested that fragmentation is the major source of compound sex chromosomes in Heteroptera. Schrader (1947) pointed out that a simple breakage of a holokinetic sex chromosome would result directly in compound sex chromosomes. Hughes-Schrader and Schrader (1961) induced artificial breakage of sex chromosomes in Pentatomidae by X-rays, supporting the idea that simple fragmentation is a factor in the evolution of compound sex chromosomes, because the fragments behaved quite normally and perpetuated themselves during the meiotic cycle.

This concept of simple fragmentation may be applied to the deviation in number of sex chromosomes in the *Cimex pilosellus* complex. The compound sex-chromosome mechanism doubtless is of more recent origin than the XX-XY mechanism. *Cimex latipennis* has an XX-XY mechanism in which the X is the largest component in the chromosome set (Fig. 10–10). *Cimex pilosellus* has an X_1X_2Y mechanism in which the X_1 and X_2 are almost the same size (Fig. 10–11). The X in *Cimex latipennis* is almost as large as the X_1 and X_2 together in *Cimex pilosellus.* Although this comparison supports the possibility of fragmentation, just how such a fragmentation can have taken place is difficult to ascertain; it may be assumed that transverse fragmentation has taken place in *Cimex pilosellus,* as has been suggested for the Pentatomidae (Manna 1951, Parshad 1957). On the other hand, Hughes-Schrader and Schrader (1961) believe that longitudinal rather than transverse fragmentation may be responsible for the increase of chromosomal autonomies. In any case, fragmentation of the sex chromosomes seems to be involved in the evolution of this species complex.

Cimex adjunctus and *Cimex brevis* have 4 quite small X chromosomes (Figs. 10–12, 10–13) instead of the 2 in *Cimex pilosellus* and the single one in *Cimex latipennis.* It seems likely that fragmentation of a single X chromosome has taken place directly or indirectly, because the total length of the 4 X chromosomes is almost the same as the single X in *Cimex latipennis* or the 2 X's in *Cimex pilosellus.* Therefore, in *Cimex adjunctus* and *Cimex brevis,* fragmentation may be considered to have occurred at least twice. The possibility of subsequent fragmentation is suggested by Schrader (1947).

A possible explanation of the evolution of the sex chromosome mechanism in the *Cimex pilosellus* complex is considered diagramatically in Fig. 10–47.

Another instance of simple fragmentation of sex chromosomes is found in the genus *Hesperocimex,* in which *sonorensis* and *cochimiensis* have the XX-XY mechanism and *coloradensis* 3 X chromosomes. The X chromosome in both *Hesperocimex sonorensis* and *Hesperocimex cochimiensis* is a large component in the set, and each of the 3 X chromosomes in

Hesperocimex coloradensis is a very small one. The total length of the 3 X chromosomes is almost the same as that of a single X in *Hesperocimex sonorensis* or *Hesperocimex cochimiensis,* suggesting that the 3 X chromosomes in *Hesperocimex coloradensis* were derived by fragmentation from a single X chromosome in *Hesperocimex sonorensis* or *Hesperocimex cochimiensis.*

SUPERNUMERARY SEX CHROMOSOMES

Compound sex-chromosome mechanisms have been reported in many species of Heteroptera, and the chromosomes have been found to be constant in number and size within species, even in some reduviids which have a fairly high number of X chromosomes (Payne 1910, 1912). But in rare cases an anomolous sex chromosome mechanism has been reported. One such case is *C. lectularius,* described by Slack (1939a) and Darlington (1939), in which the number of X's varies from one individual to another and within individuals as well. A second case is the genus *Acanthocephala* (Wilson 1907, 1909, 1910), in which the number of Y's is variable in different individuals, but the number of X's is constant. These anomolous cases are due to supernumerary sex chromosomes—supernumerary X chromosomes in *C. lectularius* and supernumerary Y chromosomes in *Acanthocephala.* During the present study, such supernumerary sex chromosomes were found in *C. lectularius* and in the species of *Paracimex.* Because the essential features of supernumerary sex chromosomes are somewhat different in *Cimex* and *Paracimex,* the 2 genera are discussed separately.

Supernumerary Sex Chromosomes in *C. lectularius*

Darlington (1939) found that the number of X chromosomes in *C. lectularius* varied from 2 to 15 in the male, not only in different individuals but within individuals, and that the number of X chromosomes was more variable in wild than in laboratory populations. Slack (1939a) suggested that the basic sex-chromosome mechanism in *C. lectularius* was X_1X_2Y and that the variability in the number of X chromosomes was caused by (a) irregular segregation of the supernumeraries at second anaphase, and (b) non-disjunction of chromatids of the univalent sex chromosomes at the first anaphase. Although Darlington's explanation was similar to Slack's, the former suggested that the segregation of numerous X's from a single Y was due to quantitative differences between centromeres, with a strong Y and weak X's.

In the present study of *C. lectularius,* the status of supernumerary X chromosomes was found to differ somewhat from that described by Slack and Darlington. Many populations from different sources were observed (at least 20 specimens each); most of them were very stable in chromosome number within a population and quite regular in mei-

osis. Only the specimens from Columbus, Ohio, showed a variable number of X chromosomes (from 7 to 9 in the male), not only among individuals but within individuals.

The specimens from Berkeley, Calif, Monterrey and La Piedad, Mexico, Nagasaki, Japan, and Durtal, France, have a consistently X_1X_2Y sex-chromosome mechanism. On the other hand, the specimens from Cairo, Egypt, and Moravia, Czechoslovakia, are consistently $X_1X_2X_3X_4X_5X_6Y$. Darlington observed lagging chromosomes (more frequently where the number of X chromosomes was high) at the first spermatocyte division, indicating that non-disjunction might have taken place. Such meiotic irregularity was never found in the present study, even in specimens from Cairo and Moravia which have 6 X's and Y. However, in the specimens from Columbus, Ohio, a little lagging of chromosomes (Fig. 10–3k) was observed at first anaphase.

As Slack (1939b) and Darlington (1939) proposed, doubtlessly the basic sex-chromosome mechanism in *C. lectularius* is X_1X_2Y in the male, and the diversity in the number of X chromosomes is due to supernumerary X chromosomes. This is further confirmed by the observation of the X_1X_2Y chromosomes during meiosis in the related species *Cimex columbarius* and *C. hemipterus.*

To obtain information on the origin and transmission of supernumerary X chromosomes, interspecific (*C. lectularius* and *Cimex columbarius*) and intraspecific (*C. lectularius* from Berkeley (X_1X_2Y) and from Cairo ($X_1X_2X_3X_4X_5X_6Y$)) hybridization was carried out. In the hybrids, meiosis reveals some irregularities, and there are lagging chromosomes at first anaphase, indicating possible non-disjunction of the X chromosomes. The results of observations of chromosome numbers in hybrids is summarized in Tables 10–3 to 10–8. In the intraspecific hybrids (Tables 10–3, 10–4), the results indicate that transmission of supernumerary X chromosomes is mainly due to maternal influence. The cross Berkeley (♀) × Cairo (♂) is fairly stable, while the reciprocal is more variable. Were meiosis in the hybrid quite normal and transmission of X chromosomes maternal, the expected number of X chromosomes in the reciprocal cross would be 6, but the result obtained (Table 10–4) was 5, suggesting that the irregularity had taken place during embryogenesis. In the reciprocal cross, no discernible results in embryogenesis were obtained, so the reason for deviation from the expected number of X chromsomes is uncertain. Further study is needed to clarify this point.

In the interspecific hybrids *C. lectularius* × *Cimex columbarius,* the results differed somewhat from those of intraspecific crosses. When female *columbarius* was used, almost no supernumerary X chromosomes were obtained (Tables 10–6, 10–8), but when female *lectularius* was used, the number of X chromosomes was more variable (Tables 10–5, 10–7), and the tendency for variation in the number of X chromosomes resembled that of the intraspecific cross. Although it is certain that the

transmission of supernumerary X chromosomes is mainly maternal, their origin is not clear.

Supernumerary X Chromosomes in *Paracimex*

The number of pairs of autosomes in *Paracimex* is consistently 18, but the number of X chromosomes is quite variable (Table 10–1). The following discussion is based principally on observations of *Paracimex borneensis* from Malaya and *Paracimex capitatus* from Wau, New Guinea, because many fresh specimens were available. The number of X chromosomes varies from 3 to 6 in the Wau species and from 7 to 9 in the Malayan species. In both, variation in the number of X chromosomes was observed among and within individuals. At the first spermatocyte anaphase, irregularity and abnormality were observed with lagging chromosomes and chromatid bridges (Figs. 10–21, 10–23), indicating that non-disjunction can take place in X chromosomes and induce variation of chromosome number in the second spermatocyte. Of course variation is observed in the number of X chromosomes in the second metaphase (the females have not been studied but presumably would reveal a corresponding variation), leading to more variations in the progeny. Such a situation is very anomalous and suggests that natural hybridization may have taken place. To obtain definitive information on the transmission and origin of these supernumerary X chromosomes, it will be necessary to culture species in the laboratory. This has been attempted but without success because of their host specificity. Further study is needed, but the cytological data already at hand permits the conclusion that the basic chromosome complement of this group is 18 pairs of autosomes with X_1X_2Y.

Table 10–1.—Sources of specimens and chromosome complements.

Species	From	2n	n
Primicimicinae			
*Primicimex cavernis**	Ney Cave, Texas	♂ (10) ♀ (10)	4A + XY
Bucimex chilensis	Dalcahue, Chile Lonquimay, Chile	♂ 28 spg ♀ 28	13A + XY
Cimicinae			
Cimex lectularius	Berkeley, Calif. Monterrey, Mexico La Piedad, Mexico Nagasaki, Japan Durtal, France	♂ 29 spg ♀ 30	13A + X_1X_2Y
	Cairo, Egypt Moravia, Czech.	♂ 33 spg ♀ 38	13A + $X_1X_2X_3X_4X_5X_6Y$
	Pittsburgh, Penn. (DDT-resistant strain)	♂ 35 spg	13A + $X_1X_2X_3X_4X_5X_6Y$ + 1
	Columbus, Ohio	♂ 34 to 36 spg	13A + (7 to 9X's) Y
Cimex columbarius	Southern Finland	♂ 29 spg ♀ 30	13A + X_1X_2Y
Cimex hemipterus	Vietnam Panama Thailand Taiwan New Guinea	♂ 31 spg ♀ 32	14A + X_1X_2Y
Cimex pipistrelli	England	♂ 31 spg ♀ 32	14A + X_1X_2Y
Cimex stadleri	Czechoslovakia	♂ 31 spg ♀ 32	14A + X_1X_2Y
Cimex japonicus	Akita, Japan	♂ 31 spg ♀ 32	14A + X_1X_2Y
Cimex latipennis	Klamath, Oreg.	♂ 30 spg ♀ 30	14A + XY
Cimex pilosellus	Colusa, Calif.	♂ 31 spg ♀ 32	14A + X_1X_2Y
Cimex adjunctus	Woodford, Ky	♂ 33 spg ♀ 36	14A + $X_1X_2X_3X_4Y$
Cimex brevis	Staples, Minn.	♂ 33 spg ♀ 36	14A + $X_1X_2X_3X_4Y$
Cimex antennatus	Pope Valley, Calif.	♂ 24 spg ♀ 24	11A + XY

Table 10-1.— (Continued)

Species	From	2n	n
Cimex incrassatus	St. David, Ariz.	♂ 22 spg ♀ 22	10A + XY
Oeciacus hirundinis	Greece	♂ 31 spg ♀ 32	14A + X_1X_2Y
Oeciacus vicarus	Colusa, Calif. Mt. Diablo, Calif.	♂ 31 spg ♀ 32	14A + X_1X_2Y
*Paracimex borneensis**	Sarawak, Borneo	♂ (39) ♀ (40)	18A + X_1X_2Y
Paracimex boreensis	Malaya	♂ 44 to 47 spg	18A + (7 to 9X's) Y
*Paracimex capitatus**	New Britain	♂ (39) ♀ (40)	18A + X_1X_2Y
Paracimex capitatus	Neth. N. Guinea	♂ (40) spg ♀ (42)	18A + $X_1X_2X_3Y$
Paracimex capitatus	Wau, New Guinea	♂ 41 to 42 spg	18A + (4 to 6X's) Y
*Paracimex caledoniae**	New Caledonia	♂ (39) ♀ (40)	18A + X_1X_2Y
Cacodminae			
Cacodmus vicinus	Cairo, Egypt	♂ 10 spg ♀ (10)	4A + XY
*Aphrania vishnou**	Cambodia	♂ (10) ♀ (10)	4A + XY
Loxaspis malayensis	Malaya	♂ 10 spg ♀ 10	4A + XY
*Stricticimex antennatus**	South Africa	♂ (24) ♀ (24)	11A + XY
Leptocimex duplicatus	Cairo, Egypt	♂ 24 spg ♀ 24	11A + XY
*Crassicimex pilosus**	Madagascar	♂ (39) ♀ (40)	18A + X_1X_2Y
Afrocimicinae			
*Afrocimex leleupi**	Katanga, Congo	♂ (25) ♀ (26)	11A + X_1X_2Y
Latrocimicinae			
*Latrocimex spectans**	Trinidad, B. W. I.	♂ (24)	11A + XY
Haematosiphoninae			
*Ornithocoris toledoi**	Brazil	♂ (10)	4A + XY

Table 10–1.—(Continued)

Species	From	2n	n
Ornithocoris pallidus	Brazil	♂ 10 spg	4A + XY
Caminicimex furnarii	Tucuman, Argentina	♂ 34 spg ♀ 34	16A + XY
Psitticimex uritui	Tucuman, Argentina	♂ 31 spg ♀ 32	14A + X_1X_2Y
Haematosiphon inodorus	Norco, Calif.	♂ 31 spg ♀ 32	14A + X_1X_2Y
Synxenoderus comosus	Mt. Diablo, Calif.	♂ 31 spg ♀ (32)	14A + X_1X_2Y
Hesperocimex coloradensis	Durango, Colo.	♂ 42 spg ♀ 44	19A + $X_1X_2X_3Y$
Hesperocimex sonorensis	Sonora, Mexico Kelvin, Ariz.	♂ 42 spg ♀ 42	20A + XY
Hesperocimex cochimiensis	Baja Calif., Mexico	♂ 40 spg ♀ 40	19A + XY

Table 10–2.—Chromosome complements of individuals in a colony of *C. lectularius* from Columbus, Ohio.

Males				Females	
	Chromosome complement				
No. observed	Spermatogonial metaphase	First metaphase	Second metaphase	No.	Chromosome no. in mitosis
14[a]	34	21	13A + $X_1 \ldots X_7Y$	1	39
4[a]	35	22	13A + $X_1 \ldots X_8Y$	6	40
7[a]	36	23	13A + $X_1 \ldots X_9Y$	2	42

[a] In some individuals the diploid chromosome number was estimated from the first and second metaphase, because no spermatogonial metaphase was observed.

Table 10–3.—Summary of observations of chromosome complements in hybrid males of *C. lectularius* Berkeley (♀) (26A + $X_1X_1X_2X_2$) × Cairo (♂) (26A + $X_1X_2X_3$ $X_4X_5X_6Y$). The first progeny were obtained by a single-pair mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1	10					10
	F_2	13	2				15
	F_3	14	1				15
	F_4	15					15
2	F_1	15					15
	F_2	15					15
	F_3	15					15
	F_4	15					15
3	F_1	15					15
	F_2	15					15
	F_3	15					15
	F_4	15					15
4	F_1	9	1				10
	F_2	11	4				15
	F_3	13	2				15
	F_4	15					15
5	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
6	F_1	5	8	2			15
	F_2	4	11				15
	F_3	9	6				15
	F_4	14	1				15
7	F_1	12	3				15
	F_2	15					15
	F_3	15					15
	F_4	15					15
8	F_1	15					15
	F_2	15					15
	F_3	15					15
	F_4	15					15
9	F_1		5		10		15
	F_2		12		3		15
	F_3		15				15
	F_4		15				15
10	F_1	10					15
	F_2	15					15
	F_3	15					15
	F_4	15					15
Totals	F_1	101	17	2	10	0	130
	F_2	118	29	0	3	0	150
	F_3	126	24	0	0	0	150
	F_4	134	16	0	0	0	150
	Σ	479	86	2	13	0	580

Table 10–4.—Summary of observations of chromosome complements in the hybrid males of *C. lectularius* Cairo (♀) (26A + $2X_1X_2X_3X_4X_5X_6$) × Berkeley (♂) (26A + X_1X_2Y). The first progeny were obtained by a single mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1			4	8	3	15
	F_2			1	13	1	15
	F_3				14	1	15
	F_4				15		15
2	F_1				12	3	15
	F_2				15		15
	F_3				15		15
	F_4				15		15
3	F_1			2	13		15
	F_2			1	14		15
	F_3				15		15
	F_4				15		15
4	F_1		6	2	7		15
	F_2		5		10		15
	F_3		2		13		15
	F_4				15		15
5	F_1		2		9	4	15
	F_2				12	3	15
	F_3				14	1	15
	F_4				15		15
6	F_1				8	7	15
	F_2				14	1	15
	F_3				15		15
	F_4				15		15
7	F_1	1	4	1	9		15
	F_2		4		11		15
	F_3		1		14		15
	F_4				15		15
8	F_1	9	5	1			15
	F_2	4	10	1			15
	F_3	2	13				15
	F_4		15				15
9	F_1		4		8	3	15
	F_2		2		11	2	15
	F_3				13	2	15
	F_4				15		15
10	F_1		3		10	2	15
	F_2		4		10	1	15
	F_3		2		13		15
	F_4				15		15
Totals	F_1	10	24	10	84	22	150
	F_2	4	25	3	110	8	150
	F_3	2	18		126	4	150
	F_4		15		135		150
	Σ	16	82	13	455	34	600

Table 10–5.—Summary of observations of chromosome complements in the hybrid males of *C. lectularius* from Berkeley (♀) ($26A + 2X_1X_2$) × *Cimex columbarius* (♂) ($26A + X_1X_2Y$). The first progeny were obtained by a single mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
2	F_1	4	6				10
	F_2	12	3				15
	F_3	15					15
	F_4	15					15
3	F_1	7	3				10
	F_2	15					15
	F_3	15					15
	F_4	15					15
4	F_1	11	4				15
	F_2	12	3				15
	F_3	14	1				15
	F_4	15					15
5	F_1	9	6				15
	F_2	11	4				15
	F_3	15					15
	F_4	15					15
6	F_1		15				15
	F_2	4	11				15
	F_3	12	3				15
	F_4	14	1				15
7	F_1	10					10
	F_2	14	1				15
	F_3	15					15
	F_4	15					15
8[a]							
9	F_1		2	5	8		15
	F_2		11	1	3		15
	F_3		14		1		15
	F_4		15				15
10	F_1	6	1				7
	F_2	15					15
	F_3	15					15
	F_4	15					15
Totals	F_1	57	37	5	8		107
	F_2	98	33	1	3		135
	F_3	116	18		1		135
	F_4	119	16				135
	Σ	390	104	6	12		512

[a] No eggs laid.

Table 10–6.—A summary of observations of chromosome complements in the hybrid males of *Cimex columbarius* (♀) (26A + $2X_1X_2$) × *C. lectularius* from Berkeley (♂) (26A + X_1X_2Y). The first progeny were obtained by a single mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
2	F_1	7					7
	F_2	15					15
	F_3	15					15
	F_4	15					15
3[a]							
4	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
5	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
6[a]							
7	F_1	4					4
	F_2	15					15
	F_3	15					15
	F_4	15					15
8	F_1	3					3
	F_2	10					10
	F_3[b]	15					15
	F_4						
9	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
10	F_1	1					1
	F_2	10					10
	F_3	15					15
	F_4	15					15
Totals	F_1	55					55
	F_2	110					110
	F_3	120					120
	F_4	120					120
	Σ	405					405

[a] No eggs laid.
[b] No further generation was obtained.

Table 10-7.—Summary of observations of chromosome complements in the hybrid males of *C. lectularius* from Cairo (♀) ($26A + 2X_1X_2X_3X_4X_5X_6$) × *Cimex columbarius* (♂) ($26A + X_1X_2Y$). The first progeny were obtained by a single mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1		3	5	7		15
	F_2		4		11		15
	F_3		9		6		15
	F_4		13		2		15
2	F_1			3	12		15
	F_2		5		10		15
	F_3		2		13		15
	F_4				15		15
3	F_1				10		10
	F_2				15		15
	F_3				15		15
	F_4				15		15
4	F_1			1	9		10
	F_2		2		13		15
	F_3		1		14		15
	F_4				15		15
5[a]							
6	F_1		6		9		15
	F_2		8		7		15
	F_3		14		11		15
	F_4		15				15
7	F_1				10		10
	F_2		4		11		15
	F_3		2		13		15
	F_4				15		15
8	F_1			1	5	9	15
	F_2				3	12	15
	F_3				1	14	15
	F_4					15	15
9	F_1		3		4		7
	F_2		4		6		10
	F_3		10	1	4		15
	F_4		14	1			15
10	F_1			1	7		8
	F_2		2		8		10
	F_3		2	3	10		15
	F_4			2	13		15
Total	F_1		12	11	73	9	105
	F_2		29		84	12	125
	F_3		40	4	77	14	135
	F_4		42	3	75	15	135
	Σ		123	18	309	50	500

[a] No eggs laid.

Table 10–8.—Summary of observations of chromosome complements in the hybrid males of *Cimex columbarius* (♀) (26A + $2X_1X_2$) × *C. lectularius* from Cairo (♂) (26A + $X_1X_2X_3X_4X_5YX_6Y$). The first progeny were obtained by a single mating, the following ones by mass matings.

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	F_1	2					2
	F_2	10					10
	F_3	15					15
	F_4	15					15
2	F_1	5	2				7
	F_2	10					10
	F_3	15					15
	F_4	15					15
3	F_1	8					8
	F_2	15					15
	F_3	15					15
	F_4	15					15
4	F_1	9	1				10
	F_2	13	2				15
	F_3	15					15
	F_4	15					15
5	F_1	3	1				4
	F_2	15					15
	F_3	15					15
	F_4	15					15
6	F_1	10					10
	F_2	15					15
	F_3	15					15
	F_4	15					15
7	F_1	8					8
	F_2	15					15
	F_3	15					15
	F_4	15					15
8	F_1	15					15
	F_2	15					15
	F_3	15					15
	F_4	15					15
9	F_1	4					4
	F_2	10					10
	F_3	15					15
	F_4	15					15
10[a]							
Total	F_1	64	4				68
	F_2	118	2				120
	F_3	135					135
	F_4	135					135
	Σ	452	6				458

[a] No eggs laid.

INHERITANCE OF X CHROMOSOMES

By H. E. McKEAN

The remarks in this section are restricted to deductions and inferences based upon 6 hybrid crosses, including reciprocals, of the Berkeley and Cairo strains of *C. lectularius* and *C. columbarius* (see Tables 10–3 through 10–8), as well as upon 4 backcrosses involving reciprocal first-generation hybrids of the *columbarius* × *lectularius* (Cairo) interspecific crosses (see Tables 10–9 through 10–12). For brevity, we shall refer to these strains as the Berkeley, Cairo, and Columbarius strains.

As was discussed previously, 10 single-pair matings of each cross were made, producing hybrid F_1's consisting entirely of full sibs. Ten males and 10 females were selected at random from these sibs to provide parents for the F_2 generation, and were mated en masse to produce F_2 progeny. This procedure was repeated for several generations. In each generation, 15 males (if available) were examined cytologically for the number of X chromosomes during spermatogenesis and the results compiled in Tables 10–3 through 10–8 for generations F_1–F_4. For the most part, males examined cytologically were distinct from those used as parents.

It is the purpose of this discussion to consider possible mechanisms by which supernumerary X's are inherited in this genus and to formulate hypotheses consistent with known genetic theory and observation.

Elsewhere in this chapter, Ueshima concluded that "transmission of supernumerary X chromosomes is mainly maternal." Consideration of the aforementioned tables reveals that there are extraordinary reciprocal differences in numbers, especially when the 12X female, or 6X,Y male, is used as one parent. That the males of the hybrid in general resemble the males of the maternal line more closely than those of the paternal line (in terms of the number of X chromosomes, which we will henceforward refer to simply as the "X number") cannot be seriously questioned. On the other hand, since the results are not predictable in this regard, it is obvious that modifications of one sort or another do occur, and the overall mechanism deserves closer scrutiny.

BACKCROSSES

To check on the actual genotypes of the F_1 females (which were not examined cytologically), backcrosses of F_1 females were made[3] to 10 males of each parental type in the Cairo × Columbarius cross, in a manner similar to the propagation of the F_2–F_4 generations. Backcross progeny (10 females chosen at random) were again backcrossed to the same 10 males of the parental line, yielding 2 backcross generations B_1 and B_2. The data are summarized in Tables 10–9 to 10–12.

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[3] Data from Ueshima.

Table 10–9.—Summary of observations of chromosome complements in the backcross of type (*C. lectularius* from Cairo × *C. columbarius*) (♀) × *C. columbarius* (♂).

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	B_1			3	12		15
	B_2			2	13		15
2	B_1		2	1	11	1	15
	B_2	1	1	2	11		15
3	B_1		5	2	8		15
	B_2	1	4		10		15
4	B_1		2	7	6		15
	B_2		1	6	8		15
5	B_1	1		11	3		15
	B_2	1	2	11	1		15
Total	B_1	1	9	24	40	1	75
	B_2	3	8	21	43		75
	Σ	4	17	45	83	1	150

The results are entirely consistent with the F_1–F_4 data. When the male parent in the backcross is of the same strain as the female line entering into the F_1 hybrid (Tables 10–10, and 10–11), the data strongly suggest approach toward that parental type, whereas in the opposite case (Tables 10–9, and 10–12) there is evidence of more variation in X number than was true in the F_1 (Tables 10–7, 10–8).

Table 10–10.—Summary of observations of chromosome complements in the backcross of type (*C. lectularius* from Cairo × *C. columbarius*) (♀) × *C. lectularius* from Cairo (♂).

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	B_1			1	9	5	15
	B_2				11	4	15
2	B_1		1	2	9	3	15
	B_2			1	10	4	15
3	B_1				10	5	15
	B_2				7	8	15
4	B_1		1		11	3	15
	B_2				12	3	15
5	B_1			1	8	6	15
	B_2			1	10	4	15
Total	B_1		2	4	47	22	75
	B_2			2	50	23	75
	Σ		2	6	97	45	150

Table 10–11.—Summary of observations of chromosome complements in the backcross of type (*C. columbarius* × *C. lectularius* from Cairo) (♀) × *C. columbarius* (♂).

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	B_1	15					15
	B_2	15					15
2	B_1	14	1				15
	B_2	15					15
3	B_1	15					15
	B_2	15					15
4	B_1	15					15
	B_2	15					15
5	B_1	15					15
	B_2	15					15
Total	B_1	74	1				75
	B_2	75					75
	Σ	149	1				150

For example, in the Columbarius (♀) × Cairo (♂) F_1–F_4 data (Table 10–8), there are only 6 cases out of 458 in which male progeny contain 3 X chromosomes, with the remainder containing the maternal number of 2. Moreover, when F_1 females were crossed to Columbarius males (Table 10–11), only one of 150 of the backcross progeny had an X count of 3, with 149 continuing the maternal number of 2. On the other hand,

Table 10–12.—Summary of observations of chromosome complements in the backcross of type (*C. columbarius* × *C. lectularius* from Cairo) (♀) × *C. lectularius* from Cairo (♂).

Exp. no.	Generation	29 13A + 2X + Y	30 13A + 3X + Y	31 13A + 4X + Y	32 13A + 5X + Y	33 13A + 6X + Y	No. observed
1	B_1	14	1				15
	B_2	15					15
2	B_1	15					15
	B_2	15					15
3	B_1	13	1	1			15
	B_2	14		1			15
4	B_1	12		2	1		15
	B_2	15					15
5	B_1	14		1			15
	B_2	14		1			15
Total	B_1	68	2	4	1		75
	B_2	73		2			75
	Σ	141	2	6	1		150

the backcross to the Cairo male still gave 141 of 150 with the normal number of 2, but this time there were 2, 6, and 1 cases with 3, 4, and 5 X chromosomes, respectively.

MECHANISMS OF INHERITANCE

Due to the extreme difficulty of obtaining good cytological material from the female germ line in *Cimex*, there is a paucity of information regarding the behavior of the X chromosome during oogenesis. There is no reason to believe that the autosomes behave in anything but the regular diploid fashion of random assortment in gametogenesis in both sexes. The X chromosomes, however, are clearly special, since a typical (XX–XY) number of X's is rare in *Cimex*. On the basis of all available information, there seems to be no advantage in carrying many or few supernumerary X chromosomes in a given strain. A real question, then, exists as to the nature of genetic segregation of the X chromosomes themselves during oogenesis—clearly laboratory techniques need to be improved to enable cytological examination of the female germ line.

Indeed, the close agreement in X number between male progeny and male sibs of females of all crosses under consideration would lead one to suspect that this segregation is not random.

Consider first Tables 10–3 through 10–8. The counts for F_1 males are certainly not surprising, since the males receive all their X chromosomes from their mother. However, the huge reciprocal differences in F_2–F_4 males from mothers presumably identical in X number virtually assure us that some mechanism is causing non-random segregation at oogenesis.

For example, in the Berkeley × Cairo reciprocals, the F_2 data reveal 118 of 150 with the Berkeley X count of 2 when Berkeley females are used, whereas in the reciprocal 110 of 150 show an X count of 5. This certainly establishes the enormous reciprocal difference in X count arising from females *known* to have inherited a total of 8 X chromosomes from the uniting Berkeley and Cairo gametes. Comparison of Table 10–5 with 10–6, and Table 10–7 with 10–8 reveals other striking reciprocal differences in F_2–F_4.

Two reasonable alternative mechanisms, not necessarily mutually exclusive, exist which, for the most part, could explain the data as they stand:

A. *Cytoplasmic Control of X Number.*—We note that the cytoplasm introduced in each of the single-pair matings remains essentially constant for all progeny of that cross. This is especially true of the filial crosses of Tables 10–3 through 10–8, and of course the cytoplasm is almost entirely that of the female strain. It is not unreasonable to suppose that the X number of the egg is determined primarily by the nature of the cytoplasm.

It is equally certain that other factors must be at work to cause variations in the X number characteristic of the female line. First, we remark that the X number is strikingly constant within all the parental lines, so

that the variation already apparent in the F_1 should not be interpreted as possibly due to irregularities in the parental contribution. Secondly, we would presume that the strains have attained an equilibrium between cytoplasm and genetic factors compatible with the characteristic X number of the strain.

With this in mind, interstrain crosses will introduce genetic influences on the female cytoplasm which are not necessarily compatible with the X number dictated by the cytoplasm, and may well cause absolute chaos during oogenesis and during development of the zygote. Continued filial crosses will involve the same genetic factors and cytoplasm, with the former undergoing reassortment and, presumably, selection in favor of genes that can reach an equilibrium condition with the relatively constant cytoplasm. It is noted that in every case in Tables 10–3 through 10–8, there is a settling toward a characteristic X number for that single-pair cross, which, because of genetic differences among the parents at the head of each series, is not constant for each type of cross. For example, in the Cairo ♀ × Columbarius ♂ cross, 5 of the 9 single-pair matings settled at an X number of 5, 1 at 6, and 3 at 3.

It is interesting that the autosomal genes of the males, which cause essentially no difference in X number in their own cytoplasmic environment, react with greatly different effect within a different cytoplasmic environment. This is typical of genotypic-environment interaction, with the cytoplasm here considered as the "environment."

Tables 10–4 and 10–7 are especially interesting, in that the characteristic X number is modally 5. It would appear from examining the tables that the Cairo strain is least capable of holding its characteristic X number in the presence of adverse genetic factors, followed by Berkeley, with Columbarius most capable.

Table 10–5 also contains a good example of interaction. One would expect that 2 strains with the same characteristic X numbers would preserve the same X number without exception in the cross. With a Berkeley female and Columbarius male, however, progeny are frequently observed with more than 2 X chromosomes.

The preceding discussion, however, does not account for discrepancies in the F_1 data, since oogenesis is presumably regular in females of the original strains. The conclusion is inescapable that the effects of interaction between male-line genetic factors and female-line cytoplasm begin in the embryo, possibly only in the germ line itself. Deficiencies can be explained by an elimination of one or more X chromosomes during early cleavage. It is possible that the genotype of the individual would preclude further development unless a reduction in X number occurred. On the other hand, excesses might be explained by nondisjunction of X chromosomes during early differentiation of the germ line, resulting in an excess of X chromosomes in the germ line and a deficiency in the soma. This

possibility could be checked by a comparison between somatic- and germ-line nuclei.

We note that the backcross data quite strongly support the hypothesis of cytoplasmic inheritance with autosomal modification, since in each backcross generation half of the remaining maternal autosomal genes are replaced by male-line autosomal factors, and further, a bit of male cytoplasm is also presumably introduced into the backcross progeny each generation. Ultimately the cytoplasm and the autosomes will become entirely male-line type, so that one would expect an approach to the male-line characteristics in the long run.

There remain two other possible modifiers, namely, Y chromosome factors and factors carried on the X chromosomes themselves. The former may be dismissed immediately, since the Y chromosome in the filial crosses is constant for each single-pair mating, and yet X numbers closely resembling the opposite parent are the general rule. The X chromosomes can be dismissed if we assume that, during oogenesis, a random sample of X chromosomes from those available are furnished to the egg. In other words, if there were the number N of X chromosomes available in a female, and her cytoplasm and genotype dictated that a characteristic number, K, of X chromosomes be transmitted to the egg, there would then be C(N,K) equally likely combinations of X chromosomes, where C(N,K) denotes the number of distinct combinations of N chromosomes taken K at a time.

The X chromosomes could not be important in determining their own X number in this case because the F_1 females would be expected to have exactly the same number and source of X chromosomes in the reciprocal crosses and therefore the F_2–F_4 generations would not be expected to have any reciprocal difference. As already pointed out, however, the F_2–F_4 show, on the whole, at least as great reciprocal differences as does the F_1, so the genetic factors on the X chromosomes appear to have little effect. This should be contrasted with the immediate disruptive effect of the autosomal factors introduced by the father.

The case of non-random sampling of X chromosomes will be considered next.

B. *Genetic Control by Factors in X Chromosomes Themselves.*—Factors on the X chromosomes control their own number, with autosomal modification. The paternal X complement is genetically inactive in the female and is not transmitted in the egg.

Figure 10–48 shows the expected pattern of transmission for all the crosses involving the Cairo and Columbarius strains, on the assumptions of X chromosome control and no autosomal modifications of any sort. Also included is the expected fraction of autosomal characters from each source in the absence of selection. (We remark that the *autosomal* pattern would have the same expectation under either mechanism A or B.)

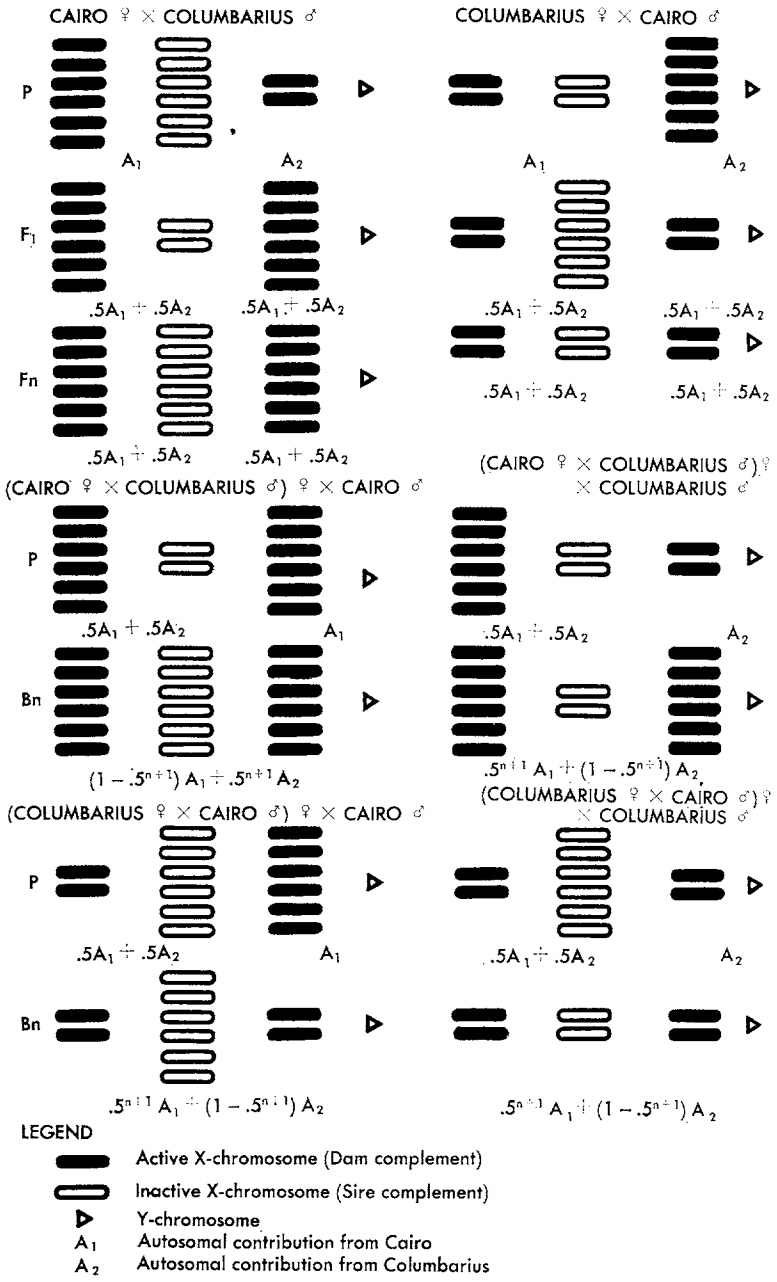

FIG. 10–48.—Chromosomal complements expected under mechanism B, with no autosomal modification.

To illustrate, the top right diagram in Fig. 10–48 shows that X chromosome complements contributed by the original Columbarius mother and the Cairo father in the P (parental) generation. In the F_1, males contain 2 X chromosomes from their Columbarius mother, whereas the F_1 females possess 2 active (shown shaded) X chromosomes from their mothers and 6 inactive (shown clear) X chromosomes from their Cairo fathers. Crosses for all future generations show an X chromosome transmission akin to the Columbarius line. The autosomal contributions, however, remain uniform, with A_1 denoting the autosomal contribution from the Cairo strain and A_2 that from the Columbarius strain. Selection against autosomal genes of the male line which affect X number might actually occur, however, which would conceivably affect the 1:1 autosomal ratio.

In the lower left diagram of Fig. 10–48, which depicts a backcross of the F_1 female just mentioned to a Cairo male, all backcross generations from the first onward will have the same X chromosome complement as shown. Note, however, that the autosomal contribution of the Columbarius strain (A_2) decreases by a factor of 2 each generation. In generation B_3, for example, only $^1/_{16}$ of the autosomal genes would be expected to be of Columbarius origin.

As can be seen, the discussion in paragraph A can be repeated again, with interaction between autosomal factors and X chromosome factors replacing interaction of the autosomal-cytoplasmic type. All the same arguments hold, and it is clear that the present design is incapable of distinguishing between the 2 possibilities. Indeed, it is not improbable that a combination of the two actually controls the X number in *Cimex*.

SUMMARY AND CONCLUSIONS

The inheritance of supernumerary X chromosomes in *Cimex*, with reference to the 3 strains studied herein, is clearly not simple. Autosomal genes almost surely play an important role in the modification of the number of X chromosomes, but it is not clear at this moment what the principal mechanism is. Two strong possibilities, not mutually exclusive, are A) cytoplasmic determination; B) genetic control by factors in the X chromosomes themselves, coupled with transmission of only the maternal complement of X chromosomes during oogenesis. It is unlikely that anything except cytological examination of female germ and somatic cells will be able to ultimately distinguish between these possibilities. Indeed, we may find that a combination of the 2 mechanisms actually prevails.

11 | Systematics

The Cimicidae are unique among the Hemiptera in the amount and types of information available to the systematist. In addition to the traditional evidence from external characters, studies of internal anatomy, cytogenetics, and experimental taxonomy are available. In the present chapter such evidence is combined with data on geographical distribution and host relations to arrive at a workable species concept and a probable phylogeny. Table 11–1 lists the subfamilies, genera, and species of Cimicidae with zoogeographic regions and hosts. The sequence is from generalized to specialized within each line, as discussed under phylogeny.

GEOGRAPHICAL DISTRIBUTION

Except for the species distributed by man, the patterns of distribution of the major groups of Cimicidae are clear and separate. Twelve genera are confined to the New World and 8 to the Old World, with only *Cimex* and *Oeciacus* common to both. Haematosiphoninae are exclusively American, and Cacodminae extend from Africa to the Oriental Region. Primicimicinae are local bat bugs in Texas and Guatemala (*Primicimex*) (Fig. 11–14) and southern Chile (*Bucimex*) (Fig. 11–1). Two anomalous groups that stand out as monotypic subfamilies are *Afrocimex* (Fig. 11–12) on fruit-eating bats in Equatorial Africa, and *Latrocimex* (Fig. 11–1) on fish-eating bats in tropical South America. Only the subfamily Cimicinae is complex, with *Propicimex* and *Bertilia* in South America (Fig. 11–1), *Paracimex* on cave swiftlets in Southeast Asia (Fig. 11–6), *Oeciacus* on swallows over most of the Holarctic Region (Fig. 11–5), and *Cimex* throughout most of the world. Excluding the semidomestic species for the moment, the genus *Cimex* comprises 2 groups: The *Cimex pipistrelli* group on bats throughout the Palearctic Region (Fig. 11–3) and the *Cimex pilosellus* group on bats throughout the Nearctic Region (Fig. 11–4). Interesting gaps are the absence of native Cimicidae in Australia and Central America, and the lack of bird bugs of any kind in the Ethiopian Region and in Central America.

The distribution of bat bugs shows a remarkable parallel with the distribution of their hosts (Allen 1939). Five genera are confined to the

Table 11–1.—Geographical distribution and hosts of Cimicidae.

Species	Distribution	Hosts
PRIMICIMICINAE		
1. *Primicimex cavernis*	Sonoran (Texas), Neotropical (Guatemala)	Molossidae (*Tadarida brasiliensis mexicana*)
2. *Bucimex chilensis*	Neotropical (S. Chile)	Vespertilionidae (*Myotis c. chiloensis*)
CIMICINAE		
3. *Bertilia valdiviana*	Neotropical (S. Argentina, Chile)	
4. *Propicimex tucmatiani*	Neotropical (Argentina, Brazil)	Molossidae (*Tadarida brasiliensis*), Vespertilionidae (*Myotis nigricans*)
5. *Propicimex limai*	Neotropical (Brazil)	"Bat"
6. *Cimex lectularius*	Cosmopolitan	Phasianidae (*Gallus gallus*), Hominidae (*Homo sapiens*), Vespertilionidae (*Lasiurus borealis, Myotis myotis, M. m. oxygnathus, M. mystacinus*), many other hosts, domestic and wild
7. *Cimex columbarius*	Palearctic (W. Europe)	Columbidae (*Columba livia*), Muscicapidae (*Muscicapa atricapilla*)
8. *Cimex hemipterus*	Tropicopolitan	Phasianidae (*Gallus gallus*), Hominidae (*Homo sapiens*), Vespertilionidae (*Scotophilus heathii, S. temminckii*)
9. *Cimex pipistrelli*	Palearctic (Britain)	Vespertilionidae (*Nyctalus noctula, Pipistrellus pipistrellus*)
10. *Cimex dissimilis*	Palearctic (Europe)	Vespertilionidae (*Myotis myotis, Nyctalus noctula*)
11. *Cimex stadleri*	Palearctic (Europe)	Rhinolophidae (*Rhinolophus ferrumequinum*), Vespertilionidae (*Myotis myotis*)
12. *Cimex cavernicola*	Palearctic (Turkmenia, Russia)	"Bats"
13. *Cimex burmanus*	Palearctic? (N. Burma)	"Pipistrell"
14. *Cimex flavifusca*	Palearctic (China)	"Bats"
15. *Cimex japonicus*	Palearctic (Japan)	Vespertilionidae (*Nyctalus lasiopterus*)
16. *Cimex pilosellus*	Nearctic (W. North America)	Vespertilionidae (*Antrozous pallidus, Eptesicus fuscus fuscus, E. f. pallidus, Lasionycteris noctivagans, Myotis californicus, M. volans longicrus, M. yumanensis, Pipistrellus hesperus merriami*)
17. *Cimex latipennis*	Nearctic (Oregon, California)	Vespertilionidae (*Myotis thysanodes*)
18. *Cimex adjunctus*	Nearctic (E. North America)	Vespertilionidae (*Eptesicus fuscus, Lasionycteris noctivagans, Myotis californicus, M. lucifugus carrissima, M. lucifugus, M. sodalis, Nycticeius crepuscularis, N. humeralis*)
19. *Cimex brevis*	Nearctic (N. E. North America)	
20. *Cimex antennatus*	Nearctic (California, Nevada)	Vespertilionidae (*Antrozous pallidus, Myotis lucifugus*)
21. *Cimex incrassatus*	Nearctic (S. California, Arizona, Mexico)	Vespertilionidae (*Antrozous pallidus, Eptesicus fuscus, Myotis thysanodes, M. velifer velifer, M. yumanensis, Pipistrellus hesperus*)
22. *Oeciacus hirundinis*	Palearctic	Hirundinidae (*Delichon urbica, Hirundo daurica, H. rustica, Riparia riparia*), other birds rarely
23. *Oeciacus vicarius*	Nearctic	Hirundinidae (*Hirundo erythrogaster, Petrochelidon albifrons*)

Table 11-1.—(Continued)

Species	Distribution	Hosts
24. *Paracimex avium*	Oriental (Sumatra)	"Birds"
25. *Paracimex setosus*	Oriental (Java)	Apodidae (*Collocalia esculenta linchi, C. vestita*)
26. *Paracimex lamellatus*	Oriental (Java)	Apodidae (*Hirund-apus cochinchinensis*)
27. *Paracimex gerdheinrichi*	Oriental (Celebes)	Apodidae (*Collocalia spodiopygia sororum*)
28. *Paracimex philippinensis*	Oriental (Philippines)	Apodidae (*Collocalia marginata, C. troglodytes*)
29. *Paracimex borneensis*	Oriental (Borneo, Malaya)	Apodidae (*Collocalia esculenta esculenta, C. lowi lowi, C. maxima, C. salangana, C. vestita*)
30. *Paracimex ignotus*	Oriental (Malay Peninsula)	Apodidae (*?Collocalia innominata*)
31. *Paracimex capitatus*	Oriental (New Britain, New Guinea)	Apodidae (*Collocalia* sp.)
32. *Paracimex reductus*	Oriental (New Guinea)	"Swift nests"
33. *Paracimex caledoniae*	Australian (New Caledonia)	Apodidae (*Collocalia spodiopygia spodiopygia* or *C. esculenta esculenta*), Hirundinidae (*Hirundo tahitica subfusca*)
CACODMINAE		
34. *Cacodmus ignotus*	Ethiopian (Uganda)	"Bat"
35. *Cacodmus indicus*	Oriental (India)	"Bat"
36. *Cacodmus sumatrensis*	Oriental (Sumatra, Java, Malaya)	Dermoptera (*Galeopithecus* sp.), Vespertilionidae (*Miniopterus* sp., *Myotis mystacinus muricola, Pipistrellus javanicus, P. stenopterus, P. tenuis, P. tralatiticus, P. tylophus*)
37. *Cacodmus sinuatus*	Ethiopian (Brazzaville, Repub. Congo)	Vespertilionidae (*Eptesicus* sp.)
38. *Cacodmus sparsilis*	Ethiopian (S. Africa)	Vespertilionidae (*Scotophilus nigritus dingani*)
39. *Cacodmus vicinus*	Palearctic (N. Africa, Middle East)	Vespertilionidae (*Pipistrellus kuhlii*)
40. *Cacodmus villosus*	Ethiopian (C., S. Africa)	Vespertilionidae (*Eptesicus capensis, Pipistrellus kuhlii, P. k. fuscatus, P. musciculus, P. nanus, Scotophilus gigas*)
41. *Aphrania barys*	Ethiopian (S. Africa)	Vespertilionidae (*Eptesicus zuluensis*)
42. *Aphrania recta*	Ethiopian (C. Africa)	Vespertilionidae (*Eptesicus tenuipennis, Scotophilus nigritus*)
43. *Aphrania elongata*	Ethiopian (C. Africa)	Vespertilionidae (*Eptesicus tenuipennis, Scoteinus schlieffenii, Scotophilus nigritus*)
44. *Aphrania vishnou*	Oriental (N. India, Cambodia, Malaya)	Pteropidae (*Cynopterus sphinx*), Vespertilionidae (*Scotophilus temminckii*)
45. *Loxaspis setipes*	Ethiopian (Congo)	"Horse-shoe bat"
46. *Loxaspis miranda*	Ethiopian (C. Africa)	Emballonuridae (*Taphozous hildegardeae*), Molossidae (*Chaerephon pumilis, Mops angolensis, Tadarida limbata*)
47. *Loxaspis barbara*	Ethiopian (C. Africa)	Molossidae (*Nyctinomus pumilis, Tadarida condylura*)
48. *Loxaspis seminitens*	Oriental (Java)	
49. *Loxaspis spinosa*	Oriental (Borneo)	Molossidae (*Cheiromeles torquatus*)
50. *Loxaspis malayensis*	Oriental (Malaya)	Molossidae (*Cheiromeles torquatus, Tadarida mops*)

Table 11-1.— (Continued)

Species	Distribution	Hosts
51. *Stricticimex pattoni*	Oriental (E. India)	"Bat"
52. *Stricticimex transversus*	Ethiopian (S. Africa)	Molossidae (*Tadarida bocagei*), Vespertilionidae (*Scotophilus nigritus*)
53. *Stricticimex namru*	Palearctic (Egypt)	Molossidae (*Tadarida a. aegyptiaca*)
54. *Stricticimex antennatus*	Ethiopian (S. Africa)	"Bats"
55. *Stricticimex intermedius*	Ethiopian (E. Africa)	"Bats"
56. *Stricticimex brevispinosus*	Ethiopian (C. Africa)	Hipposideridae (*Hipposideros caffer*)
57. *Leptocimex boueti*	Ethiopian (W. Africa)	Hominidae (*Homo sapiens*), "bat"
58. *Leptocimex vespertilionis*	Ethiopian (Sudan and Baghdad, Iraq)	Emballonuridae (*Taphozous nudiventris*)
59. *Leptocimex duplicatus*	Palearctic (Egypt)	Emballonuridae (*Taphozous nudiventris*)
60. *Crassicimex pilosus*	Ethiopian (Madagascar)	Molossidae (*Mormopterus albiventer*)
61. *Crassicimex sexualis*	Ethiopian (C. Africa)	Molossidae (*Chaerephon* sp., *Nyctinomus* sp., *Tadarida fulminans*)
AFROCIMICINAE		
62. *Afrocimex leleupi*	Ethiopian (C. Africa)	Pteropidae (*Rousettus aegyptiacus*)
63. *Afrocimex constrictus*	Ethiopian (E. Africa)	Pteropidae (*Eidolon helvum, Epmophorus* sp.)
LATROCIMICINAE		
64. *Latrocimex spectans*	Neotropical (Brazil, Trinidad)	Noctilionidae (*Noctilio leporinus*)
HAEMATOSIPHONINAE		
65. *Ornithocoris toledoi*	Neotropical (Brazil, Bolivia, Argentina)	Phasianidae (*Gallus gallus*)
66. *Ornithocoris pallidus*	Neotropical, Nearctic (Introduced?)	Apodidae (*Pygochelidon cyanoleuca*), Hirundinidae (*Progne subis*), Phasianidae (*Gallus gallus*)
67. *Caminicimex furnarii*	Neotropical (Argentina, Uruguay)	Furnariidae (*Furnarius rufus*)
68. *Psitticimex urutui*	Neotropical (Argentina)	Psittacidae (*Myiopsitta monachus cotorra*)
69. *Haematosiphon inodorus*	Nearctic (Sonoran)	Cathartidae (*Gymnogyps californianus*), Falconidae (*Aquila chrysaetos*), Strigidae (*Bubo virginianus*), Tytonidae (*Tyto alba alba*), Phasianidae (*Gallus gallus*)
70. *Cimexopsis nyctalus*	Nearctic (E. United States)	Apodidae (*Chaetura pelagica*)
71. *Synxenoderus comosus*	Nearctic (W. United States)	Apodidae (*Aeronautes melanoleucus*)
72. *Hesperocimex coloradensis*	Nearctic (W. North America)	Hirundinidae (*Progne subis* in woodpecker holes)
73. *Hesperocimex sonorensis*	Nearctic (Sonoran)	Hirundinidae (*Progne subis*)
74. *Hesperocimex cochimiensis*	Nearctic (Baja California)	Hirundinidae (*Progne subis, Tachycineta thalassina*)

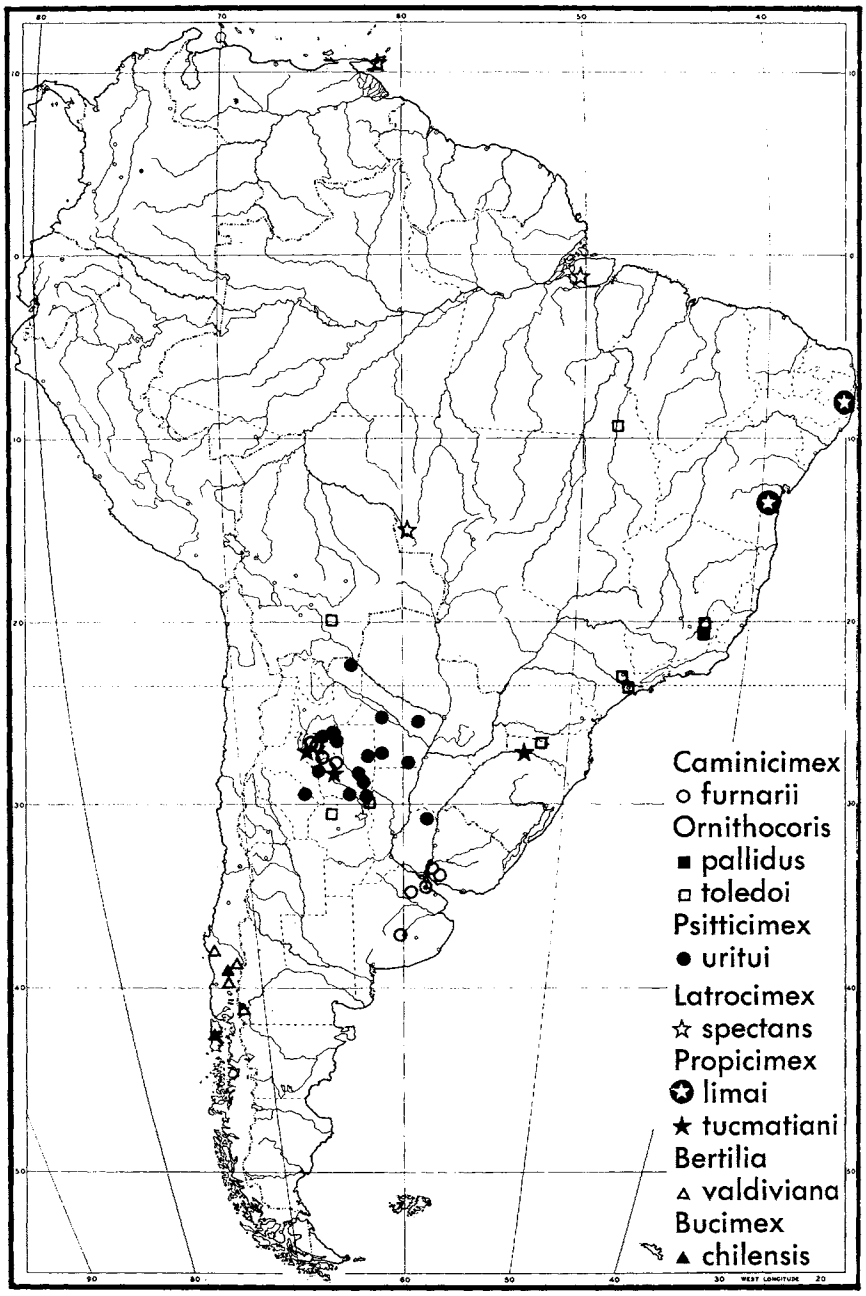

FIG. 11–1.—Distribution of bird bugs and bat bugs in South America.

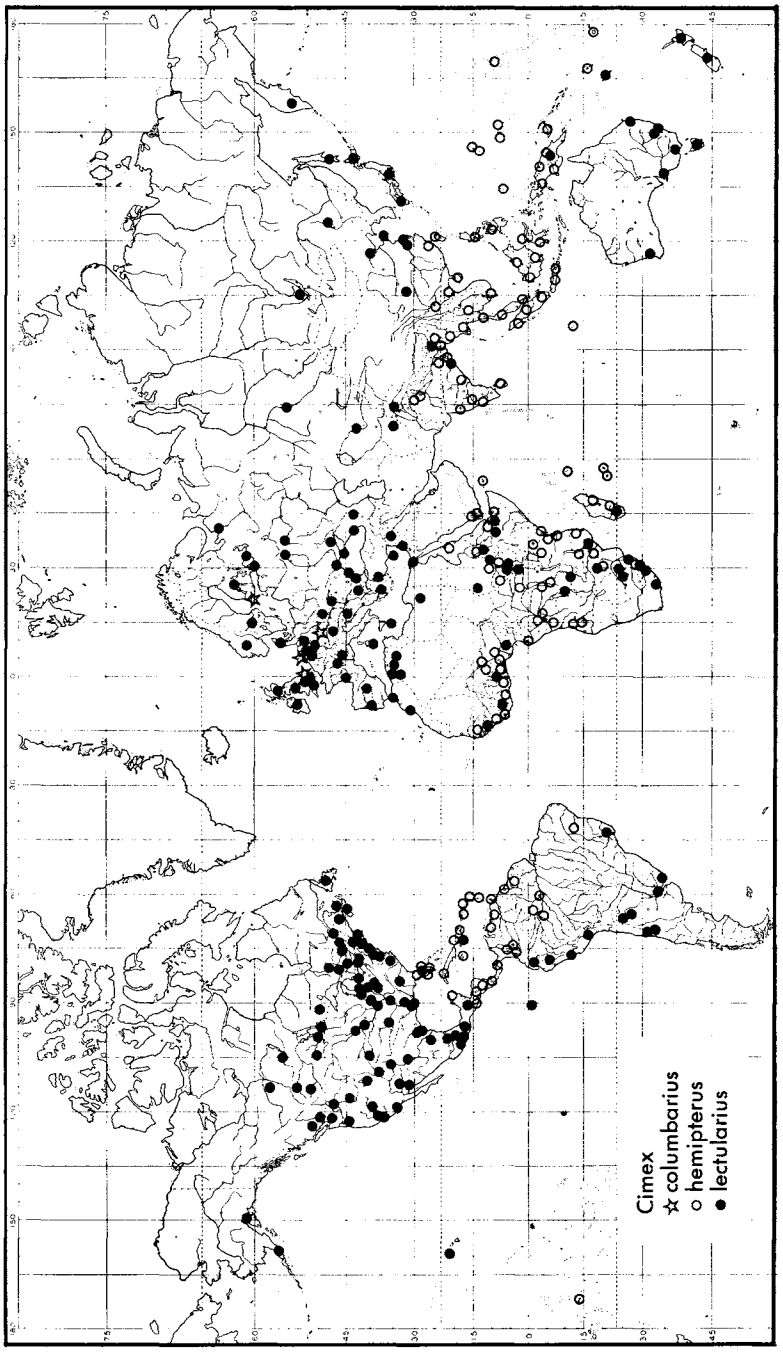

FIG. 11-2.—World distribution of the human bed bugs, *C. lectularius* and *C. hemipterus*, and the pigeon bug, *Cimex columbarius*.

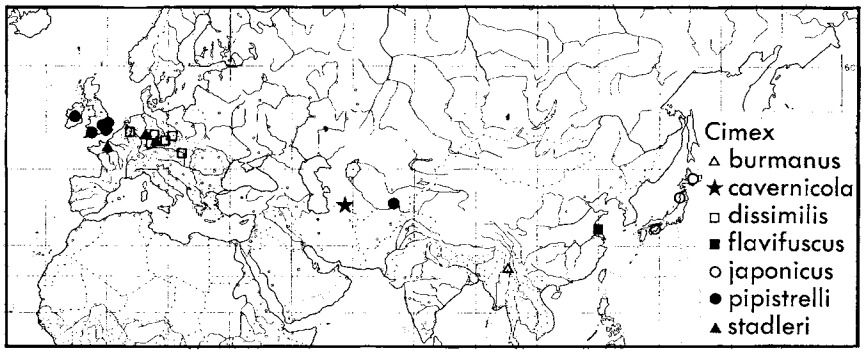

FIG. 11–3.—Distribution of bat bugs of the *Cimex pipistrelli* Group in the Palearctic Region.

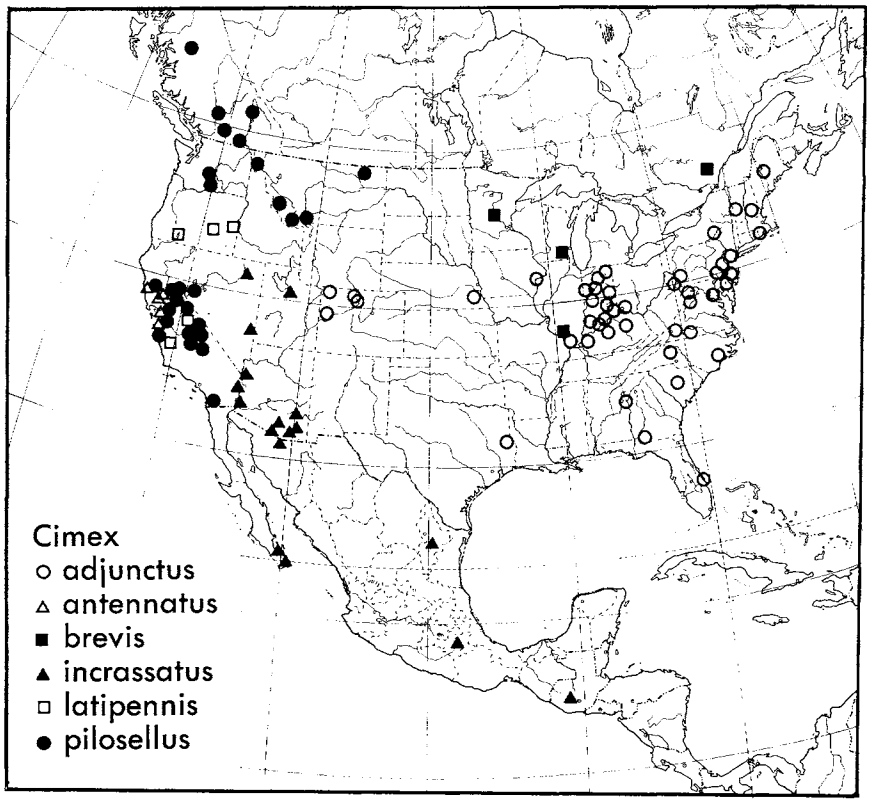

FIG. 11–4.—Distribution of bat bugs of the *Cimex pilosellus* Group in the Nearctic Region.

New World and 7 to the Old World, with only *Cimex* common to both, while comparable figures for bat families are 8, 6, and 3, respectively.

Within some groups of Cimicidae there are indications of allopatry: *Oeciacus* (Fig. 11–5), with its Palearctic species *hirundinis* and its Nearctic *vicarius,* and the Palearctic (Fig. 11–3) and Nearctic (Fig. 11–4) species groups of *Cimex* on bats.

Of the African and Asian bat bugs, the closely related *Cacodmus* (Fig. 11–7), *Aphrania* (Fig. 11–8), and *Loxaspis* (Fig. 11–9) each has representatives in Africa and the Orient; *Cacodmus* has a species, *vicinus,* that forms a connecting link in the Middle East. The other group of related genera in the Cacodminae includes *Stricticimex* (Fig. 11–10), widespread in Africa with 1 species recorded from East India, *Leptocimex* (Fig. 11–11) in Africa and the Middle East, and *Crassicimex* (Fig. 11–11) from Equatorial Africa and Madagascar.

Probably the most complicated genus, from the standpoint of local populations, is *Paracimex* (Fig. 11–6), which is spread over the vast area from Sumatra and the Malay Peninsula to New Caledonia (and perhaps from India to Australia, the Marquesas, and Samoa, to judge by the distribution of the host genus *Collocalia*). Each island or island group seems to have a slightly different species. Considering the thousands of islands and the vast mainland areas of Southeast Asia, the possibilities for allopatric differentiation seem infinite. Yet, curiously, Borneo and Malaya populations resemble each other, whereas more than one distinct type occurs in Java and in New Guinea.

Although information is not yet clear, clines are evident in several species, especially in Africa. Individuals of *Cacodmus villosus* Stål are large in South Africa but smaller in equatorial Africa and may be found to grade into *vicinus,* the small species of North Africa and the Middle East. *Afrocimex* also shows a clinal tendency in bristle number on the fore femora. Those collected at Brazzaville on the west coast have 6–12

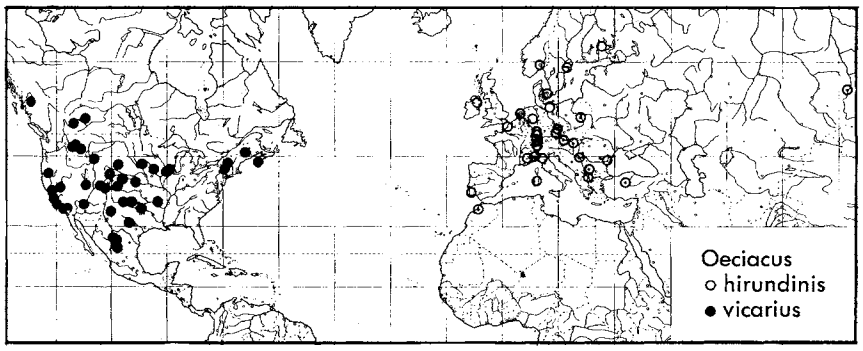

FIG. 11–5.—Distribution of swallow bugs of the genus *Oeciacus* in the Nearctic and Palearctic Regions.

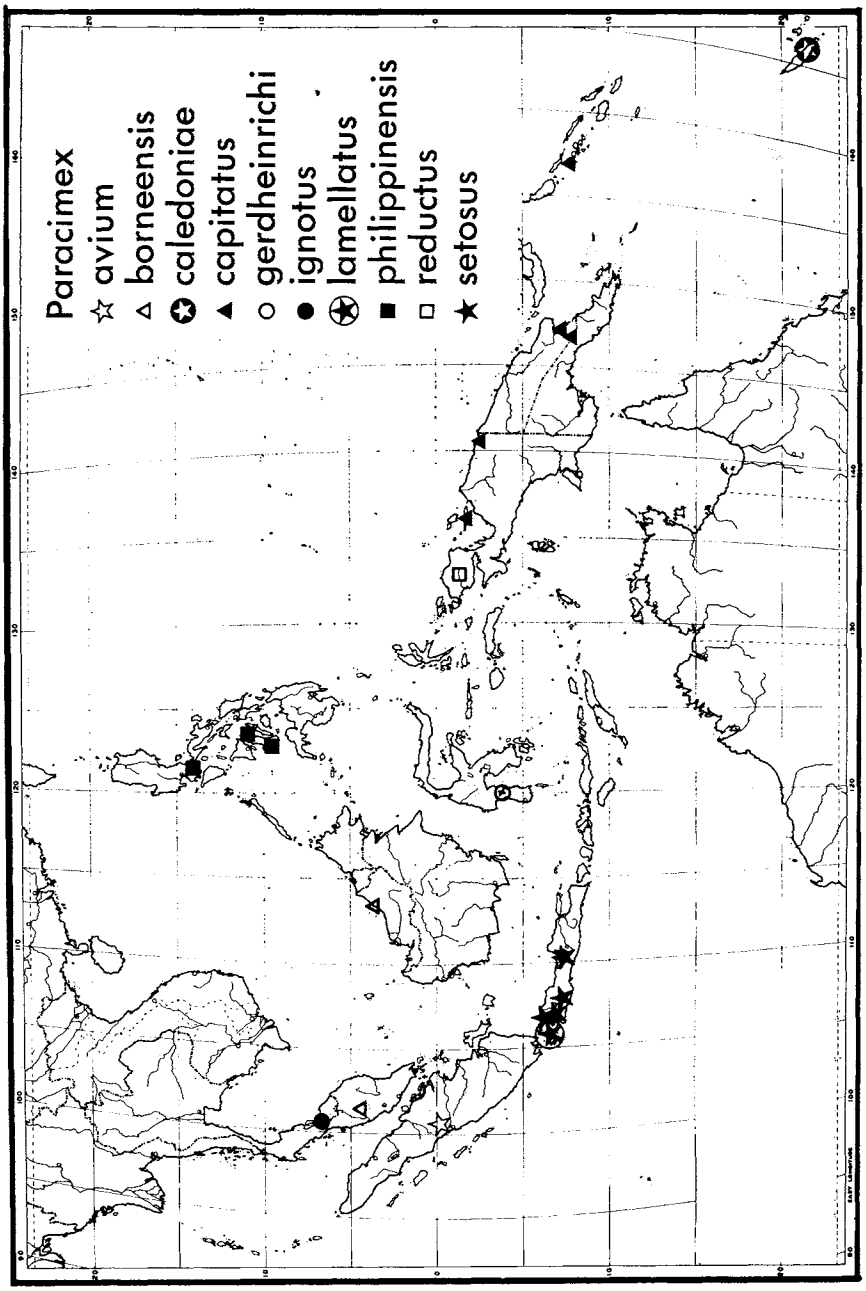

FIG. 11.6.—Distribution of cave swiftlet bugs of the genus *Paracimex* in Southeast Asia and Pacific Islands.

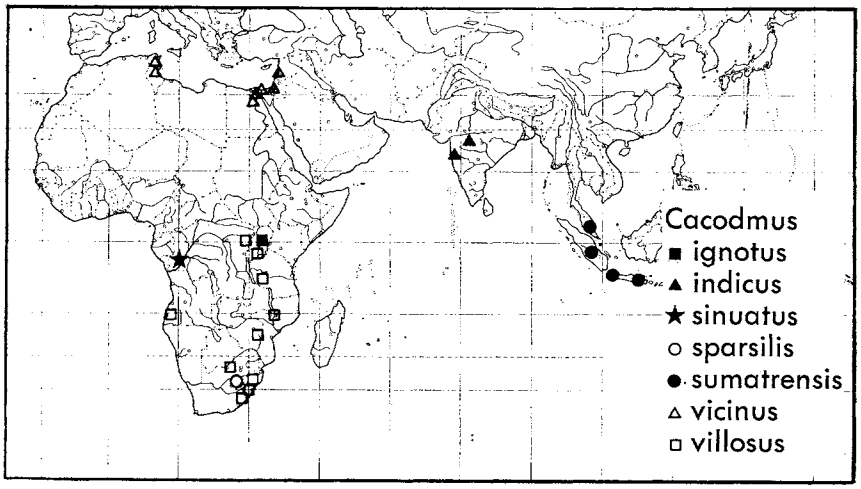

FIG. 11–7.—Distribution of bat bugs of the genus *Cacodmus* in Africa, the Middle East, and the Oriental Region.

bristles, those in the Congo in the center of Africa 12–20, and those in Kenya in the eastern part of Africa 20–36. Other possible clines include *Stricticimex transversus* Ferris and Usinger in the south and *namru* Usinger in the north, *Stricticimex intermedius* Ferris and Usinger in Kenya and *brevispinosus* in the Congo, and *Aphrania barys* Jordon and Rothschild in the south and *recta* Ferris and Usinger in Central Africa.

The American Haematosiphoninae show some interesting distributional patterns. In North America (Fig. 11–13) *Synxenoderus* is western

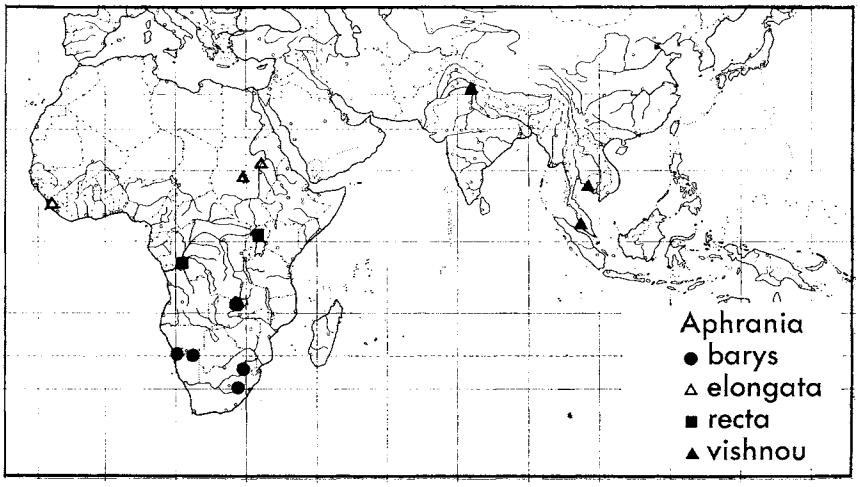

FIG. 11–8.—Distribution of bat bugs of the genus *Aphrania* in the Ethiopian and Oriental Regions.

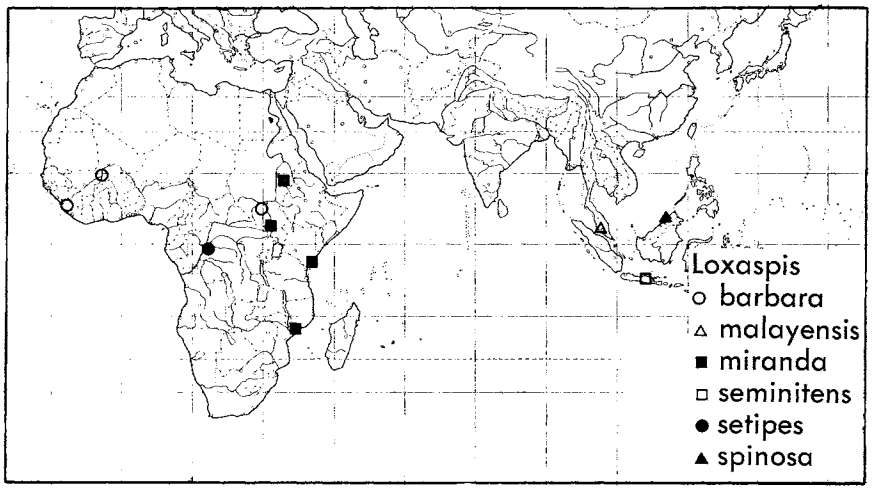

FIG. 11–9.—Distribution of bat bugs of the genus *Loxaspis* in the Ethiopian and Oriental Regions.

and *Cimexopsis* is eastern, corresponding to the distribution of their respective hosts, the white-throated swifts and chimney swifts. *Haematosiphon* is exclusively western, although its hosts (except the California condor) are widely distributed. *Hesperocimex* (Fig. 11–14) is likewise western, but its hosts, the purple martins, are also widely distributed in the eastern United States. In the southwest, 2 species, *sonorensis* and *cochimiensis,* are associated with *Progne subis hesperia* in woodpecker holes in tree cacti, and *coloradensis* occurs farther north with *Progne*

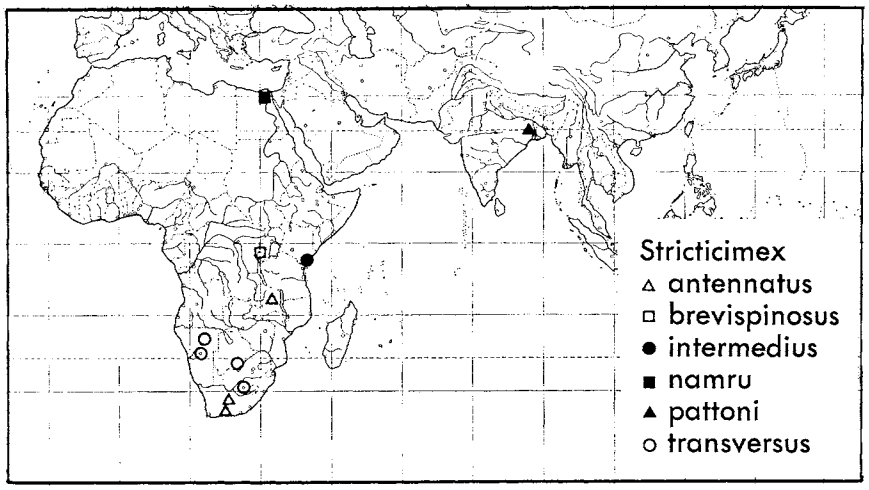

FIG. 11–10.—Distribution of bat bugs of the genus *Stricticimex* in Africa and India.

subis subis in tree trunks over most of the west. In South America (Fig. 11–1) there is a concentration in the south with none of the bird-infesting genera in the tropical rain forest areas. The occurrence of *Ornithocoris pallidus* in Florida is an anomaly; it is found in chicken houses and in manmade bird houses occupied by purple martins (*Progne subis subis*). Purple martins make annual migrations to Brazil and might have carried the bugs, or they could have been carried with chickens. However, *Ornithocoris toledoi* is the Brazilian chicken bug, while *Ornithocoris pallidus* has been found thus far only on swallows in Brazil.

The problems of the origin and spread of human bed bugs have been discussed by Horvath (1914b) and others. The general view is held that *C. lectularius* originated in the Middle East and that *C. hemipterus* was originally an oriental species. The maps of Mellanby (1935) and Geisthardt (1937) show that *C. hemipterus* is confined almost exclusively to the tropics and that *C. lectularius* is primarily north temperate but with spotty distribution elsewhere in south temperate regions and the tropics. The same pattern is shown in Fig. 11–2, based on individual records of the 2 species.[1]

[1] Records were taken from all specimens seen during this study, and from Johnson (1939) and other publications that filled important gaps. No attempt was made to canvass all the museums of the world or to give every published record. It is probable that *C. lectularius* occurs in every country, state, and province in Europe and North America, but catalogues like Van Duzee (1917) merely state that the bed bug is "cosmopolitan."

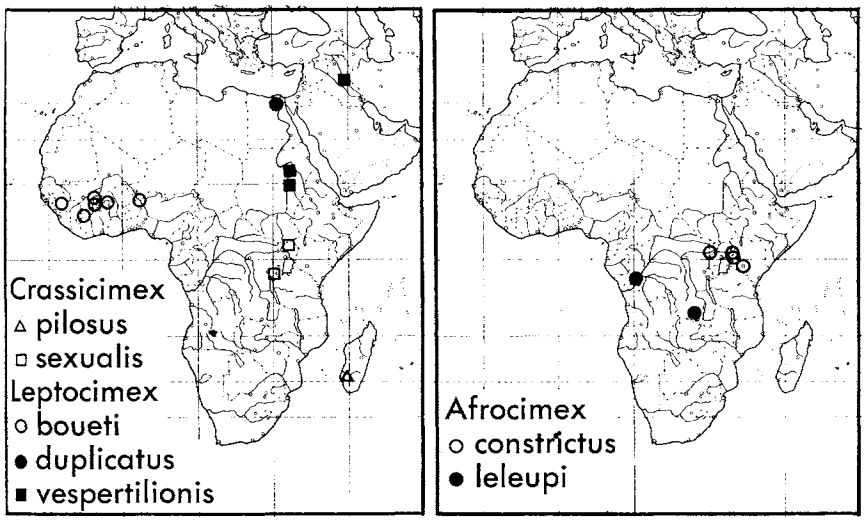

FIG. 11–11 (left).—Distribution of *Leptocimex* on bats and man in Africa and the Middle East and of *Crassicimex* on bats in Africa and Madagascar.

FIG. 11–12 (right).—Distribution of bat bugs of the genus *Afrocimex*.

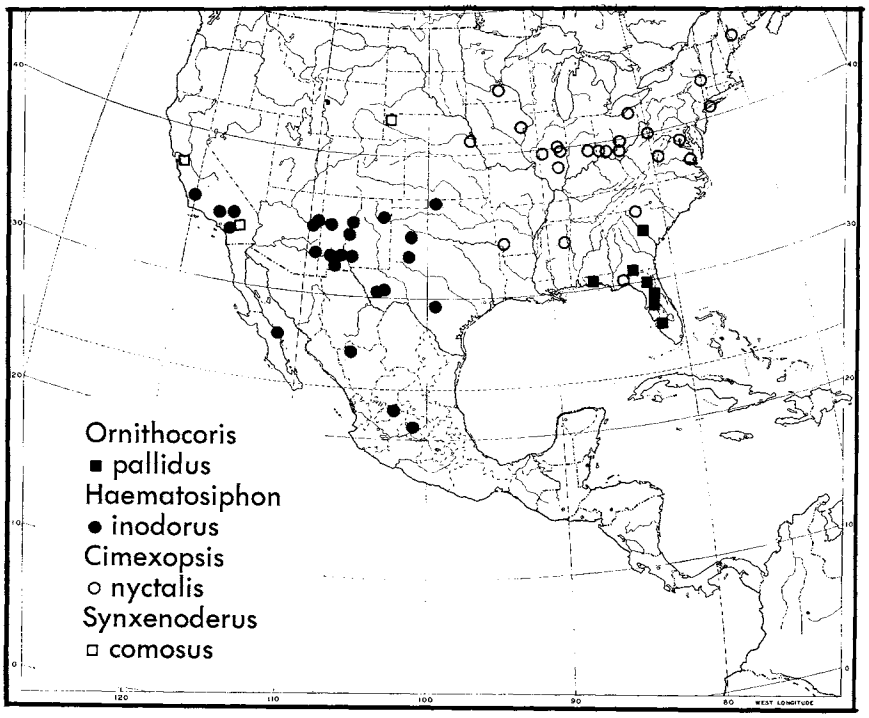

FIG. 11–13.—Distribution of North American bird bugs of the genera *Ornithocoris, Haematosiphon, Cimexopsis,* and *Synxenoderus.*

One of the anomalies is the absence of *C. lectularius* from most of India, Formosa, and Southeast Asia. This was noticed by Omori (1941), who showed on the basis of temperature that *C. lectularius* could compete successfully with *C. hemipterus* wherever the 2 species coexist. However, in crossing experiments he found that "the females of *lectularius* suffer fatal effects upon their reproductive function and generally on their lives by crossing with males of *hemipterus.*" Davis has confirmed this observation and finds that it is the sperm fluid of *C. hemipterus* that is toxic to *C. lectularius* females. Thus there may be a mechanical barrier not only to interbreeding but also, since interspecific copulation is common in Cimicidae, to coexistence of the species. Lewis (1949) and others have stated that *C. lectularius* is confined to large towns in the tropics and that *C. hemipterus* is the indigenous species in rural areas. It is interesting to note that *C. hemipterus* has not developed local populations, whereas *C. lectularius* shows considerable diversity throughout its range. The pigeon bug, *Cimex columbarius,* is a local population within the *C. lectularius* complex. Its distribution probably exceeds that shown

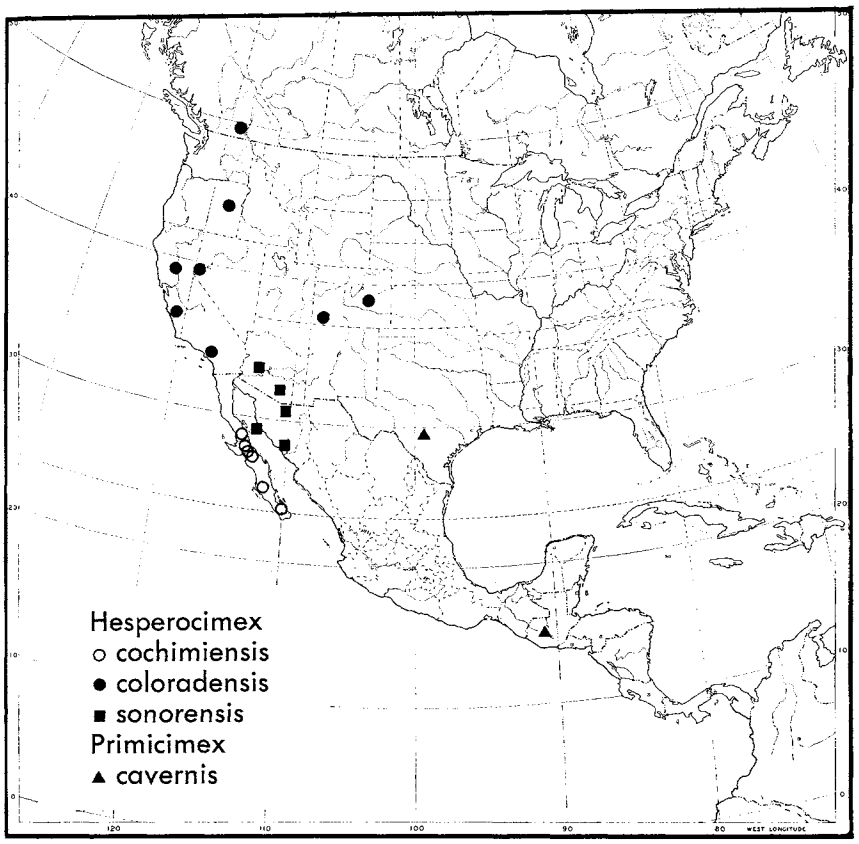

FIG. 11–14.—Distribution of purple martin bugs of the genus *Hesperocimex* in western North America and bat bugs of the genus *Primicimex* in Texas and Guatemala.

on the map (Fig. 11–2), but records prior to Johnson's (1939) study are meaningless. My collection from southern Finland is the only new record since that time. Johnson gave verified records for England, the Netherlands, and Germany. The lack of records since World War II could mean that use of residual insecticides has eliminated this species from domesticated pigeons.

C. lectularius shows distinctive but unnamed populations in parts of its range. For example, all the specimens I have seen from the Mexican Plateau have very short bristles, and a collection from Manchuria and another from Central Europe have very long bristles. Also, types with a haploid chromosome number of 13A+6X+Y occur almost exclusively in the Mediterranean Region, whereas the type $13A+X_1X_2Y$ is the rule in the circum-Pacific area.

HOST RELATIONS

The relationships of *C. lectularius* and *C. hemipterus* to man and his domesticated animals have been discussed elsewhere in this work. The original or native hosts provide the best information on the origin and evolution of the Cimicidae.

In this discussion and in Table 11–1, exceptional and unverified records are ignored (though they are fully recorded under each species). Also records from mixed colonies of bats (very common) are not included. Records of bats and of the species of *Collocalia* are subject to more than the usual hazards of misidentification because of the state of taxonomy in these groups, particularly in the 19th century. The most reliable records are of specimens taken while clinging to bats, or better, the few cases of bugs actually observed feeding on a particular species of bat. In the text, original names of hosts are given as reported by the collectors with the present valid name, if known, in parentheses. Only names valid as of the present time are used in Table 11–1.

Of the 6 subfamilies, 4 occur exclusively in association with bats, 1 with birds; only the Cimicinae has genera that live on both (Table 11–1). Twelve of the 22 genera are found on bats, 9 on birds, and only *Cimex* on both.

It appears that Cimicidae adopted birds as hosts on 4 occasions, probably in the following sequence: First, the Haematosiphoninae primarily on swifts and martins in the Western Hemisphere; second, *Paracimex* on cave swiftlets (*Collocalia*) in Southeast Asia; third, *Oeciacus* on swallows in the Holarctic; fourth, and comparatively recently, *Cimex columbarius* on pigeons in Western Europe. Each genus of Haematosiphoninae has its own distinctive host, or hosts: *Hesperocimex* on purple martins (Hirundinidae), *Cimexopsis* and *Synxenoderus* on chimney and white-throated swifts (Apodidae), respectively; *Haematosiphon* on birds of prey (Falconiformes, Strigiformes); *Caminicimex* on oven birds (Furnariidae); *Psitticimex* on a parrot (Psittacidae); and *Ornithocoris* (to judge by the single record on a native host) on South American swallows (Hirundinidae). The groups of birds have little in common except that their nests offer microhabitats suitable to the bugs. Why other birds' nests that seem equally suitable are not infested is not known (I examined hundreds in South America with negative results). Of the other bird bugs, *Paracimex* in Southeast Asia also is found on swifts (Apodidae, *Collocalia*) and *Oeciacus* in Europe and North America on swallows (Hirundinidae). Thus only 3 of the genera of bird bugs occur on birds other than Hirundinidae (swallows, martins) and Apodidae (swifts, cave swiftlets).

Hesperocimex is especially interesting because it is found in the purple martin's nest in tree or sajuaro cactus holes made by woodpeckers (Ryck-

man 1958). *Oeciacus hirundinis* in Europe may also inhabit woodpecker holes (Goidanich 1947), but it is primarily a parasite of the house martin (*Delichon urbica*) and less frequently of the swallow (*Hirundo rustica*), the sand martin (*Riparia riparia*), and other Hirundinidae. In North America the closely related *Oeciacus vicarius* occurs almost exclusively in the nests of the cliff swallow (*Petrochelidon albifrons*) and only rarely in the more open nests of the barn swallow (*Hirundo erythrogaster*) and others. The populations from each host in California show superficial differences, but they will interbreed in the laboratory and the differences are not consistent elsewhere in the range of the species.

Because 2 or 3 species of *Collocalia* may live in the same cave, it is difficult to say to what degree, if any, the species of *Paracimex* are host specific. Dimorphism has been noted in the bristles of bugs from a single cave and the supernumerary X chromosomes may be different in specimens that are collected together. The status of populations of *Paracimex* is being studied at the present time.

The adoption of a bird host by *Cimex columbarius* may have occurred after the domestication of the pigeon (bugs have never been found in the cave nests of wild rock pigeons, *Columba livia*), or it may be an older association with pied flycatchers and other birds that live in woodpecker holes and manmade bird houses in northern Europe (see discussion under *Cimex columbarius,* Chapter 12).

The behavior of bugs with respect to the bird hosts is little understood. Ryckman (1958) describes the dry sawdust "duff" at the bottom of woodpecker holes as a microhabitat for *Hesperocimex,* and the propensity of *Oeciacus* for laying its eggs on the outside of the mud nests of swallows is well known. I do not know of a verified case of bugs being found on birds in flight, although bugs must be carried from one distant nesting place to another. The occurrence of *Haematosiphon inodorus* on predatory birds (unusual cimicid hosts) and chickens suggests that the owls, condors, or eagles could have dropped (or picked up) bugs in chicken yards while preying on the chickens.

Bats were probably the original hosts of Cimicidae. The most unique and presumably most primitive genera are found on bats, as are the more specialized relatives, the Polyctenidae. Being only temporary ectoparasites, in contrast to the flies (Nycteribiidae) and polyctenids, they are found more often in the roosts of the bats and only rarely are attached to the skin of the bat. Cimicids lack many of the characteristics of the permanent ectoparasites of bats, such as typical ctenidia, reduced eyes, asymmetrical claws, and viviparous reproduction. On the other hand, they have reduced wings and some of them have "pseudojoints" of unknown function on the tibiae like nycteribiids and polyctenids (Rothschild 1916). Considering their lack of special adaptations, it is remarkable that cimicids are able to cling to bats at all. Records from bats are

particularly common for *Cacodmus* (Reuter 1913b), the Pipistrelli Group of *Cimex* (Reuter 1913b), and the Pilosellus Group (A. A. Allen 1920, G. M. Allen 1939, Usinger, and Beck). Both of the Allen records, one from *Eptesicus fuscus* in New York and the other from *Lasionycteris noctivagans* in Maine, were of bugs attached behind the ears. Beck found the bugs attached to the upper sides of the wing membrane along the thickened forelimb. There are many records "ex bat" or "on bat" that need confirmation, but *Leptocimex vespertilionis* Ferris and Usinger was definitely stated to be "on tails of bats," and Kühnelt (Fig. 11–15) photographed *Aphrania barys* on *Eptesicus zuluensis* in Southwest Africa.

Although the evidence is somewhat confusing and subject to correction with additional collecting, certain generalizations can be made about the relationships between bug genera and bat genera and families (Table 11–1). *Primicimex* seems to be associated with Molossidae (*Tadarida brasiliensis mexicana*) (Ryckman 1956), as also are at least some *Loxaspis, Crassicimex,* and *Stricticimex*. The unique subfamilies Afrocimicinae and Latrocimicinae are attached to equally unique groups of bats, the former to fruit-eating Pteropidae in Africa and the latter to fish-eating Noctilionidae in South America. Two of the 3 species of *Leptocimex* are known to be associated with Emballonuridae (*Taphozous nudiventris*), and the third, *boueti,* has adopted man as a host in West Africa but also has been recorded from a "bat."

In the Holarctic Region all bat records of *Cimex* (Pipistrelli and Pilosellus Groups) are of members of the family Vespertilionidae. Because this represents the observations of many collectors in Europe and North America, it is probably a true picture. It is interesting that Polyctenidae are found almost exclusively on Molossidae, not on Vespertilionidae. Apparently *Cacodmus* also is associated almost exclusively (the *Galeopithecus* record is surely an error) with Vespertilionids. This makes for an unusual situation in North Africa and the Middle East, where *Cacodmus vicinus* occurs commonly on *Pipistrellus kuhlii,* whereas one might have expected a member of the Pipistrelli Group to have extended into this southern part of the Palearctic Region.

As for species "specificity," very little can be said. In Europe the records for the Pipistrelli Group are confused because the taxonomy of the bugs has been in a state of flux. In North America records for the Pilosellus Group are inconclusive.

The role of man and his domesticated animals as hosts has been discussed elsewhere. It seems most likely that *C. lectularius* evolved on bats and then spread when man built houses for which it was preadapted. This is probably true also for *C. hemipterus* and is certainly true for *Leptocimex boueti.* Whether *Cimex columbarius* evolved on pigeons from an original stock on bats (via flycatchers?) or from a population already associated with man, is a moot question.

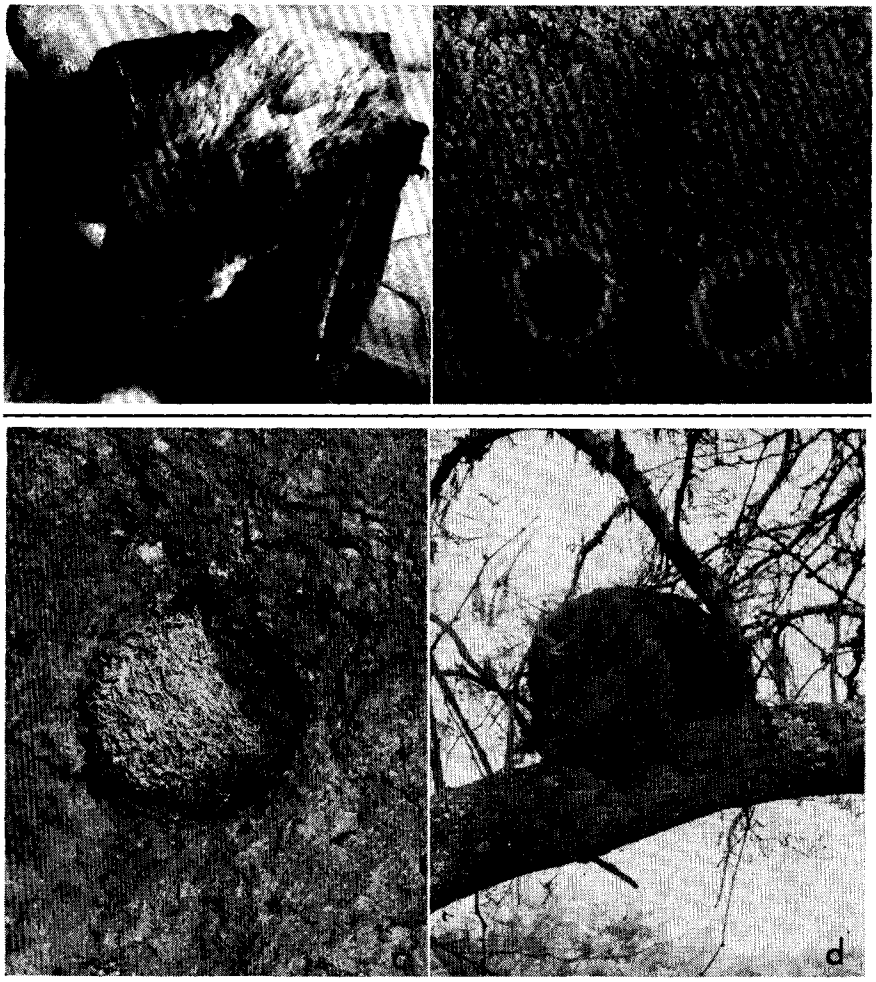

FIG. 11–15.—a. *Aphrania barys* specimens attached to wings of *Eptesicus zuluensis* in southwest Africa. (Kühnelt, original). b. Nests of cliff swallow, *Petrochelidon albifrons,* under a bridge near Colusa, California. The mud surface is covered with small black fecal spots and egg shells of *Oeciacus vicarius.* c. Nest of the cave swiftlet (*Collocalia*) in a mine tunnel near Wau, New Guinea. Habitat of *Paracimex capitatus* (Peter Shanahan, original). d. Nest of the oven bird, or "hornero," *Furnarius rufus* near Tucumán, Argentina. Habitat of *Caminicimex furnarii* (E. Bucher, original).

RELATIONSHIPS OF CIMICIDAE

The presently accepted position of Cimicidae within the Hemiptera-Heteroptera is: Geocorisae (Dufour 1833) or land bugs; Cimicomorpha (Leston et al. 1954) with distinctive male genitalia and no trichobothria; superfamily Cimicoidea (Reuter 1910, Börner 1934) with posterior coxae cardinate and hemelytra with a cuneus; Cimiciformes (Reuter 1910) without arolia between the claws. The last-named group includes the Microphysidae (and Plokiophilidae), Anthocoridae, Cimicidae, and Polyctenidae. Of these the Microphysidae differ from Cimicidae in the symmetrically developed male genitalia and 2-segmented tarsi; the Anthocoridae in the composite meso- and metasterna and, usually, paratergites at the base of the abdomen and well-developed ocelli; and the

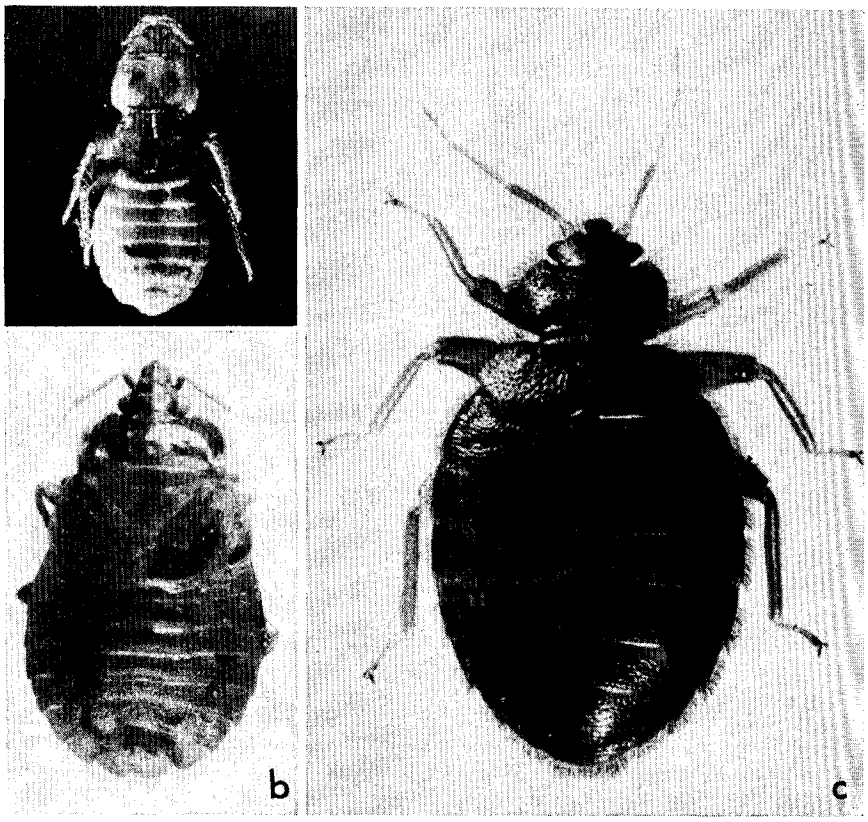

FIG. 11–16.—Representatives of three related families of Cimicoidea. a, Polyctenidae (*Eoctenes nycteridis* Horvath) (Carayon, original); b, Anthocoridae (*Astemmocoris cimicoides* Carayon and Usinger (Carayon, original); c, Cimicidae (*Cimex antennatus*, n. sp.) (Ueshima, original).

Polyctenidae in the ctenidial combs, a very broad labrum, no eyes, and no dorsal abdominal scent glands in the nymphs. Within the anthocorid-cimicid-polyctenid line (Fig. 11–16) (with the right genital clasper strongly developed and the other usually reduced or absent) there is a trend from predominantly plant-dwelling predators of aphids, mites, thrips, etc. (Anthocorinae) to predators in the nests of birds and mammals (Lyctocorinae), thence to free-living blood suckers in the nests of warmblooded animals (Cimicidae), and finally to the permanently ectoparasitic Polyctenidae, which live in the fur of bats and reproduce by viviparity. Also within this line there is a trend toward loss of wings, ocelli, and ovipositor. Hemocoelic insemination is universal and variously developed in members of this line.

Because of their close relationships with the Anthocoridae, the Cimicids have been considered by some authors to be a subfamily equivalent either to anthocorids (Stål 1873), or to be at the same level as the anthocorid subfamilies (Southwood and Leston 1959). As just mentioned, anthocorids differ in having a longitudinal suture on the meso- and metasterna, usually paratergites on the second and third abdominal segments, and usually fully developed ocelli and wings. Reuter (1913b) and others have stressed the habits of the anthocorid *Lyctocoris campestris,* which sucks the blood of birds and mammals including man. Carayon and Usinger (1965) described a new genus, *Astemmocoris,* of the Lyctocorinae with brachypterous females that bear a striking resemblance to Cimicidae. To settle the status of the cimicids it is necessary to decide whether the anthocorid subfamilies are more closely related to each other than they are to the cimicids. In my opinion they are; this was also the judgment of Stål (1873), Reuter (1910), China and Myers (1929), Carayon, and others. Therefore the Cimicidae is here recognized as a separate family.

PHYLOGENY

Although the major groups (subfamilies) of Cimicidae are reasonably distinct, we can only speculate as to the origin and probable course of evolution within the family. Barber (1941) regarded the American bat parasite, *Primicimex,* the most primitive cimicid, and Carayon (1954b) agreed, finding that it lacks a true spermalege and mycetomes, both of which are characteristic of all other Cimicidae. This theory seems more plausible than that of Reuter (1913b) which derived the Cimicinae, and in particular the swallow parasites (*Oeciacus*), from *Lyctocoris campestris,* which also lives in birds' nests. Much additional evidence is now available in support of the unspecialized nature of *Primicimex,* but it is difficult to imagine a cimicid that would look less like an anthocorid than does *Primicimex.*

Bridging the gap between *Primicimex* and the Cimicinae is *Bucimex*

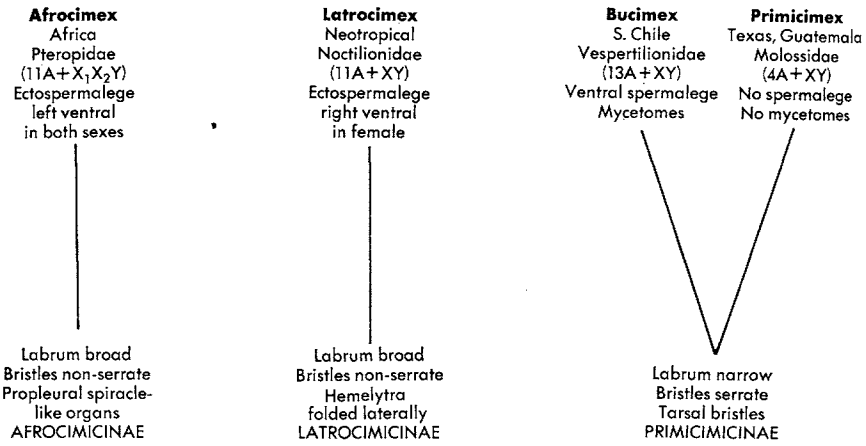

FIG. 11–17.—Dendrogram showing some diagnostic characters of 3 unique subfamilies of bat bugs.

(Usinger 1963). This genus occurs on bats in southern Chile. In external characters it is remarkably like *Primicimex*, but Carayon has shown that it has a well-developed ventral spermalege and mycetomes and that, on the basis of internal characters, it belongs in the Cimicinae. Cytological evidence supports this position, both groups having serrate bristles in contrast to other Cimicidae. Probably, then, the Primicimici-

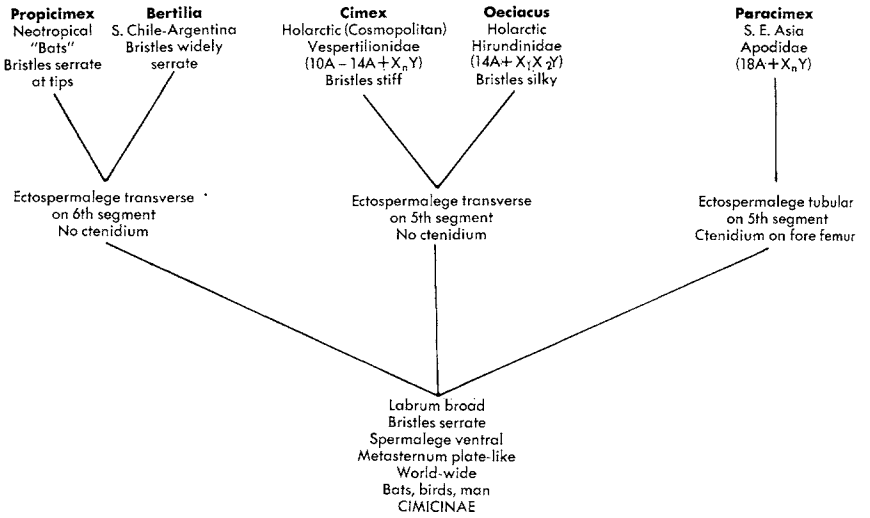

FIG. 11–18.—Dendrogram showing some diagnostic characters and relationships of genera in the subfamily Cimicinae.

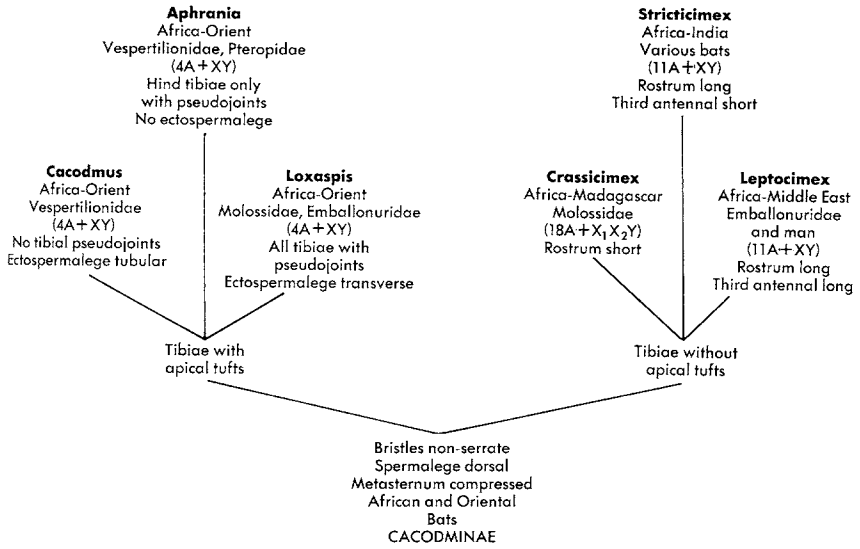

FIG. 11–19.—Dendrogram showing some diagnostic characters and relationships of genera in the subfamily Cacodminae.

nae and Cimicinae represent a single line (Fig. 11–17, 11–18) that originated on bats and only later turned to cave swiftlets in Southeast Asia (*Paracimex*) and still later to swallows in the Holarctic Region (*Oeciacus*). *Paracimex* has the most specialized spermalege in this line, with a tubular ectospermalege and conducting tissue, so that the sperm are not wasted by diffusion throughout the body cavity. The South American genera *Bertilia* and *Propicimex* are specialized branches that probably evolved in complete isolation from Holarctic *Cimex*.

In the Old World tropics a distinctive type, the Cacodminae (Fig. 11–19), evolved with simple (non-serrate) bristles and a dorsal spermalege. If evolution was from low chromosome numbers to high and from the simple XX-XY sex-chromosome mechanism to XnY, then, like *Primicimex* in America, *Cacodmus* and its near allies have only 4 autosomes and the XX-XY mechanism (haploid number, first metaphase). *Cacodmus* has the same compact body form as *Cimex* and occurs on vespertilionid bats as *Cimex* and *Bucimex* do, but is unlike *Primicimex*, which is associated with a bat of the family Molossidae. *Cacodmus* occurs throughout Africa, the Middle East, and the Orient, while its near relatives, *Aphrania* and *Loxaspis*, lack representatives in the area between Africa and the Orient. In these 3 genera some or all of the tibiae have pseudojoints (a specialized character). In *Aphrania* the ectospermalege is reduced but the mesospermalege is fully developed. *Loxaspis* has 1 African representative, *setipes* Ferris and Usinger, with long setose legs like those of the next group of African Cacodminae.

Crassicimex, Stricticimex, and *Leptocimex* are the long-legged genera with higher chromosome numbers and, each in its own way, with highly specialized ectospermalege. *Crassicimex* is the most unusual in general appearance because of the large head and short, stout beak. It and possibly also *Stricticimex* are associated with molossid bats, whereas *Leptocimex* is found on Emballonuridae. Evolution in *Leptocimex* has resulted in the only genus of Cimicidae with completely different spermaleges in the various species. *Leptocimex duplicatus* agrees in all other generic characters but has 2 separate spermaleges, bilaterally arranged, and the male has a long, sickle-like paramere to penetrate the tubular ectospermaleges. *Leptocimex boueti* has no ectospermalege.

Also in Africa occurs the unique Afrocimicinae (Fig. 11–17), a group of cave-inhabiting bugs associated with fruit-eating bats (Pteropidae). *Afrocimex* has simple bristles and long, unspecialized legs. In contrast to the Cacodminae, the spermalege is ventral and generalized. Curiously, like the females, the males have an enormously developed ectospermalege at the base of the abdomen on the left side. There is a peculiar spiracle-like organ ventrally on the prothorax near each posterolateral angle.

In the American tropics another monotypic group, the Latrocimicinae (Fig. 11–17), is confined to fish-eating bats of the family Noctilionidae. It has the same number of autosomes as *Afrocimex* and shows similarities in the internal metathoracic scent glands. The ectospermalege is ventral like that in *Afrocimex* (though on the left side) but is not developed in the male. The 2 groups are completely unlike in appearance, and despite the similarities mentioned, probably have no close connection. Actually, *Latrocimex,* although a bat parasite, has prominent bristles on the hind angles of the pronotum (most noticeable in first-instar nymphs) and stout spine-like bristles on the tibiae that are suggestive of the next subfamily.

The Haematosiphoninae (Fig. 11–20) are bird bugs of the Western Hemisphere. Having a dorsal (or in *Hesperocimex* lateroventral) spermalege and simple bristles, they might conceivably have arisen from Cacodminae or from *Latrocimex,* although it is more probable that they arose as an independent line equivalent to the Cacodminae, but on birds in the Western Hemisphere. There are 2 groups—*Haematosiphon, Ornithocoris,* and allies with a generalized spermalege; and *Hesperocimex* with a peculiar hat-shaped ectospermalege lateroventrally and some unique internal features. *Ornithocoris* is one of the least specialized South American genera and has only 4 autosomes and the simple XX-XY sex mechanism. Like so many cimicids, it occurs on birds of the family Hirundinidae and could have given rise to the more specialized *Psitticimex* on Psittacidae and *Caminicimex* on Furnariidae. Skipping the American tropics for unknown reasons, the group is represented in North America by *Cimexopsis* and *Synxenoderus* on swifts (Apodidae) and by *Haematosiphon* on birds of prey. *Hesperocimex* might represent the end

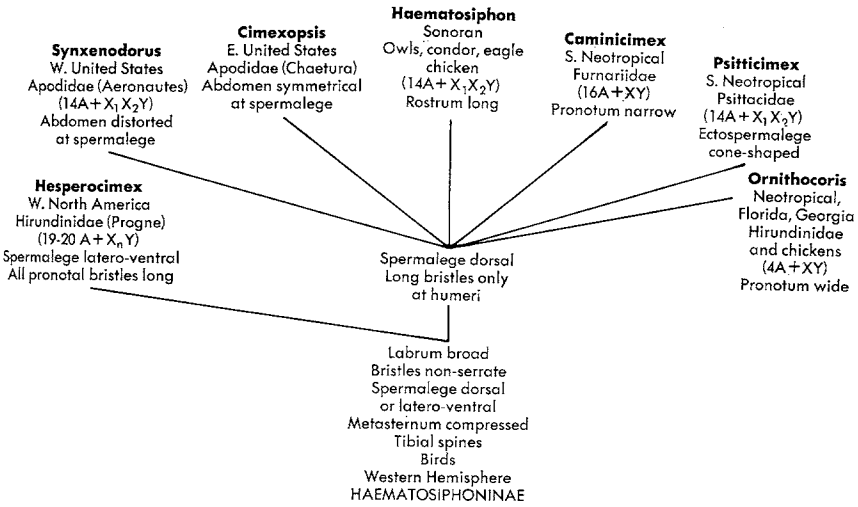

FIG. 11-20.—Dendrogram showing some diagnostic characters and relationships of genera in the subfamily Haematosiphoninae.

point in this line, being specialized as previously mentioned, with the highest number of autosomes, and occurring in the nests of purple martins (Hirundinidae) in woodpecker holes in western North America.

SPECIES CONCEPT

As in most groups of insects, species in the Cimicidae have been based largely, and in earlier times exclusively, on external characters. This traditional taxonomic approach often results in a useful and sometimes "natural" classification. In the Cimicidae it has failed to resolve the complex problems in the genus *Cimex*. Many ill-defined names had accumulated in the Lectularius Group, and the situation in the Pilosellus Group and especially in the Pipistrelli Group could best be described as chaotic. In the European literature from 1930 to the present, no 2 authors have agreed on the taxonomic status of the various names.

Hase (1938) was the first to try to resolve the question "What is a species in *Cimex*?" by cross-breeding experiments. He found that populations of *C. lectularius* from Berlin, Frankfurt, Jaffa, Cairo, Nanking, and Peiping were interfertile, as were populations of *C. hemipterus* from Ocumore (Venezuela), Havana (Cuba), and Aligarh (India), but that crosses between the 2 species were sterile. Omori (1941) and Davis confirmed that the 2 species were intersterile and added the interesting details given below.

The status of the pigeon bug, *Cimex columbarius*, had been a problem almost since it was first described because its main characters (small size

and relatively short third antennal segment) are variable and because *C. lectularius* also infests pigeons at times. Johnson (1939) and Titschack (1949) undertook to solve the problem by cross-breeding experiments. Both claimed that *Cimex columbarius* and *C. lectularius* would interbreed freely, but Johnson, who found statistically significant differences in the ratio of head width to third antennal segment length, concluded that the two should be considered as subspecies, while Titschack considered them to be full species. Ueshima (1964), using more refined techniques, showed that the two are effectively isolated due to selective mating (Table 11–2) and reduction in number of eggs laid (Table 11–3), and that, being sympatric, they must be considered as full species. This is the treatment adopted in the present work.

The situation in the Pilosellus and Pipistrelli Groups is much more involved. In the first draft of this manuscript, prepared several years

Table 11–2.—Evidence of selective mating in mixed colonies of *Cimex columbarius* and *C. lectularius* (Cairo and Berkeley strains). Number of females examined (*n*) and percent of females inseminated (%) after 24 hours (Ueshima 1964).

Females	Males	Ex.[a]	*Homogametic*		*Heterogametic*		χ^2	Isolation index[b]
			n	%	*n*	%		
columbarius, *lectularius* (from Cairo)	*columbarius*	1	10	90	10	20	9.86	0.64
		2	10	80	10	20	7.20	.60
		T	20	85	20	20	16.94	.62
columbarius, *lectularius* (from Cairo)	*lectularius* (from Cairo)	1	10	100	10	0	20.00	1.00
		2	10	80	10	10	9.89	0.78
		T	20	90	20	5	28.97	.89
columbarius, *lectularius* (from Berkeley)	*columbarius*	1	10	90	10	20	9.86	.64
		2	10	100	10	30	10.77	.54
		T	20	95	20	25	20.42	.58
columbarius, *lectularius* (from Berkeley)	*lectularius* (from Berkeley)	1	10	90	10	10	12.80	.80
		2	10	80	10	10	9.89	.78
		T	20	85	20	10	22.56	.79
lectularius, (from Cairo) *lectularius* (from Berkeley)	*lectularius* (from Cairo)	1	10	90	10	90	0.00	.00
		2	10	90	10	80	.39	.06
		T	20	90	20	85	.23	.03
lectularius, (from Cairo) *lectularius* (from Berkeley)	*lectularius* (from Berkeley)	1	10	80	10	90	.39	−.06
		2	10	100	10	90	1.05	.05
		T	20	90	20	90	0.00	.00

[a] 1, first experimental set with the bristles on the right wing pad of homogametic females removed; 2, second experimental set with the bristles on the right wing pad of heterogametic females removed; t, total of 1 and 2 above.

[b] For isolation index see Stalker (1942). An index of 1.00 indicates complete isolation; zero indicates random mating.

Table 11–3.—Number of eggs laid (mean and its standard error) in crosses (10 ♀ and 10 ♂) between *Cimex columbarius* and *C. lectularius* (Cairo and Berkeley strains) (Ueshima 1964).

	Male		
Female	*C. columbarius*	*C. lectularius* (from Cairo)	*C. lectularius* (from Berkeley)
C. columbarius	—	1.9 ± 1.32	0.4 ± 0.40
C. lectularius (from Cairo)	24.3 ± 3.26	—	40.3 ± 2.74
C. lectularius (from Berkeley)	32.5 ± 4.98	36.2 ± 2.30	—

ago, I took a broad view of species in the genus *Cimex* based on the experiments just quoted. I recognized 4 species, *C. lectularius, C. hemipterus, Cimex pipistrelli,* and *Cimex pilosellus.* Unfortunately from the point of view of simplicity, the interpretation proved to be wrong. In the following pages experimental evidence is presented on which a new species concept is based. Most of the work was done in my laboratory by several students and colleagues (N. Ueshima, N. T. Davis, R. E. Ryckman, and W. Foster).

First a word should be said about the validity of experimental crosses in taxonomic work. In vertebrates the method is not highly regarded because of behavioral patterns that are upset under artificial conditions. In Cimicidae the method seems to be valid because of the promiscuous mating behavior and because the bugs live so well in culture tubes. Mating was normal in all control colonies, so deviations from the norm in crossing may be regarded as significant.

In all hybridization studies it is necessary to define the words fertile

Table 11–4.—Length/width ratios of parameres in the two chromosomal types of *C. lectularius* (Cairo and Berkeley strains) (Ueshima).

Chromosomal form	Locality	Mean		Index	
		Length	Width	Population	Form
Mediterranean	Cairo	7.28	0.99	7.35±0.098	7.365±0.015
	Moravia	7.13	.97	7.38± .275	
Pacific	Berkeley	7.15	1.12	6.37± .043	6.35 ± .086
	Monterrey	6.86	1.09	6.33± .052	
columbarius	South Finland	6.15	.95	6.45± .031	6.45 ± .031

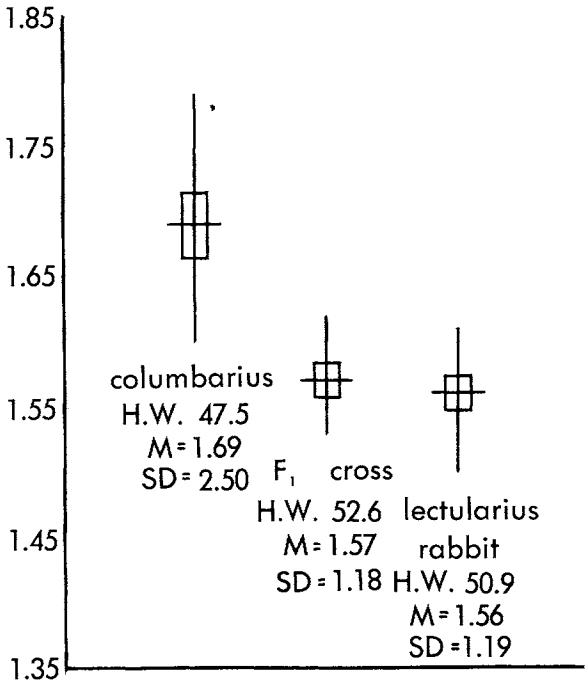

FIG. 11–21.—Head width/3rd antennal ratio in *Cimex columbarius* reared on chicken, *C. lectularius* reared on rabbit, and in F_1 hybrids. Range in variation is shown by vertical line. Rectangle shows 1 standard deviation above and below the mean in tenths of a micrometer unit. Vertical scale is in micrometer units. 1 unit = 0.17 mm.

and sterile, or to set up degrees of fertility and sterility. Like the cross between the ass and the horse and many other cases in vertebrates, F_1 progeny are obtained but they are sterile, hence reproductive isolation is complete. In Cimicidae 1) mating may occur without migration of sperm to the conceptacula so that no eggs are produced, 2) mating may occur and eggs may be laid but the eggs are infertile, 3) a low percentage of eggs may hatch and produce nymphs that die before becoming adults, 4) nymphs may reach the adult stage but the latter may be sterile, or 5) the adults may have reduced fertility so that sterility results in the F_2. Each of these cases is represented in various of the experimental crosses. For example, the crosses by artificial insemination between *C. lectularius, Oeciacus vicarius,* and *Leptocimex duplicatus* were of type 1 (Davis); the crosses between *C. lectularius* males and *Cimex columbarius* females (but not the reciprocal) were of type 3; the cross *Cimex pipistrelli* × *Cimex japonicus* and the reciprocal were of type 4; and the cross *Cimex pipistrelli* × *Cimex stadleri* and its reciprocal were of type 5. In general, any reduction in fertility in the F_1 results in complete sterility in the F_2.

Table 11–5.—Hybridization experiments involving *C. lectularius* and *Cimex columbarius* crossed with other species in the genus[a] (Ueshima).

	Cairo *lectularius*		Berkeley *lectularius*		Finland *columbarius*		Panama *hemipterus*		British *pipistrelli*	
Females	E	N	E	N	E	N	E	N	E	N
Cairo *lectularius*			+++	+++	+++	+++	+	–	++	–
Berkeley *lectularius*	+++	+++			+++	+++	+	–	++	–
Cimex columbarius	+	+	+	+			+	–	++	–

[a] E = eggs laid; N = nymphs obtained; + = less than 5 eggs/female; ++ = less than 10 eggs/female; +++ = more than 10 eggs/female.

Elsewhere in this work (Chapter 10) Ueshima describes the chromosomal aberrations in many of the crosses. Curiously, there is no reduction in fertility in crosses between *C. lectularius* populations having extreme differences in supernumerary chromosomes. Also, the supernumerary chromosomes are practically inert. The only apparent difference (Ueshima) is in the ratio length/width of the paramere (Table 11–4); the Mediterranean form with supernumerary chromosomes has a significantly higher paramere index. There is a reproductive barrier in the cross *C. hemipterus* ♂ × *C. lectularius* ♀ (Omori 1941) and Davis found, by artificial insemination, it is the sperm fluid of *C. hemipterus* that is toxic to the females of *C. lectularius.*

In the cross *C. lectularius* × *Cimex columbarius,* Ueshima (1964) found a strong intraspecific mating preference (Table 11–2) and greatly reduced egg production when females of *Cimex columbarius* were crossed with males of *C. lectularius* (Table 11–3). There was no reduction in fertile eggs in the reciprocal cross. In other experiments the hybrids showed a head width/3rd antennal ratio that was intermediate between the 2 parents but nearer the mean for *C. lectularius* (Fig. 11–21). In crosses between *Cimex columbarius* females and males of the Cairo strain of *C. lectularius* with 6 supernumerary X chromosomes (Table 10–7), all the progeny were of the female type ($13A+X_1X_2Y$). In the reciprocal (Table 10–6), the progeny varied from $13A+X_1$-X_3Y to 13A+

Table 11–6.—Hybridization experiments between species in the Pipistrelli Group. Ten ♂ and 10 ♀ were used in each cross (Ueshima).

	F_1			F_2		
Cross	Eggs	Nymphs	Adults	Eggs	Nymphs	Adults
pipistrelli × *stadleri*	137	107	62	41	19	sterile
stadleri × *pipistrelli*	119	89	73	59	27	24 sterile
pipistrelli × *japonicus*	72	49	43	–	–	–
japonicus × *pipistrelli*	97	81	74	27	–	–
stadleri × *japonicus*	139	65	61	66	39	17 sterile
japonicus × *stadleri*	83	59	53	–	–	–

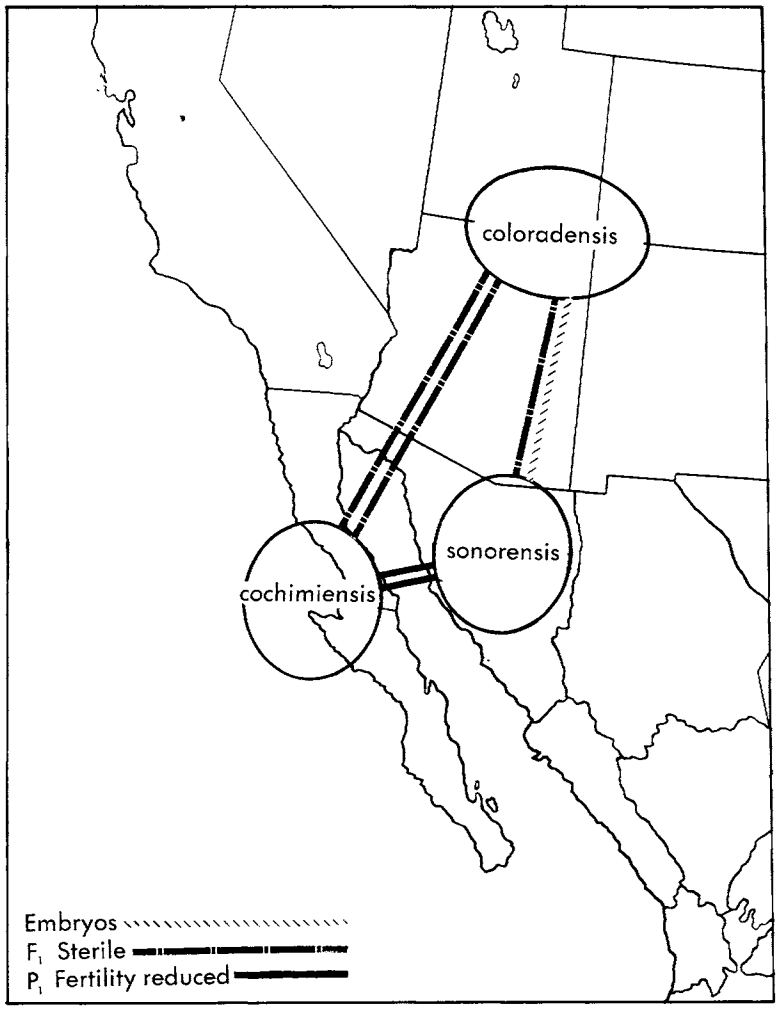

FIG. 11–22.—Results of hybridization experiments with the three species of *Hesperocimex* (Ryckman and Ueshima 1964).

X_1-X_6Y. After 14 generations, as might be expected in the first cross, the pattern was fixed at 13A+X_1X_2Y. The head width/3rd antennal ratio was 1.6, between the range of *Cimex columbarius* and that of *C. lectularius*. In the reciprocal cross the opposite was true, over 95% of the supernumerary chromosomes being fixed at 13A+X_1-X_5Y and the head width/3rd antennal ratio being 1.47 (typical *C. lectularius*). This situation indicates that a hybrid population in nature would not stabilize into parental types for a long time, if ever.

Table 11–7.—Hybridization experiments involving species in the Pilosellus Group[a] (Ueshima).

	Cimex latipennis		*Cimex pilosellus*		*Cimex antennatus*		*Cimex incrassatus*		*Cimex brevis*	
Females	E	N	E	N	E	N	E	N	E	N
Cimex latipennis			+	−	−	−	+	−	−	−
Cimex pilosellus	+	−			−	−	−	−	+	−
Cimex antennatus	+	−	−	−			+++	+++	++	++
Cimex incrassatus	+	+	−	−	++	++			+	−
Cimex brevis	−	−	+	+	++	++	+	−		

[a] E = eggs laid; N = nymphs obtained; + = less than 5 eggs/female; ++ = less than 10 eggs/female; +++ = more than 10 eggs/ female.

Crosses between *C. lectularius* and other *Cimex* species are summarized in Table 11–5. Not shown are the completely negative results with *C. lectularius* and 5 species in the Pilosellus Group (Ueshima), the 3 eggs and 1 nymph obtained in crosses between *C. lectularius* and *Cimex stadleri* from Czechoslovakia (Davis) and the negative cross of *C. lectularius* and *Oeciacus vicarius* by artificial insemination (Davis). A few sterile eggs were obtained in a cross between *C. lectularius* and *Cimex brevis* (Davis).

Crosses in the Pipistrelli Group (Table 11–6) showed reduced fertility in F_1, and all F_2 produced were sterile. In the Pilosellus Group (Table 11–7) crosses showed reduced fertility in F_1, and a majority of F_2 produced were sterile.

Hybridization studies in *Hesperocimex* were fully reported by Ryckman and Ueshima (1964). The results are shown diagrammatically in Fig. 11–22. Eggs were produced in all cases, but the numbers were greatly reduced in the *Hesperocimex cochimiensis* ♂ × *Hesperocimex sonorensis* ♀ cross owing to a traumatic effect. Ryckman states that "killer" males of *Hesperocimex cochimiensis* kill the females of *Hesperocimex sonorensis* by trauma during mating, the female abdomens being "swollen and blackened with a plug of dried serum adhering to the external abdominal wall in the region of the spermalege."

In *Oeciacus,* European *hirundinis* (Greece) and North American *vicarius* (California) were crossed and were completely intersterile (Ueshima). Crosses between California populations of *Oeciacus vicarius* on cliff swallows and barn swallows were interfertile (Foster).

Intraspecific variation is an important element in forming a species concept. In the Cimicidae very little variation is observed except in certain as yet unresolved complexes in *Paracimex* and the Pipistrelli Group and in the human bed bugs. In *C. lectularius* considerable intraspecific variation occurs in size (best expressed as pronotal width), the number of supernumerary X chromosomes, the length of bristles, the ratio of length and width of the hind femora, and in antennal proportions ex-

pressed as the head width:3rd antennal ratio. All of these have been discussed elsewhere. Here it is only necessary to point out that *C. lectularius* is by far the most variable species of Cimicidae and that differences in bristle length, for example, like those seen in populations from Moravia and Monterrey (Mexico) would be considered as specific characters elsewhere in the family. Thus we find 1 species (*C. hemipterus* is less variable) with divergent populations that are fully interfertile and most other species (bat bugs of the Pilosellus and Pipistrelli Groups) that are remarkably uniform and are sterile when crossed with closely related forms. Such an inconsistency is disconcerting but is not without parallel in other plants and animals under domestication.

TAXONOMIC CHARACTERS[2]

The spermalege and its associated structures in the paragenital system provide the best and most fundamental characters in the Cimicidae. Only the paragenital sinus is visible in most dried specimens, but this alone is sufficient to place most genera. The ectospermalege seen in cleared specimens adds a great deal, especially in differentiating species in such genera as *Cacodmus* and *Paracimex* (Fig. 11–23). The mesospermalege is more difficult to use because dissections of fresh material or histological sections are needed. But this internal structure and the seminal conceptacles give the best information on the degree of specialization of a group. It is the lack of a spermalege that provides the best evidence that *Primicimex* is primitive and that *Paracimex* and the *Stricticimex-Crassicimex-Leptocimex* group are the most specialized members of the Cimicinae and Cacodminae, respectively. The trend in each case is from a poorly delimited mass of cells to a distinct organ through which the sperm pass. Beyond this there is a tendency toward tubular conducting organs and tissues to carry the sperm to the conceptacles without the waste of dispersal throughout the body cavity. In general, evolution of the spermalege coincides with the generally accepted taxonomic grouping at the generic level. With few exceptions (*Oeciacus* and *Cimex, Ornithocoris,* and *Caminicimex*), each genus of Cimicidae can be recognized instantly by the structure of the spermalege. No other characters are needed. Curiously, evolution has gone a step farther in *Leptocimex,* and each species is distinct and in fact totally different, *L. duplicatus* having 2 separate tubular structures unknown in the rest of the family. The weight to be given spermalege characters at the subfamily level was a major question in the preparation of this work. On the basis of the

[2] The methods of measuring structures used as taxonomic characters in keys and descriptions are shown diagrammatically in Fig. 11–32.

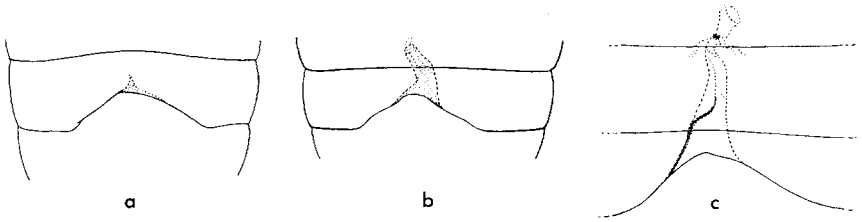

FIG. 11–23.—Distinctive shapes of the ectospermalege in *Paracimex*. a, *reductus;* b, *borneensis;* c, *ignotus*.

spermalege alone, *Bucimex* would have to be moved to the Cimicinae and *Hesperocimex* and *Leptocimex duplicatus* would require separate subfamily status. After much deliberation it was decided that, in doubtful cases, external characters would be considered decisive, if only for practical reasons.

Other internal characters are the mycetomes, small lobe-like organs near the ovaries and testes that occur on all Cimicidae except *Primicimex* and in no other Cimicoidea; the ovarioles, which number 7 in Anthocoridae and Cimicidae and 2 or 3 in Polyctenidae; the seminal conceptacles, usually a pair of lobes, 1 on each side, connected to the lateral oviducts but replaced in some Haematosiphoninae by a ring of many small lobes around the oviducts; and the metasternal scent glands, which show remarkable diversity and, with few exceptions, support the classification adopted here.

In the male, the parameres (Fig. 11–24 to 11–28) are diagnostic at the species level in *Cacodmus, Hesperocimex,* and some other genera, and at the generic level, for example, in the *Cacodmus* Group, in which the organ is bent backward in *Loxaspis* and forward in *Cacodmus* and *Aphrania.* Ueshima (Table 11–14) found slight differences in the ratio of length to width of the paramere in the 2 chromosome types of *C. lectularius.*

The internal genitalia are difficult to see in males and have not been used previously in taxonomic work. The aedeagus of *C. lectularius* has been figured more or less accurately in several studies of anatomy (Christophers and Cragg 1922, Ludwig and Zwanzig 1937), but the connections of the basal plates were not shown. It is clear from a brief survey that *Primicimex* (Fig. 11–29) and *Bucimex* differ from all other Cimicidae in having thick, strongly sclerotized basal plates and a prominent bridge like more generalized Hemiptera (Singh-Pruthi 1925). *C. lectularius,* in contrast, has very fine connections between the plates.

The female genitalia have been completely ignored in taxonomic work. Here again anatomical studies on *C. lectularius* (Davis 1956, Scudder 1959) show a specialized condition, whereas *Primicimex* (Fig. 11–30) and *Bucimex* show each of the structures in a primitive form, including

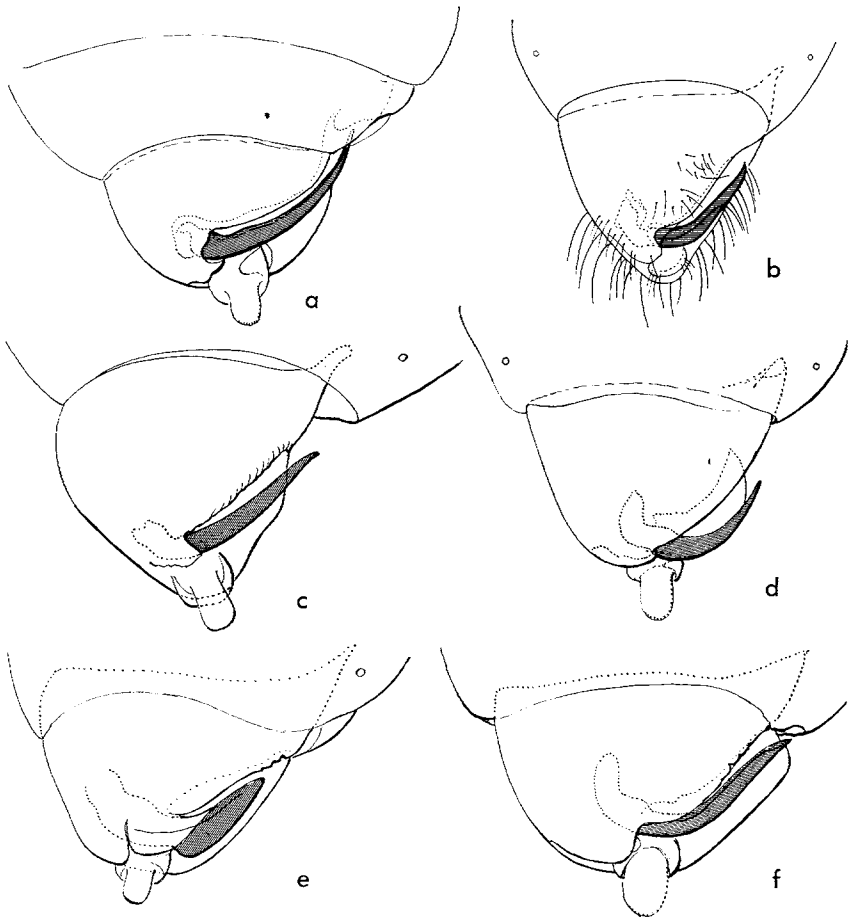

FIG. 11–24.—Male genital segments and parameres. a, *Primicimex cavernis;* b, *Paracimex reductus;* c, *Bertilia valdiviana;* d, *Oeciacus hirundinis;* e, *Propicimex limai;* f, *C. lectularius.*

the complete separation of the second gonocoxae from the ninth paratergites.

Bristles are perhaps the other most useful character at all levels in the classification. Jordan and Rothschild (1912) first used the presence or absence of serrations on the convex sides of bristles to distinguish subfamilies, and this character has held up remarkably well over the years. All Primicimicinae and Cimicinae, except for a few individuals or species in *Paracimex* and *Cimex,* have serrate bristles seen nowhere else in the Cimicidae. At the species level, the length and shape of bristles vary, and sexual dimorphism occurs in *Paracimex, Cimex,* and perhaps

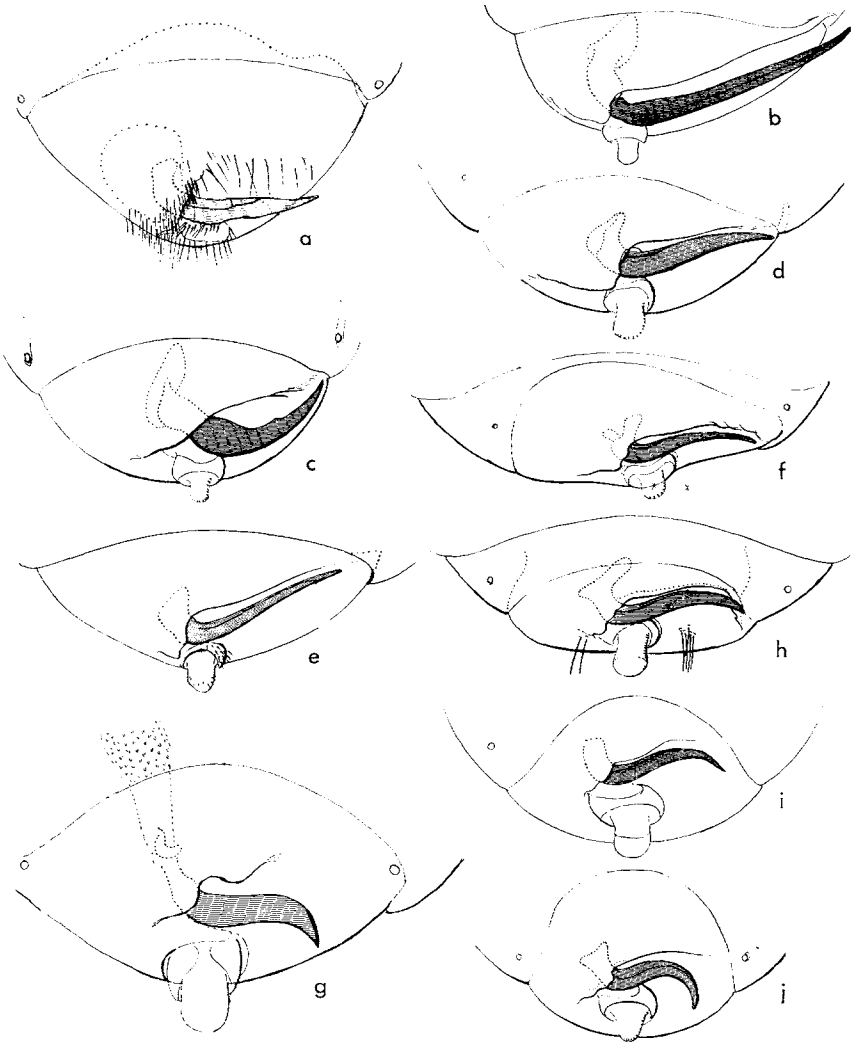

FIG. 11–25.—Male genital segments and parameres. a, *Stricticimex antennatus;* b, *Psitticimex urituí;* c, *Afrocimex constrictus;* d, *Haematosiphon inodorus;* e, *Synxenodorus comosus;* f, *Ornithocoris toledoi;* g, *Crassicimex pilosus;* h, *Loxaspis miranda;* i, *Leptocimex boueti;* j, *Leptocimex vespertilionis.*

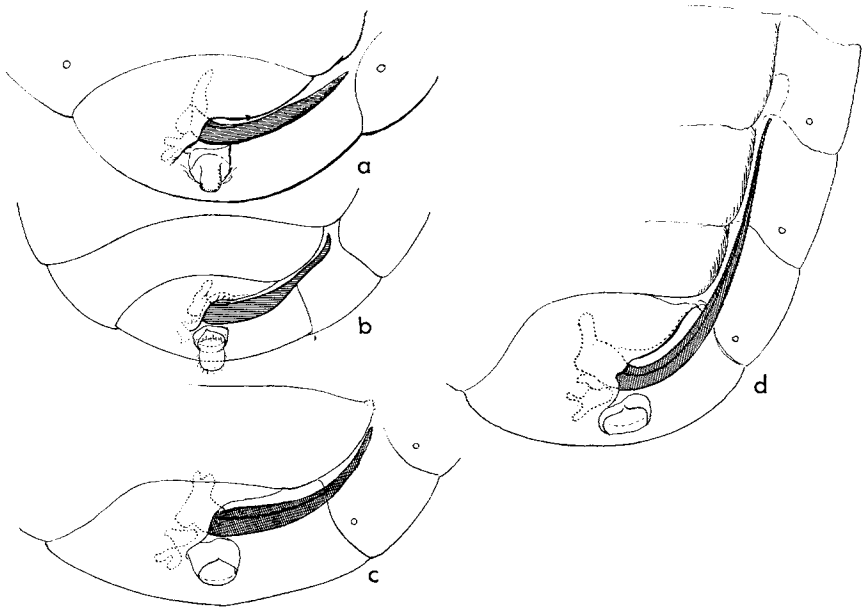

FIG. 11–26.—Male genital segments and parameres in *Cacodmus*. a, *sumatrensis;* b, *sinuatus;* c, *ignotus;* d, *sparsilis*.

in other genera. The significance of differences in bristle length is still a moot question in *Cimex*. Populations with very long and very short bristles interbreed in the Lectularius Group (Fig. 11–31) but not in the Pilosellus Group. For convenience in measuring (Fig. 11–32), the longest bristles at the sides of the pronotum were selected. Measurement is facilitated when the bristles are pressed out laterally in a slide-mounted specimen. Serrations are so fine that they should be viewed with a compound microscope. Abdominal bristle length is important in several genera. Usually the shortest bristles are anterior and median. Actual lengths were measured for a stated area in most cases, but the easiest method of referring to bristle length for routine taxonomic work is the length in relation to the distance between bristles. This is only an approximation for most bristles in an area, but it is a character that is obvious at a glance and hence is frequently used.

A few other bristles have been found useful as taxonomic characters, such as the group of stiff bristles at the apex of the tarsus in apposition to the claws in *Primicimex,* and the humeral bristles and short, stout tibial bristles in Haematosiphoninae. Bristles are easily broken off when mounting specimens on slides. The position of broken bristles on the dorsum is indicated by round pits in which the bristles were inserted.

On the head the width of the clypeus and labrum is useful, both struc-

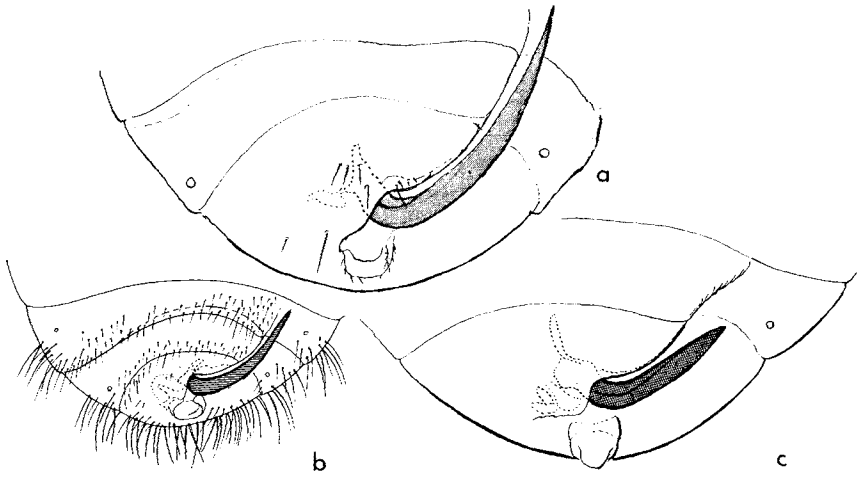

FIG. 11–27.—Male genital segments and parameres in *Aphrania*. a, *vishnou;* b, *elongata;* c, *recta*.

tures being narrow (and therefore primitive?) in Primicimicinae. The clypeus is also narrow in *Leptocimex* but is strongly widened in all other Cimicidae. In nymphs the shape of the ecdysial sutures provides a useful character. The head is measured (Fig. 11–32) to the front of the clypeus but not to the labrum and, most important, to the actual base as seen in cleared specimens, even though the head is more or less retracted within the pronotum.

The antennae (Fig. 11–33) are useful at the generic and especially at

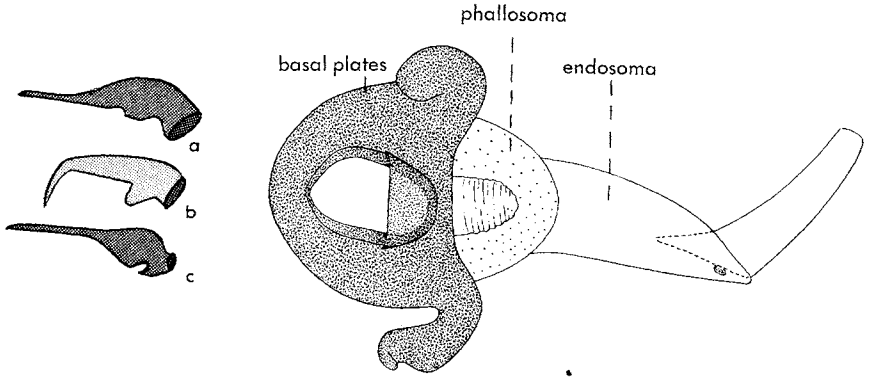

FIG. 11–28 (left).—Male parameres of *Hesperocimex*. a, *coloradensis;* b, *sonorensis;* c, *cochimiensis* (Ryckman and Ueshima 1964).

FIG. 11–29 (right).—Aedeagus of *Primicimex cavernis* with asymmetrical and strongly joined basal plates.

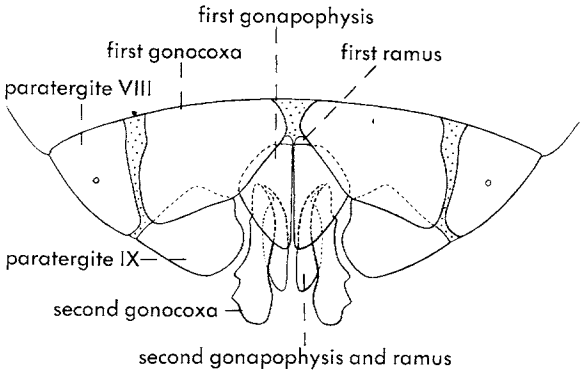

FIG. 11–30.—Female genitalia of *Primicimex cavernis*.

the specific level. Unfortunately, measurement is difficult, and specialists have come to quite different conclusions by measuring the same type specimens, depending on their method of measuring the segments. In dried specimens the problem seems simple, but when cleared and expanded, the second segment is seen to have a subbasal pale ring (pseudojoint) which is included in measurements (Fig. 11–32) in this work. Also between the second and third and the third and fourth segments are small intercalary segments (excluded in measurements in this work). All antennal measurements were made from slide-mounted specimens. The total length was obtained by adding the lengths of individual segments, hence it may not agree with an overall measurement, expanded or otherwise, that includes the intercalary segments.

The relative lengths of second, third, and fourth antennal segments have long been used as distinguishing characters in the genus *Cimex*. Part of the confusion in the Pipistrelli Group was due to different techniques of measurement. In distinguishing *Cimex columbarius* from *C. lectularius,* Johnson (1939) found that differences between second and third segments were not statistically significant but that, when related to a fixed measurement such as head width, the resulting ratios were significant and provided the most useful character for separating the 2 species. Fig. 11–34 shows the head width/3rd antennal ratios of the 2 species plotted in graph form, and Fig. 11–35 shows a scatter diagram of ratios plotted against head widths with regression lines drawn for *C. lectularius* and *Cimex columbarius.*

The rostrum often provides useful characters in the Hemiptera. In the Cimicidae it is difficult to use. Even the number of segments is a matter of dispute, the primitively 4-segmented rostrum of Hemiptera having been reduced to 3 segments in the Anthocorid–Cimicid line by the more or less complete loss of the basal segment. In dried specimens only 3 segments are seen, and the length can be indicated fairly accurately

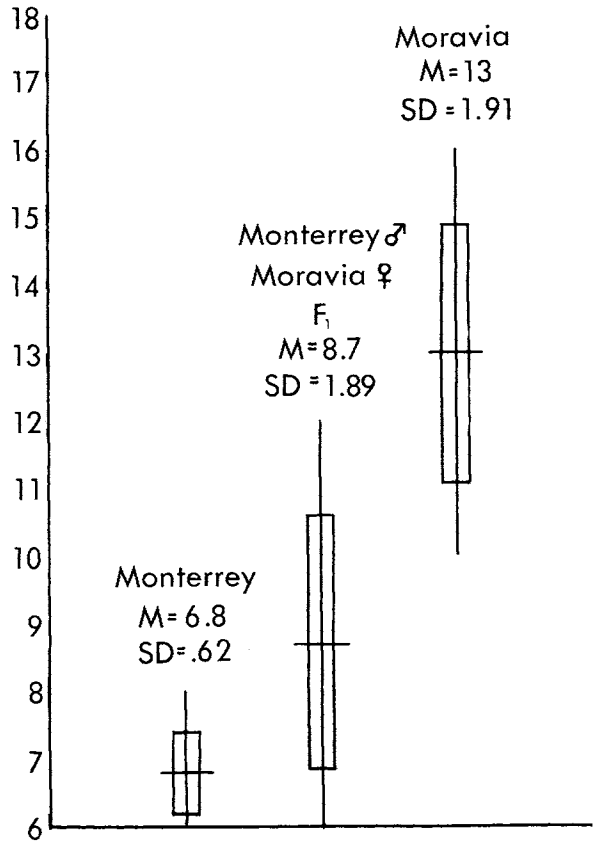

FIG. 11–31.—Length in micrometer units of bristles on hemelytral disks in *C. lectularius* colonies from Monterrey, Mexico and Moravia, Czechoslovakia, and F_1 hybrids between them. Vertical lines represent total range, rectangles 1 standard deviation on each side of mean.

by stating whether the rostrum attains the fore coxae, middle coxae, etc. It was by this means that *Haematosiphon* was first recognized as a genus, and the long rostrum was used by Jordan and Rothschild (1912) as a subfamily character in their monotypic Haematosiphoninae. Other groups with diagnostic rostra are *Primicimex* and *Crassicimex,* in neither of which does the rostrum reach the base of the head, and *Leptocimex,* which has an unusually long third segment. In all other Cimicidae the length and proportions of the segments are rather meaningless. Accurate measurements of individual segments are difficult in dry specimens and impossible in slide-mounted specimens because of the different degrees of expansion of the intersegmental membranes. Overall length in slide-mounted specimens is useless as a taxonomic character. It not only varies

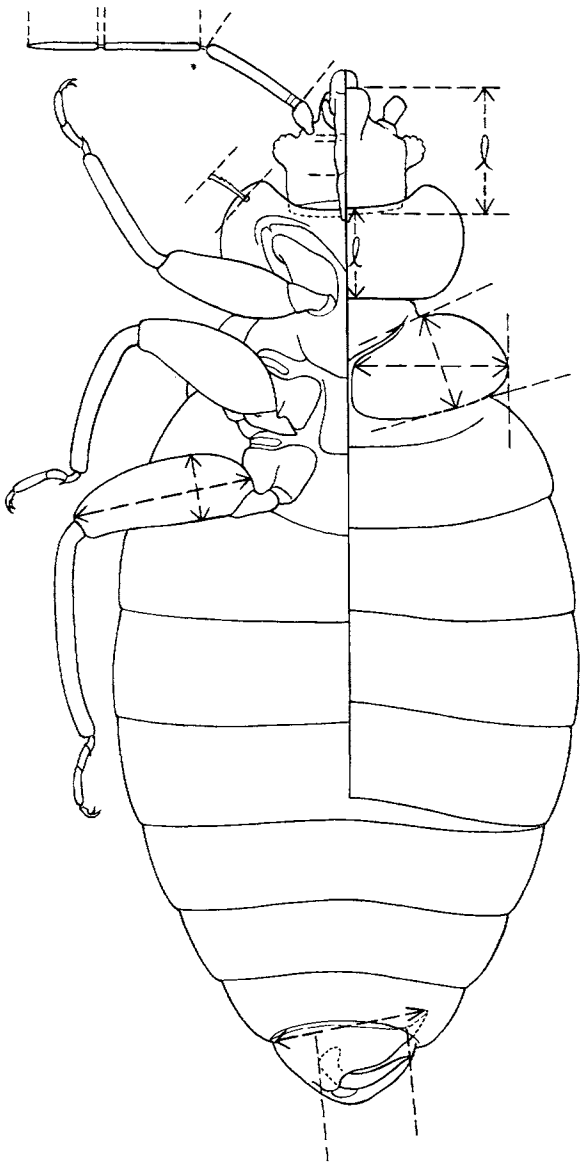

FIG. 11–32.—Diagram showing the methods used in measuring various structures as taxonomic characters.

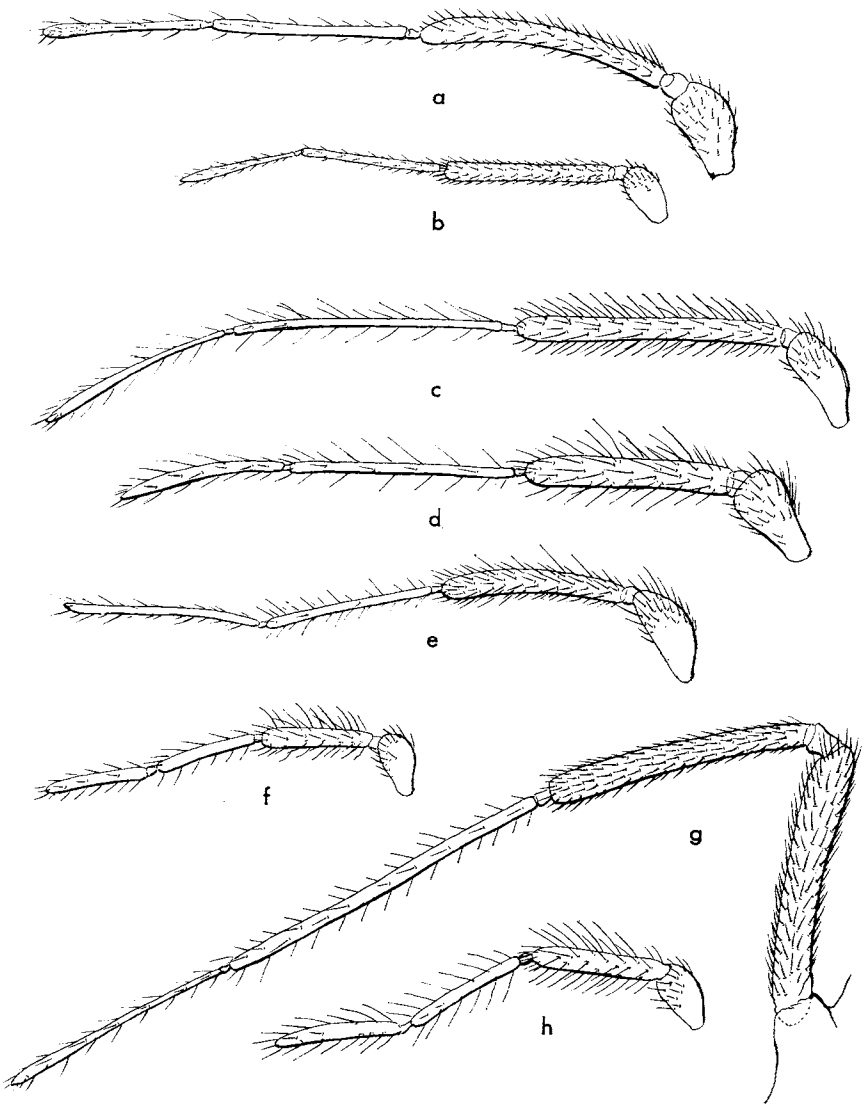

FIG. 11–33.—Details of antennae. a, *Haematosiphon inodorus;* b, *Ornithocoris toledoi;* c, *Cimex lectularius;* d, *C. adjunctus;* e, *Cacodmus sumatrensis;* f, *Oeciacus hirundinis;* g, *Primicimex cavernis;* h, *Oeciacus vicarius* (Ferris, original).

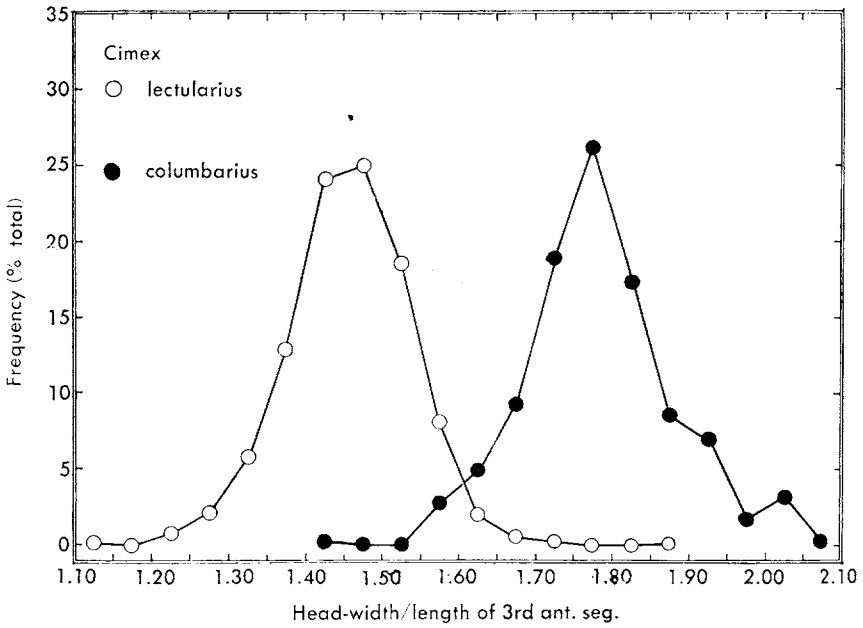

FIG. 11–34.—Frequency distribution of the ratio head width/3rd antennal segment length in *Cimex columbarius* and *C. lectularius* (Johnson 1939).

with the degree of expansion of the intersegmental membranes, but the rostrum may reach anywhere from the prosternum to the middle coxae, depending upon the degree to which the head is telescoped into the prothorax. In the descriptions and illustrations no reliance should be placed on apparent differences in rostral proportions.

Head, pronotum, and hemelytral proportions are especially useful at the specific level and were measured as indicated in the diagrams. In all cases, because of possible distortions in the semidorsal-semiventral drawings, proportions should be taken as given in the descriptions rather than in the illustrations. This applies to relative lengths of other structures as well.

Surface texture, sculpture, and punctures are best seen in dried specimens, hence were described from such material whenever possible.

The external evaporating areas of the metathoracic scent glands are strikingly distinct in some genera (lobulately produced in *Latrocimex*) and show differences at the species level in the genus *Cimex*. Unfortunately the areas, being lateral, are not visible in slide-mounted specimens and often are hidden by the legs in pinned material. In the future, more use may be made of these areas if specimens are especially prepared to reveal the pleural areas of the thorax.

The legs (Fig. 11–36) provide some of the most useful characters at

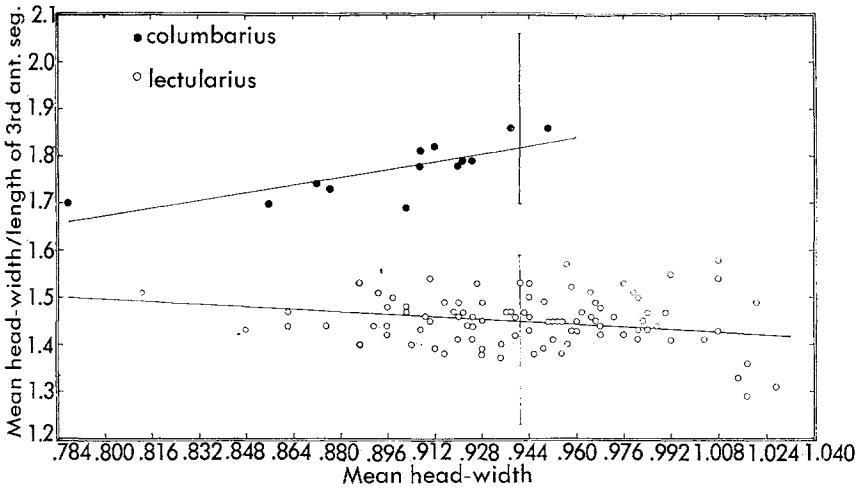

FIG. 11–35.—Local means of the ratio head width/3rd antennal segment length (vertical) and local mean head widths (horizontal in mm) for *Cimex columbarius* and *C. lectularius*. Regression lines are drawn between localities for each species (Johnson 1939).

all levels. The curiously mottled tibiae of Primicimicinae are diagnostic, as are subapical pale "rings" or pseudojoints in the tibiae of *Aphrania* and *Loxaspis* and the narrowed and subapically bent tibiae of *Leptocimex* and *Stricticimex*. The apical tufts on the tibiae of most Cimicidae, their absence in others (*Leptocimex, Stricticimex, Crassicimex*), and the sexual dimorphism in some Haematosiphoninae provide useful characters. The rows of stiff spines on the femora of *Afrocimex* and *Leptocimex* and the ctenidium-like structures of *Paracimex* are also diagnostic. As a routine measurement to indicate degree of incrassation of legs, the ratio of length to width of the hind femur is given in all descriptions.

Body length is perhaps the most elusive of all characters. The species and genera of Cimicidae obviously differ in size, but the abdomen is so expandable (to accommodate large blood meals) and therefore so variable in cleared and slide-mounted specimens that overall length is not very meaningful. Wherever possible, length is given both for slide-mounted and dried specimens. A fixed and easily measured indication of size is the width of the pronotum.

The size, shape, and number of chromosomes, details of which are given in Chapter 10, have proved of great value in this study. For consistency the haploid number at first metaphase is used in all the taxonomic discussions in this work. Autosome numbers range from 4 in *Primicimex, Ornithocoris,* and the *Cacodmus-Aphrania-Loxaspis* group to 18 in *Paracimex* and 19 or 20 in *Hesperocimex*. In general, the number of autosomes is constant or falls within a narrow range for each

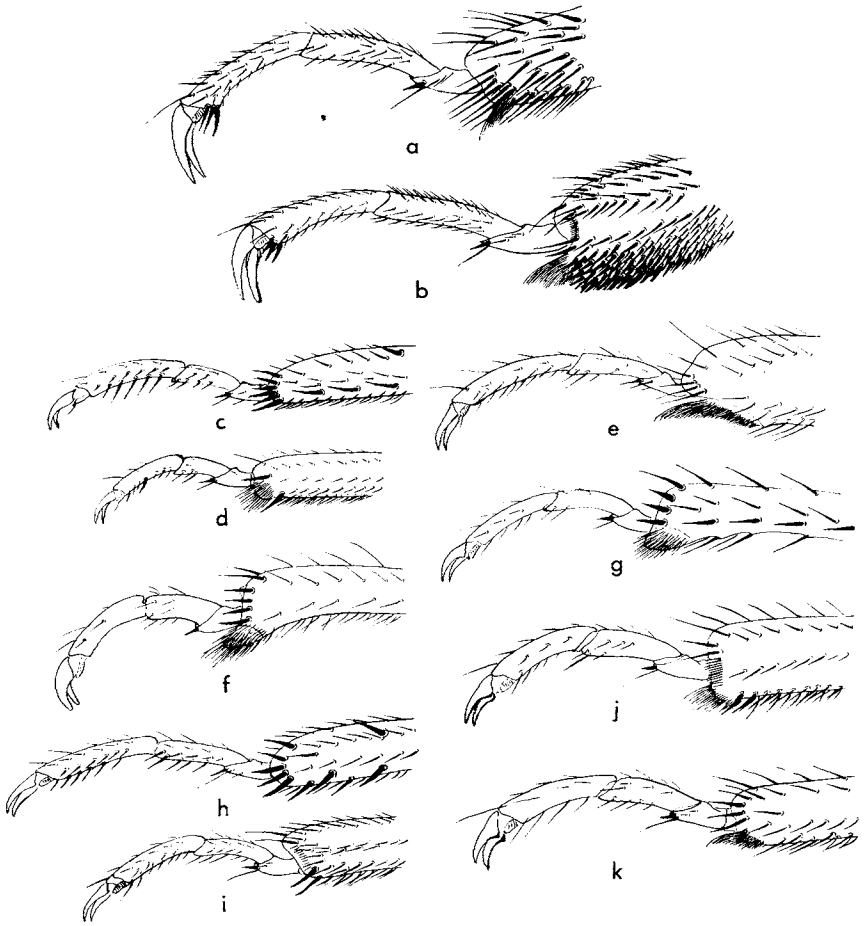

FIG. 11–36.—Apices of tibiae and tarsi of females. *Primicimex cavernis:* a, hind leg; b, front leg. *Synxenoderus comosus:* c, hind leg; d, front leg. *Paracimex caledoniae:* e, hind leg. *Oeciacus vicarius:* f, hind leg. *Oeciacus hirundinis:* g, hind leg. *Haematosiphon inodorus:* h, front leg; i, hind leg. *C. lectularius:* j, front leg; k, hind leg.

genus. Within each subfamily there is a striking trend from the low autosome number of 4A and the primitive XX-XY sex chromosome arrangement to the highest autosome number and the X_1X_2Y arrangement. Thus *Primicimex* has the primitive arrangement, *Bucimex* has a higher number of autosomes but retains the primitive sex chromosome arrangement, and the Cimicinae show a progression culminating in *Paracimex* with 18 autosomes and the X_1X_2Y mechanism. In the Cacodminae, *Cacodmus, Aphrania,* and *Loxaspis* have both primitive conditions (4A and XY); *Stricticimex* and *Leptocimex* have 11 autosomes

and the XY mechanism; and *Crassicimex* has 18 autosomes and the X_1X_2Y mechanism. Likewise in the Haematosiphoninae the trend is from the simple condition in *Ornithocoris* through higher numbers and a more complex mechanism to *Hesperocimex* with 19 or 20 autosomes and, in *Hesperocimex coloradensis,* with $X_1X_2X_3Y$. Since, in each case the sequence corresponds exactly with that derived independently from other evidence, including degree of specialization of the spermalege, the chromosomes provide important confirmation of the arrangement adopted in this work. The supernumerary X chromosomes offer still more characters. In the Lectularius Group the number of supernumerary X chromosomes is correlated with geographical distribution but reproductive isolation does not seem to have evolved. A complicated pattern of supernumerary X chromosomes exists in *Paracimex,* a situation which is under investigation at present.

Unfortunately, cimicid chromosomes are exceptionally small, but the standard technique is used, collecting in Ueshima's modification of Carnoy's fixative (3 parts pure isopropyl alcohol and 1 part glacial acetic acid) for 24 hours or more. The testes of late-instar nymphs or young adults are likely to show most active cell division. They are dissected out, stained with acetocarmine for about 24 hours and squashed on a microscope slide with a coverslip. In an emergency under field conditions isopropyl alcohol alone (obtainable in any drug store) will serve as a fixative. An important event for the completion of this study was the development of a technique for counting chromosomes of old museum specimens collected in ethyl alcohol (Ueshima 1963b), a procedure recommended for use only when fresh material cannot be obtained. The technique is as follows:

a. Dissect out testes or ovaries in alcohol, then transfer to glacial acetic acid.
b. Gently heat the acid for 10 minutes, being careful not to boil it. Remove from heat and immediately add a few drops of ferric acetate saturated in propionic acid.
c. Keep the specimen in the mixture until it has nearly reached room temperature, when the testes or ovaries usually have become soft enough for squashing. If not, heat again.
d. Transfer the specimens to acetocarmine. The next day remove from the stain, put onto a slide glass with a few drops of 45% acetic acid, cover with coverslip, and treat in the usual manner for squash preparations.

DESCRIPTIONS

Old species have been redescribed [except *Stricticimex pattoni* (Horvath), the type of which is lost] to facilitate comparison. Any inconsistencies are due to the use of different optical equipment and techniques

during a period of several years while visiting the various museums. Descriptions were nearly always made from types or type material mounted on slides. Abdominal segments are numbered according to their morphological sequence; the first segment is reduced to a median plate beneath the hemelytral pads. The first visible segment at the side of the abdomen is the second segment. An effort (not always successful) has been made to avoid mention of characters in species descriptions if they are common to all members of a genus or higher group, hence given in other descriptions in the heirarchy.

SYNONYMIES AND LITERATURE CITATIONS

For each taxonomic category the valid name, author, original reference, and full synonymy are given. At the species level, synonyms cited by others have been checked wherever possible by examining the types, and new synonymy is indicated. For all species except *C. lectularius,* the references given are reasonably complete, omitting only those publications that merely list the species and add no new information. *C. lectularius,* of course, is a special case. Extensive bibliographies have been published by Girault (1906b) and by Smart et al. (1942). It seemed unnecessary to republish this material, so references before 1942 are given only when they contain information of value on the group or point in question. The bibliographies contain hundreds of references in the fields of dermatology, disease transmission, and control that are now of historical interest only. Textbook references are ignored entirely unless, as in the case of Patton and Cragg (1913), Herms (1939), and a few others, original work is included or new nomenclatorial combinations occur. Also the numerous State and Federal bulletins (in various editions) are not cited unless they contain original information. The standard catalogues of Hemiptera (Lethierry and Severin 1896, Oshanin 1912, Van Duzee 1916, etc.) are listed under each name only if original combinations are proposed or if different endings are given for higher group names. In a few cases authors of technical papers have mentioned all of the species found in the literature up to the time of publication. Goidanich (1947) and Weidner (1958) are examples. Such references are included even though little if any new information is given. The same is true for the extensive work of Kassianoff (1937)—all parts of this ambitious work are cited except the final "tableau simplifié de classification" on p. 402 and 403. The table in question is at variance with much of the rest of the work. All genera are reduced to "espèces-types" under *Cimex* and all species are listed as "sous-espèces ou varietés."

Locality records are given as cited in the original publications or on the locality labels. Since names of countries and political boundaries are changing so rapidly, any attempt to update locality data would be of temporary use only and might actually lead to confusion. Host records

are given as originally cited, but the presently accepted names and authors are included in parentheses.

To facilitate cross reference from keys to descriptions and figures, each species is assigned a number which is used consistently for it throughout. The sequence of species given in Table 11–1 is the same as that used in Chapter 12.

12 Taxonomy of Adults

Family CIMICIDAE Latreille

Cimicides Latreille, 1802, Hist. Nat. Crust. Ins. 3: 240 (part).
Acanthilles Latreille, 1807, Genera Crust. Ins. 3: 135 (part).
Cimicida Leach, 1815, Brewster's Edinburgh Encycl. 9: 122 (part).
Cimicidae Samouelle, 1819, Entomol. Useful Compend., p. 223 (part).
Cimicites Laporte, 1833, Essai Classif. Syst. Hemip., p. 51 (part).
Cimicina Newman, 1834, Entomol. Mag. 2: 426 (part).
Lecticolae Amyot et Serville, 1843, Hist. Nat. Ins. Hemip., p. 309.
Acanthides Amyot et Serville, 1843, Hist. Nat. Ins. Hemip., p. 310.
Cimicini Costa, 1847, Cimic. Regni Neapol. Cent. 3 (7) : 160.
Cimicoideae Spinola, 1850, Tavola Sinottica, p. 39.
Cimicidea, Fieber, 1851, Genera Hydroc., p. 9.
Acanthidae Dohrn, 1859, Cat. Hemip., p. 44.
Acanthiadae Fieber, 1860–1861, Europ. Hemip., p. 24, 37, 135, 402.
Acanthiidae Costa, 1852, Cimic. Regni Neapol. Cent. 4: 67.
Acanthiini Costa, 1852, Cimic. Regni Neapol. Cent. 4: 67.
Acanthiida Stål, 1865, Hemip. Afr. 3: 24.
Acanthiina Reuter, 1871, Öfvers. Sven. Vet-Akad. Förhandl. 28: 407.
Cimicaria Populus, 1880, Cat. Hemip. Dep. l'Yonne, p. 24.
Cimicini Puton, 1886, Cat. Hemip. Palae., 3rd ed., p. 42.
Acanthiinae Comstock, 1888, Introd. Entomol., p. 204.
Cimicidi Acloque, 1897, Faune de France 2: 358, 392.
Cacodmidae Kirkaldy, 1899b, Bull. Liverpool Mus. 2: 45.
Cacodminae Kirkaldy, 1902, Fauna Haw. 3 (2) : 129.
Clinocoridae Kirkaldy, 1906, Trans. Amer. Entomol. Soc. 32: 147.
Clinocorina Reuter, 1908, Entomol. Mon. Mag. 44: 27.

Body form oval or elongate-oval, flattened or subflattened above. Surface more or less beset with bristles which may be serrate at sides and serrate, cleft, or acute at tips.

Head without ocelli. Clypeus usually widened apically. Labrum usually short and wide. Eyes ¼ to ⅛ as wide as interocular space. Antennae 4-segmented, the last 2 segments slender. Rostrum 3-segmented.

Pronotum transverse to subquadrate, with front margin more or less concave to receive the head. Sides depressed and lamellate in some, scarcely so in others.

Mesonotum-scutellum triangular or subrectangular.

Metapleural scent glands opening on an evaporating area. Mesosternum and metasternum without longitudinal suture.

Hemelytra reduced to pads which are variously shaped. Hind wings absent.

Abdomen in nymphs with 3 dorsal scent gland openings at hind margins of third, fourth, and fifth segments. Adults with first tergite forming a broad plate beneath hemelytral pads but not reaching lateral margins. Sides of abdomen without distinct

paratergites (connexivum). Spiracles ventral. Male paramere well developed on right side, directed to the left, grooved for the reception of aedeagus. Left paramere absent. Female with a spermalege (except *Primicimex*) of ectodermal and mesodermal tissue. Fertilization by traumatic insemination through the hemocoel.

Legs stout or slender, the tibiae with or without apical tufts. Tarsi of adults 3-segmented, with a pair of claws that lack arolia. Tarsi of nymphs 2-segmented.

Color ochraceous to fulvous with a few species darker brown, appendages usually paler. A few (*Hesperocimex*) with distinctive color pattern.

Size from 3 to 13 mm.

Type-genus: *Cimex* L.

The principal works on higher classification of the Cimicidae are Stål (1873), Jordan and Rothschild (1912), Reuter (1913b), Kassianoff (1937), and Weidner (1958). Lethierry and Severin (1896) cataloged the species known at that time.

Regional works include Horvath (1910b), Wendt (1941a), and Stichel (1959) (Europe); Southwood and Leston (1959) (British Isles); Usinger (1960) (Egypt); Distant (1904) (India); Horvath (1912), Usinger (1939) (North America); Champion (1900) (Central America); Costa Lima (1940) (Brazil); and Wygodzinsky (1951) (Argentina). Jaczewski (1962) reviewed the status of family-group names for *Cimex* and proposed that Cimicidae be placed on the official List of Family Group Names in Zoology.

KEY TO THE SUBFAMILIES OF CIMICIDAE

1. Tibiae mottled. Tarsi with several stout spines at inner apex in apposition to claws. Labrum over twice as long as wide. Size large, unexpanded specimens mostly over 7 mm long. Western Hemisphere. Bats. . . . . **Primicimicinae** (p. 294)

   Tibiae not mottled. Tarsi without stout spines in apposition to claws. Labrum short and broad. Size usually less than 7 mm in unexpanded specimens. 2

2. Bristles at sides of pronotum minutely serrate on outer sides or, rarely, only at obliquely truncate tips. Females with paragenital sinus always ventral. Metasternum commonly forming a flat plate between coxae. Worldwide. Bats, birds, or man. . . . . **Cimicinae** (p. 301)

   Bristles at sides of pronotum not minutely serrate on outer sides or at oblique tips, minutely cleft at tips or acute. Females with paragenital sinus usually dorsal, rarely ventral or absent. Metasternum a rounded lobe more or less compressed between coxae. 3

3. Middle and hind tibiae with fine bristles which may be short or very long but never with additional short, stout, spinelike bristles. African and Oriental Regions. 4

   Middle and hind tibiae with short, stout, spinelike bristles as well as finer bristles. Western Hemisphere. 5

4. Tibiae bent subapically. Paragenital sinus dorsal and on females only, rarely lacking. African and Oriental Regions. Bats and man. . . . . **Cacodminae** (p. 389)

   Tibiae straight. Paragenital sinuses large, left-ventral near base of abdomen in both sexes. Africa. Bats. . . . . **Afrocimicinae** (p. 451)

5. Hemelytral pads folded downward at sides. Paragenital sinuses right-ventral near base. Neotropical Region. Fish-eating bats (*Noctilio*). . . . . **Latrocimicinae** (p. 458)

Hemelytral pads not folded downward at sides. Paragenital sinus right-ventral near lateral margin of sixth or seventh abdominal segment. Nearctic and Neotropical Regions. Birds..... **Haematosiphoninae** (p. 461)

Subfamily PRIMICIMICINAE Ferris and Usinger

Primicimicinae Ferris and Usinger, 1955, *in* China and Miller, Ann. Mag. Nat. Hist. (12) 8: 263.
Primicimicinae, Miller, 1956, Biol. Heterop., p. 8, 120.
Primicimicinae, Povolný, 1957, Folia Zool. 6 (20) : 62.

Large (7 mm or more in unexpanded state). Head with a long bristle behind each eye. Clypeus widened a little beyond base, then narrowed to subtruncate apex. Labrum long and slender, more than twice as long as wide. Rostrum short, not or scarcely reaching base of head. Pronotum with long lateral bristles which are serrate at outer sides and cleft or serrate at tips. Scutellum well developed, subtriangular. Hemelytral pads large and subrounded, with hairs laterally on under surface. Metasternum lobe-like and somewhat compressed between middle coxae. Front and middle tibiae with small apical tufts. All tibiae with bristles of uniform type and with pale spotting (mottled) between areas of insertion of bristles. Tarsi with several stiff bristles at apex in apposition to claws. Female second gonocoxae as separate elongate lobes, not fused with lateral plates of ninth segment. Male basal plates joined by a strong bridge, forming a yoke with a hole in the center.

Type-genus: *Primicimex* Barber.

This subfamily contains 2 very different genera, both associated with bats in the Western Hemisphere. *Primicimex* is the most remarkable of all Cimicidae, being larger than other species and possessing many unique and probably primitive characters. Aside from the distinctive external characters mentioned in the descriptions and keys, it is unique among Cimicidae in lacking mycetomes and a spermalege (Carayon 1954b). It is known only from bat caves in Texas and Guatemala.

Bucimex in many ways bridges the gap between *Primicimex* and the Cimicinae. In external characters it resembles *Primicimex,* but it has mycetomes and a well-developed ventral spermalege. Both genera have serrate bristles like those in some Cimicinae. *Bucimex* occurs in southern Chile on bats that roost in trees.

KEY TO THE GENERA OF PRIMICIMICINAE

1. First antennal segment exceeding apex of head, as long as second segment. No paragenital sinus or ectospermalege but, in cleared specimens, usually with a transverse pigmented area between fifth and sixth abdominal tergites on left side. Length 10–13 mm. Texas and Guatemala..... ***Primicimex***
First antennal segment much shorter than second. Paragenital sinus and ectospermalege well developed between fourth and fifth ventral segments on right side. Length 6.8–9.6 mm. Chile..... ***Bucimex***

Genus *Primicimex* Barber

Primicimex Barber, 1941, J. Wash. Acad. Sci. 31 (7) : 315.

Size 10–13 mm (dry vs. slide-mounted). Bristles dense over most of body, those of sides of pronotum and hemelytral pads of about equal length.

Head longer than wide, 55:47, much wider subbasally than across interocular space, 43:34; head bristles dense on clypeus and on either side of clypeus, extending back of middle of vertex; naked at base and on either side to inner margins of eyes, with 1 very long bristle on each jugum and another just behind each eye. First antennal segment thick and long, subequal to width of interocular space; second segment as long as first, thick; third and fourth segments slender, the third longest, fourth shortest.

Rostrum short, reaching to middle (slide-mounted) or base (pinned) of head, third segment less than half as long as second.

Pronotum nearly twice as wide as long, with sides strongly depressed and impressed submarginally, anterior angles only moderately produced, hind margin broadly, shallowly concave; disk impunctate except for small points of insertion of bristles.

Mesonotum unique among the Cimicidae, subtriangular like the scutellum of other Hemiptera, ⅜ as long as wide, prominently raised with apex rounded, disk with long bristles.

Hemelytral pads nearly or quite as long as wide, nearly round behind; lateral margins a little reflexed, not bent around metathorax at base; disk deeply, densely, coarsely punctured and densely beset with bristles; under surfaces with long, fine bristles laterally.

Legs long, front femora narrowed subbasally, all femora narrowed slightly subapically. Tibiae mottled, long and broadly curved. Tarsi long, with 2 stiff bristles at apex of short first segment and 3 or 4 stout spines in a clump at apex of last segment in apposition to base of claws.

Male genital segment bent to the left, the paramere exceeding lateral margin. Female without a paragenital sinus or ectospermalege, the place of entry of paramere more or less fortuitous but most often marked (in cleared specimens) by a transverse pigmented area between fifth and sixth abdominal tergites on left side.

Type-species: *Primicimex cavernis* Barber.

Primicimex is known only from Ney Cave near Bandera, Texas, and from a cave near Chocoyos, Chimaltenango, Guatemala. The Mexican free-tailed bat, *Tadarida mexicana* (Saussure), is found in both caves and may be the host.

1. ***Primicimex cavernis*** Barber

(Fig. 12–1)

Primicimex cavernis Barber, 1941, J. Wash. Acad. Sci. 31 (7) : 315–317.
Primicimex cavernis, Kohls and Jellison, 1948, Nat. Speleological Soc. Bull. 10: 117.
Primicimex cavernis, Usinger, 1950, *in* Herms, Med. Entomol., 4th ed., p. 99.
Primicimex cavernis, Sailer, 1950, Proc. Entomol. Soc. Wash. 52: 308.
Primicimex cavernis, Sailer, 1952, Pest Control Mag. 20 (10) : 22, 27, 70, 72, fig.
Primicimex cavernius, Carayon, 1954b, Compt. Rend. Acad. Sci. 239: 1542–1544.
Primicimex cavernis, Ryckman, 1956, Amer. Midland Nat. 56: 187.
Primicimex cavernis, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 25.
Primicimex cavernius, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 95.

Female.—Head 1.34 mm wide; $^1/_7$ longer than wide, 54:47; interocular space 6 times as wide as an eye, 35:6. Antennae 4.37 mm long; proportion of segments (including pseudojoints) 37:37:49:30; first segment slightly longer than interocular space. Rostrum (dried specimen) reaching to base of head; length 1.31 mm; proportion of segments 17:20:9.

Pronotum 2.23 mm wide; ratio of length to width, 47:78; sides evenly arcuate, front margin shallowly concave, anterolateral angles briefly produced; longest bristles at sides

about 0.43 mm, dense; discal bristles shorter but numerous. Mesonotum (scutellum) almost completely exposed in slide-mounted specimens; ¼ wider at base than long; sides subparallel at base, then converging to blunt apex.

Hemelytral pads contiguous, appearing as large subrounded flaps which partially overlap in dried specimens and may just meet in slide-mounted specimens; as long as wide, hind margin rounded; bristles much as on pronotum.

Female with eighth segment gonapophyses distinctly lobulate, reaching halfway to tip of abdomen; ninth segment gonocoxae elongate, not fused with ninth paratergites.

Hind femora 8 times as long as greatest thickness; hind tibiae ⅓ longer than femora.

Male.—Genital segment over half as long as wide, 28:48; total length of paramere ¾ the width, 38:48; paramere exceeding left side of segment. Basal plates joined to form a stout yoke with a hole in middle.

Size.—Male, length 10.57 mm, width (pronotum) 2.14 mm, (abdomen) 5 mm; female, length 12.3 mm, width (pronotum) 2.23 mm, (abdomen) 5 mm.

Redescribed from slide-mounted male and female paratypes, Ney bat cave, Medina Co., Texas, Sept. 14, 1940 (Kohls and Jellison). The types are in the U. S. National Museum. Also at hand are a slide-mounted female paratype from the same series as above and a dried point-mounted paratype with the same data as above. Drs. G. M. Kohls and W. L. Jellison kindly sent additional material from the Rocky Mountain Laboratory at Hamilton, Mont. Also from Ney Cave is a paratype collected on Feb. 5, 1939 (K. E. Stager).

In addition, many nymphs and adults are at hand from the same locality, "Ney Cave, Texas, July 13, 14, 1954" (R. E. Ryckman, C. P. Christianson, and Dean Spencer). Another large collection was taken June 30, 1955 (R. E. Ryckman, D. Spencer, and K. C. Fisher).

Ryckman (1956) writes details concerning the 1954 collection: "The Ney Cave is located ten miles southwest of Bandera and contains a very high population of the Mexican free-tailed bat, *Tadarida mexicana* . . . . The temperature was relatively high in this cave, that is, 86°F. inside the entrance and 91°F. in the central portion of the cave. *Primicimex* . . . was readily collected on the floor and walls; eggs and miniature instars were usually found in small crevices in the rock walls and ceiling. Feeding was observed on bats clinging to the ceiling and later on bats anesthetized with sodium nembutal. *Primicimex* repeatedly strikes the prospective host with its front legs and proboscis until no twitching or response is registered by the bat. Then the bug lunges forward and grasps a section of the folded wing or leg of the bat with its fore legs and starts to feed."

On Aug. 27, 1957, R. E. Ryckman again visited the cave and found no living bugs. He writes: "Hatched eggs and dead bodies of *Primicimex* were still recoverable when pieces of broken rock were chipped away. It would seem quite possible that someone may have sprayed this cave with a residual insecticide . . . and that this colony . . . may have been completely destroyed."

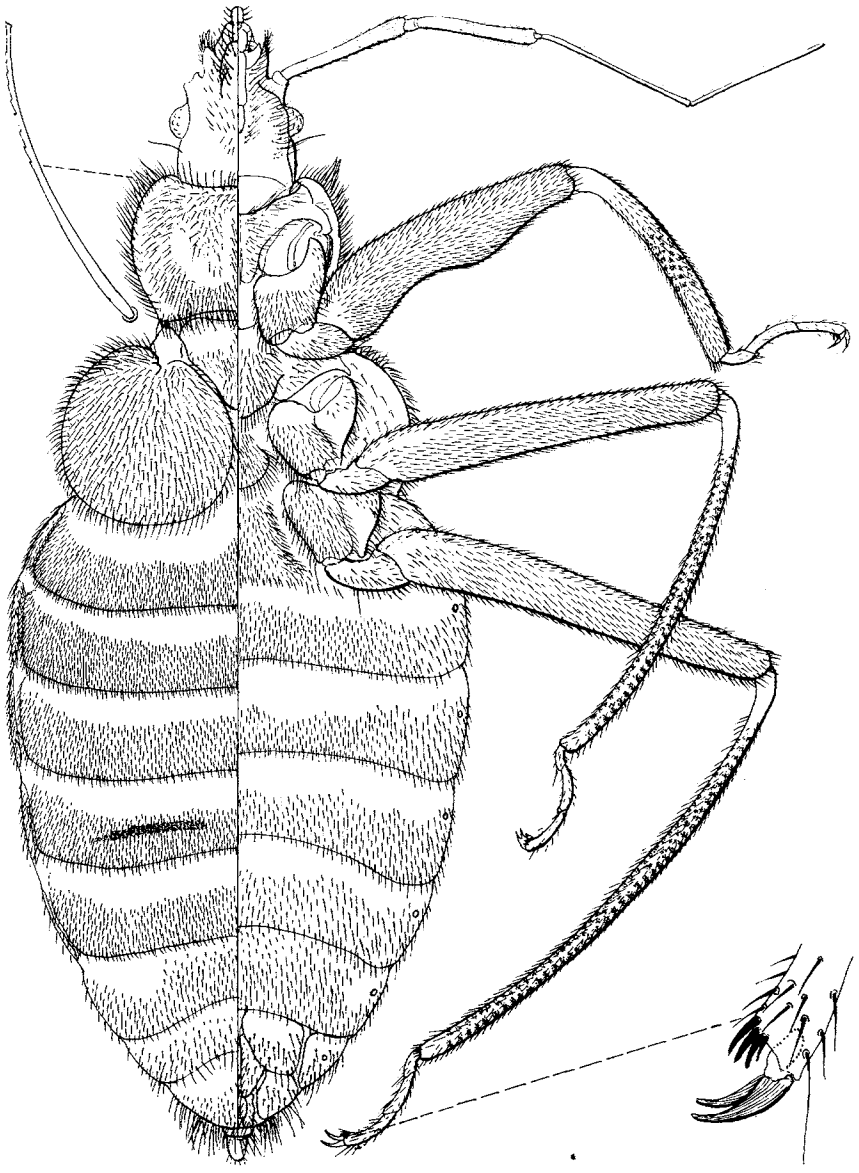

FIG. 12–1.—*Primicimex cavernis* Barber. Female paratype. Ney Cave near Bandera, Texas (Ferris, original).

A second locality was reported by Sailer (1950). It is a cave near Chocoyos, Chimaltenango, Guatemala, April 28, 1948 (R. L. Wenzel and R. Mitchell). Mr. Luis de la Torre writes that "the exact locality of the Chocoyos cave is . . . on the main highway between Guatemala City and Panajachel, 4 miles northwest of the village of Patzun." The elevation is about 5000 ft. Both *Tadarida brasiliensis mexicana* Saussure and *Myotis velifer velifer* (Allen) were found in the cave. A second Guatemala record is a single female in the U.S. National Museum bearing the label "Yepocapa, Guatemala, May, 1948 (H. T. Dalmat)."

Genus ***Bucimex*** Usinger

Bucimex Usinger, 1963, Pan-Pacific Entomol. 39: 51.

Size 6.8 mm (dried) to 9.6 mm (slide-mounted). Body suboval, flattened above. Bristles dense and long, the individual bristles curved, minutely notched at tip and serrate on outer side.

Clypeus not widened anteriorly, the sides subparallel. Labrum over twice as long as wide, gradually tapering to rounded tip. A prominent bristle behind each eye. Antennae about half again as long as width of pronotum; second segment 3 times as long as first, 1/8 longer than third; fourth 2/3 as long as third. Rostrum short, reaching only to base of head or a little onto prosternum.

Pronotum transverse; disk convex at middle, depressed sublaterally; sides rounded. Hemelytral pads broadly suboval, with bristles on undersides as well as above. Metasternum not platelike, forming a subrounded lobe between middle coxae.

Spermalege located ventrally between fourth and fifth segments on right side, the ectospermalege saclike, longer than wide, extending forward from narrow paragenital sinus at intersegmental membrane.

Legs with hind femora 4 times as long as wide. Tibiae with mottled markings, front and middle pair with small but distinct apical tufts in both sexes. Tarsi with 3 stout spines at inner apex of third segment in apposition to claws.

Type-species: *Bucimex chilensis* Usinger.

Bucimex is related to *Primicimex* in the large size, short rostrum, narrow clypeus, long slender labrum, long, fine, serrate bristles, suboval hemelytral pads, separate second gonocoxae, strongly fused basal plates, mottled tibiae, and stiff spines at inner apex of third tarsal segment. Also there is a long lone bristle behind each eye in both of these genera. On the other hand, *Primicimex* lacks a spermalege and usually receives sperm between the fifth and sixth tergites on the left side, there being a transverse pigmented area at that point. *Bucimex* differs radically in having a distinct sclerotized ectospermalege between the fourth and fifth ventral segments on the right side. The organ is saclike, enlarged apically, and bent toward the middle of the body. The mesospermalege is very large and saclike, exceeding the size of an ovary. Also *Bucimex* possesses a pair of mycetomes situated in the middle of the fat tissue near the dorsal membrane of the abdomen at the level of the fifth abdominal segment. *Primicimex* is unique among the Cimicidae in lacking discrete mycetomes. In *Bucimex* the chromosome number is 13 + XY (1st metaphase, n ♂).

This is close to certain colonies of *C. lectularius*. The chromosome number of *Primicimex* is 4 + XY.

2. ***Bucimex chilensis*** Usinger
(Fig. 12–2)

Bucimex chilensis Usinger, 1963, Pan-Pacific Entomol. 39: 52.

Female.—Head as long as wide, 1.05 mm, eyes less than ⅓ width of interocular space, 2:6, small and round in outline; sides of clypeus subparallel, a little sinuate, apex truncate; sides of head narrowed immediately behind eyes and then widened near base; clypeus beset with long, erect bristles except on either side of base, the rest of head smooth and without bristles except adjacent to clypeus and forward near anterior margins of eyes to antenniferous tubercles; postocular area with 1 prominent bristle behind each eye. Antennae 3.3 mm; proportion of segments 8:24:21:14. Rostrum short, reaching only to base of head in slide-mounted specimens (attaining apex of prosternum in dried specimens), proportion of segments 6:10:5.

Pronotum 2.1 mm wide, about twice as wide as long at middle; disk convex, rough and beset with long bristles, depressed sublaterally and narrowly before hind margin; margins thickened and slightly reflexed; lateral margins evenly arcuate; anterior angles rounded, anterior margin roundly emarginate behind head; disk glabrous along 2 vertical pale marks at middle and laterad at about basal fourth; lateral bristles very long, about as long as first antennal segment, 0.4 mm.

Scutellum more than half as wide as pronotum, 24:42; exposed part in slide-mounted specimens about half as long as wide; disk smooth or minutely granular on semilunate yellow areas on either side of middle; the middle brown, feebly punctured, and with some bristles; posterior and lateral areas dark brown to black, coarsely rugose and beset with longer bristles; apex moderately swollen or inflated; lateral margins constricted at apical third.

Hemelytral pads transversely suboval, nearly straight at contiguous inner margins, broadly, evenly rounded posterolaterally, the articulations at sides of scutellum smooth, conspicuous, yellow; length 1.3 mm; ratio of length to width 26:35; disk coarsely punctured and beset with long bristles, anterolateral margin thick, the disk depressed submarginally.

Abdomen widened above; ratio of width across fourth segment: hemelytral pads: pronotum: head including eyes 88:70:42:22; hind margins of segments sinuate, thin, translucent; disk rugosely punctate and with numerous erect bristles; fifth, sixth, and seventh segments each with 2 pale spots at middle, possibly corresponding to paired nymphal scent gland openings, though the latter are at anterior margin of each segment, whereas pale spots in adults approach middle of each segment.

Under surface with many bristles; prosternum not produced as a point between front coxae; mesosternum with hind margin thickened and arcuate; metasternum a somewhat inflated lobe, separating middle coxae by a distance approximately equal to width of a coxa.

Female genital segments consisting of lateral spiracle-bearing eighth paratergites, 2 sublateral gonocoxal plates, and 2 elongate first gonapophyses of eighth segment. Behind this are 2 ninth-segment paratergites, 2 separate elongate second gonocoxae that are slightly inflated apically and densely beset with long bristles, and a pair of second gonapophyses.

Legs rather long and slender; hind femora 2.8 mm long, 4 times as long as wide, 56:14; hind tibiae ¼ longer than femora, 80:56, distinctly curved and mottled on apical half. Hind tarsi ⅓ the length of tibiae, the second and third segments subequal, third segment with 3 stout spines on inner apex, claws angulately produced sub-basally.

Male.—Genital segment slightly wider across base than long, 28:24, bent slightly to left; paramere as long as segment, curved and slightly sinuate at tip, tapering gradually

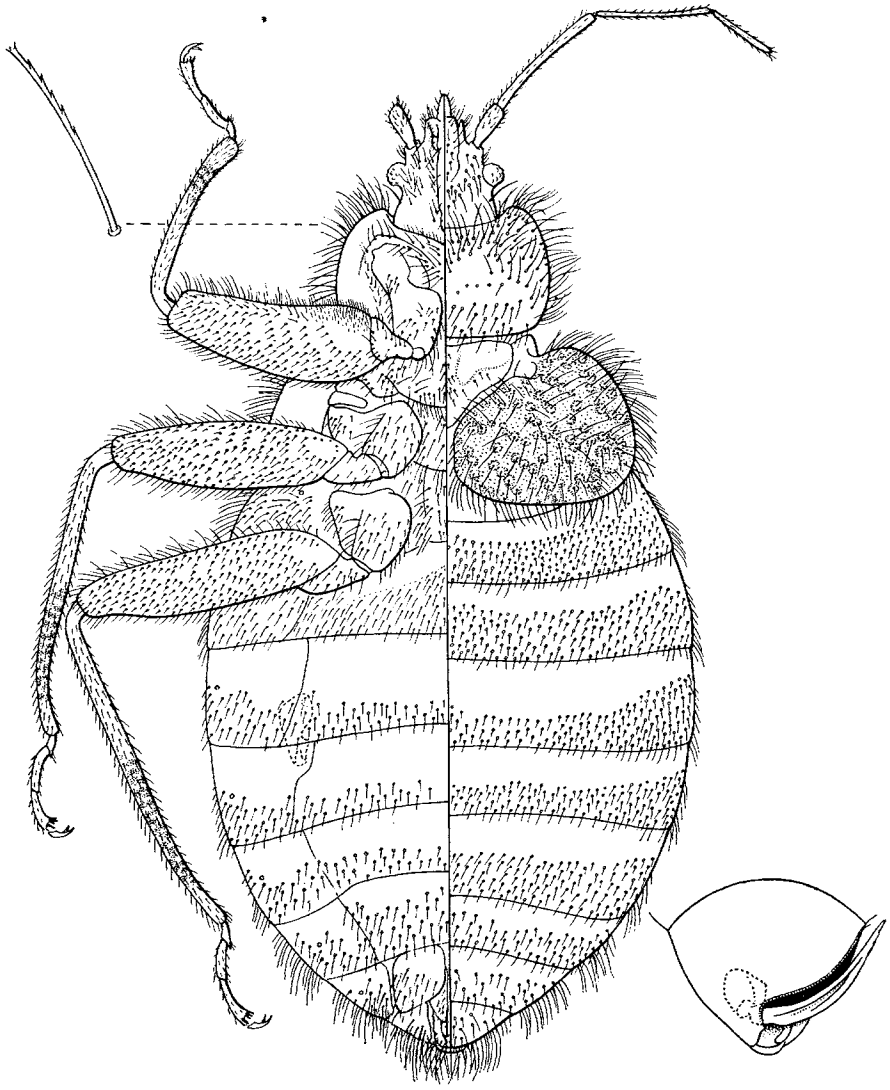

FIG. 12–2.—*Bucimex chilensis* Usinger. Female and male genital segment. Paratypes, Lonquimay, Malleco, Chile (Usinger 1963).

to acute apex which reaches an open pocket at left side of asymmetrical eighth segment. Basal plates asymmetrical and joined by a prominent bridge.

Size.—Female, length (slide-mounted) 8.6 mm, width (pronotum) 2.05 mm; male, length 9.6 mm, width (pronotum) 2.15 mm; female (dry, pinned), length 6.8 mm, width (pronotum) 2.15 mm.

Holotype female, 10 km south of Lonquimay, Malleco, Chile, Jan. 11, 1962 (R. L. Usinger); allotype male, same data as holotype; paratypes, 12 specimens, same data as type, and 6 males and several nymphs near Dalcahue, Chiloe I., Chile, Jan. 22, 1962 (R. L. Usinger). Nymphs only were taken at Tolhuaca, Malleco, Chile, Jan. 11–25, 1959, and Dalcahue, Chiloe I., Chile, Feb. 10–12, 1954, by Luis E. Peña. The holotype is in the U. S. National Museum.

At Tolhuaca in 1959 Luis Peña found small nymphs in the hollow trunk of an Araucaria tree in a dense moist forest of tall trees. These specimens were associated with the bat *Myotis chiloensis chiloensis* (Waterhouse). Unfortunately, local inhabitants of the region built a fire in the hole and destroyed the colony. Near Lonquimay in 1962 a hollow *Nothofagus* tree was found with bats present and bugs hiding in cracks inside the hollow trunk. Near Dalcahue bats and bugs were found beneath a piece of loose bark of a large *Nothofagus* tree. The area had been burned several years earlier and the open type of country was quite dry. Nymphs, adults, cast skins, and eggs were found in a compact cluster about 15 ft from the ground. A third collection was made beneath loose bark of a *Nothofagus* tree about 25 km north of Dalcahue. Under bark near the latter place the bat *Histiotus montanus magellanicus* (Philippi) was taken.

Subfamily CIMICINAE Latreille

Cimicides Latreille, 1802, Hist. Nat. Crust. Ins. 3:240 (part).
Clinocorinae Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Cimicinae Van Duzee, 1916, Check List Hemip. Amer. N. Mex., p. 33 (part).

Head with numerous bristles on clypeus, juga, and middle of vertex, and with bristles along inner margin of eyes extending backward and inward. Head wider than long or subequal. Antennae with first segment stout and short, second thick and nearly as long or longer than third, third and fourth slender or fusiform and nearly as thick as second, the last segment subequal to or shorter than third. Rostrum reaching about to middle of prosternum or longer, the segments subequal.

Pronotum more or less flattened at sides and produced forward behind eyes, with lateral bristles curved and serrate or cleft at tips and usually serrate also on outer sides.

Metasternum forming a platelike lobe between middle coxae, lobe rarely somewhat compressed. Legs moderately stout; tibiae usually with well-developed apical tufts in both sexes on all legs, without mottling or pseudojoints. Tarsi without stiff bristles in apposition to claws at apices.

Spermalege ventral, opening between fifth and sixth or sixth and seventh segments.

Type-genus: *Cimex* L.

This is the commonest and most widespread subfamily, consisting of the genus *Paracimex* on *Collocalia* birds in southeast Asia; *Bertilia* and *Propicimex,* probably both on bats in South America; and the closely related *Oeciacus* and *Cimex,* the former exclusively on swallows in the Holarctic region and the latter on a great variety of hosts throughout the world but primarily on bats, pigeons, and man.

KEY TO THE GENERA OF CIMICINAE

1. Front and middle femora each with a row of short, stout spines (ctenidium) subapically. Ectospermalege in the form of a forwardly-directed, usually tubular extension of anterior margin of sixth ventral segment. Southeast Asia. Cave swiftlets (*Collocalia*).....***Paracimex***
   Front and middle femora without a subapical row of short, stout spines. Female with ectospermalege as a transverse thickening of anterior margin of sixth or seventh ventrite..... 2
2. Pronotum over twice as wide as head. Hemelytral pads with hind margins concave. Tibiae with serrate bristles on outer sides. Southern Chile and Argentina. .....***Bertilia***
   Pronotum less than twice as wide as head. Hemelytral pads with hind margins convex. Tibiae with simple bristles on outer sides..... 3
3. Metasternum partially compressed between coxae. Bristles at sides of pronotum serrate only at obliquely truncate tips. Female seventh ventrite produced forward, conelike, into sixth at middle, the ectospermalege at middle of anterior margin of sixth segment. Neotropical Region. Bats.....***Propicimex***
   Metasternum a broad, discrete plate between coxae. Bristles at sides of pronotum more or less serrate on their convex sides. Female fifth ventrite cleft or emarginate on right side, the ectospermalege on anterior margin of sixth segment at right..... 4
4. Body clothed with pale hairlike bristles. Second antennal segment ⅔ or less as long as interocular space. Pronotum less than 1½ times as wide as head. Holarctic Region. Swallows.....***Oeciacus***
   Body with shorter, thicker bristles. Second antennal segment subequal to interocular space. Pronotum 1½ or more times as wide as head. Holarctic Region on bats, cosmopolitan on man and domestic animals.....***Cimex***

Genus ***Bertilia*** Reuter

Bertilia Reuter, 1913a, Wien. Entomol. Zeitung 32: 237.
Bertilia, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 361.
Bertilia, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Bertilia, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Bertilia, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 18.
Bertilia, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 193.

Size 4.7 (pinned) to 7.5 mm (slide-mounted). Surface densely punctured. Color reddish brown. Bristles short and dense over entire body, the individual bristles thick, wide, and serrate.

Head wider than long, 36:29; approximately 1 mm wide across eyes; eyes strongly exserted, ¼ as wide as interocular space; clypeus about half as wide anteriorly as interocular space; bristles covering most of upper surface, with subcircular bare areas following vaguely the ecdysial lines and then, with interruptions, curving inward near eyes. Antennae long and slender, a little longer than width of pronotum; second

segment slightly longer than interocular space; third segment longest; fourth shorter than second. Rostrum (slide-mounted) reaching only to middle of prosternum; second segment attaining base of head.

Pronotum over twice as wide as head; 2½ times as wide as long; sides broadly lamellate, appearing as laterally elevated plates with sinuate edges; bare areas on convex median disk forming a vaguely vermiculate pattern.

Mesonotum-scutellum broadly exposed, triangular, rugose with many bristles. Metasternum slightly compressed between middle coxae, appearing as a posteriorly widening rounded lobe. Scent gland evaporating canal curved around outer margin of metapleuron.

Hemelytral pads strongly transverse, twice as wide as long, contiguous only briefly just behind scutellum, then with inner margins widely divergent; hind margins shallowly concave.

Legs long and slender; hind femora 5 times as long as broad; hind tibiae ⅓ longer than femora, straight. Tibial tufts inconspicuous and seen only on front and middle legs of male. Outer edges of tibiae with serrate bristles.

Female ectospermalege ventral between sixth and seventh segments; hind margin of sixth segment deeply, roundly emarginate at middle.

Male genital segment strongly asymmetrical to the left, the paramere reaching beyond middle.

Type-species: *Acanthia valdiviana* Philippi.

This genus is known only from southern South America (Chile and Argentina). The host is not known. It is related to *Cimex* but differs in the position of the spermalege, in the greatly expanded pronotum, the unique shape of hemelytral pads, and especially in the broad, serrate bristles.

3. ***Bertilia valdiviana*** (Philippi)
(Fig. 12-3)

Acanthia valdiviana Philippi, 1865, Stett. Entomol. Z. 26: 64.
Cimex valdivianus, Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 104.
Cimex valdivianus, Lethierry and Severin, 1896, Cat. Gen. Hemip., p. 236.
Acanthia valdiviana, Reed, 1901, Rev. Chil. Hist. Nat. 5: 92.
Cimex valdivianus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 260.
Bertilia valdiviana, Reuter, 1913a, Wien. Entomol. Zeitung 32: 237.
Bertilia valdiviana, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 361.
Bertilia valdiviana, Horvath, 1914, IX[e] Int. Congr. Zool., p. 295.
Cimex valdivianus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 317.
Bertilia valdiviana, Wygodzinsky, 1950, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (1) : 119.
Bertilia valdiviana, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 193.
Bertilia valdiviana, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Bertilia valdiviana, Ronderos, 1961, Notas Mus. La Plata 20: 34.

Female.—Head 1 mm wide; ratio of length to width 29:36; ratio of eye width to interocular space 6:23. Antennae 2.37 mm long; proportion of segments 7:25:30:21. Rostrum 0.88 mm long; proportion of segments 10:9:12.

Pronotum 2.11 mm wide; ratio of length to width 29:74; anterior lobes broadly rounded, hind margin sinuate sublaterally.

Exposed part of scutellum about twice as wide as long, the apex subacute.

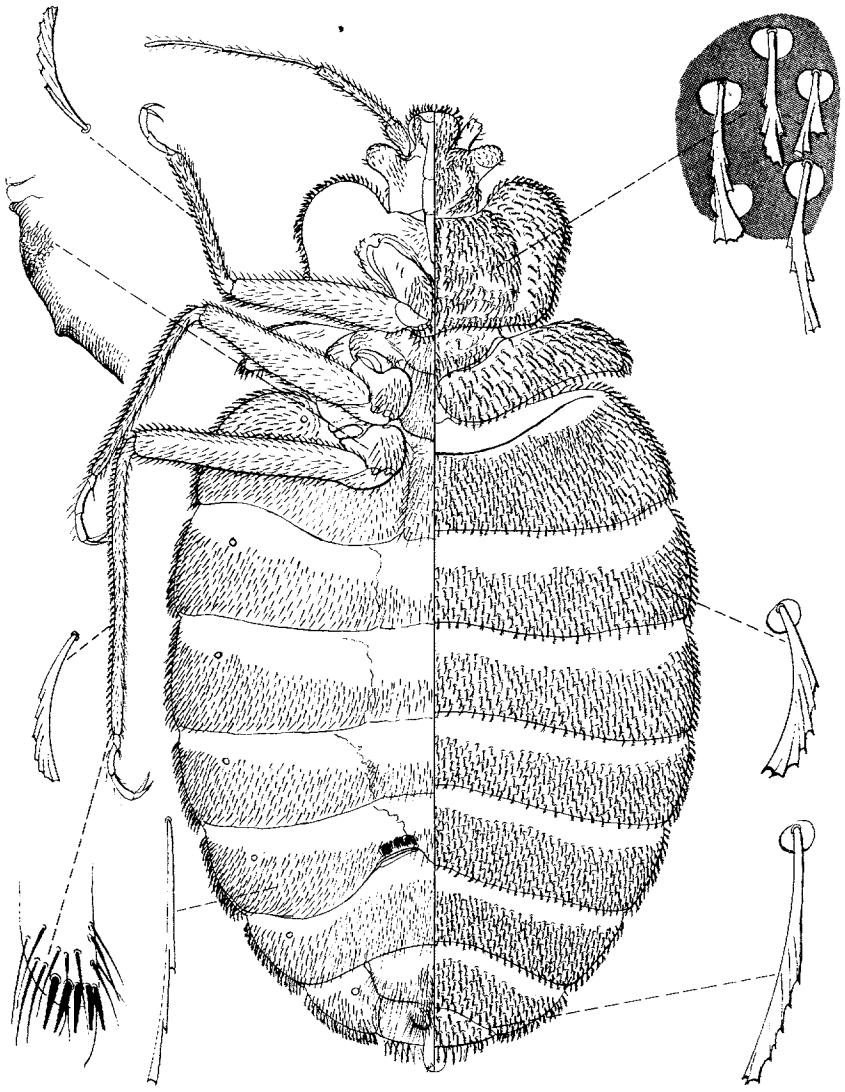

FIG. 12-3.—*Bertilia valdiviana* (Philippi). Female. Bariloche, Argentina (Ferris, original).

Hemelytral pads each over twice as wide as long, 50:22; total width to narrowly rounded lateral margins of both pads 2.85 mm.

Abdomen with bristles at sides and on disk short and dense, 7 or 8 ill-defined rows on all tergites except the second, the latter with basal bristles much more dense.

Legs with normal tapering bristles on inner sides and broad serrate bristles on outer sides.

Under surface of body also with fine tapering bristles.

Male.—Paramere reaching ⅔ distance from apex of genital segment back along left margin to base, tapering and curved.

Size.—Male, length 7.43 mm, width (pronotum) 2.05 mm, (abdomen) 3.5 mm; female, length 7.71 mm, width (pronotum) 2.11 mm, (abdomen) 4.1 mm.

Redescribed from a male and female, Lago Trebol, San Carlos de Bariloche, Rio Negro, Argentina, Nov. 23, 1950 (P. Wygodzinsky). A female (presumably the type) and nymph are in the Helsinki Museum received by Reuter from Carlos Berg. There is also a female in the Vienna Museum labeled "Chile, Coll. Signoret" and "Acanthia valdiviana Phil. Valdivia, Chile. Berg." Material before me includes a female, Cordillera de Pemehue, Prov. Malleco, Chile, 1800 m (W. Kuschel); a male, Rinihue, Valdivia, Jan.-Feb. 1948 (L. E. Peña); and a male, Crest of Sierra Nahuelbuta, W. of Angol, Chile, Jan. 3, 1951 (E. S. Ross, A. E. Michelbacher). Wygodzinsky (1951) figures the egg and nymphs of this species. Philippi and Ross and Michelbacher record the species from under bark. Wygodzinsky and Kuschel took their specimens under stones. No vertebrate host has been found associated with the bugs.

There is considerable variation, especially in size, in the few specimens before me. The Ross and Michelbacher male has the pronotum 1.7 mm wide; the Peña male is 1.8 mm. In the Kuschel female the pronotum is 1.9 mm wide. The Bariloche male and female are over 2 mm. In the latter the hind femora are over 5 times as long as wide whereas they are less than 5 times as long as wide in the Chilean specimens.

Propicimex, new genus

Size 5.5 (alcohol preserved) to 7.25 mm (slide-mounted). Surface densely, finely punctured. Bristles short, rather evenly and densely covering dorsum, those at sides of pronotum serrate only at or near apex.

Head a little less than ½ again as wide as long; eyes large, ¼ as wide as interocular space; clypeus wide, ½ as wide as interocular space, truncate at apex; bristles short and evenly spaced over upper surface of head except at base and along 2 pale anteriorly convergent lines near eyes. Antennae longer than width of pronotum; second segment longest, equal to width of interocular space; third segment shorter; fourth still shorter. Rostrum reaching front coxae, the segments subequal.

Pronotum about twice as wide as long but much less than twice as wide as head; sides relatively narrowly flattened and evenly arcuate; disk with a mottled appearance.

Mesonotum-scutellum subtriangular, with small bristles. Scent gland peritreme expanded posterolaterally beyond edge of metapleuron. Metasternum narrowly compressed between middle coxae, a little wider posteriorly.

Hemelytral pads ⅔ as long as wide, the sides arcuate and hind margins nearly straight.

Legs short and stout, the hind femora 3 times as long as wide; hind tibiae ¼ longer than femora; all tibiae bent subapically, the hind pairs with vague indication of a pseudojoint; all tibiae with apical pads in both sexes.

Females with spermalege (in cleared specimens) visible as a sclerotized area at middle of suture between fifth and sixth ventrites; sixth segment bent strongly forward and seventh segment extending far forward into it.

Male paramere very short and thick, not exceeding middle of left side of genital segment.

Type-species: *Cimex limai* Pinto.

Propicimex is related to *Cimex* but differs in the bristles, which are dentate only apically, and in the spermalege, which resembles that of *Bertilia.*

KEY TO THE SPECIES OF *PROPICIMEX*

1. Pronotum relatively narrow, 2 times as wide as long (1.45–1.6 mm). Female seventh ventrite produced forward as a triangular cone. Northern Brazil and Colombia.....5. ***limai***
   Pronotum broader, 2.1–2.25 times as wide as long (1.7–1.8 mm). Female seventh ventrite produced forward as a broadly rounded cone. Argentina and S. Brazil.....4. ***tucmatiani***

4. ***Propicimex tucmatiani*** (Wygodzinsky)

(Fig. 12–4)

Cimex tucmatiani Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 190.
Cimex tucmatiani, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 21.
Cimex tucmatiani, Ronderos, 1961, Notas Mus. La Plata 20: 34.

Female.—Head 1.08 mm wide; ratio of length to width 29:38; interocular space 4 times as wide as an eye. Antennae 2 mm long; proportion of segments 7:25:23:16. Rostrum 0.85 mm; proportion of segments about 10:10:11.

Pronotum 1.8 mm wide; ratio of length to width 30:63; much less than twice as wide as head, 63:37; disk with very short, fine bristles.

Mesonotum about twice as wide as long, 38:20, with very short, fine bristles on disk.

Ratio of length to width of hemelytral pads 46:28; sides arcuate; posterior margin nearly straight, bristles of disk much longer than those of pronotum.

Female seventh ventral segment produced forward as a broadly rounded median lobe, at middle reaching level of fifth tergite; length of compressed sixth ventrite about equal to that of fifth ventrite at middle.

Legs with hind femora in the ratio of 48:17, hind tibiae longer than femora in the ratio of 55:47.

Male.—Paramere narrower than in *limai,* not broadened into a blade.

Size.—Male, length 7.2 mm, width (pronotum) 1.7 mm; female, length 7.1 mm, width (pronotum) 1.8 mm.

Redescribed from a paratype female, El Chorillo, Tucumán, Argentina, on *Myotis nigricans* (Schinz) (P. Wygodzinsky). Also at hand is a male from Nova Teutonia, Brazil, Nov. 4, 1935 (Fritz Plaumann), and 2 males

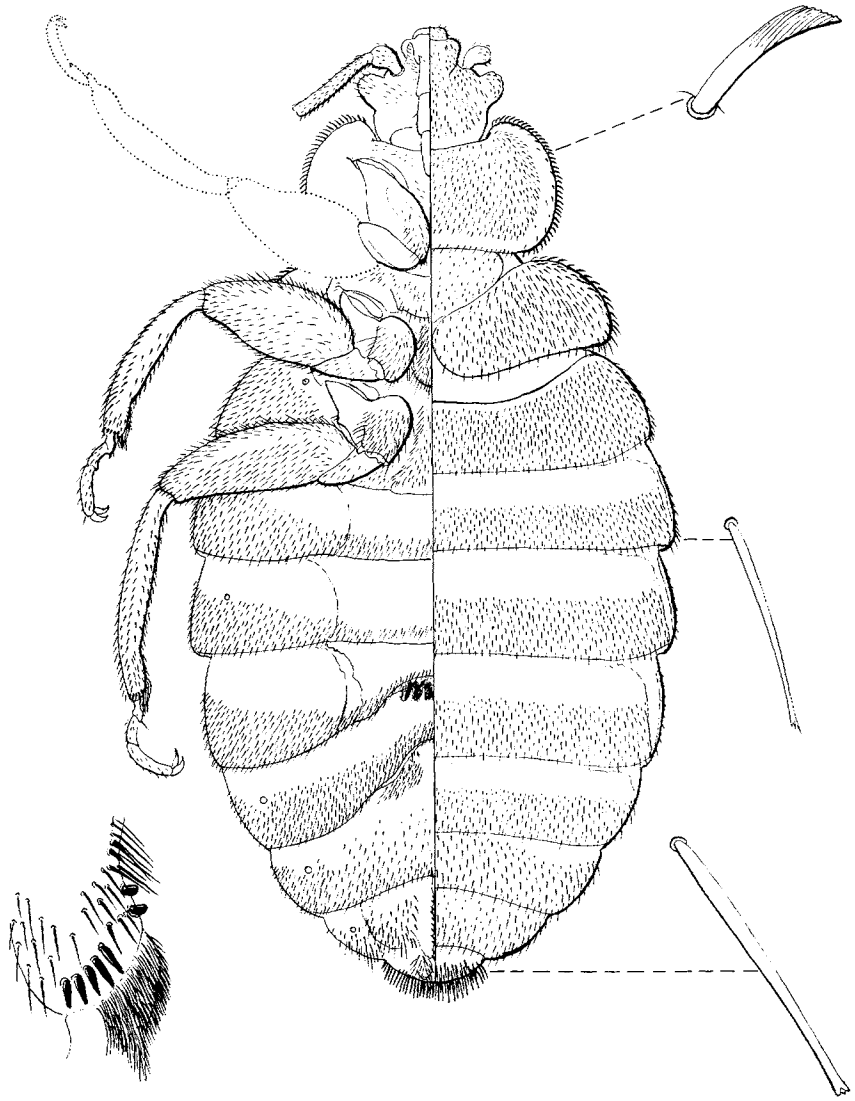

FIG. 12–4.—*Propicimex tucmatiani* (Wygodzinsky). Female paratype. El Chorillo, Tucumán, Argentina (Ferris, original).

and a female, Santiago del Estero, Argentina (J. W. Abalos), Oct. 22, 1964, *Tadarida brasiliensis* (I. Geof. St. Hilaire). In the British Museum are additional specimens, Nova Teutonia, Brazil, 27°15′ lat, 52°23′ long, May, 1936 (Fritz Plaumann). The type is in the Instituto Miguel Lillo, Tucumán, Argentina.

Wygodzinsky (1951) has figured a first-instar nymph.

5. ***Propicimex limai*** (Pinto)

(Fig. 12–5)

Cimex limai Pinto, 1927b, Bol. Biol. 10: 186.
Cimex limai, Lent and Proença, 1937, Mem. Inst. Oswaldo Cruz 32: 211.
Cimex limai, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 315.
Cimex limai, Pinto, 1945, Zoo-Parasitos, p. 119.
Cimex limai, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Cimex limai, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 192.
Cimex limai, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 21.

Female.—Head 1 mm wide; ratio of length to width 30:36; interocular space 4 times as wide as an eye; ratio of clypeal width to interocular space 15:24. Antennae (male) 1.8 mm long; proportion of segments 6:22:20:15. Rostrum 0.91 mm long; proportion of segments approximately 10:10:12.

Pronotum 1.6 mm wide; twice as wide as long or less, much less than twice as wide as head, 56:37; sides narrowly depressed and rather evenly arcuate; bristles very short and fine on disk, coarser and longer on edges.

Mesonotum about twice as wide as long, subtriangular.

Hemelytral pads with ratio of length to width 25:40; bristles at edges stiff like those of sides of pronotum; bristles of disk finer but distinctly longer than bristles on disk of pronotum.

Female seventh ventrite produced forward as a cone with its apex reaching just past hind margin of fifth tergite; length of sixth ventrite at middle much less than fifth.

Legs with ratio of length to width of hind femora 48:17.

Male.—Paramere very short and broad, the blade beyond median enlargement about ⅓ as wide as long.

Size.—Male, length 6.51 mm; width (pronotum) 1.47 mm; female, length 7.2 mm, width (pronotum) 1.6 mm.

Redescribed from a male and female kindly loaned from the type series in the Instituto Oswaldo Cruz by Dr. Herman Lent. The only data on the slides are the numbers 276 and 285. The type is a female, no. 266, from Tapera, Pernambuco, Brazil (D. B. Pickel) on bat. In the British Museum (Nat. Hist.) are a male and female from Taperinha, Santarem, Pará, Brazil, Aug. 1936 (H. Lent). The allotype male in the Instituto Oswaldo Cruz, no. 2942, is from the latter locality.

A male from 2 miles S. of Vijes on the road to Cali, Departamento del Valle, Colombia, 1000 m, on *Molossus major* (Kerr) July 16, 1964 (A. Arata) was sent by Dr. H. Trapido too late to be included in the map and distribution table.

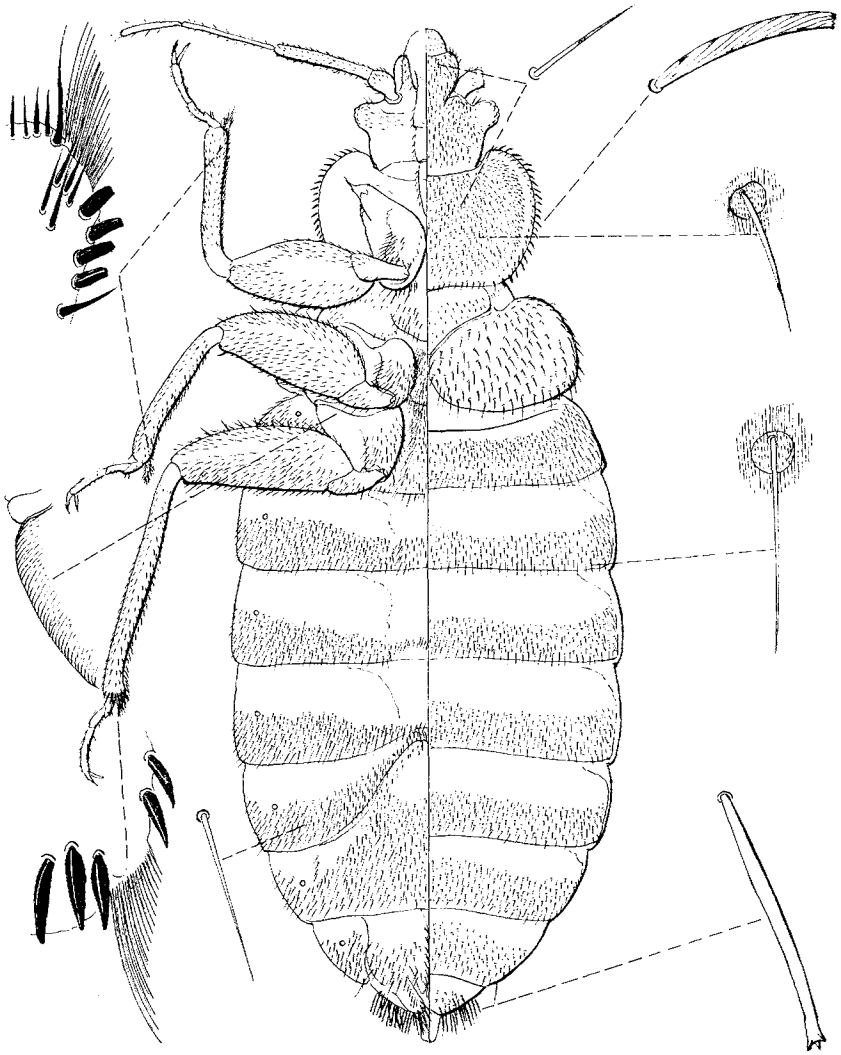

FIG. 12-5.—*Propicimex limai* (Pinto). Female no. 276, Tapera, Pernambuco, Brazil (Ferris, original).

Genus *Cimex* Linnaeus

Cimex Linnaeus, 1758, Syst. Nat., 10th ed., p. 441.
Acanthia Fabricius, 1775, Syst. Entomol., p. 693.
Acanthia, Fabricius, 1803, Syst. Rhyng., p. 112.
Cimex, Latreille, 1804, Hist. Nat. Crust. Ins. 12: 254.
Cimex, Latreille, 1810, Consid. Gen. Ord. Nat. Crust. Arach. Ins., p. 257, 433.
Clinocoris Fallén, 1829, Hemip. Suec., p. 141.
Cimex, Laporte, 1833, Essai Class. Syst. Hemip., p. 51 (part).
Acanthia, Amyot and Serville, 1843, Hist. Nat. Ins. Hemip., p. 310.
Cimex, Spinola, 1850, Tavola Sinottica, p. 39.
Acanthia, Fieber, 1861, Europ. Hemip., p. 135.
Acanthia, Douglas and Scott, 1865, Brit. Hemip., p. 37, 509.
Acanthia, Stål, 1865, Hemip. Afr., p. 24.
Cimex, Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 104.
Cimex, Saunders, 1892, Hemip. Heterop. Brit. Is., p. 186.
Cimex, Hueber, 1893, Fauna Germ., Wanzen, p. 188.
Klinophilos Kirkaldy, 1899a, Entomologist 32: 219.
Clinophilus Blanford, 1903, Nature 69: 200.
Cimex, Distant, 1904, Fauna Brit. India, Rhynch., II, p. 410.
Cimex, Brumpt, 1910, Précis Parasitol., p. 557.
Clinocoris, Horvath, 1910b, Ann. Mus. Nat. Hung. 8: 362.
Clinocoris, Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Cimex, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 258.
Cimex, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 305.
Cimex, Horvath, 1914b, IX^{e} Int. Congr. Zool., p. 295.
Clinocoris, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 762.
Clinocoris, Jordan, 1922, Ectoparasites 1: 284.
Cimex, Butler, 1923, Biol. Brit. Hemip. Heterop., p. 309–322.
Cimex, Stichel, 1926, Illus. Bestimm. Deut. Wanzen, Lief. 4, p. 119.
Cimex, Hedicke, 1935, Tierwelt Mitteleuropas IV, 3, X, p. 36.
Cimex, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Cimex, Darlington, 1939, J. Genet. 39: 101.
Cimex, Lima, 1940, Ins. Brasil 12: 247 (part).
Cimex, Wendt, 1941, *in* Gulde, Wanzen Mitteleuropas 8: 121.
Cimex, Kiritshenko, 1951, Hemip. Europ. Russia, p. 103.
Cimex, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 188 (part).
Cimex, Povolný, 1957, Zool. Listy, Folia Zool. 20:57.
Cimex, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19 (part).
Cimex, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3) : 76.
Cimex, Usinger and Ferris, 1960, Ins. Micronesia 7 (5) : 286.
Cimex, Lansbury, 1961, Entomologist 94: 133.

Size 3.85 to 6.43 mm. Bristles long or short, bent, those at sides of pronotum serrate apically and usually on their outer sides.

Head wider than long; eyes 4 to 7 times as wide as interocular space. Clypeus about half as wide as interocular space. Bristles dense on clypeus, middle of head behind clypeus extending forward onto juga and backward near inner margins of eyes, with a line of bristles posteriorly. Antennae about as long or much longer than width of pronotum; first segment short and stout; second segment stout, subequal to (shorter or longer than) third; third and fourth segments slender, fourth always shorter than third. Rostrum (pinned specimens) reaching about to apices of fore coxae; segments subequal.

Pronotum 2 or 2½ times as wide as long; sides narrowly or broadly flattened; disk and sides with numerous bristles, those of the sides thicker and bent upward and back.

Mesonotum-scutellum over twice as wide at base as long, subtriangular, with short, tapering apex; disk bare of bristles on either side at base and extending backward on either side of middle.

Hemelytral pads ½ again as wide as long or more than ½ again as wide as long with dense, longer, stiffer bristles at sides, usually shorter bristles arising from prominent punctures on disks.

Legs moderately stout; hind femora about 2 to 4 times as long as wide and shorter than tibiae. Tibiae nearly straight, without pseudojoints, and with apical tufts on all legs in both sexes.

Metasternum broad and platelike between middle coxae.

Female spermalege right ventral on anterior margin of sixth segment; sclerotized part as seen in cleared specimens transverse. Hind margin of fifth segment at spermalege cleft or emarginate (paragenital sinus).

Male genital segment broader along oblique base than long, asymmetrical; paramere broadly curved and fitting into a groove on left side.

Type-species: *Cimex lectularius* L.

The type of the genus *Cimex* was fixed by the International Commission on Zoological Nomenclature (1924). The reason for the confusion was that Linnaeus (1758) used *Cimex* in a broad sense, including nearly all Hemiptera. He did not name a type, and his generic description mentions 4 wings, whereas the bed bug is described as without wings. Thus, *lectularius* could hardly be regarded as "typical" of the Linnaean genus *Cimex*. The next available name was *Acanthia* proposed by Fabricius (1775), also in a broad sense. Here, again, no type was designated (though many considered that Fabricius meant the first species listed under each genus, in this case *lectularius,* to be the type). Later the name *Cimex* was applied to a genus of Pentatomidae and *Acanthia* was used for a genus of Saldidae (Latreille 1796). Latreille (1804) restricted *Cimex* to the bed bug, and, in a work that has been ruled as definitely designating types (Opinion 11), he (Latreille 1810) cites *"Acanthia lectularia,* Fab." as type of *Cimex* and *"Lygaeus saltatorius,* Fab." as type of *Acanthia.* Fallén (1829) suggested *Clinocoris* as a better name, and Kirkaldy (1899a) overlooked *Clinocoris* and proposed still another name, *Klinophilos.* The International Commission, in a divided opinion, settled the matter and the decision has been generally accepted. *Cimex* Linnaeus, 1758, with *Cimex lectularius* Linnaeus, 1758, as type, is listed as no. 275 in the Official List of Generic Names in Zoology (Hemming and Noakes 1958a). *Acanthia* Fabricius (1775), *Clinocoris* Fallén (1829), and *Klinophilos* Kirkaldy (1899a) are junior objective synonyms of *Cimex* with the same type-species. *Clinophilus* Blanford (1903) is an invalid emendation of *Klinophilos.* All these later names were placed on the "Official Index of Rejected and Invalid Generic Names in Zoology" (Hemming and Noakes 1958b) under "Direction 63" of the International Commission on Zoological Nomenclature.

Cimex, as restricted in the present work, is Holarctic and presumably also Old World tropical in original distribution, no endemic species being known from the Neotropical or Australian Regions. Its species are primarily associated with bats, but man and pigeons must be counted as natural hosts at present. Other birds and mammals are occasional hosts.

The status of the various names applied to members of this group is

Table 12–1.—Main characteristics of species groups in the genus *Cimex*.

Group	Paragenital sinus	Pronotum ratio l/w	Hind femora l/w	Distrib.	Principal hosts
Lectularius	cleft with bristles	2.5+	3.4 –4.1	cosmopolitan	man, bats, chickens, pigeons
Hemipterus	cleft with bristles	1.9–2.3	2.9 –3.5	tropicopolitan	man, bats, chickens
Pilosellus	rounded with bristles	2.0–2.8	2.1 –2.8	nearctic	bats
Pipistrelli	cleft, naked	2.0–2.5	2.36–3.6	palearctic	bats

discussed under each species. Here it should be mentioned that there are 4 species groups within the genus *Cimex:* the Lectularius Group and the Hemipterus Group primarily on man in the temperate and tropical regions respectively; the Pipistrelli Group in the Palearctic Region on bats, and the Pilosellus Group in the Nearctic Region on bats. The essential characters of these groups are summarized in Table 12–1.

KEY TO THE SPECIES OF *CIMEX*

1. Hind margin of fifth (fourth visible) ventral abdominal segment in female narrowly cleft (paragenital sinus) on right side at spermalege. Hind femora usually more than 2.6 times as long as wide 2
   Paragenital sinus roundly emarginate on right side. Hind femora usually less than 2.6 times as long as greatest width. Nearctic Region. Bats. Pilosellus Group 11
2. Area around paragenital sinus with bristles like those on other parts of abdominal venter. Hind margins of hemelytral pads broadly rounded on inner halves. Hemipterus and Lectularius Groups 3
   Area around paragenital sinus naked. Hind margins of hemelytral pads usually only feebly rounded, their inner margins broadly contiguous. Palearctic Region. Bats. Pipistrelli Group 5
3. Pronotum less than 2½ times as wide as long at middle. Man, bats, chickens. Tropics ..... 8. ***hemipterus***
   Pronotum more than 2½ times as wide as long. Lectularius Group 4
4. Ratio of head width to third antennal segment 1.45 (SD 0.079). Man, bats, chickens. Cosmopolitan ..... 6. ***lectularius***
   Ratio of head width to third antennal segment 1.78 (SD 0.096). Pigeons, pied flycatcher. Western Europe ..... 7. ***columbarius***
5. Hind femora slender, 3.4 or more times as long as wide. Antennae relatively long, ratio of head width to third antennal segment less than 1.4. Bakharden Cave, Russia ..... 12. ***cavernicola***
   Hind femora 3.4 times or less as long as wide. HW/3rd ant. ratio more than 1.4. 6
6. Hind femora stout, 2.36 times as long as wide. Antennae relatively short, HW/3rd ant. ratio 1.92. Burma ..... 13. ***burmanus***
   Hind femora 2.54–3.37 times as long as wide. HW/3rd ant. ratio 1.64 or less 7
7. Longest bristles at sides of pronotum longer than width of first antennal segment, more than 0.13 mm. Bristles of abdominal tergites mostly longer than distance between bristles. British Isles ..... 9. ***pipistrelli***

Longest bristles at sides of pronotum usually shorter than or subequal to width of first antennal segment, 0.13 mm or less. Bristles of abdominal tergites usually shorter than distance between bristles, especially at middle.... 8

8. Size small; pronotum less than 1.4 mm wide. Oriental.... 9
Size larger; pronotum more than 1.42 mm wide. European.... 10

9. Bristles at sides of pronotum mostly serrate on outer sides apically. Scutellum with about 25 bristles on either side posteriorly. China.... 14. ***flavifusca***
Bristles at sides of pronotum scarcely serrate on outer sides. Scutellum with only about 12 bristles on either side posteriorly. Japan.... 15. ***japonicus***

10. Bristles at middle of hemelytral pads 0.1 mm or more, mostly longer than distance between bristles. Germany, Hungary.... 10. ***dissimilis***
Bristles at middle of hemelytral pads less than 0.1 mm, shorter than distance between bristles. Germany, France, Czechoslovakia.... 11. ***stadleri***

11. Head relatively broad; pronotum less than 1.6 times as wide as head.... 12
Head relatively narrow; pronotum more than 1.6 times as wide as head.... 13

12. Bristles at sides of pronotum subequal to width of first antennal segment. Northern California and Nevada.... 20. ***antennatus***
Bristles at sides of pronotum longer than width of first antennal segment. S. W. United States and Mexico.... 21. ***incrassatus***

13. Longest bristles of hind tibiae longer than width of tibia (1.25). Size small; pronotum 1.1 mm wide. Minnesota, Illinois, Michigan, Quebec.... 19. ***brevis***
Longest bristles of hind tibiae shorter than or subequal to width of tibia. Pronotal width usually 1.2 mm or more.... 14

14. Long bristles at sides of pronotum long and thin, over 0.2 mm and not or only feebly serrate. Longest bristles of hind tibiae almost as long as width of tibia (0.90 mm). Eastern United States to Colorado.... 18. ***adjunctus***
Long bristles at sides of pronotum usually less than 0.2 mm, thicker and distinctly serrate. Longest bristles of hind tibiae shorter, 0.8 or less times as long as width of tibia.... 15

15. Hemelytral pads relatively short and broad, nearly twice as wide as long, ratio of width to length 1.8–1.9. Calif., Ore., Idaho, Mont., B. C.... 17. ***latipennis***
Hemelytral pads longer and narrower, ratio of width to length 1.6 or 1.7. Western U. S.... 16. ***pilosellus***

6. *Cimex lectularius* L.

(Fig. 12–6)

Cimex domesticus Moufet, 1634, Theatrum Ins., p. 269.
Cimex lectularius Ray, 1710, Hist. Ins., p. 7.
Cimex apterus Linnaeus, 1746, Fauna Svecica, 1st ed., p. 203.
Cimex lectularius Linnaeus, 1758, Syst. Nat., 10th ed., p. 441.
Cimex lectularius apterus Linnaeus, 1761, Fauna Svecica, 2d ed., p. 245.
Acanthia aptera, Fabricius, 1775, Syst. Entomol., p. 693.
Acanthia lectularia, Fabricius, 1775, Syst. Entomol., p. 693.
Cimex lectularius, DeGeer, 1780, Abh. Geschichte Ins. 3: 195.
Acanthia lectularia, Fabricius, 1803, Syst. Rhyng., p. 112.
Clinocoris lectularius, Fallén, 1829, Hemip. Svec., p. 141.
Cimex improvisus Reuter, 1882b, Wien. Entomol. Zeitung 1: 307.
Klinophilos lectularius, Kirkaldy, 1899a, Entomologist 32: 217.
Clinophilus lectularius, Blanford, 1903, Nature 69: 200.
Cimex lectularius, Girault, 1906b, Zool. Ann. 2: 143–201 (bibliography to 1906).
Acanthia pipistrelli, Bowhill, 1906, J. Hyg. 6: 246.
Cimex vespertilionis Poppius, 1912, Medd. Soc. Fauna Flora Fenn. 38: 56.
Clinocoris peristerae Rothschild, 1912a, Entomol. Mon. Mag. 23: 87.
Cimex lectularius, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 325.

Cimex improviso, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 763.
Cimex lectularius, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 763.
Acanthia pipistrelli, Galli-Valerio, 1927, Zentralbl. Bakt. 103: 181 (Kassianoff, p. 205).
Cimex lectularius, Halbert, 1935, Proc. Roy. Irish Acad. (B) 42: 211.
Cimex lectularius, Stichel, 1937, Illus. Bestimm. Deut. Wanzen, Lief. 13, p. 376–7.
Cimex lectularius, Darlington, 1939, J. Genet. 39: 103.
Cimex lectularius, Lima, 1940, Ins. Brasil 2: 247.
Cimex lectularius, Wendt, 1941, *in* Gulde, Wanzen Mitteleurop. 8: 123.
Cimex roubali Hoberlandt, 1942, Časopis Č. Spol. Entomol. 39: 130.
Cimex lectularius, Smart, 1942, Rep. Comm. Bed-bug Inf. 1935–1940. Med. Res. Counc., Spec. Rep. Ser. No. 245, p. 58–63. (Bibliography through 1941; continuation of Rep. Publ. Health Med. Subj. no. 72, 1934, bibliography to 1933.)
Cimex columbarius f. *roubali* Hoberlandt, 1944, Sb. Entomol. Odd. Zem. Mus. Prage 21–22: 277.
Cimex lectularius, Dubinin, 1947, Entomol. Oboz. 29: 241.
Cimex lectularius, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.
Cimex lectularius, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2) : 188.
Cimex lectularius, Massee, 1955, Entomol. Mon. Mag. 91: 14–15.
Cimex lectularius, Rothschild and Clay, 1952, Fleas, Flukes, and Cuckoos, p. 36.
Cimex lectularius, Miller, 1956, Biol. Hemip., p. 120.
Cimex lectularius, Ferris and Usinger, 1957a, Microentomology 22: 2–6.
Cimex lectularius, Povolný, 1957, Zool. Listy, Folia Zool. 20: 57–80.
Cimex lectularius, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 20.
Cimex lectularius, Hicks, 1959, Check-List and Bibliogr., p. 242; 1962, Suppl. I, Iowa State J. Sci. 36: 260 (bibliogr. of occurrence on birds, much confusion with *C. columbarius*).
Cimex lectularius, Scudder, 1959, Trans. Roy. Entomol. Soc. Lond. 111: 430.
Cimex lectularius, Southwood and Leston, 1959, Land and Water Bugs Brit. Is., p. 188.
Cimex lectularius lectularius, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3) : 77.
Cimex lectularius, Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 83.
Cimex lectularius, Beaucournu, 1961, Bull. Soc. Sci. Bretagne 36: 328.

Male.—Head 0.88 mm wide; ratio of width to length 31:28; interocular space about 4 times as wide as an eye, 21:5. Antennae 1.74 mm long; proportion of segments (dried specimen) 6:19:20:16. Rostrum (dried specimen) reaching level of apices of front coxae; 0.85 mm long; proportion of segments 10:9:11.

Pronotum 2½ times as wide as long, 46.5:18.5; 1.33 mm wide; sides broadly expanded, especially anteriorly, depressed and a little reflexed at edges; disk depressed near basal angles of scutellum; longest bristles at sides about 0.085 mm to 0.11 mm; discal bristles shorter, but distinctly longer than distance between bristles.

Scutellum with numerous scattered bristles on posterior half.

Hemelytral pads half again as wide as long, 33:21; contiguous at center for a distance about ½ that of exposed part of scutellum; disks with prominent, large punctures from each of which arises a bristle; bristles mostly longer than distance between bristles.

Abdominal disk clothed with rows of bristles, most of which are about as long as distance between bristles, the last row of bristles on each tergite exceeding edge, sometimes by as much as ½ their length.

Paramere ⅔ as long as basal width of genital segment, evenly curved.

Legs relatively slender; hind femora over 3 times as long as wide, 40:12 (40:11 in a dried specimen).

Female.—Similar to male but with bristles slightly shorter, especially on abdominal tergites, about as long as distance between bristles. Ectospermalege right ventral, transverse and (as seen in cleared specimens) with dark pigmented areas. Paragenital sinus at hind margin of fifth ventrite, a narrow cleft surrounded by a continuous coat of bristles.

Size.—Male, length 5.34 mm, width (pronotum) 1.33 mm, (abdomen) 2.6 mm; male (dried), 4.5 mm; female, length 5.57 mm, width (pronotum) 1.4 mm, (abdomen) 2.6 mm.

Redescribed from a series from Bordeaux, France, infesting human dwellings and maintained for several years as a colony at the Museum National d'Histoire Naturelle, Entomologie Agricole Tropicale, by Dr. Jacques Carayon. It was felt that specimens infesting man in western Europe could be regarded as most nearly "typical." The actual type is in the Linnaean collection in London. According to W. E. China (in litt.) it is a male with the head and thorax missing. It is labeled "lectularius" in Linnaeus' own handwriting. The type of *Cimex vespertilionis* Poppius is a male, no. 3036, Hattula, Finland, (A. Wegelius) in the museum in Helsinki. The head and pronotum are lacking. The type of *Cimex improvisus* Reuter is a male from Schönbrunn, near Vienna, Austria, "20/4" (Ferrari), in the Vienna Museum; that of *Clinocoris peristerae* Rothschild, a male, Simla, N. W. Himalayas, India, Sept. 12, 1911, from pigeon house (P. T. Dodsworth) in the British Museum (Nat. Hist.). Hoberlandt's type of *Cimex roubali* is a nymph, "Praha-Troja, V, 1941" (J. Roubal) in the author's collection.

Cimex lectularius is one of the few truly cosmopolitan insects, having followed man over most of the world. Specimens or published records are at hand from all continents except Antarctica. The distribution is summarized in Fig. 11–2. Previous small-scale maps have been published by Mellanby (1935) and Geisthardt (1937). Records for each country in Europe are summarized by Stichel (1937). Johnson (1939) gives world-wide records of specimens actually studied by him. From the map it is evident that, unlike *hemipterus, lectularius* knows no geographical boundaries. It is common in tropical as well as temperate regions but is absent over wide areas of the Orient. Omori (1941) attributes its absence there to the fatal effects when males of *hemipterus* mate with females of *lectularius.* Judging by the narrowly cleft paragenital sinus, *lectularius* evolved from Old-World bat bugs, all of which have a similar structure. In America the bat bugs have a roundly concave sinus.

Where in the Old World it first turned to man is difficult to say. As mentioned earlier in this work, the shift to man may have occurred very early when man shared the same caves with bats. Since *lectularius* has rarely been recorded from caves (Povolný, in litt., has found it only in Domica Cave, a classical Cro-Magnon locality in Czechoslovakia, and in a

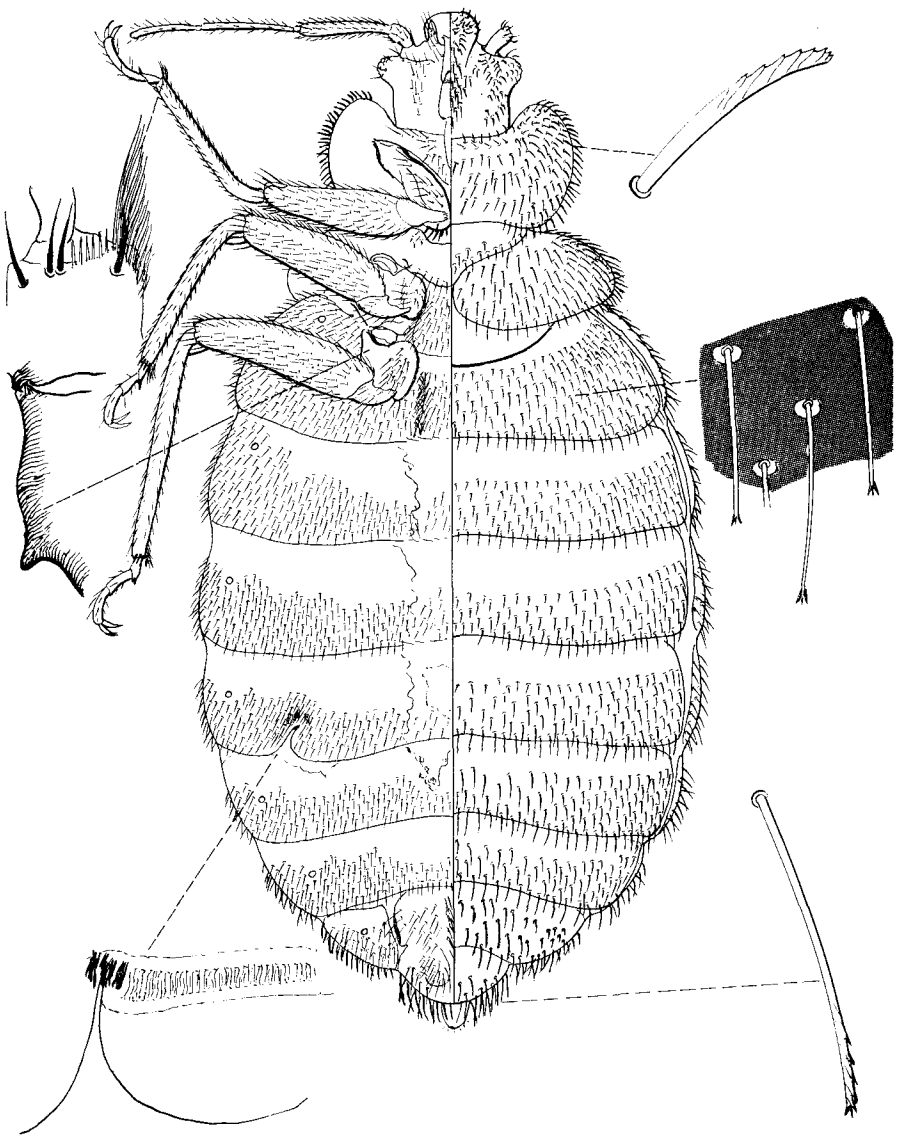

FIG. 12–6.—*Cimex lectularius* L. Female. Missoula, Montana (Usinger 1960).

cave near Kabul, Afghanistan), this theory would require that the species was preadapted to man's dwellings and that it left its original habitat when it turned to man. The *lectularius* colonies that we now find infesting bats in man-made structures in Europe are probably secondary infestations in which the bugs returned to their original hosts under semidomestic conditions.

Another possibility is that *lectularius* evolved on bats in tree holes. Members of the Pipistrelli Group are the typical tree-hole breeders in northern Europe today (to N. Bohemia and Moravia, Povolný, in litt.) but *lectularius* has been reported rarely from tree holes (Reuter 1913a), and it was first reported on man in ancient times in southern Europe. There and in the Middle East the total ecology was altered with advancing civilization and especially with the domestication of the goat. With the obliteration of forests and hence of tree holes, a species that was preadapted to human habitations could have survived and spread with advancing civilization to northern Europe, reaching England in the 16th Century.

The literature on *lectularius* is so extensive and repetitious that a full treatment here would serve no useful purpose. Instead, I have tried to give a full account of the different names that have been applied to the bed bug, and references to the extensive bibliographies of Girault (1906b), Smart (1942), and Hicks (1959, 1962) are included. The principal works on biology are by Hase (1917), Kemper (1936), Omori (1941), and Johnson (1940).

There is no agreement on the synonymy of names within the *lectularius* complex. Povolný (1957) recognized only the single species with no subspecies or "forms," whereas Stichel (1959) attempted to key out all named forms. On the basis of chromosome similarity (13A + 6X + Y) and free interbreeding (Hase 1938 and crosses reported elsewhere in the present work), as well as a study of the type specimens, I am inclined to synonymize all European names except *columbarius*. This course is not consistent with the treatment of other species complexes in Cimicidae (where each difference, however slight, is accompanied by a difference in chromosomes and each such population is reproductively isolated), but a semi-domestic species would be expected to show complexities due to migration and mixing like the races of mankind.

The principal differences that have been used to separate forms of *lectularius* are: 1) size; 2) relative lengths of third and fourth antennal segments; and 3) length of bristles. Johnson (1939) has shown that size varies from a head width of 0.816 mm to 1.024 mm. Although length is subject to individual variation due to expansion of the abdomen after feeding, and slide-mounted specimens cannot be compared with those on pins, still Horvath (1910b) gives a range of 4–6 mm. The most useful

indication of size is pronotal width, which varies in the material before me from 1.3 to 1.9 mm.

Relative proportions of the third and fourth antennal segments were shown by Johnson (1939) to be unreliable in separating *columbarius* from *lectularius,* although differences were noted between different localities. He states that such differences in ratio "are too slight and have too much scatter in a population to be of much use to the museum systematist." The ratio of head width/3rd antennal segment proved to be more useful. The male type of *vespertilionis* (Helsinki Museum) has a ratio of 1.5 and the male type of *peristerae* (British Museum) 1.57. *C. improvisus* (Vienna Museum) has a ratio of 1.66. The first two fall well within the range of typical *lectularius* (Johnson 1939), while *improvisus* is intermediate but nearer *columbarius. C. roubali* was based on an immature specimen and cannot be compared with adults.

Length of bristles is a conspicuous and easily measured character but proves to be of little or no taxonomic significance in this species. The extremes are specimens from the Hingan Mts., Manchuria, with the longest bristles at the sides of the pronotum 0.15 mm, in contrast to a series from Tejupilco, Temascaltepec, Mexico, with bristles measuring 0.057 mm. Abdominal bristles show some sexual dimorphism, but specimens from bats (*Myotis*) in Moravia (long bristles at the sides of pronotum 0.14 mm) have discal bristles that mostly exceed the distance between bristles in both sexes, whereas the bristles on abdominal tergites of Mexican specimens are much shorter than the distance between bristles. The length of bristles on the hemelytral disk (in units) is shown for the Moravia population and for a colony from Monterrey, Mexico (Fig. 11–31). The differences between parental types are statistically significant, and the hybrids overlap the ranges of both parents.

C. lectularius is primarily a parasite of man, but it also occurs on a wide variety of other mammals and birds. Chickens and bats are the other commonly reported hosts, and laboratory animals are often infested. The original host was undoubtedly bats, as most species in the genus are found exclusively on the Chiroptera. Reuter (1913b) reports "vespertilionis" was taken on *Myotis mystacinus* (Leisler *in* Kuhl) in Finland, and there are specimens in the Helsinki Museum from Koxlio, 1920 (Suomalainen) on *Vesperugo borealis* Müller (= *Lasiurus*). During the course of this study, colonies were established from natural infestations found on man, chickens, and bats [Povolný—*Myotis myotis* (Borkh.) and *Myotis blythi oxygnathus* (Monticelli) (= *Myotis myotis oxygnathus*), Chlaba, southern Slovakia].

Slack (1937) and Eichler (1937) suggested that morphological differences resulted from feeding on different hosts. Johnson (1939) denied this, but his data on bugs from animal and fowl houses are intermediate between *lectularius* and *columbarius.* In the present study, bugs from a

single colony (originally from man in Berkeley, Calif.) were separated and fed on different hosts—chicken, pigeon, rabbit, human, mouse, and bat. After 6 generations, differences were evident in the head width/3rd antennal segment ratios, but the greatest differences were well within the normal range of *lectularius*.

All specimens of *lectularius* examined thus far have 13 autosomes at second metaphase (haploid number), but differences are seen in the number of X chromosomes. Darlington (1939) found that the number of X's was variable and that the average number in natural populations was 9. In the present study the number has almost always been found to be constant for each naturally occurring population, with 6 the rule in Europe and the Mediterranean region and 2 the rule for the circum-Pacific area. An exception is a $13A + X_1X_2Y$ count for a population on *Myotis* in France.

Ueshima found that bristle length and the HW/3rd antennal ratio did not differ significantly between the 2 chromosomal forms of *lectularius*. However, the ratio of length to width of the paramere was significantly higher (7.35–7.38) in the Mediterranean type with 6 supernumerary X chromosomes than in the Pacific form (6.33–6.45) or *columbarius* (6.45) (see Table 11–4).

In summary, *lectularius* is here regarded as a cosmopolitan parasite of mankind and his associated animals (chickens, etc.). Its original host was probably bats, and the place of origin was definitely the Old World and probably southern Europe or the Middle East. Morphological variation is considerable, especially in the HW/3rd antennal ratio, bristle length, paramere ratio, and number of supernumerary X chromosomes. However, except for *columbarius*, the various names proposed to date do not represent distinguishable natural populations. Also the types of variation are not correlated in any way that would support taxonomic treatment at the subspecies level.

7. ***Cimex columbarius*** Jenyns

(Fig. 12–7)

Cimex columbarius Jenyns, 1839, Ann. Nat. Hist. 3: 242.
Acanthia columbaria, Douglas and Scott, 1865, Brit. Hemip., p. 510.
Acanthia columbaria, Douglas, 1871, Entomol. Mon. Mag. 8: 64.
Cimex columbarius, Schenck, 1877, Entomol. Nachr. 3: 182.
Cimex columbarius, Puton, 1886, Cat. Hemip. Palearct., 3rd ed., p. 42.
Cimex columbarius, Saunders, 1892, Hemip. Heterop. Brit. Is., p. 187.
Cimex columbarius, Hueber, 1893, Fauna Germanica, Wanzen 5: 191.
Cimex columbarius, Girault and Strauss, 1905, Psyche 12: 117.
Cimex columbarius, Oshanin, 1909, Verzeichn. Palaeark. Hemip. 1: 610.
Cimex columbarius, Horvath, 1910b, Ann. Mus. Nat. Hung. 8: 362.
Clinocoris columbarius, Rothschild, 1912b, Novitates Zool. 19: 93.
Cimex columbarius, Girault, 1913, Entomol. News 24: 341.
Cimex columbarius, Horvath, 1914b, IX^e Int. Congr. Zool. 2: 295.
Clinocoris columbarius, Jordan, 1922, Ectoparasites 1: 284.

Clinocoris columbarius, Rothschild, 1922, Ectoparasites 1: 216.
Cimex columbarius, Butler, 1923, Biol. Brit. Hemip.-Heterop., p. 319.
Cimex columbarius, Stichel, 1926, Illus. Bestimm. Deut. Wanzen 4: 119.
Cimex columbarius, Bedford, 1932, Rep. Vet. Res. S. Afr., 2nd ed., 18: 415.
Cimex columbarius, Börner, 1935, Tierwelt Mitteleuropas, Insekten, 1er Teil 4 (3) : 36.
Cimex columbarius, Slack, 1937, Scot. Nat. 225: 91.
Cimex columbarius, Eichler, 1937, Zool. Anz. 120: 267.
Cimex columbarius, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 193.
Cimex columbarius, Stichel, 1937, Illus. Bestimm. Deut. Wanzen, Lief. 13, p. 376–7.
Cimex columbarius, Hase, 1938, Z. Parasitenk. 10: 9.
Cimex columbarius, Darlington, 1939, J. Genet. 39: 103.
Cimex lectularius columbarius, Johnson, 1939, Trans. Roy. Entomol. Soc. Lond. 89: 543.
Cimex columbarius Wendt, 1941a, *in* Gulde, Wanzen Mitteleuropas 8: 126.
Cimex columbarius, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Cimex columbarius, Hoberlandt, 1944, Sb. Entomol. Odd. Zem. Mus. Prage 21–22: 277.
Cimex columbarius, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Cimex columbarius, Titschack, 1949, Verhandl. deut. Ges. angew. Entomol. 11: 71–7.
Cimex columbarius, Rothschild and Clay, 1952, Fleas, Flukes, and Cuckoos, p. 247.
Cimex lectularius columbarius, Dasgupta and Ray, 1955, Proc. Zool. Soc. Calcutta 8: 1.
Cimex columbarius, Massee, 1955, Entomol. Mon. Mag. 91: 14–15.
Cimex columbarius, Povolný, 1957, Zool. Listy, Folia Zool. 20: 64 (synon. of *C. lectularius*) .
Cimex lectularius columbarius, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3) : 78.
Cimex columbarius, Hicks, 1959, Check-List and Bibliogr., p. 240. 1962, Suppl. 1, Iowa State J. Sci. 36: 260.
Cimex lectularius columbarius, Southwood and Leston, 1959, Land and Water-bugs Brit. Is., p. 191.
Cimex columbarius, Ueshima, 1964, Pan-Pacific. Entomol. 40: 47.

Male.—Head 0.9 mm wide; ratio of width to length 27:22; interocular space almost 7 times as wide as an eye. Antennae 1.5 mm long; proportion of segments 5:14:14:12. Rostrum (slide specimen) 0.73 mm long, reaching apices of front coxae (pin-mounted) ; segments approximately equal in length.

Pronotum 2.84 times as wide as long, 44:15.5; 1.45 mm wide; sides broadly expanded and rounded anteriorly, a little reflexed; disk coarsely punctured, transversely depressed sub-basally; longest bristles at sides approximately 0.1 mm; discal bristles about as long as distance between bristles.

Scutellum-metanotum with short bristles posteriorly.

Hemelytral pads not quite half again as wide as long, 26:18; briefly contiguous at middle; hind margins only feebly concave; disk with rather large, shallow punctures; discal bristles distinctly longer than distance between bristles.

Abdomen with numerous bristles mostly shorter than distance between bristles, slightly longer laterally and posteriorly. Paramere ⅔ as long as width of base of genital segment.

Legs relatively slender, hind femora 3.44 times as long as greatest width.

Size.—Male (slide-mounted) , length 5.6 mm; width (pronotum) 1.45 mm, (abdomen) 2.6 mm (dried specimens from Finland, 3.2–4 mm long) .

Redescribed from a specimen in the Horvath collection at Budapest labeled "Brittania, Shrewsbury, Columba domest." This is one of the series included by Johnson (1939) in his *columbarius* measurements. Jenyns' type is a male in the Hope Department, University Museum, Oxford. Specimens are at hand from "Bosworth" (Boxworth), Cambridgeshire, Sept. 19, 1911, on *Columba livia* (E. H. Thornhill) (British Museum (Nat. Hist.)) and from the Island of Korpo in southern Finland, July 4, 1958 (R. L. Usinger). The latter were in natural-appearing bird houses built from hollow sections of logs with holes for the birds to enter and leave. Boards were used to close the top and bottom. The houses were fastened about 8 ft high on tree trunks in the forest. The pied flycatcher, *Muscicapa atricapilla* L., was nesting in the houses. In 1949 in these same houses, Mr. Axel Vergelius had collected bugs that are now in the Helsinki Museum. He reported to me that to his knowledge the bird houses had been there for 40 years and that bird houses of this type are very common in Finland.

The specimens from Finland are consistently at the lower end of the size range of *columbarius* (3.2–4 mm), but Horvath (1910b) and later authors give as a minimum 3.5 mm. The ratio HW/3rd antennal segment (1.69) falls in the *columbarius* range (Johnson 1939), and the chromosomes agree with *columbarius* and differ from typical European *lectularius*. Massee (1955) lists *columbarius* from 12 counties in England and Stichel (1959) records it from Germany (Schlesien, Prov. Sachsen, Brandenburg, Bayern), The Netherlands, France, S. Russia, Cyprus, and Czechoslovakia. Until Johnson's study (1939), identifications were mostly by host—bugs taken from pigeon cotes were recorded as *columbarius*. Since *lectularius* also occurs on pigeons, no records before 1939 are accepted here unless verified by reference to Johnson's work. Positive records are: ENGLAND—Boxworth (W. Cambs.), Shrewsbury (Shropshire), Ashen (N. E. Essex), Ashton Wold nr. Oundle (Northampton); NETHERLANDS—Schmeeda; GERMANY—Frankendorf; and FINLAND—Korpo. Johnson regarded his South Africa (Kokstad) material as doubtful or intermediate and the North American records of Girault and Strauss (1905) and Girault (1913) as erroneous.

The taxonomic status of *columbarius* has been debated for many years. Hase (1938) questioned that it is a species, Johnson (1939) considered it to be a subspecies, and Titschack (1949) regarded it as a separate species. In general, Johnson's views have been followed because 1) he proposed a statistically significant character by which the 2 forms can be separated (Fig. 11–34; 11–35); 2) he was successful in cross-breeding *columbarius* and *lectularius;* and 3) he reared *columbarius* and *lectularius* side by side on rabbit for 3–4 generations with no significant change in characters. Eichler (1937) and Slack (1937) had suggested the opposite—that the characters were determined by the host. I have

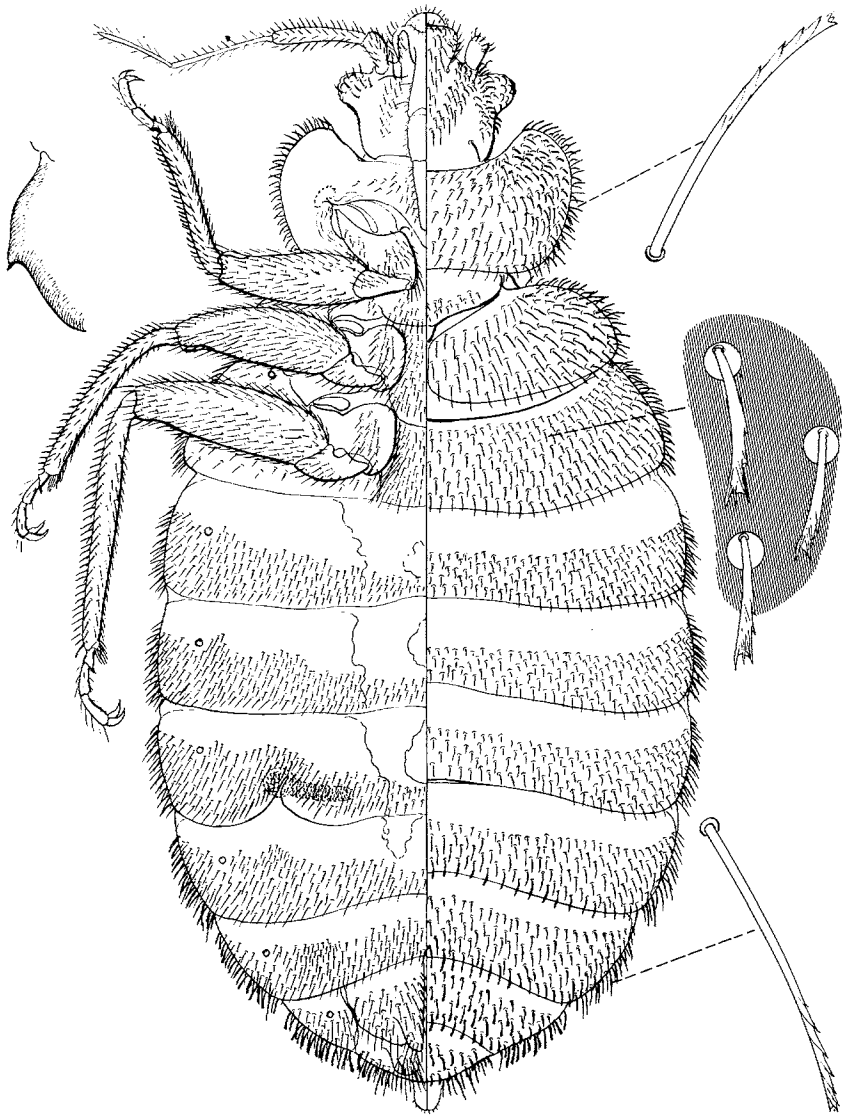

FIG. 12–7.—*Cimex columbarius* Jenyns. Female. Ashen, Essex, England (Ferris, original).

confirmed Johnson's views—*columbarius* and *lectularius,* after 30 generations on rabbit, have HW/3rd antennal ratios of 1.71 and 1.45 respectively. After 30 generations *lectularius* on pigeons had a ratio of 1.47, and the ratios for *columbarius* on rabbit were 1.71 and on chicken 1.72.

According to Johnson's interpretation, *columbarius* is an ecological subspecies of *lectularius* associated with a different host, the pigeon. The difficulty with this theory is that the bugs are only occasional ectoparasites, not actually attached to their hosts. Therefore the 2 forms are not really allopatric, even in the special sense of the parasitologist. It is true that some pigeon cotes are built apart from human dwellings like the Roman columbaria, but pigeons are also commonly housed in attic lofts with the owners living on the lower floors.

Ueshima (1964), working with the Korpo (Finland) colony, added substantially to an understanding of the situation. First he confirmed Darlington's (1939) observation that *columbarius* has a stable number of chromosomes ($13A + X_1X_2Y$). In contrast, European *lectularius* usually has supernumerary chromosomes in the pattern $13A + 6X + Y$. Second, he showed that there is a high degree of reproductive isolation due to selective mating (Table 11–2) (See Stalker 1942 for Isolation Index) and a reduction in number of eggs laid (Table 11–3). These facts led Ueshima to the conclusion that, in nature, the 2 forms are essentially sympatric and effectively isolated and thus, by definition, are full species.

There remains the question of the origin of the pigeon bug. According to verified records, *columbarius* has a limited distribution in northwestern Europe well within the range of the cosmopolitan *lectularius.* Therefore, it has been assumed that it evolved (sympatrically?) as a local race after the pigeon was domesticated. However, Levi (1941) states that "There is no record of fancy domestic pigeons indigenous to the soil of Germany, France, Great Britain or of America. Most breeds of domestic pigeons of these countries can be traced back to importations from countries of ancient civilization—Persia, India, Asia Minor." The presence of *C. columbarius* in the Middle East has not been verified, but the pigeon was domesticated over a wide area in the ancient world, even reaching England in Roman times.

Two possibilities are suggested that avoid the difficulties of sympatric speciation. A population of *lectularius* from bats or from man could have become attached to pigeons and carried to western Europe during Roman times. There are remains of ancient pigeon cotes in England dating from the 13th Century. Pigeon cotes would have provided a continuous blood supply and a warm microhabitat at a time when human dwellings in northern Europe were too cold in the winter to sustain *lectularius* (Buxton and Johnson 1942). According to this theory, *columbarius* would not have met with a resident population of *lectularius* in Britain

until the 16th century, by which time it could have evolved the degree of reproductive isolation that we see today.

The other possibility is suggested by my discovery of *columbarius* in southern Finland in man-made bird houses occupied by the pied flycatcher (*Muscicapa atricapilla* L.). This could have been an accidental infestation, or it might point to an aboriginal host for *columbarius*. The pied flycatcher occurs over the entire range of *columbarius*. It is described as essentially a tree-hole breeder, often inhabiting woodpecker's holes and returning to the same nesting place year after year. *Hesperocimex* occupies an identical habitat throughout western North America (Ryckman 1958). It is possible that sometime before or after *lectularius* turned from bats to man in southern Europe or the Middle East, a population became isolated on birds in woodpecker holes. Later, in Germany, France, and England, this population proved to be preadapted to man-made shelters for wild birds such as the pied flycatcher and for domestic pigeons. Reproductive barriers had already developed under geographic and host isolation. Then, with the advent of *lectularius* into northern Europe, the 2 species became sympatric but maintained their distinctness.

8. ***Cimex hemipterus*** (F.)

(Fig. 12–8)

Acanthia hemiptera Fabricius, 1803, Syst. Rhyng., p. 113.
Acanthia rotundata Signoret, 1852, Ann. Soc. Entomol. France (2) 10: 540.
Acanthia foeda Stål, 1854, Öfv. Vet.-Akad. Förh. (1854) : 237. **New synonymy.**
Acanthia macrocephala Fieber, 1861, Europ. Hemip., p. 135.
Acanthia rotundata, Stål, 1865, Hemip. Afr., p. 25.
Acanthia hemiptera, Stål, 1868, Kongl. Sven. Vet.-Akad. Handl. 7 (11) : 91.
Cimex hemipterus, Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 104.
Cimex foedus, Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 104.
Klinophilos horrifer Kirkaldy, 1899b, Bull. Liverpool Mus. 2: 45.
Cimex macrocephalus, Distant, 1904, Fauna Brit. India, Rhynch. 2: 411.
Cimex rotundatus, Patton, 1907, Indian Med. Gaz. 42 (2) : 2.
Cimex rotundatus, Patton, 1908, Rec. Indian Mus. 2 (2) : 153.
Clinocoris rotundatus, Horvath, 1909, Ann. Mus. Nat. Hung. 7: 632.
Cimex rotundatus, Distant, 1910, Fauna Brit. India, Rhynch. 5: 227.
Cimex rotundatus, Brumpt, 1910, Précis Parasitol., p. 561.
Cimex foedus, Rothschild, 1912b, Novitates Zool. 19: 94.
Cimex hemipterus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 259.
Cimex foedus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 260.
Cimex rotundatus, Balfour, 1912, Bull. Entomol. Res. 2: 179.
Cimex rotundatus, Kunhikannan, 1912, J. Bombay Nat. Hist. Soc. 21: 1342.
Cimex rotundatus, Patton and Cragg, 1913, Textb. Med. Entomol., p. 506.
Cimex hemipterus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 306.
Cimex foedus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 306.
Cimex hemipterus, Horvath, 1914b, IX^{e} Int. Congr. Zool. 2: 297.
Clinocoris hemiptera, Rothschild, 1914a, Bull. Entomol. Res. 4: 345.
Clinocoris hemiptera, Rothschild, 1914b, Suppl. Entomol. 3: 118.
Cimex foedus, Horvath, 1914b, IX^{e} Int. Congr. Zool. 2: 295.
Cimex rotundatus, Castellani and Chalmers, 1914, Man. Trop. Med., 3rd ed., p. 765.

Clinocoris hemipterus, Jordan, 1922, Ectoparasites 1: 284.
Cimex rotundatus, Cornwall, 1923, Indian J. Med. Res. 10: 687.
Cimex rotundatus, Dunn, 1924, Amer. J. Trop. Med. 4: 77.
Cimex hemipterus, Bequaert, 1926, Med. Rep. Hamilton Rice 7th Exped. Amazon. p. 184.
Cimex foedus, Pinto, 1928, Bol. Biol. 13: 85.
Cimex hemipterus, Bequaert, 1930, Afr. Repub. Liberia and Belgian Congo 2: 823.
Cimex rotundatus, Hase, 1930, Z. Parasitenk. 2: 368.
Cimex hemipterus, China, 1930, Ins. Samoa 2 (3) : 160.
Cimex rotundatus, Hase, 1931, Z. Parasitenk. 3: 55.
Cimex rotundatus, Schouteden, 1932, Rev. Zool. Bot. Afr. 23: 70.
Cimex hemipterus, Mellanby, 1935, Parasitology 27: 111.
Cimex rotundatus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 289.
Cimex rotundatus, Geisthardt, 1937, Z. Parasitenk. 9: 150.
Cimex rotundatus, Hase, 1938, Z. Parasitenk. 10: 1–30.
Cimex hemipterus, Usinger, *in* Herms, 1939, Med. Entomol., 3rd ed., p. 92.
Cimex hemipterus, Barber, 1939a, Sci. Surv. Porto Rico, Virgin Is. 14: 398.
Cimex hemipterus, Lima, 1940, Ins. Brasil 2: 248.
Cimex hemipterus, Omori, 1941, J. Med. Ass. Formosa 40: 555.
Cimex hemipterus, Hixson, 1943, Florida Entomol. 26: 47.
Cimex hemipterus, Pinto, 1945, Zoo-Parasitos, 2nd ed., p. 119.
Cimex foedus, Pinto, 1945, Zoo-Parasitos, 2nd ed., p. 119.
Cimex hemipterus, Lewis, 1949, Parasitology 39: 295.
Cimex hemipterus, Wygodzinsky, 1951, An. Inst. Med. Reg. Mus. Nac. Tucumán 3: 188.
Cimex hemipterus, Miller, 1956, Biol. Heterop., p. 120.
Cimex hemipterus, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 21.
Cimex rotundatus, Hicks, 1959, Check-List and Bibliogr., p. 243.
Cimex hemipterus, Usinger and Ferris, 1960, Ins. Micronesia 7: 286.
Cimex hemipterus, Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 83.
Cimex hemipterus, Wattal and Kalra, 1961, Indian J. Malariol. 15: 139–71.

Male.—Head 0.88 mm wide; ratio of width to length 31:25; interocular space about 4 times as wide as an eye, 21:5. Antennae 1.94 mm long; proportion of segments 7:22:21:18 (dried specimen). Rostrum (dried specimen) reaching about to level of apices of front coxae; second segment surpassing base of head; total length about 0.82 mm; proportion of segments 9:9:11.

Pronotum a little more than twice as wide as long, 47:22; 1.34 mm wide; sides more rounded anteriorly than behind middle, not broadly expanded, rather narrowly depressed; posterior disk with a submarginal impression; surface transversely rugose anteriorly; longest bristles at sides and on disks about 0.057–0.085 mm.

Mesonotum-scutellum with short but numerous bristles on posterior half.

Hemelytral pads half again as wide as long; contiguous for a distance about ½ that of exposed part of scutellum, broadly rounded at inner and outer angles, nearly straight at middle. Bristles on inner part of disk about as long or a little longer than distance between bristles, those at sides about 0.114 mm long.

Abdominal tergites clothed with moderately long bristles which generally equal or exceed in length the distance between bristles. Posterior row of bristles on each segment exceeding edge by over ½ their length.

Paramere ⅔ as long as diagonal width of genital segment at base, strongly curved apically.

Legs relatively slender; hind femora over 3 times as long as broad, 42:13.

Female.—Similar to male but with the bristles of dorsum much shorter, those of hemelytral pads and abdomen generally shorter than distance between bristles, and bristles of hind margins of abdominal tergites exceeding edges by less than ½ their length. Ectospermalege in cleared specimens appearing as a transverse dark area enclosed in a membrane. Hind margin of fifth ventral segment deeply, narrowly cleft over spermalege, the surrounding area beset with a continuous coat of bristles.

Size.—Male, length 6.65 mm, width (pronotum) 1.34 mm, (abdomen) 2.7 mm; female, length 7 mm, width (pronotum) 1.4 mm, (abdomen) 2.9 mm (dried specimens vary from 4.2 to 4.6 mm).

Redescribed from a slide-mounted male and female, sleeping quarters, Ta'izz, Yemen, alt. 4100 ft, Jan. 16, 1951 (H. Hoogstraal). Pinned specimens from the same series were used to describe the bristles.

Fabricius' type, a female, is in the Zoological Museum at Copenhagen. The last 2 antennal segments are lacking on both sides and there is a large pin hole through the thorax. It bears the label "ex Am. mer. Schmid." The type of *Acanthia macrocephala* Fieber is a male from "Ost-Indien." It is labeled "Type de Fieber," "*Cimex rotundatus* Sign. det Horvath," and "Museum Paris Coll. Noualhier, 1898." The antennae and most of the legs are gone. Signoret's type of *Acanthia rotundata* is a female, here chosen as lectotype from 2 females in the Vienna Museum from "Bourbon"—it has only the first 2 antennal segments on each side. Kirkaldy's type of *Klinophilos horrifer,* a male from Sokotra, "Adho Dumellus, 3500 ft. Febr. 16, 1899" (W. E. Ogilvie Grant) is in the British Museum (Nat. Hist.). Stål's type of *Acanthia foeda,* a female from Remedios, Colombia (Nisser), is in the Stockholm Museum. Stål (1868) reported on Fabricius' type, and Rothschild (1914a) studied the types of *hemipterus* and *foedus.* I have examined all of the types and concur with the synonymy first proposed by Horvath (1909). In addition I here propose to relegate *Acanthia foeda* Stål to synonymy. It falls well within the limits of variation of the widespread *hemipterus.*

Dimorphism in bristle length like that described above is seen in a series from Aligarh, "Ost-Indien," 1937 (A. Hase). A female before me from Fan Ta, Hainan Island, June 4, 1935 (J. L. Gressitt), has bristles shorter than the female described above, the individual bristles being much shorter than the distance between bristles; in fact, near the middle the individual bristles scarcely exceed the limits of their basal punctures. In contrast to this, a female from Pt. Antonio, Jamaica, April 1906 (E. P. Van Duzee), has bristles longer than the male described above. A specimen with rather long bristles is at hand from Sarasota, Fla.

Despite the variation in bristles, *Cimex hemipterus* is a relatively homogeneous species. The chromosomes were found to be $14A + X_1X_2Y$ in colonies that I have cultured from Vietnam, Taiwan, and Panama. This agrees with findings of Darlington (1939) based on a colony from Uganda. Experimental crosses by Hase (1938) gave fertile offspring from

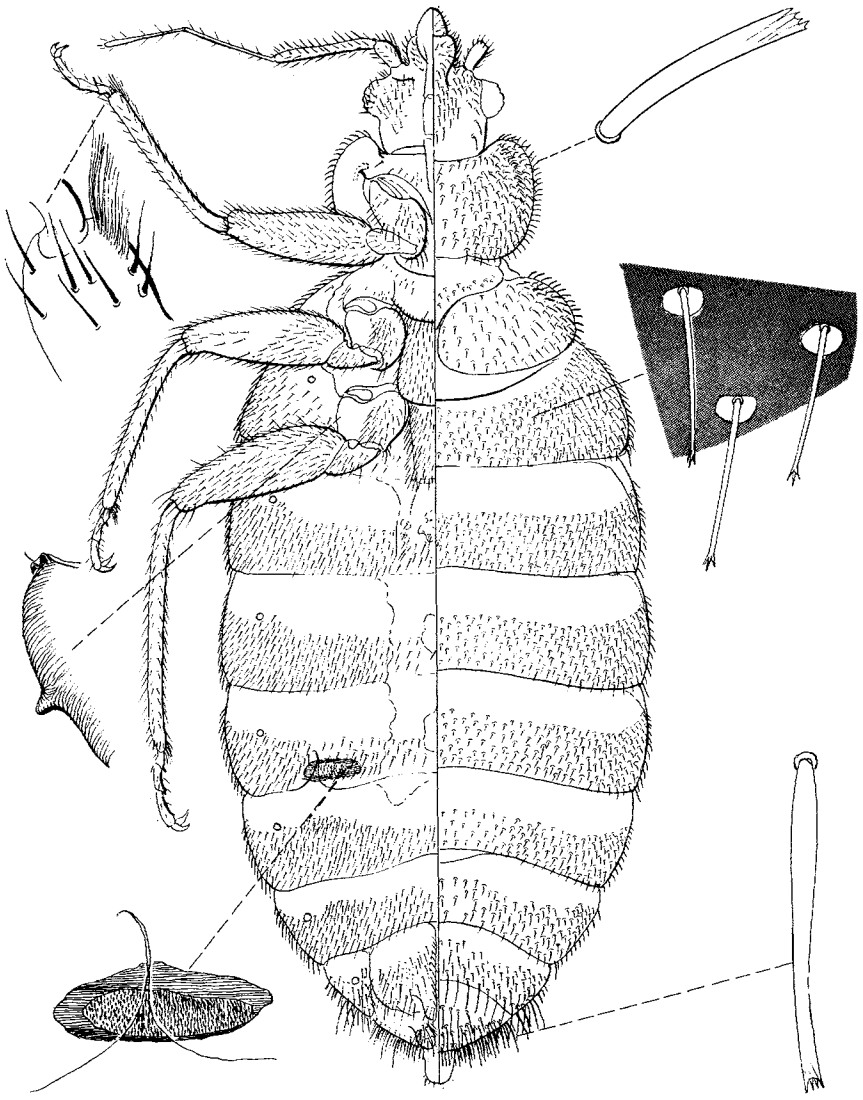

FIG. 12–8.—*Cimex hemipterus* (F.). Female, from colony bred at London School of Hygiene and Tropical Medicine (Usinger and Ferris 1960).

parent colonies originating in Venezuela, Cuba, and India. Also crosses between my Panama and Vietnam colonies were fully fertile. On the other hand, attempts by Hase, Omori, Davis, and myself to cross *hemipterus* with *lectularius,* while occasionally producing eggs in the F_1, failed to produce F_2 adults. Omori (1941) and Davis (pers. comm.) report that mating between males of *hemipterus* and females of *lectularius* is fatal to the latter.

C. hemipterus is mainly a parasite of man, but Patton (1908) and Kunhikannan (1912) record it from bats (*Scotophilus kuhlii* Leach) (?=*Scotophilus heathii* (Horsfield)) in India, and a specimen is at hand from "bats," Java, Toeloengagoeng, July 1932 (C. J. Louwerens) from the G. B. Thompson Collection. Horvath (1913d) recorded it from *Scotophilus temminckii* (Horsfield) in Java. Horvath (1912) reports specimens from St. Ann's Bay, Jamaica, collected on poultry and in poultry houses. Distant (1910) cites it from India in nests of the common swift. The last record could be based on a misidentification, but it seems clear that *hemipterus,* while primarily a parasite of man, occurs also on chickens and, like other species of *Cimex,* was originally a parasite of bats.

The most extensive works on the biology of *Cimex hemipterus* are by Patton and Cragg (1913), Dunn (1924), Hase (1930, 1931), Mellanby (1935), Geisthardt (1937), Omori (1941), and Wattal and Kalra (1961).

C. hemipterus is tropicopolitan in distribution. Mellanby (1935) and Geisthardt (1937) give small-scale maps which indicate that the species rarely extends beyond the tropics. Because of the large number of records at hand it seems best not to list them individually but rather to show them on a map (see Fig. 11–2). Definite records for Florida are given by Hixson (1943).

9. ***Cimex pipistrelli*** Jenyns
(Fig. 12–9)

Cimex pipistrelli Jenyns, 1839, Ann. Nat. Hist. 3: 243.
Acanthia pipistrelli, Kolenati, 1857, Paras. Chir., p. 30.
Cimex pipistrelli, Saunders, 1892, Hemip. Heterop. Brit. Is., p. 188.
Cimex pipistrelli, Hueber, 1893, Fauna Germ., Wanzen, p. 192 (part).
Cimex pipistrelli, Horvath, 1910b, Ann. Mus. Nat. Hung. 8: 362, 363 (part).
Cimex pipistrelli, Brumpt, 1910, Précis Parasitol., p. 564.
Cimex pipistrelli, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 305.
Cimex pipistrelli, Kiritshenko, 1913, Ann. Mus. Zool. Acad. Imp. Sci. 18: 544.
Cimex pipistrelli, Horvath, 1914b, IX^e Int. Congr. Zool., p. 295.
Cimex pipistrelli, Pringault, 1914, Compt. Rend. Soc. Biol., Paris 76 (19) : 881.
Cimex pipistrelli, Britten, 1916, Entomol. Mon. Mag 59: 142.
Cimex dissimilis, Rothschild, 1922, Ectoparasites 1: 216.
Cimex pipistrelli, Jordan, 1922, Ectoparasites 1: 285.
Cimex pipistrelli, Butler, 1923, Biol. Brit. Hemip. Heterop., p. 320.
Cimex dissimilis, Butler, 1923, Biol. Brit. Hemip. Heterop., p. 320.
Cimex pipistrelus, Drenski, 1928, Trav. Soc. Bulg. Sci. Nat. 13: 63–96.

Cimex pipistrelli, Hedicke, 1935, Tierwelt Mitteleurop. IV, 3, X, p. 36 (part).
Cimex pipistrelli, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 199.
Cimex pipistrelli, China, 1938, *in* Stichel, Illus. Bestimm. Deut. Wanzen, 15: 456.
Cimex pipistrelli, Hase, 1938, Z. Parasitenk. 10: 15.
Cimex pipistrelli, Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 127 (part).
Cimex pipistrelli, Wendt, 1941b, Z. Parasitenk. 12: 259 (part).
Cimex pipistrelli, Dubinin, 1947, Entomol. Oboz. 29: 239.
Cimex pipistrelli, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.
Cimex pipistrelli, Kiritshenko, 1951, Hemip. Europ. Russia, p. 103, 104.
Cimex pipistrelli, Kiritshenko, 1952, Trudy Zool. Inst. Akad. Nauk SSSR 10: 182.
Cimex pipistrelli, Massee, 1955, Entomol. Mon. Mag. 91: 14–15.
Cimex dissimilis, Massee, 1955, Entomol. Mon. Mag. 91: 14–15.
Cimex dissimilis, Woodroffe, 1956, Entomol. Mon. Mag. 92: 138.
Cimex pipistrelli, Woodroffe, 1956, Entomol. Mon. Mag. 92: 138.
Cimex pipistrelli, Povolný, 1957, Zool. Listy, Folia Zool. 6 (20) : 68 (part).
Cimex pipistrelli, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 20 (part).
Cimex pipistrelli, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3) : 79 (part).
Cimex pipistrelli, Southwood and Leston, 1959, Land and Water Bugs Brit. Is., p. 191.
Cimex dissimilis, Southwood and Leston, 1959, Land and Water Bugs Brit. Is., p. 191.
Cimex pipistrelli, Beaucournu, 1961, Bull. Soc. Sci. Bretagne 36: 328.
Cimex pipistrelli pipistrelli, Lansbury, 1961, Entomologist 94: 133.

Male.—Head 0.91 mm wide, distinctly wider than long, 17:14; interocular space about 8 times as wide as an eye, 17:2. Antennae 1.8 mm long; proportion of segments 3:14: 13:10. Rostrum 0.73 mm long, not reaching apex of triangular prosternum, expanded due to mounting, but proportion of segments appearing as 10:9.5:4.5.

Pronotum 1.25 mm wide; slightly more than twice as wide as long on median line, 25:12; sides evenly arcuate except for attenuated anterior angles; posterior angles rounded; hind margin straight; anterior angles produced beyond level of middle of anterior margin by 1/6 of length on median line; disk gradually depressed to lateral margins, not lamellately expanded laterally. Longest bristles at sides of pronotum distinctly longer than width of first antennal segment, 6:5, tapering apically, directed upward, and longer than discal bristles.

Scutellum with only a few very short, inconspicuous bristles.

Hemelytral pads over 1/2 again as wide as long, 18:11; broadly contiguous on basal half at middle; densely clothed with long bristles, longer than distance between bristles.

Abdominal disk evenly clothed with fine bristles; longest bristles near hind margins of tergites about 1/2 or 2/3 as long as bristles of side margins of pronotum. Lateral bristles longer, especially on anterior segments and last abdominal segment.

Male paramere about 2/3 as long, 22:30, as width of terminal segment at base, strongly and rather evenly bent forward and upward.

Legs relatively stout; hind femora less than 3 times as long as wide, 20:7; 1/5 shorter than hind tibiae, 20:25.

Size.—Male, length 4.5 mm, width (pronotum) 1.25 mm, (abdomen) 2.25 mm.

Described from the male holotype, Cambridge, England, 1838, (L. Jenyns) from the collection of the Cambridge Philosophical Society (now in the collection of the British Museum (Nat. Hist.))

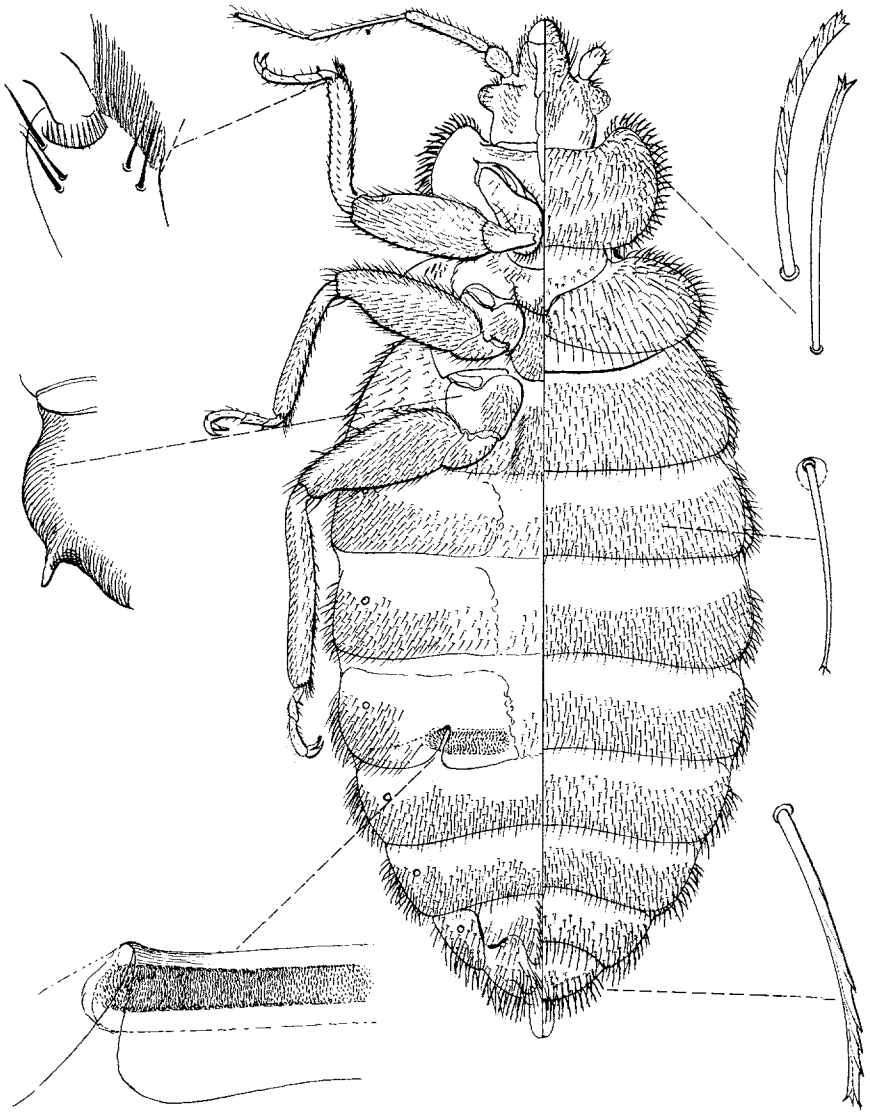

FIG. 12–9.—*Cimex pipistrelli* Jenyns. Female. Exeter, England (Ferris, original).

A female from a series (Wanstead Park, Essex, England, Oct. 11, 1952, E. E. Syms) sent by T. R. E. Southwood shows no sexual dimorphism in development of bristles. Measurements for the female are: Head 0.94 mm wide; ratio of width to length 33:30. Ratio of interocular width to eye width 23:5. Antennae 1.85 mm long; proportion of segments 7:23:19:16. Rostrum (dried specimen) reaching a little beyond apex of prosternum; length approximately 0.74 mm. Pronotum 1.48 mm wide; ratio of width to length 52:21. Lateral bristles mostly not serrate on outer sides. Scutellum with 12–25 rather long bristles posteriorly. Ratio of width to length of hemelytral pads 38:23. Long bristles at hind margins of abdominal tergites about 110μ. Spermalege long and narrow, appearing as if enclosed in a tube in cleared specimens; fifth ventrite at this point narrowly cleft and bare of bristles. Ratio of length to width of hind femora 42:16. Outer bristles of hind tibiae shorter than thickness of a tibia.

The most obvious difference in the 2 sexes is in the relative length of the second and third antennal segments, yet this varies in the series before me from Wanstead Park, dried specimens being especially difficult to measure. A slide-mounted (figured) female from Exeter, Devonshire, England, June, 1937, *Nyctalus noctula* (Schreber) (L. A. Harvey, in G. B. Thompson collection), has the antennal proportions 7:22:20:15.

This species is known from 12 counties in England and from Ireland (Massee 1955). Records for the continent [Stichel 1959: Germany (Thüringen, Brandenburg, Mecklenburg, Rheinland, Hessen, Bayern), Sweden, Denmark, Netherlands, Switzerland, Czechoslovakia, Turkestan; Povolný 1957: France, Belgium, Poland, Byelorussia, Moscow, Kursk, Kiev] probably apply to other species. However, a single male sent by R. Linnavuori seems to agree with typical *pipistrelli*. It is a specimen recorded by Kiritshenko (1952, p. 182) as *Cacodmus vicinus* from Kurgantube, Tadzhikistan. American records before 1910 refer to *pilosellus* (Horvath) (Chittenden 1898) or *Oeciacus vicarius* Horvath (Gillette 1890). The record (Bowhill 1906, Bedford 1932) from South Africa pertains to *lectularius* (Horvath 1910b). Priesner and Alfieri (1953) list *pipistrelli* doubtfully from Egypt. It is likely that this record refers to *Stricticimex namru*.

Host records are *Nyctalus noctula* (Schreber) (L. A. Harvey) and *Pipistrellus pipistrellus* Schreber (Jenyns 1839, Woodroffe 1956, Southwood 1954).

C. dissimilis Horvath has been recorded from Britain on several occasions (Butler 1923, Woodroffe 1956). The specimens were identified by Jordan and by W. E. China. A female specimen in the Rothschild collection at the British Museum (Nat. Hist.) from Coombe, Warwickshire (J. W. Saunders), "from Pipistrelle" has the abdominal bristles shorter than the distance between bristles. However, this character is

variable, females often having shorter abdominal bristles than males. Specimens with short bristles are rare in England, but they predominate on the continent. Much remains to be done to clarify the status of populations in central Europe and especially in Germany. Recent authors vary in their treatment—Povolný (1957) considers all named forms as synonyms of *pipistrelli;* Stichel (1959) recognizes *dissimilis* as a distinct species from *pipistrelli* with the "forms" *stadleri* and *singeri;* and Lansbury (1961) considers all forms as subspecies of *pipistrelli.* In the present work, each distinguishable population is recognized as a full species because it was found by experimental crosses that a long-bristled population from England (T.R.E. Southwood from Hartley Witner, Hampshire), when crossed with short-bristled *stadleri* from Czechoslovakia, produced F_1 adults, but the F_2 generation was reduced by 50% and all were sterile. Also crosses between *japonicus* and both *pipistrelli* and *stadleri* were sterile.

Antennal proportions have long been used as key characters for the separation of the various "forms" in the *pipistrelli* complex. But in the *lectularius* complex (Johnson 1939) and in the *pipistrelli* complex (Wendt 1941b), the ratio of second to third antennal segments has proved to be very unreliable. It is difficult to measure the segments accurately. Dried specimens seldom show the subbasal pseudojoint on the second segment or the small intercalary segment at the base of the third segment. If the former is included and the latter excluded when measuring slide-mounted specimens, the second segment is usually found to be subequal to or slightly longer than the third segment in all populations of the *pipistrelli* complex except the Oriental *flavifusca.* Horvath's type of *dissimilis* is said to have the second segment distinctly longer, but I found that the two are subequal. The type of *stadleri* has the second seg-

Table 12-2.—Main characteristics of species in the Pipistrelli Group.

				Bristles		
Species	Distr.	HW/3rd	Hind femur l/w	Sides pronotum	Hemelytral pads	Abdom. tergites
pipistrelli	Britain	1.4–1.6	3.0–3.4	long, few serrate	long	long
dissimilis	Hungary, Germany	1.5–1.6	2.8–3.2	short, serrate	long	short
stadleri	Czechoslovakia, France, Germany	1.3–1.6	2.8–3.1	short, serrate	short	vary
flavifusca	China	1.4	2.7–2.8	short, serrate	short	short
burmanus	Burma	1.9	2.36	long, not serrate	long	long
japonicus	Japan	1.6	2.5–2.7	short, not serrate	short	short
cavernicola	Turkmenia, Russia	1.3	3.6	long, serrate	long	long

ment slightly shorter than the third, but in other specimens from the type series the reverse is true. Wendt (1941b) has given the most complete analysis of bristle length in the *pipistrelli* complex. His conclusion that only a single species is represented cannot be maintained if, as seems to be the case, the various populations are reproductively isolated. Of greatest interest would be crossbreeding experiments between the sympatric *stadleri* and *dissimilis* in Germany.

Main characteristics of species in the Pipistrelli Group are given in Table 12–2.

10. ***Cimex dissimilis*** (Horvath)
(Fig. 12–10)

Clinocoris dissimilis Horvath, 1910b, Ann. Mus. Nat. Hung. 8: 361.
Cimex dissimilis, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 306.
Acanthias lectularia, Roubal, 1913b, Časopis 10: 122.
Cimex dissimilis, Horvath, 1913b, Časopis 10: 141.
Cimex dissimilis, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Cimex dissimilis, Roubal, 1917, Arch. Naturgesch., Abt. A, 83 (3) : 22–5.
Cimex dissimilis, Jordan, 1922, Ectoparasites 1: 284.
Cimex dissimilis, Hedicke, 1935, Tierwelt Mitteleurop. IV (3) X: 36.
Cimex dissimilis, Horvath, 1935, Mitt. Deut. Entomol. Ges. 6: 14.
Cimex dissimilis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 205.
Cimex dissimilis, China, 1938, *in* Stichel, Illus. Bestimm. Deut. Wanzen 15: 456.
Cimex pipistrelli f. *dissimilis,* Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 126.
Cimex pipistrelli f. *dissimilis,* Wendt, 1941b, Z. Parasitenk. 12: 259.
Cimex pipistrelli f. *dissimilis,* Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.
Cimex pipistrelli, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 20.
Cimex pipistrelli, Povolný, 1957, Zool. Listy, Folia Zool. 6 (20) : 68.
Cimex dissimilis, Stichel, 1959, Illus. Bestimm. Wanzen II, Europa 3 (3) : 79.
Cimex pipistrelli dissimilis, Lansbury, 1961, Entomologist 94: 133.

Female.—Head 1.03 mm wide, 1/3 wider across eyes than long, 30:23, interocular space more than 5 times as wide as an eye, 22:4. Antennae with second segment twisted and damaged but approximately 2.14 mm long; proportion of segments 7:20:20:15. Rostrum about 0.86 mm long, not reaching apex of prosternum in this slide-mounted specimen, second segment not reaching base of head; proportion of segments about 8:8:8.

Pronotum over twice as wide as long on median line, 48:20, 1.65 mm wide, the sides rather evenly arcuate. Longest bristles at sides of pronotum as long as width of first antennal segment. Bristles on disk a little shorter than, or subequal to, distance between bristles, at least laterally. At middle there are very few bristles (perhaps broken off). Scutellar disk without visible bristles.

Hemelytral pads about 1/2 again as wide as long, 84:54, broadly rounded laterally and posteriorly and contiguous on inner half at middle. Discal bristles dense and long, distinctly longer than distance between bristles, the bristles mostly about 0.10 mm long.

Abdomen with bristles mostly about as long as distance between bristles, becoming longer sublaterally and posteriorly and shorter at middle of segments. Posterior row of bristles on each segment slightly to distinctly exceeding hind margin of segment

except at middle. Longest bristles at posterior segment of body. Paragenital sinus narrowly cleft, surrounded by a bare area.

Hind femora less than 3 times as long as wide, 38:14, much shorter than hind tibiae, 38:48.

Size.—Female, length (very expanded slide-mounted specimen) 6.55 mm, width (pronotum) 1.65 mm, (abdomen) 3.24 mm.

Holotype, female, Csép (F. Cerva), Hungary, in the Hungarian National Museum. It is mounted in balsam between 2 coverslips and fixed to a pinned card. The specimen was mounted and the illustration made by Dr. W. E. China. Also in the Budapest collection is a male labeled *dissimilis* by Horvath. It is from Bohemia (J. Roubal), Chudenice, Aug. 23, 1913. As this specimen was collected after the species was originally described (1910), it is not a type. The antennal proportions are 10:48:42:34. The abdominal bristles are very short, shorter than the distance between bristles over most of the center of the abdomen.

A series of specimens that seem to be typical of *dissimilis* have been received from Drs. Eckerlein, Stichel, and Hoberlandt, collected by Dr. H. Eckerlein in Martins-Kirche, Bamberg, Germany, June 18, 1958, and March 11, 1959, on *Myotis myotis* Borkh. The lateral bristles on these and other *dissimilis* before me are thickened apically and serrate at tips and on outer sides. In this series the females are consistent in having very short bristles, those of the hind rows of abdominal tergites not reaching the edges of the tergites. The males, however, show some variation; 1 male has bristles almost but not quite as short as the females, whereas in other males the bristles surpass the hind margins of the tergites by as much as ½ their length.

The distribution of *dissimilis* stands at the moment (Stichel 1959) as Germany (Bayern), Netherlands, and England, with Horvath records from Hungary and Bohemia. Of these, only the type from Hungary and the Eckerlein material mentioned above from Germany are certain. In addition, specimens with long bristles are before me from the Eifel Mts. and from Ludwigsburg, Germany, Sept. 1952, on *Nyctalus noctula* (Schreber) (H. Kemper).

11. ***Cimex stadleri*** Horvath

(Fig. 12–11)

Cimex stadleri Horvath, 1935, Mitt. Deut. Entomol. Ges. 6: 13.
Cimex stadleri, Hedicke, 1935, Tierwelt Mitteleurop. IV (3) X, p. 36.
Cimex stadleri, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Cimex pipistrelli f. *singeri* China, 1938, *in* Stichel, Illus. Bestimm. Deut. Wanzen 15: 456.
Cimex stadleri, Michalk, 1938, Sitzungsber. Naturforsch. Ges. Leipzig 63–64: 102.
Cimex stadleri, Darlington, 1939, J. Genet. 39: 107.
Cimex pipistrelli f. *stadleri,* Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 127.
Cimex pipistrelli f. *singeri,* Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 127.

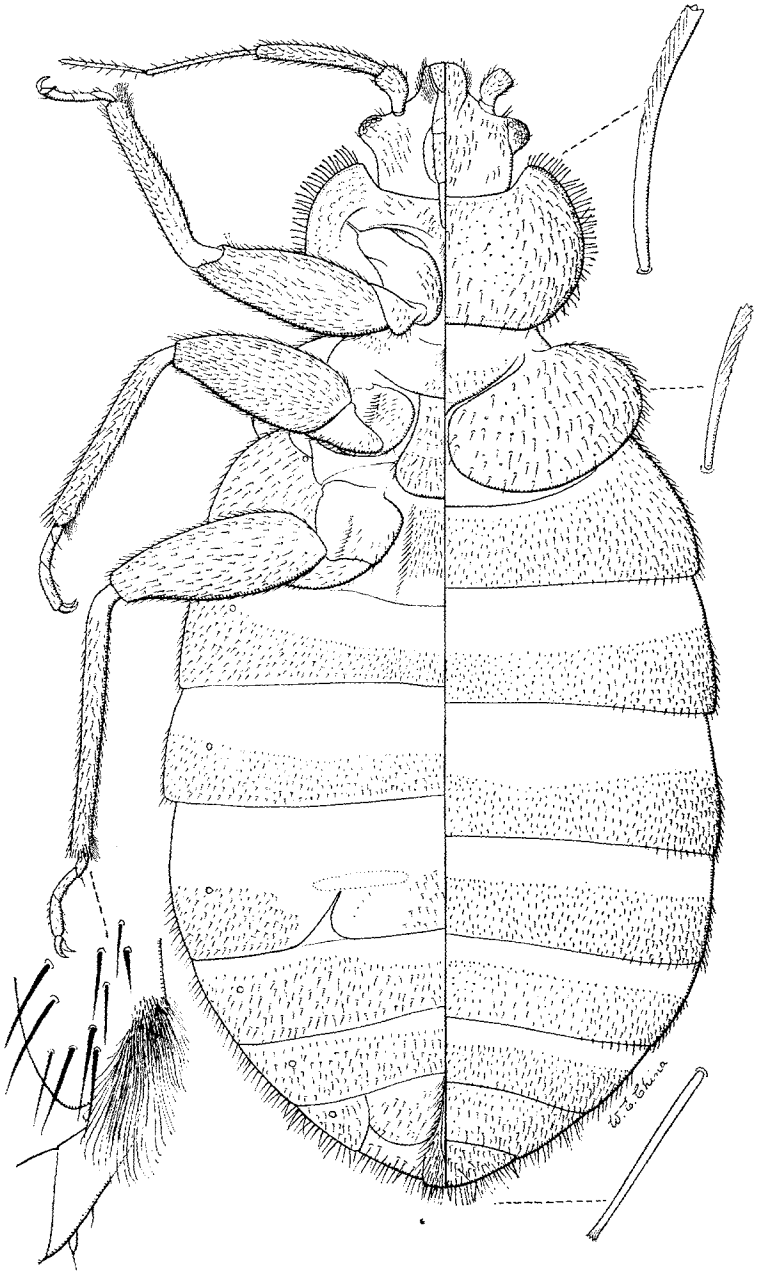

FIG. 12–10.—*Cimex dissimilis* Horvath. Female type. Csép, Hungary (W. E. China, original).

Cimex pipistrelli f. *stadleri,* Wendt, 1941b, Z. Parasitenk. 12: 259.
Cimex pipistrelli f. *singeri,* Wendt, 1941b, Z. Parasitenk. 12: 259.
Cimex pipistrelli f. *stadleri,* Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 17: 7.
Cimex pipistrelli f. *singeri,* Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 17: 7.

Male.—Head 1 mm wide; distinctly wider than long, 19:16; interocular space about 7 times as wide as an eye, 15:2. Antennae 2.1 mm long; proportion of segments 4:13: 13:9. Rostrum 0.82 mm long; proportion of segments roughly 10:10:10, not reaching apex of triangular prosternum.

Pronotum slightly over twice as wide as long, 31:14; sides rather evenly arcuate; anterior angles relatively feebly produced, about $^1/_7$ as far beyond level of anterior margin at middle as length at middle; hind margin feebly concave. Long bristles at sides of pronotum relatively short and blunt, not longer than width of first antennal segment, serrate at tips and on outer sides.

Scutellar disk with very small, scattered bristles.

Hemelytral pads about $1/2$ again as wide as long, 22:14, broadly rounded laterally and posteriorly and contiguous on anterior half at middle; discal bristles shorter or about as long as distance between bristles.

Abdominal disk with very fine, even bristles, those at middle distinctly shorter than distance between bristles, those of hind margins of tergites slightly exceeding the edge and extending briefly onto the base of following segment.

Male paramere about $2/3$ as long as width of terminal segment at base, strongly bent forward and upward.

Hind femora about 3 times as long as wide, 25:8.5, $1/6$ shorter than tibiae, 25:30.

Female.—Very similar to male but with bristles on abdominal tergites shorter, those of hind margins (except on apical segments) not reaching posterior edges of segments. Paragenital sinus narrowly cleft and surrounded by a bare area.

Size.—Male, length 5.8 mm, width (pronotum) 1.52 mm, (abdomen) 2.98 mm; female, length 5.75 mm, width (pronotum) 1.48 mm, (abdomen) 2.85 mm.

Described from a male and female in the British Museum (Nat. Hist.) received from Dr. Singer and, since he designated no type of *singeri* China, presumably representing typical material of that form. The specimens are labelled "Hobbach, Spessart, Brit. Mus. 1933–570, Sept. 12, 1933, Dr. Singer." A series in the Hungarian National collection is from the same locality, Hobbach in Spessart, Germany, but is dated Oct. 13, 1934. The latter, determined by Horvath as *Cimex stadleri,* presumably constitute his type series. Apparently all specimens were first collected from a colony of "Vespertilio murinus" (=*Myotis myotis* (Borkh.)) in a school house at Hobbach in Elsavatal (Spessart) by Hans Stadler and later by Karl Singer. They were sent to G. Horvath and to W. E. China by Karl Singer of Aschaffenburg. It seems clear from the material before me that the name *stadleri* was proposed for females with very short bristles, and that *singeri* pertains to the males with somewhat longer bristles. Additional material before me includes a colony of live bugs received from Dr. D. Povolný collected at Cerna Hora near Brno, Czechoslovakia,

FIG. 12–11.—*Cimex stadleri* Horvath. Female. Hobbach, Spessart, Germany (Celeste Green, original).

June 6, 1963; a male from Waldmünchen, Upper Bavaria, Germany (Gerd Heinrich) on *Myotis myotis* (Borkh.) (Chicago Nat. Hist. Mus.); and a male and female from a church at Vouvray-sur-Huisne (Sarthe), France, in a mixed colony of *Rhinolophus ferrumequinum* (Schreber) and *Myotis emarginatus* (Geoffroy), June 20, 1964 (J. C. Beaucournu). Specimens from the type colony in Spessart were mass-cultured from 1935 to 1939 according to Darlington (1939), who studied their chromosomes.

The synonymy of *singeri* and *stadleri* seems clear enough. Whether both are synonyms of *dissimilis* can be determined only by cross-breeding experiments and by cytological studies. In the North American *pilosellus* complex, reproductive isolation has developed in separate but sympatric populations—a comparable process may have occurred in the bat bugs of central Europe.

12. ***Cimex cavernicola*** Usinger, n. sp.

(Fig. 12–12)

Cimex lectularius, Vlasov, 1929, Russ. J. Trop. Med. 7: 688–92.
Cimex lectularius, Kiritshenko, 1951, True Bugs Europ. U.S.S.R., p. 36.

Female.—Head 0.93 mm wide; wider than long, 28:25; interocular space about 5 times as wide as an eye. Antennae 2.16 mm long; proportion of segments 5:22:21:17. Rostrum about 0.86 mm long; proportion of segments approximately 10:8:8.

Pronotum 1.4 mm wide; 2.3 times as wide as long at middle, 18:42; 1.5 times as wide as head; sides rather evenly arcuate anterolaterally, less so behind middle; longest bristles at sides 0.16 mm, longer than width of first antennal segment, distinctly serrate at tips and on outer sides; discal bristles longer than distance between bristles submarginally, generally shorter at middle.

Scutellum with sparse bristles in a short longitudinal and transverse pattern.

Hemelytral pads over ½ again as wide as long, 31:19, broadly rounded at inner half and only briefly contiguous; discal bristles long, exceeding distance between bristles; longest marginal bristles about as long as those on pronotal margins.

Abdominal tergites with some bristles at middle shorter than distance between bristles, most bristles slightly to distinctly longer than distance between bristles. Paragenital sinus narrowly cleft and surrounded by a bare area.

Legs relatively long and slender, the hind femora about 3½ times as long as wide, 40:11.5; hind femora about ⅛ shorter than tibiae.

Male.—Like the female, but with bristles slightly longer. Paramere about ⅔ as long as width of genital segment at base.

Size.—Male, length 4.0 mm, width (pronotum) 1.13 mm, (abdomen) 2.26 mm; female, length 5.1 mm, width (pronotum) 1.4 mm, (abdomen) 3.2 mm.

Holotype female, allotype male, 5 paratypes, and many nymphs, Bakharden Cave at the foot of the northern slope of the Kopet Mountains, Turkmen S. S. R., Russia, Aug. 13 to Sept. 16, 1927 (J. P. Vlasov). Kiritshenko (1951) states that the cave is far from human settlements and that entry is only by ladder because the walls fall away perpendicularly from the entrance. There are no traces of habitation by prehistoric man.

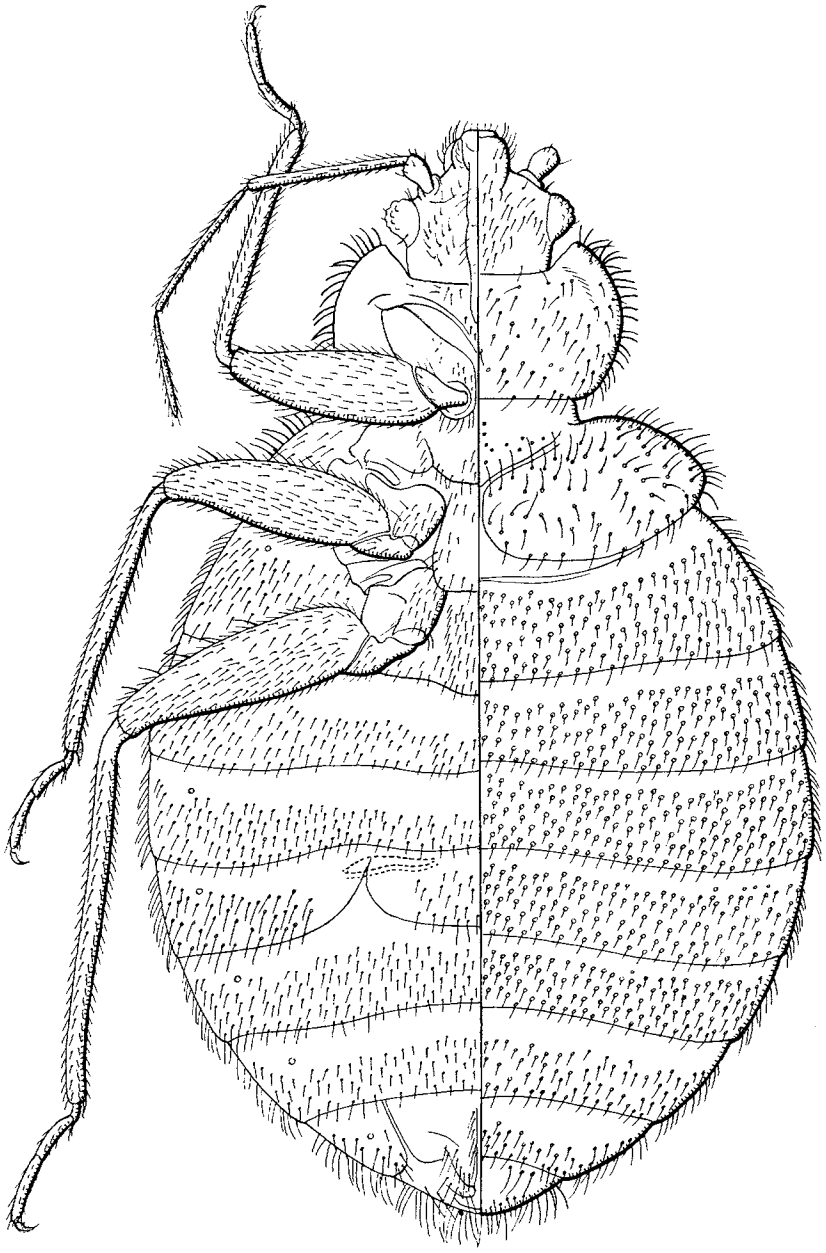

FIG. 12–12.—*Cimex cavernicola,* n. sp. Female holotype. Bakharden Cave, Kopet Mtns. Turkmenia, Russia (Celeste Green, original).

Large numbers of bugs and bats were found in total darkness. The bats were identified as *Miniopterus, Myotis,* and *Rhinolophus.*

C. cavernicola has the naked area surrounding the paragenital sinus and hence belongs to the pipiştrelli complex. The bristles on the hemelytral pads are nearly as long as in typical *pipistrelli,* but the ratio HW/3rd antennal segment is quite low, 1.40 or less, and the ratio of length to width of hind femora is high, 3.4 or more. It is this last characteristic that suggests *lectularius,* in which the ratio ranges from 3.4 to over 4.

I am indebted to I. M. Kerzhner for the loan of this material. The holotype has been returned to the Leningrad Museum.

13. ***Cimex burmanus*** Usinger, n. sp.
(Fig. 12–13)

Female.—Head 0.8 mm wide; nearly ½ again as wide as long, 24:17; interocular space about 5 times as wide as an eye, 17:3.5. Antennae 1.36 mm long; proportion of segments 5:13:13:10. Rostrum 0.57 mm long; proportion of segments approximately 7:5:5.

Pronotum 1.32 mm wide, 2.32 times as wide as long, 39.5:17; 1.64 times as wide as head, 39.5:24; sides rather evenly arcuate throughout; lateral bristles notched at tips but not at sides; longest bristles about 0.13 mm, slightly longer than greatest width of first antennal segment; discal bristles longer than distance between bristles submarginally, sparser and somewhat shorter at middle.

Scutellum with a pattern of short, sparse bristles longitudinally at middle and transversely behind middle.

Hemelytral pads just ½ again as broad as long, broadly rounded on inner posterior margins; discal bristles distinctly longer than distance between bristles.

Abdominal tergites mostly with bristles longer than distance between bristles. Paragenital sinus narrowly cleft and surrounded by a bare area.

Legs very short and stout, the hind femora 2.36 times as long as wide; hind tibiae scarcely longer than femora, 28:26.

Size.—Female, length 4.9 mm, width (pronotum) 1.3 mm, (abdomen) 2.3 mm.

Holotype, female, Myitkyina, Burma, Oct. 3, 1945, "Pipestrell," AP no. 22167, received from the Rocky Mountain Laboratory of the U. S. Public Health Service, Hamilton, Montana. The type has been deposited in the U. S. National Museum.

C. burmanus is unique in the *pipistrelli* group because of its short, stout hind femora and short third antennal segment (HW/3rd antennal ratio=1.92).

14. ***Cimex flavifusca*** Wendt
(Fig. 12–14)

Cimex hemipterus f. *flavifusca* Wendt, 1939b, Z. Parasitenk. 11: 199.

Male.—Head 0.77 mm wide; a little shorter than wide, 24:27; interocular space nearly 5 times as wide as an eye, 19:4. Antennae 1.66 mm long; proportion of segments 5:17:20:16. Rostrum (slide-mounted) reaching about to front margins of fore coxal cavities; proportion of segments approximately 7:8:8.

Pronotum 1.1 mm wide; less than 2½ times as wide as long, 39:17; long bristles at

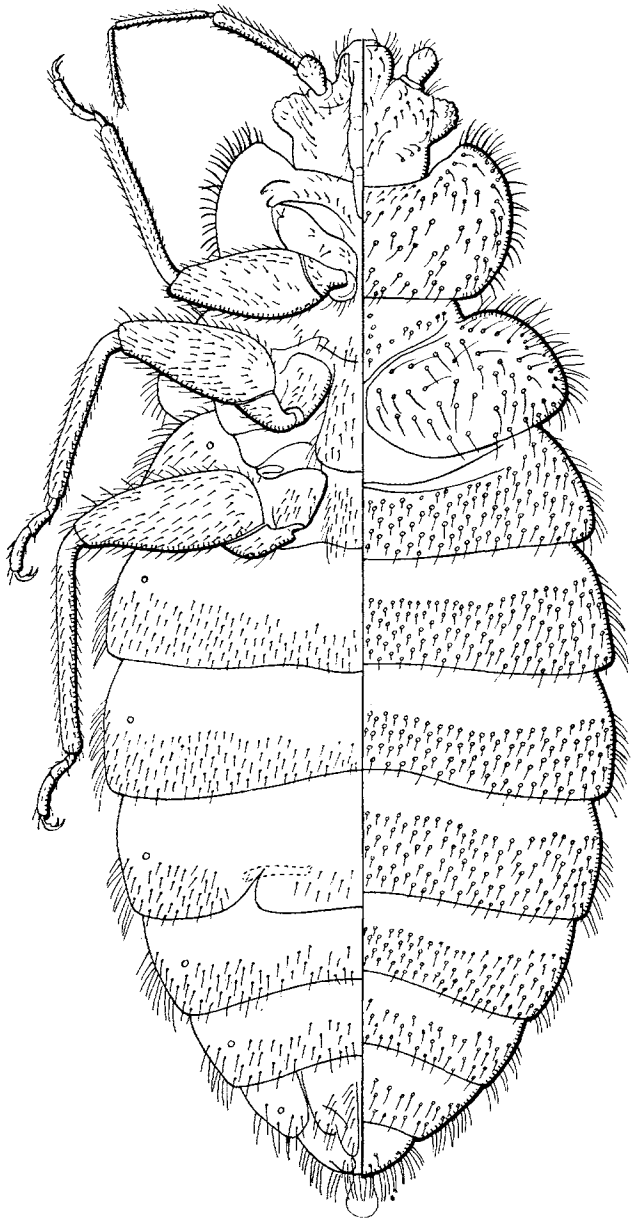

FIG. 12–13.—*Cimex burmanus,* n. sp. Female holotype. Myitkyina, Burma (Celeste Green, original).

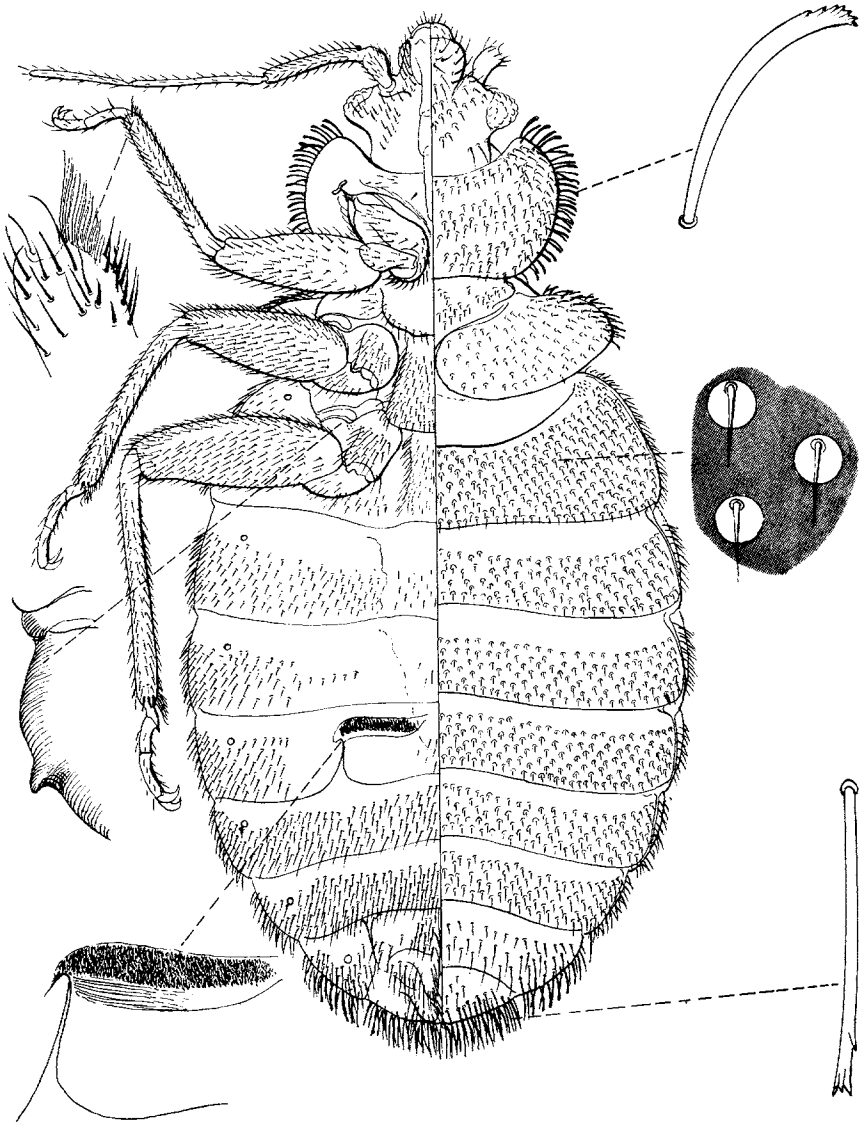

FIG. 12–14.—*Cimex flavifusca* Wendt. Female paratype. Kiangsu, China (Ferris, original).

sides approximately 0.11 mm, bent and thickened apically and serrate at tips and usually also on outer sides, those of disk shorter and finer, not or only a little longer than distance between bristles.

Scutellum with bristles rather numerous.

Hemelytral pads not quite twice as wide as long, 26:14; discal bristles shorter than distance between bristles.

Abdominal tergites with anterior rows of bristles shorter than distance between bristles; posterior row of bristles longer, exceeding edge by as much as ½ their length.

Legs with hind femora almost 3 times as long as wide, 31:11; posterior tibiae with outer bristles shorter than thickness of tibia.

Male paramere difficult to measure in the slide-mounted specimen but strongly curved and surpassing subbasal notch on left side of genital segment.

Female.—Similar to male but with bristles shorter, those of hemelytral pads about ½ as long as distance between bristles, those of hind row on abdominal tergites not or scarcely surpassing edge. Paragenital sinus narrowly cleft, surrounding area bare.

Size.—Male, length 4.88 mm, width (pronotum) 1.1 mm, (abdomen) 2.0 mm; female, length 4.66 mm, width (pronotum) 1.16 mm, (abdomen) 2.4 mm.

Redescribed from male and female paratypes, Hsü-tschou, Kiangsu, China, on bats (A. Hase), kindly sent from the Berlin Museum.

C. flavifusca was originally described as a "form" of *hemipterus,* but the bare area around the paragenital sinus shows clearly that it belongs in the pipistrelli group. A series is at hand from China received from Dr. Marshall Hertig with the following notes: "Parents of a strain collected in Hsuchowfu, Kiangsu, China, in summer of 1925 or 1926, by Marshall Hertig. Crawling on bathroom wall of house in compound of Southern Presbyterian Mission. Associated by occupants with bats living under eaves or in roof. These bugs were not known to bite the occupants and did not become established in beds, etc. Reared by Marshall Hertig in China, usually in container with Chinese striped hamster, up to 1927. Continued in Boston on some animal or other. Not later than 1937, put in feeding cage with Marshall Hertig as sole host, until 1943–44." In the Hertig series the bristles vary, sometimes being as long in the females as described above for the male. Unfortunately the last 2 antennal segments are broken off in every specimen, so the relative length of the second segment cannot be checked.

15. ***Cimex japonicus*** Usinger, n. sp.

(Fig. 12–15)

Female.—Head 0.93 mm wide; nearly ⅓ wider than long, 28:22; interocular space 5 times as wide as an eye. Antennae 1.83 mm long; proportion of segments 6:19:17:13. Rostrum approximately 0.73 mm long; proportion of segments (slide-mounted) 7:7:8.

Pronotum 1.46 mm wide; 2.2 times as wide as long, 44:20; 1.57 times as wide as head, 44:28; sides rather evenly arcuate except just behind middle; longest lateral bristles less than 0.13 mm, not longer than width of first antennal segment, serrate at tips but not on outer sides; discal bristles shorter than distance between bristles.

Scutellum with bristles of posterior half short and sparse, about 12 on each side.

Hemelytral pads over ½ again as wide as long, 32:20, broadly contiguous at middle;

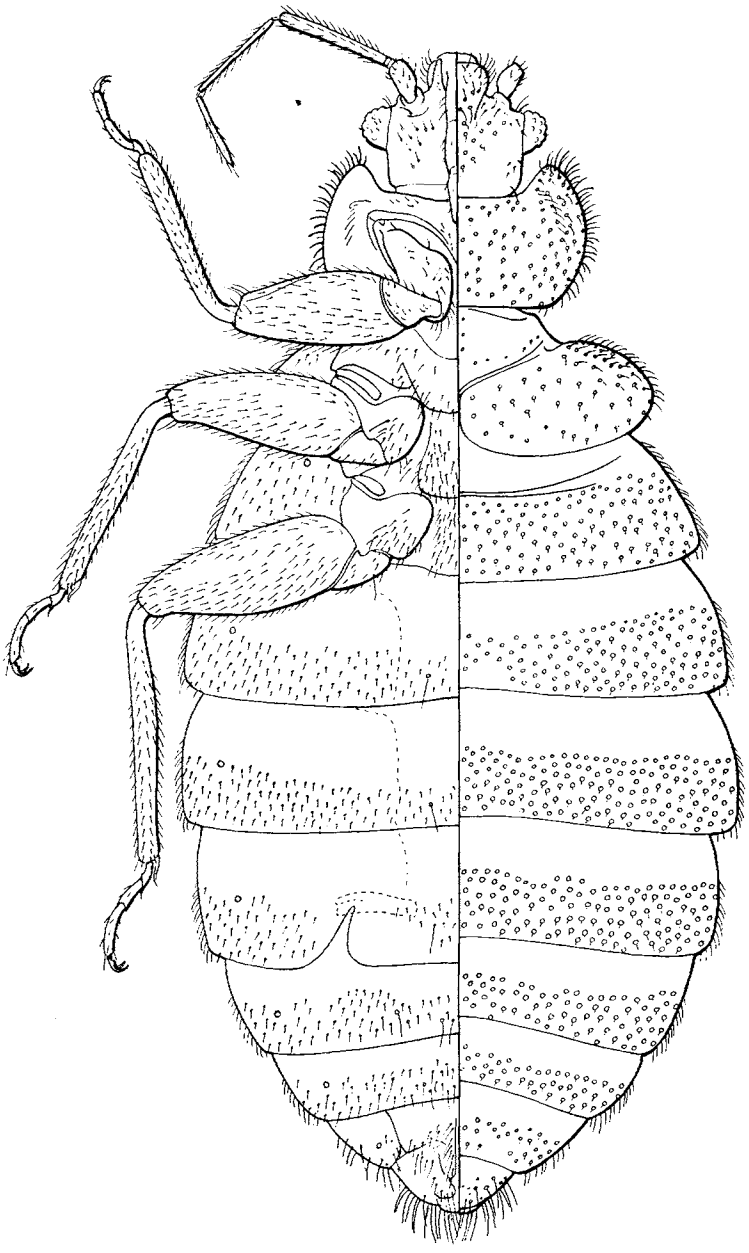

FIG. 12–15.—*Cimex japonicus,* n. sp. Female. Hokkaido, Japan (Celeste Green, original).

lateral bristles widened and serrate at tips but not on outer sides; discal bristles shorter than distance between bristles.

Abdominal disk with short bristles, mostly shorter than distance between bristles. Area around paragenital sinus naked.

Legs relatively stout; hind femora 2.77 times as long as wide; hind tibiae 1/6 longer than femora.

Male.—Paramere broadly, evenly bent forward, the tip slightly recurved.

Size.—Male, length 6.7 mm, width (pronotum) 1.35 mm, (abdomen) 2.45 mm; female, length 7 mm, width (pronotum) 1.46 mm, (abdomen) 2.9 mm.

Holotype female, allotype male, and 1 female paratype, Hokkaido, Japan, Aug. 1952 (J. Yamashita) ex *Nyctalus maximus* (=*Nyctalus lasiopterus* (Schreber)), sent by Norihiro Ueshima. The holotype is deposited in the British Museum (Nat. Hist.), and the paratype is in the Ueno National Museum, Tokyo. Additional specimens are at hand from Aki, Kochi Pref., Shikoku, 1954 (Hiromatsu) on *Nyctalus;* and Akita, Honshu, 1964 (Ueshima). Specimens from the latter locality have been reared for cytological study and cross-breeding experiments. They are smaller (pronotum 1.2 mm) and the hind femora are about 3 times as long as wide. In addition to the nonserrate outer edges of the longest lateral pronotal bristles and the sparse bristles on scutellum, *japonicus* differs from *flavifusca* in having the second antennal segment longer than third in the specimens before me.

As shown in the discussion of cross-breeding, females of the Akita population, when mated with males of *pipistrelli* or *stadleri,* produced a few F_1 adults, but the F_2 bugs were completely sterile. In the reciprocal cross with *stadleri* as the female, the F_2 was greatly reduced in fertility.

16. ***Cimex pilosellus*** (Horvath)

(Fig. 12–16)

Cimex pipistrelli, Chittenden, 1898, USDA, Div. Entomol., Bull. (N. S.) 18: 97.
Clinocoris pilosellus Horvath, 1910a, Entomol. Mon. Mag. (2) 21: 12.
Cimex pilosellus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 259.
Cimex pilosellus, Horvath, 1914b, IX^e Int. Congr. Zool., p. 295.
Cimex pipistrelli, Zimmer, 1914, Entomol. News 25: 418.
Cimex pilosellus, Van Duzee, 1917, Cat. Hemip., p. 287 (part).
Cimex pilosellus, Jordan, 1922, Ectoparasites 1: 285.
Cimex pilosellus, Downes, 1927, Proc. Entomol. Soc. Brit. Columbia 23: 11.
Cimex pilosellus, Spencer, 1935, Proc. Entomol. Soc. Brit. Columbia 31: 44.
Cimex pilosellus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Cimex pilosellus, Barber, 1939b, Proc. Entomol. Soc. Wash. 41: 245, fig. 2.
Cimex pilosellus, Usinger, 1939, *in* Herms, Med. Entomol., 3rd ed., p. 93.
Cimex pilosellus, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Cimex pilosellus, Matheson, 1950, Med. Entomol., 2nd ed., p. 178.

Female.—Head 0.83 mm wide, 0.70 mm long, ratio of width to length 25:21; interocular space 6 times as wide as an eye, 18:3. Antennae 1.7 mm long; proportion of segments 5:17:17:12. Rostrum reaching well onto prosternum, the second segment attaining base of head (limits of basal segments not visible).

Pronotum 1.43 mm wide, 0.6 mm long, ratio of width to length 43:18; ratio of pronotal width to head width 43:25; sides rather evenly arcuate on anterior half, less so behind middle, subdepressed laterally and subbasally; longest bristles at sides about 0.166 mm, a little longer than width of first antennal segment, 5:4; bristles on disk sparse at middle but generally much longer than distance between bristles.

Hemelytral pads 1.66 times as wide as long, 30:18; bristles on disk dense and much longer than distance between bristles.

Abdomen with longest bristles at hind margins of anterior tergites about 0.1 mm, exceeding hind margins by ½ or ⅔ their length. Paragenital sinus shallow. Ectospermalege transverse, tubular, the limits ill-defined mesad.

Legs relatively stout, the hind femora 2.48 times as long as wide, 31:12.5. Bristles of hind tibiae distinctly shorter than thickness of tibia, 2:4.

Size.—Length 5.7 mm, width (pronotum) 1.4 mm, (abdomen) 2.8 mm.

Described from a female of the type series from Okanagan Landing, British Columbia, Oct. 20, 1903, from *Myotis longicrus* (True) (Allan Brooks). This slide-mounted specimen is in the Rothschild collection at the British Museum (Nat. Hist.). The Hungarian National Museum has a male and a female from the same type series. I hereby designate the female as lectotype.

A male from Wilbur Springs, Colusa Co., Calif. (Ueshima) differs in that the bristles on the hind tibiae are a little longer than, but not equal to, the width of a tibia, and the hind femora are 2.66 times as long as wide. Length 5.3 mm, width (pronotum) 1.2 mm, (abdomen) 2.4 mm. The haploid chromosome number at second metaphase is $14A + X_1X_2Y$.

The following specimens are at hand: CALIFORNIA: Sequoia National Park, Fresno Co., ex *Myotis* sp., Febr. 24, 1924 (R. Hopping); Bishop, Inyo Co., Dec. 8, 1963 (J. D. Birchim); Pioneer, 4000 ft elev., Amador Co., July 8, 1961, ex *Eptesicus fuscus* (Palisot de Beauvois) (A. J. Beck); SE Porterville, Aug. 5, 1935, on *Pipistrellus hesperus merriami* (Richardson); Yosemite Valley, 1915, from *Pipistrellus h. merriami* (G. F. Ferris); Walker Basin, Kern Co., Aug. 31, 1921, ex *Pipistrellus* sp. (A. B. Howell); Stanford University, Aug. 1923, from *Antrozous pallidus* (Le Conte) (G. F. Ferris); Moraga Vy., Contra Costa Co. (F. M. Woods); Wilbur Springs, Colusa Co., Sept. 23, 1945, on *Myotis yumanensis* (H. Allen) (S. B. Benson); 5 mi. W. Woodland, Yolo Co., ex *Myotis californicus* (A. J. Beck); La Grange, Stanislaus Co., July 25, 1948, ex *Myotis yumanensis* (H. Allen) (R. P. Allen); Tahoe City, June 23, 1946 (H. H. Keifer); Kernville, July 1911, *Vesperugo hesperus* (= *Pipistrellus hesperus* H. Allen) (A. K. Fisher); Agua Caliente Springs, San Diego Co., ex *Pipistrellus hesperus* (H. Allen); Waddel Creek, Santa Cruz Co., Sept. 1945, *Myotis yumanensis* (H. Allen) (S. B. Benson). IDAHO: Hope, July 28, 1940, ex *Myotis y. sociabilis* (C. B. Philip). NEVADA: Reno, Nov. 1962; Reno, Jan. 1963 (O. A. Steen). MONTANA: Hamilton, Aug. 1938 (W. L. Jellison); Gallatin Co., Aug. 4, 5, 1949 (W. L. Jellison); Ravalli Co., Aug. 22, 1961 (Bell and Jellison); Chinook, Mar. 27, 1944 (Chas.

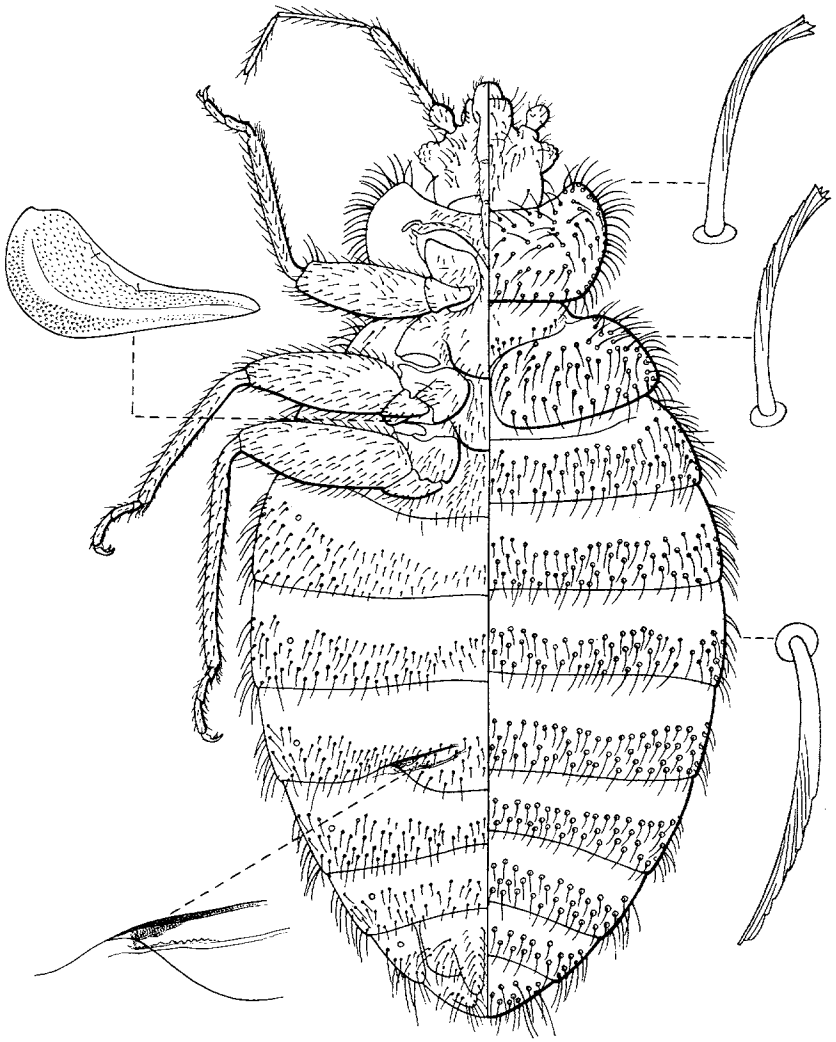

FIG. 12–16.—*Cimex pilosellus* Horvath. Female lectotype. Okanagan Landing, British Columbia (Celeste Green, original).

Ivey); Centennial Vy., Beaverhead Co., July 4, 1953 (W. L. Jellison). WASHINGTON: Yakima, Aug. 18, 1953 (E. J. Newcomer); Toppenish, Aug. 1, 1924 (M. C. Lane). BRITISH COLUMBIA: Lytton, Aug. 30, 1931 (G. R. Spencer); Burns L., Sept. 10, 1934 (W. Downes); Salmon Arm, Apr. 27, 1929 (H. B. Leech); Anarchist Mt. near Keremeos, July 1931 (Kenneth Racey).

Spencer (1935) says of *Cimex pilosellus:* "I have rarely found it on the animals themselves, but it may readily be taken from their roosting places in trees or in buildings. One of my records is from the loose bark of a cedar tree where bats were in the habit of sleeping. Another record shows a very well known summer hotel in the Dry Belt whose log construction afforded splendid hiding for bats. Up to the time of our visit in July, no less than 72 bats had been destroyed because they harboured the bugs which swarmed into the neighboring rooms through cracks in the plaster, especially in one of the bathrooms. Although human beings had not been actually bitten by the bugs, the guests seemed to resent their presence and the management was much concerned over the situation. The bat in question was *Eptesicus fuscus fuscus* (Beauvois).

"From the log roof of a root cellar near Lytton in the Dry Belt I obtained a large number of the bugs, which were occupying a deserted termite nest whose tunnels afforded them splendid protection. There were five of these same bats roosting immediately below the termite nest but no bugs were found on the animals themselves, although all stages of the insects occurred in the termite nest. This brood was taken in August.

"Very large specimens of this same insect, in fact the largest of all the bedbugs I have, were taken by that ardent mammalogist and ornithologist, Mr. Kenneth Racey of Vancouver, from specimens of the bats *Lasionycteris noctivagans* (Le Conte), the silver haired bat, and *Eptesicus fuscus pallidus* (Young), the pale brown bat, which were captured in July, 1931 in a talus slope on Anarchist Mt. near Keremeos. There were 10 specimens of these bugs, all females, 4 on *pallidus* and 6 on *noctivagans,* attached by their beaks firmly implanted in the bats' skin with their bodies sticking up at right angles to the skin, practically concealed in the long dense fur behind the ears. The bats were found in two separate locations at Keremeos."

I have examined the large specimens from Anarchist Mt. They differ from typical *pilosellus* in that the head is relatively narrow. When material is available for chromosome study this form may prove to be a distinct species.

17. ***Cimex latipennis*** Usinger and Ueshima
(Fig. 12–17)

Cimex latipennis Usinger and Ueshima, 1965, Pan-Pacific Entomol. 41: 114.

Female.—Head 0.76 mm wide, 0.63 mm long, the ratio of width to length 23:18; interocular space over 5 times as wide as an eye, 16:3. Antennae 1.53 mm long, pro-

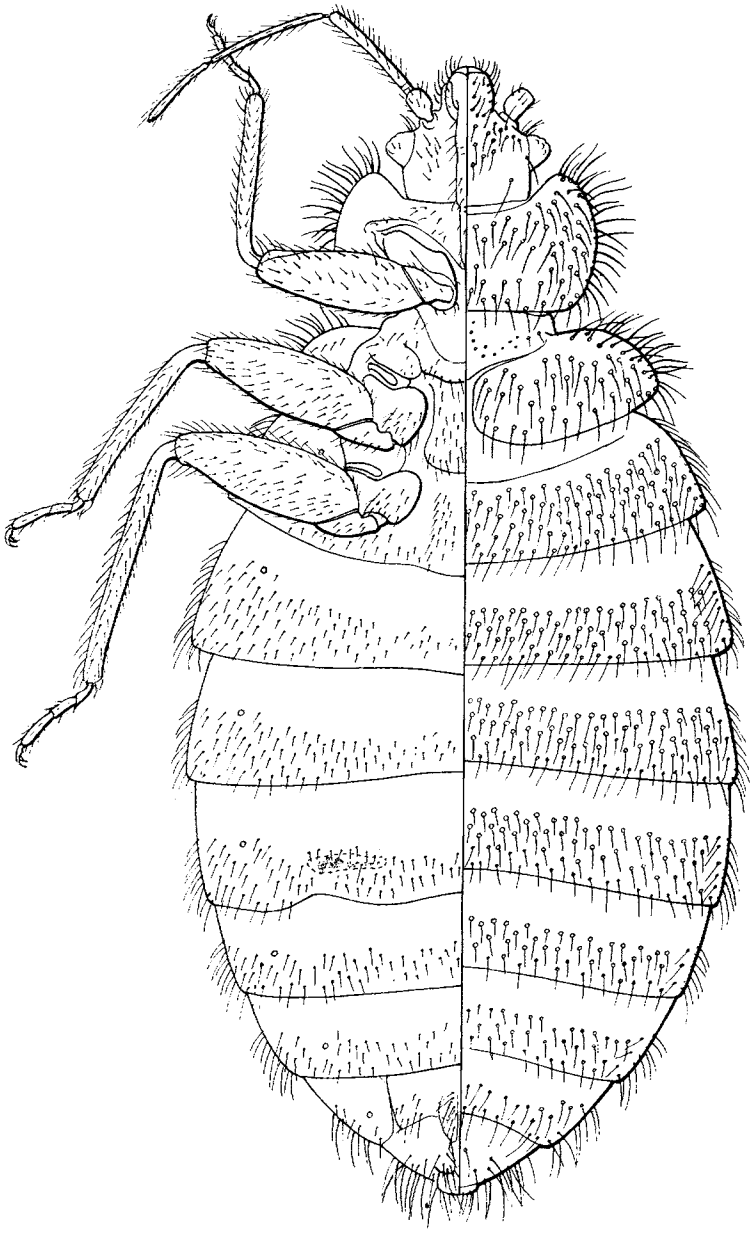

FIG. 12–17.—*Cimex latipennis* Usinger and Ueshima. Female allotype. Klamath Lake, Oregon (Celeste Green, original).

portion of segments 5:15:17:12. Rostrum with second segment reaching about to base of head, proportion of segments 7:6:7.

Pronotum 1.2 mm wide, 0.46 mm long, ratio of width to length 36:14; ratio of pronotal width to head width 36:23; sides broadly rounded on anterior half, less so posteriorly, subdepressed laterally and subbasally; longest bristles at sides about 0.166 mm, distinctly longer than width of first antennal segment, 5:3; bristles on disk fine and much longer than distance between bristles.

Hemelytral pads 1.85 times as wide as long, 25:13.5, bristles on disk much longer than distance between bristles.

Abdomen with longest bristles at hind margins of anterior tergites approximately 0.13 mm, exceeding hind margins by ¾ their lengths. Paragenital sinus very broad and shallow, the ectospermalege transverse and tubular.

Legs with hind femora 2.84 times as long as wide, 27:9.5. Bristles of hind tibiae shorter than thickness of tibia, 2:2.5.

Male.—Like the female but with longest bristles at sides of pronotum slightly shorter, and longest bristles of hind tibiae about as long as thickness of tibia.

Size.—Female, length 5 mm, width (pronotum) 1.2 mm, (abdomen) 2.5 mm; male, length 4.8 mm, width (pronotum) 1.2 mm, (abdomen) 2.2 mm.

Holotype female, allotype male, and 11 paratypes (slide-mounted), near Klamath Lake, Ore. The types are in the U. S. National Museum. Specimens are also at hand from Vale, Ore., May, 1934, and French Glen, Harney Co., Ore., Aug. 14, 1954 (G. G. Hansen); Miami Ranger Station, Mariposa Co., Calif., July 23, 1946 (R. L. Usinger); Coalinga, Fresno Co., Calif., June 15, 1945, *Myotis thysanodes* Miller (W. W. Balquest). These agree with the types but are not included in the paratype series.

This species is closest to typical *C. pilosellus* but differs in the wider hemelytral pads; smaller size; and distinctive chromosome pattern, the haploid number at second metaphase being 14A + XY.

18. ***Cimex adjunctus*** Barber
(Fig. 12–18)

Cimex adjunctus Barber, 1939b, Proc. Entomol. Soc. Wash. 41: 244, fig. 1.
Cimex adjunctus, Usinger, 1950, *in* Herms, Med. Entomol., 4th ed., p. 100.
Cimex adjunctus, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 21.

Male.—Head 0.8 mm wide; ratio of width to length 28:24; interocular space about 5 times as wide as an eye, 20:4. Antennae 1.7 mm long; proportion of segments 6:20: 20:14. Rostrum 0.71 mm long, reaching about to middle of prosternum (slide-mounted); proportion of segments approximately 9:8:8.

Pronotum 2½ times as wide as long, 48:19; 1.37 mm wide; sides rather evenly arcuate; disk (dried specimen) depressed laterally, more broadly so anteriorly than posteriorly, submarginally impressed posteriorly on either side; longest bristles at sides much longer than width of an eye, 7:4, 0.22 mm long; discal bristles much longer than distance between bristles.

Hemelytral pads over ½ again as wide as long, 33:20; contiguous at middle for a distance greater than ½ that of exposed part of scutellum; disk with bristles nearly twice as long as distance between bristles.

Abdominal disk clothed with rows of fine long bristles, the longest bristles near hind

margins of tergites exceeding edges in some cases by as much as ¾ their length. All bristles much longer than distance between bristles.

Legs stout; hind femora more than 2½ times as long as wide, 38:14. Outer erect bristles of hind tibiae nearly as long as thickness of tibiae.

Female.—Similar to male in essential characters, the bristles not sexually dimorphic. Spermalege transverse and tubular, the hind margin of fifth segment over it roundly emarginate and the bristles continuous across area of spermalege.

Size.—Male, length 5.51 mm, width (pronotum) 1.37 mm; female, length 6 mm, width (pronotum) 1.4 mm.

Described from a male and female, paratypes, Allentown, Penn., March, 1939, type no. 53750, U. S. National Museum.

Cimex adjunctus has the relatively broad pronotum of *pilosellus* but differs in the usually much longer bristles at the sides of pronotum and longer bristles on hind tibiae. It is widely distributed over the eastern United States and reaches Colorado. The haploid chromosome number at second metaphase in specimens from Woodford, Kentucky was 14A + $X_1X_2X_3X_4Y$.

In the U. S. National Museum are paratypes from the following localities: Lancaster, Penn., July 26, 1937 (H. W. Young); Reading, Penn., June 8, 1934 (Seibert); Rennocetarville, N. Y., June 15, 1921; Bowman's Bluff, N. C., July 16, 1898, on *Nycticeius crepuscularis* Le Conte; Contoocook, N. H., Aug. 10, 1936 (G. & E. Wheeler); Newark, Del., July 26, 1938 (V. L. Simpson); Ramsey, N. J., June 10, 1938 (H. B. Arnold); Masontown, Penn., Oct. 10, 1933 (R. J. Shields); Walton, N. Y., Aug. 26, 1934 (Mrs. Edmund More); Grady Co., Ga., June 24, 1935 (Komarek), from Florida brown bat; Clifton, Cincinnati, Ohio, May 9, 1932 (J. G. Stroebel); Harrisburg, Va. (J. H. Dyerle); Nelson Co., Va., June 28, 1916 (W. Robinson); Smyrna, Del., Aug. 20, 1936 (Bishopp no. 25792).

Specimens in the U. S. National Museum in addition to the paratypes are from Muscatine, Iowa, May, 1940 (G. J. Collins); Ft. Collins, Colo., June 29, 1916 (O. G. Babcock); Camp Ogontz, Maine, July 10, 1942; Chaptico, Md., Aug. 29, 1953 (C. E. Yunkers); Morris Plains, N. J., July 16, 1919 (A. Mitchell and A. H. Wood); Chatam, Va., Dec. 1943 (L. A. Heterick); Jackson Co., Ind. (N. Wilson) on *Myotis l. lucifugus* (Le Conte); Hamptonville, N. C., June 26, 1944 (H. C. Ball); Wayne Co., Ind., on *Myotis sodalis* Miller; S. Kingston, R. I., Apr. 25, 1955 (J. Mathewson); Irwin, Penn., June 19, 1952 (G. E. Smetak); Salisbury, Vt., June 20, 1950 (H. B. Hitchcock), ex *M. l. lucifugus* (Le Conte); Park Co., Ind. (N. Wilson) on *Eptesicus fuscus* (Palisot de Beauvois); Greeley, Colo., May 24, 1933.

Other specimens before me are from: Nacogdoches, Texas, June 25, 1962 (J. S. Weiseman) ex *Nycticeius humeralis* (Rafinesque); Columbia, S. C., ex *Nycticeius humeralis* (Rafinesque); Garfield Co., Colo., July 10, 1937 (K. E. Staeger), ex *Myotis carissima* Thomas; Ft. Collins, Colo.,

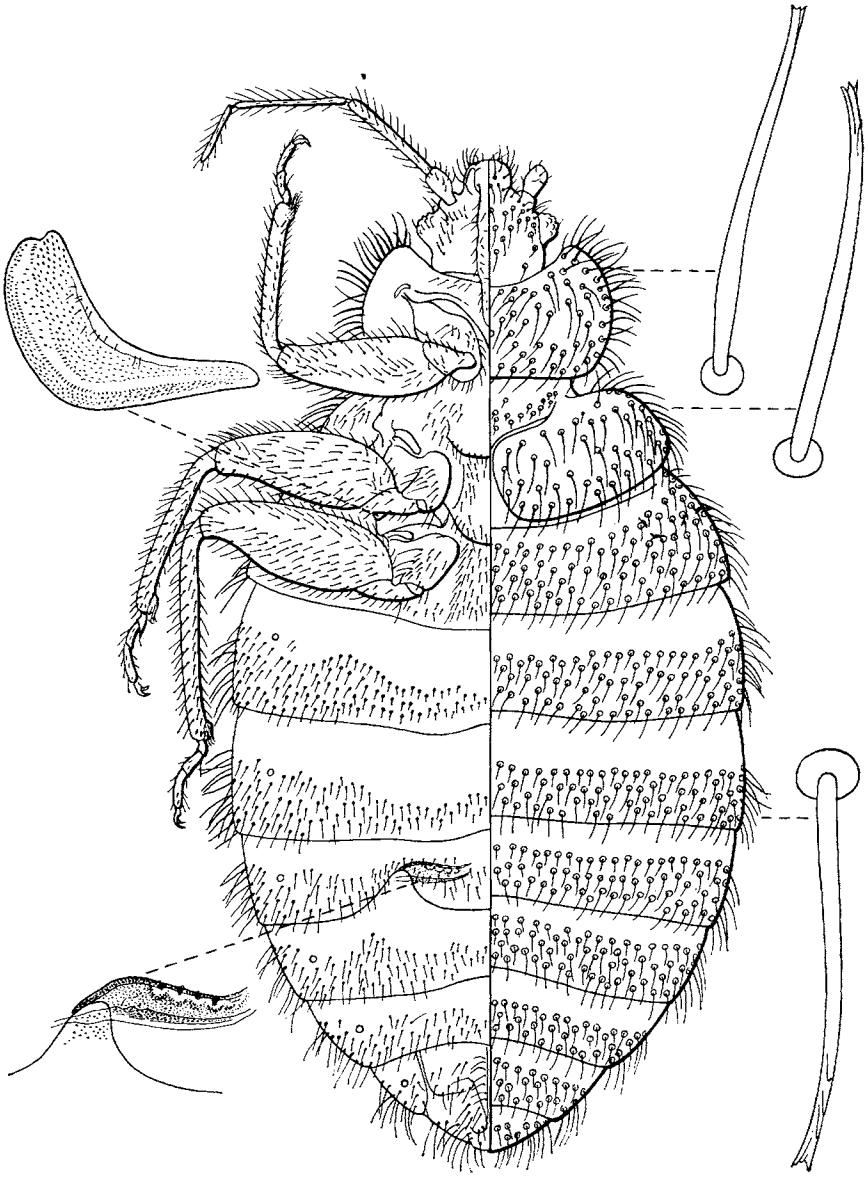

FIG. 12–18.—*Cimex adjunctus* Barber. Female paratype. Allentown, Pennsylvania (Celeste Green, original).

July 24, 1899; Smelter Ranch, Maybell, Colo., June 18, 1942 (J. L. Swauger) ex *Myotis californicus* (Audubon and Bachman); Lincoln, Nebr., Aug. 28, 1910 (J. T. Zimmer) ex *Lasionycteris noctivagans* (Le Conte); Auburn, Ala., May 24, 1938 (F. S. Barkalow) ex *Nycticeius humeralis* (Rafinesque); Melbourne, Brevard Co., Fla., June 26, 1952 (Wm. Duelmann) ex *Nycticeius humeralis* (Rafinesque); 5 mi. S. Moorefield, Hardy Co., W. Va. (L. W. Wilson) ex *Myotis l. lucifugus* (Le Conte); Virginia (R. E. Ryckman).

Records in the collection at Purdue University sent by Leland Chandler (determinations by Nixon Wilson) are as follows: INDIANA: Bartholomew Co., Azalia, July 4, 1957, *Myotis l. lucifugus* (Le Conte) (N. Wilson), and Columbus, July 29, 1958, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Boone Co., Thorntown, Aug. 19, 1959, *Myotis l. lucifugus* (Le Conte) (N. Wilson); Carroll Co., Pittsburg, Aug. 5, 1959, *Myotis l. lucifugus* (Le Conte) (N. Wilson), and Rockfield, Aug. 5, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson); Clark Co., Nabb, July 10, 1959, *Myotis l. lucifugus* (Le Conte) (B. Gross); Clay Co., Ashboro, June 21, 1958, *Myotis l. lucifugus* (Le Conte) (R. Mumford); Crawford Co., Alton, Aug. 11, 1959, *Eptesicus fuscus* (Beauvois) (B. Gross); De Kalb Co., Waterloo, July 20, 1959, *Eptesicus fuscus* (Beauvois) (J. B. Cope); Fulton Co., Fulton, July 24, 1959, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Grant Co., Fairmount, April 15 and June 11, 1958, *Eptesicus fuscus* (Beauvois) (R. Kirkpatrick); Hamilton Co., Cicero, Aug. 19, 1959, *Myotis l. lucifugus* (Le Conte) (N. Wilson); Henry Co., Grant City, July 29, 1959, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Jackson Co., Cortland, May 28 and June 14, 1954, *Myotis l. lucifugus* (Le Conte) (R. Mumford); Jay Co., Bluff Point, July 15, 1959, *Eptesicus fuscus* (Beauvois) (J. B. Cope); La Grange Co., Topeka, July 19, 1959, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Lawrence Co., Tunnelton, July 4, and Oct. 7, 1956, and July 4, 1957, *Myotis l. lucifugus* (Le Conte) (N. Wilson); Martin Co., Shoals, Aug. 12, 1959, *Myotis l. lucifugus* (Le Conte) (B. Gross); Montgomery Co., Yountsville, July 3, 1958, *Eptesicus fuscus* (Beauvois) (N. Wilson); Orange Co., Millersburg, Aug. 7, 1958, *Nycticeius humeralis* (Rafinesque) (J. B. Cope); Park Co., Turkey Run State Park, May 8, 1953, July 24, 1954, Sept. 7, 1957, and May 3, 1958, *Eptesicus fuscus* (Beauvois) (J. B. Cope and N. Wilson); Putnam Co., Reelsville, Aug. 8, 1959, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Ripley Co., Friendship, July 17, 1957 and July 10, 1959, and Olean, July 10, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson); Rush Co., Milroy, July 31, 1959, *Myotis l. lucifugus* (Le Conte) (J. B. Cope); Tippecanoe Co., Raub, July 22, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson), and W. Lafayette, May 23 and June 25, 1957, *Eptesicus fuscus* (Beauvois) (N. Wilson and B. Munyon); Washington Co., July 20, 1954, *Nycticeius humeralis* (Rafinesque) (R. Mumford); Wayne Co., Dalton,

July 29, 1959, *Eptesicus fuscus* (Beauvois) (J. B. Cope), and Pershing, Aug. 11, 1954, *Eptesicus fuscus* (Beauvois) (G. L. Ward); White Co., Norway, Aug. 20, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson). KENTUCKY: Clark Co., Winchester, Aug. 18, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson); Nelson Co., Bardstown, Dec. 23, 1955, and Aug. 15, 1959, *Eptesicus fuscus* (Beauvois) (N. Wilson); Webster Co., Onton, Aug. 1, 1958 and Aug. 17, 1959, *Nycticeius humeralis* (Rafinesque) (N. Wilson).

19. ***Cimex brevis*** Usinger and Ueshima

(Fig. 12–19)

Cimex brevis Usinger and Ueshima, 1965, Pan-Pacific Entomol. 41: 117.

Female.—Head 0.67 mm wide, 0.55 mm long, the ratio of width to length 27:24; interocular space 0.52 mm wide, 7 times as wide as an eye. Antennae 1.42 mm, proportion of segments 4:18:19:16. Rostrum with second segment surpassing base of head, proportion of segments 8:7:8.

Pronotum 1.1 mm wide, 0.45 mm long, the ratio of width to length 44:18; ratio of pronotal width to head width 44:27; sides almost evenly arcuate, subdepressed laterally, the longest bristles at edges 0.44 mm, very thin, twice as long as width of first antennal segment; bristles on disk generally longer than distance between bristles, even at center.

Hemelytra over twice as wide as long, 34:14, the disk with bristles generally twice or more as long as distance between bristles.

Abdomen with bristles more than 0.25 mm long, those near hind margins of segments surpassing the margin by more than ½ their length. Ectospermalege widened, the notch in hind margin of fourth visible ventral segment rather narrowly emarginate.

Legs with hind femora slightly more than 2½ times as long as wide, 32:12.

Male.—Like the female but pronotum 42:18. Hemelytra twice as wide as long, 32:16.

Size.—Male, length 4.85 mm, width (pronotum) 1.1 mm, (abdomen) 2.2 mm; female, length 4.75 mm, width (pronotum) 1.1 mm, (abdomen) 2.3.

Holotype female, allotype male, and 23 paratypes, Staples, Minn. (R. Ryckman) associated with unidentified bat. The types are in the U. S. National Museum. Chromosome complement at second metaphase, $14A + X_1X_2X_3X_4Y$.

Other records are: Carbondale, Ill., Sept. 1940, ex *Myotis l. lucifugus* (Le Conte); Ontario, Mich., Sept. 2, 1963 (C. W. Schaefer); Brownsburg, Quebec, Canada, Aug. 22, 1965 (W. Gagné).

This species is closest to *adjunctus* but differs in the long tibial bristles and smaller size.

20. ***Cimex antennatus*** Usinger and Ueshima

(Fig. 12–20)

Cimex pilosellus strain A, Ueshima, 1963a, Chromosoma 14: 512.
Simex antennatus Usinger and Ueshima, 1965, Pan-Pacific Entomol. 41: 115.

Female.—Head 0.85 mm wide, including eyes, the ratio of width to length (excluding labrum) 34:28; width of interocular space 0.65 mm, 6 times as wide as an eye. An-

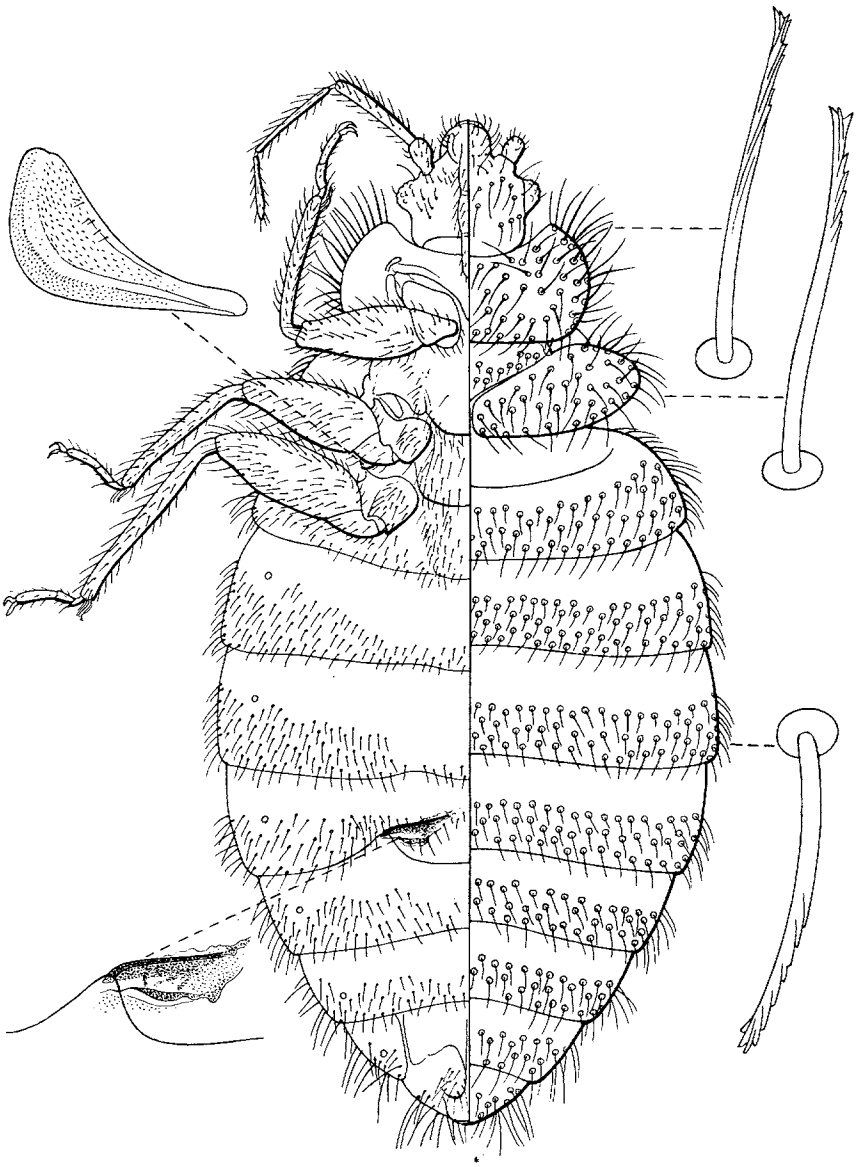

FIG. 12–19.—*Cimex brevis* Usinger and Ueshima. Female paratype. Staples, Minnesota (Celeste Green, original).

FIG. 12–20.—*Cimex antennatus* Usinger and Ueshima. Female paratype. Pope Valley, Napa County, California (Celeste Green, original).

tennae 1.7 mm long, proportion of segments 6:22:23:17. Rostrum 0.75 mm long, the second segment reaching hind margin of head, proportion of segments approximately 9:8:10.

Pronotum 1.3 mm wide and 0.55 mm long at middle, the ratio of width to length 50:22 and ratio of pronotal width to head width 50:34; sides evenly arcuate and narrowly sublaterally depressed; disk with bristles longer than distance between bristles except at middle; side bristles relatively stout, truncate and serrate, the longest 0.31 mm, exceeding width of first antennal segment.

Hemelytral pads nearly twice as wide as long, 37:20; disks with bristles more than twice as long as distance between bristles.

Abdomen with bristles of terga about 0.25 mm long, much longer than distances between bristles; posterior rows of bristles exceeding edge by much more than ½ the length of bristles.

Ectospermalege tubular beneath asymmetrical emargination of hind margin of fourth visible ventral segment.

Legs stout, the hind femora 2.5 times as long as wide, 40:16.

Male.—Like the female but pronotum 1.26 mm wide.

Size.—Male, length 5.8 mm, width (pronotum) 1.26 mm, (abdomen) 2.6 mm; female, length 5.35 mm, width (pronotum) 1.3 mm, (abdomen) 2.6 mm.

Holotype female, allotype male, and 19 paratypes (slide-mounted), Pope Valley, Calif., ex *Antrozous pallidus* (Le Conte) (A. J. Beck and N. Ueshima). The types are in the U. S. National Museum. This species has a haploid chromosome count of 11A + XY. It differs from *pilosellus* and *adjunctus* in the relatively narrower pronotum. It differs from *incrassatus* in having shorter bristles and less incrassate hind femora.

Additional specimens are at hand as follows: 1 adult and 4 nymphs, San Jose, Calif., Apr. 24, 1942; 1 specimen near Woodland, Yolo Co., Calif., ex *Tadarida brasiliensis mexicana* (Saussure); 1 specimen, Alameda Co., Calif., Apr. 5, 1945, ex *Antrozous,* no. AP 21677; 1 specimen Gualala River, Mendocino Co., Calif. (H. S. Fuller); 1 specimen, Hail Rindy, Little Shasta Rd., Siskiyou Co., Calif., July 13, 1963, *on Antrozous pallidus* (Le Conte) (A. J. Beck); 20 specimens, Murphys, Calaveras Co., Calif., Oct. 30, 1965 (N. Ueshima and P. Rubtzoff); Happy Valley, Contra Costa Co., Calif., Sept. 21, 1965, on *Antrozous pallidus* (Le Conte) (N. Ueshima and P. Rubtzoff); Carson City, Nev., Oct. 29, 1965 (N. Ueshima and P. Rubtzoff).

21. ***Cimex incrassatus*** Usinger and Ueshima
(Fig. 12–21)

Cimex pilosellus, Bradshaw and Ross, 1961, J. Ariz. Acad. Sci. 1: 110–11.
Cimex pilosellus strain B, Ueshima, 1963a, Chrômosoma 14: 512.
Cimex incrassatus Usinger and Ueshima, 1965, Pan-Pacific Entomol. 41: 115.

Female.—Head 0.8 mm wide, 0.625 mm long, the ratio of width to length 32:25; interocular space 0.60 mm, 6 times as wide as an eye. Antennae 1.5 mm long, pro-

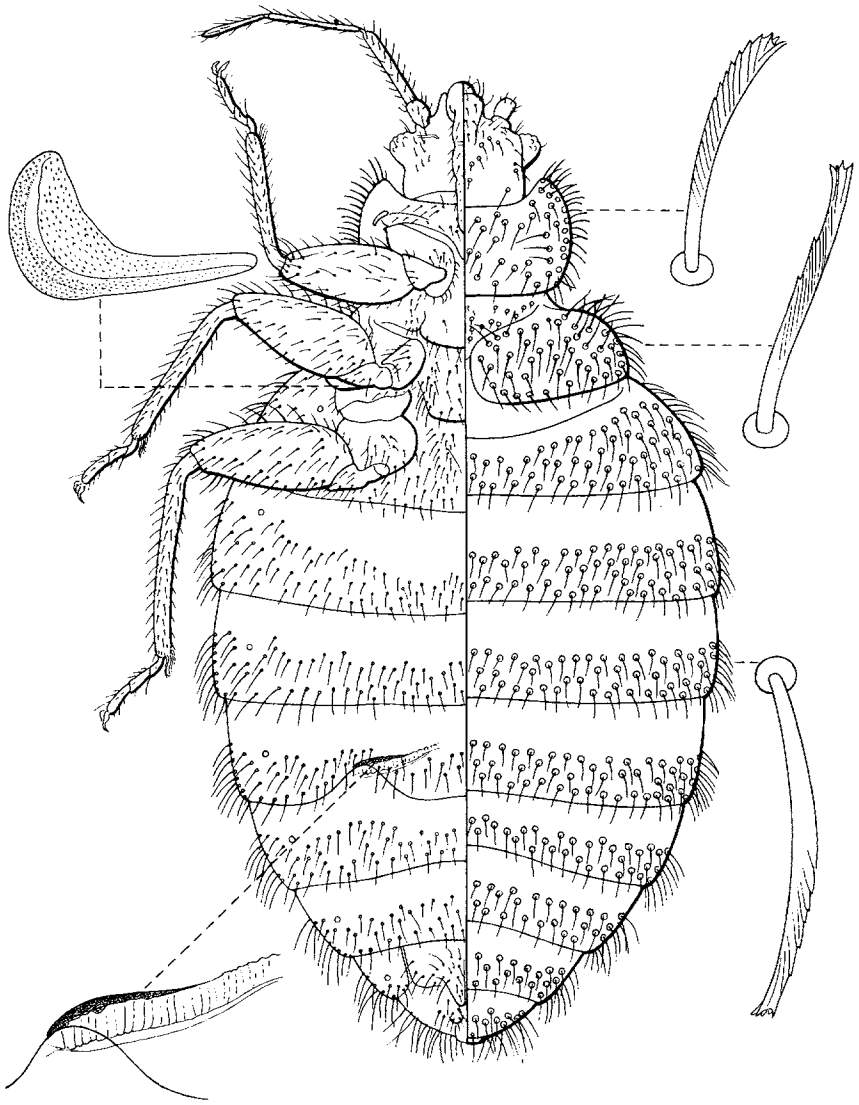

FIG. 12–21.—*Cimex incrassatus* Usinger and Ueshima. Female paratype. St. David, Arizona (Celeste Green, original).

portion of segments 6:18:20:16. Rostrum with second segment not quite reaching hind margin of head, proportion of segments 8:8:10.

Pronotum 1.2 mm wide and 0.5 mm long, the ratio 48:20; ratio of pronotal width to head width 48:32; sides slightly more arcuate anteriorly, feebly depressed laterally, the longest side bristles about 0.28 mm, distinctly longer than width of first antennal segment, 23:18, relatively stout and serrate on outer edges; bristles of disk generally longer than distance between bristles except at middle.

Hemelytra nearly twice as wide as long, 36:19; disk with bristles generally over twice as long as distance between bristles.

Abdomen with bristles of terga about 0.25 mm, much longer than distance between bristles, the posterior row of bristles on each segment exceeding hind margin by much more than ½ a bristle length. Ectospermalege tubular beneath rather broadly and evenly emarginate hind margin of fourth visible ventral segment.

Legs stout, the hind femora 2.17 times as long as wide, 37:17.

Male.—Similar to female but with lateral bristles of pronotum somewhat thinner and hind femur 0.40 times as stout as long.

Size.—Male, length 5.2 mm, width (pronotum) 1.1 mm, (abdomen) 2.49 mm; female, length 5.25 mm, width (pronotum) 1.2 mm, (abdomen) 2.8 mm.

Holotype female, allotype male, and 16 paratypes, St. David, Cochise Co., Ariz., ex *Eptesicus fuscus* (Palisot de Beauvois) (N. Ueshima). The types are in the U. S. National Museum. The chromosome complement is 10A + XY at second metaphase.

This species differs from *antennatus* not only in number of autosomes but also in the slightly longer bristles, stouter hind femora, and different antennal proportions.

Additional specimens in the U. S. National Museum are from the following localities. ARIZONA: Mine tunnel, Picacho Peak, May 24, 1940 (G. M. Kohls), no. AP17865; near Red Rock, 1940, biting *Myotis velifer velifer* (J. A. Allen) (J. Bequaert); Burney Mine Road, *Eptesicus fuscus* (Beauvois) (G. Vr. Bradshaw); 8 mi. S. Winkleman, May 23, 1959 (A. Ross), on *Myotis velifer* (J. A. Allen) (all Pinal Co.); Mescal, July, 1928 (R. H. Beamer); Willcox, Aug. 4, 1909 (A. K. Fisher), from *Antrozous*; July, 1961 (C. R. Ash); Aug. 1, 1959 (A. Ross), on *Eptesicus fuscus* (Beauvois); July 30, 1959 (A. Ross), on *Antrozous pallidus* (Le Conte); June 10, 1959 (L. Cockrum), on *Eptesicus fuscus* (Beauvois); June 21, 1959 (G. Vr. Bradshaw), on *Eptesicus fuscus* (Beauvois) (all Cochise Co.); Mine tunnel, Arivaca, May 27, 1940 (G. M. Kohls), no. AP17873; Madera Cyn., April 15, 1959 (A. Ross), on *Eptesicus fuscus* (Beauvois); Beehive Mine, Tucson Mtn., May 30, 1959 (G. Vr. Bradshaw), on *Myotis velifer* (J. A. Allen) (all Pima Co.); Nogales, Oct. 7, 1940 (Ehinger); White Oak Mine, Walker Cyn., May 28, 1959 (A. Ross), on *Eptesicus fuscus* (Beauvois) (all Santa Cruz Co.); Graham Mtns., Aug. 1951, *Myotis;* Highway bridge, U. S. 70, 7.3 mi. NW of Pima, Sept. 20, 1959 (G. Vr. Bradshaw), on *Myotis yumanensis* (H. Allen), no. 1754 (both Graham Co.); Twin Windmills, 5 mi. SE Kingman, July 11, 1959

(Wm. Musgrove) on *Pipistrellus hesperus* (H. Allen) (Mohave Co.). UTAH: Salt Lake City, Oct. 4, 1948 (K. R. Kelson) no. 90876. NEVADA: Lincoln Co., Panaca, Sept. 2, 1955 (R. F. Koontz); Elko Co., Elko, Dec. 19, 1956, Apr. 27, 1957, July 25 and Sept. 28, 1959, Mar. 21, 1960, June 5, 1961 (J. M. Del Curto). CALIFORNIA: San Bernardino Co., Vidal, June 17, 1940 (G. M. Kohls) on *Corynorhinus rafinesquii pallescens* Miller, no. AP17886; Mine Tunnel, Laguna Dam, May 21, 1940 (G. M. Kohls), no. AP17859.

MEXICO: Baja California, Mina la Republica, 4000 ft, July 31, 1949 (S. B. Benson), ex *Myotis thysanodes* Miller; La Paz, 9 mi. SW, July 22, 1964, ex bat in *Pachycereus* woodpecker hole (R. E. Ryckman, C. P. Christianson); Santiago, *Tadarida brasiliensis mexicana* (Saussure); Puebla, 9 mi. NE Acatzingo, Aug. 3, 1954 (R. A. Alcorn), *Eptesicus.*

Two additional specimens may belong here but have the head slightly narrower with respect to the pronotum: Mexico, Santa Catarina, Nuevo Leon, April, 1940, on *Pipistrellus hesperus* (E. V. Miller), and Chocoyos, Chimaltenango, Guatemala, elev. 6300 ft, April 28, 1948, on floor of cave containing *Myotis velifer* and *Tadarida mexicana* (= *Tadarida brasiliensis* (I. Geof. St.-Hilaire)) (R. L. Wenzel, R. D. Mitchell).

Genus *Oeciacus* Stål

Oeciacus Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2): 104.
Oeciacus, Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Oeciacus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 260.
Oeciacus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 254.
Oeciacus, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Oeciacus, Jordan, 1922, Ectoparasites 1: 284.
Oeciacus, Myers, 1928, Parasitology 20: 162.
Oeciacus, Börner, 1935, Tierwelt Mitteleurop. 4 (3);X: 36.
Oeciacus, Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 130.
Oeciacus, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 295 (part).
Oeciacus, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 1.
Oeciacus, Kiritshenko, 1951, Hemip. Europ. Russia, p. 103.
Oeciacus, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3): 79.

Size 3 (pinned) to 5 mm (slide-mounted). Bristles long, dense, often described as "silky", the long bristles of sides of body approximately of equal length, minutely serrate on their outer sides. Surface rugose but not punctured, abdominal tergites transversely rugose.

Head a little wider than long, approximately 0.7 mm to 0.8 mm wide across eyes. Eyes relatively small, not strongly exserted, about ⅕ as wide as interocular space. Clypeus about ½ as wide as interocular space. Bristles long and numerous on labrum, clypeus, juga, and vertex ½ way from base of clypeus to hind margin of head, and a row of long bristles along inner margins of eyes extended by 2 long bristles on each side back toward base of head. Antennae a little longer or shorter than width of pronotum; first segment short and stout; remaining segments longer and subequal, or second a little longer than third and fourth. Rostrum (pinned specimen) reaching nearly to apices of front coxae; second segment attaining base of head.

Pronotum over twice as wide as long and ½ again as wide as head; sides narrowly

subflattened and evenly arcuate; disk and sides with long curved bristles, the longest being about 0.2 mm.

Mesonotum-scutellum broadly exposed, subtriangular; apex distinctly produced; disk with fine short bristles posteriorly.

Hemelytral pads ⅔ as long as broad, arcuate anterolaterally and less so on posterior margin; bristles of disk shorter than those of sides.

Legs moderately stout; hind femora about 3 times as long as broad; tibiae ¼ longer than femora, straight, apices with tufts in both sexes.

Metasternum broad and platelike between coxae.

Female spermalege right ventral on anterior margin of sixth segment; sclerotized part as seen in cleared specimens transverse but short. Hind margin of fifth segment narrowly cleft into a paragenital sinus like that in *C. lectularius* and allies.

Male genital segment a little broader than long, sloping to left with a ventral groove for paramere; the latter reaching ⅔ or ¾ the distance to base of left margin.

Type-species: *Cimex hirundinis* Lamarck.

This is a Holarctic genus, occurring in Eurasia and North America south to Morocco in North Africa and Durango in Mexico. It occurs in the mud nests of swallows. *Oeciacus* differs from *Cimex* in its smaller size, longer bristles, thicker third and fourth antennal segments, higher ratio of head width to third antennal length, and shorter ectospermalege. These might be regarded as specific rather than generic characters. However, when taken in conjunction with the host differences, they seem adequate to justify separate genera. The chromosomes ($14A + X_1X_2Y$) are within the range of types seen in the genus *Cimex*.

In folk-lore, swallows are said to bring bed bugs and the bugs do, indeed, bite man when nests are disturbed. However, there is no record of *Oeciacus* becoming attached to man.

KEY TO THE SPECIES OF *OECIACUS*

1. Size small, width of pronotum 0.83–0.9 mm. HW/3rd ant. ratio 2.5 or more. Palearctic Region. ..... 22. ***hirundinis***
   Size larger, width of pronotum 1.0 mm or more. HW/3rd ant. ratio less than 2.3. Nearctic Region. ..... 23. ***vicarius***

22. ***Oeciacus hirundinis*** (Lamarck)

(Fig. 12–22)

Cimex hirundinis Lamarck, 1816, Hist. Nat. Anim. sans Vertebr. 3: 502–503.
Cimex sp. Latreille, 1829, *in* Cuvier, Règne Animal, 2nd ed. 5: 201.
Acauthia hirundinis Schummel, 1832, *in* Gravenhorst, Arb. Schles. Ges. Vaterl. Kultur, Breslau (1832) : 73–4.
Cimex hirundinis Jarocki, 1838, Zool. Zwierz. ogólne VI. Warsaw, p. 55–8.
Cimex hirundinis Jenyns, 1839 (June) , Ann. Nat. Hist. 3: 243.
Acanthia hirundinum Siebold, 1839 (December) , Preuss. Provinzialbl. 22: 552.
Acanthia ciliata Eversmann, 1841, Bull. Imp. Soc. Nat. Moscou 14: 359.
Cimex nidularius Rondani, 1842, Bol. Accad. Aspir. Nat. Napoli 1: 98–99.
Cimex hirundinis Herrich-Schäffer, 1853, Alph. Synon. Verz. Wanzenart. Ins., Index, p. 52 (*nomen nudum*) .
Acanthia hirundinis, Dohrn, 1859, Cat. Hemip., p. 44.
Cimex nidularius, Costa, 1860, Addit. Cent. Cim. Reg. Neap. 1, f. 2.
Acanthia generalii Picaglia, 1884, Atti Soc. Nat. Modena (Rendic.) (3) 2: 44.

Cimex hirundinis, Saunders, 1892, Hemip. Heterop. Brit. Is., p. 187.
Cimex hirundinis, Hueber, 1893, Fauna Germ. Wanzen, p. 192.
Cimex generalii, Horvath, 1910b, Ann. Mus. Nat. Hung. 8: 362.
Cimex hirundinis, Brumpt, 1910, Précis Parasitol., p. 562.
Oeciacus hirundinis, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 261.
Oeciacus hirundinis, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 254.
Clinocoris ciliatus, Castellani and Chalmers, 1913, Man. Trop. Med., 2nd ed., p. 640.
Oeciacus hirundinis, Castellani and Chalmers, 1913, Man. Trop. Med., 2nd ed., p. 640.
Oeciacus hirundinis, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Oeciacus hirundinis, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 766.
Oeciacus hirundinis, Bacot, 1921, Proc. Entomol. Soc. London, p. ii.
Cimex hirundinis, Butler, 1923, Biol. Brit. Hemip.-Heterop., p. 321.
Cimex hirundinis Lamarck, Stiles, 1924, Smiths. Misc. Collect. 73 (2) : 22.
Cimex hirundinis Lamarck, Sherborn, 1927, Index Animalium, Part 12, p. 3010.
Oeciacus hirundinis, Myers, 1928, Parasitology 20: 161.
Oeciacus hirundinis, Börner, 1935, Tierwelt Mitteleurop. 4 (3) ;X: 36.
Oeciacus hirundinis, Eichler, 1937, Zool. Anz. 120: 267.
Oeciacus hirundinis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 206.
Oeciacus hirundinis, Hase, 1938, Z. Parasitenk. 10: 1.
Oeciacus hirundinis, Michalk, 1938, Sitzungsber. Naturforsch. Ges. Leipzig 63–64: 102.
Oeciacus hirundinis, Wendt, 1939a, Arch. Ver. Naturgesch. Mecklenburg, N.F., 14: 71–94.
Oeciacus hirundinis, Wendt, 1941a, *in* Gulde, Wanzen Mitteleurop. 8: 130.
Oeciacus hirundinis hirundinis, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Oeciacus hirundinis, Dubinin, 1947, Entomol. Oboz. 29: 232.
Oeciacus hirundinis, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 1.
Oeciacus hirundinis, Kiritshenko, 1951, Hemip. Europ. Russia, p. 104.
Oeciacus hirundinis, Rothschild and Clay, 1952, Fleas, Flukes and Cuckoos, p. 247, pl. 36.
Oeciacus hirundinis, Massee, 1955, Entomol. Mon. Mag. 91: 14–15.
Oeciacus hirundinis, Povolný, 1957, Zool. Listy, Folia Zool. 6 (20) : 73.
Oeciacus hirundinis, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Oeciacus hirundinis, Stichel, 1959, Illus. Bestimm. Wanzen II. Europa 3 (3) : 79.
Oeciacus hirundinis, Hicks, 1959, Check-List and Bibliogr., p. 244; 1962, Suppl. 1, p. 261.
Oeciacus hirundinis, Southwood & Leston, 1959, Land and Water Bugs Brit. Is., p. 187.
Oeciacus hirundinis (Schummel) , Jabłońska, 1964, Bull. Entomol. Pologne 34: 186.

Female.—Body small and generally pale. Surface obscurely, rugosely punctured.

Head 0.65 mm wide; ratio of length to width 18:23; ratio of eye width to interocular space 3:17. Antennae 1 mm long; proportion of segments 4:11:10:10. Rostrum 0.56 mm long; proportion of segments approximately 7:6:7.

Pronotum 0.94 mm wide; ratio of length to width 13:33; longest bristles at sides about 0.14 mm.

Mesonotum a little more than twice as wide as long, 20:9; short bristles of disk about 1/5 as long as side bristles of pronotum.

Hemelytral pads meeting briefly at middle; ratio of length to width 14:23.

Bristles on abdominal disk long, forming 3 or 4 ill-defined rows on segments after

the second; anterior bristles on each segment only slightly longer than distance between bristles; posterior bristles much longer, extending beyond edge of segment by more than ½ their length.

Legs stout; ratio of length to width of hind femora 25:9.5.

Male.—Paramere reaching ¾ of distance to base of left margin of genital segment.

Size.—Male, length 3.70 mm, width (pronotum) 0.75 mm, (abdomen) 1.6 mm; female, length 3.80 mm, width (pronotum) 0.84 mm, (abdomen) 1.65 mm (dried specimens measure 2.9–3.1 mm).

Redescribed from specimens collected at Tvärmine, southern Finland, July, 1958 (R. L. Usinger) in swallow nests. Jenyns' type in the museum at Oxford University is from Cambridgeshire. Additional material is at hand from Germany, Greece, Lebanon, and Morocco. Massee (1955) lists it from Ireland and from 16 counties in the south of England. Stichel (1959) adds Norway, Sweden, Denmark, Russia, France, Netherlands, Poland, Austria, Albania, Czechoslovakia, Hungary, Yugoslavia, and Roumania. In the British Museum (Nat. Hist.) spirit collection are specimens from Switzerland, Portugal, and Algeria. Drenski (1928) adds a record from Bulgaria. Hoogstraal (in litt.) reports *hirundinis* from Turkey, and Jellison (in litt.) adds Sardinia.

Wendt (1939a) and Dubinin (1947) give accounts of the life history of *Oeciacus hirundinis*. The principal host is the house martin (Mehlschwalbe, hirondelle de fenêtre), *Delichon urbica* (L.). Other hosts that have been reported are the European barn swallow, *Hirundo rustica* L.; the red-rumped swallow, *Hirundo daurica* L.; the sand martin, *Riparia riparia* L.; the house sparrow, *Passer domesticus* L.; the starling, *Sturnus vulgaris* L.; the swift, *Apus apus* L.; the woodpecker *Dendrocopus major* (L.); the rock sparrow, *Petronia petronia* L.; the wheatear, *Oenanthe oenanthe* (L.); the skylark, *Alanda arvensis* L.; the lesser short-toed lark, *Calandrella rufescens* (Vieillot); the tawny pipit, *Anthus campestris* (L.); Richard's pipit, *Anthus novaeseelandiae richardi* (Vieillot); the yellow wagtail, *Motacilla flava* L.; the white wagtail, *Motacilla alba* L.; the Siberian blue robin, *Luscinia cyane* (Pallas); and the Mongolian lark, *Melanocorypha mongolica* (Pallas). The bugs are found in large numbers in martins' nests during the breeding season of the birds. In the winter when the birds migrate as far as South Africa, some bugs survive in nest crevices and wait for the return of their hosts in the spring.

Hicks (1959, 1962) gives an extensive bibliography with many references not repeated here. Records of *hirundinis* from America prior to 1912 refer to the American swallow bug, *Oeciacus vicarius* Horvath.

The variation in bristle length is considerable, female specimens from Finland having the longest bristles at sides of pronotum 0.1 mm, whereas those from Greece measured 0.2 mm. Kassianoff (1937) described a "Forme aberrante" but gave no name and no details as to locality. Kassianoff (1937) and Eichler (1942) considered *hirundinis* and *vicarius* as

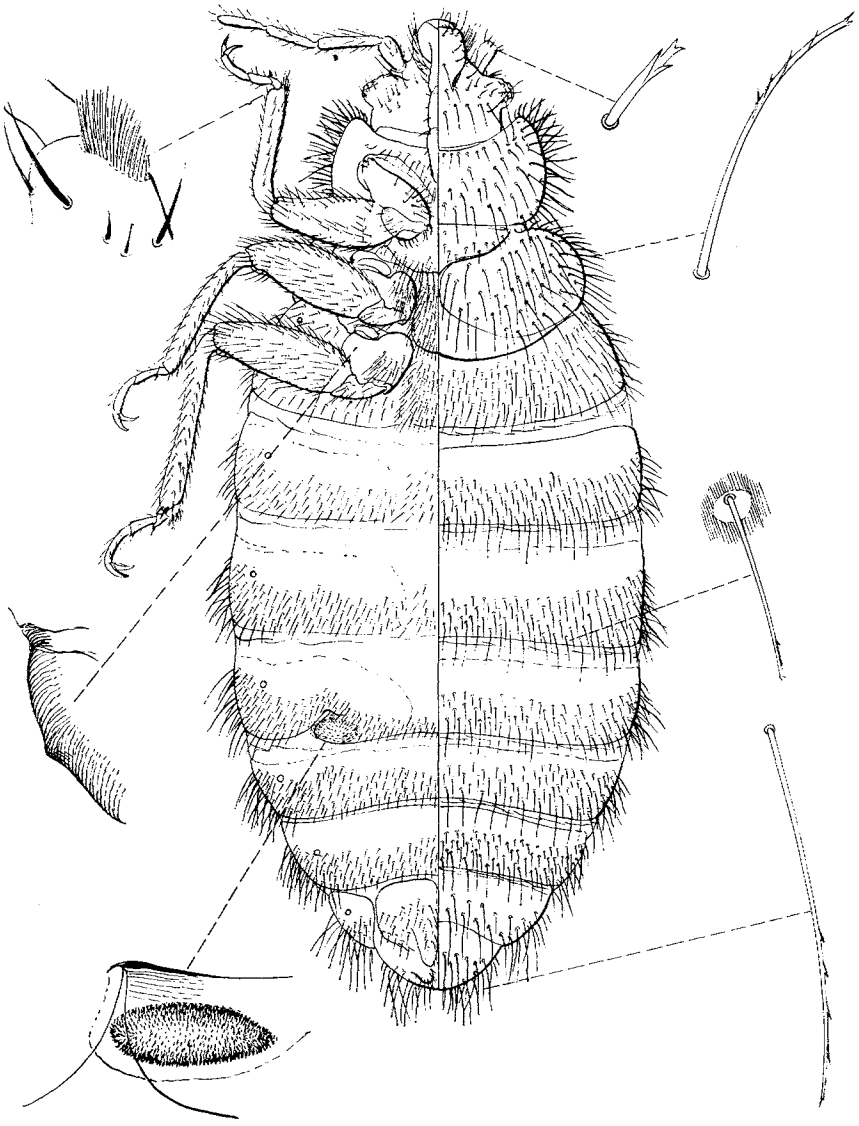

FIG. 12–22.—*Oeciacus hirundinis* (Lamarck). Female. Göttingen, Hanover, Germany (Ferris, original).

subspecies. My attempts to cross the two have failed, so they are here considered as separate species.

The synonymy is complicated by the apparently independent choice of the name *hirundinis* by several early authors. Jenyns' name has been generally accepted as the first, but such well known bibliographical sources as Stiles (1924) in an Opinion of the International Commission on Zoological Nomenclature, and Sherborn (1927) in Index Animalium, called attention to Lamarck's (1816) name. Since Lamarck's work was one of the classics in 19th century natural history and went through at least 2 subsequent editions (1835 and 1839) under the editorship of G. P. Deshayes and H. Milne Edwards, it is astonishing that the briefly but clearly described *Cimex hirundinis* was overlooked. Latreille (1829) referred unmistakably to the species but did not name it. I am indebted to W. E. China for the reference to *Acanthia hirundinum* Siebold (December 1839) and to Dennis Leston for *Acauthia hirundinis* Schummel (1832). The latter name is accepted as valid by Jabłońska (1964), having priority over Jenyns (1839). Jabłońska also cites *Cimex hirundinis* Jarocki (1838).

In the opinion of W. E. China (in litt.) all of the names prior to Jenyns are *nomina oblita,* having been overlooked for more than 50 years. However, Article 23b of the International Code of Zoological Nomenclature has been questioned by entomologists, and the International Commission has not yet published the modifications and clarifications of this controversial rule. Under the circumstances, I have chosen to follow priority and attribute the name to Lamarck.

23. ***Oeciacus vicarius*** Horvath

(Fig. 12–23)

Abcanthia papistrilla Gillette, 1890, Entomol. News 1: 26.
Cimex hirundinis, Osborn, 1892b, Can. Entomol. 24: 264.
Acanthia hirundinis, Gillette and Baker, 1895, Hemip. Colo., p. 56.
Acanthia hirundinis, Osborn, 1896, USDA Div. Entomol. Bull. (n.s.) 5: 161.
Acanthia hirundinis, Lugger, 1900a, Ann. Rep., Div. Entomol., Minn. 6: 51.
Acanthia hirundinis, Kellogg, 1904, Amer. Ins., p. 206.
Oeciacus vicarius Horvath, 1912, Ann. Mus. Nat. Hung. 10: 261.
Oeciacus vicarius, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 254.
Clinocoris hirundinis, Parshley, 1914, Psyche 21: 143.
Oeciacus vicarius Horvath, 1914b, IX^{e} Int. Congr. Zool., p. 295.
Oeciacus vicarius, Blatchley, 1926, Heterop. East. N. Amer., p. 619.
Oeciacus vicarius, Myers, 1928, Parasitology 20: 159–72.
Oeciacus vicarius, Spencer, 1930, Can. Entomol. 62: 20.
Oeciacus vicarius, Spencer, 1935, Proc. Entomol. Soc. Brit. Columbia 31: 43.
Oeciacus vicarius, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 215.
Oeciacus vicarius, Hase, 1938, Z. Parasitenk. 10: 15.
Oeciacus vicarius, Usinger, 1939, *in* Herms, Med. Entomol., 3rd ed., p. 92.
Oeciacus hirundinis vicarius, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Oeciacus vicarius, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 5.
Oeciacus vicarius, Beck, 1953, Proc. Utah Acad. Sci., Arts, Lett. 30: 41.

Oeciacus vicarius, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Oeciacus vicarius, Hicks, 1959, Check-List and Bibliogr., p. 247; 1962, Suppl. 1, p. 261.

Female.—Body larger and darker in color than *hirundinis,* with brown markings laterally or over most of head, center of pronotum, scutellum, and abdomen. Pronotal margins and all of hemelytral pads pale. Surface transversely rugose on abdominal tergites, elsewhere obscurely punctured.

Head 0.74 mm wide; ratio of length to width 22:26; ratio of eye width to interocular space 3:20. Antennae 1.31 mm long; proportion of segments 5:14:14:13. Rostrum 0.6 mm long; segments subequal.

Pronotum 1.06 mm wide; ratio of length to width 16:37; long bristles at sides about 0.2 mm.

Mesonotal length to width ratio 12:25, gradually narrowed to an acute apex; disk with short bristles, several of which extend beyond margins.

Hemelytral pads less than twice as wide as long, 29:18; discal bristles about as long as those on pronotal disk.

Abdomen with bristles very long, those of hind rows of tergites extending ¾ their length beyond edges of segments.

Legs stout; ratio of length to width of hind femora 30:10.5.

Male.—Paramere reaching ⅔ the length of left side of genital segment.

Size.—Male, length 4.6 mm, width (pronotum) 1.12 mm, (abdomen) 2.20 mm; female, length 4 mm, width (pronotum) 1.06 mm, (abdomen) 2.4 mm (pinned specimens 3.6–4 mm).

Redescribed from a male and female, Yankton Bridge, Cedar Co., Nebr., Aug. 10, 1955 (W. F. Rapp and H. E. Baumgarten), in nests of *Petrochelidon albifrons* (Rafinesque). The type, a male, is in the Hungarian National Museum. It is from Los Angeles, Calif. (Coquillett). Material before me ranges from New York to California and from Canada to Mexico. Specimens have been collected throughout the year. R. E. Ryckman has collected *Oeciacus* intensively and is responsible for many of the new records indicated in Fig. 11–15. Although the swallows fly south each winter, *Oeciacus* has never been reported from the Southern Hemisphere. I looked in the mud nests of swallows in Lima, Peru, and Guayaquil, Ecuador, but found no bugs. Curiously, *vicarius* has not been recorded from the southeastern United States, and it is less common throughout the East than in California, where every cliff swallow nest that I have examined has been infested.

O. vicarius is primarily a parasite of cliff swallows, *Petrochelidon albifrons* (Rafinesque). Rarely, it has been reported from the barn swallow, *Hirundo erythrogaster* Boddaert. I found it with *Synxenoderus comosus* List in a nest of the white-throated swift, *Aeronautes saxatalis* (Woodhouse), on a cliff at Mt. Diablo, Calif., but cliff swallows were very abundant on the same cliff. An inexplicable record is the occurrence of specimens which were sent to me for determination by D. Elden Beck from the nest of a wood-rat, *Neotoma cinerea,* in a small cave north of Thistle, Utah County, Utah. Another strange record is from mud-dauber nests

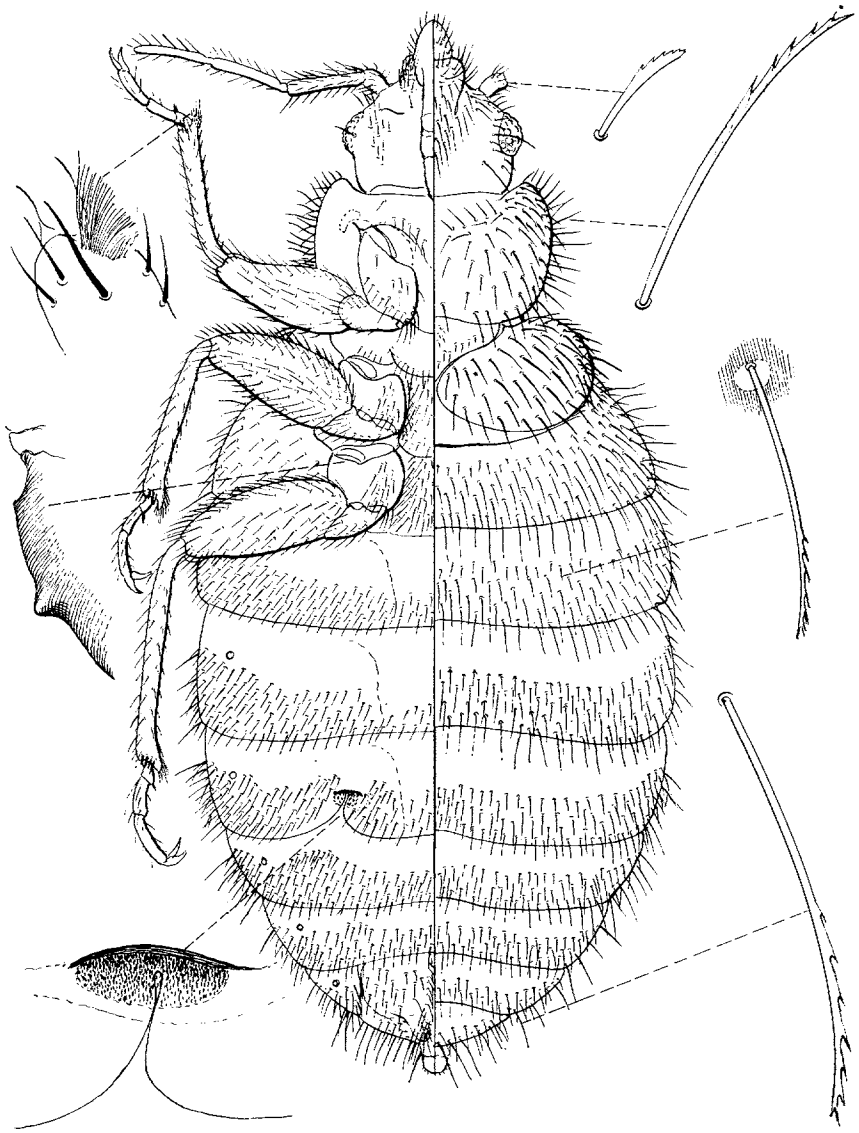

FIG. 12–23.—*Oeciacus vicarius* Horvath. Female. Stanford University, California (Ferris, original).

(*Sceliphron*) under a bridge 7 mi N. of Davis, Calif., Jan. 18, 1960. Records of *Oeciacus* from the purple martin (Horvath 1912) and blue birds nesting in woodpecker holes (Gregson 1949) probably refer to *Hesperocimex*. C. W. Johnson's (1925) record from chimney swifts probably was *Cimexopsis nyctalis* List.

Myers (1928) gives an account of the life history of *vicarius*. The curious features are the large numbers of individuals in a single nest (1333+), the ability to survive in various stages of development during the winter months when the swallows are away, and the masses of egg shells and fecal spots on the outside of the mud nests. Presumably, the swallows do not eat the bugs because of the "buggy" odor. Spiders were observed to be the chief enemies of the bugs.

There is considerable variation in the series before me. Specimens from the nests of cliff swallows in California are rather uniformly brown and have a HW/3rd antennal ratio of about 2. Barn swallow bugs from California are much paler, with brown spots at the sides of the abdomen, and have a HW/3rd antennal ratio above 2. Also the longest bristles at the sides of the pronotum are slightly longer on the cliff swallow bugs. Such differences, however, are not consistent elsewhere in the United States, and a series from cliff swallows in northern Mexico is intermediate in color and has long bristles and a high HW/3rd antennal ratio. Cross-breeding tests were successful between the 2 types in California (W. A. Foster) so it does not seem likely that separate taxonomic status is justified.

Genus ***Paracimex*** Kiritshenko

Paracimex Kiritshenko, 1913, Ann. Mus. Zool. Acad. Imp. Sci. St. Petersbourg 18: 542.
Neotticoris Horvath, 1914a, Ann. Mus. Nat. Hung. 12: 660.
Paracimex, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.

Size 3.7 (pinned) to 8 mm (slide-mounted). Body narrowed anteriorly, shining, with superficial punctures except on hemelytral pads. Bristles short to relatively long, 0.08–0.17 mm at sides of pronotum, with convex side minutely serrate in some species, the apices with two to several serrations. Antennae 1/6 to 1/3 longer than width of pronotum; first segment short and stout; second about 1/2 as thick as first and shorter than length of pronotum on median line; third and fourth segments slender, the third slightly longer than fourth and subequal to or longer than second. Rostrum reaching about to apices of fore coxae in pinned specimens.

Pronotum 1 1/2 to nearly 2 times as wide as head; about twice as wide as long on median line; strongly produced anteriorly on either side of head; anterior lobes rounded, attenuated or bent inward, forming a deep concavity for reception of head.

Hemelytral pads about 1/2 again as wide as long, broadly rounded posteriorly and laterally.

Metasternum broad, widened posteriorly. Fore coxae contiguous, middle and hind coxae widely separated.

Legs relatively stout; hind femora slightly shorter than width of pronotum; 3 or more times as long as wide; about 2/3 as long as hind tibiae. Front and middle femora

each with an outer row of spines extending almost the entire length of femur and an inner row which consists of only a few short pegs; bristles of outer row concentrated and contiguous subapically to form a distinct ctenidium; inner margin of femur more or less dilated at this point; front and middle tibiae slightly enlarged opposite ctenidia with an obsolescent row of pegs; all tibiae with apical tufts and without pseudojoints.

Terminal segment of male abdomen conical, about as long as wide at base, paramere reaching about ½ the distance to base, directed obliquely forward.

Ectospermalege usually subtubular, consisting of an anterior projection from broadly concave paragenital sinus at hind margin of fifth ventral segment.

Sexual dimorphism striking in some species, the females having shorter bristles than males. In extreme cases the female pronotal disk, abdominal tergites, and inner ⅔ of hemelytral pads have very short bristles and the scutellum is nude.

Type-species: *Paracimex avium* Kiritshenko.

Paracimex has a broad metasternal plate and ventral spermalege, hence is related to *Cimex* and *Oeciacus*. However, the bristles are serrate only in a few species and much less so than in *Cimex* and *Oeciacus*. The spermalege is more specialized, as well. The ctenidia of front and middle femora are diagnostic for this genus. It is apparently confined to cave swiftlets (*Collocalia*) of the East Indies, although there are 2 records from *Hirund-apus* and *Hirundo*. The female ectospermalege is distinctive for each species.

Considerable variation exists within the broadly defined species as recognized here, and sexual dimorphism further complicates the picture. The chromosome numbers differ between the New Britain and New Guinea specimens of *capitatus,* for example, and the number of supernumerary X chromosomes varies within the Malayan specimens of *borneensis*. The presence or absence of serrations on the outer sides of bristles is usually a stable character (present in *caledoniae,* absent in *setosus,* etc.) but both types of bristles occur within the series of *capitatus* from various places in New Guinea and even within series from a single locality (Davaon).

Part of the difficulty may be attributed to the isolation of caves where colonies of swiftlets nest. However, the real problem probably is with the birds, which are distributed over a vast area from India to Samoa and the Marquesas Islands. Mayr (1937) states: "Every author who has ever worked with these small swiftlets of the Indo-Australian region will contend that their classification presents the most difficult problem in the taxonomy of birds." Added to the complications of *Collocalia* taxonomy, the entomologist must contend with the common situation of 2 and sometimes even 3 species of *Collocalia* nesting in the same cave. This situation makes associating the bugs with their particular hosts difficult and, of course, suggests the possibility that the bugs may move from 1 host to another.

Some of the cave swiftlets make nests almost entirely of a hardened salivary secretion prized by the Chinese for "birds' nest soup." Other

species glue feathers and plant materials together with their saliva. Apparently the bugs occur in both kinds of nest.

KEY TO THE SPECIES OF *PARACIMEX*

1. Lateral margins of pronotum broadly, evenly rounded anteriorly and usually slightly convex behind middle. Ectospermalege tubular, bent to left, with a small sclerotized tube bent backward subbasally. New Caledonia....33. ***caledoniae***
   Lateral margins of pronotum not evenly rounded anteriorly, the anterior lobes more or less attenuated, the margins slightly to distinctly concave behind middle. 2
2. Ctenidia of front and middle femora strongly convex, the bristles inserted on preapical rounded lobes of inner margins of femora. Anterior lobes of pronotum broadly, lamellately produced. Third antennal segment longer than second. Java.....26. ***lamellatus***
   Ctenidia of front and middle femora only feebly convex, the bristles inserted on normal or scarcely more rounded inner margins of femora. Anterior lobes of pronotum not broadly lamellate. Third antennal segment subequal to or shorter than second..... 3
3. Bristles relatively dense, approximately 50 bristles on lateral margin of pronotum. Ectospermalege arising on right side in front of deeply rounded paragenital sinus, then tapering and tubular. Java.....25. ***setosus***
   Bristles relatively sparse, 25 to 30 or 40 on lateral margin of pronotum..... 4
4. Anterior lobes of pronotum long and attenuated, as long as wide at base. Ectospermalege arising at middle in front of broad paragenital sinus, tubular. Sumatra. .....24. ***avium***
   Anterior lobes of pronotum shorter, broader, shorter than wide at base..... 5
5. Male genital segment in cleared specimens distinctly wider than long (left) side; paramere extending well beyond middle of long side. Celebes.....
   .....27. ***gerdheinrichi***
   Male genital segment rarely wider than long side, if so, paramere not extending well beyond middle of long side..... 6
6. Ectospermalege broadly tubular, curved to the right and then recurved forward at tapering apex. Paramere short, not or scarcely reaching middle of long side of genital segment. Philippines.....28. ***philippinensis***
   Ectospermalege not curved in an "S" shape. Paramere longer, exceeding middle of long side of genital segment..... 7
7. Ectospermalege reduced to a sclerotized edge of broadly, shallowly concave hind margin of fifth ventral segment, without anteriorly directed tube. Vogelkop, New Guinea.....32. ***reductus***
   Ectospermalege well developed, tubular..... 8
8. Ectospermalege broadly sclerotized, especially on right side and diagonally across tube, then tapering and membranous. "Koshiha," Malay Peninsula
   .....30. ***ignotus***
   Ectospermalege without subbasal diagonal sclerotized area..... 9
9. Ectospermalege a curved cylindrical tube first inclined to the right and then towards apex, bent to left. Apex with a round cap. New Guinea, New Britain. .....31. ***capitatus***
   Ectospermalege first inclined to the left and then, subbasally bent to the right and straight to truncate apex which has a small appendage at tip. Borneo, Malaya .....29. ***borneensis***

24. ***Paracimex avium*** Kiritshenko

(Fig. 12–24)

Paracimex avium Kiritshenko, 1913, Ann. Mus. Zool. Acad. Imp. Sci. St. Petersbourg 18: 542.

Paracimex avium, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 319.
Paracimex avium, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 294, 296.
Paracimex avium, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Paracimex avium, Hicks, 1959, Check-List and Bibliogr., p. 249.

Female.—Head 0.9 mm wide, as long as wide across eyes; eyes small, $^1/_7$ as wide as interocular space. Antennae 1.7 mm long; proportion of segments 10:32:32:32. Rostrum about 1 mm long; proportion of segments approximately 15:18:20.

Pronotum 1.34 mm wide; twice as wide as long, 79:39; sides concave behind middle, convergent anteriorly to attenuated anterior lobes; anterior lobes produced beyond inner angles of anterior concavity by $^1/_5$ of median length; anterior concavity in shape of a shallow "U"; long bristles at sides of pronotum about as long as first antennal segment, relatively sparse, with about 25 on each side of pronotum; apices of bristles minutely serrate.

Mesonotum-scutellum practically naked, with only a few very small bristles.

Hemelytral pads broadly contiguous on anterior half of inner margins. Bristles relatively stout and sparse as on pronotum.

Ectospermalege arising from broad concavity in middle of fifth ventral segment, the sclerotized tube bent, reaching almost to second segment.

Male.—Paramere extending a little more than half way from tip to base of left side of genital segment, the latter in cleared specimens slightly longer on left side than wide across base, 32:30.

Described from a female specimen, Sumatra, Grot van Buo, March, 1914 (Jacobson), British Museum (Nat. Hist.) 1938–212, and a male, same data. There is a second female with the same data in the pinned collection of the British Museum and 2 nymphs, Pajacombo, Sumatra, March 19, 1913 (O. John), in nests of birds (A. N. Kiritshenko). The type is presumably in the zoological museum in Leningrad.

Also before me are 3 females and 4 nymphs from the Leiden Museum and 2 females and a male from the Hungarian National Museum, Grot van Buo, Sumatra, March, 1914 (Jacobson), Cat. 42 to 50. The collection at Budapest contains a series of about 100 specimens from Grot van Buo. According to J. G. Betrem "Buo" is 70 km N.E. of Padang.

P. avium is readily distinguished by the long pronotal lobes.

25. ***Paracimex setosus*** Ferris and Usinger
(Fig. 12–25)

Paracimex setosus Ferris and Usinger, 1957a, Microentomology 22: 9.

Female.—Head 1 mm wide; slightly wider across eyes than long, 63:58; interocular space about 8 times as wide as an eye. Antennae 2 mm long; proportion of segments 13:38:37:34. Rostrum approximately 1 mm long; proportion of segments 17:17:17.

Pronotum 1.85 mm wide; twice as wide as long on median line, 91:45; sides convex anteriorly, feebly concave behind middle; anterior lobes attenuated apically, produced beyond inner angles of anterior concavity $^1/_4$ of median length of pronotum; long bristles at sides nearly as long as first antennal segment.

Mesonotum-scutellum with only a few very obscure bristles.

Hemelytral pads over $^1/_2$ again as wide as long, 58:35, very broadly rounded laterally and behind and contiguous only briefly at middle.

Terminal abdominal segment in male about as long as width across oblique base; paramere slightly more than $^1/_2$ as long as width across oblique base.

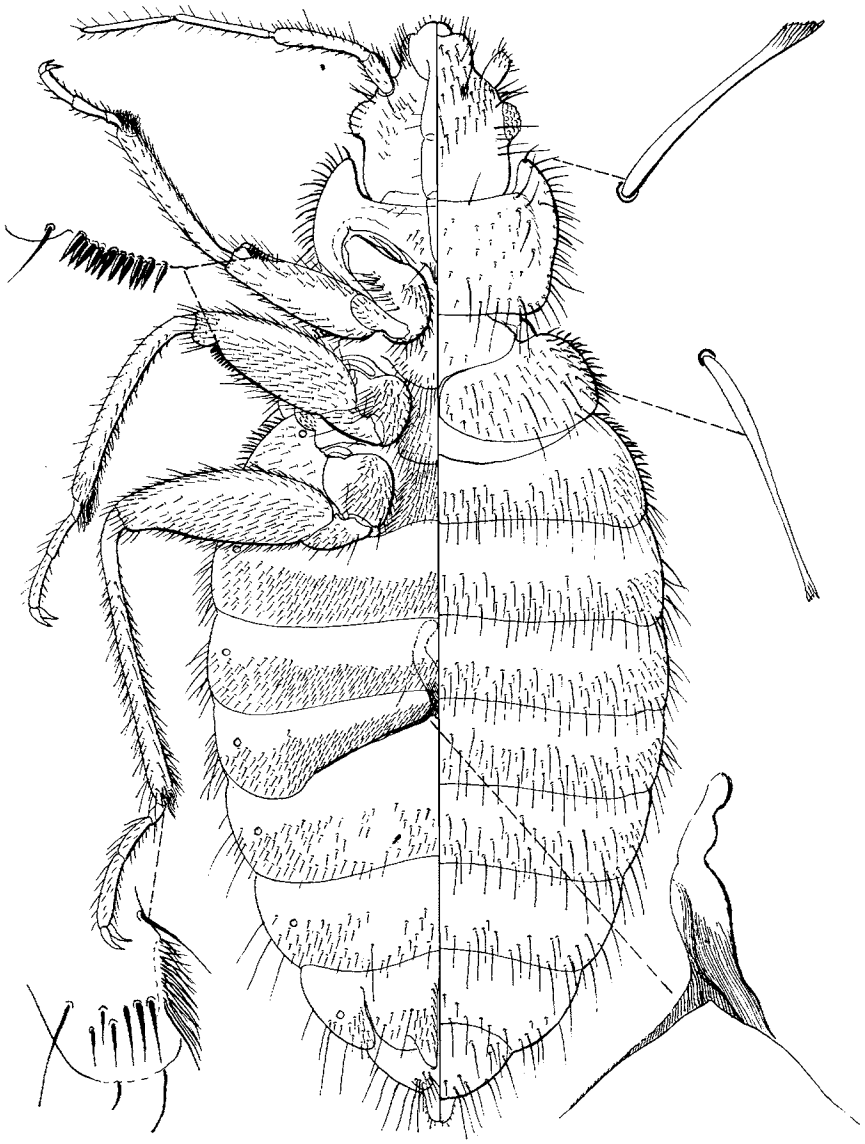

FIG. 12-24.—*Paracimex avium* Kiritshenko. Female. Grot van Buo, Sumatra (Ferris, original).

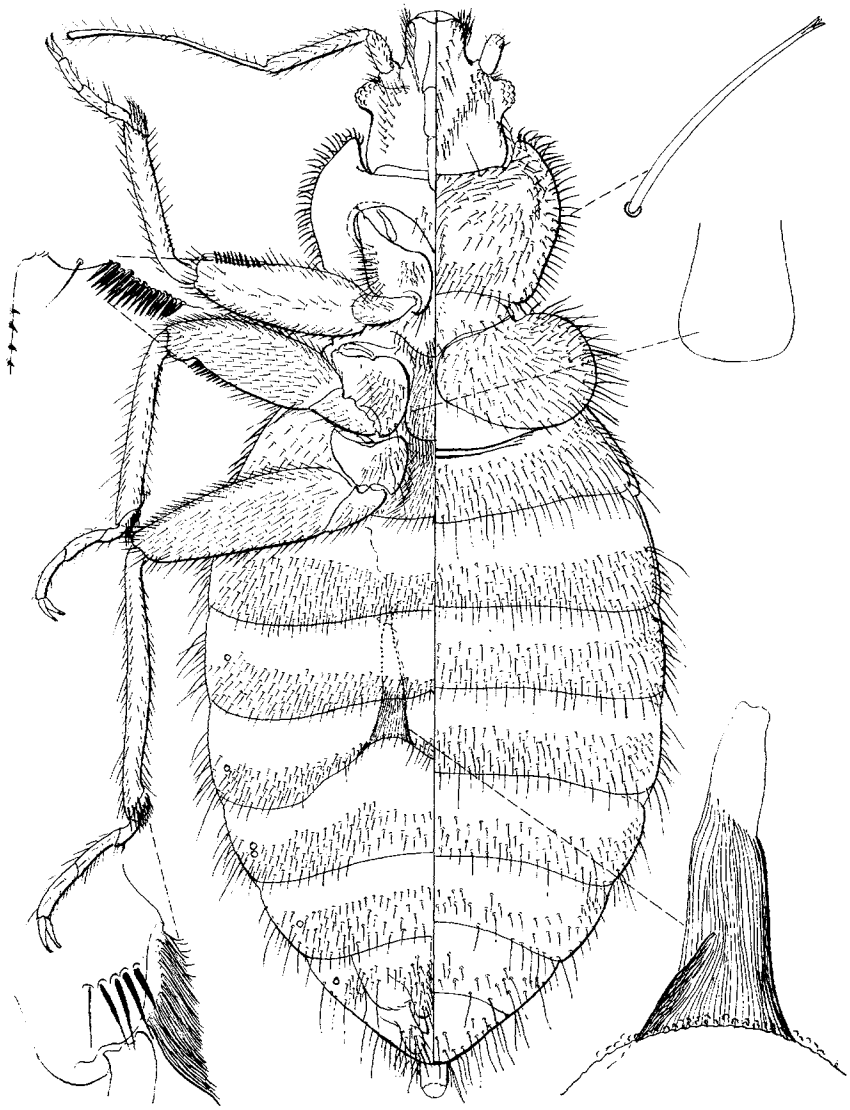

FIG. 12-25.—*Paracimex setosus* Ferris and Usinger. Female paratype. Wijnkoopabaai, West Java (Ferris and Usinger 1957a).

Female ectospermalege arising to the right of middle of hind margin of fifth ventral segment, the margin deeply, roundly concave and the sclerotized tube directed forward, tapering, just reaching second visible abdominal segment.

Hind femora slightly less than 3 times as long as broad, 82:28. Hind tibiae ¼ longer than femora. Ctenidia of front and middle femora short and not prominently produced. All tibiae straight.

Size.—Male, length 7.5 mm, width (pronotum) 1.85 mm; female, length 6.6 mm, width (pronotum) 1.6 mm (a pinned male is 4.5 mm and a female 4.3 mm).

Holotype female, allotype male, and 2 female paratypes, Wijnkoopabaai, W. Java, June 21, 1936 (M. A. L.) in cave in nest of *Collocalia esculenta linchi* Horsfield and Moore, collection of G. B. Thompson. A male and female are at hand from Depok, Java, July 10, 1909, *Collocalia esculenta linchi* Horsfield and Moore (Bryant and Palmer, USNM). A series from the Berlin Museum agrees exactly in structure of the ectospermalege and key characters. This collection is from *Collocalia vestita* (Lesson), Java. Series in the Leiden Museum bear the following data: Batavia, 1931–32 (W. C. v. Heurn), and Garoet, W. Java, 700 m, Jan. 15, 1929, *Collocalia esculenta linchi* Horsfield and Moore (W. C. van Heurn). In the Bishop Museum is a series from Sarangan, W. Java, Feb. 27, 1962 (P. Jauffret).

P. setosus is very close to *avium* but differs conspicuously by the denser bristles at the sides of the pronotum, the shorter anterior pronotal lobes, and, of course, by the distinctive ectospermalege.

26. ***Paracimex lamellatus*** Ferris and Usinger
(Fig. 12–26)

Paracimex lamellatus Ferris and Usinger, 1957a, Microentomology 22: 10.

Male.—Head about as wide across eyes as long; interocular space 6 times as wide as an eye. Proportion of first to fourth antennal segments 12:46:50:40. Rostral proportions approximately 18:16:15.

Pronotum about twice as wide as long on median line, 110:54; sides strongly, lamellately dilated in front of middle, narrowed and concave behind middle; anterior lobes produced beyond inner angles of anterior concavity for ⅓ of median length of pronotum. Long bristles at sides of pronotum about ½ as long as first antennal segment.

Mesonotum-scutellum with short scattered bristles.

Hemelytral pads broadly rounded behind, broadly contiguous along inner margins.

Abdomen relatively long and slender; terminal segment almost as long as wide across base, subconical; paramere about ⅔ as long as width of terminal segment at base.

Hind femora a little more than 3 times as long as wide, 103:31. Hind tibiae about ⅓ longer than femora, 145:103. Ctenidia of front and middle femora prominently dilated preapically, with a row of short pegs in apposition on tibiae. Front and middle tibiae curved, hind tibiae straight.

Size.—Male, length 7.8 mm, width (pronotum) 1.85 mm.

Holotype male and 1 male paratype, Soekaboemi, Tjiparij, W. Java,

FIG. 12–26.—*Paracimex lamellatus* Ferris and Usinger. Male paratype. Soekaboemi, Tjiparij, West Java (Ferris and Usinger 1957a).

1200 m, Jan. 18, 1938 (M. Bartels), on tail feathers of *Hirund-apus cochinchinensis* (Oustalet), G. B. Thompson collection.

Strikingly distinct because of the large size, short bristles, long third antennal segment, and especially the roundly produced femoral ctenidia.

27. ***Paracimex gerdheinrichi*** (Eichler)
(Fig. 12–27)

Oeciacus gerdheinrichi Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 293.

Male.—Head 0.86 mm wide, as long as wide; interocular space about 6 times as wide as an eye. Antennae 1.83 mm long; proportion of segments 7:20:20:17. Rostrum approximately 1 mm long; proportion of segments about 10:11:12.

Pronotum 1.34 mm wide; a little more than twice as wide as long, 47:22; sides a little concave behind middle, strongly arcuate anteriorly and then with anterior lobes slightly attenuated, rounded at apices, ⅔ as long beyond inner angles of concavity as wide at that level; largest bristles at sides about 0.2 mm; number of prominent bristles on each side about 30; disk of pronotum with scattered long, fine bristles.

Mesonotum with long fine bristles posteriorly.

Hemelytral pads ⅔ as long as broad, with long stiff bristles laterally and shorter finer bristles on inner half, the latter only slightly longer than distances between bristles.

Abdominal tergites with very long bristles, both at sides and on disks, those near posterior margins of segments extending well over ½ their length beyond edge of segment. Male paramere extending ⅔ of distance from tip to base of left side of genital segment, the latter slightly wider at base than long on left side.

Legs moderately robust; hind femora a little more than 3 times as long as wide, 43:113; ctenidia of middle femora inserted on only slightly more rounded area than regular curve of femur.

Size.—Male, length 5 mm, width (pronotum) 1.34 mm, (abdomen) 2.4 mm.

Redescribed from a paratype loaned by the Berlin Museum, Celebes, Latimodjong-Gebirge, Oeroe, 800 m, Aug. 1930 (G. Heinrich), in nest of *Collocalia spodiopygia sororum* Stresemann. According to J. B. Betrem "Latimotjung" is a mountain range in the north half of the S.E. arm of Celebes.

This species was described in the genus *Oeciacus* but clearly belongs in *Paracimex*. Detailed comparisons with other species must await a study of the ectospermalege. Unfortunately the original collection consisted of 4 males and no females.

28. ***Paracimex philippinensis*** Usinger
(Fig. 12–28)

Paracimex philippinensis Usinger, 1959b, Entomologist 92: 22.

Female.—Head 0.83 mm wide, as long as wide; interocular space 7 times as wide as an eye. Antennae 1.7 mm long; proportion of segments 6:20:18:18. Rostrum (slide preparation) reaching to apex of prosternum; length approximately 1 mm; proportion of segments about 13:10:12.

Pronotum 1.23 mm wide; a little less than twice as wide as long, 43:23; sides feebly or scarcely concave behind middle, attenuated anteriorly; anterior lobes about

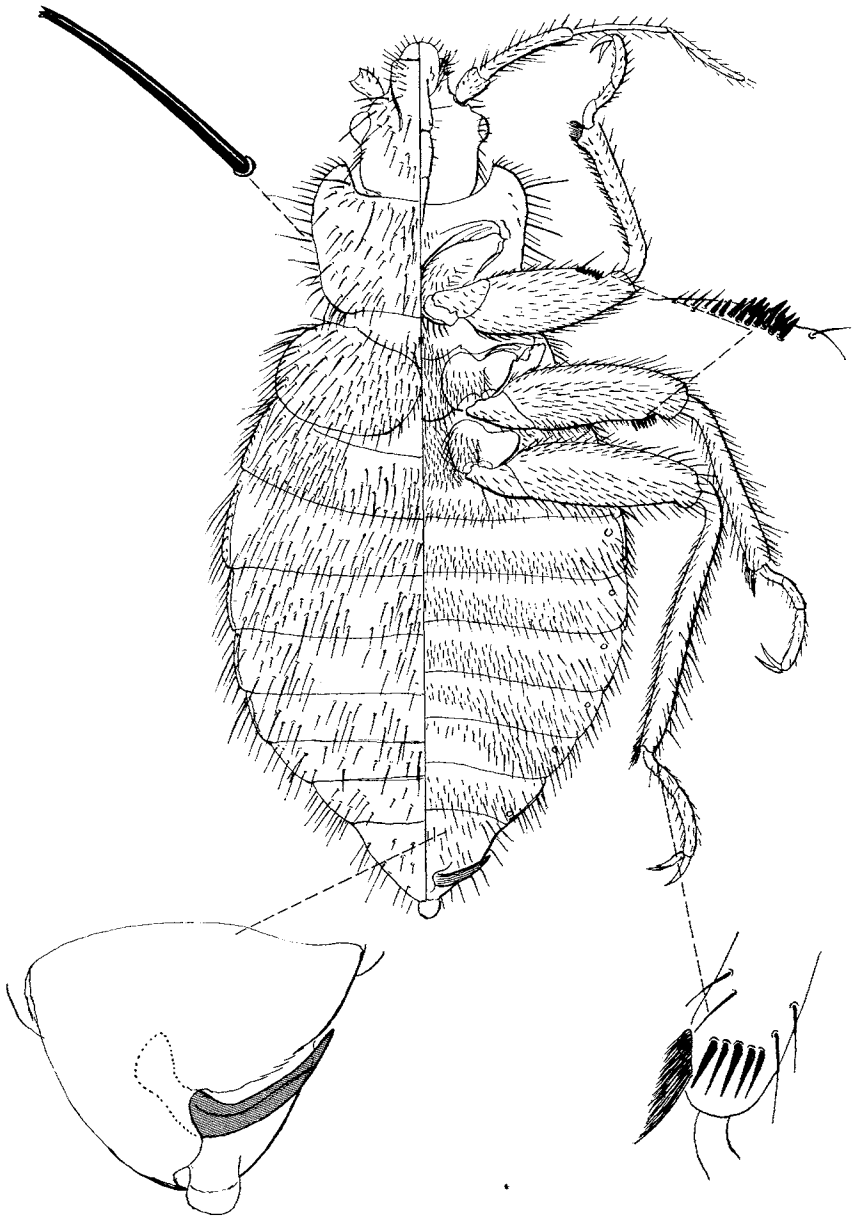

FIG. 12–27.—*Paracimex gerdheinrichi* (Eichler). Male paratype. Latimodjong Gebirge, Oeroe, Celebes (Ferris, original).

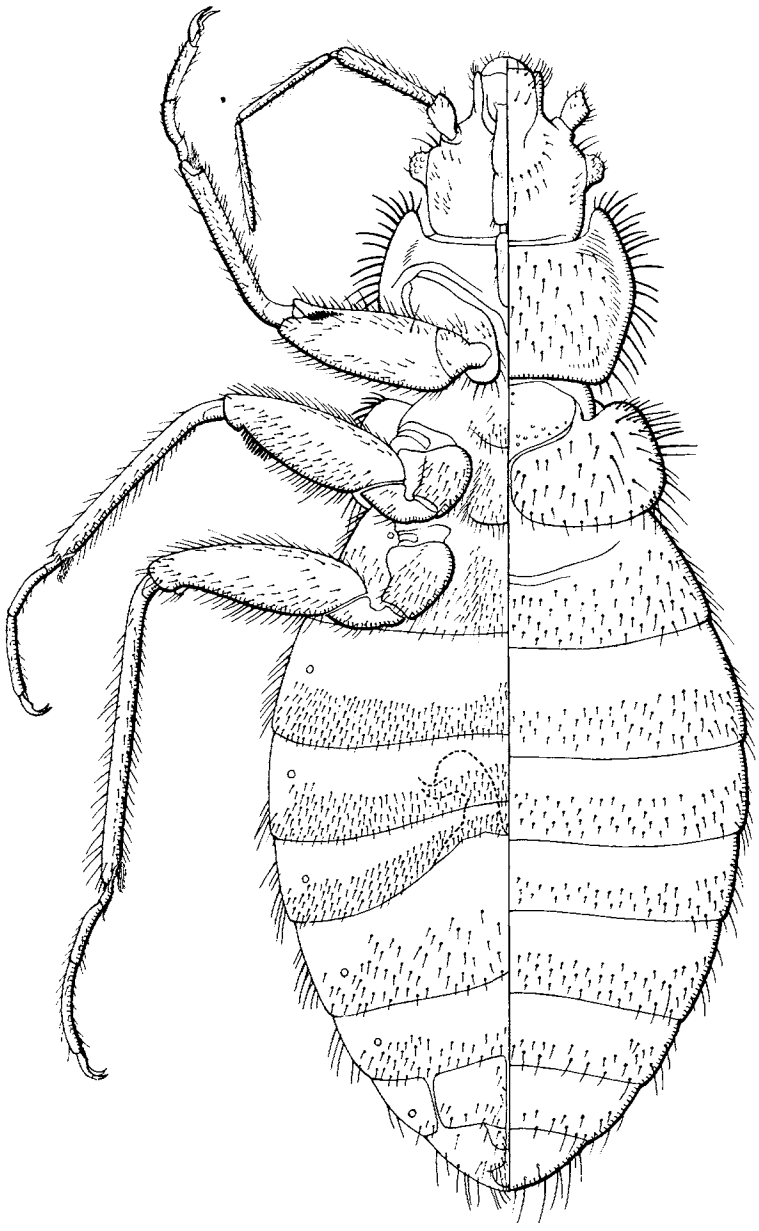

FIG. 12–28.—*Paracimex philippinensis* Usinger. Female. Basay, Negros Orient, Philippine Islands (Celeste Green, original).

as long beyond inner angles of anterior concavity as wide at that point; edges on each side with about 30 or 35 bristles, the longest bristles about 0.14 mm.

Mesonotal disk without bristles.

Hemelytral pads approximately ⅔ as long as wide; margins arcuate; sides with many short but stout bristles; disk with short fine bristles which are shorter than distance between bristles, at least on inner basal part.

Abdominal tergites mostly with bristles short and sparse.

Legs moderately stout; hind femora 3 times as long as broad; front and middle femora with subapical ctenidia following well the curve of the femur or (middle femora) only slightly more convex.

Spermalege (as seen from above in cleared specimen) arising a little to right and directly forward from a rounded concavity, then broadly bent to the right and gradually narrowed, the apex curved abruptly to the left, forming an "S" shape.

Size.—Female, length 5.88 mm, width (pronotum) 1.25 mm, (abdomen) 2.3 (a pinned male is 4.2 mm and a female 3.9 mm).

Holotype female and 1 female paratype, Desmarinas, Philippine I., Sept. 26, 1929 (R. Wheeler), from nests of *Collocalia marginata* Salvadori, Museum of Comparative Zoology.

In addition to the types, a male and a female are at hand from Sagay, Occ. Negros, P. I., May 23, 1928 (W. D. Pierce), from cave Buyog on *Collocalia,* and a male from Mt. Maquilling, Luzon, P. I., Sept. 14, 1929 (R. Wheeler). In the Bishop Museum is a series from Basay, Negros Orient. south of Dumaguete City, P. I., Dec. 16, 1959 (L. W. Quate). Dr. Quate writes that these were taken in small caves in an elevated coral ridge less than 100 m in elevation within 5 km of the coast. *Collocalia troglodytes* Gray (det. Rabor) were nesting in these caves.

The males have distinctly longer bristles than the females, especially on the abdominal tergites, and the paramere does not extend to the middle of the long side of the genital segment.

Although there is considerable variation in bristle length and development of the anterior lobes of the pronotum, all the Philippine specimens agree in the "S"-shaped ectospermalege and differ from all other species in this respect.

29. ***Paracimex borneensis*** Usinger
(Fig. 12–29)

Paracimex borneensis Usinger, 1959b, Entomologist 92: 220.

Female.—Head 0.8 mm wide, as long as wide; interocular space 7 times as wide as an eye. Antennae (pinned specimen) 1.8 mm long; proportion of segments 6:20:20:17. Rostrum (pinned specimen) reaching apices of front coxae; 1 mm long; proportion of segments 11:11:12.

Pronotum 1.25 mm wide; slightly less than twice as wide as long, 44:23; sides broadly rounded anteriorly, slightly concave on posterior half; anterior projections broad, ratio of length to width 4:7, lobes produced beyond inner angles of anterior concavity ⅙ of median length of pronotum, 4:23; long bristles at sides about 0.17 mm, the number of bristles at edge about 40 on each side; disk with scattered long bristles, more densely beset with fine, long bristles posteriorly.

Mesonotum-scutellum nude.

Hemelytral pads ⅔ as long as wide, 20:29; broadly rounded behind and at sides; sides densely beset with stiff bristles; disk with numerous fine long bristles, the latter much longer than distance between bristles.

Legs moderately stout; hind femora more than 3 times as long as wide, 44:13. Ctenidia of front and middle femora on rather evenly arcuate margin of each femur, not produced or arched.

Abdominal tergites with fine long hairlike bristles greatly exceeding distance between bristles, the individual bristles on posterior margins extending more than ½ their length beyond margins of tergites. Spermalege as seen from above in cleared specimens long and broad, tubelike, directed to the left at base and then immediately bent a little to the right, truncate at apex with a small apical tube.

Male.—Genital segment long and narrow, a little longer on left side than wide at base; paramere extending a little beyond middle of left side.

Size.—Male, length 6.71 mm, width (pronotum) 1.3 mm, (abdomen) 2.5 mm; female, length 6.3 mm, width (pronotum) 1.26 mm, (abdomen) 2.6 mm (a pinned male is 4.1 mm and a female 4.2 mm).

Holotype female, allotype male, and several paratypes (slide-mounted), a male and female (pinned), and other specimens in alcohol, all from Bidi, Sarawak, Borneo, Sept. 3, 1958, *Collocalia* nest in cave (T. C. Maa), Bishop Museum. The type series is very homogeneous, showing uniformity in development of bristles in both sexes, except that there are several long bristles on the mesonotum in the male.

In the British Museum (Nat. Hist.) there is a series of 14 specimens from Niah Cave, Sarawak, March 13, 1957, *Collocalia salangana* Streubel, the males of which agree with the type material but some females of which have shorter bristles. Especially on the hemelytral pads the bristles on the inner half are only slightly longer than the distance between bristles. Lord Medway reports that both *Collocalia salangana* and *maxima* Hume were in total darkness in the caves at Bidi and Niah. Also in the British Museum are a male and female, Baram Caves, Sarawak, May 8, 1957, *Collocalia vestita* (Lesson), which show strong dimorphism, as do 4 specimens from Gunong Sta'at Cave, Jan. 1, 1958, in nest of *Collocalia lowi lowi* (Sharpe) (Lord Medway).

Such dimorphism is difficult to interpret, but as all basic characters agree, it is assumed for the present that it represents intraspecific variation. It is not correlated with different caves.

Another long series that seems clearly to belong here was collected by Lord Medway at Semangko Pass, 2700 ft ("The Gap"), Ulu Selangor, Malaya, May, 1962, in nests of *Collocalia esculenta esculenta* (L.). Lord Medway reports that the nests consisted of vegetable material and that they were not in total darkness. All specimens were taken in nests of the 1 species of bird.

The great Niah Cave in Sarawak has long been exploited for the edible nests which are harvested by natives using long ladders and scaffolding (Harrisson 1958, Medway 1958).

FIG. 12–29.—*Paracimex borneensis* Usinger. Female paratype. Bidi, Sarawak, Borneo (Celeste Green, original).

30. ***Paracimex ignotus*** Usinger, n. sp.
(Fig. 12–30)

Female.—Head 0.9 mm wide, slightly wider than long; interocular space 7 times as wide as an eye. Antennae 1.73 mm long; proportion of segments 5:17:17:16. Rostrum 0.9 mm long, reaching well onto prosternum (slide-mounted specimen); proportion of segments 9:8:8.

Pronotum 1.45 mm wide; about twice as wide as long; sides only feebly concave behind middle; anterior lobes shorter than wide at base, 5:7; bristles at lateral margins short, 0.13 mm, serrate on outer side, about 40 on each side.

Mesonotum-scutellum nude (a few bristles posteriorly in male).

Hemelytral pads less than ⅔ as long as wide, 17:28; broadly rounded behind and at sides; disk with prominent erect bristles laterally.

Legs with hind femora less than 3 times as long as wide, 37:13. Ctenidia of front and middle femora not at all arched, following the curve of femur.

Abdominal tergites with fine, scattered bristles, those of lateral margins longer and more conspicuous. Ectospermalege arising from a broad concavity (paragenital sinus) in hind margin of fifth ventrite a little to the right of middle, tubular and tapering, the broad base sclerotized on right side with sclerotized margin, then bent to the left and again forward apparently within membranous tube. Apex of tube narrowed and then inflated with a round cap and 2 posteriorly directed, membranous arms.

Male.—Bristles somewhat longer, the longest at sides of pronotum 0.16 mm. Genital segment slightly narrower than length on left side, the paramere extending well beyond middle of left side.

Size.—Male, length (slide-mounted) 6.3 mm, width (pronotum) 1.35 mm, (abdomen) 2.4 mm; female, length 5.1 mm, width (pronotum) 1.45 mm, (abdomen) 2.7 mm.

Holotype female and allotype male, "Koshiha, Tale Sub. R. E. 29.3.99. Skeat Coll." In a list of localities for the Skeat expedition (Skeat 1901), further details are given as "Birdsnest Islands" (Ko Si Ha) in the "Inland Sea" or "Big Lake" (Tălē Sap) near Songkhla, Singgora State, Malay Peninsula, Thailand. "R. E." presumably refers to the collector, Richard Evans. The label also states, "Bugs from the nests of edible nest birds." Two specimens of *Collocalia innominata* Hume were collected by the Skeat Expedition (Bonhote 1901), but no locality data or other particulars are given. *P. ignotus* differs from other *Paracimex* species in the form of the ectospermalege.

These specimens were found by Dr. John Smart in the Museum at Cambridge University, England, at the suggestion of Prof. G. E. Hutchinson, who remembered seeing them when he was a student at Cambridge. The types have been deposited in the British Museum (Nat. Hist.).

31. ***Paracimex capitatus*** Usinger, n. sp.
(Fig. 12–31)

Female.—Head 1 mm wide, as wide as long; interocular space 7 times as wide as an eye. Antennae 1.8 mm long; proportion of segments 5:18:16:15. Rostrum 1.16 mm long; reaching apices of front coxae (specimen preserved in alcohol); proportion of segments 12:11:11.

Pronotum 1.4 mm wide, twice as wide as long; sides concave behind middle; anterior lobes produced ⅔ as far forward as width at base; longest bristles at sides short, 0.13

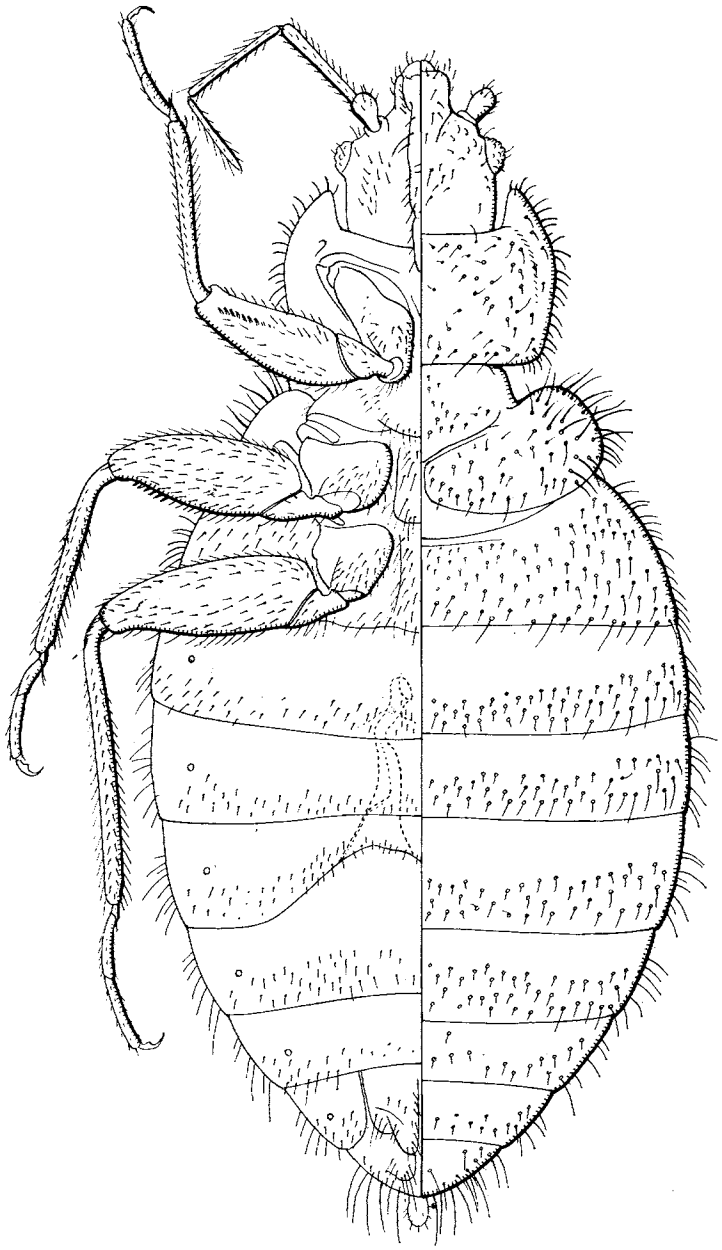

FIG. 12–30.—*Paracimex ignotus,* n. sp. Female holotype. Ko-si-ha, Songkhla, Singgora, Malay Peninsula, Thailand (Celeste Green, original).

FIG. 12–31.—*Paracimex capitatus,* n. sp. Female paratype. Keravat, Rabaul, New Britain (Celeste Green, original).

mm, serrate at apices and on outer sides near tips; number of bristles on each side about 35.

Mesonotum-scutellum with a few bristles posteriorly.

Hemelytral pads ⅔ as long as wide, 18:27, broadly rounded behind and at sides, contiguous at middle for a distance less than ½ the length of scutellum; disk laterally with prominent stiff bristles, inner ⅔ with finer bristles.

Legs with hind femora 3 times as long as wide; ctenidia of front and middle femora compact, only slightly dilated from even curve of femur.

Abdominal tergites with only fine, inconspicuous bristles except laterally. Ectospermalege as seen from above in cleared specimens arising from a broad paragenital sinus formed by a concavity of hind margin of fifth ventrite, the rounded apex at right of middle. Tubular ectospermalege bent to the right and then, near apex, briefly curved to left with a sclerotized cap at tip.

Male.—Genital segment about as wide as long on left side; paramere reaching about to middle of left side.

Male bristles longer, those of sides of pronotum to 0.23 mm, those on abdominal tergites long and stiff.

Size.—Male, length 6 mm; width (pronotum) 1.45 mm, (abdomen) 2.55 mm; female, length 5.6 mm, width (pronotum) 1.4 mm, (abdomen) 2.55 mm (a pinned male is 5.6 mm and a female 5.2 mm).

Holotype female, allotype male, and a series of paratypes, Keravat, Rabaul, New Britain, Nov. 21, 1959 (T. C. Maa), from *Collocalia* nests (B. P. Bishop Museum). Additional material with similar ectospermalege is at hand as follows: S. side of Humboldt Bay, New Guinea, Dec. 24, 1961 (L. W. Quate); S. side of Sentani, Ajappo, New Guinea, Dec. 31, 1961 (L. W. Quate); Dawson, New Guinea (H. W. Clissold); Taliligap, New Guinea (H. W. Clissold); Bulolo River Gorge, Wau, New Guinea, 2400 ft, May, 1963 (H. W. Clissold); Papua, New Guinea, Aug. 20, 1963 and Edie Creek, Wau, New Guinea, 2000 m, Oct. 4–10, 1961 (J. H. Sedlacek); Cyclops Mtns., nr. Kota Nica, New Guinea, 400 m, Dec. 20, 1961 (L. W. Quate); cave at Kanyon Batu, 10 mi E. Sumberbaba, Japen I., New Guinea, Nov. 1, 1962 (Nixon Wilson); Vella Lavella, Gingola, B.S.I.P., Nov. 28, 1963 (P. Shanahan), on edible swiftlets in limestone caves.

32. ***Paracimex reductus*** Usinger, n. sp.
(Fig. 12–32)

Female.—Head 0.9 mm wide; slightly wider than long; interocular space 7 times as wide as an eye. Antennae 1.7 mm long; proportion of segments 5:17:15:14. Rostrum 1.07 mm; reaching to apices of front coxae (specimen in alcohol); proportion of segments 11:10:10.

Pronotum 1.3 mm wide, about twice as wide as long at middle, sides slightly concave behind middle; anterior lobes attenuated, not quite as long as width at base; longest bristles at sides to 0.22 mm, serrate at apices, and a few serrations on outer sides; approximately 35 bristles on each side margin.

Mesonotum-scutellum with a few bristles posteriorly.

Hemelytral pads over ⅔ as long as broad, 17:23, broadly rounded behind and at sides; disk with long, erect bristles laterally.

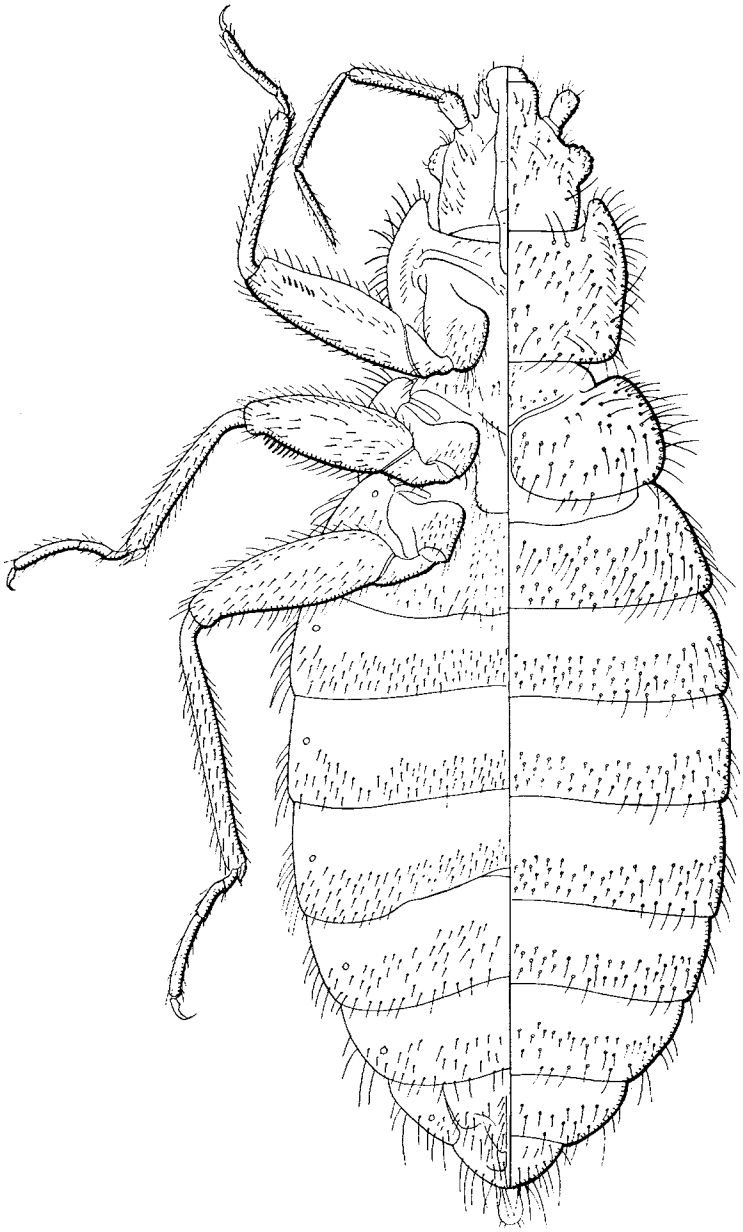

FIG. 12–32.—*Paracimex reductus,* n. sp. Female. Kebar Valley, Vogelkop, New Guinea (Celeste Green, original).

Legs with hind femora slightly more than 3 times as long as broad, 35:11; ctenidia dilated a little beyond the curve of femur.

Abdominal tergites with fine bristles. Ectospermalege seen from above in a cleared specimen greatly reduced, consisting of a short sclerotized triangle arising from middle of broad paragenital sinus.

Male.—Bristles longer and more conspicuous, the longest at sides of pronotum about as in female, but with more reaching the maximum length. Genital segment a little narrower than long on left side, the paramere reaching only slightly beyond middle of long side.

Size.—Male, length 5.9 mm, width (pronotum) 1.2 mm, (abdomen) 2.1 mm; female, length 6 mm, width (pronotum) 2.3 mm, (abdomen) 2.4 mm (a pinned female is 4.4 mm long and a pinned male 5 mm).

Holotype female, allotype male, and a series of paratypes, Kebar Valley, Vogelkop, New Guinea, Jan. 9, 1962 (L. W. Quate), in swift nests in small cave on side of hill (B. P. Bishop Museum).

This species differs from all other *Paracimex* in lacking a tubular ectospermalege.

33. ***Paracimex caledoniae*** Ferris and Usinger

(Fig. 12–33)

Paracimex caledoniae Ferris and Usinger, 1957a, Microentomology 22: 9.

Male.—Head 0.9 mm wide; scarcely wider across eyes than long, 52:50; interocular space almost 7 times as wide as an eye. Antennae 1.7 mm long; proportion of segments 10:33:30:27. Rostral proportions approximately 12:12:15; rostrum about 0.71 mm long.

Pronotum 1.4 mm wide; over twice as wide as long on median line, 84:36; sides convexly rounded throughout, feebly so at and behind middle, strongly and rather evenly rounded on anterior lobes; anterior lobes produced beyond inner angles of anterior concavity ⅕ of median length of pronotum; long bristles at sides of pronotum about as long as first antennal segment.

Mesonotum-scutellum with numerous fine bristles medially and posteriorly.

Hemelytral pads broadly rounded, even on inner margins, contiguous only adjacent to apex of scutellum.

Male paramere more than ½ as long as width of terminal segment at base, 30:55, feebly sinuate.

Hind femora slightly more than 3 times as long as broad, 73:23. Hind tibiae about ¼ longer than femora, 92:73. Ctenidia of front and middle femora rounded to conform to subapical concavity but not inserted on a strongly rounded elevation of femoral margin. Front and middle tibiae feebly bent inward, hind tibiae straight.

Female.—Ectospermalege tubular, arising slightly to right of middle of hind margin of fifth (fourth visible) ventral segment; sclerotized tube bent mesad and not extending to anterior margin of fourth visible segment, with a small sclerotized tube bent backward subbasally.

Size.—Male, length 6.2 mm, width (pronotum) 1.45 mm, (abdomen) 2.4 mm; female, length 5.7 mm, width (pronotum) 1.55 mm, (abdomen) 2.7 mm (a pinned male is 4.2 mm and a female 3.9 mm).

Holotype male, allotype female, and a long series of paratypes, 10 mi SE La Foa, New Caledonia, March 13, 1945 (C. L. Remington), in nests

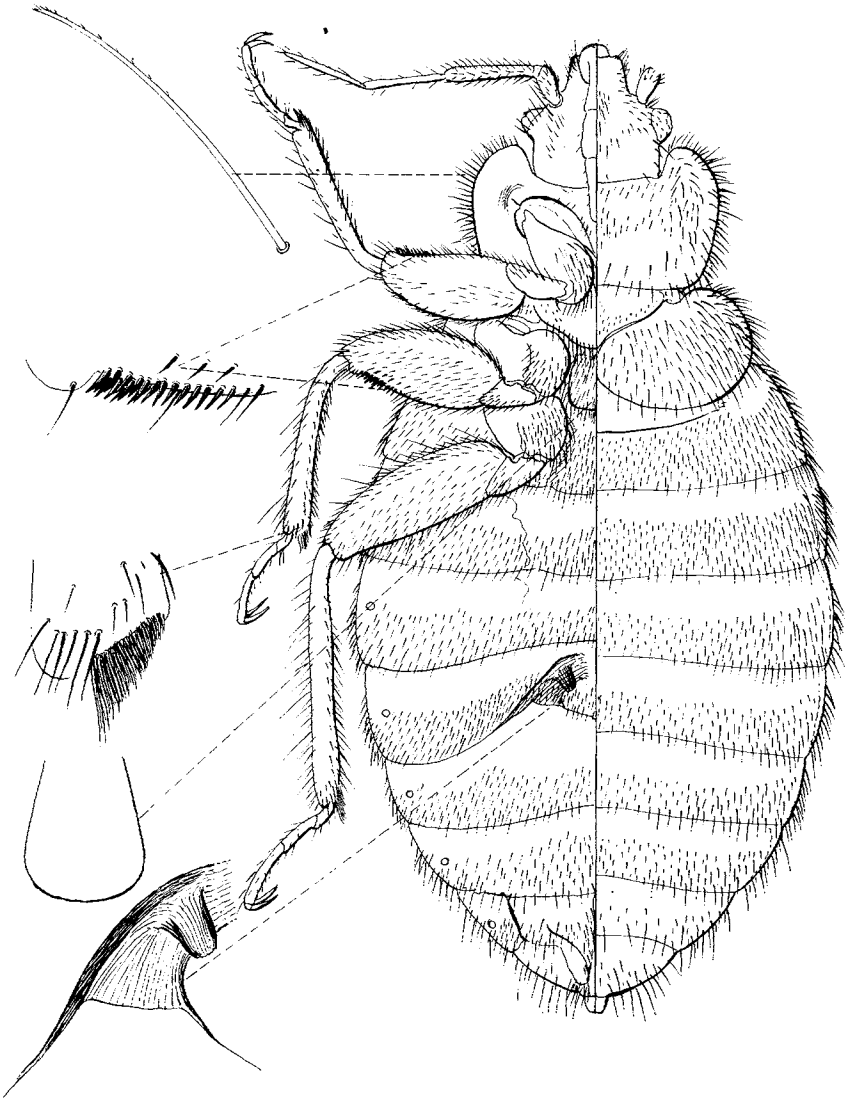

FIG. 12–33.—*Paracimex caledoniae* Ferris and Usinger. Female paratype. Near La Foa, New Caledonia (Ferris and Usinger 1957a).

of *Collocalia spodiopygia spodiopygia* (Peale) or *C. esculenta esculenta* (L.). Several nymphs were taken at Sarraméa (E. Coast), New Caledonia, Dec. 22, 1955, in nests of *Hirundo tahitica subfusca* Gould (J. Rageau). The types are in the British Museum (Nat. Hist.).

As shown in the key, this species is widely divergent from the rest of the members of the genus, structurally as well as geographically. The rounded margins of the pronotum are distinctive.

Subfamily CACODMINAE Kirkaldy

Cacodminae Kirkaldy, 1899b, Bull. Liverpool Mus. 2: 45.
Cacodminae, Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Cacodminae, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Cacodminae, Horvath, 1913a, Bull. Soc. Entomol. France, p. 372.
Cacodminae, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.
Cacodminae, China and Miller, 1955, Ann. Mag. Nat. Hist. (12) 8: 263.
Cacodminae, Miller, 1956, Biol. Heterop., p. 120.
Cacodminae, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 18.

Bristles at sides of pronotum tapered, not serrate at sides, usually bifid at tips. Clypeus scarcely to strongly widened anteriorly. Labrum not elongate. Head with few to many bristles on clypeus, juga, and vertex; narrower, subequal to, or wider than long. Antennae of various lengths and proportions but with the first segment always shortest and thickest, second subequal or shorter than remaining segments. Third segment longer than all the others together in *Leptocimex;* fourth usually shorter than third. Rostrum long and slender with apex attaining level of apices of front coxae (*Leptocimex*) or shorter; rarely shorter than head and very wide (*Crassicimex*); always with 1 or 2 pairs of prominent bristles on first segment.

Pronotum broadly rounded at sides and transverse (*Cacodmus*) or subquadrate, with few or many bristles.

Scutellum very short and broad, subrectangular, very briefly produced into a short apex, usually without bristles.

Metasternum usually compressed between middle coxae but sometimes (*Aphrania*) broader, platelike.

Legs short and stout with thick curved tibiae or long and slender. Tibiae with short bristles and with long, erect bristles as well (*Crassicimex*). Tibiae with pseudojoints on all legs, on hind legs only, or on none of the legs. Apical tufts on all tibiae, on front and middle tibiae, or on none.

Spermalege usually dorsal on seventh segment, rarely dorsal and more anterior (*Leptocimex duplicatus*) or with no external opening visible (*Leptocimex boueti, Crassicimex sexualis, Aphrania*).

Type-genus: *Cacodmus* Stål.

This is a diverse subfamily but probably belongs as a single unit because intermediates seem to connect the extreme types. As originally proposed by Jordan and Rothschild (1912), the group was homogeneous, including only *Cacodmus, Aphrania,* and *Loxaspis.* We now know that these 3 genera have a uniform and low metaphase chromosome number of 4A+XY. The other 3 genera, *Leptocimex, Stricticimex,* and *Crassicimex,* have a very different appearance, but *Loxaspis* seems to be somewhat intermediate, having the recurved paramere and, in *L. setipes,* long

legs. *Leptocimex* and *Stricticimex* both have the chromosome number 11A+XY; *Crassicimex* has 18A+XY. In all Cacodminae the spermalege is dorsal, but there is no ectospermalege in *Aphrania*. *Leptocimex* has one species (*duplicatus*) with 2 completely separate organs.

The Cacodminae are widely distributed in the Ethiopian and Oriental Regions with species also inhabiting the arid parts of North Africa and the Middle East and 1 species in Madagascar. All species live on bats, and one, *Leptocimex boueti* Brumpt, also lives on man in West Africa.

KEY TO THE GENERA OF CACODMINAE

1. Tibae with apical tufts on front and middle legs and usually also on hind legs 2
   Tibiae without apical tufts 4
2. Front and middle tibiae only with apical tufts. All tibiae with subapical pseudojoints. Paramere bent posteriorly. Paragenital sinus right dorsal between fifth and sixth segments. Africa and Orient. Bats. ..... ***Loxaspis***
   All tibiae with apical tufts. Paramere bent anteriorly. 3
3. Tibiae without subapical pseudojoints. Ectospermalege left dorsal and produced forward internally as a tube from front margin of seventh tergite. Africa and Orient. Bats. ..... ***Cacodmus***
   Hind tibiae usually with more-or-less distinct pseudojoints. No paragenital sinus. Point of entry of paramere sometimes indicated by pigmented area on left side between fifth and sixth or sixth and seventh tergites. Africa and Orient. Bats. ..... ***Aphrania***
4. Rostrum very stout, shorter than head. Middle and hind tibiae with very long, erect bristles in addition to shorter ones. Africa and Madagascar. Bats. ..... ***Crassicimex***
   Rostrum slender, longer than head. Middle and hind tibiae with only short bristles, scarcely longer than thickness of tibia 5
5. Third antennal segment longer than remaining segments combined. Apical segment of rostrum longer than second. Hemelytral pads very short, ⅓ or ¼ as long as wide. Africa. Bats and man. ..... ***Leptocimex***
   Third antennal segment shorter than remaining segments. Third segment of rostrum shorter than second. Hemelytral pads longer, ⅔ as long as wide. Africa and Orient. Bats. ..... ***Stricticimex***

Genus ***Cacodmus*** Stål

Cacodmus Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 103, 104.
Cacodmus, Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Cacodmus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Cacodmus, Rothschild, 1913, Entomol. Mon. Mag. 49: 102–103.
Cacodmus, Patton and Cragg, 1913, Textb. Med. Entomol., p. 512.
Cacodmus, Rothschild, 1914a, Bull. Entomol. Res. 5: 41–42.
Cacodmus, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Cacodmus, Jordan, 1922, Ectoparasites 1: 285–6.
Cacodmus, Bedford, 1932, Rep. Vet. Res. S. Afr. 18: 416.
Cacodmus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 299–307.
Cacodmus, Lent and Abalos, 1946, An. Inst. Med. Reg. 1: 347.
Cacodmus, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Cacodmus, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 25.

Size 3.8 (dried) to 7 mm (slide-mounted). Bristles long and rather uniformly densely distributed over the body, not serrate on sides, minutely bifid or indented at

tips. Antennae about ¼ longer than width of pronotum, first segment short, second longest, third and fourth usually shorter in that order. Rostrum reaching front coxae.

Pronotum 1¾ to 2 times as wide as head, transverse, about twice as wide as long; disk superficially punctured, distinctly impressed sublaterally and subbasally.

Hemelytral pads strongly transverse, about twice as wide as long, disk distinctly, evenly punctured.

Mesonotum-scutellum smooth, shining, practically devoid of bristles.

Metasternum a posteriorly broadened, rounded lobe. Fore coxae contiguous, middle and hind coxae progressively farther apart.

Abdominal tergites finely punctured; male paramere bent forward and to the left, relatively long, extending well onto preapical segment and sometimes over the preceding 2 segments. Female paragenital sinus roundly indented on left side of sixth abdominal tergite, the ectospermalege produced forward, elongate and variously shaped.

Legs relatively short, the hind femora shorter than width of pronotum, 2 to 3 times as long as wide and subequal to hind tibiae. Tibiae relatively stout, usually slightly inwardly curved subapically, without pseudojoints. All tibiae with tufts at apices.

Type-species: *Cacodmus villosus* Stål.

Cacodmus most closely resembles *Aphrania* and *Loxaspis* but differs in the unique type of spermalege and absence of pseudojoints on all tibiae. Each species has a different ectospermalege and the parameres are often distinctive. All records are from bats of the family Vespertilionidae.

KEY TO THE SPECIES OF *CACODMUS*

1. Last 2 antennal segments subequal or the fourth segment longer than third. Male paramere short, reaching only onto penultimate (eighth) ventral segment. 2
   Third antennal segment longer than fourth. Male paramere long, reaching across penultimate (eighth) ventral segment to seventh segment. 5
2. Size relatively large, the width of pronotum 1.9 mm. Africa. 3
   Size smaller, the width of pronotum 1.17–1.45 mm. Orient (India, Java, Sumatra, Malaya). 4
3. Male paramere evenly curved and tapered, reaching a little beyond middle of penultimate segment. Spermalege short, stumpy. Uganda. ..... 34. ***ignotus***
   Male paramere abruptly tapered near middle, bent inward at apex and reaching nearly to base of eighth segment. Congo. ..... 37. ***sinuatus***
4. Fourth antennal segment subequal to third. Male paramere sinuous. Spermalege not bent outward at tip. India. ..... 35. ***indicus***
   Fourth antennal segment longer than third. Male paramere not sinuous. Spermalege bent to the left at tip. (Java, Sumatra, Malaya). ..... 36. ***sumatrensis***
5. Pronotum less than twice as wide as long. Paramere longer than width of genital segment. Ectospermalege twisted apically. ..... 38. ***sparsilis***
   Pronotum twice or more than twice as long. Paramere shorter than width of genital segment. Ectospermalege bent but not twisted at apex. 6
6. Pronotum 1.24–1.5 mm wide, less than twice as wide as head. Longest bristles at sides of pronotum less than ⅓ mm. North Africa. ..... 39. ***vicinus***
   Pronotum 1.5–1.7 mm wide, twice as wide as head. Longest bristles at sides of pronotum more than ⅓ mm. South Africa. ..... 40. ***villosus***

34. *Cacodmus ignotus* Rothschild

(Fig. 12–34)

Cacodmus ignotus Rothschild, 1912a, Entomol. Mag. 48: 85.
Cacodmus ignotus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.

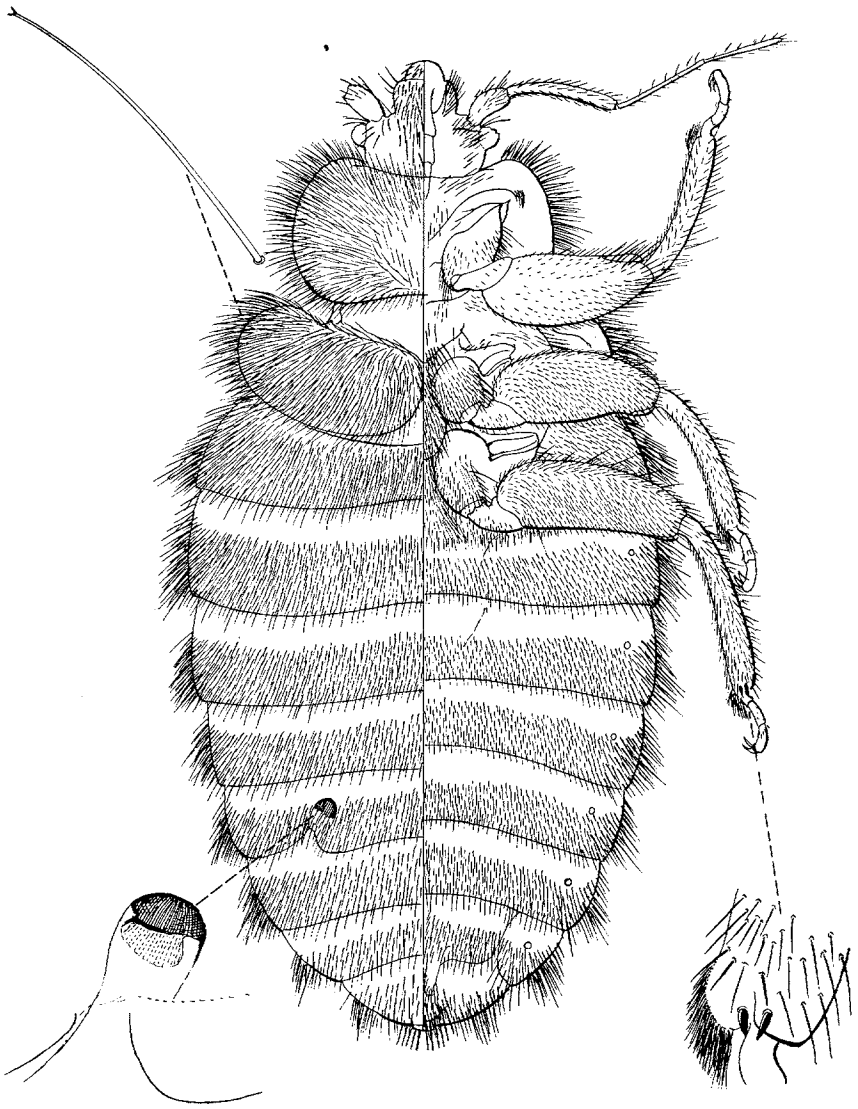

FIG. 12–34.—*Cacodmus ignotus* Rothschild. Female. Entebbe, Uganda (Ferris, original).

Cacodmus ignotus, Rothschild, 1913, Entomol. Mon. Mag. 49: 103.
Cacodmus ignotus, Rothschild, 1914a, Bull. Entomol. Res. 5: 42.
Cacodmus ignotus, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Cacodmus ignotus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 318.
Cacodmus ignotus, Mathur, 1953, Indian J. Entomol. 14: 260.

Female.—Head 0.96 mm wide, 1/3 wider across eyes than long, 28:21, interocular space about 6 times as wide as an eye. Antennae 2.27 mm long, proportion of segments approximately 10:24:18:18. Rostrum 0.68 mm long, proportion of segments about 20:16:20, reaching about 3/4 of distance to apex of triangular prosternum.

Pronotum 1.86 mm wide, about twice as wide as long on median line, 55:28, rather evenly rounded laterally; anterior margin distinctly sinuate sublaterally behind eyes; longest pubescence at sides about as long as first antennal segment.

Hemelytral pads approximately twice as wide as long, inner margins straight and contiguous only at base.

Abdomen with bristles a little shorter posteriorly than anteriorly. Female ectospermalege short, apically rounded.

Hind femora 2 1/3 times as long as greatest width, 42:18, as long as hind tibiae. All tibiae very slightly incurved subapically.

Male.—Paramere (Uganda specimen) relatively short, a little more than 1/2 as long as width of terminal segment at base, 25:45, extending across preapical segment but not onto seventh segment; strongly tapered to thin apical half but not sinuous apically.

Size.—Male, length 6.55 mm, width (pronotum) 1.82 mm, (abdomen) 3.34 mm; female, length 6.9 mm, width (pronotum) 1.86 mm, (abdomen) 3.48 mm.

Described from the holotype female, received by the British Museum (Nat. Hist.) from Oldfield Thomas without locality data. Male characters described from a specimen collected by C. C. Gowdey at Entebbe, Uganda, June 20, 1913, "From bat." A female bearing the same data (Entebbe, Uganda) agrees perfectly with the type, so that the type locality of this species is almost certainly some place in or near Uganda.

35. ***Cacodmus indicus*** Jordan and Rothschild
(Fig. 12–35)

Cacodmus indicus Jordan and Rothschild, 1912, Novitates Zool. 19: 353.
Cacodmus indicus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Cacodmus indicus, Rothschild, 1913, Entomol. Mon. Mag. 49: 103.
Cacodmus indicus, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Cacodmus indicus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 317.
Cacodmus indicus, Mathur, 1953, Indian J. Entomol. 14: 260.
Cacodmus indicus, Hiregander and Bal, 1957, Agra Univ. J. Res. (Sci.) 5: 82.

Male.—Head 0.7 mm wide, 1/3 wider than long, interocular space approximately 7 times as wide as an eye. Antennae 1.36 mm long, proportion of segments 16:36:34:33. Rostrum 0.54 mm long, proportion of segments approximately 12:16:18, reaching well past middle of triangular prosternum.

Pronotum 1.17 mm wide, twice as wide as long on median line; sides slightly more broadly rounded anteriorly than posteriorly; anterior margin relatively shallowly concave, scarcely sinuate behind eyes; long hairs of lateral margins longer than first antennal segment.

Hemelytral pads half again as wide as long, straight and contiguous only on anterior third.

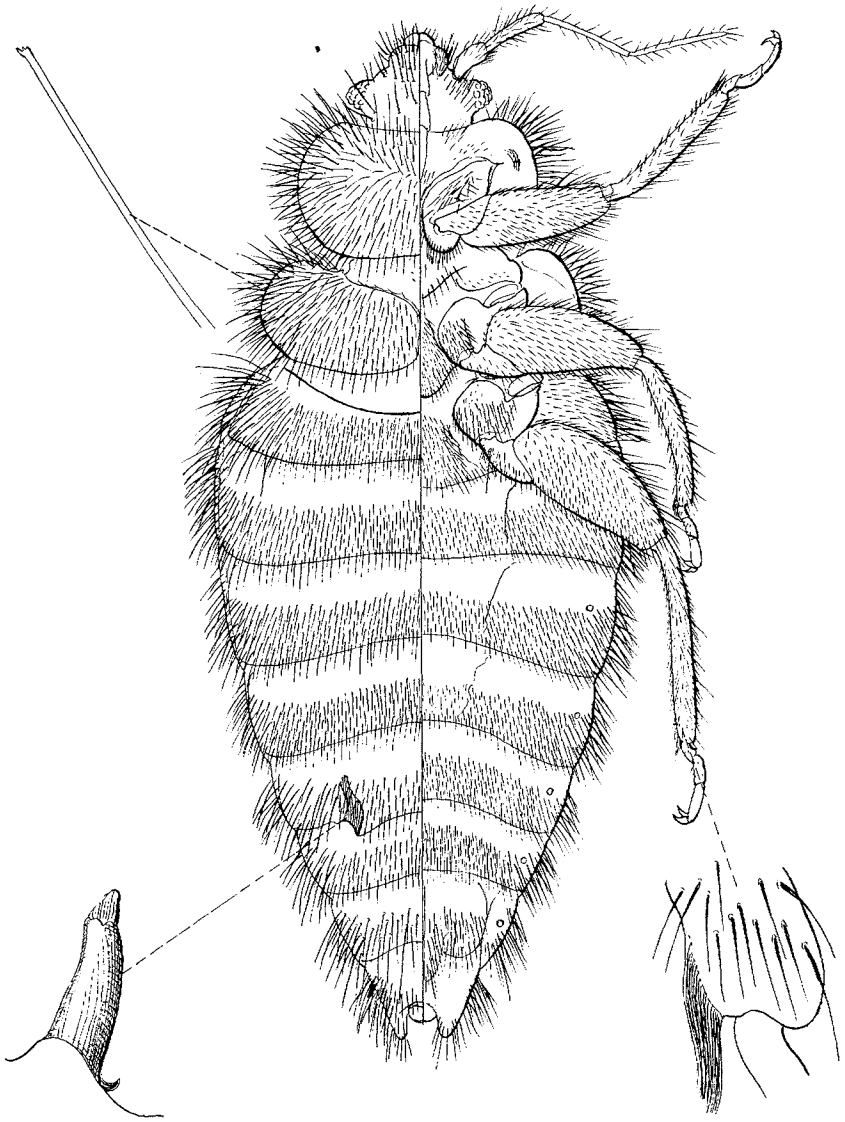

FIG. 12–35.—*Cacodmus indicus* Jordan and Rothschild. Female. Chikalda, Berars, North of Ellichpur, India (Ferris, original).

Abdomen relatively uniformly clothed with bristles. Male paramere ½ as long as width of terminal abdominal segment at base, distinctly sinuous apically, extending well onto but not across preapical segment.

Hind femora 2½ times as long as greatest width, 25:10; only slightly shorter than hind tibiae, 25:28; tibiae nearly straight, with only slight concavities on inner side subapically.

Female.—Ectospermalege elongate and tapering.

Size.—Male, length 3.8 mm, width (pronotum) 1.17 mm, (abdomen) 1.86 mm; female, length 4.48 mm, width (pronotum) 1.31 mm.

Described from the holotype male, Khandala, Bombay Presidency, Apr. 26, 1911, "From bat," (F. Assmuth), and a female bearing the same data but collected on Apr. 24, 1911. There are 2 small nymphs bearing the same data but collected in Nov., 1911.

A female specimen, also from the Rothschild collection in the British Museum (Nat. Hist.), bears the label "Chikalda, Berars, N. of Ellichpur, Nov. 1913. From *Pachyura* sp. N. B. Kinnear." It has a strongly tapered abdomen, but the ectospermalege is similar to that of the topotypic female mentioned previously.

36. ***Cacodmus sumatrensis*** Ferris and Usinger
(Fig. 12–36)

Cacodmus sumatrensis Ferris and Usinger, 1957a, Microentomology 22: 11.

Male.—Head 0.8 mm wide, slightly more than ⅓ wider than long, 49:35; interocular space approximately 5 times as wide as an eye. Antennae 1.91 mm long, proportion of segments 17:34:30:35. Rostrum about 0.63 mm long, reaching well past middle of triangular prosternum; proportion of segments approximately 11:15:13.

Pronotum 1.1 mm wide; nearly twice as wide as long on median line, 81:42; sides more broadly rounded anteriorly than posteriorly; anterior margin shallowly, evenly concave, not sinuate behind eyes; longest hairs of lateral margins subequal to length of first antennal segment.

Mesonotum-scutellum devoid of bristles.

Hemelytral pads more than ½ again as wide as long, 56:32.

Abdominal bristles longest laterally and posteriorly. Male paramere more than ½ as long as terminal abdominal segment at base, not sinuous, extending onto preapical segment.

Hind femora almost 3 times as long as greatest width, 70:24, slightly shorter than hind tibiae; tibiae slightly but distinctly inwardly bent apically.

Female.—Paragenital sinus a distinct but shallow emargination. Ectospermalege tubular, as long as sixth segment, bent to the left apically.

Size.—Male, length 5.25 mm, width (pronotum) 1.4 mm, (abdomen) 2.45 mm; female, 6.4 mm; width (pronotum) 1.45 mm, (abdomen) 2.55 mm (2 dried, pinned males, 2.6 and 3.4 mm long).

Holotype male, allotype female, and 1 male and 3 female paratypes, *Galeopithecus,* Sumatra, received from Prof. Jean G. Baer, University of Neuchatel, Switzerland. The types have been deposited in the British Museum (Nat. Hist.).

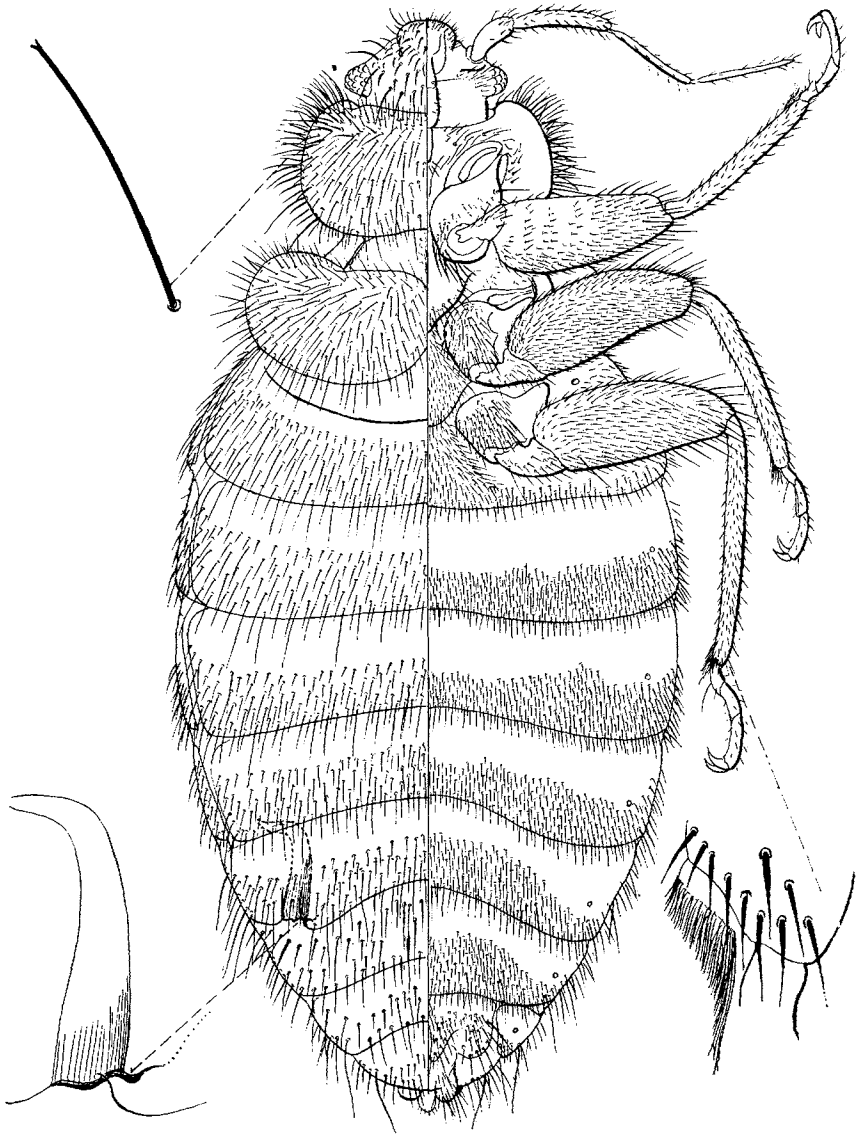

FIG. 12–36.—*Cacodmus sumatrensis* Ferris and Usinger. Female paratype. Sumatra (Ferris and Usinger 1957).

This is the first record of a cimicid from a lemur, although the record needs confirmation; other specimens are at hand from Sumatra, Java, and Malaya collected on bats. When questioned as to details of the host record, Professor Baer wrote as follows: "All I know is that they have been for many years in our slide collection, and were probably collected by my predecessor, Prof. O. Fuhrmann from skins that had been sent from Sumatra to Switzerland."

Additional localities are Garoet, W. Java, 700 m, 1931, (W. C. van Heurn), ex *Pipistrellus tralatiticus* Horsfield (G. B. Thompson coll.), and a long series, same locality and collector, 1929, insectivore vleermuizen (Mus. Leiden); a series with slightly longer hemelytral pads from Buitenzorg, Java, Feb. 18, 1910 (Bryant and Palmer Coll.) (Mus. Comp. Zool.); 2 specimens from Malay Penin., *Nyctalus,* AP no. 23475 (Jellison), from Raffles Museum, and *Miniopterus,* AP no. 23472 (Jellison), received from the Rocky Mountain Laboratory, Hamilton, Mont.; a series, Bukit Lagong, Malaya, April 11, 1953; Sungei Buloh, Selangor, Malaya, Dec. 10, 1962, on *Nyctalus stenopterus* (= *Pipistrellus (Nyctalus) stenopterus* (Dobson)) (R–65972–985; Fog. no. 23164), and same locality and date on *Myotis muricola* (= *Myotis mystacinus muricola* (Gray)) (R66542–544; Fog. no. 23279), the last 3 lots received from the Institute of Medical Research, Kuala Lumpur. Finally several collections were received from T. C. Maa, who obtained specimens from bats in the spirit collection of the Leiden Museum as follows: Sumatra, Deli, ex *Vesperugo tylophus* Dobson (= *Pipistrellus (Glischropus) tylophus* (Dobson)) on tail membrane of new-born bats (Leiden Museum no. 333); Java, E. Malang, ex *Scotophilus temminckii* (Horsfield), Oct. 1912 (P. Buitendijk) (Leiden Mus. no. 1768); Java, Mt. Gedeh, ex *Vesperugo abramus* (= *Pipistrellus javanicus* (Temminck)) (Leiden Mus. no. 1514); Java, Batavia, ex *Vesperugo tenuis* (= *Pipistrellus tenuis* (Temminck)), and Java, Modjokert, ex *Scotophilus pallidus* Dobson (= *Scotophilus temminckii* (Horsfield)), inside rolled tail membrane, the last 2 collections originating from the Embryological Institute, Utrecht.

37. ***Cacodmus sinuatus*** Usinger, n. sp.
(Fig. 12–37)

Male.—Head 0.95 mm wide, ½ again as wide across eyes as long, 14.25:9.5; interocular space 5 times as wide as an eye. Antennae 2.06 mm long, proportion of segments approximately 4:11:8:8. Rostrum 0.66 mm long, proportion of segments about 4:3:3.

Pronotum 1.86 mm wide, twice as wide as long on median line and twice as wide as head, the sides a little more rounded anteriorly than at posterior third; anterior margin sinuate behind eyes; longest bristles at sides approximately equal to first antennal segment.

Hemelytral pads slightly less than twice as wide as long, 20:11.5; bristles about as long and dense as on pronotum.

Abdomen broadest before middle, densely beset with bristles, those at sides of anterior segments longer than those at apex. Male paramere more than ½ as long as

FIG. 12–37.—*Cacodmus sinuatus,* n. sp. Male holotype. Brazzaville, République du Congo (Celeste Green, original).

width of genital segment, 14:20, extending across eighth ventral segment but not onto seventh segment, narrowed in apical half and bent inward at tip.

Hind femora 2.2 times as long as greatest width, 20:9, about as long as hind tibiae.

Size.—Male, length 6.2 mm, width (pronotum) 1.86 mm, (abdomen) 3.4 mm.

Holotype male and 1 male paratype, Brazzaville, République du Congo, Nov. 11, 1964, on *Eptesicus* (J.-P. Adam). The holotype is deposited in the Paris Museum. *C. sinuatus* is closest to *ignotus* but differs in the uniquely sinuate paramere. The simple paramere of *ignotus* is illustrated by Rothschild (1915) and is shown here for ease of comparison (see Fig. 11–6c).

38. ***Cacodmus sparsilis*** Rothschild

(Fig. 12–38)

Cacodmus villosus, Rothschild, 1912c, Entomol. Mon. Mag. 23: 85.
Cacodmus villosus, Rothschild, 1913, Entomol. Mon. Mag. 49: 102 (part).
(C)acodmus sparsilis Rothschild, 1914a, Bull. Entomol. Res. 5: 41.
Cacodmus sparsilis, Bedford, 1932, Rep. Vet. Res. S. Afr. 18: 416.
Cacodmus sparsilis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.

Female.—Head 0.91 mm wide; ½ again as wide across eyes as long on median line, 26:18; interocular space about 6 times as wide as an eye. Antennae 2 mm long; proportion of segments (Pietermaritzburg specimen) 7:20:17:15. Rostrum 0.77 mm long; proportion of segments approximately 10:20:25.

Pronotum 1.62 mm wide, less than twice as wide as long on median line, 47:25; sides more broadly rounded anteriorly than posteriorly, faintly depressed sublaterally; anterior margin feebly sinuate laterally behind eyes; longest hairs on lateral margins distinctly longer than first antennal segment.

Mesonotum-scutellum completely devoid of bristles.

Hemelytral pads about ⅔ as long as greatest width, 19:32; inner margins straight and contiguous only on anterior half.

Abdominal bristles a little longer anteriorly than posteriorly. Female ectospermalege twisted in a loop.

Legs with hind femora 2½ times as long as greatest thickness, 38:15, almost as long as hind tibiae, 38:40. Tibiae scarcely bent subapically.

Male.—Paramere (Pietermaritzburg specimen) very long, longer than width of apical abdominal segment at base, just reaching sixth abdominal segment, slender, sinuate at apex.

Size.—Male, length 5.8 mm, width (pronotum) 1.45 mm, (abdomen) 2.55 mm; female, length 5.76 mm, width (pronotum) 1.62 mm, (abdomen) 3.07 mm.

Described from the holotype female, Port Natal (Durban), on *Vespertilio dingani* (=*Scotophilus nigrita dingani* A. Smith). The characters not shown on the holotype were described from a male and a female, Pietermaritzburg, S. Africa, Feb. 22, 1918 (G. A. H. Bedford). The female from Pietermaritzburg seems to agree perfectly with the type. Two males from this same Bedford collection are in the British Museum (Nat. Hist.)

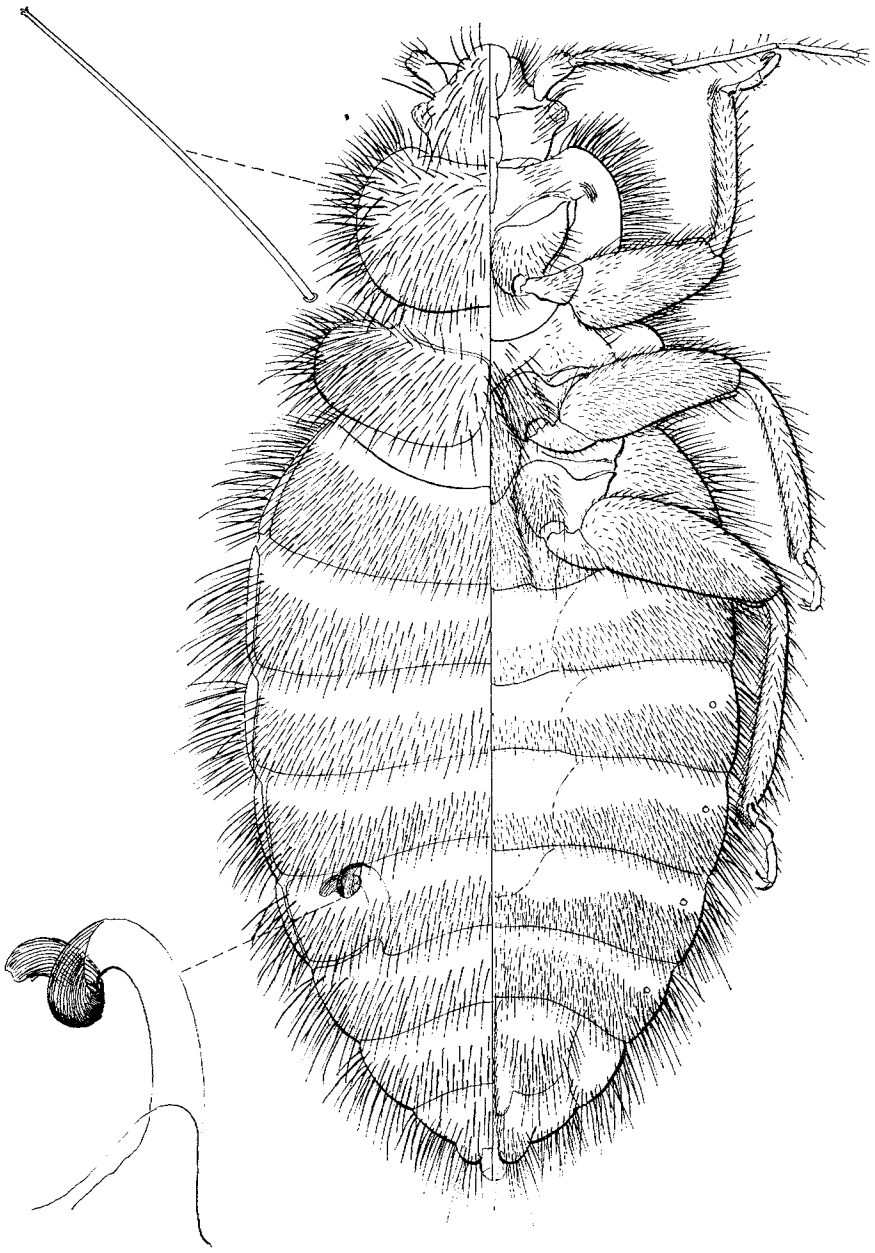

FIG. 12–38.—*Cacodmus sparsilis* Rothschild. Female. Pietermaritzburg, South Africa (Ferris, original).

spirit collection, one labeled *sparsilis* and the other *villosus*. The illustrations were made from the Pietermartizburg specimens.

39. ***Cacodmus vicinus*** Horvath
(Fig. 12–39)

Cacodmus vicinus Horvath, 1934, Bull. Soc. Entomol. France 39: 23.
Cacodmus tunetanus Horvath, 1934, Bull. Soc. Entomol. France 39: 22.
Cacodmus vicinus, Kassianoff, 1937, Ann. Par. Hum. Comp. 25: 299–307.
Cacodmus tunetanus, Kassianoff, 1937, Ann. Par. Hum. Comp. 25: 299–307.
Cacodmus vicinus Mathur, 1953, Indian J. Entomol. 14: 260.
Cacodmus aridus Ferris and Usinger, 1957a, Microentomology 22: 10.
Cacodmus tunetanus, Usinger, 1960, J. Egyptian Pub. Health Ass. 35: 84.
Cacodmus tunetanus, Linnavuori, 1964, Ann. Zool. Fenn. 1: 322.

Male.—Head 0.77 mm wide, about ⅓ wider than long; interocular space about 6 times as wide as an eye. Antennae 1.68 mm long, proportion of segments 7:18:15:13. Rostrum reaching well onto fore coxae, approximately 0.65 mm long, proportion of segments approximately 18:17:23.

Pronotum 1.3 mm wide, twice as wide as long on median line, 39:20, rather evenly rounded laterally, anterior margin not or scarcely sinuate sublaterally, though the distinctness of this character depends to some extent on the view; margins feebly impressed sublaterally, longest bristles distinctly longer than first antennal segment.

Mesonotum-scutellum devoid of bristles in slide-mounted specimens, but with several minute light spots on either side of midline which may represent points of insertion of small bristles.

Hemelytral pads nearly twice as wide as long, 29:15, inner margins straight and contiguous for more than anterior half (but not over entire length as figured by Horvath).

Abdominal bristles slightly longer on anterior segments than on posterior segments. Male paramere a little shorter than width of terminal segment at base, 26:32, extending across preapical segment but only onto basal fourth of sixth visible segment, though the pale impression extends to anterior third; paramere distinctly bent outward at apex and outer margin distinctly but feebly sinuate before middle. Ectospermalege tubular, broadly, roundly curved to the left, apex more or less curved.

Hind femora 2⅔ as long as wide, 34:13, and as long as hind tibiae. All tibiae distinctly curved inward, the apices with 2 minute but relatively short, stout spines on ventral side.

Female.—Antennal proportions 8:20:17:14. Longest bristles at sides of pronotum 0.30 mm. Hind femora 2½ times as long as wide. Ectospermalege bent roundly to the left at apex.

Size.—Male, length 5.8 mm, width (pronotum) 1.34 mm, (abdomen) 2.68 mm; female, length 5 mm, width (pronotum) 1.4 mm, (abdomen) 2.7 mm.

Described from the male holotype of *aridus* (British Museum (Nat. Hist.)), Palestine, Yesod, Humaalah, Sept. 20, 1946, *Pipistrellus* (O. Theodor). Female characters were taken from a specimen from Abu Rawash, Imbaba, Giza, Egypt, Aug. 19, 1959 (H. Hoogstraal), *Pipistrellus kuhlii* (Kuhl).

C. vicinus and *tunetanus* were described by Horvath from 3 specimens sent by Kassianoff from Tunis. Actually, Kassianoff had 1 specimen of

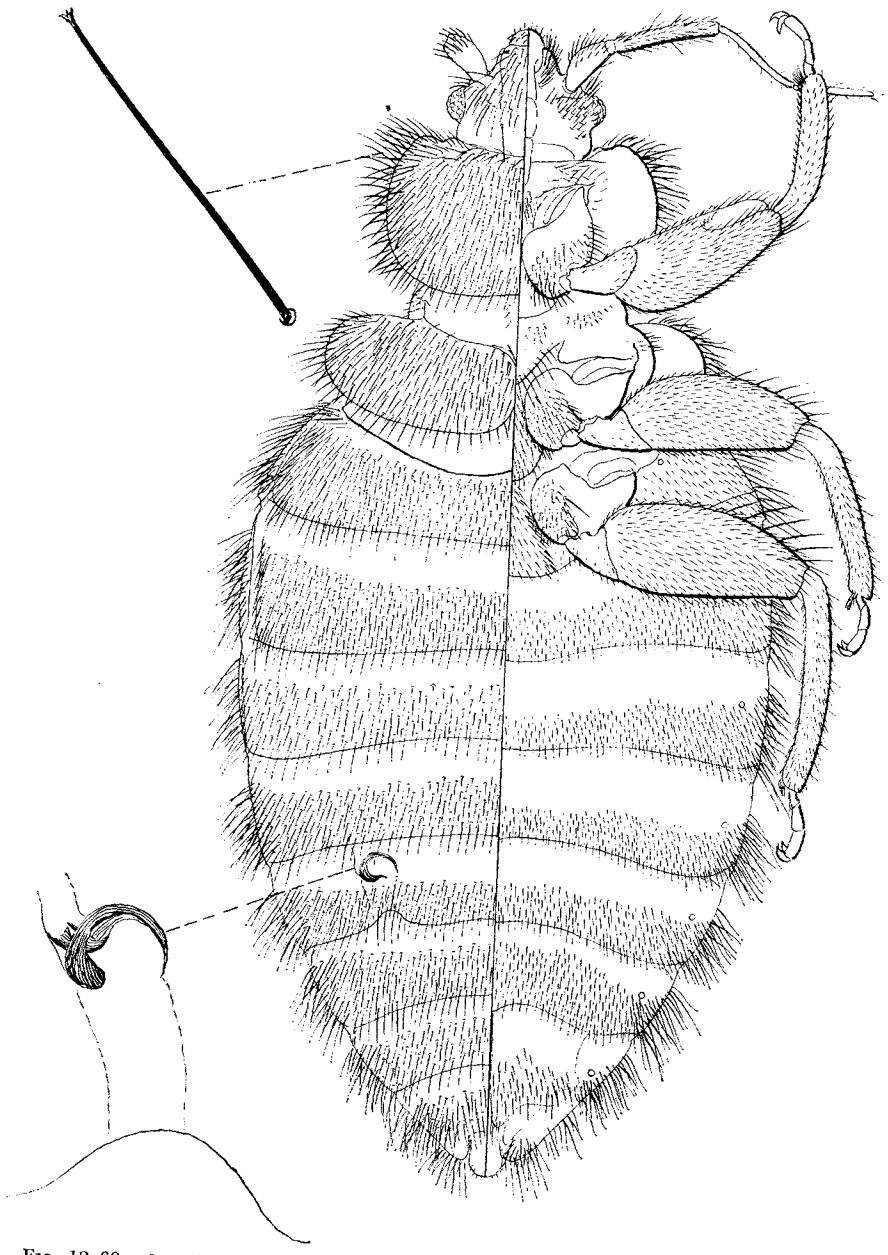

FIG. 12-39.—*Cacodmus vicinus* Horvath. Female holotype of *Cacodmus aridus* Ferris and Usinger. Yesod, Palestine (Ferris and Usinger 1957).

tunetanus and 3 of *vicinus*. I have not been able to locate Kassianoff's specimens in Paris or Lausanne, but the type of *Cacodmus vicinus* Horvath is in the slide collection at the Hungarian National Collection in Budapest. There is a crack across the cover slip and the specimen is not cleared or expanded, but it is intact. The following description was made from the type:

Male.—Head 0.75 mm wide, ½ again as wide as long (22:15); interocular space about 5 times as wide as an eye (16:3). Antennae 1.69 mm long, proportion of segments 6:16:14:13. Longest bristles at sides of pronotum 0.33 mm. Hind femora 2.76 times as long as wide.

Size.—Length 4.03 mm, width (pronotum) 1.24 mm, (abdomen) 2.41 mm.

Tunis, 1930, on *Pipistrellus kuhlii* (Kuhl).

The type of *tunetanus* may have been destroyed with some other slides in 1956, according to Dr. Soos. According to Kassianoff (1937), who studied the types in detail before sending them to Horvath, the differences were so slight (in effect, only in size) that she could not see how they could be considered as 2 separate species. The type locality of *tunetanus* is Kairouan, Tunis. In the material before me is a pair of specimens from "Gabes, Tunis Mer. Exp. Abenb." sent by Hoberlandt. The female is the same size as that given for the type of *tunetanus* (pronotal width 1.5 mm) and agrees in spermalege and other characters with specimens from Israel and Egypt. The male is smaller (pronotal width 1.4 mm) and agrees with other specimens in shape of the paramere. It seems safe to conclude that only a single species occurs from Jordan and Lebanon through Israel and Egypt to Tunis and Algeria. In general these agree with South African *villosus* in shape of ectospermalege and form of paramere. They differ in smaller size (pronotal width 1.24–1.5 mm) and shorter bristles (less than $^1/_3$ mm).

Additional material in the British Museum (Nat. Hist.) includes the allotype of *aridus,* a female presented by the Commonwealth Institute of Entomology, Palestine, Jerusalem, Aug. 1943, O. Theodor; a nymph from Gesod; a male and female from Tiberias, Palestine, July 6, 1919 (P. C. Schmitz); a female, Jericho, Palestine, Jan. 31, 1922 (P. A. Buxton), *Pipistrellus kuhlii* (Kuhl); a pair from Beison, Jordan Valley, Palestine, "Pipistrelle," June 16, 1922 (P. A. Buxton); 2 females, Ojama, S. Algeria, Feb. 20.

The longest series before me has been received over several years from Harry Hoogstraal via the Chicago Natural History Museum. Specimens were collected in Egypt as follows: 4 km W. of El Mansuriya, Giza Province, May 28, 1951 (HH6859–6867); Abu Rawash, Imbaba, Giza Province, Sept. 24, 1951 (HH7293–7304), Oct. 21, 1953, Aug. 19, 1959, Sept. 25, 1959; Sinnuris, Faiyum Prov., July 7, 1953; and 15 mi. N. W. of

Mersa Matruh, Western Desert Governorate, Sept. 23, 1959 (HH12260–12337). According to Hoogstraal and Makram Kaiser, the specimens are found between palm fronds in the roofs of houses where *Pipistrellus kuhlii* (Kuhl) roosts. The bats are migratory and are absent in the winter months.

Other material before me includes specimens from the east bank of the Jordan River near Lake Galilee, (A4695a–'46–16054) (J. Palmoni) (U. S. National Museum); a pair, Alexandria, collection of E. de Bergevin (Paris Museum); and a series, Barja, Lebanon, July 21, 1960, *Pipistrellus kuhlii* (Kuhl) (S–6048–56), sent by R. E. Lewis.

Kiritshenko (1952) reports *vicinus* from Stalinabad and Kurgan-tube in Tadzhikistan (*Pipistrellus*) and from Chira (Lake Sajat). A specimen from Kurgan-tube determined by Kiritshenko and sent by Linnavuori proved to be *Cimex pipistrelli* Jenyns, so Kiritshenko's records are not accepted as *Cacodmus*.

40. *Cacodmus villosus* Stål

(Fig. 12–40)

Acanthia villosa Stål, 1855, Öfv. Vet.-Akad. Förhandl., vol. 12, p. 38.
Acanthia villosa Stål, 1865, Hemip. Afr. 3: 24.
Cacodmus villosus Stål, 1873, Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 104.
Cacodmus villosus, Jordan and Rothschild, 1912, Novitates Zool. 19: 353.
Cacodmus villosus, Rothschild, 1913, Entomol. Mon. Mag. 49: 102–3 (part).
Cacodmus villosus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Cacodmus villosus, Rothschild, 1914a, Bull. Entomol. Res. 5: 41–2.
Cacodmus villosus, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Cacodmus villosus, Jordan, 1922, Ectoparasites 1: 285.
Cacodmus villosus, Bequaert, 1930, Rep. Harvard Afr. Exped. Liberia, Belgian Congo, p. 823.
Cacodmus villosus, Bedford, 1932, Rep. Vet. Res. S. Afr. 18: 416.
Cacodmus villosus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 403.

Male.—Head 0.83 mm wide, ⅓ wider across eyes than long on median lines; interocular space about 5 times as wide as an eye. Antennae 1.9 mm long; proportion of segments 9:24:19:14. Rostrum 0.65 mm long; proportion of segments approximately 20:18:20; tip extending beyond apex of triangular prosternum.

Pronotum 1.54 mm wide; twice as wide as long on median line and about twice as wide as head; lateral margins rather evenly rounded and anterior margin feebly sinuate sublaterally behind eyes; longest bristles of side margins nearly ½ again as long as first antennal segment; margins distinctly depressed sublaterally.

Mesonotum-scutellum devoid of bristles.

Hemelytral pads about twice as wide as long, 30:16, inner margins straight and contiguous for anterior ⅔ or more.

Abdomen densely and rather uniformly beset with bristles, those of posterior segments slightly shorter than those of anterior segments. Male paramere only slightly shorter than width of terminal abdominal segment at base, 28:32, slender and distinctly bent outward apically; extending well onto antepenultimate segment.

Hind femora 2½ times as long as broad and equal in length to hind tibiae. All tibiae distinctly but only moderately bent inward.

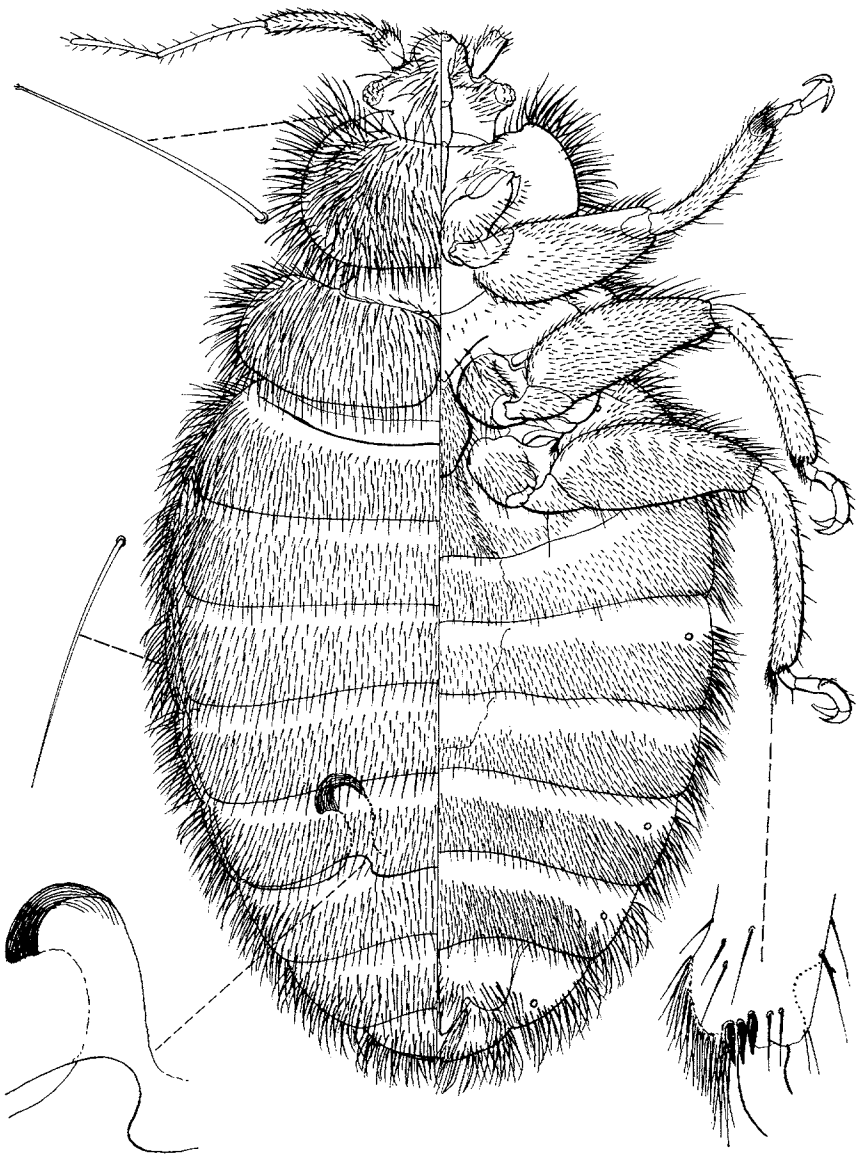

FIG. 12–40.—*Cacodmus villosus* Stål. Female. 'Mlangi, Nyasaland, Africa (Ferris, original).

Female.—Similar to male. Ectospermalege bent roundly to the left and notched before tip.

Size.—Male, length, 4.5 mm, width (pronotum) 1.48 mm, (abdomen) 2.76 mm; female, length 5 mm, width (pronotum) 1.6 mm, (abdomen) 3.1 mm.

Described from a male in the British Museum (Nat. Hist.), Mlangi, Nyasaland, May 30, 1913 (S. A. Neave). Measurements of head, pronotum, and appendices are from a male, Rukwa Valley, Tanganyika. Female characters were described from Stål's type (Stockholm Museum), which Dr. Lars Brundin kindly permitted me to clear and mount on a slide. It bears the labels "Caffraria" and "J. Wahlb."

Specimens in the British Museum (Nat. Hist.) include a male from Angola; 2 females on slides and 6 males and females in alcohol from Lichtenberg, Transvaal, Dec. 1906, from *Vespertilio capensis* (=*Eptesicus capensis* Smith) (A. Brauns), received from O. M. Reuter; 2 males from Greenwood Park, Natal, Oct. 11, 1914, from *V. capensis* (=*Eptesicus capensis* Smith) (D. R. Boyce), received from C. C. Chubb; a pair from Malvern, Natal, Sept. 24, 1897, bearing the note, "2 bugs taken off bat. They feed on wing membrane on its outer side and close to body where bat can't touch them. Bites leave distinct scar."; 2 females, Tsolo, S. Africa, June 28, 1917, *Pipistrellus kuhlii fuscatus* R. Godfrey; a male, female, and nymph, Rukwa Valley, Tanganyika, Aug. 15, 1955, from *Eptesicus capensis* (A. Smith); a male and female, Pietermaritzburg, Natal, S. Africa, Sept. 1954, ex *Pipistrellus nanus* (Peters) (R. F. Lawrence); and a series, Huila, Angola, Nov. 26 and Dec. 31, 1954 (G. Hendrich).

Specimens of uncertain position include 2 males, 2 females, and a nymph, Lutoto, N. W. Ankole, Uganda, 4800 ft, Sept. 22, 1929 (C. R. S. Pitman), and a female, "Congo." The latter specimen is smaller than typical *villosus* (pronotum 1.45 mm wide) but has the pronotum broad compared with the head, and has long bristles. The ectospermalege is not twisted.

Bequaert (1930) records a male of *villosus* from Avakubi, Belgian Congo, off *Pipistrellus musciculus* Thomas, Feb. 26, 1914 (J. P. Chapin). He mentions that the paramere agrees with Rothschild's drawing but gives no details that would indicate a relationship to *vicinus* or the South African species.

A male and female from Odzi District, S. Rhodesia, Aug. 27, 1946, ex *Scotophilus gigas* Dobson (N. C. E. Miller), are in the geographical range of *villosus,* but the pronotal width (1.38 mm) would require that they be placed with the North African *vicinus.*

Genus ***Aphrania*** Jordan and Rothschild

Aphrania Jordan and Rothschild, 1912, Novitates Zool. 19: 353.
Aphrania, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.

Aphraniola Horvath, 1913a, Bull. Soc. Entomol. France, p. 131 (n. n. for *Aphrania* J. and R., not *Afrania* Stål).
Aphraniola (*Aphrania*), Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 17, 26.
Afranya Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Aphraniola, Mathur, 1953, Indian J. Entomol., 14: 257.
Aphramia, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 766.

Size intermediate, 3.5 to 4 mm (4 to 5.5 mm when expanded on slides). Bristles moderately long and rather uniformly distributed over the body, not serrate on sides, bristles of pronotal margins minutely notched at tip. Antennae 1/3 longer than width of pronotum (African species) to over twice as long as width of pronotum (Oriental), first segment short, second longest, third and fourth shorter in that order. Rostrum reaching onto anterior half or third of prosternum. Metasternum a simple, rounded lobe narrowed anteriorly and posteriorly between middle and hind coxae.

Pronotum 1/4 or 1/5 wider than head, transverse, twice or less than twice as wide as long. Hemelytral pads slightly to distinctly transverse.

Fore coxae contiguous, middle and hind coxae progressively more widely separated, hind coxae separated by a width less than that of 1 coxa. Legs relatively short, hind femora shorter than, or about as long as, width of pronotum. Hind femora 2 to 3 times as long as greatest width, slightly to distinctly shorter than hind tibiae. Tibiae relatively stout, slightly inwardly bent subapically, all tibiae with tufts at apices, hind tibiae with a more or less distinct subapical pseudojoint.

Male genital segment rounded posteriorly following curve of abdomen, bent forward on left ventral side where the paramere groove extends even onto preapical segments mesad of spiracles. Paramere bent anteriorly to the left, extending only slightly, if at all, onto preapical segment in African species, longer and extending well beyond preapical segment in Oriental species. Female spermalege dorsal but not visible externally, without a paragenital sinus or ectospermalege, but often with pigmented traces of copulation in membrane between sixth and seventh tergites on left side or at middle. Mesospermalege rather large and not sharply delimited.

Type-species: *Aphrania barys* Jordan and Rothschild.

Aphrania was based on a negative character—lack of a visible spermalege. This is still the most significant difference between it and the closely related *Cacodmus,* although some *Aphrania* species show pigmented areas in the intersegmental membranes at the point of insertion of the paramere. *Cacodmus* has a distinct paragenital sinus and a well developed tubular ectospermalege on the left side between the sixth and seventh tergites. Also, no trace of subapical pseudojoints appears on any of the tibiae, whereas they are usually distinct on the hind tibiae in *Aphrania.*

Except for Mathur's (1953) record from palm leaves where fruit-eating bats, *Cynopterus marginatus* Blyth, were roosting, all hosts are Microchiroptera. Kühnelt's record on *Rhinolophus* (Rhinolophidae) is particularly significant because the specimens of *Aphrania barys* were attached to the wings of the bat (Fig. 11–15). Other records are from Vespertilionidae (*Eptesicus* and *Scotophilus*).

Aphrania, in common with *Cacodmus* and *Loxaspis,* has the exceptionally low haploid chromosome number of 4A + XY.

Aphrania Jordan and Rothschild (1912) was thought to be a homonym of *Afrania* Stål, so the new name *Aphraniola* Horvath (1913a) was proposed. According to the Paris Proceedings of the International Commission (Bull. Zool. Nomencl, 4:243, 1950) this action was justified, thus the name *Aphraniola* was used correctly by Ferris and Usinger (1953) and Mathur (1953). However, the present International Code recognizes the 1953 Copenhagen decision—the so-called "one-letter rule"—for determining homonymy of generic names. Therefore Horvath's new name is now unnecessary and is suppressed.

KEY TO THE SPECIES OF *APHRANIA*

1. Pronotum relatively long and narrow, ratio of length on median line to greatest width 1:1.75 or less. Hemelytral pads much less than ½ again as wide as long. Second antennal segment much longer than interocular space. Oriental Region. ..... 44. ***vishnou***

   Pronotum relatively short and broad, the ratio of length on median line to greatest width 1:1.84 or even broader. Hemelytral pads distinctly broader, more than ½ again as wide as long. Second antennal segment subequal or shorter than interocular space. Africa. 2

2. No pseudojoints on hind tibiae; clypeus with 3 erect inwardly curved bristles submarginally on each side; paramere long, reaching past eighth segment and into groove beyond level of spiracle of seventh segment; spermalege indicated in cleared specimens by a transverse pigmented area in intersegmental membrane on left side between fifth and sixth tergites. Sudan, Sierra Leone ..... 43. ***elongata***

   A distinct pseudojoint subapically on each hind tibia; clypeus with 2 erect, inwardly curved submarginal bristles on each side; paramere shorter, scarcely surpassing margin of genital segment, not reaching beyond groove at level of seventh segment spiracle; spermalege without visible pigmented area in cleared specimens. 3

3. Male paramere ½ or more than ½ as long as width of genital segment at base, 33:60. S. Africa. ..... 41. ***barys***

   Male paramere less than ½ as long as width of genital segment at base, 27:63. Central Africa. ..... 42. ***recta***

41. *Aphrania barys* Jordan and Rothschild
(Fig. 12–41)

Aphrania barys Jordan and Rothschild, 1912, Novitates Zool. 19: 353.
Aphraniola barys, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Aphrania barys, Scott, 1928, Entomol. Mon. Mag. 64: 108.
Afranya barys, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 317.
Afranya barys, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.

Body suboval, rather coarsely punctured on hemelytral pads and abdominal tergites, more finely so on pronotum, the head at center and scutellum impunctate. Color reddish brown to dark brown with paler hemelytral pads and appendages. Longest bristles of body about 0.23 mm.

Male.—Head transverse, 0.81 mm wide, ratio of width across eyes to length 48:35, interocular space about 6 times as wide as an eye; clypeus with 2 erect, inwardly bent bristles on each side near lateral margins. Antennae 1.68 mm long; proportion of

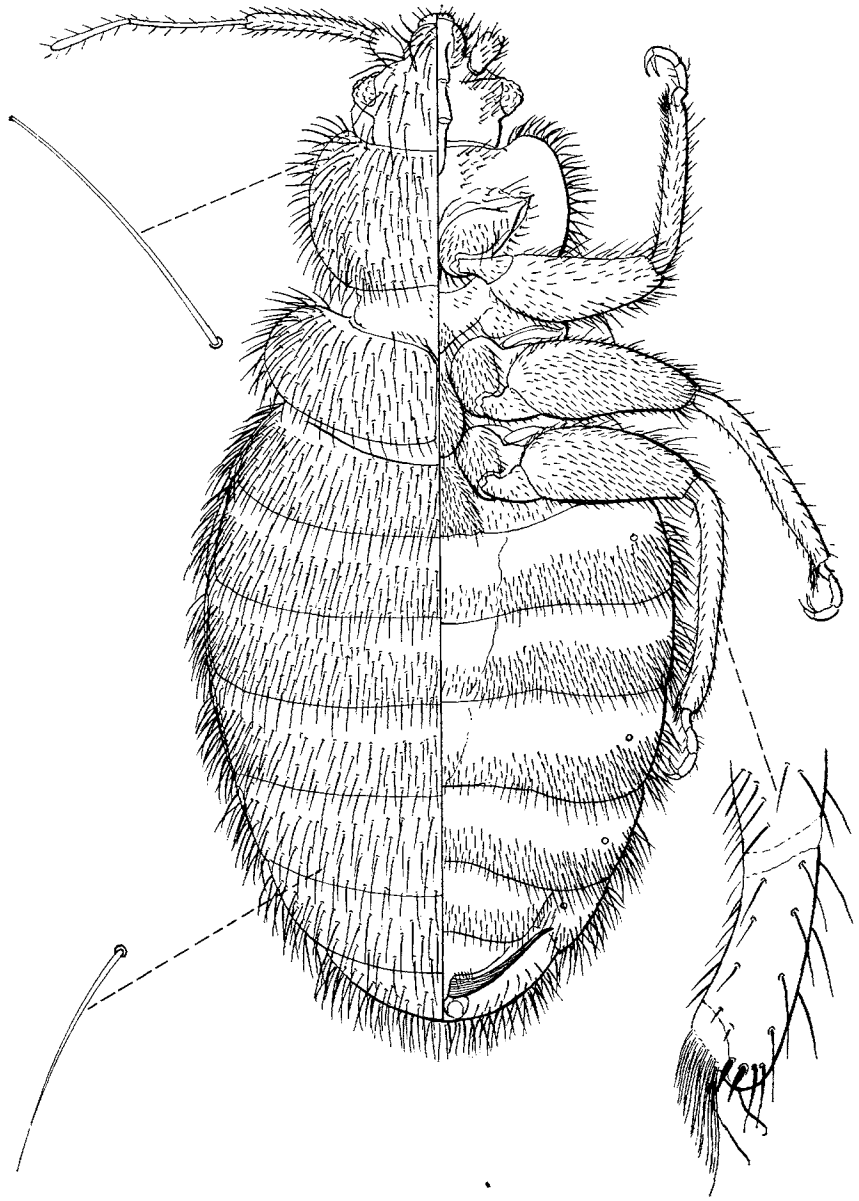

FIG. 12–41.—*Aphrania barys* Jordon and Rothschild. Male paratype. Maseru, Basutoland, Africa (Ferris, original).

segments 11:35:33:26. Rostrum 0.68 mm long, proportion of segments approximately 13:10:16.

Pronotum less than twice as wide as long on median line, 72:39, rather evenly arcuate laterally, the long bristles at sides about equal to length of first antennal segment.

Mesonotum-scutellum practically devoid of hairs or bristles, with only 1 or 2 obscure bristles on each side at hind margin.

Hemelytral pads distinctly transverse, ½ again as broad as long, inner margins straight and in contact over most of their length.

Abdomen with bristles rather uniformly developed throughout. Paramere more than ½ as long as width of terminal abdominal segment at base, 31:55, sinuate or slightly bent outward apically, its tip extending onto preapical segment.

Legs relatively stout, the hind femora about 2½ times as long as greatest thickness and 5/6 as long as hind tibiae.

Female.—Like the male but with abdomen symmetrical and without pigmented copulatory tracts.

Size.—Male, length (expanded, slide-mounted specimen) 4.7 mm, width (pronotum) 1.2 mm, length (pinned specimen) 3.9 mm, width (abdomen) 2.38 mm; female, length (slide-mounted) 4.9 mm, width (pronotum) 1.15 mm, (abdomen) 2.15; pinned specimen, length 3.8 mm, width (pronotum) 1.10 mm, (abdomen) 2.0 mm.

Holotype male and 2 male paratypes, British Museum (Nat. Hist.), Maseru, Basutoland (L. Wroughton), and a pinned paratype, male, same data. Also 2 males and a female, Gobabeb, Namib Desert, S. W. Africa, March 15, 1964, on wings of *Eptesicus zuluensis* Roberts (W. Kühnelt). Prof. Kühnelt reported that the bats were hiding in cracks in the exfoliating granite domes that are characteristic of this part of the Namib Desert. Other collections are 2 males and a female, Otjitambi, S. W. Africa, January, 1952, British Museum (Nat. Hist.), 1956–275, det. W. E. China (fewer rows of bristles on abdominal tergites); a male, 5 mi NE of Kapiri, Mposhi, N. Rhodesia, Feb. 10, 1958 (E. S. Ross and R. E. Leech), in *Brachystegia* woodland under bark of stump; and a female and nymph, Westminster, Orange Free State, South Africa, "from sleeping place of bats" (Capt. E. E. Helme). The latter cannot be placed with certainty because of the lack of male specimens.

42. ***Aphrania recta*** Ferris and Usinger
(Fig. 12–42)

Aphrania recta Ferris and Usinger, 1957a, Microentomology 22: 11.

Body suboval, coarsely punctured as in *barys*. Longest bristles about 0.27 mm.

Male.—Head 0.77 mm wide, transverse, the ratio of width across eyes to length 50:35, interocular space about 4 times as wide as an eye; clypeus with 2 erect inwardly curved bristles on each side. Proportion of antennal segments 13:30:29:26. Rostrum approximately 0.56 mm long; proportion of segments 10:10:15.

Pronotum 1.24 mm wide, slightly more than twice as wide as long on median line, 75:36, the sides a little more broadly arcuate anteriorly than posteriorly; long bristles at sides distinctly longer than first antennal segment.

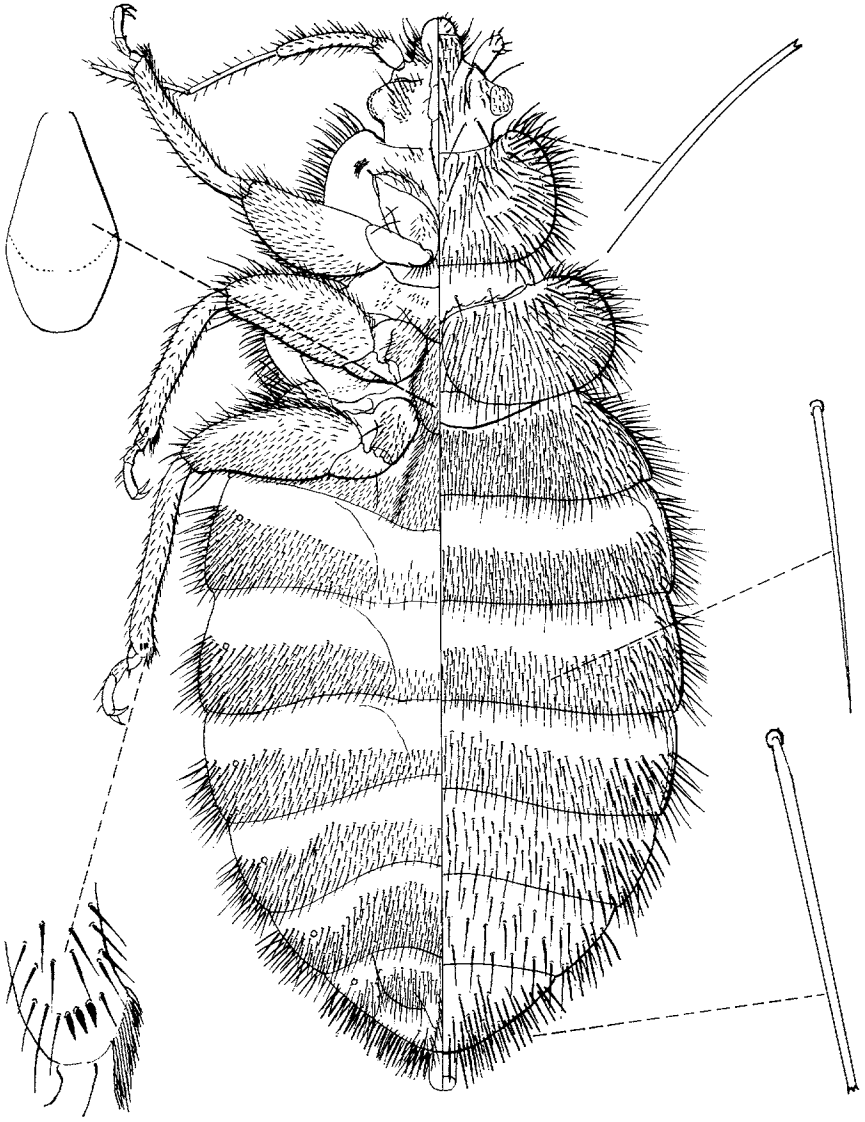

FIG. 12–42.—*Aphrania recta* Ferris and Usinger. Female paratype. Mutir, Uganda (Ferris and Usinger 1957).

Mesonotum-scutellum with at least 2 well developed bristles on either side at hind margin.

Hemelytral pads strongly transverse, more than ½ again as wide as long, inner margins straight and contiguous except narrowly at posterior angles.

Abdominal bristles dense and relatively uniformly developed throughout, second tergite with 7 or 8 irregular rows and other tergites with about 6 rows. Paramere less than ½ as long as width of terminal abdominal segment at base, not sinuate apically and not extending onto preapical segment.

Hind femora 2⅓ times as long as greatest thickness and ⅚ as long as hind tibiae.

Female.—Like male, abdominal tergites symmetrical, without traces of copulation.

Size.—Male, length 5 mm, width (pronotum) 1.24 mm, (abdomen) 2.45 mm (expanded, slide-mounted specimen); female, length 5.86 mm, width (pronotum) 1.38 mm.

Holotype, allotype, and 1 male and 3 female paratypes, all taken at Mutir, Uganda, left bank, Albert Nile, March 13, 1926, (C. R. S. Pitman), British Museum (Nat. Hist.). A series of 14 specimens, Matadi, Belgian Congo (U. Rahm), "on bat."

A. recta differs from *barys* in the shorter paramere. Whether this difference is significant at the species level is not known, but all specimens from South Africa (*barys*) have the long paramere and all from Central Africa have the short paramere.

43. ***Aphrania elongata*** Usinger, n. sp.
(Fig. 12–43)

Male.—Body elongate-oval, surface finely punctured except for coarse punctures on hemelytral pads. Bristles long, erect, the longest bristles at sides of pronotum 0.3 mm.

Head 0.83 mm wide, ¼ wider than long; interocular space about 5 times as wide as an eye, 9:1.75; clypeus with 3 erect, inwardly bent bristles on each side near lateral margins in addition to several erect but backwardly directed spines on disk. Antennae 2 mm long; proportion of segments 4:9:9:8. Rostrum 0.62 mm long; proportion of segments 10:12:15. Pronotum 1.31 mm wide, a little less than twice as wide as long, 79:41, and slightly more than ½ again as wide as head, 79:51; sides more arcuate anteriorly than posteriorly; bristles rather evenly spaced on disk, much longer than distance between bristles, dense at sides and up to 0.3 mm long.

Mesonotum-scutellum with 2 or 3 bristles on each side posteriorly.

Hemelytral pads more than ½ again as wide as long, 53:33; broadly contiguous in a straight line at middle, surface with rather evenly spaced bristles over twice as long as distance between bristles.

Abdomen with relatively sparse, long bristles, the longest 0.25 mm, those of second tergite in about 5 irregular rows, those of other tergites in 4 or 5 irregular rows. Paramere ¼ longer than greatest width of genital segment, extending beyond edge of genital segment in a groove that crosses eighth segment and reaches level of spiracle on seventh segment.

Legs rather stout, hind femora 2½ times as long as wide, hind tibiae ⅕ longer than femora, with scarcely a trace of pale "pseudojoint."

Female.—A distinct transverse pigmented area sublaterally on left side in intersegmental membrane between fifth and sixth tergites.

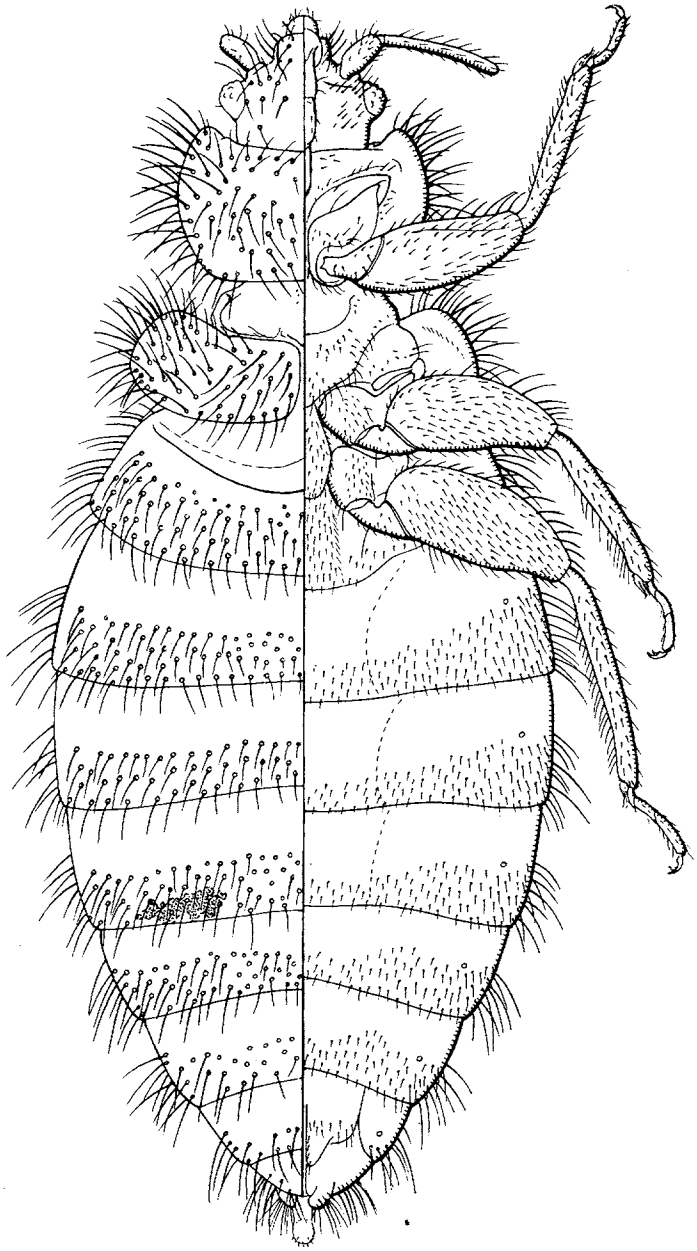

FIG. 12–43.—*Aphrania elongata,* n. sp. Female allotype. Kordofan, El Obeid, Sudan (Celeste Green, original).

Size.—Male, length 5.53 mm, width (pronotum) 1.31 mm, (abdomen) 2.53 mm; female, length 6.53 mm, width (pronotum) 1.36 mm, (abdomen) 2.8 mm (slide-mounted).

Holotype male, allotype female, and 1 male paratype, Kordofan, El Obeid, Sudan, Jan. 30 to Feb.'1, 1963 (R. Linnavuori). The holotype is in the collection of R. Linnavuori. A second series, including 1 male and 2 females from Khartoum, Sudan, Nov. 28, 1962 (R. Linnavuori), agrees except for smaller size, the male being 4.6 mm long with the pronotum 1.1 mm wide and the female 5.3 mm long with the pronotum 1.2 mm wide. A third collection consists of 1 female with a pronotal width of 1.2 mm from Musaia, Sierra Leone, Apr. 6, 1962, alt. 1135 ft, on *Scotophilus nigritus* A. Smith (F. R. Allison), sent by Dr. O. Theodor.

Other specimens that probably belong here include 2 males in the Rothschild Collection (British Museum (Nat. Hist.)), 35 mi east of Kordofan, Sudan, from *Scoteinus schlieffenii* (Peters) (Rear Adm. W. Hynes), and 4 males, Njala, Sierra Leone, March 29, 1955, on *Eptesicus tenuipennis* (Peters) (T. S. Jones).

A. elongata differs from *barys and recta* in the fewer rows of longer bristles on the abdominal tergites, the obsolete pseudojoints on the hind tibiae, the much longer paramere, and the pigmented area on the left side between the fifth and sixth abdominal tergites. The Oriental *vishnou* also has a long paramere and a pigmented insemination area, but the latter is between the sixth and seventh tergites.

44. ***Aphrania vishnou*** (Mathur)

(Fig. 12–44)

Aphraniola vishnou Mathur, 1953, Indian J. Entomol. 14: 257.
Aphraniola orientalis Ferris and Usinger, 1953, Rev. Franç. Entomol. 20: 138.
Aphraniola orientalis, Carayon, 1953a, Rev. Franç. Entomol. 20: 139.

Body elongate-oval, superficially punctured, light brown with hemelytral pads even paler. Bristles long, the longest at sides of pronotum 0.33 mm.

Male.—Head 0.8 mm wide, much wider (eyes included) than long, 52:35, the interocular space about 3 times as wide as an eye. Antennae about 2.23 mm long, proportion of segments 15:55:50:34. Rostrum 0.54 mm long, reaching to anterior fifth of prosternum, proportion of segments approximately 15:11:15.

Pronotum 1 mm wide, more than ½ again as wide across anterior half as long on median line, 66:40, narrowed posteriorly, the sides not evenly rounded. Long bristles of sides of pronotum longer than first antennal segment.

Mesonotum-scutellum devoid of hairs or bristles.

Hemelytral pads nearly as long as broad, 35:40, inner margins nearly straight except posteriorly.

Abdomen with lateral bristles of posterior segments stiffer, longer, and denser than those of anterior segments. Paramere only slightly, evenly curved, not sinuate near apex; nearly as long as width of genital segment at base, 22:27, extending in a groove over eighth ventral segment and nearly across seventh segment.

Legs relatively long and slender, the hind femora 3 times as long as greatest thickness and ¾ as long as hind tibiae.

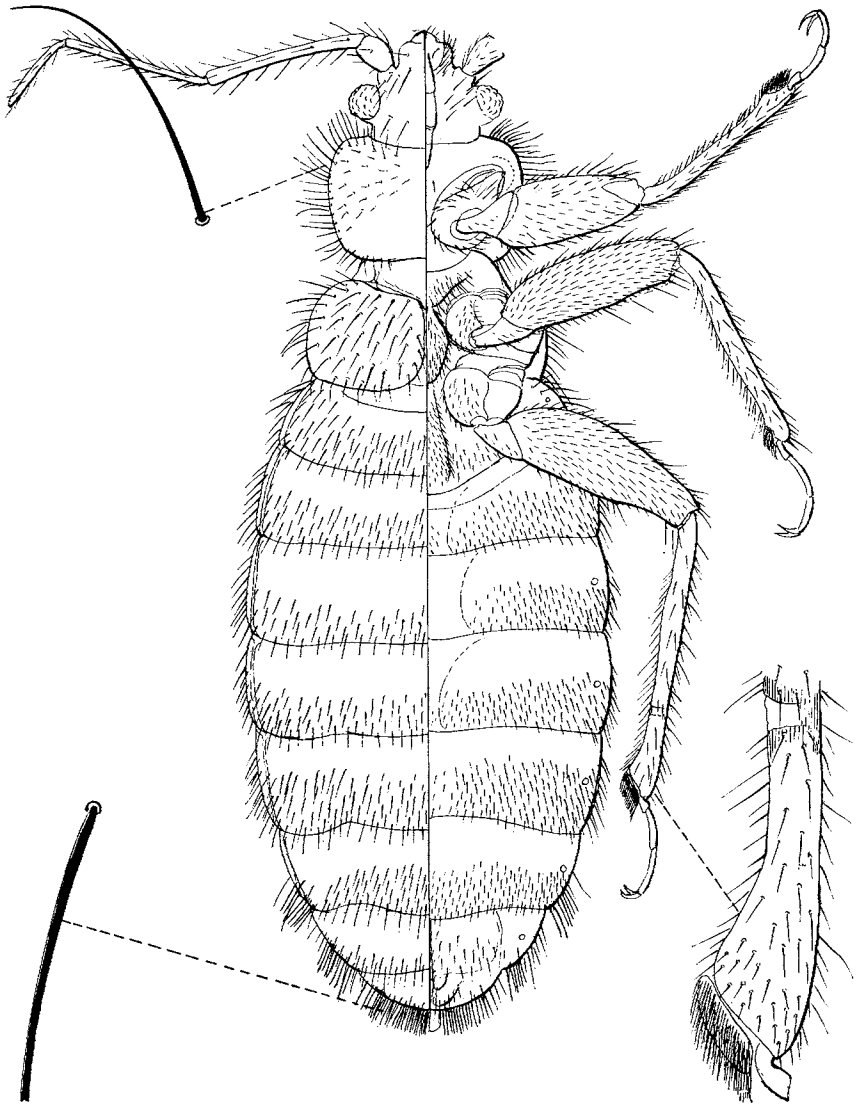

FIG. 12–44.—*Aphrania vishnou* (Mathur). Female paratype of *Aphrania orientalis* Ferris and Usinger. Pnom Penh, Cambodia (Ferris and Usinger 1957).

Female.—Abdominal tergites with no paragenital sinus.

Size.—Expanded, slide-mounted specimens: Male, length 5.2 mm, width (pronotum) 1 mm, (abdomen) 2 mm; female, length 5.5 mm, width (abdomen) 2 mm. Length of pinned specimens: Male 3 mm, female 3.2 mm. Length of female in ethyl alcohol: 4.0 mm.

Described from the holotype male, allotype female, and 7 male and 1 female paratypes of *orientalis* (Paris Museum) collected on bats, *Scotophilus temminckii castaneus* Gray (= *Scotophilus temminckii* (Horsfield)), at the farm school of Prek-Léap near Pnom Penh, Cambodia, October, 1952, by Mr. Ho Tong Peng. A male and female are at hand from Port Dickson, Malaya, July 10, 1958 and Feb. 27, 1960, on *Scotophilus temminckii* (Dobson) (= *Scotophilus temminckii* (Horsfield)).

Comparison with a male of *vishnou* kindly sent by R. N. Mathur shows that these 2 names represent the same, apparently widely distributed, species. The type of *vishnou* is in the collection of the Forest Research Institute, Dehra Dun. *A. vishnou* was collected from dry palm leaves of *Livistoma chinensis* Br. where bats, *Cynopterus marginatus* Blyth (=*Cynopterus sphinx* (Kohl)), were roosting at Dehra Dun, U. P., May 20, 1951. Mathur (4 Nov. 1959) writes that the date of publication of his description of "*Aphraniola vishnou*" is January, 1953, though the volume is for December, 1952 (Indian Journal of Entomology, vol. 14, pt. 3). The date of publication of the Revue Francaise d'Entomol., vol. 20, was July 25, 1953.

According to Mathur (1953), "*Cynopterus marginatus* Blyth (=*Cynopterus sphinx* (Kohl), a species of bat which roosts in large numbers on the above-mentioned palms, does considerable damage to the litchi (*Nephelium litchi*) fruits of the garden every year. In order to drive away the bats, the author got all the dry leaves cut down from his palm trees in May 1951. The men engaged for the work complained that they had been bitten very badly by bugs harboured on the leaves. On examination, their clothes were found infested with a good number of bugs knocked down from the leaves. It would appear that these bugs subsist on the blood of the bats and after gorging, leave the bats and secrete themselves in the suspended dry leaves at night. When the bats return again in the early morning, the bugs visit their hosts for a feed and thus breed actively there."

A. vishnou differs strikingly from the African species. Dried specimens reveal punctures that are more superficial. The hemelytral pads are longer and more roundly produced posterolaterally. The bristles are longer, the antennae are longer, the pronotum is narrower and distinctly margined, and the paramere is longer. Yet the ectospermalege is wanting as in the African species, and the unusually low chromosome number is like other members of this group (*Cacodmus* and *Loxaspis*). There are

distinct traces of copulation in the membrane between the sixth and seventh tergites at the middle or on the left side.

Genus *Loxaspis* Rothschild

Loxaspis Rothschild, 1912d, Bull. Entomol. Res. 2: 363.
Loxaspis, Jordan and Rothschild, 1912, Novitates Zool. 19: 353.
Loxaspis, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Loxaspis, Patton and Cragg, 1913, Textb. Med. Entomol., p. 512.
Loxaspis, Jordan, 1922, Ectoparasites 1: 285.
Loxaspis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 307, 318.

Body oval with narrowed pronotum, finely, rather superficially punctured and with dense short bristles interspersed with longer bristles, especially at sides of pronotum and hemelytra and on femora. Females of some species with longer bristles throughout. Bristles not serrate, the tips acute or minutely cleft. Color reddish brown with paler appendages. Size 3.75 mm (dried specimens) to 5.75 mm (expanded, slide-mounted specimens).

Antennae 2 or 2½ times as long as width of pronotum, first segment short and stout, second segment 3 to 5 times as long as first, third subequal or much shorter than second, fourth a little shorter than third. Rostrum with segments approximately subequal or third slightly longer than others, surpassing apex of triangular prosternum, reaching about to level of middle of front coxae, without stout bristles.

Pronotum ½ again as wide as head or less, about ½ again as wide as long, narrowly depressed laterally and sharply impressed subbasally.

Mesonotum-scutellum with many small bristles.

Hemelytral pads about ½ again as wide as long, broadly contiguous along straight inner margins.

Metasternum compressed between middle coxae, the hind coxae a little farther apart than front and middle coxae.

Legs moderately long, the hind femora from 3 to 5 times as long as wide, slightly shorter than tibiae. All tibiae bent inward subapically with pseudojoints at point of bend. Front and middle tibiae with apical tufts. Femora with several long bristles. Tibiae with short bristles except in 1 species.

Genital segment in male deeply set in preapical segment, 2 or 3 times as wide as long, the paramere transverse, directed to the left and bent backward apically, tapering and slightly exceeding the lateral margin of terminal segment.

Females with hind margin of fourth visible tergite sinuate or concavely notched sublaterally on the right side over spermalege.

Type-species: *Loxaspis miranda* Rothschild.

Loxaspis is close to *Aphrania* and *Cacodmus* but differs from both in the type of spermalege, in the backwardly bent male paramere, and in the tibial tufts, which are present only on the front and middle tibiae.

KEY TO THE SPECIES OF *LOXASPIS*

1. Hind femora more than 5 times as long as greatest width. Longest bristles of middle and hind tibiae distinctly longer than diameter of tibia. Belgian Congo ..... 45. ***setipes***
   Hind femora about 4 times or less as long as greatest width. Longest bristles of middle and hind tibiae shorter than diameter of tibia..... 2
2. Second antennal segment slightly to distinctly shorter than width of head. Sides of pronotum slightly converging behind middle. Africa..... 3

Second antennal segment subequal or distinctly longer than width of head across eyes. Sides of pronotum subparallel behind middle. Asia..... 4

3. Male paramere ⅔ as long as width of genital segment. Hind margin of fifth abdominal tergite in female with sinus just mesad of right margin. East Africa. .....46. ***miranda***

Male paramere about ⅘ as long as width of genital segment. Hind margin of fifth abdominal tergite in female with sinus distinctly removed from right margin. West Africa (French Soudan).....47. ***barbara***

4. Hind femora 4 times as long as wide. Java.....48. ***seminitens***

Hind femora 3½ times as long as wide. Borneo and Malaya..... 5

5. Second antennal segment subsequal to width of head. Malaya.....50. ***malayensis***

Second antennal segment distinctly longer than width of head. Borneo...49. ***spinosa***

45. *Loxaspis setipes* Ferris and Usinger
(Fig. 12–45)

Loxaspis setipes Ferris and Usinger, 1957a, Microentomology 22: 10.

Body abruptly dilated at abdomen. Legs relatively long and slender. Bristles of dorsal surface very fine and inconspicuous. Middle and hind tibiae with a few bristles longer than thickness of tibia.

Male.—Head 0.83 mm long; scarcely wider than long, 48:46, the interocular space about 8 times as wide as an eye. Antennae 2.9 mm long, proportion of segments 15:55:57:50. Rostrum 1 mm long; proportion of segments approximately 20:20:25, apex reaching well beyond tip of triangular prosternum.

Pronotum 1.14 mm wide; ½ again as wide as long on median line, 68:43, distinctly but only slightly narrowed just behind middle; long bristles at sides sparse, about 12 on each side, the longest distinctly shorter than first antennal segment; disk with very short, fine bristles.

Mesonotum-scutellum with very short, fine bristles, visible only under high magnification.

Hemelytral pads more than ½ again as wide as long, 39:25, broadly rounded posterolaterally, narrowly, roundly produced anterolaterally, outer margin with about 8 long bristles; disk with very short fine bristles except for 1 or 2 long ones submarginally.

Abdomen subrounded in outline, the tergites with such small bristles that the disk appears naked under magnification of 27 diameters; a few longer bristles laterally on first visible segment, small but distinct bristles along hind margins of ventrites, and a short, dense pubescence at middle of base between hind coxae. Male paramere ⅘ as long as width of terminal segment at base, extending beyond margin of terminal segment at side, evenly bent to the left and gradually tapering, not sinuous apically.

Hind femora more than 5 times as long as wide, 107:20, distinctly shorter than hind tibiae, 107:143. Longest bristles of hind tibiae much longer than diameter of tibia.

Size.—Slide-mounted male, length 5.65 mm, width (pronotum) 1.14 mm, (abdomen) 2.5 mm.

Holotype male and 2 male paratypes, Lukolela, Belgian Congo (J. P. Chapin), Museum of Comparative Zoology, off horse-shoe bat.

This is the most distinct species in the genus, being readily separable from the other described species by the relatively long slender femora, the long tibial bristles, and the extremely small bristles on most of the dorsal surface of the body.

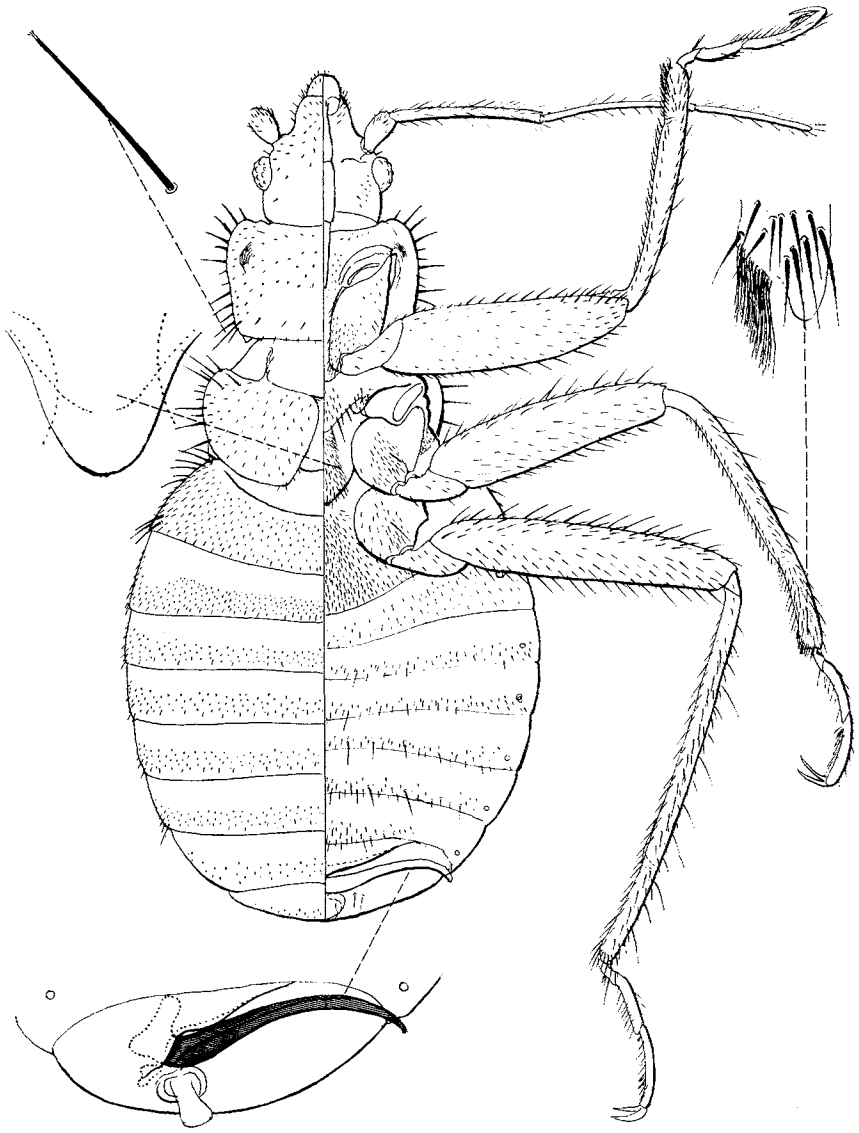

FIG. 12–45.—*Loxaspis setipes* Ferris and Usinger. Male holotype. Lukolela, Congo (Ferris and Usinger 1957).

46. *Loxaspis miranda* Rothschild
(Fig. 12–46)

Loxaspis miranda Rothschild, 1912d, Bull. Entomol. Res. 2: 363.
Loxaspis mirandus, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Loxaspis mirandus, Patton and Cragg, 1913, Textb. Med. Entomol., p. 512.
Loxaspis miranda, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Loxaspis mirandus, Scott, 1928, Entomol. Mon. Mag. 64: 108–9.
Loxaspis miranda, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 318.
Loxaspis miranda, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Loxaspis mirandus, Mathur, 1953, Indian J. Entomol. 14: 260.
Loxaspis mirandus, Miller, 1956, Biol. Heterop., p. 119.
Loxaspis miranda, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 26.

Body with dense, relatively short bristles in both sexes. Pronotum only slightly narrowed behind middle. Hemelytral pads longest on inner half, roundly narrowed laterally.

Male.—Head only slightly wider than long, 23:20, 0.82 mm wide; interocular space 6 times as wide as an eye. Antennae 2.2 mm long; proportion of segments 5:22:19:17.

Pronotum slightly more than ½ again as wide as long on median line, 31:19, narrowed posteriorly, the sides feebly concave behind middle; long bristles at sides not longer than first antennal segment.

Mesonotum-scutellum with many short, fine bristles, especially on posterior half.

Hemelytral pads ½ again as wide as long, broadly rounded laterally, straight and contiguous at inner basal three-fourths; outer fourth of disk with long bristles, inner disk with short, fine bristles.

Abdomen relatively short and round, covered with very short bristles except along hind margins of tergites; a few more prominent bristles laterally at base of first visible segment and a cluster of stouter spines surrounding anus. Male paramere about ⅔ as long as width of terminal segment at base, evenly bent to the left and gradually tapering, not sinuous apically.

Hind femora over 3 times as long as wide, 37:10.5, slightly shorter than tibiae, 37:44. Tibial bristles very short.

Female.—Paragenital sinus a shallow emargination sublaterally at right on hind margin of fifth tergite.

Size.—Slide-mounted male, length 3.71 mm, width (pronotum) 1.1 mm; female, length 3.8 mm, width (pronotum) 1.07 mm.

Described from the holotype male, Kolidini near Mombasa, Kenya, Feb. 12, 1911, probably from *Taphozous hildegardeae* (F. S. Jackson). A female from the same series was used for describing the female characters. A nymph is also in the British Museum (Nat. Hist.) from the same collection.

Additional specimens include a male from Entebbe, Uganda, Nov. 11, 1960, on *Tadarida limbata* Peters (T. S. Jones); a male and a nymph, Fambani R., Zambesia, E. Africa, in hollow trunk of *Borassus* palm with *Mops angolensis* Peters (H. B. Cott); 3 males and 2 females, Equatoria, Juba-Terakeka-2, Mar. 6, 1963 (R. Linnavuori); and 2 males and 2 females, Singa Sennar Province, Sudan, 1913, from *Chaerephon pumilus*

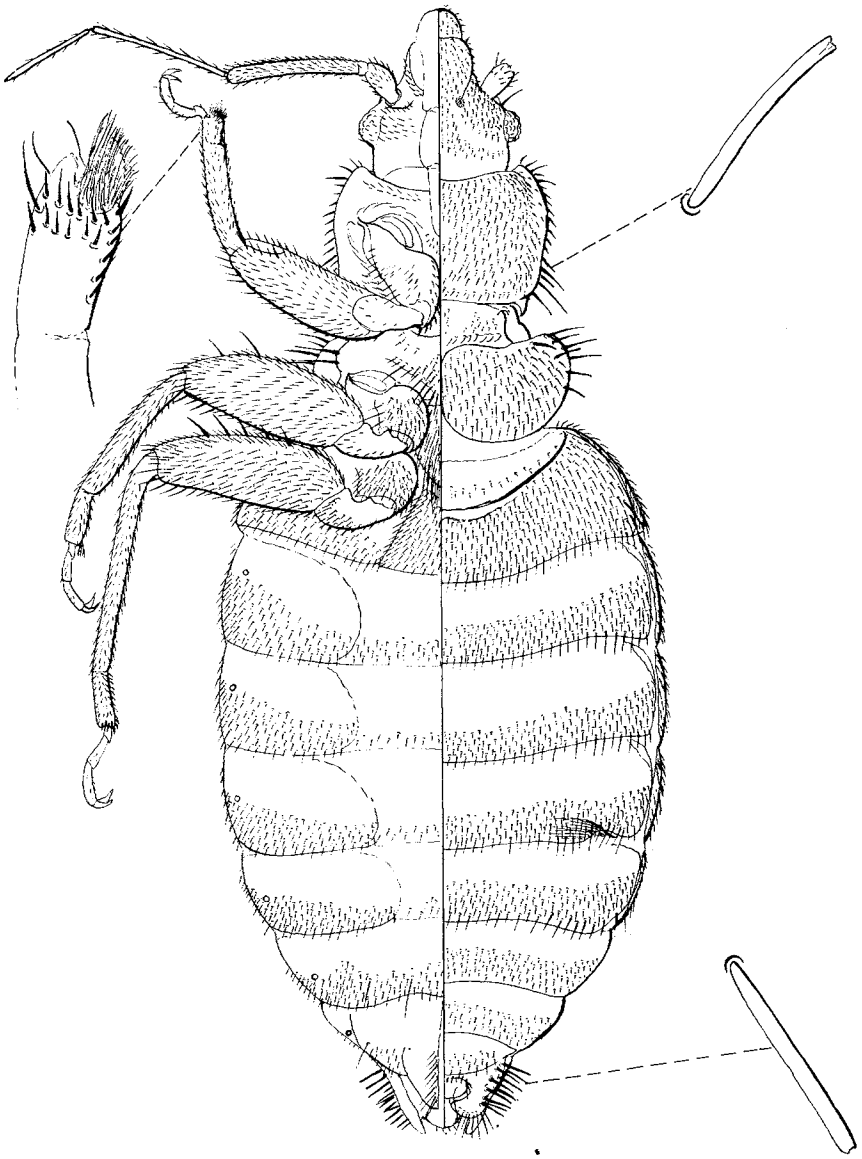

FIG. 12–46.—*Loxaspis miranda* Rothschild. Female. Kolidini near Mombasa, Kenya. (Ferris, original).

(Cretzchmar) (N. E. Marshall). There are additional specimens from the Marshall collection in the spirit collection of the British Museum (Nat. Hist.), 3 specimens in the Hungarian National Collection, and 1 in the U. S. National Museum.

The bristles are difficult to see in the types. In specimens from Singa Sennar they are very short but dense on the pronotal disk, a little longer on the hemelytral pads (with long erect bristles anterolaterally) and still longer (0.10 mm in the female) posteriorly on the abdominal tergites. The latter are a little shorter on the male.

47. *Loxaspis barbara* (Roubaud)

(Fig. 12–47)

Leptocimex barbarus Roubaud, 1913, Bull. Soc. Entomol. France, p. 350.
Loxaspis barbara, Horvath, 1913a, Bull. Soc. Entomol. France, p. 372.
Loxaspis barbara, Horvath, 1914b, IX^{e} Int. Congr. Zool., p. 295.
Loxaspis barbara, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 307–312.
Loxaspis barbara, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Loxaspis barbara, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 26.

Body bristles fine and appressed on pronotal disk, longer on hemelytral pads, with scattered bristles 0.17–0.20 mm long on abdomen of female. Longest bristles on abdominal tergites in male about 0.10 mm.

Female.—Head 0.85 mm wide, only slightly wider than long, 50:47, interocular space about 7 times as wide as an eye. Ratio of antennal segments 6:21:17:15. Rostrum approximately 1 mm long, reaching apices of fore coxae; proportions about 10:8:10.

Pronotum 1 mm wide, more than ½ again as wide as long on median line, 60:35, feebly sinuate just behind middle; long bristles at sides only about ½ as long as first antennal segment; disk with extremely fine, inconspicuous bristles and a few more prominent ones.

Mesonotum-scutellum with a few very minute bristles.

Hemelytral pads ½ wider than long, broadly rounded laterally, and not longest on inner half, with several stout bristles laterally and a mixture of short and longer bristles on disks.

Abdomen oval in outline, the tergites clothed with dense, fine bristles and with longer bristles along hind margins. Under surface rather uniformly clothed with fine bristles except for a cluster of longer ones at apex. Paragenital sinus distinctly notched ⅓ of distance mesad from right side of hind margin of fifth tergite. Ectospermalege forming a prominent thickening that is transverse beneath and mesad of sinus.

Hind femora 3½ times as long as wide, 70:20, distinctly shorter than hind tibiae, 70:85. Tibiae with very short bristles not nearly as long as diameter of tibia.

Male.—Abdominal bristles short. Paramere ⅕ shorter than width of genital segment.

Size.—Slide-mounted female, length 4 mm, width (pronotum) 1 mm, (abdomen) 2.2 mm; pinned male, length 3 mm, width (pronotum) 0.95 mm, (abdomen) 2.05 mm.

Described from a female specimen, "Soudan Français" (West Africa—Mali) presented by Dr. Henri Schouteden and received by him from Roubaud. The illustration was made from a British Museum (Nat. Hist.) specimen. The British Museum material includes 5 males and 3

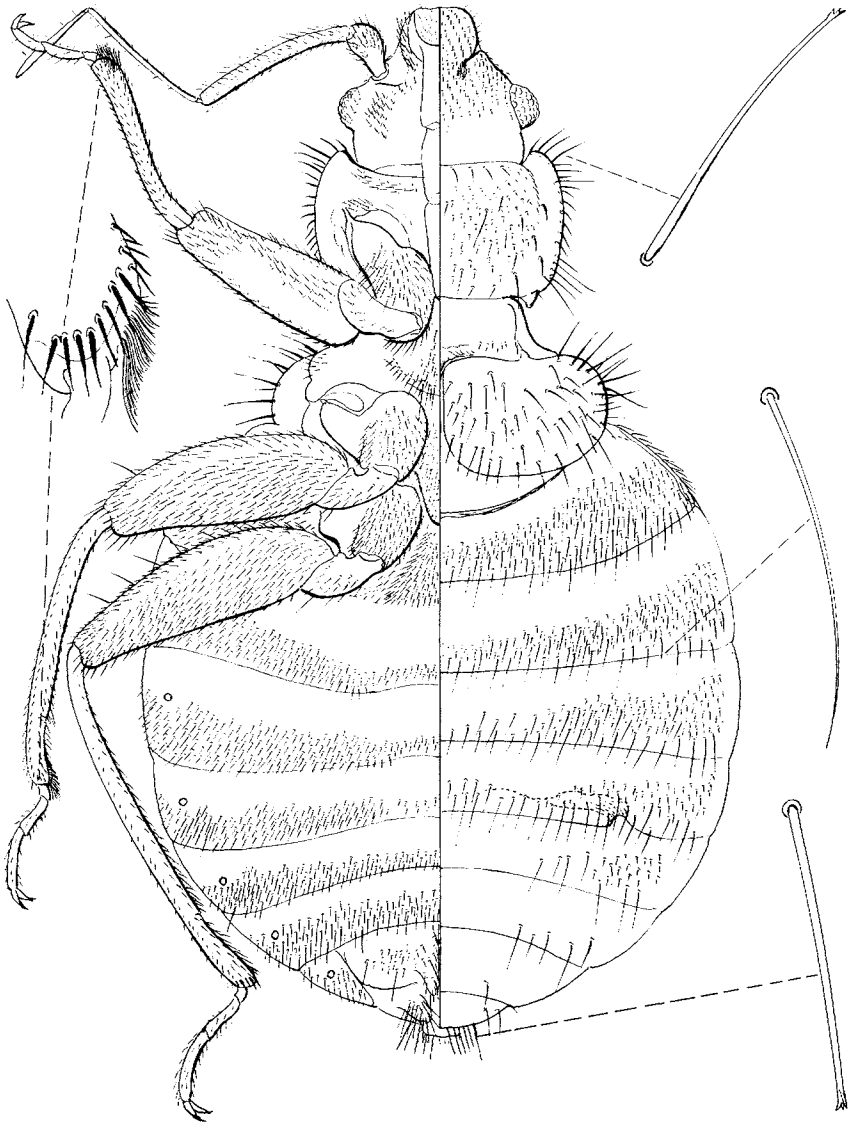

FIG. 12–47.—*Loxaspis barbara* (Roubaud). Female. Hte. Senegal-Niger, Saramela, near Mopti, West Africa—Mali (Ferris, original).

females mounted on slides, a pair in the pinned collection, and additional material in the spirit collection. The detailed locality data are, "Hte Senegal-Niger, Saremala nr. Mopti in nesting hole of bat *Nyctinomus pumilus* Erety." The type, male, and 2 additional males and a female are in the Paris Museum. They bear the following labels "Chauve-souris, Mopti, Bouet-Roubaud," and "Institut Pasteur." One of these males was used to prepare the above description. Three additional specimens, presumably from the same type series, "Mopti," are in the Budapest Museum.

A male and 2 nymphs were sent by Dr. O. Theodor from Sierra Leone, Makeni, Jan. 8, 1962, alt. 275 ft, *Mops condylura* (F. R. Allison). The length of the paramere indicates that this is typical *barbara*.

A male and female from Gogrial, Sudan (East Africa), Feb. 5, 1950 (P. Z. MacKenzie), Commonwealth Institute of Entomology, resemble *barbara* in every way except that the female lacks the long bristles. The sexual dimorphism in bristle length and the loss of long bristles in some slide preparations makes identification difficult in the African *Loxaspis*. The Gogrial collection is in the general range of *miranda* but the paragenital sinus is exactly as in *barbara*.

48. ***Loxaspis seminitens*** Horvath

(Fig. 12–48)

Loxaspis seminitens Horvath, 1912, Tidj. Entomol. 55: 344.
Loxaspis seminitens Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Loxaspis seminitens, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Loxaspis seminitens, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 26.

Male.—Head 0.9 mm wide, including eyes, interocular space more than 5 times as wide as an eye, 19:3.5; ratio of width to length (through cleared pronotum) 26:21. Antennae 2.31 mm long, ratio of segments 6:29:16:16, second segment about $^1/_8$ longer than width of head. Rostrum apparently exceeding apex of prosternum, but third segment turned up in balsam mounted specimen.

Pronotum more than ½ again as wide as long, 36:22, 1.24 mm wide, widest in front of middle, the sides slightly sinuate (narrowed) behind middle. Longest bristles anteriorly and posteriorly on sides a little shorter than width of first antennal segment, 4:5.

Hemelytral pads ½ again as wide as long, 58:38, with margins rounded except for long, straight inner margins that are contiguous. Lateral bristles long and stiff, discal bristles shorter than distance between bristles.

Abdomen broadly suboval in outline with short, fine discal bristles above, becoming longer at hind margins of segments, especially sublaterally. Male paramere about ⅔ as long as width of terminal segment, 44:64, extending a little beyond margin of segment, evenly bent and tapering, not sinuous.

Hind femora 4 times as long as wide, 48:12, ⅕ shorter than hind tibiae, the tibial bristles much shorter than thickness of tibia.

Size.—Male, length 4.9 mm (slide-mounted), pronotum 1.24 mm wide, abdomen 2.68 mm wide.

Holotype male, Hungarian National Museum, "Java Nrt. 1911. Goewalawa (grot) E. Jacobson. Babakan. (Banjoemas)." Horvath says the type is a female but it is clearly a male.

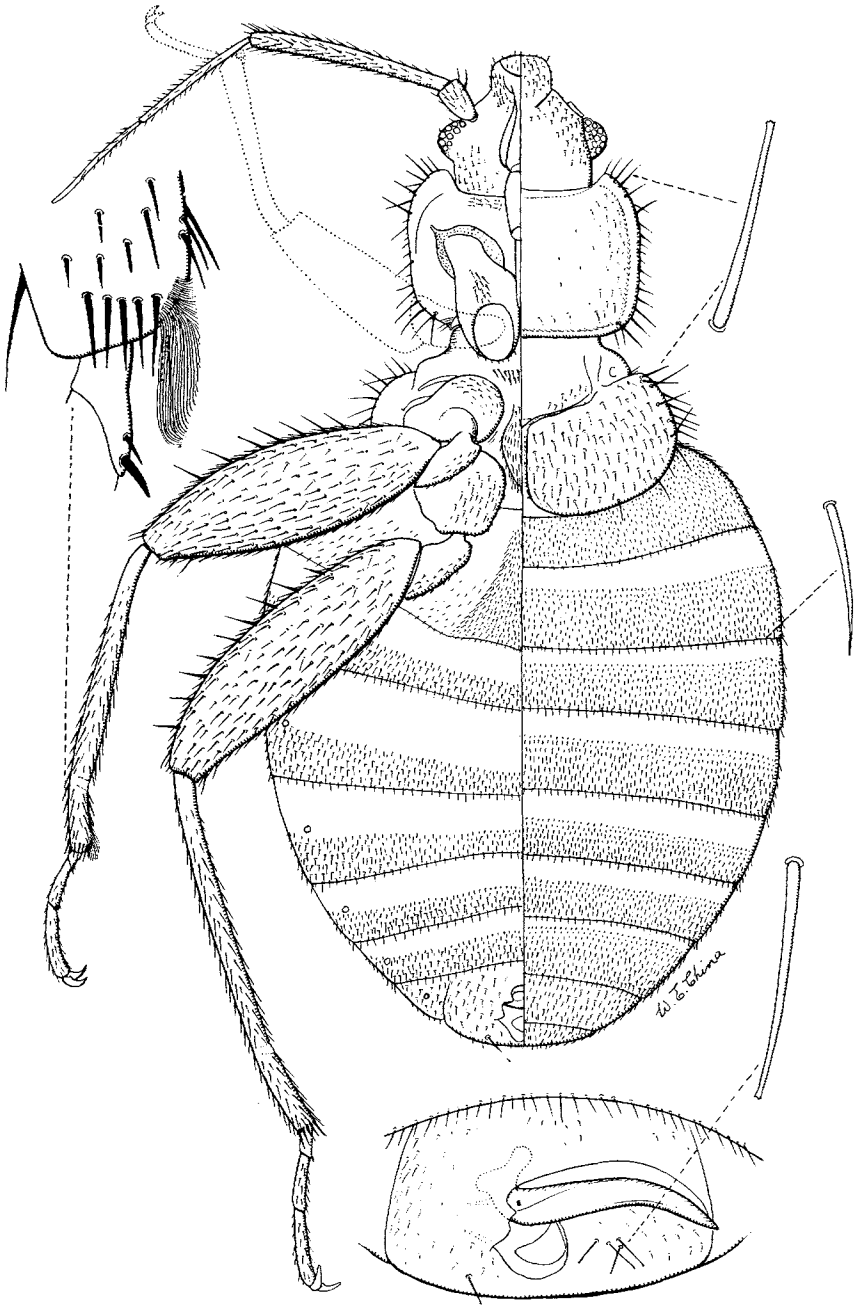

FIG. 12–48.—*Loxaspis seminitens* Horvath. Male holotype. Goewalawa, Java (W. E. China, original).

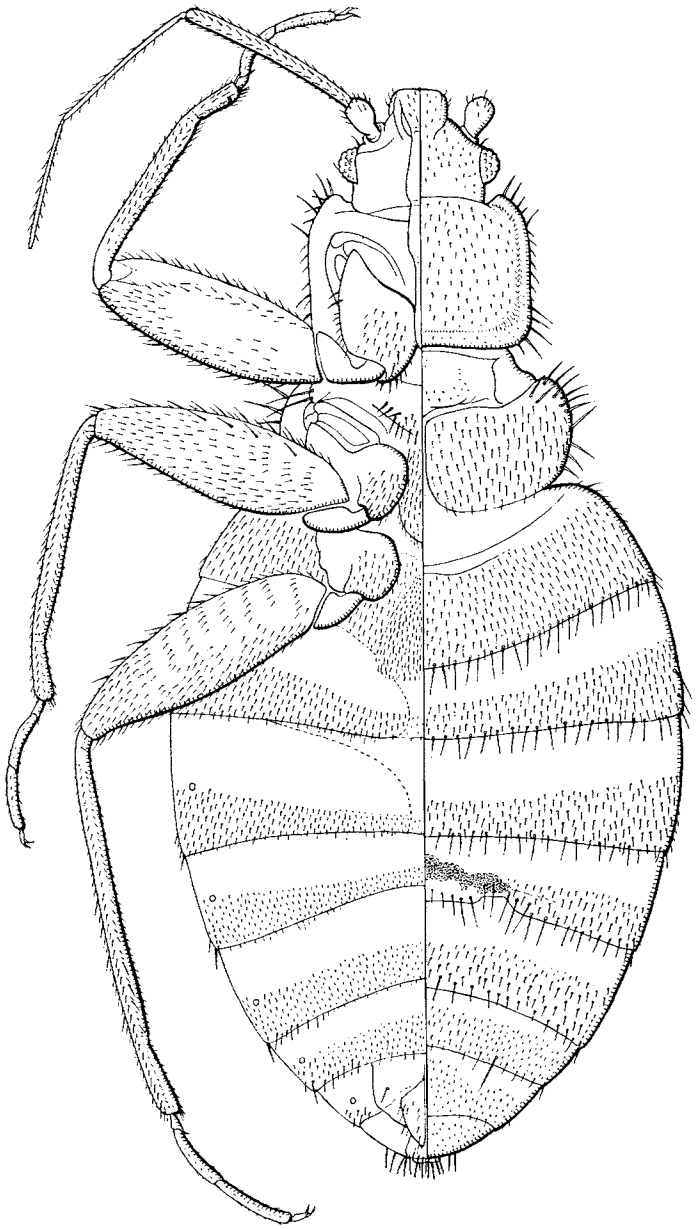

FIG. 12–49.—*Loxaspis spinosa* Usinger. Female paratype. Niah Cave, Sarawak, Borneo (Celeste Green, original).

The description is based on the type specimen, mounted by Dr. W. E. China. The figure was drawn by Dr. China.

The Asiatic species of *Loxaspis* differ from the African forms by the longer second antennal segment.

49. ***Loxaspis spinosa*** Usinger
(Fig. 12–49)

Loxaspis spinosus Usinger, 1959b, Entomologist 92: 218.

Male.—Head 0.94 mm wide, ratio of width to length 33:28; interocular space more than 4 times as wide as an eye, 23:5. Antennae 2.83 mm long, proportion of segments 8:38:27:26; second segment about 1/6 longer than width of head. Rostrum reaching about to middle of fore coxae (slide-mounted), the proportion of segments about 7:11:14.

Pronotum 1.3 mm wide; 1/2 again as wide as long, longest bristles anteriorly and posteriorly almost as long as an eye, the bristles near middle much shorter; bristles of disk extremely fine, scarcely visible.

Scutellum with minute pale spots posteriorly which may represent points of insertion of fine bristles that are not visible in slide preparation.

Hemelytral pads 1/2 again as wide as long, rather evenly and continuously rounded behind and at sides and contiguous for a distance greater than length of scutellum; disk with very fine, dense bristles about as long as distance between bristles, the sides with about 10 prominent bristles about as long as those on humeri.

Abdominal tergites with numerous rows of very fine bristles about as long as distance between bristles, the last row on each tergite much stouter and at least twice as long as the others.

Male paramere about 2/3 as long as width of genital segment, extending beyond lateral margins of terminal segment, evenly curved and tapering, not sinuous.

Hind femora 3.5 times as long as wide, distinctly shorter than hind tibiae, 64:85, the longest bristles of hind tibiae much shorter than thickness of tibia.

Female.—Like the male but with posterior row of bristles on each abdominal tergite even longer than in male. Spermalege, as seen in a cleared specimen, consisting of thickened anterior margin of sixth abdominal tergite near middle, the hind margin of fifth tergite sinuate, the strongest asymmetry to the right of middle.

Size.—Male, length 5.45 mm, width (pronotum) 1.3 mm; female, length 6 mm, width (pronotum) 1.23 mm.

Holotype male, allotype female, and a series of paratypes, Sarawak, The Great Cave, Niah, April 2, 1958, *Cheiromeles torquatus* Horsfield (Lord Medway), British Museum (Nat. Hist.) 1958–431. In addition there are 2 specimens taken on April 1, 1957, same locality and host, British Museum (Nat. Hist.) 1957–723.

This species is related to *seminitens* from Java but has the hind femora only 3 1/2 times as long as wide.

50. ***Loxaspis malayensis*** Usinger, n. sp.
(Fig. 12–50)

Body brown with paler hemelytra and appendages. Bristles on hind margins of

abdominal tergites a little longer in female than in male. Second antennal segment subequal to width of head. Size a little smaller than *spinosa*.

Male.—Head 0.8 mm wide, ratio of width to length 24:20, interocular space 5 times as wide as an eye, 17.5:3.5, bristles very short and sparse. Antennae 2.13 mm long, proportion of segments 6:24:18:16, second segment subequal to width of head. Rostrum reaching apices of fore coxae, proportion of segments approximately 8:9:10.

Pronotum 1.1 mm wide, half again as wide as long, 33:22, widest in front of middle and very slightly narrowed behind this. Disk with very fine appressed hairs much shorter than distance between hairs. Long bristles of lateral margins anteriorly (3 or 4) and posteriorly (4), the longest about 0.125 mm, short bristles between.

Scutellum with very short, hairlike bristles, especially posteriorly.

Hemelytral pads a little less than ½ again as wide as long, 20:15, contiguous for a distance greater than length of scutellum, broadly rounded behind and laterally; shallowly but roughly punctured and clothed with fine, white, hairlike bristles that are about as long as distance between bristles; the margins and anterolateral region with long, stiff bristles like those on pronotal margins.

Abdominal tergites with fine punctures and bristles, longer (to 0.10 mm) along hind margins, especially laterally.

Male paramere more than ⅔ as long as width of genital segment, 34:45, extending beyond lateral margin of genital segment to sublateral spiracle, curved and tapering, not sinuous apically.

Hind femora 3½ times as long as wide, 39:11, shorter than hind tibiae, 39:48. Tibiae with longest bristles shorter than thickness of tibia.

Female.—Longest bristles on hind margins of abdominal tergites 0.17 mm. Paragenital sinus at right of middle on hind margin of fifth tergite broadly, shallowly emarginate, the ectospermalege forming a thickened area at middle.

Size.—Male, length 4.8 mm, width (pronotum) 1.1 mm, (abdomen) 2.2 mm; female, 4.8 mm, width (pronotum) 1.05 mm, (abdomen) 2.15 mm (pinned specimens 3.6 and 3.8 mm).

Holotype male, allotype female, and a series of paratypes, at Fort Iskandar, Tasik Bera, Pahang, in hollow palm tree (serdang) where *Cheiromeles torquatus* Horsfield and *Tadarida mops* (Cuvier) (=*Tadarida mops* (de Blainville)) were roosting, Dec. 29, 1962 (Lord Medway). Two males are also at hand from Malaya, taken in 1952 in hollow trees inhabited by *Cheiromeles torquatus* Horsfield (Dr. J. R. Audy) (Brit. Mus. (Nat. Hist.) 1955–126).

This species is very close to *spinosa* Usinger, described from Niah Cave, Sarawak, on *Cheiromeles torquatus* Horsfield, but differs consistently in its smaller size and shorter second antennal segment.

Genus ***Stricticimex*** Ferris and Usinger

Stricticimex Ferris and Usinger, 1957b, S. Afr. Animal Life 4: 374.
Stricticimex, Usinger, 1959a, Rev. Zool. Bot. Afr. 60: 61.
Stricticimex, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 81–104.
Stricticimex, Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 86.

Relatively small, with head and thorax narrow and abdomen suboval. Appendages long and slender. Head and pronotum impunctate, hemelytral pads and abdominal

FIG. 12–50.—*Loxaspis malayensis,* n. sp. Female paratype. Fort Iskandar, Tasik Bera, Pahang, Malaya (Celeste Green, original).

tergites rough but only vaguely if at all punctate, the surface with wartlike elevations. Color whitish with brown on pronotum and with broad, transverse brown stripes anteriorly on abdominal tergites.

Bristles scattered but numerous, stiff, erect, the longest bristles at sides of pronotum to about 0.33 mm; sides of bristles not serrate, tips minutely cleft. Antennae 2½ to 4 times as long as width of pronotum, first segment short and stout, second segment 2 to 4 times as long as first, ½ to ⅔ as long as third which, in turn, is ½ again or even twice as long as fourth. Rostrum (pinned specimens) reaching well onto front coxae, second segment attaining base of head; first segment widest and longest with 2 well developed but short bristles on each side; second segment ½ or ⅔ as wide as long; third segment subequal to or shorter than second. Anteocular portion of head about as long as length behind level of front margins of eyes, not inflated at level of antennae. Eyes moderately exserted. Head margins concave behind eyes, converging to hind margin of head.

Pronotum more or less than twice as wide as long and wider than head; sides roundly converging posteriorly; anterior margin shallowly concave, resulting in a slight projection of lateral angles; lateral and posterior margins forming a continuous, narrowly depressed edge.

Mesonotum naked. Hemelytral pads transverse, longest at inner sides.

Gula entirely naked. Metasternum roundly lobate, compressed between middle coxae.

Legs relatively long and slender, the hind femora 3 to 5½ times as long as wide. Hind tibiae ½ again as long as femora, tapered and bent inward at apical third, with pseudojoints and without apical tufts.

Abdomen with edges wrinkled and somewhat reflexed.

Male paramere short, less than ½ as wide as genital segment, bent backward. Paragenital sinus forming a large opening at right side between third and fourth tergites, the hind margin of third tergite bent forward before lateral margin. Ectospermalege broadly tubular, directed mesad and bent backward at apex, with a slender diverticulum arising subapically.

Type-species: *Stricticimex antennatus* Ferris and Usinger.

Stricticimex is in some ways intermediate between *Crassicimex* and *Leptocimex*. It lacks tufts on all tibiae, and the tibiae are tapering and bent. The male paramere is backwardly bent. The spermalege is unique and highly specialized. The type-species is from Cape Province, and *namru* is from Cairo. *S. pattoni* extends the distribution to India.

KEY TO THE SPECIES OF *STRICTICIMEX*

1. Fore femora a little longer than tibiae. Size small, the pronotum 0.6 mm wide. Total length 2.5 mm. India.....51. ***pattoni***
   Fore femora a little shorter than tibiae. Size larger, the pronotum 0.74 mm or more in width. Total length (small pinned specimens) 3 mm to (large slide-mounted specimens) 6.8 mm. Africa..... 2
2. Second antennal segment much shorter than width of head..... 3
   Second antennal segment longer than width of head..... 4
3. Hind femora less than 4 times as long as wide. South Africa.....52. ***transversus***
   Hind femora 4 times as long as wide. Egypt.....53. ***namru***
4. Third antennal segment more than twice as long as fourth. Size large, the pronotum 1 mm or more wide. South Africa.....54. ***antennatus***
   Third antennal segment less than twice as long as fourth. Size smaller, the pronotum less than 1 mm wide..... 5
5. Last antennal segment longer than width of head. Longest bristles at sides of pronotum, wing pads, and abdomen about 0.37 mm. Kenya.....55. ***intermedius***

Last antennal segment subequal to width of head. Longest bristles at sides of pronotum, wing pads, and abdomen about 0.31 mm. Belgian Congo. ..... 56. ***brevispinosus***

51. ***Stricticimex pattoni*** (Horvath)

Macrocranella pattoni Horvath, 1925, Rec. Indian Mus. 27: 191.
Leptocimex (Macrocranella) pattoni, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Macrocranella pattoni, Mathur, 1953, Indian J. Entomol. 14: 260.
Leptocimex puttoni, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 25.

Whitish, shining, densely clothed with long, erect, fusco-testaceous bristles.

Head with eyes scarcely broader than long and a little narrower than pronotum; vertex more than 4 times broader than an eye; eyes black, but little prominent. Antennae somewhat shorter than body, covered with semiappressed short hairs; first segment not reaching apex of head; second segment 4 times as long as preceding segment; third ½ longer than second; fourth ⅓ shorter than third. Rostrum with first segment longer than third.

Pronotum somewhat less than twice as broad as long at middle; posteriorly and laterally narrowly margined; anteriorly dilated; sides lightly arcuate; provided with bristles longer than first antennal segment. Scutellum fully 3½ times as wide as long at middle. Hemelytral pads $^{3}/_{10}$ broader than long, apex obliquely round-truncate, with sutural and costal margins nearly straight, inner and outer apical angles rounded. Abdomen quite orbicular. Femora and tibiae densely clothed with short, semiappressed bristles; proportional lengths of femora and tibiae, 40:38, 37:40, 45:56.

Size.—Female, length 2.5 mm, width (pronotum) 0.6 mm, (abdomen) 1.6 mm.

The type locality is East India. The type specimen is apparently lost—it could not be found in Horvath's collection in Budapest, nor in the Indian Museum. The description just given is based on Horvath's Latin diagnosis. The species was placed in *Leptocimex,* but it lacks the distinctive long third antennal segment, the short broad hemelytral pads, and the long apical rostral segment of that genus. It cannot be placed with certainty until additional material is available to allow study of the spermalege and paramere. However the description and figure agree in all respects with *Stricticimex; pattoni* differs from the known species in its smaller size and relatively longer fore femora.

52. ***Stricticimex transversus*** Ferris and Usinger
(Fig. 12–52)

Stricticimex transversus Ferris and Usinger, 1957a, Microentomology 22: 8.

Body suboval, whitish, with a broad brown band across anterior part of each abdominal tergite and also brown on head, pronotum, scutellum, and second antennal segment.

Male.—Head 0.8 mm wide, wider across eyes than long, 15.5:14; interocular space 5½ times as wide as an eye; eyes only moderately exserted, margins of head concave behind eyes and then tapering posteriorly; length of head in front of eyes subequal to length of head from level of front margins of eyes to hind margin of head. Antennae 2.23 mm; proportion of segments 4:9:19:12. Rostrum 0.57 mm long, reaching

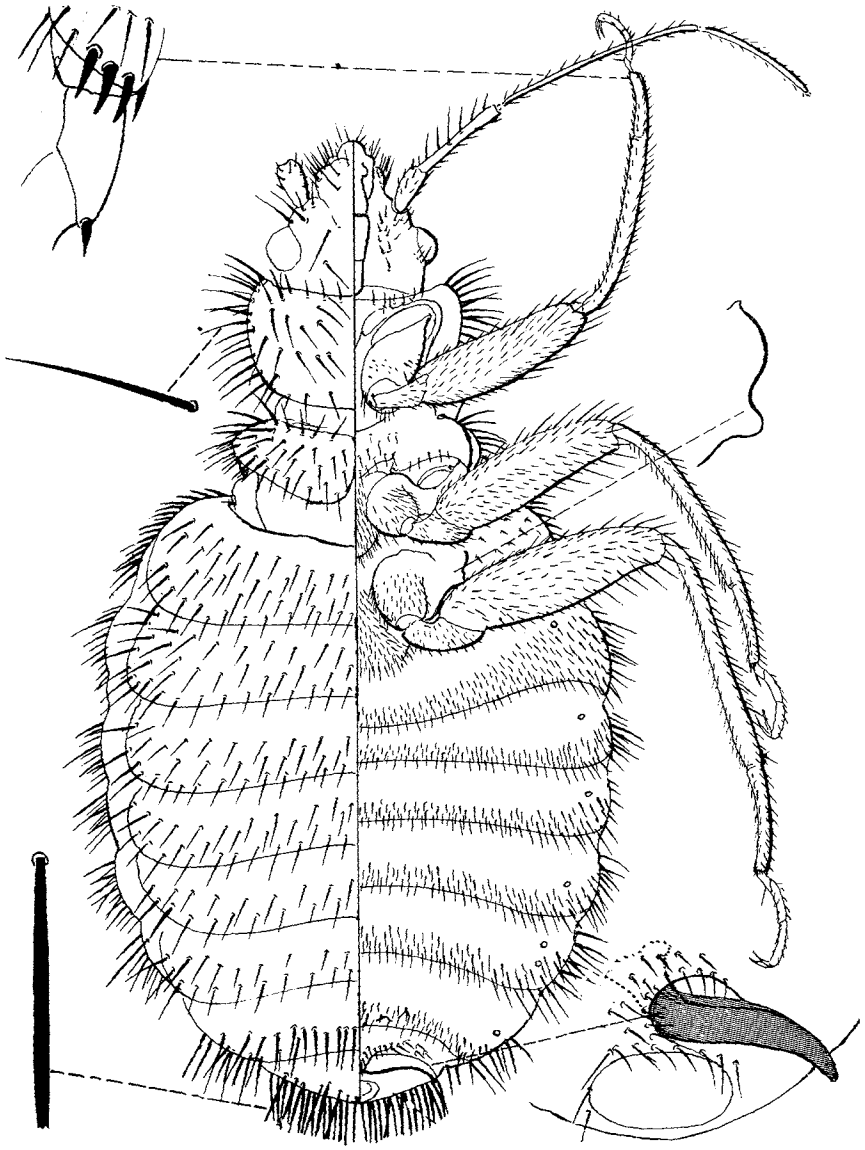

FIG. 12–52.—*Stricticimex transversus* Ferris and Usinger. Male holotype. Blomfontein, Orange Free State, South Africa (Ferris and Usinger 1957)

onto prosternum; proportion of segments approximately 10:7:5, second segment ⅔ as wide as long; first segment with several small bristles, including 2 moderately prominent ones on each side.

Pronotum 0.95 mm wide; more than twice as wide as long, 40:17.5; wider than head, 40:32; anterolateral angles roundly angular, slightly produced but scarcely interrupting the concavity of anterior margin; side margins rather smoothly rounded and a little convergent posteriorly; disk with a few scattered long stiff bristles as also on the head; side margins each with about 20 long, stiff bristles, 0.23 mm, a few ½ the length of longest bristles.

Hemelytral pads ½ again as wide as long (approx. 23:14) with many long, stiff bristles laterally, and scattered ones on disk.

Abdominal disk with many stiff bristles arranged more or less in rows. Male paramere short, less than ½ as long as width of genital segment.

Hind femora less than 4 times as long as greatest width, 45:12. Hind tibiae less than ½ again as long as femora, 63:45.

Female.—Paragenital sinus between third and fourth abdominal tergites a sublateral opening on the right. Hind margin of third segment bent forward at this point and with several backwardly directed spines on edge.

Size.—Male, length 4.07 mm (3.5 mm in dried specimen), width (pronotum) 0.95 mm, (abdomen) 2.25 mm; female, length 5.3 mm, width (pronotum) 0.97 mm, (abdomen) 2.1 mm.

Holotype male, Blomfontein, Orange Free State, South Africa, Sept. 1953 (F. Zumpt), British Museum (Nat. Hist.). The female was described from an additional collection sent recently by Dr. Zumpt.

Additional material includes a series from Kanye, Bechuana Protectorate, Oct. 24, 1957, roof of house, *Tadarida bocagei* Seabra (F. Zumpt); a series from Windhoek, Southwest Africa, Feb., 1961 and Mar. 22, 1961, *Scotophilus nigritus* (Schreber) (F. Zumpt); and a collection from Grootfontein, S. W. Africa, July 11, 1963 (B. du Toit).

53. ***Stricticimex namru*** Usinger
(Fig. 12–53)

Cimex pipistrelli?, Priesner and Alfieri, 1953, Bull. Soc. Fouad 1er Entomol. 37: 81.
Stricticimex namru Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 85.
Stricticimex namru, Linnavuori, 1964, Ann. Zool. Fenn. 1: 322.

Male.—Head 0.85 mm wide; wider across eyes than long, 51:42; interocular space 3½ times as wide as an eye. Bristles of head relatively short and thick. Antennae 2.43 mm long; proportion of segments 6:16:32:19. Rostrum 0.61 mm long, exceeding base of head; proportion of segments approximately 8:5:6; stout, second segment ⅚ as wide as long.

Pronotum 1 mm wide; about twice as wide as long, 61:30; ⅛ wider than head, 61:51; longest lateral bristles about 0.266 mm; anterolateral angles only slightly produced, following curve of anterior margin, rounded; side margins rounded onto hind margin and convergent posteriorly.

Hemelytral pads ⅜ as long as wide (21:35), rounded laterally, and straight and contiguous on inner edges.

Abdominal disk and sides with relatively short, stiff bristles posteriorly on each

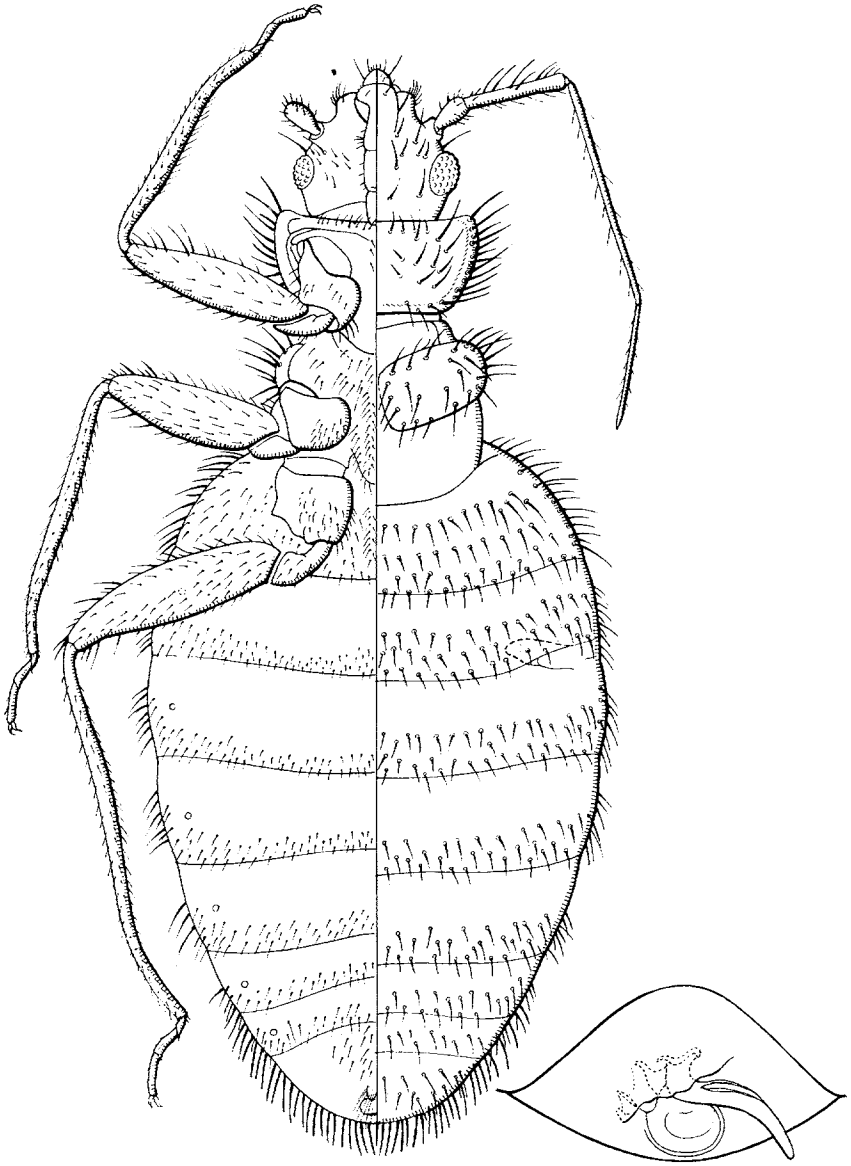

FIG. 12–53.—*Stricticimex namru* Usinger. Female paratype and male genitalia. Giza, Egypt (Usinger 1960).

segment, bristles in 3 irregular rows on middle segments. Male paramere less than ½ as long as width of genital segment at base, rather evenly curved and tapering.

Hind femora more than 4 times as long as greatest width, 77:18. Hind tibiae more than ½ again as long as femora, 123:77.

Female.—Similar to the male but with slightly longer bristles, longest bristles at sides of pronotum a little more than ½ as long as pronotum. Paragenital sinus bordered by sinuate posterior margin of third tergite sublaterally.

Size.—Male, 4.7 mm, width (pronotum) 1 mm, (abdomen) 2.3 mm; female, 4.75 mm, width (pronotum) 1 mm, (abdomen) 2.25 mm.

Holotype male, Giza, Egypt, June 25, 1959, ex *Tadarida a. aegyptiaca* (E. Geoffroy) (H. Hoogstraal) (U. S. National Museum). Allotype female, same data (Chicago Mus. Nat. Hist.). Paratypes, same locality, July 15, 1959, R. L. Usinger and Makram Kaiser, in deep cracks in rocky outcrops in Western Desert. Narrow fissures, otherwise inaccessible, were blasted open with dynamite by a group of quarry workers.

This species differs from all others except the South African *transversus* in having the second antennal segment distinctly shorter than the width of the head, 16:26. In *transversus* the hind femora are about 3 times as long as wide, whereas they are 4 times as long as wide in *namru.*

The reference to *Cimex pipistrelli* Jenyns (?) (in Priesner and Alfieri 1953) almost certainly pertains to *namru.*

54. ***Stricticimex antennatus*** Ferris and Usinger

(Fig. 12–54)

Stricticimex antennatus Ferris and Usinger, 1957b, S. Afr. Animal Life 4: 376.
Stricticimex antennatus, Ferris and Usinger, 1959, Ann. Entomol. Soc. Amer. 52: 82.
Stricticimex antennatus, Usinger, 1959a, Rev. Zool. Bot. Afr. 60: 61.

Relatively large, with longer, slender appendages and with longest bristles at sides of pronotum to 0.33 mm.

Female.—Head 0.88 mm wide; wider across eyes than long, 55:50; interocular space 5 times as wide as an eye; disk of head with several erect bristles and with 4 bristles along inner margin of each eye. Antennae 3.8 mm long; proportion of segments 20:70:100:45. Rostrum 0.85 mm long; proportion of segments about 9:8:9.

Pronotum 1.1 mm long; a little less than twice as wide as long, 38:21; with long bristles along anterior (10) and lateral (14) margins, several very long bristles on hind margin at sides, 2 each in front of hind margin on either side, and with a few shorter bristles on disk.

Hemelytra ¾ as long as wide, longest and straight on inner sides, narrowed and rounded laterally. Longest bristles at sides 0.4 mm.

Abdomen more than twice as wide as pronotum in dried specimens, suboval and with membranous lateral margins pale, slightly elevated at edges, encircling the abdominal disk above. Abdominal tergites roughened by elevations at the insertions of bristles (visible only in dried specimens), except narrowly along hind margins of segments. Surface of abdomen beset with many long erect bristles and with long bristles also on lateral margins, the abdominal bristles longer, denser, and stiffer on

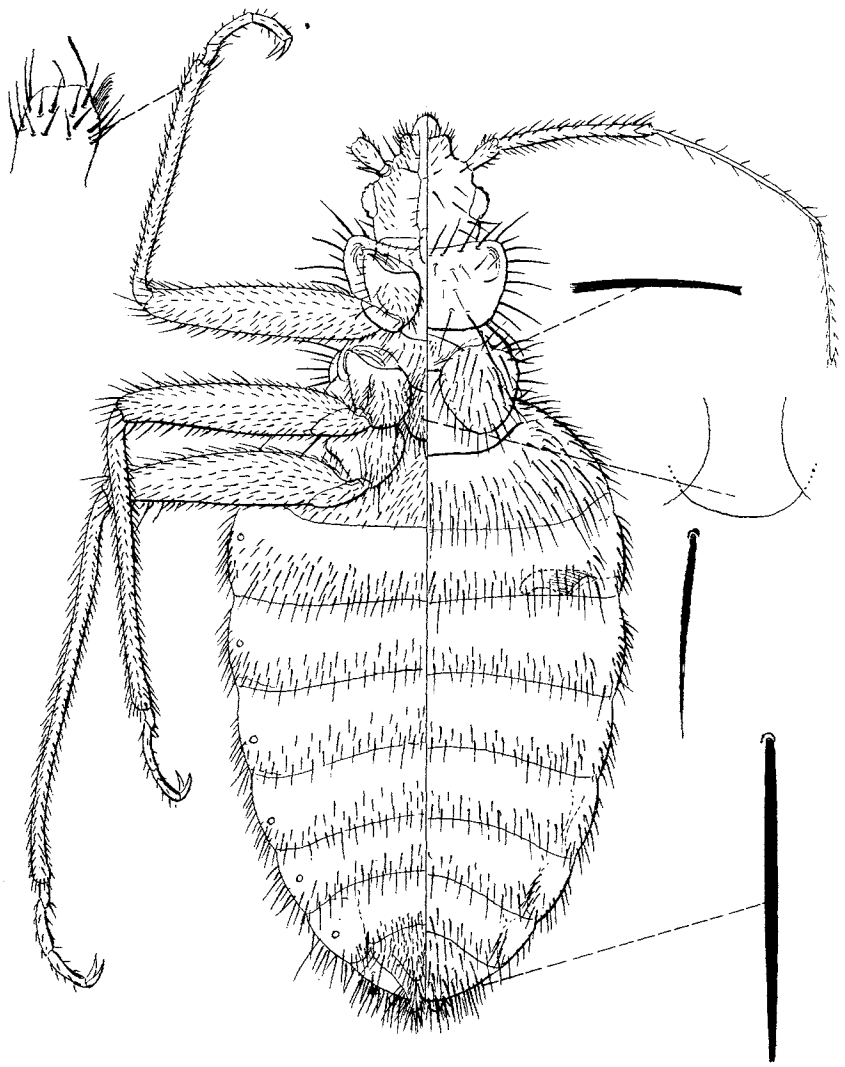

FIG. 12–54.—*Stricticimex antennatus* Ferris and Usinger. Female paratype. DeHoop Vlei, near Bredasdorp, Cape Province, South Africa (Ferris and Usinger 1957).

last segment. Paragenital sinus strongly bent forward sublaterally and margined by several long bristles, the aperture wide. Ectospermalege coneshaped.

Legs relatively long and slender, hind femora over 5 times as long as wide. Hind tibiae more than ½ again as long as femora.

Male.—Paramere ½ as long as width of genital segment.

Size.—Male, length 5.5 mm, width (pronotum) 1.1 mm, (abdomen) 2.5 mm; female, 6.8 mm, width (pronotum) 1.1 mm, (abdomen) 3.3 mm (4.5 mm long in a dried female).

Holotype female, allotype male, and 4 paratypes, Cape Province, De Hoop Vlei, 20 mi. ENE of Bredasdorp, in bat cave (guano), Jan. 1, 1951 (Loc. No. 105) (Brinck and Rudebeck Swedish South African Expedition).

Other material includes a series of 10 specimens, S. Africa, Kleinemunde Bats' Cave, Three Sisters' Rocks, Jan.-Feb., 1955 (P. and W. Omer-Cooper) (British Museum (Nat. Hist.) 1955–204), and a collection from a small cave in Northern Rhodesia sent by A. de Barros Machado.

55. ***Stricticimex intermedius*** Ferris and Usinger

(Fig. 12–55)

Stricticimex intermedius Ferris and Usinger 1959, Ann. Entomol. Soc. Amer. 52: 81.

Stricticimex intermedius, Usinger, 1959a, Rev. Zool. Bot. Afr. 60: 61.

Female.—Head 0.74 mm wide; about as long to tips of mandibular plates (juga) as wide across eyes; longer to apex of clypeus than wide (51:44); interocular space 4 times as wide as an eye (30:7); bristles of upper surface sparse but long, ½ as long as interocular space, with 3 bristles along inner margin of each eye, 4 on vertex, 3 on either side of base of clypeus, and about 20 bristles on clypeus. Antennae 3.1 mm long; about 4 times as long as width of pronotum (209:52); proportion of segments 14:55: 90:50. Rostrum about 0.7 mm long, with apex of second segment just reaching hind margin of head, entire third segment extending onto prosternum; proportion of segments approximately 15:15:10.

Pronotum widest anteriorly, 0.9 mm wide; briefly produced forward anterolaterally; sides rounded and convergent posteriorly; hind margin following curve of sides; disk with very long bristles; longest bristles at sides about 0.33 mm; ratio of pronotal width to length on median line 52:31.

Hemelytral pads ⅔ as long as wide, beset with numerous bristles, the longest ⅔ as long as width of 1 hemelytron.

Abdominal disk with rows of bristles. Lateral margins with longest bristles at base and with the usual clump of long, posteriorly directed bristles on terminal segment.

Paragenital sinus broad, the hind margin of third tergite gradually bent forward toward the side. Ectospermalege broad at opening, tapering and bent mesad and then backward.

Legs with hind femora about 5 times as long as greatest width; tibiae less than ½ again as long as femora, 50:36.

Male.—Paramere directed to the left and curved backward, ½ as long as width of genital segment at base.

Size.—Male, length 4.15 mm, width (pronotum) 0.9 mm, (abdomen) 2.1 mm; female, length 5 mm, width (pronotum) 0.9 mm, (abdomen) 2.4 mm.

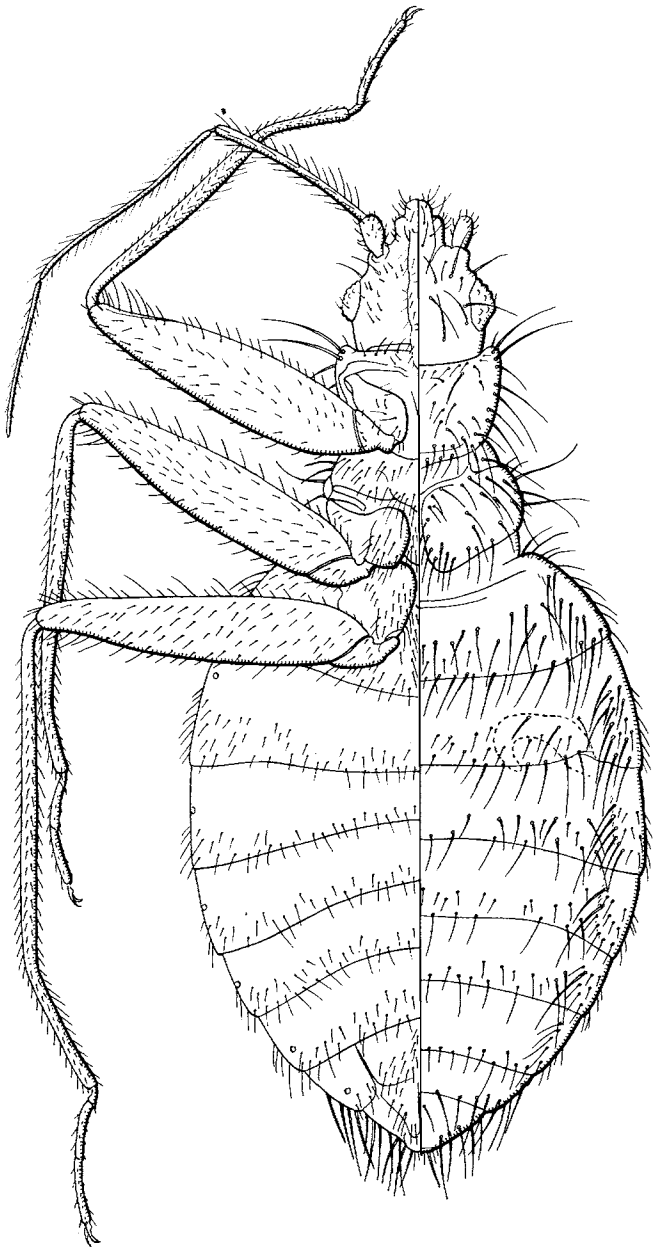

FIG. 12–55.—*Stricticimex intermedius* Ferris and Usinger. Female holotype. Mgahein bat cave, near Mombasa, Kenya, East Africa (Ferris and Usinger 1959).

Holotype female, allotype male, 1 male paratype, and several nymphs, Mgaheni bat cave, 5 mi. S. of Mombasa, Kenya, East Africa, July 17, 1956 (Glen M. Kohls). Also at hand is a series from a bat-infested coral sea-coast cave, Ngombeni, Kwail, Kenya, July 17, 1956 (H. Hoogstraal). The type is in the U. S. National Museum.

56. ***Stricticimex brevispinosus*** Usinger
(Fig. 12–56)

Stricticimex brevispinosus Usinger, 1959a, Rev. Zool. Bot. Afr. 60: 63.
Stricticimex brevispinosus, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 81–104.
Stricticimex brevispinosus, Berghe, Chardome, and Peel, 1959, Folia Sci. Afr. Centr. 5 (2) : 36–37.

Female.—Head 0.77 mm wide; slightly wider than long, 27:25; interocular space 4 times as wide as an eye; labrum with several pairs of bristles, posterolateral pair longest; clypeus with 5 pairs and vertex with 3 long bristles on each side behind clypeus; 3 short bristles on each side between antennae and eyes; 3 long bristles along inner margins of eyes, and 1 bristle on each side, mesad of hind margin of eye; 3 short bristles on each eye.

Antennae about 3 mm long; proportion of segments 7:29:45:26; first segment with short, stiff bristles, second with longer stiff bristles, third and fourth with fine, hairlike bristles; second segment longer than width of head, 29:27.

Rostrum reaching apices of fore coxae; second segment reaching just to base of head; length, excluding inflated basal region and labrum, approximately 0.7 mm; proportion of segments 10:8:7.

Pronotum (in dried specimen) 0.74 mm wide; the ratio of width to length 26:16; disk transversely rugose near concave anterior margin, strongly convex with side margins and posterior margin narrowly flattened; longest bristles at sides of pronotum slightly curved but not strongly bent, 0.28–0.31 mm.

Hemelytral pads wider than long, 16:13, straight along inner margins, narrowly rounded at inner apices and broadly rounded laterally; surface roughened and with erect bristles, longest bristles about as long as those on pronotum.

Abdominal disk roughened; second and third segments with 3 or 4 ill-defined rows of bristles, the remaining segments with 2 rows and with the usual cluster of terminal bristles. Paragenital sinus formed by broadly sinuate hind margin of third tergite at right. Ectospermalege inwardly directed and then curved around and backward.

Under surface with much finer, more numerous bristles, especially on metasternum and base of abdomen, with 2 ill-defined backward rows on posterior part of each segment from third segment.

Legs long and slender, the ratio of length to thickness of hind femora 54:12.

Male.—Paramere ½ a long as width of terminal segment, curved.

Size.—Male, length 4.5 mm, width (pronotum) 0.8 mm, (abdomen) 2.1 mm; female, length 5.4 mm, width (pronotum) 0.91 mm, (abdomen) 2.5 mm (length of dried female 3.2 mm).

Holotype female, allotype male, and 4 slide-mounted paratypes and 2 pinned paratypes, Biot. 21, Urundi, small cave, near Nyanza Lac, Lake Tanganyika, 783 m, Sept. 1958 (N. Leleup). Much additional material was collected by N. Leleup and R. L. Usinger on July 24, 1959. The bat has been identified as *Hipposideros caffer* (Sundevall). The types are

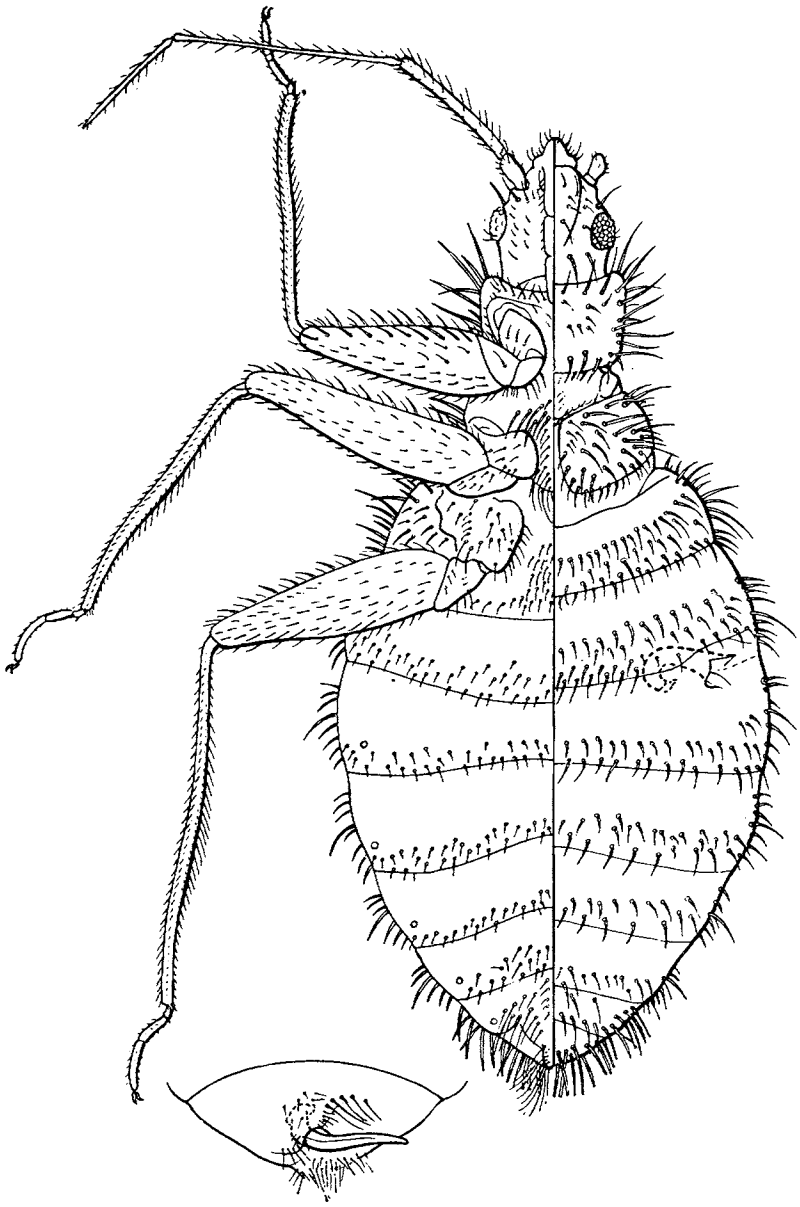

FIG. 12–56.—*Stricticimex brevispinosus* Usinger. Female holotype and male genitalia. Nyanza Lac, Lake Tanganyika, Africa (Usinger 1959).

in the Congo Museum, Terveuren, Belgium. The cave, not limestone, is at the edge of the lake; it is short (perhaps 10 yards of darkness) and dry. There were hundreds of bats, and *Stricticimex* was common on the walls and in the cracks.

Genus ***Leptocimex*** Roubaud

Leptocimex Roubaud, 1913, Bull. Soc. Entomol. France, p. 349.
Macrocranella Horvath, 1913a, Bull. Soc. Entomol. France, p. 371 (n. n. for *Leptocimex*).
Macrocranella, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Leptocimex, Kassianoff, 1937, Ann Parasitol. Hum. Comp. 15: 99.
Leptocimex, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 97.
Leptocimex, Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 88.

Body suboval, narrowed in front. Surface variously roughened or wrinkled but not distinctly punctate. Size 2.5 (pinned) to 4.3 mm. Bristles very stiff and sparse on head and thorax; longest bristles at sides of thorax about 0.20 mm; sides of bristles not serrate, tips minutely cleft.

Head with sides of clypeus subparallel. Antennae nearly 4 times as long as width of pronotum, 150:40; first segment short and stout; second about ½ as thick and twice as long as first, ½ as wide as pronotum; third over 4 times as long as second; fourth less than ½ as long as third. Rostrum reaching backward beyond apices of fore coxae, even attaining middle of hind coxae in pinned specimens; first segment narrowed subbasally, widened apically, with a stout, laterally directed bristle on each side; second segment about as long and wide as first; third segment much narrower and twice as long as second.

Pronotum $^{1}/_{10}$ wider than head including eyes, a little less or more than twice as wide as long, moderately produced anteriorly on either side of head; sides and hind margin distinctly, submarginally impressed.

Hemelytral pads transverse, oval, very small, not contiguous at middle.

Mesonotum and especially metanotum broadly exposed, naked.

Metasternum compressed between middle coxae. Hind coxae farther apart than front and middle coxae. Legs relatively long and slender; hind femora more than 5 times as long as greatest width, nearly twice as long as width of pronotum. Hind tibiae more than ½ again as long as hind femora. Front femora with scattered short bristles, 2 rows of bristles on inner face, and a more-or-less distinct row of bristles on ventral face. All femora with 2 pairs of longer bristles at inner apex. All tibiae tapering and bent inward at apical third. No apical tufts on tibiae.

Abdomen broadly rounded, thickly reflexed at sides, first tergite semilunar in outline and fully exposed, wrinkled. Terminal abdominal segment in male about 4 times as wide as long, measured from above; paramere about ½ as long as width of base of segment, bent at base and strongly recurved apically, or much longer and broadly curved.

Females with or without distinct openings (paragenital sinuses) dorsally.

Type-species: *Cimex boueti* Brumpt.

Leptocimex is mainly associated with bats, even though 1 species has attached itself to man. The long third antennal segment and short, flaplike hemelytral pads are unique.

The general form of the ectospermalege is usually similar and characteristic for each genus of Cimicidae. Only in *Leptocimex* does one find

totally different structures, ranging from *boueti,* with no visible ectospermalege, through *vespertilionis,* with openings on 1 side only, to *duplicatus* with double tubes. It is clear from this evidence that evolution of the paragenital structures has proceeded at very different rates in the genera of Cimicidae.

KEY TO THE SPECIES OF *LEPTOCIMEX*

1. Front femora with a distinct longitudinal row of 15–20 bristles on inner posterior face, in addition to 2 rows on ventral face, the bristles as long or longer than distance between bristles. Female without distinct apertures for the spermalege. French Soudan. Bats and man.....57. ***boueti***
   Front femora with an ill-defined row of about 6–12 bristles on ventral face, the bristles shorter than distance between bristles. Two rows on ventral face less prominent. Female with 2 exposed or concealed apertures for spermalege 2
2. Front femora with 6 bristles in poorly defined row. Female with very distinct, transversely oval apertures on the right side between middle and lateral margin at hind margins of fifth and sixth abdominal tergites. Male paramere briefly bent and tapered apically. Sudan and Iraq.....58. ***vespertilionis***
   Front femora with 12 bristles in a distinct row on posterior face, in addition to 2 ventral rows. Female with 2 separate apertures bilaterally, situated between fifth and sixth abdominal tergites, the tubelike ectospermaleges curved. Male paramere broadly curved, sickleshaped, and thin on apical half. Egypt. .....59. ***duplicatus***

57. ***Leptocimex boueti*** (Brumpt)

(Fig. 12–57)

Cimex boueti Brumpt, 1910, Précis Parasitol., p. 563.
Cimex boueti, Joyeux, 1913, Arch. Parasitol., p. 140–146.
Cimex boueti, Patton and Cragg, 1913, Textb. Med. Entomol., p. 512.
Leptocimex boueti, Roubaud, 1913, Bull. Soc. Entomol. France, p. 349.
Macrocranella boueti, Horvath, 1913a, Bull. Soc. Entomol. France, p. 371.
Macrocranella boueti, Horvath, 1914b, IX^{e} Int. Congr. Zool., p. 295.
Leptocimex boneti, Castellani and Chalmers, 1919, Man. Trop. Med., 3rd ed., p. 763.
Leptocimex boueti, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 294.
Leptocimex boueti, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Leptocimex boueti, Ferris and Usinger, 1957a, Microentomology 22: 9.
Leptocimex (Macrocranella) boueti, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg, 59:25.
Leptocimex boueti, Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 88.

Female.—Head 0.8 mm wide; about as wide across eyes as long, 42:41; interocular space 4 times as wide as an eye. Antennae about 3.2 mm long; proportion of segments 7:12:45:23. Rostrum 0.85 mm long; proportion of segments approximately 17:17:25.

Pronotum 0.88 mm wide; nearly twice as wide as long, 48:25; narrowed posteriorly; anterior lobes very short, subrounded; long bristles at sides about as long as first antennal segment, 0.23 mm.

Hemelytral pads 4 times as wide as long, with about 5 long bristles along hind margins.

Female with abdominal tergites showing no indication of a paragenital sinus. Fourth and fifth tergites without distinct oval apertures.

Hind femora nearly 6 times as long as wide, 80:14. Hind tibiae more than ½ again

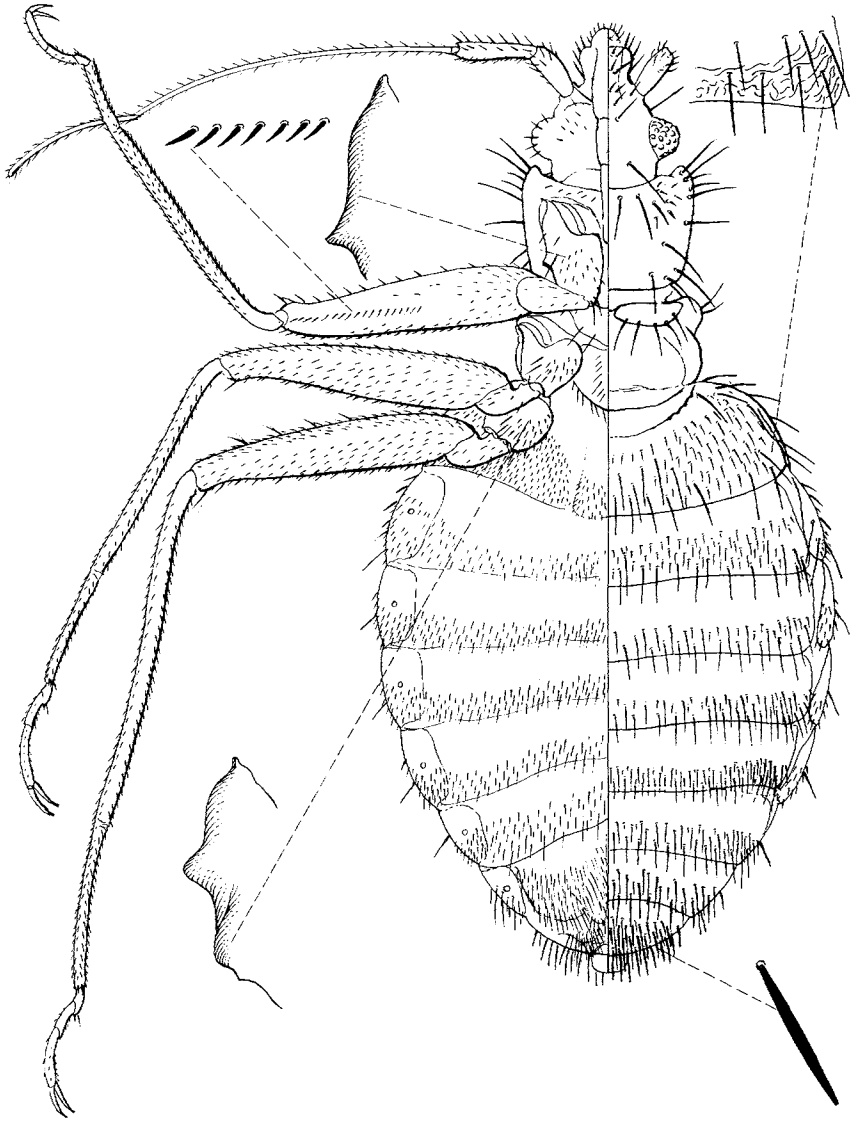

FIG. 12–57.—*Leptocimex boueti* (Brumpt). Female. Bobo-Dioulasso, Haute Volta, West Africa (Ferris, original).

as long as hind femora, 140:80. Bristles of under face of fore femora 15 to 20 in number, arranged in a longitudinal row, the individual bristles longer than spaces between bristles.

Male.—Paramere moderately curved, tapering, and slightly recurved at apex.

Size.—Male, length 2.75 mm, width (pronotum) 0.88 mm; female, length 4 mm, width (pronotum) 0.8 mm.

Described from a female, Djenné, French Soudan, 1911 (E. Roubaud), and a male bearing the same data. Both of these are from the Rothschild collection in the British Museum (Nat. Hist.) and are presumably part of the original type material collected by Roubaud and described by Brumpt. There are 3 additional males and 3 females in the British Museum from the Roubaud collection. Two specimens in the Hungarian National collection are labeled "Ht. Dahomey. Bouet-Roubaud." Roubaud reports the species from Djenné to Karimama in French Soudan; from Dendi, Haute Dahomey; from Odienné, Hte. Cote d'Ivoire; and from Haute Guinée.

Still another collection is from "Nissikoro Grottes à chauves souris (Cercle de Sikasso) Soudan. June 17, 1959 (Dr. Bailey-Choumarz). Sour paroi rocheuse." Joyeux (1913) gives details of the life history of the species.

Additional material bearing the label "Bobo-Dioulasso, Haute Volta (A.O.F.), Dec. 1950, sur homme" is at hand from Dr. J. Carayon. These specimens agree with the Roubaud material except for a dark coloration which may be due to the method of preservation. Dr. Carayon collected the specimens in huts of natives; they were never associated with Europeans. Specimens would not feed on him but fed readily on his native assistant. Specimens were also found in a bat cave.

58. ***Leptocimex verspertilionis*** Ferris and Usinger
(Fig. 12–58)

Leptocimex vespertilionis Ferris and Usinger, 1957a, Microentomology 22: 8.

Female.—Head 0.6 mm wide; as wide across eyes as long; interocular space about 5 times as wide as an eye. Antennae about 2.5 mm long; proportion of segments 10:20: 85:35. Rostrum about 1 mm long; proportion of segments approximately 15:19:26.

Pronotum 0.68 mm wide; nearly twice as wide as long, 44:24; rather evenly arcuate laterally and then abruptly rounded to hind margin; long lateral bristles longer than first antennal segment, 0.2 mm; anterior lobes of pronotum short but distinctly produced, subrounded, about $^1/_{12}$ as long as median length of pronotum.

Hemelytral pads 3 times as wide as long, transversely oval, not meeting at center, with 5 prominent bristles on hind margins.

Female paragenital sinuses on 2 segments, seen as 2 conspicuous, transversely oval apertures at hind margins of fifth and sixth tergites on right side.

Bristles of abdominal disk sexually dimorphic—numerous, short and relatively fine, especially on anterior half, in female; sparse, stout, and longer in male. Approximate length of bristles 0.07 mm in female, 0.12 mm in male.

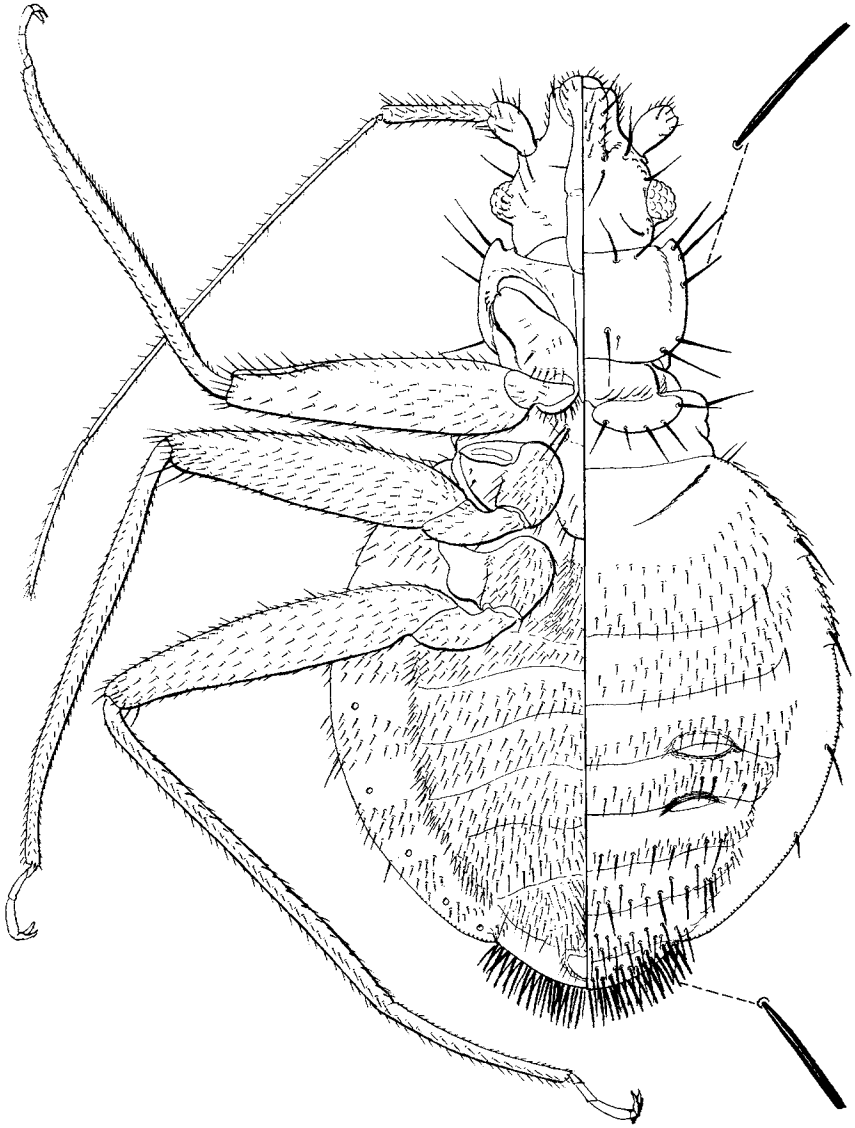

FIG. 12–58.—*Leptocimex vespertilionis* Ferris and Usinger. Female paratype. Zeidab, Sudan, Africa (Ferris and Usinger 1957).

Hind femora more than 5 times as long as wide, 80:15. Hind tibiae more than ½ again as long as femora, 130:80.

Bristles of under face of fore femora about 6 in number in an ill-defined row; individual bristles much shorter than distance between bristles.

Male.—Paramere strongly recurved and tapering on apical half.

Size.—Male, length 3.33 mm, width, (pronotum) 0.7 mm; female, length 3.25 mm, width (pronotum) 0.75 mm.

Holotype male, allotype female, Zeidab, Anglo-Egyptian Sudan, Nov. 1935 (W. P. L. Cameron), on tails of bats. These specimens and an additional male and 2 females are in the collection of the British Museum (Nat. Hist.). Another series in the British Museum includes 4 males and 6 females bearing the labels Khartoum, Anglo-Egyptian Sudan, July 9, 1925 (H. B. Johnston) ex *Taphozous (Liponycteris) nudiventris* (Cretzschmar). A male and female were received from R. Linnavuori collected at Baghdad, Iraq, June 15, 1962.

59. ***Leptocimex duplicatus*** Usinger

(Fig. 12–59)

Leptocimex duplicatus Usinger, *in* Carayon, 1959, Rev. Zool. Bot. Afr. 60:97, footnote.
Leptocimex duplicatus Usinger, 1960, J. Egypt. Pub. Health Ass. 35: 86.
Leptocimex duplicatus, Linnavuori, 1964, Ann. Zool. Fenn. 1: 322.

Male.—Head 0.58 mm wide; a little longer than wide, 37:35; interocular space 5 times as wide as an eye. Antennae 2.88 mm long; proportion of segments 12:23:98:40. Rostrum reaching to apices of fore coxae (slide-mounted specimen); apex of second segment just attaining base of head; total length 1 mm; proportion of segments 14:16:28.

Pronotum 0.68 mm long; a little more than ½ again as wide as long, 41:26; longest bristles at sides about as long as first antennal segment, 0.16 mm.

Hemelytral pads about twice as wide as long, 15:7, arcuate behind and bearing 5 stiff bristles on posterior margin.

Abdomen with each tergite, except the first visible and last with about 14 stiff bristles arranged in 2 ill-defined rows. Second (first visible) tergite with 2 rather widely separated rows of stiff bristles and with 3 or 4 stiff bristles at sides. Surface of abdomen between long bristles with scattered, very short, inconspicuous bristles.

Legs long and slender; hind femora about 7 times as long as wide. Hind tibiae ½ again as long as femora. Row of bristles of inner (lower) face of fore femora about 12 in number, the individual bristles shorter than distance between bristles. Fore femora on inner anterior face with other rows of slightly longer and more erect bristles.

Male paramere very long and slender, sickleshaped, nearly 1 mm long; bent to the left and then posteriorly.

Female.—Abdomen with stiff bristles of dorsum largely concentrated on last 5 segments; anterior tergites with only short, inconspicuous bristles. Spermalege double, consisting of a pair of bilaterally symmetrical apertures between fifth and sixth abdominal tergites on each side midway between center and lateral margins. Internally (cleared specimens) from each opening a tubular ectospermalege extends inward and coils backward.

Size.—Male, length 3.8 mm, width (pronotum) 0.75 mm; female, length 3.65 mm, width (pronotum) 0.70 mm.

FIG. 12–59.—*Leptocimex duplicatus* Usinger. Female paratype and male genitalia. Mycerinus Pyramid, Giza, Egypt (Usinger 1960).

Holotype male, allotype female, and designated paratypes, Giza, Mycerinus Pyramid, Egypt, July 14, 1959, on bat, *Taphozous nudiventris* (Cretzschmar) (R. L. Usinger and Makram Kaiser). One paratype, same data but March 1, 1955 (H. Hoogstraal). Several additional lots of specimens, collected at the type locality, have been received from Dr. Hoogstraal. Other localities are "Bat-infested crevices" in temple beside Sphinx, Giza Governorate, Egypt, July 10, 1962; Abu Rawash, Imbaba, Giza, Egypt, July 17, 1959, "Bat-inhabited crevice in a rocky mound;" Sakkara, El Badrshein, Giza Prov., Egypt, May 23, 1960, in "bat-infested cave;" Sultan Hassan Mosque, Cairo, Egypt, Aug. 8, 1960, all sent by Dr. Hoogstraal. The types are in the U. S. National Museum.

The type specimens were collected in a small tunnel part way up the face of the smallest (Mycerinus) of the 3 great pyramids at Giza. The tunnel was excavated by grave robbers in 1837. Bats were abundant in the 30-ft horizontal shaft and in a deep vertical shaft. Bugs, Nycteribiids, and ticks were common on the walls where the bats had been roosting before being disturbed. The bugs were difficult to collect because they moved rapidly with their long legs and clung to the rough walls so that an aspirator was useless. Many small cracks in the walls showed fecal spots and contained eggs of the bugs. The tunnel was hot, dry, and very dusty.

Genus ***Crassicimex*** Ferris and Usinger

Crassicimex Ferris and Usinger, 1957a, Microentomology 22: 6.

Body suboval, head and pronotum relatively large. Head and pronotum without distinct punctures. Hemelytral pads and abdominal tergites roughened but not distinctly punctured. Bristles very long, at least at sides of pronotum, on hind legs, and at tip of abdomen; longest bristles at sides of pronotum about 0.33 mm; sides of bristles not serrate, tips minutely cleft.

Antennae more than twice as long as width of pronotum; first segment short and stout, inserted on under side of inflated lateral margin of head; second segment 3 or 4 times as long as first, subequal to or a little shorter than third (1/8 shorter); fourth a little more than 1/2 the length of third. Rostrum about 2/3 as long as head, very stout; first segment widened apically, wider than long, with a pair of very long stiff bristles on each side; second segment about as wide as long; third segment wider than long.

Head with eyes deeply set so that they scarcely interrupt the curve of lateral margins; margins behind eyes convexly rounded to hind margin; anteocular portion long, 1/2 again or twice as long as head behind level of front margins of eyes; anteocular margins sinuate, convex at level of antennae.

Pronotum slightly more or less than twice as wide as long, as wide or wider than head; lateral angles not at all produced; rounded at sides and posteriorly, the edges distinctly impressed sublaterally.

Mesonotum naked.

Hemelytral pads about as long as wide, rounded.

Gula with a dense patch of bristles. Pro-, meso-, and metasterna with numerous stiff bristles; prosternum formless, without a longitudinal carina. Mesosternum also a simple, formless lobe. Coxae not contiguous.

Legs relatively long and slender; hind femora 4 or 5 times as long as wide. Hind

tibiae ½ again as long as femora; all tibiae tapering, bent, and with pseudojoints at apical third; without apical tufts.

Abdomen with edges thick and reflexed. Male genital segment about 3 times as wide as long, measured from above; paramere about ½ as long as width of base of segment, bent at base and curved backward apically.

Female.—Abdomen of *sexualis* with an ill-defined spermalege opening at right side of hind margin of second visible abdominal tergite. No evidence of a spermalege in *pilosus*.

Type-species: *Crassicimex pilosus* Ferris and Usinger.

Crassicimex is related to *Leptocimex* in the form of the paramere, tibial pseudojoints, and lack of tibial tufts. It differs in head form, antennal proportions, and especially in the short, stout rostrum.

KEY TO THE SPECIES OF *CRASSICIMEX*

1. Pronotum more than twice as wide as long. Bristles of dorsum dense and long, up to ¼ mm long. Madagascar.....60. ***pilosus***
   Pronotum less than twice as wide as long. Bristles of head, pronotum, hemelytra, and abdominal disks very short, long only at sides of pronotum and at tip of abdomen. Africa.....61. ***sexualis***

60. ***Crassicimex pilosus*** Ferris and Usinger
(Fig. 12–60)

Crassicimex pilosus Ferris and Usinger, 1957a, Microentomology 22: 7.

Male.—Head 1.2 mm wide; wider across eyes than long, 24:20 (24:18 excluding labrum); interocular space 6 times as wide as an eye, 17.5:3. Eyes deeply set in head; margins of head rounded behind eyes; anteocular margins convexly rounded at level of antennae; anteocular length of head (including labrum) ½ again as long as from level of anterior margins of eyes to hind margin. Antennae 2.8 mm long; proportion of segments 5:12.5:20:13. Rostrum 0.65 mm long; about ⅔ as long as head; proportion of segments approximately 8:11:6; second segment slightly wider than long; first segment with a pair of very long, stiff bristles on each side near apex.

Pronotum 1.3 mm wide; more than twice as wide as long, 25.5:11, and wider than head, 25.5:23; longest lateral bristles about ⅔ as long as length of pronotum; anterolateral angles rounded, not at all produced; lateral margins posteriorly convergent; disk with numerous stiff bristles, the bristles sparser on head, absent on mesonotum.

Hemelytral pads about as wide as long, rounded, disks densely beset with stiff, long bristles.

Abdomen with long, stiff bristles on tergites and lateral margins. Paramere about ½ as long as width of genital segment.

Hind femora about 4 times as long as wide, 31:7. Hind tibiae ½ again as long as hind femora, with some exceedingly long bristles as well as moderately long and short ones.

Female.—Similar to male but with bristles of pronotal and abdominal disks shorter. No trace of a spermalege.

Size.—Male, length 5.75 mm, width (pronotum) 1.3 mm, (abdomen) 2.5 mm; female, length 6 mm, width (pronotum) 1.2 mm, (abdomen) 2.6 mm. Length of pinned female 3.4 mm.

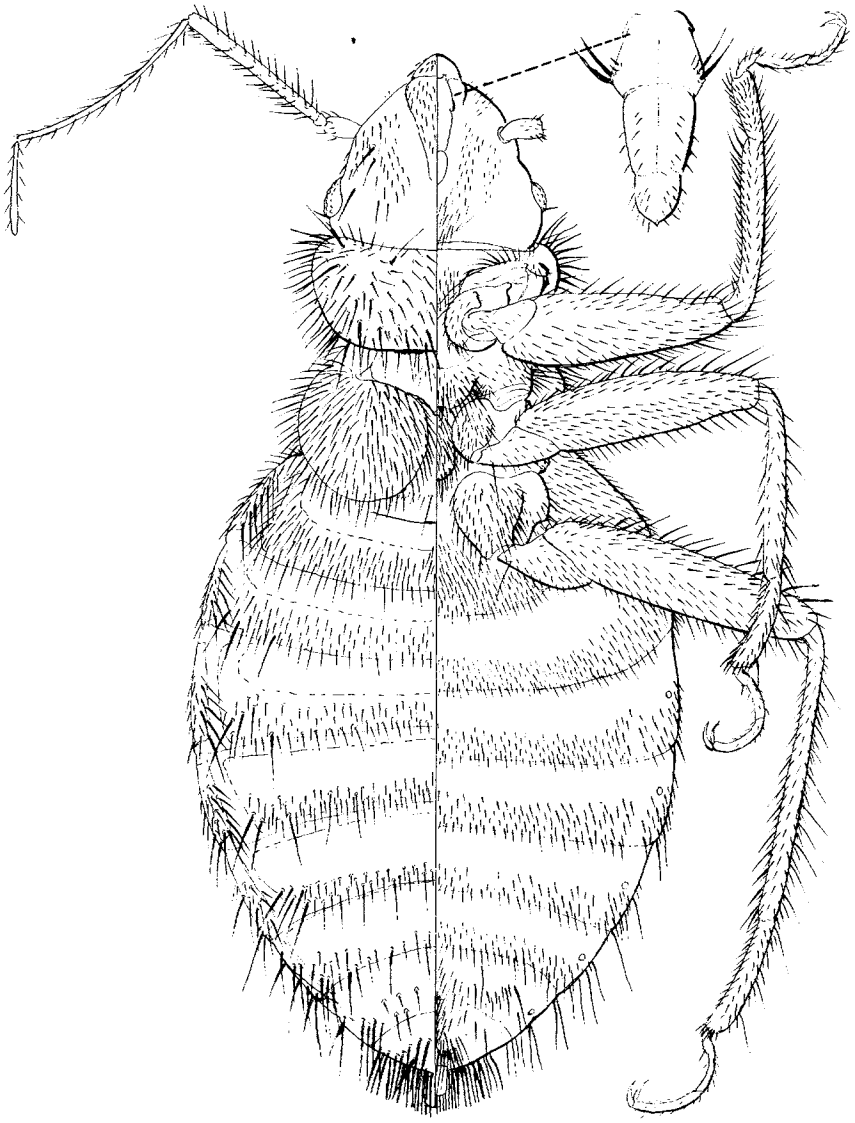

FIG. 12–60.—*Crassicimex pilosus* Ferris and Usinger. Female holotype. Sakaraha, Madagascar (Ferris and Usinger 1957).

Holotype female, allotype male, and several paratypes, Sakaraha, Madagascar, May, 1951, on *Mormopterus albiventer* Dobson (R. Paulian). Also, same locality, roof gable bat roost, Dec. 16, 1959 (E. S. Ross). The type is in the British Museum (Nat. Hist.).

61. ***Crassicimex sexualis*** Ferris and Usinger
(Fig. 12–61)

Crassicimex sexualis Ferris and Usinger, 1957a, Microentomology 22: 7.

Female.—Head 1.23 mm wide; narrower across eyes than long, 71:80 (71:74, excluding labrum); interocular space 7 times as wide as an eye, 55:8. Eyes deeply set in head; margins of head rounded behind eyes. Antennae 2.7 mm long; proportion of antennal segments approximately 15:65:65:35 (last 2 segments bent). Rostrum 0.73 mm long; about ⅔ as long as head; proportion of segments approximately 17:17:10; second segment about as wide as long; first segment widest at apex, wider at this point than long; a pair of prominent spines on each side, about ½ as long as greatest width of segment.

Pronotum 1.23 mm wide; nearly twice as wide as long, 71:38; width equal to width of head across eyes; longest lateral bristles nearly equal to length of pronotum; anterolateral angles not at all produced; side margins feebly rounded anteriorly, nearly straight posteriorly; disk nearly naked, with very sparse, minute bristles as also on head and mesonotum.

Hemelytral pads about as wide as long, rounded even on inner margins, disk with scattered minute bristles and numerous small spots which may represent points of insertion of broken bristles.

Abdominal disk with very short bristles except posteriorly. Hind margin of second visible tergite with an ill-defined spermalege as figured.

Hind femora more than 5 times as long as greatest width, 108:20. Hind tibiae ½ again as long as femora, with some exceedingly long bristles as well as shorter ones.

Size.—Female, length 6.5 mm; width (pronotum) 1.23 mm, (abdomen) 2.75 mm.

Holotype female, Ikotos, 50 mi. S. E. of Torit, Uganda, July 5, 1951, ex *Nyctinomus*? (E. T. M. Reid). This unique specimen is in the collection of the British Museum (Nat. Hist.). A second female, in the Congo Museum (Tervuren), is from Astrida, Ruanda, Aug. 1955, on *Tadarida fulminans* Thomas (Dr. A. Fain). A nymph that clearly belongs to *Crassicimex* is at hand from Musaia, Sierra Leone, Feb. 25, 1962, alt 1135 ft, on *Chaerephon* sp. (F. R. Allison), sent by Dr. O. Theodor.

Subfamily AFROCIMICINAE, new subfamily

Bristles long, without serrations on outer sides and without teeth or a cleft at apices. Head with clypeus widened anteriorly. Pronotum subquadrate. A large, oval spiracle-like organ posterolaterally on each propleuron. Metasternum a simple, rounded lobe between coxae. Legs long, slender, with fine, subappressed hairs and a few very long, erect bristles. All tibiae straight, with apical tufts and without pseudojoints.

Female spermalege left ventral, the hind margins of second and third ventral segments asymmetrical, with heavily sclerotized serrate or crenulate margins. Male ventral segments modified in the same way with the addition of the fourth segment, but without a true mesospermalege.

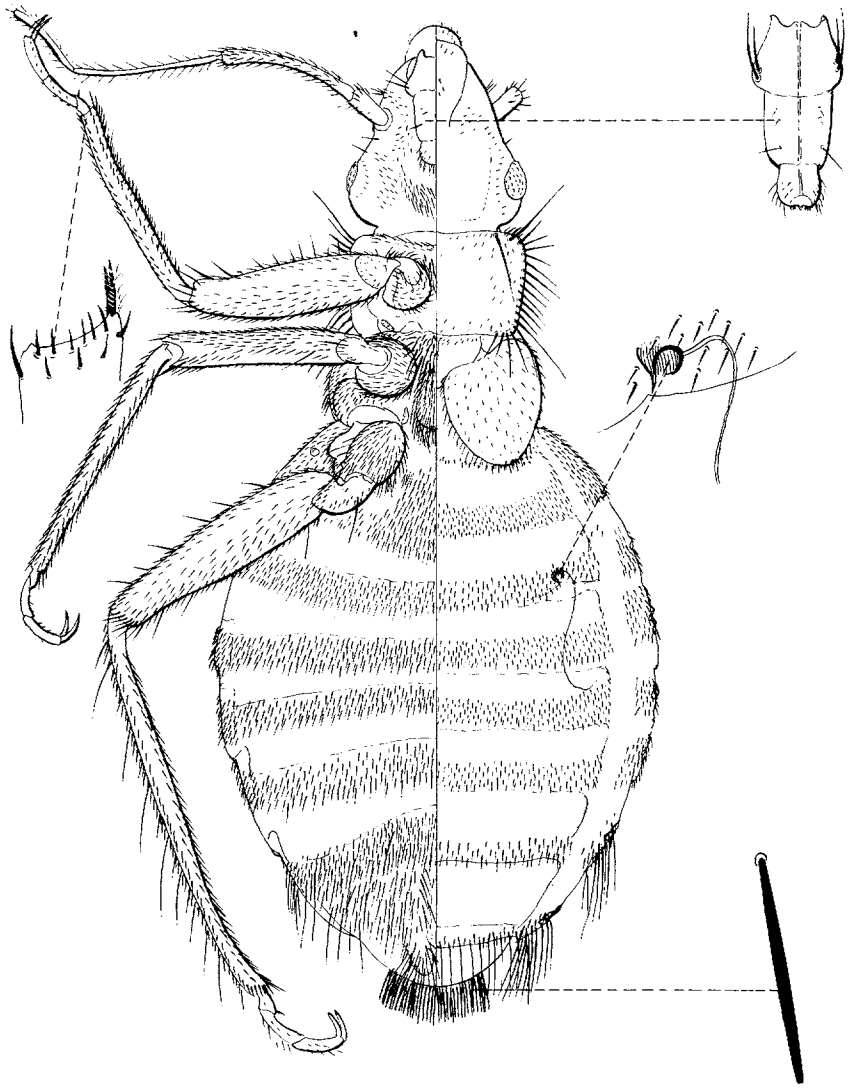

FIG. 12–61.—*Crassicimex sexualis* Ferris and Usinger. Female holotype. Ikotos, near Torit, Uganda, Africa (Ferris and Usinger 1957).

Type-genus: *Afrocimex* Schouteden.

Afrocimex is unique in the Cimicidae in having fully functional male paragenital openings. The spiraclelike organs on the prothorax are also distinctive, and the straight tibiae with no pseudojoints are not seen elsewhere among African bat bug genera. The chromosomes are similar to those of *Leptocimex* and *Stricticimex* but have a second X (11A + X_1X_2Y). It would be logical to assume a relationship to the latter 2 genera, but all members of the Cacodminae have a dorsal spermalege, and the inclusion of *Afrocimex* would make the Cacodminae an almost meaningless group, the separate elements of which would share only the general characters of the family.

Genus *Afrocimex* Schouteden

Afrocimex Schouteden, 1951, Rev. Zool. Bot. Afr. 44: 279.
Afrocimex, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 98.

Size relatively large, 5–7 mm. Bristles long and fine, without notches or teeth, even at apex, the longest bristles about 0.8 mm. Body narrowed anteriorly, abdomen oval, surface without distinct punctures. Antennae 3 times as long as width of pronotum, the first segment shortest, the second longest. Rostrum (pinned specimen) reaching apices of fore coxae, the first and third segments subequal.

Pronotum narrow, about ¼ or ⅕ wider than head, subrectangular, distinctly margined laterally and posteriorly.

Scutellum naked.

Hemelytral pads rather evenly rounded posteriorly, broadly rounded laterally, definitely shorter at middle than at sides.

Abdomen 2½ to 3 times as wide as pronotum, rounded at apex in both sexes. Male with a relatively short, stout, anteriorly curved paramere.

Legs relatively long, slender; fore coxae contiguous, middle coxae subcontiguous, hind coxae separated by a distance much less than the width of a coxa; hind femora more than 5 times as long as broad, ¾ as long as hind tibiae, all legs beset with fine, subappressed hairs and also with a few long erect hairs, the fore femora each with a more-or-less distinct row of about 6 to 36 short, stout, erect spines on inner apical half, the spines about $^1/_{10}$ the width of femur. Hind femora also with a row of short, stiff spines along posterior margin.

Type-species: *Afrocimex leleupi* Schouteden.

Afrocimex is a parasite of bats in caves and is widely distributed in Equatorial Africa.

KEY TO THE SPECIES OF *AFROCIMEX*

1. Comb on hind margin of fore femur with 20 or more short, stout spines placed much closer to each other than length of spines. Second antennal segment 1⅓ times as long as third segment. Hemelytral pads more than ⅔ as long as wide. Kenya and Mt. Hoyo, Congo. . . . . 63. ***constrictus***
   Comb of fore femur with fewer spines only slightly closer to each other than length of spines and difficult to distinguish from adjacent bristles. Second antennal segment less than 1⅓ times as long as third segment. Hemelytral pads ⅔ as wide as long. Katanga, Brazzaville. . . . . 62. ***leleupi***

62. *Afrocimex leleupi* Schouteden
(Fig. 12–62)

Afrocimex leleupi Schouteden, 1951, Rev. Zool. Bot. Afr. 44: 279.
Afrocimex leleupi, Ferris and Usinger, 1957a, Microentomology 22: 8.
Afrocimex leleupi, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 26.

Male.—Surface sparsely clothed with long bristles with longer and much denser bristles on hemelytral pads and first 2 abdominal tergites. Head 1.08 mm wide, about as long as wide across eyes, 65:65; interocular space about 4½ times as wide as an eye; clypeus slightly diverging from base, subtruncate at apex. Rostrum 1.4 mm long; about ⅓ longer than width of head across eyes, 83:65; proportion of segments 32:22:29. Antennae 4.1 mm long, 3 times as long as width of pronotum, 236:80; proportion of segments 18:90:75:53.

Pronotum 1.25 mm wide; nearly twice as broad as long, 40:25; sides slightly arcuate at middle; front margin shallowly, evenly concave with rounded anterolateral angles extending beyond concavity; hind margin feebly sinuate at middle and more distinctly so sublaterally.

Disks of head and pronotum with long, sparse, erect bristles, the head bare on either side of middle on posterior half, pronotum bare at middle. Scutellum broadly exposed and nearly or quite nude. Hemelytral pads densely beset with long bristles.

Abdominal disk densely beset with long bristles on first 2 visible tergites, except for nearly nude basal tergite just behind hemelytral pads. Third visible tergite with long bristles at base. Remaining tergites very sparsely beset with bristles. First 2 ventral segments densely beset with short bristles, especially in the vicinity of the asymmetrically placed paragenital sinuses.

Fore femora with 12 (in the male) and up to 20 (in the female) short, stiff bristles.

Size.—Male, length 7.5 mm, width (pronotum) 1.3 mm, (abdomen) 3.5 mm.

Paratype male, Katanga, Kakontwé, Grot. Defrenne, Oct. 17, 1948 (N. Leleup), on fruit-eating bat, Congo Museum, Tervuren, kindly sent by Dr. Henri Schouteden. The holotype is also in the Congo Museum. Additional collections are from the same cave, Jan. 15, 1957, and Apr. 3, 1957. The temperature in the cave varies from 22° to 24°C.

This species differs from *constrictus* (from Kenya) in the smaller number of stout bristles in the femoral comb (12–20 instead of 20–36), and also in the relatively longer third antennal segment.

An additional series was collected by E. S. Ross, Dom. Felix Anciaux de Faveaux, and R. Leech, Feb. 6, 1958, ex Grotte Salomoni at Kakontwé, a suburb of Jadotville, Katanga, Congo, in crevices on ceilings of damp walls in complete darkness.

Dom. F. Anciaux de Faveaux (1959), in a mimeographed publication "La Voix de l'Orycterope," listed the collections of *Afrocimex leleupi* from various caves in Katanga as follows: Grotte Salomoni, Kakontwe; Grotte Mwanga (=Grotte Defrenne), Pempéré, on *Rousettus aegyptiacus* (E. Geoffroy); Grotte Katembarikulu (=Grotte aux Crevettes), Pempéré; Grotte de la Mura, Swanepoel; Goueffre Swanepoel; Grotte de Kalumbu, Swanepoel; Grotte Kyasala, Lubudi.

Recently, Dr. René Paulian sent a collection from République du

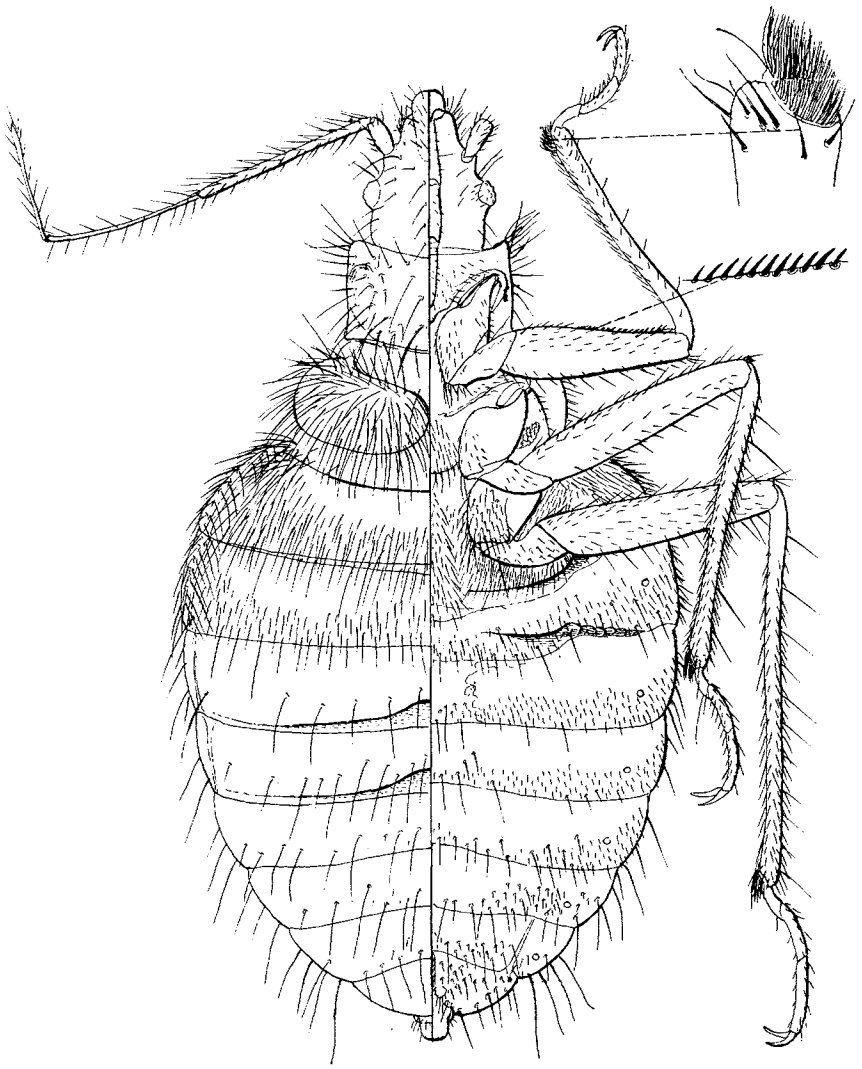

FIG. 12–62.—*Afrocimex leleupi* Schouteden. Female paratype. Kakontwe, Grotte Defrenne, Katanga, Congo (Ferris, original).

Congo, Préfecture du Pool, Ss-Pref. de Kindamba, Gr. de Meya Nzouari, lat 3.53° S; long 14.31° E, 8–1–62 (J. P. Adam). The locality is in Niari Valley SW of Brazzaville. The bugs were collected in fissures of the roof in a part of the cave occupied by a colony of *Rousettus aegyptiacus* (E. Geoffroy).

63. *Afrocimex constrictus* Ferris and Usinger
(Fig. 12–63)

Afrocimex constrictus Ferris and Usinger, 1957a, Microentomology 22: 8.
Afrocimex constrictus, Carayon, 1959, Rev. Zool. Bot. Afr. 60: 98.

Male.—Surface clothed with long (up to 0.66 mm) bristles, without fine pubescence. Head 1.05 mm wide; longer than wide across eyes, 75:66; interocular space 4½ times as wide as an eye; clypeus diverging at base, then subquadrate, apex truncate. Rostrum 1.34 mm long; about as long as width of head across eyes; proportion of segments 20:22:26. Antennae 3.7 mm long; 3 times as long as width of pronotum, 235:80; proportion of segments 20:90:75:50.

Pronotum 1.25 mm wide; much less than twice as broad as long, 79:46; sides slightly arcuate, front margin shallowly, evenly concave, hind margin feebly sinuate at middle; disk with long but sparse erect bristles except at middle. Scutellum broadly exposed, wide, with a very short, triangular projection at middle of hind margin.

Hemelytral pads about ⅔ as long as wide, inwardly broadly rounded and only briefly contiguous, longest sublaterally, the sides bent downward; disk with long bristles.

Abdominal disk with long bristles especially dense at margins of first 3 visible segments, but very short, dense bristles on margins of first segment adjacent to hemelytral pads.

Male paramere more than ½ as long as width of genital segment, curved forward and tapering; paragenital sinuses appearing as transverse apertures beneath sinuate hind margins of second (first visible), third, and fourth ventral segments on left side, the edges densely beset with bristles.

Legs with long bristles on tibiae to 0.7 mm long; fore femoral combs with 20 to 36 short, stout spines spaced closer than the length of spines; hind femora more than 5 times as long as wide.

Female.—Abdomen densely beset with short bristles as well as long bristles on first 2 tergites, anterior margins of fifth and sixth tergites bent forward at middle beneath the straight hind margins of the anterior segments. Paragenital sinuses very conspicuous on the left side of second and third ventral segments, appearing as strongly sclerotized, transverse apertures widening and then tapering mesad and fluted laterally.

Size.—Male, length 6.83 mm, width (pronotum) 1.25 mm, (abdomen) 3.33 mm; female, length 7.19 mm, width (pronotum) 1.4 mm, (abdomen) 3.83 mm.

Holotype male and allotype female, Ndurugu River, 8000 ft, near Ruiru, Kenya, Feb. 1945 (G. R. C. van Someren), from a cave haunted by the bat *Eidolon helvum* (Kerr), Commonwealth Inst. of Entomology Coll. no. 10650 (British Museum (Nat. Hist.)). Four male paratypes, same data as type, and 1 nymph are on slides; and 4 males, 1 female, and 3 nymphs are pinned. Also there is a series of nymphs and adults in alcohol. Also in the British Museum are 1 male and 1 female from a bat cave at Kiambu, near Nairobi, Kenya, Sept. 1950 (Dr. Heisch) and

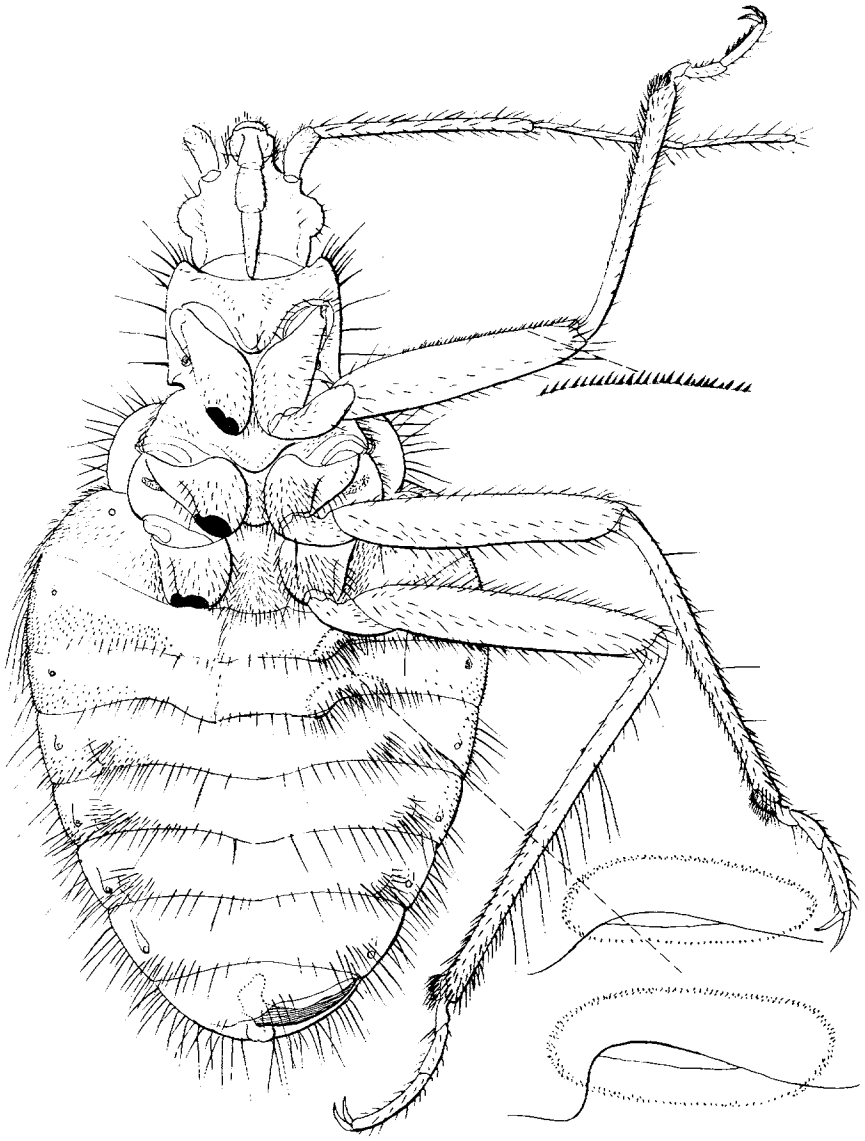

FIG. 12–63.—*Afrocimex constrictus* Ferris and Usinger. Male holotype. Ndurugu River, Near Ruiru, Kenya, East Africa (Ferris and Usinger 1957).

a series from Transnzoia, Kenya, 20 mi. SW of Kitale, in bat cave, SE slope of Mt. Elgon, Feb. 1, 1954 (W. H. R. Lumsden).

An additional series is at hand from a cave with a spring and *Epomophorus* bats, crater of Mt. Menengai, Subukia, Rift Valley, Kenya, 7000 ft, Aug. 24, 1956 (H. Hoogstraal and M. Kaiser) (Chicago Nat. Hist. Mus.).

My own collecting was at Atshokabi Cave about 4 km from Mt. Hoyo and from the main road from Beni to Bunia, Oriental Province, Congo, Aug. 4, 1959. The cave was moist with no dust arising from the guano floor. The bugs walked rather slowly on the ceiling of the cave where the bats were roosting.

Subfamily LATROCIMICINAE, new subfamily

Body surface shining and only superficially punctate. Bristles short and sparse, not serrate at sides or tips. Head with clypeus strongly widened anteriorly. Hemelytral pads folded downward at sides. Ostiolar evaporating area produced as a flaplike lobe above and beyond edge of metapleuron. Spiracles large, those of thorax to 0.07 mm in diameter. Spermalege right ventral near base of abdomen. Femora and tibiae with stiff spinelike bristles in addition to finer hairlike bristles.

Type-genus: *Latrocimex* Lent.

This monotypic subfamily occurs only with bats of the genus *Noctilio* in the Neotropical Region. *Noctilio* belongs to the primitive Noctilionidae, a family of fish-eating bats known only in the American tropics.

Latrocimex has no close relatives among bat bugs of the Western Hemisphere. Although very different in most characters, it resembles *Afrocimex* in that the spermalege is ventral (but does not occur in the male), the internal thoracic scent glands are similar, and both have 11 autosomes (haploid number). The non-serrate bristles and stout tibial spines might suggest affinities with the Haematosiphoninae, but all members of that subfamily are associated with birds and have a dorsal or lateroventral spermalege.

Genus ***Latrocimex*** Lent

Latrocimex Lent, 1941, Rev. Brasil. Biol. 1 (1) : 41.

Size 4 (dried) to 5.1 mm (slide-mounted). Bristles very sparse and short, pronotum with only a single short bristle near each humerus, and hemelytral pads with 2 or 3 short bristles at sides near base and none on rest of side margins; sides of abdomen also with only short bristles except on genital segment; head surface naked except for a single bristle on each jugum. Clypeus more than ½ as wide as interocular space, with a prominent bristle on each side. Antennae more than ½ again as long as width of pronotum; second segment slightly longer than interocular space. Rostrum (dried specimen) reaching about to apices of front coxae; first segment not reaching base of head.

Pronotum ½ again as wide as long, widest in front of middle, the sides nearly straight and slightly converging posteriorly, strongly depressed and very narrowly carinate; hind margin a little convex except for brief concavity at middle.

Mesonotum broadly exposed, naked, the hind margins roundly carinate.

Hemelytral pads difficult to measure because they bend downward around sides; visible portion measured from above contiguous at middle for a distance about equal to exposed part of mesonotum, ⅔ as long laterally as wide, and posterolaterally angulate at point of side fold; sides arcuate and narrowly, submarginally impressed; hind margins very feebly arcuate.

Male genital segment sloping to left, the long paramere exceeding its lateral margin.

Female spermalege right ventral between third-fourth and fourth-fifth segments, paragenital sinus appearing as a transverse thickening of anterior margins of segments, the margins of segments sinuate over the organ.

Abdominal spiracles about 0.13 mm in diameter and appearing as rings, the thoracic openings even larger.

Legs moderately stout and beset with prominent, thick bristles on femora and thick bristles as well as fine ones on middle and hind tibiae. Males with apical tufts on all tibiae, females with tufts reduced, absent on hind tibiae.

Type-species: *Latrocimex spectans* Lent.

This genus differs from all others in the "wrap around" hemelytral pads and the curiously large spiracles. The right ventral spermalege is unique as is the reduced chaetotaxy. *Latrocimex* is a monotypic genus. It has thus far been found only in hollow mangrove trees inhabited by fish-eating bats of the genus *Noctilio* in Brazil and Trinidad.

64. ***Latrocimex spectans*** Lent
(Fig. 12–64)

Latrocimex spectans Lent, 1941, Rev. Brasil. Biol. 1 (1) : 43.
Latrocimex spectans, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 26.

Female.—Head 0.67 mm wide; ⅕ wider than long, 23.5:19; interocular space 8 times as wide as an eye, 19:2.5. Antennae 1.88 mm long; proportion of segments 7:20:19:20. Rostrum about 0.8 mm in length (dried specimen) ; proportion of segments 7:9:12.

Pronotum 1.1 mm wide; ratio of length to width 23:38; sides with 3 or 4 very small bristles anteriorly and 1 or 2 bristles at humeri, with 4 anteriorly and 4 posteriorly on disk.

Hemelytral pads sparsely beset with short bristles.

Abdominal tergites with very sparse, short bristles. Female ventrites with several prominent bristles along sinuate margins over spermalege (third and fourth segments) and also with a mat of fine bristles on the right side of second segment.

Legs with hind femora 3 times as long as broad, 45:14; hind tibiae ⅓ longer than femora. Femora with several very stout bristles. Middle and especially hind tibiae with stout bristles nearly as long as thickness of tibia. Hind tibiae slightly bent apically in males.

Male.—Paramere $^1/_7$ shorter than width of genital segment at base.

Size.—Male, length 5.1 mm, width (pronotum) 1 mm; female, length 5.1 mm, width (pronotum) 1.1 mm.

Redescribed from a male and female, Oropouche Lagoon, Avocat, Trinidad, B.W.I., Oct. 16, 1957 (T. H. G. Aitken), in hollow mangrove tree inhabited by *Noctilio leporinus* L. Other specimens of both sexes and nymphs were collected by Dr. Aitken. Previously he had taken a

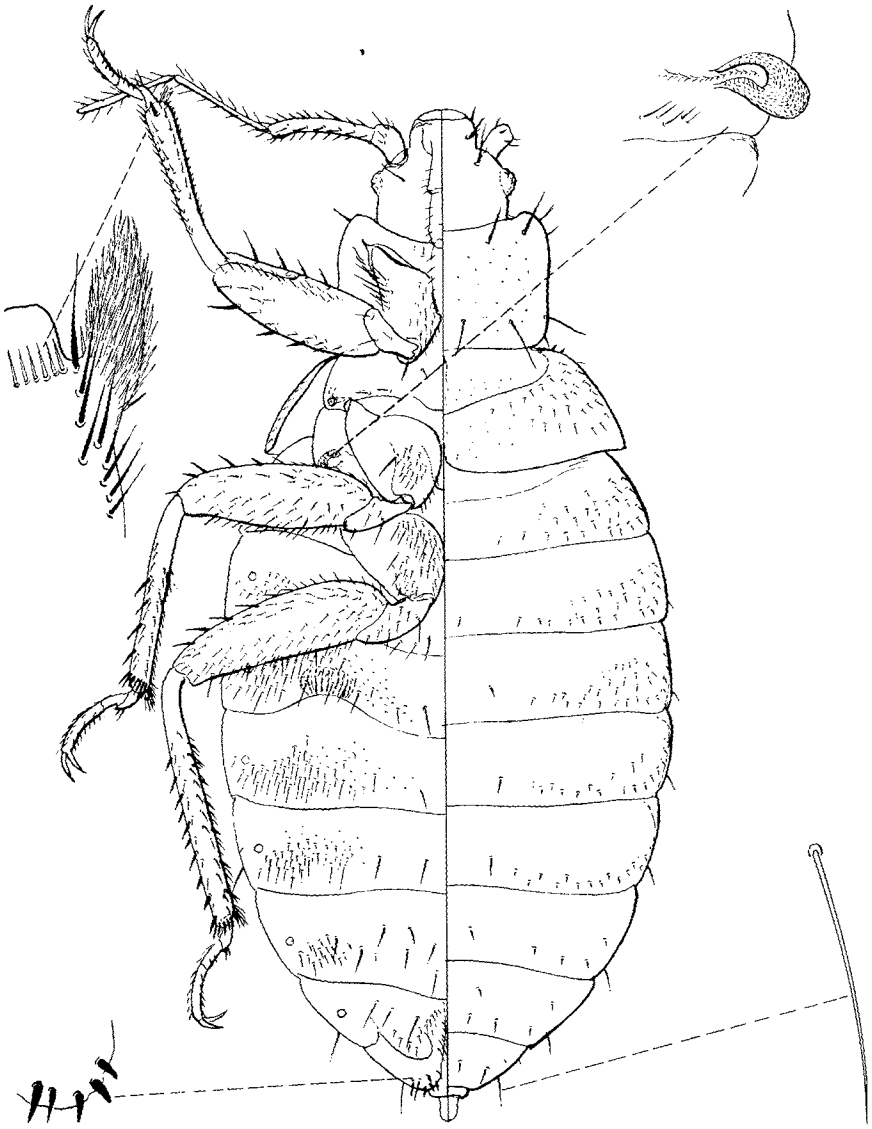

FIG. 12-64.—*Latrocimex spectans* Lent. Female paratype. Rio S. Francisco, Matto Grosso, Brazil (Ferris, original).

single male under the same conditions in a mangrove swamp at North Manzanilla, Trinidad, Mar. 20, 1957. The specimen was found on a piece of rotten wood pulled from a hollow tree. I accompanied Dr. Aitken to the same huge tree in September and, with the help of professional woodcutters, felled it in order to reach the roosting place of the bats. Unfortunately, the bats were gone and no bugs were found.

Also at hand are a male and female from the type series loaned by Dr. Herman Lent from the collection of the Instituto Oswaldo Cruz. These are the specimens used for the figures. They are from Fazenda Limoeiro, Rio S. Francisco, Estado de Matto Grosso, Brazil, in nest of *Noctilio leporinus* L., Aug. 18, 1936 (M. Caralcante). They differ from the Trinidad specimens only in the slightly longer pronotal and head bristles. In the female there are 2 humeral bristles on 1 side, whereas there is only one on a side in the other material.

A single male was kindly supplied by R. Damasceno of Belem, collected in 1941 at Fazenda Sta. Maria on the island of Marajo at the mouth of the Amazon in a mangrove tree inhabited by "Morcego."

Subfamily HAEMATOSIPHONINAE Jordan and Rothschild

Haematosiphoninae Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Haematosiphoninae, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Haematosiphoninae, Lima, 1940, Ins. Brasil 2: 246.
Haematosiphoninae, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.
Haematosiphoninae, China and Miller, 1955, Ann. Mag. Nat. Hist. (12) 8: 263.
Haematosiphoninae, Miller, 1956, Biol. Hemip., p. 8, 120.
Haematosiphoninae, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 17.

Body suboval, shallowly punctate. Bristles not serrate on edges but longest bristles at margins minutely bifid at tips. Clypeus very broad anteriorly. Pronotum with 1 or 2 long bristles posterolaterally or with long bristles throughout. Metasternum lobelike, more or less compressed between coxae. Spermalege dorsal with paragenital sinus on sixth or seventh tergites or ventral near the lateral margin between sixth and seventh abdominal segments. Tibiae with stiff, short, spinelike bristles as well as fine hairlike bristles. Tibiae without pseudojoints, their apices with tufts on front and middle legs in males.

Type-genus: *Haematosiphon* Champion.

This subfamily is distributed over most of the Western Hemisphere from Canada to Argentina. The species are associated with birds of diverse type. Five of the 7 genera are monotypic, an unusual feature in the Cimicidae. This fact has led to the suggestion that the number of genera should be reduced. However, in addition to detailed character differences, each genus has a unique spermalege, and *Ornithocoris* has only 4 autosomes (haploid number), *Hesperocimex* has 19 or 20, and of the other genera *Haematosiphon, Synxenoderus,* and *Psitticimex* have 14

and *Caminicimex* has 18. Also, each genus is associated with a different bird host and distinctive nest habitat. *Haematosiphon* has only 4 nymphal instars (Lee 1955b), a rare occurrence in the Hemiptera. *Ornithocoris* (Carvalho 1939) and *Hesperocimex* (Ryckman 1958) have the usual number of 5 instars.

Because of its lateroventral "hat-shaped" ectospermalege and its unique internal anatomy, described elsewhere, *Hesperocimex* is the most isolated genus in the Haematosiphoninae.

KEY TO THE GENERA OF *HAEMATOSIPHONINAE*

1. Bristles at sides of pronotum numerous and of equal length. Ectospermalege "hat-shaped," right ventral near lateral margin between sixth and seventh segments. Purple martins (*Progne*) in woodpecker holes. Western North America. ..... ***Hesperocimex***
   Bristles at sides of pronotum short or variable but with 1 or 2 long bristles at posterolateral angles. Ectospermalege dorsal either at middle or on right side on sixth or seventh tergites. 2
2. Second antennal segment longer than interocular space. Ectospermalege on anterior margin of a long internal lobe produced forward from anterior margin of seventh tergite at middle. Paramere long, exceeding side of genital segment. *Myiopsitta* nests. Argentina. ..... ***Psitticimex***
   Second antennal segment subequal or shorter than interocular space. Ectospermalege not produced into an internal lobe as above. Paramere not exceeding side of genital segment. 3
3. Head as wide as long (cleared specimens), the gula swollen at strongly arched front margin of prosternum. Spermalege right dorsal. Fourth to seventh abdominal tergites (males) or sixth and seventh (females) strongly asymmetrical on the right side. White-throated swifts. Western United States ..... ***Synxenoderus***
   Head wider than long. Gula not swollen. Spermalege at middle or on right side, but tergites not asymmetrical at right margin and not at all in males 4
4. Rostrum long, more than 1 mm, reaching beyond apices of middle coxae in pinned specimens. Second antennal segment subequal to interocular space. Spermalege mid-dorsal. Birds of prey. Southwestern U S. and Mexico ..... ***Haematosiphon***
   Rostrum shorter, less than 1 mm, reaching to or a little beyond apices of front coxae in pinned specimens. Second antennal segment shorter than interocular space. Spermalege opening on right side 5
5. Pronotum about twice as wide as long, widest in front of middle. Eastern North America. Chimney swifts. ..... ***Cimexopsis***
   Pronotum 2½ or more times as wide as long, widest behind middle. Brazil and Argentina (also Florida and Georgia, introduced?) on swallows, and chickens and, in Florida, on purple martins in bird houses 6
6. Several long bristles at sides of pronotum. Size small, the pronotum less than 1 mm wide. Uruguay and Argentina, in mud nests of the oven bird (*Furnarius*) ..... ***Caminicimex***
   Bristles at sides of pronotum short and dense except for 2 long bristles posterolaterally. Size larger, pronotum 1 mm or more wide. Brazil and Argentina (also Florida and Georgia, introduced?) on swallows (*Pygochelidon*) and chickens, and purple martins (*Progne*) in bird houses in Florida ..... ***Ornithocoris***

Genus *Ornithocoris* Pinto

Ornithocoris Pinto, 1927a, Rev. Biol. Hyg. 1 (2) : 17.
Ornithocoris, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Ornithocoris, Lima, 1940, Ins. Brasil 2: 247 (part) .
Ornithocoris, Pinto, 1945, Zoo-Parasitos Int. Med. Vet., 2nd ed., p. 119 (part) .
Ornithocoris, Lent and Abalos, 1946, An. Inst. Med. Reg. Univ. Tucumán 1: 347 (part) .
Ornithocoris, Wygodzinsky, 1951, An. Inst. Med. Reg. Univ. Tucumán 3: 194 (part) .

Size 2.74 (dried) to 4.3 mm (slide-mounted) . Body suboval, surface finely, shallowly punctured and covered with short, regularly spaced bristles except for long ones on humeri and sides of hemelytral pads. Also with 2 long bristles at apex of clypeus and a few long bristles at end of abdomen.

Head with clypeus strongly widened anteriorly, nearly twice as wide beyond middle as at base and more than twice as wide as interocular space. Antennae shorter or about as long as width of pronotum; second segment distinctly shorter than interocular space. Rostrum (in dried specimens) slightly exceeding apices of front coxae; first segment just reaching base of head.

Pronotum 2½ to 3 times as wide as long; more than ½ again as wide as head; widest behind middle; sides depressed and arcuate; humeri rather abruptly subangulate; hind margin sinuate with transverse depressions in front of basal angles of mesonotum.

Mesonotum broadly exposed, with distinct but short bristles.

Hemelytra twice as wide as long, contiguous for a distance equal to about ½ the length of exposed part of mesonotum, broadly rounded on inner half at apices, sinuate on outer half of apical margin; depressed and a little reflexed laterally; disks shallowly punctate and with a shagreened area at inner half.

Legs moderately stout; front and middle tibiae with prominent tufts in males, reduced but present on front legs in females.

Male genital segment feebly sloping to the left; paramere not exceeding lateral margin of genital segment.

Female spermalege between sixth and seventh tergites to the right of middle, consisting of a transverse thickened and pigmented area along anterior margin of seventh segment, visible only in cleared specimens. Hind margin of sixth segment slightly asymmetrical over ectospermalege. Internally a thickening can be seen between fifth and sixth segments.

Type-species: *Ornithocoris toledoi* Pinto.

This genus is distinguished by the broad pronotum. The spermalege is like that in *Cimexopsis* and *Caminicimex* and only slightly different in position from that of *Haematosiphon.* The very low number of autosomes (4A) is known elsewhere only in *Primicimex* and the *Cacodmus-Aphrania-Loxaspis* group.

The type species has been found only on chickens and is known from Brazil, Argentina, and Bolivia in South America. The second species, *pallidus,* is known from swallows (*Pygochelidon*) in Brazil, from purple martin nests (*Progne*) in Florida, and from chickens and a house (attacking man?) in Georgia.

KEY TO THE SPECIES OF *ORNITHOCORIS*

1. Pronotum nearly twice as wide as head (more than 1.8 times) ..... 65. ***toledoi***
   Pronotum about 1⅔ as wide as head (1.6 or 1.7 times) ..... 66. ***pallidus***

65. *Ornithocoris toledoi* Pinto

(Fig. 12–65)

*Ornithocoris toledo*i Pinto, 1927a, Rev. Biol. Hyg. 1 (2) : 17.
Ornithocoris toledoi, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 319.
Ornithocoris toledoi, Carvalho, 1939, Ceres 1: 128–140.
Ornithocoris toledoi, Snipes, Carvalho, and Tauber, 1940, Iowa State Coll. J. Sci. 15 (1) : 27–37.
Ornithocoris toledoi, Lima, 1940, Ins. Brasil 2: 253.
Ornithocoris toledoi, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Ornithocoris toledoi, Pinto, 1945, Zoo-Parasitos, 2nd ed., p. 119.
Ornithocoris toledoi, Lent and Abalos, 1946, An. Inst. Med. Reg. Univ. Tucumán 1 (3) : 347.
Ornithocoris toledoi, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Ornithocoris toledoi, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Ornithocoris toledoi, Hicks, 1959, Check-List and Bibliogr., p. 248.
Ornithocoris toledoi, Ronderos, 1961, Notas Mus. La Plata 20: 35.

Female.—Head 0.8 mm wide; ⅔ as long as wide, 19:28; interocular space 4 times as wide as an eye. Antennae 1.17 mm long; proportion of segments 4:15:11:11. Rostrum (in pinned specimen) slightly exceeding level of apices of front coxae; 0.6 mm long; proportion of segments 6:6:9.

Pronotum 1.45 mm wide; ratio of length to width 19:51; sides flaring backward; widest point just in front of humeral bristles; bristles of sides very small, those of humeri (2 each) relatively short, only ⅓ the length of pronotum, 0.17 mm.

Hemelytra with sides bearing several bristles of intermediate length.

Abdominal tergites with numerous rows of fine bristles but also, on posterior third of second segment and most of the remaining segments, with dark longitudinal lines amidst the bristles (seen only in dried specimens) .

Legs with hind femora 3 times as long as broad, 30:10; hind tibiae ⅕ longer than femora.

Color generally darker brown with pale only on inner posterior part of hemelytral pads.

Male.—Genital segment ½ again as wide as total length of paramere, 22:14.

Size.—Male, length 3.94 mm, width (pronotum) 1.4 mm, (abdomen) 2.05 mm; female, length 4.2 mm, width (pronotum) 1.46 mm, (abdomen) 2.2 mm.

Redescribed from a male and female, Sumampa, Quebrachos, Santiago del Estero, Argentina, Sept. 28, 1943 (M. A. Alvarado) , on chickens, sent by Dr. P. Wygodzinsky.

The type of *toledoi* is in the Instituto Oswaldo Cruz. It was collected at Limeira, Sorocaba, São Paulo, Brazil. Attempts to collect the species there in 1957 were unsuccessful, but an infestation was found at Ponte Nova, Minas Gerais, Brazil, on chickens (J. Becker and R. L. Usinger) . Wygodzinsky (1951) records Cruz del Eje, Cordoba, Argentina (Prosen) . Material before me is as follows: Cana Brava, Goias, Brazil, Oct. 8, 1932 (José Blaser) ; Nova Teutonia, S. Catarina, Brazil, 1942, Sept. 4, 1948, 1949 (Fritz Plaumann) ; São Paulo, Proc. Jau, Brazil, 1949 (G. B. Thompson) ; and Azero, Bolivia, Jan. 4, 1940 (P. Echalar) .

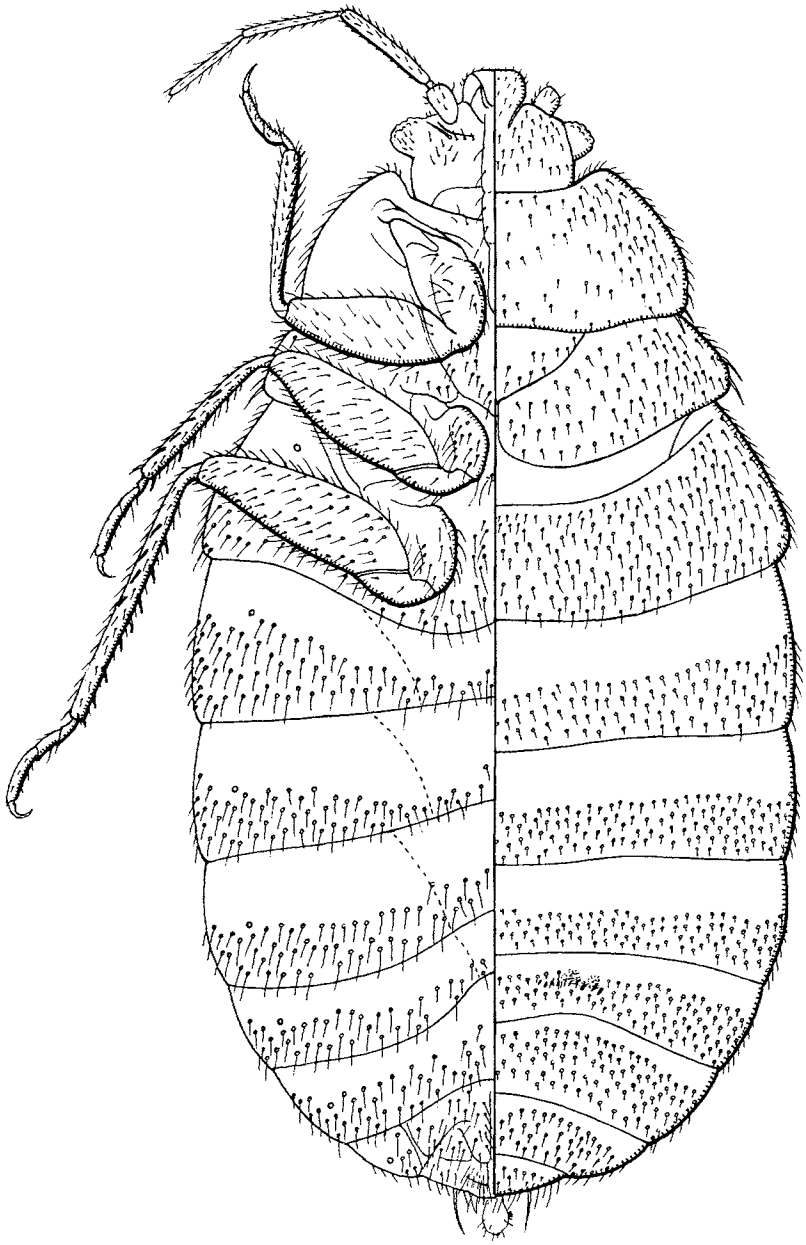

FIG. 12–65.—*Ornithocoris toledoi* Pinto. Female. Ponte Nova, Minas Gerais, Brazil (Celeste Green, original).

This is the so-called "Brazilian chicken bug" or "percevejo dos galinheiros." Thus far it has been taken only on chickens which are, of course, introduced into the Western Hemisphere. A diligent search in the nests of hundreds of wild birds in South America in 1957 failed to reveal a native host, although one must surely exist. The species has become rare, even on chickens in Brazil, as a result of the widespread use of benzene hexachloride and other residual insecticides.

66. ***Ornithocoris pallidus*** Usinger
(Fig. 12–66)

Haematosiphon inodorus, Blatchley, 1928, Florida Entomol. 12: 43.
Ornithocoris pallidus Usinger, 1959b, Entomologist 92: 219.

Female.—Head 0.71 mm wide; ¾ as long as wide, 19:25; interocular space about 4 times as wide as an eye. Antennae 1.03 mm long; proportion of segments 4:13:10:9. Rostrum (dried specimens) exceeding level of apices of front coxae; 0.6 mm long; proportion of segments 7:6:8.

Pronotum 1.08 mm wide; ratio of length to width 15:38; sides arcuate; greatest width at about basal third, converging behind that level to humeri; bristles of sides relatively short and dense, those at humeri (2 on each side) erect, 0.17 mm long.

Hemelytra with sides bearing 2 or 3 bristles almost as long as those of humeri.

Abdominal tergites with only faint rastrate lines (as seen in dried specimens). Hind margin of sixth tergite asymmetrical, bent forward over spermalege. The latter, in cleared specimens, appearing as a pigmented thickening on anterior margin of seventh tergite to the right of middle.

Male with paramere ⅔ as long as width of genital segment at base, 11:18.

Legs with hind femora 3 times as long as broad, 28:9; hind tibia ¼ longer than femur; front and middle tibiae with prominent apical tufts, reduced in female.

Color paler than in *toledoi,* with hemelytral pads broadly pallid.

Size.—Male, length 3.28 mm, width (pronotum) 1 mm, (abdomen) 1.85 mm; female, length 4 mm, width (pronotum) 1.25 mm, (abdomen) 2.1 mm.

Holotype female, allotype male, and a long series of paratypes, Viçosa, Minas Gerais, Brazil, July 22, 1957, in nest of *Pygochelidon cyanoleuca* (Vieillot) (R. L. Usinger) (U. S. National Museum). In addition to the types, 4 additional series are at hand: Pensacola, Fla., Jan. 27, 1957 (A. F. Wicke), on *Progne subis* (Linnaeus), in bird houses; Ft. Myers, Fla., Aug. 8, 1942 (Wm. V. Chester), in chicken nests; Augusta, Ga., June 16, 1945 (Mrs. R. F. Hauck), "biting collector"; and Quitman, Ga., May 13, 1937 (L. V. Cawley), in poultry house. Blatchley (1928) recorded *Haematosiphon inodorus* (Dugès) from Lakeland, Fla., July 15, 1928 (J. R. Watson); and near Tavares, Lake Co., Fla. (J. R. Watson) on chickens. Thanks to Dr. Leland Chandler, I have examined these specimens and found that they are *Ornithocoris pallidus.* An additional specimen in the Blatchley collection bears the label "Agric. Exp. Sta., Gainesville, Fla. JRW 7032." Specimens from Florida and Georgia resemble the Brazilian types in every way. Presumably they were intro-

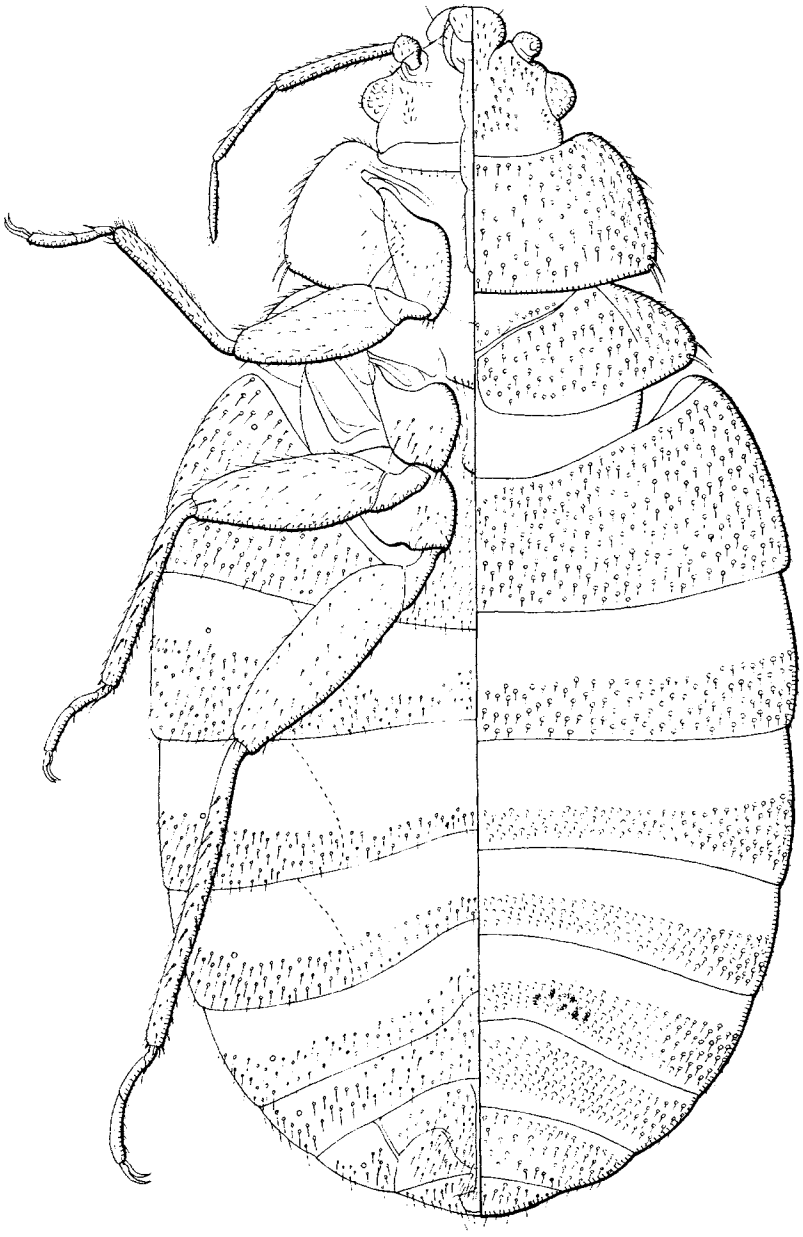

FIG. 12–66.—*Ornithocoris pallidus* Usinger. Female holotype. Viçosa, Minas Gerais, Brazil (Celeste Green, original).

duced into the United States but by what means is not known. The capture of specimens in the nest of a purple martin is especially interesting, since this is the host of *Hesperocimex* in western North America. The nests of *Pygochelidon* in Brazil are different from those of the swallows of Europe and North America, as no mud is used. They are simply straw nests hidden in protected places, in this case under eaves of a shed.

O. pallidus differs from *toledoi* in its smaller size, paler color, and narrower pronotum.

Caminicimex, new genus

Size 3–4 mm. Body suboval, pale, punctures superficial. Bristles short and inconspicuous above, except at sides of pronotum and hemelytral pads, on basal abdominal segment, and at apex of abdomen. Under surface with longer bristles.

Clypeus strongly widened anteriorly, nearly twice as wide beyond middle as at base and more than ½ as wide as interocular space, with a very long seta on each side at apex. Head disk with numerous bristles on each side near eyes and at middle, naked behind level of hind margins of eyes. Antennae about equal to width of pronotum; second segment longest, third and fourth slender, slightly shorter and subequal. Rostrum in dried specimens reaching apices of front coxae; first and third segments subequal, second slightly shorter.

Pronotum 2½ times as wide as long, about ½ again as wide as head; sides arcuate and posteriorly nearly straight and converging to roundly angulate posterior angles; sides with conspicuous bristles, the longest 0.114 mm in contrast to 2 very long (0.28 mm) bristles at humeri.

Hemelytral pads a little less than twice as wide as long, contiguous for a distance equal to length of mesonotum, broadly rounded behind and at sides; sides depressed, with several short bristles and 2 long ones.

Legs short and stout; front and middle tibiae with very short but distinct tufts at extreme apices, tufts small but distinct also in females.

Male genital segment slightly sloping to left; paramere curved, surpassing a little the lateral margin of segment.

Female ectospermalege right dorsal between sixth and seventh and also more or less between fifth and sixth segments, the organ appearing in cleared specimens as an aggregate of pigmented spots on anterior margin of each segment. Tip of abdomen with fused plates as small rounded lobes, each beset with numerous bristles.

Type-species: *Cimex furnarii* Cordero and Vogelsang.

Caminicimex may be distinguished by the long bristles at the sides of the pronotum and the distinct female genital lobes. The number of autosomes (18A) is unique insofar as is known in the Haematosiphoninae.

The genus was described from Uruguay and recorded by Wygodzinsky from several localities in northern Argentina. The host, *Funarius rufus* (Gmelin), occurs widely in Brazil, but no bugs have yet been found there.

67. ***Caminicimex furnarii*** (Cordero and Vogelsang)

(Fig. 12–67)

Cimex furnarii Cordero and Vogelsang, 1928, Bol. Inst. Clin. Quir. 4: 671.
?Cimex passerinus Cordero and Vogelsang, 1928, Bol. Inst. Clin. Quir. 4: 674.
Cimex furnarii, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 403.
?Cimex passerinus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 403.

Ornithocoris furnarii, Carvalho, 1939, Ceres 1: 128–40.
Ornithocoris furnarii, Lima, 1940, Ins. Brasil 2: 247.
Ornithocoris furnarii, Snipes, Carvalho, and Tauber, 1940, Iowa State Col. J. Sci. 15 (1) : 27–37.
?Oeciacus passerinus, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
?Cimex passerinus, Pinto, 1945, Zoo-Parasitos Int. Med. Vet., 2nd ed., p. 116.
Ornithocoris furnarii, Pinto, 1945, Zoo-Parasitos Int. Med. Vet., 2nd ed., p. 119.
Cimex furnarii, Lent and Abalos, 1946, An. Inst. Med. Reg. Tucumán 1 (3) : 347.
Ornithocoris furnarii, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Ornithocoris furnarii, Wygodzinsky, 1951, An. Inst. Med. Reg. Tucumán 3 (2) : 195.
Ornithocoris furnarii, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Ornithocoris furnarii, Hicks, 1959, Check-List and Bibliogr., p. 248.
Ornithocoris furnarii, Ronderos, 1961, Notas Mus. La Plata 20: 34.

Female.—Disks of head, pronotum, mesonotum, and hemelytral pads with short but distinct, fine bristles.

Head 0.65 mm wide; more than ⅔ as long as wide, 17:23; interocular space 5 times as wide as an eye. Antennae 0.94 mm long; proportion of segments 4:11:9:9. Rostrum 0.5 mm long; proportion of segments (slide-mounted) 5:5:8.

Pronotum 0.94 mm wide; ratio of length to width 13:33; bristles of sides regularly spaced, those of humeri longest; hind margin of pronotum in dried specimens feebly sinuate sublaterally. Mesonotum slightly raised along middle. Exposed part of metanotum naked, broadly, shallowly emarginate at middle.

Abdomen above with conspicuous bristles on basal segment, those near hind margin extending well beyond edge. Bristles on posterior terga very inconspicuous, marked mainly by fine punctures on posterior half of each segment.

Legs stout; hind femora about 3 times as long as greatest width; hind tibiae about ⅙ longer than femora.

Male.—Front and middle tibiae with apical tufts about $^1/_7$ the length of tibia. Total length of sclerotized paramere about ⅔ the width of genital segment.

Size.—Male, length 3 mm, width (pronotum) 0.9 mm, (abdomen) 1.7 mm; female, length 3.43 mm, width (pronotum) 0.94 mm, (abdomen) 1.8 mm.

Redescribed from a male and a female (slide-mounted) from a laboratory culture first collected near Tucumán, Argentina, in August, 1957 (R. L. Usinger and P. Wygodzinsky). Additional material is at hand from San Ramon, Santiago del Estero, Argentina, Aug. 15, 1944 (Romaña and Abalos); Santa Maria, Catamarca, Argentina, Sept. 10, 1952 (Ramón Guanco). Wygodzinsky (1951) adds La Banda, Santiago del Estero, Oct. 14, 1943 (Abalos); Tucumán, 10 km from the city on Route 9, Aug. 19, 1944 (Romaña and Abalos); Isla Antequeda, Corrientes (Romaña); Estancia "La Juanita," Rocha, Buenos Aires. Ronderos (1961) gives the following additional localities: Chivilcoy, Buenos Aires; Capital Federal; San Miguel de Tucumán; Colonia and Nueva Palmira, República Oriental del Uruguay.

The host records indicate that this species occurs exclusively in the mud nests of the "oven bird," "hornero," or "joão de barro," *Furnarius*

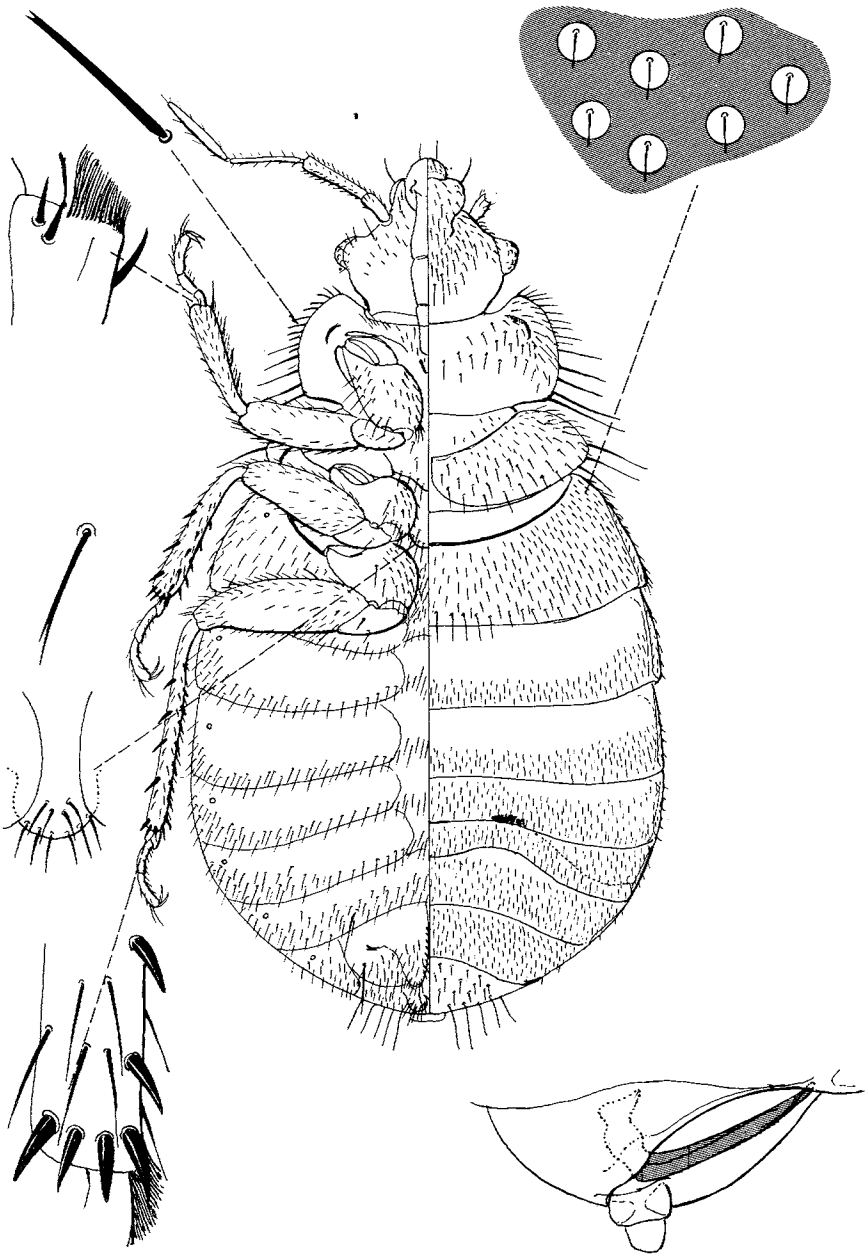

FIG. 12–67.—*Caminicimex furnarii* (Cordero and Vogelsang). Female and male genitalia. Tucumán, Argentina (Ferris, original).

rufus (Gmelin). The nests are heavy and rounded, about 6 to 8 inches in diameter, made of hardened mud with thick walls. They are built singly in a limb crotch high in a tree. The opening is small and directed away from the wind and weather. Dr. Wygodzinsky and I found many specimens in a single nest near Tucumán (Fig. 11–15d). Since there are periods of the year when the nests are empty, it is presumed that the bugs will feed on other species of birds, especially those that occupy the vacant nests. Nests were examined in Minas Gerais and São Paulo, Brazil with negative results.

Wygodzinsky (1951) figures the first nymphal instar and distinguishes it from other Haematosiphoninae by the pair of long subapical bristles on the second tarsal segment.

Cimex passerinus Cordero and Vogelsang, described from a single male from *Passer domesticus,* seems to fall well within the limits of variation of *furnarii* in size and other characters that can be gleaned from the confusing figure and non-diagnostic description. The type is apparently lost.

Psitticimex, new genus

Size 3 (dried) to 4.8 mm (slide-mounted). Body suboval, broadly rounded behind. Punctures superficial on head and pronotum, coarse but shallow on hemelytra, fine on abdomen. Bristles longest at sides of pronotum, hemelytral pads, and tip of abdomen, with 1 or 2 very long bristles at each humerus and a long bristle on each side of clypeus apically.

Clypeus strongly widened anteriorly, twice as wide beyond middle as at base and a little more than ½ as wide as interocular space. Antennae ¼ longer than width of pronotum; first segment short and thick, second longest, as long as interocular space, third and fourth shorter and more slender, the fourth shorter than third. Rostrum (in dried specimens) slightly surpassing front coxae, the apical segment longest; first segment not reaching base of head.

Pronotum about twice as broad as long; ½ again as wide as head; sides depressed and arcuate; humeri roundly subangulate; hind margin shallowly concave at middle; disk with only very fine punctures; depressed subbasally in front of each basal angle of mesonotum.

Hemelytral pads ½ again as wide as long; contiguous for ¾ the length of mesonotum and leaving only a small part of metanotum exposed; sides and posterior margins almost continuously rounded; disks convex sublaterally and then strongly depressed at lateral margins.

Legs stout, the front and middle tibiae with prominent apical tufts in males, reduced in females.

Female posterior margins of fourth and fifth tergites bent forward at middle and bisinuate, spermalege at end of strongly produced median area of hind margin of sixth tergite, forming a coneshaped internal projection reaching forward to fourth segment.

Type-species: *Ornithocoris uritui* Lent and Abalos.

P. uritui has a unique ectospermalege, but Carayon has shown that it is not fundamentally different from that of *Haematosiphon* and its allies, which also have the anterior margin of seventh tergite thickened but not so strongly produced. Other unique characters of *Psitticimex* are the relatively long, narrow pronotum, the long antennae, and the large eyes.

The host is a parrot, *Myiopsitta monachus cotorra* (Vieillot), which builds a community of nests, closely woven, in trees. *Psitticimex* has thus far been recorded only from Argentina.

68. ***Psitticimex uritui*** (Lent and Abalos)
(Fig. 12–68)

Ornithocoris uritui Lent and Abalos, 1946, An. Inst. Med. Reg. 1 (3) : 337.
Ornithocoris uritui, Wygodzinsky, 1951, An. Inst. Med. Reg. 3 (2) : 196.
Ornithocoris uritui, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Ornithocoris uritui, Hicks, 1959, Check-List and Bibliogr., p. 248.
Ornithocoris uritui, Ronderos, 1961, Notas Mus. La Plata 20: 35.

Female.—Head 0.8 mm wide, 4/5 as long as wide, 22:28; interocular space less than 4 times as wide as an eye, measured at level of anterior margins of eyes; inner margins of eyes distinctly posteriorly divergent. Antennae 1.51 mm long; proportion of segments 5:19:16:13. Rostrum (pinned specimen) 0.91 mm long; proportion of segments 10:9:12.

Pronotum 1.22 mm wide; ratio of length to width 20:43; bristles at sides short, 0.14 mm, and backwardly directed, those of humeri longer, 0.23 mm, and erect. Hemelytral margins with several bristles as long as humeral bristles. Hemelytral pads not pale, dark brown as is the rest of body.

Mesonotum with numerous hairlike bristles, some of which are long.

Abdomen with many rows of fine, backwardly directed bristles. Hind margins of third to sixth tergites sinuate and asymmetrical in female.

Legs with hind femora a little more than 3 times as long as broad, 36:11. Hind tibiae less than 1/3 longer than femora, 43:136. Stout spines of tibiae a little more than 1/2 the thickness of a tibia.

Male.—Genital segment 3 times as wide as long; paramere in total length almost as great as width of segment at base, 36:39.

Size.—Male, length 4.8 mm, width (pronotum) 1.2 mm, (abdomen) 2.2 mm; female, length 4.63 mm, width (pronotum) 1.23 mm, (abdomen) 2.3 mm.

Redescribed from a male and female collected near Tucumán, Argentina, Aug. 1957 (R. L. Usinger and P. Wygodzinsky). The types are in the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil. Ronderos (1961) summarizes the locality records, all Argentina, as follows: Tapso, Catamarca, Apr. 24, 1945 (Romaña and Abalos); El Pintado, Guemes, Chaco; Loro Blanco, Chacabuco, Chaco, June 2, 1946 (Romaña and Abalos); La Aurora, San Fernando, Chaco, May 28, 1946 (Romaña and Abalos); Villa Federal, Feliciano, Entre Rios, Sept. 19, 1947 (Romaña and Abalos); Comandante Fontana, Patino, Formosa, Oct. 9, 1947 (M. Conejos); Ruta 38a, 0.7 km del limite con Catamarca, La Rioja, Jan. 16, 1944 (Romaña and Abalos); Colonia Dora, Avellaneda, Santiago del Estero, May 26–27, 1948 (Laserna); El Mojon, Pellegrini, Santiago del Estero, Mar. 18, 1945 (Romaña and Abalos); Girardet, Moreno, Santiago del Estero, Nov. 6, 1944 (Romaña and Abalos); La Victoria, Rivadavia, Santiago del Estero; Puente Negro, Avellaneda, Santiago del Estero, Sept. 14, 1949 (R. Guanco); Sumampa, Quebrachos, Santiago del Estero, Sept. 2, 1945 (Romaña and Abalos); Villa Nueva Esperanza, Copo, Santiago

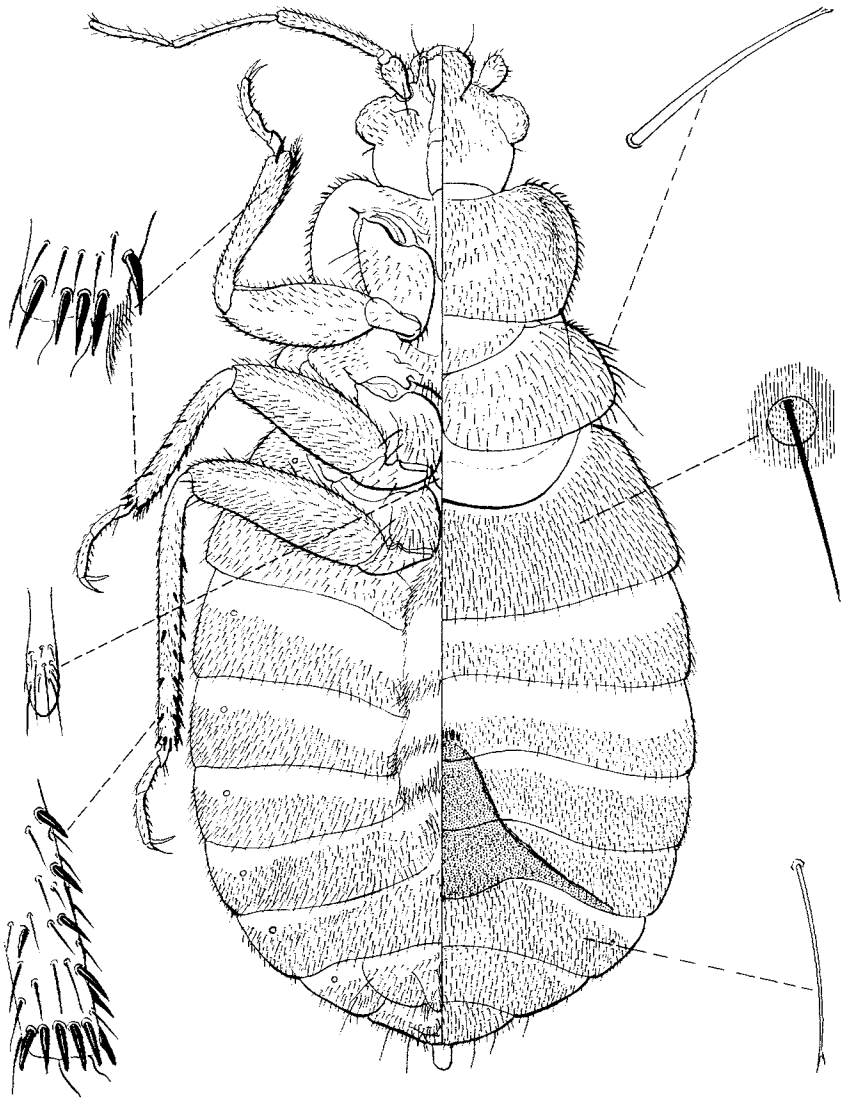

FIG. 12–68.—*Psitticimex uritui* (Lent and Abalos). Female. Santiago del Estero, Argentina (Ferris, original).

del Estero, Oct. 11, 1943 (Romaña and Abalos); Santa Victoria Este, Rivadavia, Salta, Apr. 7; Buruyacú, Tucumán, Mar. 15, 1945 (Romaña and Abalos).

All specimens have been collected in the nests of the parrot "cotorra," *Myiopsitta monacha cotorra* (Vieillot). These nests are attached in the limbs of trees. They are multiple with the entry hole in the bottom. The nest material is closely woven with twigs visible at the sides. Hundreds of specimens were found in 1 multiple nest.

Genus ***Haematosiphon*** Champion

Haematosiphon Champion, 1900, Biol. Cent.-Amer. Rhynch, 2: 337.
Haematosiphon, Jordan and Rothschild, 1912, Novitates Zool. 19: 352.
Haematosiphon, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 261.
Haematosiphon, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 363.
Haematosiphon, Patton and Cragg, 1913, Med. Entomol., p. 498, 512.
Haematosiphon, Horvath, 1914b, IX[e] Int. Congr. Zool., p. 295.
Haematosiphon, Jordan, 1922, Ectoparasites 1: 285.
Haematosiphon, List, 1925, Proc. Biol. Soc. Wash. 38: 106.
Haematosiphon, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 318, 403.
Haematosiphon, Lima, 1940, Ins. Brasil 2: 246.
Haematosiphon, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 295.
Haematosiphon, Usinger, 1947, Pan-Pacific Entomol. 23: 140.
Haematosiphon, Lee, 1954c, J. Econ. Entomol., 47: 1144.

Size 3.1 (dried) to 4.5 mm (slide-mounted). Body elongate oval, surface shining, superficially punctured on head and pronotum, more distinctly so on abdominal tergites. Bristles fine and short except on margins of pronotum, hemelytral pads and tip of abdomen with 2 long humeral bristles and several long bristles at sides of hemelytra. Clypeus strongly widened anteriorly, nearly twice as wide beyond middle as at base and ½ as wide as interocular space, with a long bristle on each side near apex. Antennae ¼ longer than width of pronotum; first segment short and thick, second longest, about as long as interocular space, third and fourth shorter, more slender and subequal. Rostrum in slide-mounted specimens reaching beyond apices of front coxae, the apical segment longest; in pinned specimens reaching beyond apices of middle coxae, the first segment attaining base of head.

Pronotum less than 2½ times as broad as long, ½ again as wide as head; sides rounded anteriorly and scarcely produced behind eyes, straighter behind and then roundly subangulate at humeri; hind margin broadly, shallowly concave at center.

Mesonotum with short, fine bristles.

Hemelytral pads with a pale, finely granular surface except laterally; twice as broad as long, contiguous for ½ the length of metanotum, evenly curved behind on inner half, nearly straight sublaterally; side margins rounded and broadly reflexed.

Legs stout; front and middle tibiae in males with distinct apical tufts ($^1/_7$ the length of a tibia on front legs). Females without tufts.

Male genital segment feebly sloping to the left, the paramere curved to the left and forward, tapering, ⅔ as long as width of segment, fitting in a groove that extends to side of segment at base.

Female spermalege opening between sixth and seventh segments, sometimes also between fifth and sixth; hind margins of fifth and sixth segments bent forward (concave) at or a little to the right of the middle.

Type-species: *Acanthia inodora* Dugès.

Haematosiphon is related to the other bird bugs of North America, *Cimexopsis* and *Synxenoderus,* but differs in the long rostrum and the nearly median position of the spermalege. The native hosts are birds of prey and especially owls, the California condor, and eagles. The known distribution includes western North America from California, Arizona, New Mexico, Texas, and Oklahoma to Mexico, with 1 anomalous record from Argentina.

69. ***Haematosiphon inodorus*** (Dugès)
(Fig. 12–69)

Acanthia inodora Dugès, 1892, La Naturaleza (2) 2: 169.
Acanthia inodora, Townsend, 1894, Proc. Entomol. Soc. Wash. 3: 40.
Haematosiphon inodora, Champion, 1900, Biol. Cen.-Amer. Rhynch. II, p. 337.
Haematosiphon inodorus, Horvath, 1912, Ann. Mus. Nat. Hung. 10: 262.
Haematosiphon inodorum, Reuter, 1913b, Z. Wiss. Insektenbiol. 9: 362.
Haematosiphon inodorus, Horvath, 1914b, IX^{e} Int. Congr. Zool., p. 295.
Haematosiphon inodorum, Jordan, 1922, Ectoparasites 1: 285.
Cimex inodorus, Lahaye, 1931, Rep. XIth Vet. Congr. London 3: 801–13.
Haematosiphon inodorus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 99.
Haematosiphon inodora, Usinger, *in* Herms, 1939, Med. Entomol., 3rd ed., p. 92.
Haematosiphon inodora, Lima, 1940, Ins. Brazil 2: 246.
Haematosiphon inodora, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Haematosiphon inodora, Usinger, 1947, Pan-Pacific Entomol. 23: 140.
Haematosiphon inodorus, Goidanich, 1947, Bol. Ist. Entomol. Stud. Bologna 16: 6.
Haematosiphon inodorus, Kaupp and Surface, 1947, Poult., Sanit., Dis. Contr. Ed. 3, p. 170–1.
Haematosiphon inodora, Biester and Schwarte, 1952, Diseases of Poultry, 3rd ed., p. 797.
Haematosiphon inodorus, Lee, 1954a, Pan-Pacific Entomol. 30: 159–160.
Haematosiphon inodorus, Lee, 1954b, J. Econ. Entomol. 47: 224–6.
Haematosiphon inodorus, Lee, 1954c, J. Econ. Entomol. 47: 1144.
Haematosiphon inodorus, Lee, 1955b, Pan-Pacific. Entomol. 31: 47–61.
Haematosiphon inodorus, Muñez Andrade, 1956, Med. Rev. Mex. 21: 45–51.
Haematosiphon inodorum, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 17.
Haematosiphon inodorus, Hicks, 1959, Check-List and Bibliogr., p. 243; 1962, Suppl. 1, p. 260.

Female.—Head 0.89 mm wide; 5/6 as long as wide, 26:31; interocular space 4 times as wide as an eye. Antennae 1.68 mm long; proportion of segments 7:21:17:14. Rostrum (pinned specimen) 1.08 mm long; proportion of segments 11:12:15. Pronotum 1.08 mm wide; ratio of length to width, 16:38; bristles at sides of pronotum relatively short and backwardly directed, 0.086 mm long; humeral bristles twice that length. Hemelytral margins with several bristles as long as humeral bristles; hemelytral disks pale and shallowly punctate.

Abdomen above finely punctured and beset with rather even rows of short, appressed bristles; middle of seventh tergite in female with several long erect bristles and apex of male genital segment with conspicuous long bristles. Under surface with longer bristles than dorsal surface.

Legs relatively slender; hind femora about 4 times as long as broad; hind tibiae about

⅓ longer than femora. Stout spines of tibiae only about ½ as long as thickness of tibia.

Male.—Paramere evenly curved and tapering.

Size.—Male, length 4.56 mm, width (pronotum) 1.22 mm, (abdomen) 2.3 mm; female, length 4.65 mm, width (pronotum) 1.28 mm, (abdomen) 2.6 mm.

Redescribed from a slide-mounted female from the nest of California condor, *Gymnogyps californianus* (Shaw), near Santa Maria, Ventura Co., Calif., Sept. 16, 1939 (A. H. Miller and C. B. Koford), and a male, Coyote Cove, Conception Bay, Baja Calif., Mexico, July 1, 1938 (E. S. Ross and A. E. Michelbacher). For measurements on dried specimens, a male and a female were used from a large collection from Norco, Riverside Co., Calif., bank along Santa Ana River, Aug. 5, 1958 (R. E. Ryckman and R. D. Lee). The Norco specimens were collected in tunnels occupied by barn owls (*Tyto alba alba* Scopoli) in the banks of the Santa Ana River. Specimens from Oklahoma (see below) were found in nests of the great horned owl (*Bubo virginianus* (Gmelin)). Another host record is the golden eagle (*Aquila chrysaëtos* (L.), 10 mi S. of Post, Garza County, Texas, April 7, 1954 (R. W. Strandtmann and R. Mitchell), and Briscoe County near Silverton, Texas (R. W. Strandtmann). Other locality records, mostly from chickens, are as follows: TEXAS: Marfa, Presidio County, June 21, 1909 (F. C. Bishopp); Sabinal, Uvalde County, June, 1910 (F. C. Pratt); Alpine, Brewster County, Oct. 26, 1910 (F. C. Bishopp). NEW MEXICO: Deming, Luna County, May 17, 1909 (F. C. Pratt); Silver City, Grant County, July 15, 1916 (W. B. McFarland); Albuquerque, Bernalillo County, Sept. 3, 1928 (J. Menifield); Lava Cave, Socorro Co., May 22, 1962 (D. G. Constantine); Dona Ana Co. (Townsend); Valencia Co. (Lee); Lake Valley, April 7, 1910 (J. D. Mitchell); 50 mi N. E. Tucumcori, Quay Co., June 25, 1961 (R. E. Ryckman). CALIFORNIA: Red Mountain, Atolia Dist., San Bernardino County, Feb. 1940 (Mrs. J. Van N. Dorr); Caliente Cr., 25 mi S. E. Bakersfield, Kern Co., May 18, 1941 (G. E. Bohart); Corona, Riverside Co., April 25, 1939 (L. E. Wilson). ARIZONA: Lupton, Apache Co., Aug. 12, 1928 (J. W. Bennett); Navajo Co. and Greenlee Co. (Lee 1954a). OKLAHOMA: Freedom, alt 3000 ft, Oct. 31, 1940 (Bubordorf and D. E. Howell). MEXICO: Tepehuanes, Durango (Wickham); Aguas Calientes. The original collection was from Guanajuato, Mexico (Dugès). The British Museum (Nat. Hist.) has a male and female from the type series, and Champion's figure in the Biologia Centrali-Americana was made from the male. Specimens from the type series are also in the Paris and Budapest museums.

A single male specimen in the U. S. National Museum is labelled "Calisaya, Rio Bopi, Argentina (G. L. Harrington)." It seems to agree with typical specimens from North America. Unless substantiated by further records, this should be regarded as an error in labeling.

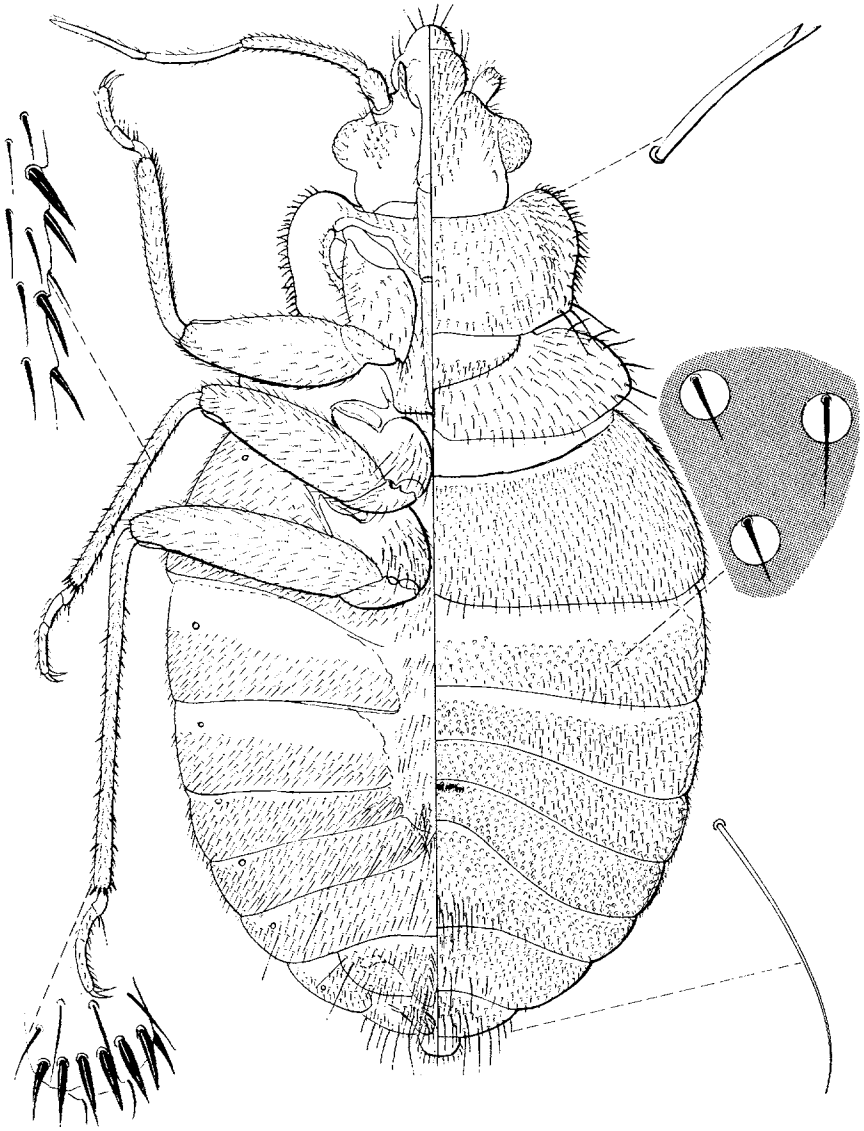

FIG. 12–69.—*Haematosiphon inodorus* (Dugès). Female. Lupton, Apache County, Arizona (Ferris, original).

The records from Florida (Blatchley 1928) pertain to *Ornithocoris pallidus* Usinger.

This species is known as the Mexican chicken bug or, in New Mexico, "coruco."

Genus *Cimexopsis* List

Cimexopsis List, 1925, Proc. Biol. Soc. Wash. 38: 106.
Cimexopsis, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Cimexopsis, Usinger, 1947, Pan-Pacific Entomol. 23: 140.
Cimexopsis, Lee 1954c, J. Econ. Entomol. 47: 1144.

Size 3 (dried) to 4 mm (slide-mounted). Body elongate-oval, shining, with superficial punctures. Bristles very fine and short over most of dorsum, with 1 or 2 longer bristles at each humerus and several at sides of hemelytral pads, a few at tip of abdomen, and 2 at anterior angles of clypeus.

Head with clypeus strongly widened anteriorly, ½ again as wide beyond middle as at base and ½ as wide as interocular space. Antennae about ⅛ longer than width of pronotum; first segment short and thick, second, third, and fourth subequal, each about ⅔ the width of interocular space. Rostrum (dried specimen) exceeding apex of prosternum but not reaching apices of front coxae; first segment not nearly reaching base of head.

Pronotum more than twice as broad as long; ½ again as wide as head; sides arcuate anteriorly, moderately produced forward behind eyes, scarcely arcuate posteriorly to roundly subangulate humeri; hind margin shallowly concave; disk distinctly depressed laterally.

Mesonotum-scutellum broad, rounded behind, the disk with short bristles.

Hemelytral pads more than ½ again as wide as long, contiguous for about ⅔ the length of exposed part of mesonotum, margins rounded, except for nearly straight outer half of posterior margin.

Legs rather stout; front and middle tarsi with prominent apical tufts in males, reduced in females.

Male genital segment sloping a little to left; paramere reaching just to lateral margin.

Female spermalege dorsal between sixth and seventh tergites a little to right of middle, consisting of a mere thickening of anterior margin of seventh segment with transverse black sclerotized area as seen in slide-mounted specimens cleared in KOH.

Type-species: *Cimexopsis nyctalis* List.

Cimexopsis has a spermalege almost like that of *Caminicimex* and *Ornithocoris* (though there is no sign of a thickening between fifth and sixth segments as in those genera). It differs from the former in that the posterior gonapophyses are less lobulate and the pronotal bristles are shorter, and from the latter in the narrower pronotum.

Thus far, *Cimexopsis* has been reported only from the eastern United States in the nests of chimney swifts, *Chaetura pelagica* (L.).

70. *Cimexopsis nyctalis* List

(Fig. 12–70)

Cimexopsis nyctalis List, 1925, Proc. Biol. Soc. Wash. 38: 106.
Cimexopsis nyctolis, Riley and Johannsen, 1932, Med. Entomol., p. 148, 158.
Cimexopsis nyctalis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 319.
Cimexopsis nyctalis, Usinger, *in* Herms, 1939, Med. Entomol., 3rd ed., p. 93.

Haematosiphon nyctalis, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Cimexopsis nyctalis, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 6.
Cimexopsis nyctalis, Lee, 1955a, Bull. Brooklyn Entomol. Soc. 50: 51–52.
Cimexopsis nyctalis, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Cimexopsis nyctalis, Hicks, 1959, Check-List and Bibliogr., p. 243; 1962, Suppl. 1, p. 260.

Female.—Head 0.71 mm wide, 4/5 as long as wide, 20:25; interocular space 5 times as wide as an eye, 18:3.5. Antennae 1.2 mm long; proportion of segments 5:13:12:12. Rostrum in a pinned specimen 0.71 mm long; proportion of segments 10:6:9.

Pronotum 1.05 mm wide; ratio of length to width 15:37; bristles at sides very short, those of humeri relatively short, 0.14 mm. Hemelytral margins with several bristles nearly as long as humeral bristles. Hemelytral pads about the same color as head, pronotum, and mesonotum. Exposed part of mesonotum with scattered short bristles.

Abdomen with many rows of very fine bristles above and with longer bristles on ventral surface. Hind margins of fifth and sixth tergites in female very slightly sinuate at spermalege, almost imperceptible.

Legs with hind femora more than 3 times as long as wide, 30:8.5; hind tibiae 1/3 longer than femora, 40:30; stout spines of tibiae nearly as long as thickness of tibiae, 2.5:3.

Male.—Genital segment 1/2 again as wide as total length of paramere, 20:14.

Size.—Male, length 3.2 mm, width (pronotum) 1.03 mm, (abdomen) 1.65 mm; female, length 3.82 mm, width (pronotum) 1.06 mm, (abdomen) 2.0 mm.

Redescribed from slide-mounted male and female paratypes, Zoological Park, Washington, D. C., July, 1921 (USNM no. 52306). Also at hand are 2 point-mounted male paratypes, Nebraska City, Nebr., Oct. 8, 1912 (Mrs. W. Wessel). Description of the ectospermalege was made from a slide-mounted specimen, Georgia, 1939 (H. C. Essick).

Lee (1955a) summarizes locality records for 12 states, to which I am now able to add New York, Indiana, Georgia, and Mississippi. The host in all cases where known is the chimney swift, *Chaetura pelagica* (L.). NEBRASKA: Nebraska City, Otoe Co., Oct. 8, 1912 (Mrs. W. Wessel). MINNESOTA: Northfield, Rice Co., Apr. 29–May 17, 1942 (Maude G. Stewart). ILLINOIS: Springfield, Sangamon Co., Oct. 15, 1941 (J. H. Smith); Wayne City, Nov. 7, 1962 (Leo Holman); Champaign, July 24, 1942 (M. M. Petrakis); Marshall, Clark Co., Dec. 6, 1940 (D. F. Heidlerider). ARKANSAS: Washington Co., Jan. 1940. IOWA: Muscatine, Muscatine Co., Dec. 27, 1940. OHIO: Chardon, Geauga Co., July, 1945; Reynoldsburg, Liking Co., Feb. 13, 1945; Lynchburg, Highland Co., July 10, 1942; Ross Co., May 2, 1952; Wilkesville, Vinton Co., June 27, 1939 (Mrs. E. L. Newson); Hillsboro, Highland Co., Aug. 11, 1941 (Miller); Portsmouth, Scioto Co., July 14, 1959. PENNSYLVANIA: Frederickstown, Fayette Co., 1928 (F. R. Smith). NEW YORK: Cold Spring Harbor, Long Island, Aug. 15, 1921 (H. M. Parshley); Albany, July 20, 1907 (Felt); Ithaca, Aug. 1, 1937 (A. A. Allen). MAINE: Clinton, Kennebec Co., Aug. 24, 1944. VIRGINIA: Staunton, Augusta Co., Mar. 11, 1943 (A. M. Woodside);

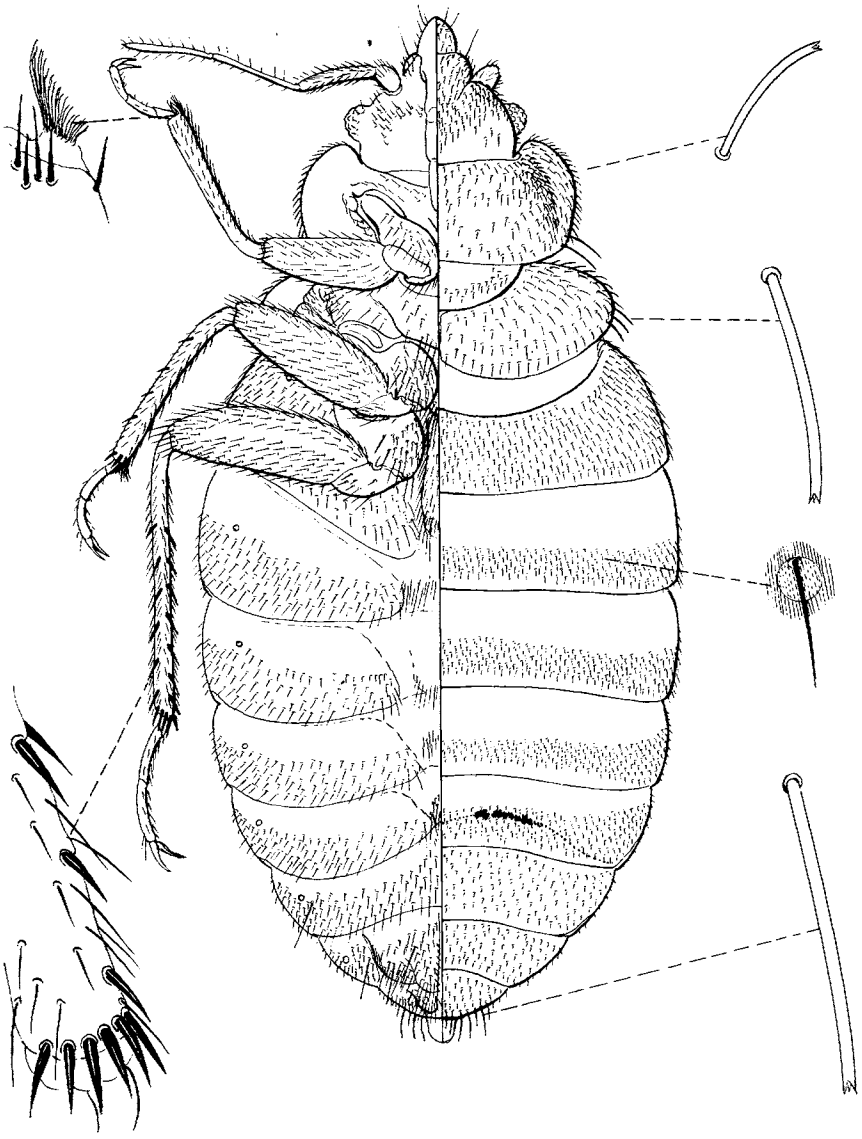

FIG. 12–70.—*Cimexopsis nyctalis* List. Female. Georgia (Ferris, original).

West Point, King William Co., July 31, 1941 (L. A. Hetrick). WASHINGTON, D. C.: Aug. 10, 1944 (Miss Bailey); Zoological Park, July, 1921. SOUTH CAROLINA: Clemson, Oconee Co., Sept. 14, 1913. GEORGIA: 1939 (H. C. Essick). FLORIDA: Tallahassee, Leon Co., April 9, 1936 (F. C. Bishopp). MISSISSIPPI: State College, Aug. 26, 1946 (Clay Lyle). INDIANA: Rushville, Rush Co., July 20, 1959 (R. Suttle).

Genus *Synxenoderus* List

Synxenoderus List, 1925, Proc. Biol. Soc. Wash. 38: 108.
Synxenoderus, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Synxenoderus, Usinger, 1947, Pan-Pacific Entomol. 23: 140.
Synxenoderus, Lee, 1954c, J. Econ. Entomol. 47: 1144.

Size 3 (dried) to 4.8 mm (slide-mounted). Body elongate-oval, superficially punctate. Bristles longest at sides of pronotum, hemelytral pads and tip of abdomen, with several very long bristles on sides of pronotum, as long as humeral bristles; also with 1 or 2 very long bristles at sides of hemelytral pads.

Clypeus strongly widened anteriorly, nearly twice as wide beyond middle as at base and ½ as wide as interocular space. Antennae with second segment a little shorter than interocular space. Rostrum reaching to apices of front coxae; second segment attaining base of head. Under surface of head inflated, especially at hind margin just in front of prosternum, where it is bulbous.

Pronotum more than twice as broad as long; less than ½ again as wide as head; sides and hind margin depressed; anterior angles rather strongly anteriorly produced and rounded behind eyes; hind margin very feebly concave at middle.

Hemelytral pads less than twice as wide as long, contiguous for about ½ the exposed length of mesonotum; sides and posterior margin rounded about as in related genera.

Legs moderately stout; front and middle tibiae in males with prominent tufts, reduced in females.

Male genital segment short and broad, sloping a little to the left, the paramere not quite reaching its lateral margin.

Third to seventh male abdominal segments strongly asymmetrically bent forward on the right side, the sixth segment very large with an abrupt deep trough leading to right margin.

Female spermalege at the extreme right between sixth and seventh segments, the seventh segment produced far forward almost to level of front margin of sixth segment at right margin. The actual organ, however, appears in cleared specimens to be not very different from that of *Cimexopsis* and others, being merely a thickening of the anterior margin of the seventh segment with a small pigmented area.

Type-species: *Synxenoderus comosus* List.

Synxenoderus is closely allied to other Haematosiphoninae but differs strikingly in its long bristles at the sides of the pronotum, swollen under surface of the head, and asymmetry of the abdomen in both sexes. It is apparently confined to the nearly inaccessible nests of white-throated swifts, *Aeronautes melanoleucus* Baird, on steep cliffs. The known distribution is Nebraska and California.

71. *Synxenoderus comosus* List

(Fig. 12–71)

Synxenoderus comosus List, 1925, Proc. Biol. Soc. Wash. 38: 108.

Synxenoderus comosus, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 319.
Synxenoderus comosus, Usinger, *in* Herms, 1939, Med. Entomol., p. 92.
Haematosiphon comosa, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Synxenoderus comosus, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 7.,
Synxenoderus comosus, Hicks, 1959, Check-List and Bibliogr., p. 249; 1962, Suppl. 1, p. 261.

Male.—Head 0.77 mm wide; almost as long as wide, 25:27; interocular space about 6 times as wide as an eye, 20:3.5. Antennae 1.23 mm long, first segment stout and short, second shorter than interocular space, 13:15; proportion of segments 4:13:11:9. Rostrum 0.83 mm long; proportion of segments 9:8:12.

Pronotum 1.1 mm wide; ratio of length to width 16:38.5; bristles of sides numerous and erect, the short ones 0.03 mm to 0.086 mm, the 2 or 3 very long ones as long as humeral bristles, 0.3 mm.

Hemelytra with marginal bristles not so long as those of pronotum. Hemelytral pads not pale, concolorous with rest of body.

Mesonotum with a few scattered bristles like those of the rest of tergum.

Abdomen with rows of distinct, backwardly-directed bristles except around and in right dorsal trough, which is nude.

Male genital segment wide, the paramere more than ½ as wide as segment at base, 17:29.

Legs with hind femora nearly 4 times as long as wide, 35:9.5; tibiae ¼ longer than femora; stout tibial spines a little shorter than thickness of tibia.

Size.—Male, length 4.3 mm, width (pronotum) 1.08 mm, (abdomen) 2.0 mm; female, length 4.8 mm, width (pronotum) 1.2 mm, (abdomen) 2.1 mm.

Redescribed from a slide-mounted male paratype, Warbonnet Canyon, Sioux County, Nebr., June 2, 1901 (M. A. Carriker, Jr.), in white-throated swift nest, and a slide-mounted female, determined by G. M. List, from Pine Canyon, Mt. Diablo, Contra Costa County, Calif., July 5, 1919. Also at hand are 2 pinned male paratypes from Warbonnet Canyon, Nebr., same data as above, a pinned male and slide-mounted male, Colton, Calif., May 22, 1918 (W. C. Hanna); and a series of specimens collected at Pine Canyon, June 17, 1963 (P. D. Ashlock, N. Ueshima, and R. L. Usinger). The types are in the U. S. National Museum, and paratypes bearing the manuscript name *"Cimex micropodidorum"* of Wehr and Worley are in the University of Nebraska collection. At each known locality the host is recorded as the white-throated swift. At Pine Canyon the swifts were greatly outnumbered by cliff swallows, and specimens of *Oeciacus vicarius* (Horvath) were mixed with *Synxenoderus* in the 1 nest of white-throated swifts that we were able to reach.

Genus ***Hesperocimex*** List

Hesperocimex List, 1925, Proc. Biol. Soc. Wash. 38: 104.
Hesperocimex, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Hesperocimex, Usinger, 1947, Pan-Pacific Entomol. 23: 140.

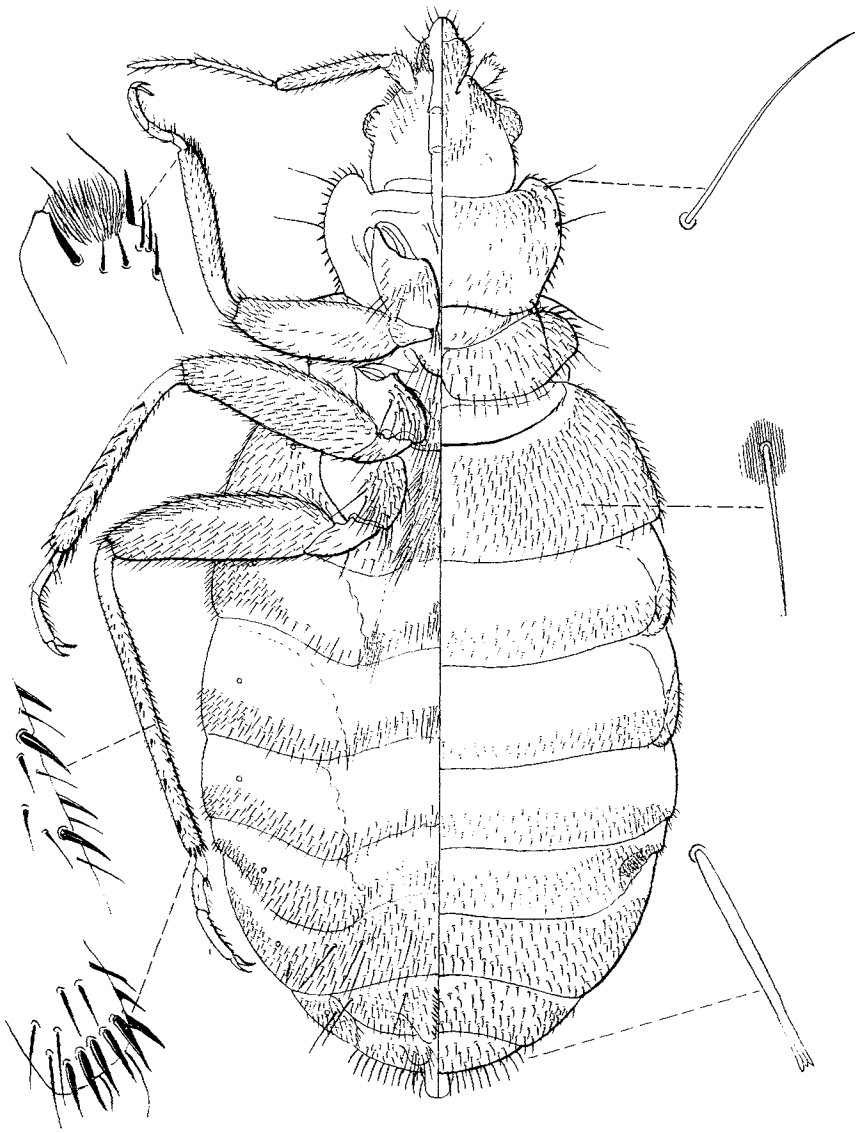

FIG. 12–71.—*Synxenoderus comosus* List. Female. Pine Canyon, Mt. Diablo, California (Ferris, original).

Hesperocimex, Lee, 1954c, J. Econ. Entomol. 47: 1144.
Hesperocimex, Ryckman and Ueshima, 1963, Proc. Entomol. Soc. Wash. 65: 247.
Hesperocimex, Ryckman and Ueshima, 1964, Ann. Entomol. Soc. Amer. 57: 624–38.

Size 4.2–5.6 mm. Bristles long over most of body. Head naked behind level of eyes, with 3 long setae along inner margin of each eye. Clypeus strongly widened anteriorly, nearly twice as wide beyond middle as at base, with several very long setae on either side. Antennae slightly to distinctly shorter than width of pronotum; first segment short and stout, second longest or subequal to third, stout, third and fourth slender, fourth a little shorter than third. Rostrum (slide-mounted specimens) reaching almost to or slightly beyond apex of prosternum, the 3 segments subequal.

Pronotum 2½ times as wide as long; more than ½ again as wide as head; sides broadly rounded and anterior angles scarcely produced; bristles dense and long at sides. Mesonotum broadly rounded and a little raised behind and at middle, with 1 or 2 rows of bristles.

Hemelytral pads ⅗ as long as wide, with long, dense bristles.

Legs short and stout; front and middle tibiae in the males with very prominent apical tufts occupying about ¼ the length of tibiae. Females without tibial tufts.

Male genital segment more strongly rounded at the right, sloping to the left, the paramere about ⅔ as long as width of segment.

Female ectospermalege small, round, with an internal projection in the form of a hat, located between the sixth and seventh abdominal segments right ventrally just mesad of the row of abdominal spiracles.

Type-species: *Hesperocimex coloradensis* List.

Hesperocimex has sclerotized areas and infuscated areas that give it a color pattern unique among the Cimicidae. The entire center of the abdominal venter is clear and presumably membranous. Laterally the segments are infuscated. On the dorsal surface the edges of the pronotum and first 4 abdominal segments are pale. In general the abdomen appears infuscated laterally or sublaterally and along the middle.

Hesperocimex is clearly a member of the Haematosiphoninae but is the most distinct genus of that subfamily. The dense long bristles, unique spermalege, high chromosome numbers, and internal characters set it apart.

The hosts are the purple martin, *Progne subis subis* L., woodpeckers of several species in the United States, and *Progne subis hesperia* in Sonora, Mexico. The habitat, according to Ryckman (1958), is abandoned woodpecker holes in the Saguaro cactus, *Carnegiea gigantea* (Engelm.), and a saguaro-like cactus, *Pachycereus pecten-aboriginum* (Engelm.) in Arizona and Sonora, and tree holes in the western United States and Canada. Specimens are now known from British Columbia, Oregon, Colorado, Nevada, California, Arizona, Sonora, and Baja California. Ryckman and Ueshima (1964) have analyzed the differences between the 3 species and studied the cytology of experimental crosses. Their original illustrations (Fig. 12–73, 12–74) were generously loaned for inclusion in this work. A summary of diagnostic characters is given in Table 12–3.

Table 12–3.—Diagnostic comparison of *Hesperocimex* species (Ryckman and Ueshima 1964).

Species	Head length ♀, mm	Pronotum width ♀, mm	Body color	Wing pads	Male genitalia	Habitats
coloradensis	0.74	1.60	light golden	pale	straight	tree cavities
sonorensis	.65	1.06	dark brown	dark	curved	saguaro cavities
cochimiensis	.66	1.03	yellowish brown	proximal and distal portions dark	straight	cardon cavities

KEY TO THE SPECIES OF *HESPEROCIMEX*

1. Size large; pronotum 3 times as wide as long; hemelytral pads almost entirely pale. Colorado, California, Oregon, B. C. ..... 72. ***coloradensis***
   Size smaller; pronotum 2½ times as wide as long; hemelytral pads partially or entirely dark. Mexico, Arizona. 2
2. Hemelytral pads nearly concolorous; male paramere bent abruptly beyond middle. Arizona; Sonora, Mexico. ..... 73. ***sonorensis***
   Hemelytral pads dark at base and apex, pale at middle; paramere straight. Baja California. ..... 74. ***cochimiensis***

72. *Hesperocimex coloradensis* List

(Fig. 12–72)

Hesperocimex coloradensis List, 1925, Proc. Biol. Soc. Wash. 38: 104.
Hesperocimex coloradensis, Riley and Johannsen, 1932, Med. Entomol., p. 158.
Hesperocimex coloradensis, Kassianoff, 1937, Ann. Parasitol. Hum. Comp. 15: 319.
Hesperocimex coloradensis, Usinger, *in* Herms, 1939, Med. Entomol., 3rd ed., p. 93.
Oeciacus coloradensis, Eichler, 1942, Mitt. Zool. Mus. Berlin 25: 296.
Hesperocimex coloradensis, Goidanich, 1947, Bol. Ist. Entomol. Univ. Stud. Bologna 16: 1–22.
Hesperocimex coloradensis, Ryckman, 1958, Ann. Entomol. Soc. Amer. 51: 33–47.
Hesperocimex coloradensis, Weidner, 1958, Nachr. Naturwiss. Mus. Aschaffenburg 59: 19.
Hesperocimex coloradensis, Lattin and Schuh, 1959, Pan-Pacific Entomol. 35: 175–6.
Hesperocimex coloradensis, Ryckman and Ueshima, 1963, Proc. Entomol. Soc. Wash. 65: 248.
Hesperocimex coloradensis, Ryckman and Ueshima, 1964, Ann. Entomol. Soc. Amer. 57: 624–38.

Female.—Head 1 mm wide; more than ¾ as long as wide, 27:34.5; interocular space 5 times as wide as an eye. Antennae 1.2 mm long; proportion of segments 6:15:11:9. Rostrum 0.86 mm long; proportion of segments 10:10:10. Pronotum broad, 1.6 mm wide, the ratio of length to width 18:54; sides rather evenly rounded, densely beset with long bristles, the longest being about 0.3 mm; hind margin very slightly concave at middle. Hemelytral pads twice as wide as long, contiguous only briefly at middle,

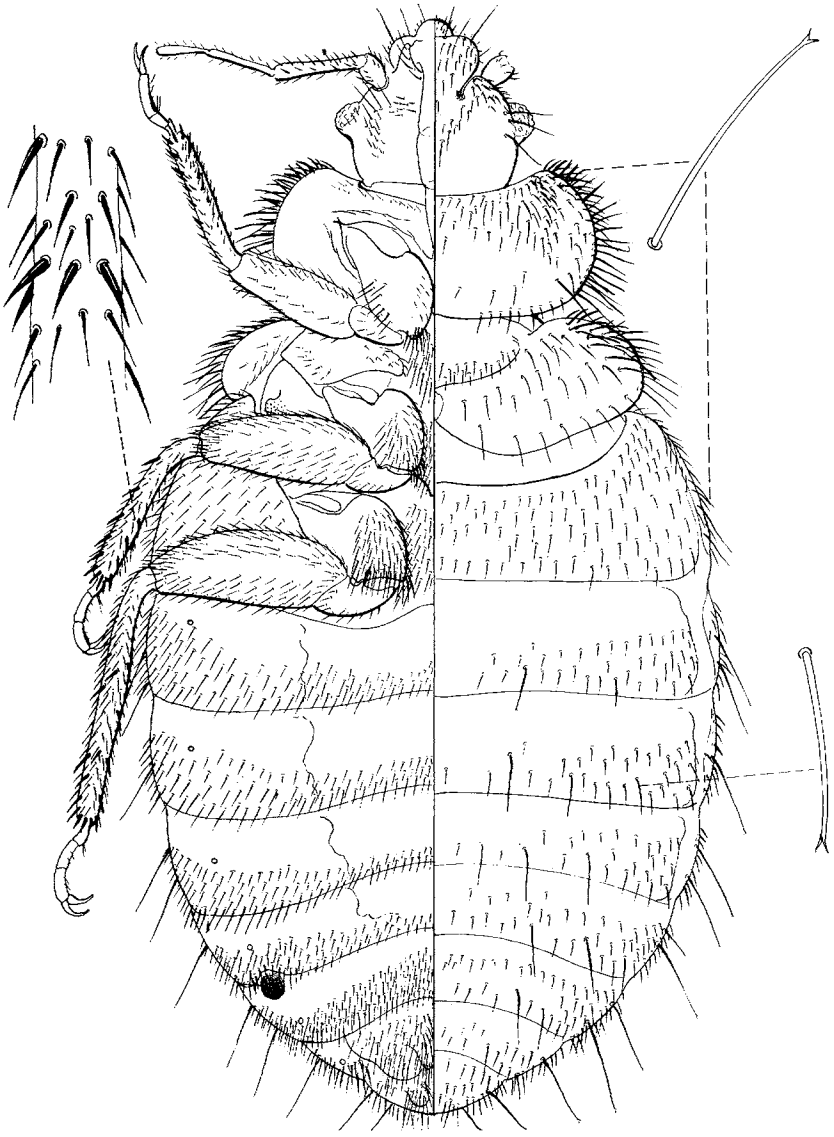

FIG. 12–72.—*Hesperocimex coloradensis* List. Female paratype. Colorado Springs, Colorado (Ferris, original).

broadly rounded behind near middle, nearly straight on outer half of apex, the outer angles abruptly rounded; surface rugose.

Abdomen above with 5–7 rows of bristles on basal segment and about 3 rows on posterior segments, each segment with 1 or more very long bristles on lateral margins. Under surface densely beset with bristles, the basal portions of abdominal ventrites naked.

Legs stout; hind femora about 2½ times as long as broad; coxae densely beset with bristles; trochanters less so; short, stout bristles of tibiae slightly shorter than thickness of a tibia, the finer bristles even shorter; hind tibiae ⅕ longer than femora.

Male.—Front and middle tibiae widened apically at tufts. Paramere tapering and straight at apex.

Size.—Male, length 5 mm, width (pronotum) 1.66 mm; female, length 5.1 mm, width (pronotum) 1.6 mm, (abdomen) 2.4 mm.

Redescribed from a female paratype and male allotype, Colorado Springs, Colo., March 13, 1916 (W. D. Edmonston) USNM. Type no. 52305 (slide-mounted). In addition there is a single pinned female paratype at hand, on loan from the University of Nebraska.

Other records are Cachagua Creek (Hastings Reservation), Monterey County, Calif. Dec. 4, 1955 (J. M. Linsdale and D. D. Linsdale), in an abandoned woodpecker nest cavity occupied the previous summer by purple martins; 13 mi. E. of Durango, Montezuma Co., Colo., Aug. 7, 1958 (R. E. Ryckman, A. E. Ryckman, and J. V. Ryckman) in sawdust-like duff in the bottom of a woodpecker hole, approximately 12 ft from the ground, in a willow tree; Prairie City, Grant Co., Ore., April 25, 1959 (J. Schuh) in a woodpecker's nest in a fallen poplar; Lytle Creek Camp, S. slope of San Gabriel Mts., San Bernardino Co., Calif., June 12, 1960 (R. E. Ryckman and J. V. Ryckman); British Columbia, Canada, (J. G. Spencer) in nest of red-shafted flicker; Sacramento, Calif., Sept. 20, 1932 (H. H. Keifer) from walls in a house; Reno, Nev., Sept. 27, 1962 (P. C. Ting). Purple martins, *Progne subis* (L.), nest commonly in man-made bird houses east of the Rocky Mountains, but careful search of such houses by R. E. Ryckman from Texas and Oklahoma to Minnesota and Wisconsin was negative for *Hesperocimex*.

73. ***Hesperocimex sonorensis*** Ryckman
(Fig. 12–73)

Oeciacus vicarius Horvath, 1912, Ann. Mus. Nat. Hung. 10: 261 (part).
Hesperocimex coloradensis, Lee and Ryckman, 1955, Proc. Entomol. Soc. Wash. 57: 164.
Hesperocimex sonorensis Ryckman, 1958, Ann. Entomol. Soc. Amer. 51: 33–47.
Hesperocimex sonorensis, Ryckman and Ueshima, 1963, Proc. Entomol. Soc. Wash. 65: 248.
Hesperocimex sonorensis, Ryckman and Ueshima, 1964, Ann. Entomol. Soc. Amer. 57: 624–38.

Female.—Head 0.8 mm wide; more than ¾ as long as wide, 24:28; interocular space

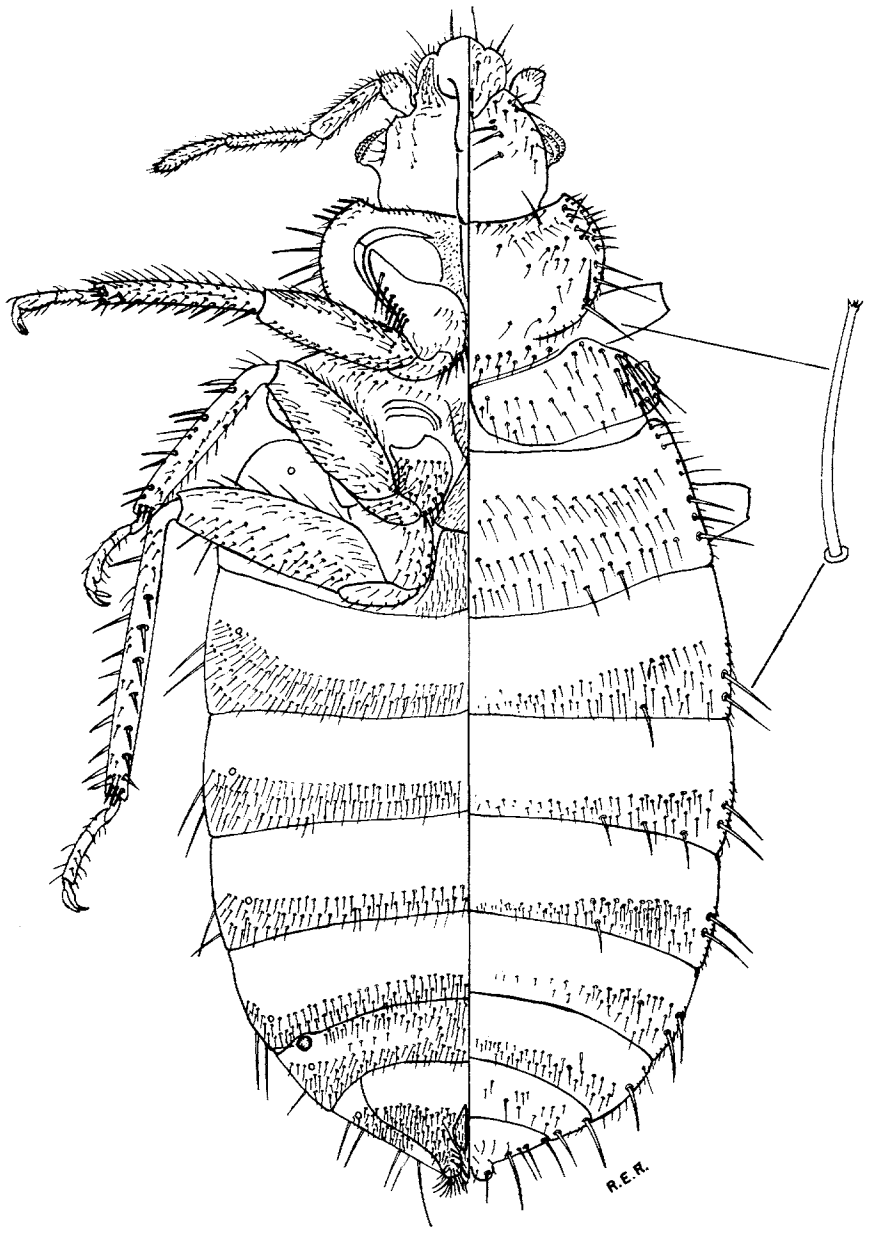

FIG. 12–73.—*Hesperocimex sonorensis* Ryckman. Female holotype. Near Guaymas. Sonora, Mexico (Ryckman 1958).

5 times as wide as an eye. Antennae 0.91 mm long; proportion of segments 4:10:9:7. Rostrum 0.79 mm long; proportion of segments 7:6:9.

Pronotum 1.06 mm wide; ratio of length to width 45:18; sides rounded and depressed, hind margin slightly concave at middle, carinate on either side; sides with fewer bristles than in *coloradensis*, but with the longest bristles about as long.

Hemelytral pads twice as wide as long, briefly contiguous at middle; outer apical margins straight or even a little concave in dried specimens.

Mesonotum with a few bristles at middle as well as behind middle. Metanotum naked. Abdominal tergites with bristles somewhat sparser than in *coloradensis* but arranged in the same pattern. Under surface with bristles essentially as in *coloradensis*.

Hind femora about 3 times as long as broad; hind tibiae 1/3 longer than femora.

Male.—Front and middle tibiae enlarged apically, the apical tufts extending about 1/4 the length of tibia. Paramere bent abruptly before apex.

Size.—Male, length 4.48 mm, width (pronotum) 1.17 mm, (abdomen) 1.8 mm; female, length 4.57 mm, width (pronotum) 1.17 mm, (abdomen) 1.9 mm.

Redescribed from a male and female from the type series, 18 miles SE of Guaymas, Sonora, Mexico, Aug. 24, 1954 (R. E. Ryckman, D. Spencer, and C. P. Christianson), collected in a woodpecker hole occupied by a pair of purple martins (*Progne subis* (L.)). The nest cavity was approximately 15 ft above the ground in a saguaro-like cactus, *Pachycereus pecten-aboriginum*. The type is in the U. S. National Museum.

Additional localities are as follows: 15 mi. NE of Imuris, Sonora, Mexico, July 26, 1957, elev. 3500 ft (R. E. Ryckman, J. V. Ryckman, A. E. Ryckman, and D. Spencer). The hosts, a pair of purple martins (*Progne subis* (L.)), were nesting in the upper portion of a very large saguaro in an unused woodpecker hole; 9 mi. SE of Kelvin, Pinal Co., Ariz., July 29, 1957 (R. E. Ryckman, A. E. Ryckman, and J. V. Ryckman), from woodpecker-nest cavities in 2 branches of a saguaro; 4.7 mi. NE of Morristown, Maricopa Co., Ariz. Feb. 10, 1958 (R. E. Ryckman and E. T. Ryckman), in a fallen saguaro cactus; Cholla Valley, S.W. Tiburon Island, Sonora, Mexico June 20, 1963 (R. E. Ryckman and P. J. Williams), in a woodpecker nest cavity in a large cactus, *Pachycereus pringlei*.

74. ***Hesperocimex cochimiensis*** Ryckman and Ueshima
(Fig. 12–74)

Hesperocimex cochimiensis Ryckman and Ueshima, 1963, Proc. Entomol. Soc. Wash. 65: 247.

Hesperocimex cochimiensis Ryckman and Ueshima, 1964, Ann. Entomol. Soc. Amer. 57: 634.

Female.—Body color light brown (intermediate between golden *H. coloradensis* and dark brown *H. sonorensis*). Head sparsely clothed with setae, width including eyes 0.73 mm; interocular width 0.58 mm; length 0.66 mm. Proportion of antennal segments 10:19:20:16; sparsely clothed with bristles. Tip of rostrum reaching anterior margin of mesosternum; proportion of segments 15:13:15.

Pronotal width 1.03 mm; length 0.42 mm; lateral margins fringed with long bristles.

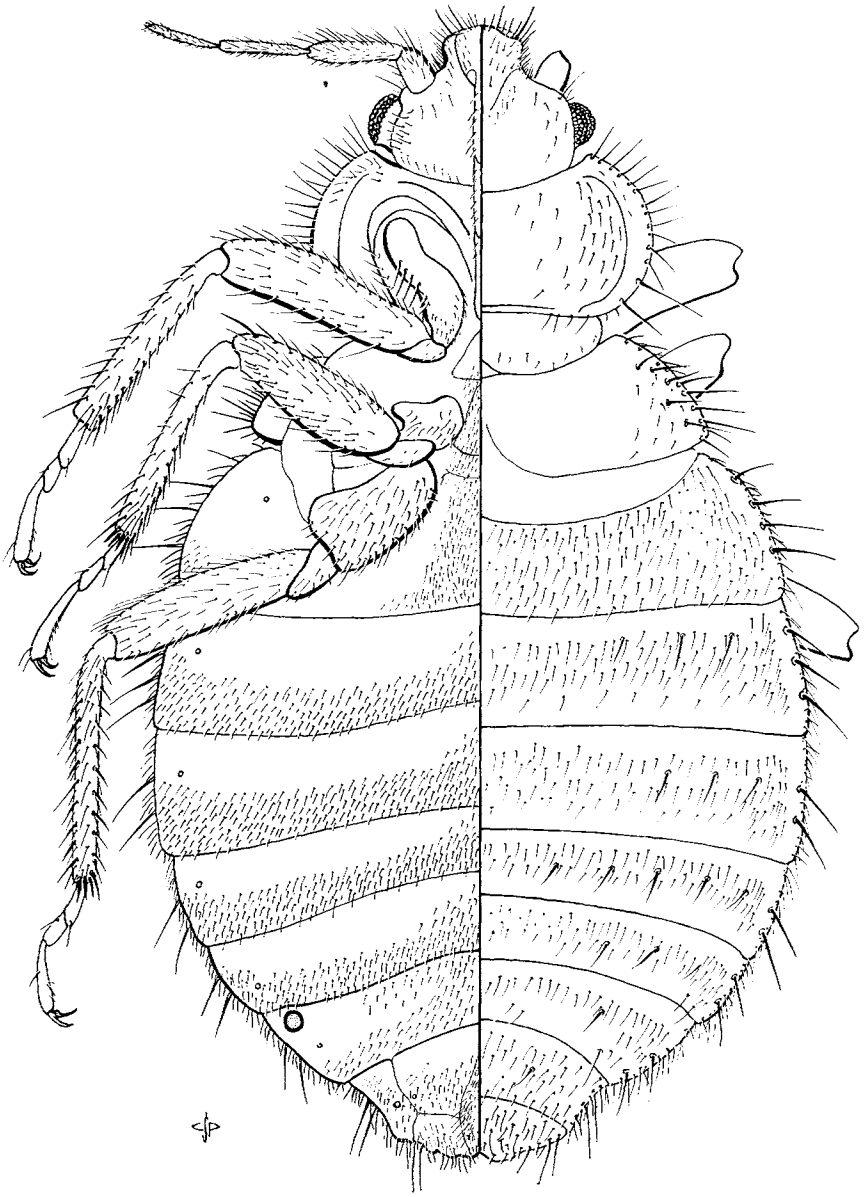

FIG. 12–74.—*Hesperocimex cochimiensis* Ryckman and Ueshima. Female holotype. Near Punta Prieta, Baja California, Mexico (Ryckman and Ueshima 1963).

Hemelytral pads dark on proximal and distal surfaces, central area relatively light. Keel of metasternum triangular, length 0.25 mm, greatest width 0.3 mm.

Legs with coxae progressively more separated (fore to hind) 5:17:22. Length of fore legs: femur 37, tibia 35, tarsus and claws 18; mid legs, femur 40, tibia 44, tarsus and claws 25; hind legs, femur 50, tibia 64, claws and tarsus 26.

Abdomen sparsely clothed with setae; long bristles on margin of abdomen (first apparent segment to last), as follows: 4–3–2–2–2–2–2; number of bristles variable; a few short bristles on dorsal abdominal surface.

Male.—Similar to female but long bristles on margin of abdomen more numerous; i.e. 7–4–3–3–2–3, merging to a brushlike condition on posterior abdomen; well developed tibial tufts present at inner apices of the first and second pairs of legs. Paramere tapering and straight.

Holotype female (USNM no. 65009) and allotype male collected 28 mi. S. of Punta Prieta, Baja California Norte, Mexico, July 2, 1957, elev. 1300 ft (R. E. Ryckman, A. E. Ryckman, and D. Spencer). Two collections were made at this site, one associated with a purple martin nesting in a woodpecker hole in a cardon cactus (a saguarolike cactus), *Pachycereus pringlei.* The other collection was made nearby in a woodpecker hole in a cirio tree, *Idria columnaris;* the host was the violet green swallow, *Tachycineta thalassina.*

Additional records are as follows: 30 mi. S. of El Arco, T. S. (El Tablon Ranch), elev. 800 ft, July 4, 1957 (R. E. Ryckman, A. E. Ryckman, J. V. Ryckman, and D. Spencer), associated with a purple martin (*Progne subis* (L.)) nesting in a woodpecker hole in the branch of a large cardon; 9 and 45 mi. NE of San Ignacio, T. S., July 5, 1957 (R. E. Ryckman, A. E. Ryckman, D. Spencer) under the same conditions as above; 127 mi. NW La Paz, Baja California, T. S., Mexico, July 20, 1964 (R. E. Ryckman and C. P. Christianson); 9 mi. W. and 9 mi. SW La Paz, Baja California, T. S., Mexico, July 22 and 23, 1964 (R. E. Ryckman and C. P. Christianson), all in woodpecker-nest cavities in *Pachycereus pringlei.*

13 | Immature Stages

In many ways, Cimicidae are ideal for life-history studies. Specimens are easy to transport in small boxes or tubes. No moisture is required or desirable, as it may cause mold. In my studies, laboratory cultures were kept in small shell vials (3×9 cm is a convenient size) and confined by a cap of fine netting secured around the vial with masking tape. Two strips of blotting paper slit half way and fitted at right angles, are provided as a substrate for the bugs. These surfaces, and especially the corners, provide an ideal situation for the bugs. The blotting paper should be shorter than the vial to keep the bugs away from the net except when they are feeding, at which time (with the vial inverted) the filter paper slides down on the net cap and the bugs are in position to start feeding at once. None of the species I have reared has failed to feed through the netting. Blotting paper must be changed when it becomes covered with fecal matter, egg shells, and cast skins. Hundreds of colonies of this size will fit in a small incubator. For massive rearings, larger jars may be used, and for individual rearings to obtain precise life history data or virgin females, small tubes 7 mm in diameter are convenient.

Feeding may be accomplished simply by holding the vial against the skin (Fig. 13–1), but much time can be saved by confining the animal (a rabbit or chicken in most of my rearings) and holding the vials against a shaved or bare area of skin with a test tube holder or strap. Ryckman's (1952) technique, devised for mass rearing of Triatominae but applicable to cimicids, confines a rabbit in a wooden frame with a screened top jar inserted against the animal from below (Fig. 13–2c). Small vials containing individual rearings may be bound together with rubber bands so that a group of vials is held against the animal at one time. Davis (1956) (Fig. 13–2) straps the vials to the rabbit. For convenience, many of the leading students of bed bug biology seem to have fed the bugs on themselves. Rearing methods have been reviewed by Adkins and Arant (1959) and Wattal and Kalra (1961).

Studies on life history, developmental rates, etc., have been carried out by many investigators, starting with Southall (1730). The most noteworthy papers for *C. lectularius* are Girault (1905), Hase (1917, 1930),

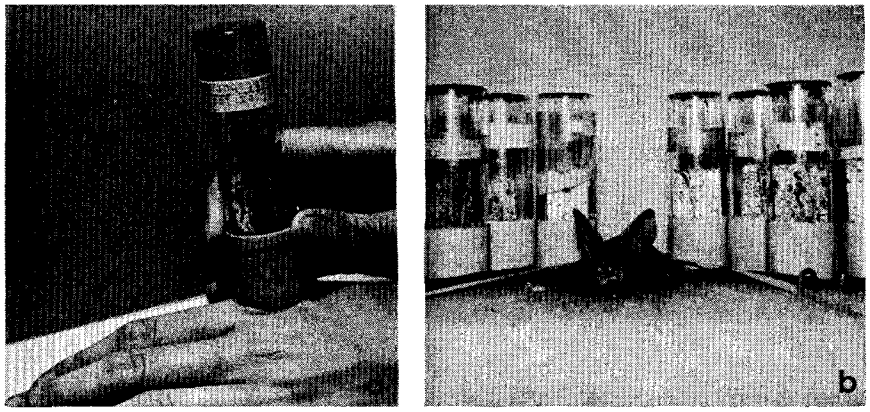

FIG. 13-1.—Feeding methods. a, vial inverted so that blotting paper slides against net permitting bugs to feed. b, *Antrozous pallidus* held with wings spread on Styrofoam block. Bugs feed on wing membrane through net-covered ends of rearing vials.

Titschack (1930), Jones (1930), Janisch (1935), Mellanby (1935, 1939b), Kemper (1936), Geisthardt (1937), Omori (1941), and Johnson (1942); for *C. hemipterus* (=*rotundatus*), Patton and Cragg (1913), Dunn (1924), Hase (1931), Mellanby (1935), Geisthardt (1937), Omori (1941), and Wattal and Kalra (1961); for *Cimex pipistrelli* auct., Wendt (1941b); *Oeciacus vicarius,* Myers (1928); *Oeciacus hirundinis,* Wendt

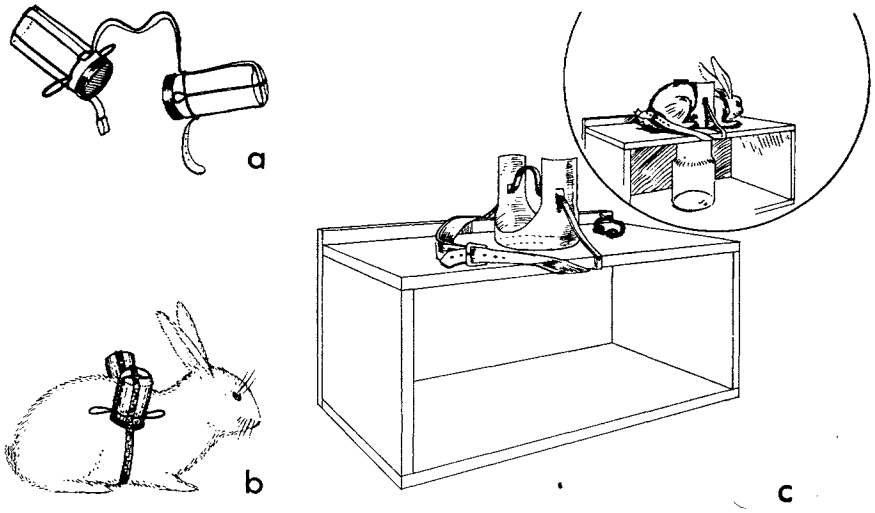

FIG. 13-2.—Feeding methods. a and b, rearing vials strapped to rabbit (Davis 1956); c, apparatus for confining rabbit (inset) and feeding bugs in jar from below (Ryckman 1952).

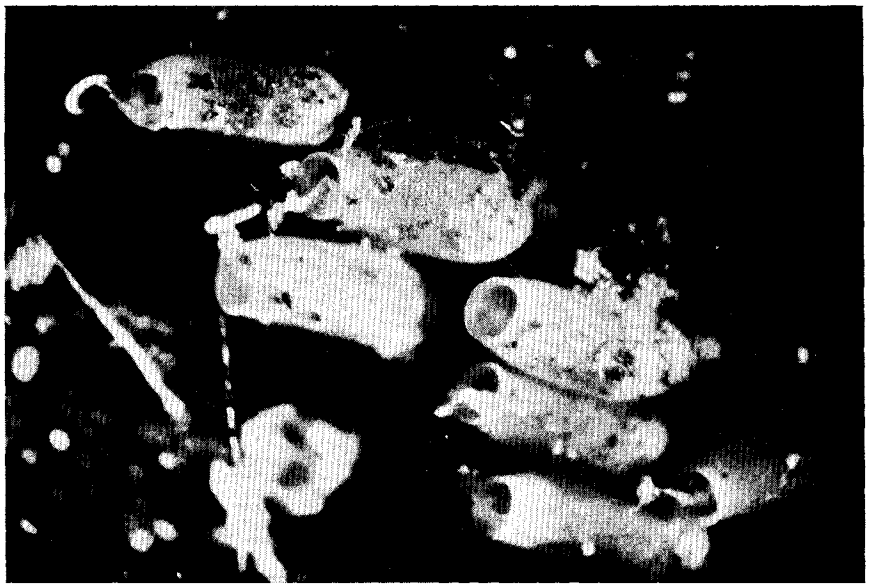

FIG. 13–3.—*Bucimex chilensis*. Hatched eggs showing reticulate surface of chorion, caps, and embryonic membrane.

(1939a); *Ornithocoris toledoi,* Snipes et al. (1940); *Leptocimex boueti,* Joyeux (1913); *Haematosiphon inodorus,* Lee (1955b); and *Hesperocimex sonorensis,* Ryckman (1958). Life history studies here reported for the first time are for *Primicimex cavernis, Paracimex capitata, Leptocimex duplicatus, Bucimex chilensis,* and *Caminicimex furnarii.* Table 2–4 summarizes developmental times from the studies cited above, and new comparative descriptions of life history stages have been prepared for a representative of each genus when available in my cultures.

EGGS

Cimicid eggs are elongate-oval with the anterior (cap) end bent obliquely and with a well-developed, slightly reflexed flange around it. Diagnostic characters are size, shape, and detailed sculpturing of the chorion. Descriptions were prepared mostly from eggs preserved in alcohol. Surface details were often clearer when seen on egg shells after hatching (Fig. 13–3).

KEY TO SOME EGGS OF CIMICIDAE
(Figs. 13–4, 13–5)

1. Length 1.26 mm or more 2
   Length less than 1.1 mm 3

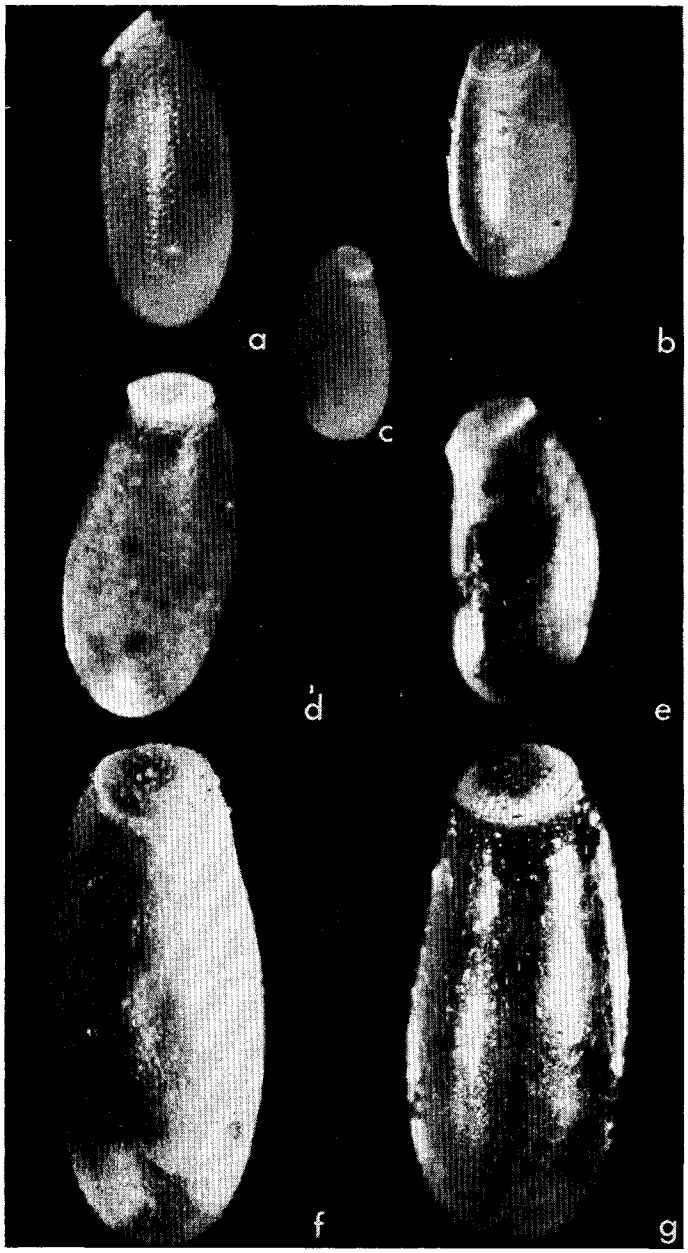

FIG. 13-4.—Eggs of Cimicidae. a, *Cacodmus vicinus;* b, *Haematosiphon inodorus;* c, *Leptocimex duplicatus;* d, *Oeciacus vicarius;* e, *Synxenoderus comosus;* f, *Primicimex cavernis;* g, *Paracimex capitatus.*

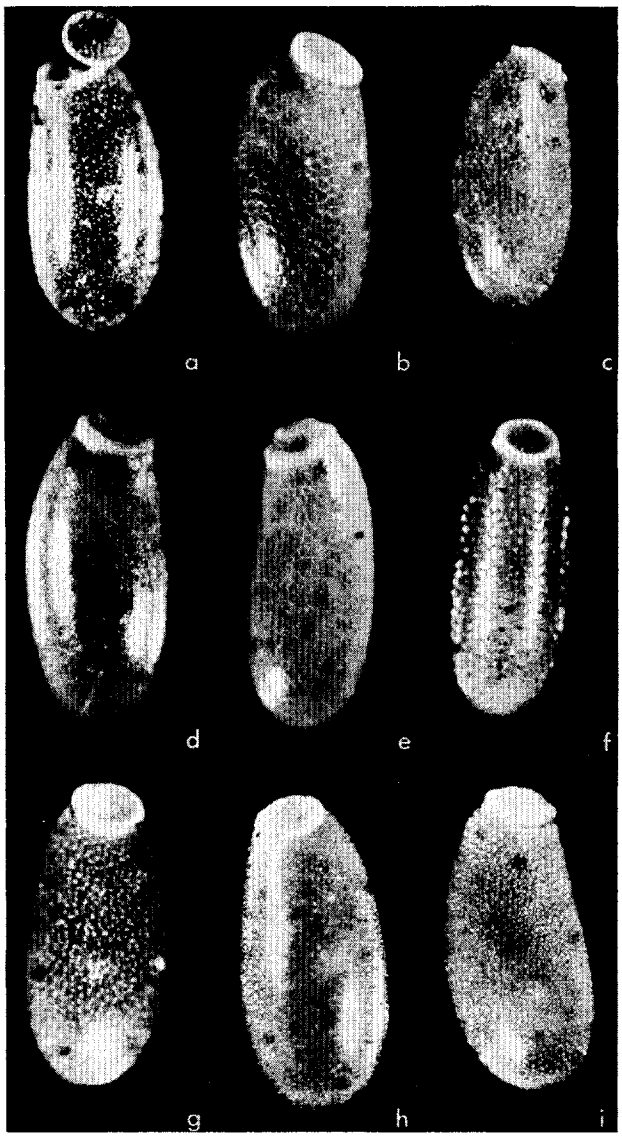

FIG. 13–5.—Eggs of *Cimex* species. a, *Cimex pilosellus;* b, *C. pipistrelli;* c, *C. brevis;* d, *C. lectularius;* e, *C. columbarius;* f, *C. hemipterus;* g, *C. antennatus;* h, *C. latipennis;* i, *C. incrassatus* (Ueshima, original).

2. Surface longitudinally rugose. Length 2 mm or more ..... ***Primicimex***
   Surface reticulate and minutely spined. Length less than 2 mm ..... ***Bucimex***
3. Cap end less than ½ the greatest width of egg ..... ***Leptocimex***
   Cap end more than ½ the greatest width of egg 4
4. Surface smooth or minutely granular, not reticulate. Shape oval, twice (2–2.28×) as long as wide. Length usually distinctly less than 1 mm (0.73–0.97 mm) 5
   Surface more-or-less distinctly reticulate or minutely spined. Shape elongate-oval, 2.32 to 2.6 times as long as wide. Length about 1 mm (0.93–1.08 mm) 8
5. Greatest width of egg about 1.5 times that of cap end. Size small (0.73–0.75 mm) 6
   Greatest width of egg 1.7 or 1.8 times that of cap end. Size 0.88–0.97 mm 7
6. Ratio of length to greatest width 2.28 ..... ***Caminicimex***
   Ratio of length to greatest width 2.25 ..... ***Cimexopsis***
   Ratio of length to greatest width 2.1 ..... ***Synxenoderus***
7. Length 0.88 mm ..... ***Haematosiphon***
   Length 0.74 mm ..... ***Hesperocimex***
8. Shape elongate, 2.6 times as long as wide, greatest width of egg only 1.38 times that across cap end ..... ***Paracimex***
   Shape more elongate-oval, 2.32–2.5 times as long as wide; greatest width of egg 1.5–1.8 times that across cap end 9
9. Cap surface flat ..... ***Cacodmus***
   Cap surface convex 10
10. Surface distinctly reticulate near cap end, minutely spinously granular elsewhere ..... ***Oeciacus***
    Surface not as above ..... ***Cimex*** 11
11. Surface distinctly spinously granular, not reticulate ..... ***Cimex pilosellus*** Complex
    Surface not spined, more or less distinctly reticulate 12
12. Shape suboval, 2.1 times as long as greatest width ..... ***Cimex pipistrelli***
    Shape more elongate, 2.4–2.5 times as long as wide 13
13. Greatest width of egg 1.8 times that of cap end. Surface coarsely reticulate ..... ***Cimex hemipterus***
    Greatest width of egg 1.5–1.6 times that of cap end. Surface finely reticulate 14
14. Surface distinctly reticulate throughout ..... ***Cimex columbarius***
    Surface very faintly reticulate over most of egg, more distinctly so near cap end ..... ***Cimex lectularius***

NYMPHS

In general, nymphs differ from adults in smaller size, undeveloped reproductive organs, absence of wing pads, fewer bristles, 2-segmented tarsi, and in the presence of 3 prominent dorsal abdominal scent glands. Diagnostic characters not seen in the adults are the ecdysial lines, width of scent gland openings, and degree and pattern of sclerotization of basal abdominal tergites. There are 5 nymphal instars in all species that have been reared except *Haematosiphon inodorus* and, probably, *Caminicimex furnarii*. Progression in growth is by a factor of approximately 1.20 (based on head-width measurements).

KEY TO THE GENERA OF CIMICIDAE

(First-instar nymphs)

1. Tarsi with 2 or more stout bristles at inner apices in apposition to claws ..... **Primicimicinae** 2
   Tarsi without a clump of stiff bristles at inner apices 3
2. First 2 antennal segments subequal, each as long as interocular space ... ***Primicimex***
   First antennal segment much shorter than second and shorter than interocular space ..... ***Bucimex***
3. Marginal bristles of pronotum serrate on their tips and usually also on outer edges 4
   Marginal bristles of pronotum not serrate 8
4. Ecdysial lines broadly and deeply U-shaped. Marginal bristles long and tapering, cleft at tip ..... ***Paracimex***
   Ecdysial lines V-shaped, though shallowly so. Marginal bristles blunt at apices 5
5. Second antennal segment nearly as long as third ..... ***Oeciacus***
   Second antennal segment much shorter than third 6
6. Abdominal tergites with long bristles only laterally, the central area with small bristles in various rows ..... ***Propicimex***
   Abdominal tergites with a transverse row of long bristles 7
7. Bristles of dorsal surface of head much shorter than those of thorax and abdomen. Bristles of antennae not longer than diameter of segments .... ***Bertilia***
   Bristles of dorsal surface of head as long as those of thorax and abdomen. Bristles of antennae longer than diameter of respective segments ..... ***Cimex***
8. Margins of pro-, meso-, and metanota and second abdominal segment each with a very long bristle at posterolateral angle in addition to various smaller, often inconspicuous bristles. Third antennal segment distinctly shorter than fourth 9
   Marginal bristles of pro-, meso-, and metanota and second abdominal segment subequal in length. Third antennal segment as long as or longer than fourth 14
9. A long bristle at side of each abdominal segment, like the long ones of pro-, meso-, and metanota. Middle and hind tibiae with bristles much longer than thickness of tibiae 10
   Bristles at sides of third to seventh abdominal segments short. Middle and hind tibiae with bristles shorter than thickness of tibiae 11
10. Dorsal abdominal scent gland openings nearly as wide as head. Head without bristles near and behind bend of eyes ..... ***Latrocimex***
    Dorsal abdominal scent gland openings less than ½ as wide as head. Head with several bristles near inner margins of eyes and behind ecdysial lines ..... ***Hesperocimex***
11. Rostrum long, reaching to middle coxae, the overall length 0.6 mm, first segment reaching base of head ..... ***Haematosiphon***
    Rostrum shorter, reaching about to front coxae, the first segment not reaching base of head 12
12. Long bristles of posterolateral angles of pronotum shorter than length of pronotum ..... ***Ornithocoris***
    Long bristles of posterolateral angles of pronotum as long or longer than length of pronotum 13
13. Second tarsal segment dorsally and subapically with 2 long bristles ... ***Caminicimex***
    Second tarsal segment without 2 long bristles subapically ..... ***Psitticimex***
14. Scent gland orifices wider than clypeus 15
    Scent gland orifices narrower than clypeus 16
15. Ecdysial lines U-shaped, not sinuate. Long bristles at sides of body almost

as long as width of head. Fore femora with a row of small, stout bristles forming an incipient comb ..... *Afrocimex*
Ecdysial lines sinuate. Long bristles at sides of body only ¼ as long as width of head. Fore femora with several rows of bristles but not in the form of a fine comb ..... *Loxaspis*
16. Rostrum shorter than head, stout ..... *Crassicimex*
Rostrum exceeding base of head, slender 17
17. Third antennal segment longer than the others combined. Third rostral segment much longer than second ..... *Leptocimex*
Third antennal segment shorter than the others combined. Second and third rostral segments subequal ..... *Stricticimex*

KEY TO THE GENERA OF CIMICIDAE
(Last-instar nymphs)

1. Clypeus narrowed anteriorly or the sides subparallel. Tarsi with several short, stout bristles at inner apex in apposition to claws. Second abdominal tergite broadly and evenly sclerotized like posterior segments. ..... **Primicimicinae** 2
Clypeus usually widened anteriorly. Tarsi without a clump of short, stout bristles at inner apex. Second abdominal tergite with sclerotized area reduced and variously broken up or absent 3
2. First and second antennal segments subequal ..... *Primicimex*
First antennal segment much shorter than second ..... *Bucimex*
3. Bristles usually minutely serrate at sides and tips ..... **Cimicinae** 4
Bristles not minutely serrate at sides 8
4. Second abdominal tergite broken up into a median transverse sclerotized area and a small area on each side 5
Second abdominal tergite with only a single transverse sclerotized area 6
5. Second antennal segment ¾ or more as long as interocular space ..... *Cimex*
Second antennal segment ⅔ or less the width of interocular space ..... *Oeciacus*
6. Front and middle femora each with a row of stout spines on inner apical third (ctenidium) ..... *Paracimex*
Front and middle femora lacking a row of stout spines on inner apical third 7
7. Sides of pronotum broadly lamellate. Bristles set in conspicuous round pits ..... *Bertilia*
Sides of pronotum narrowly depressed. Bristles set in simple depressions .... *Propicimex*
8. Scent gland openings on abdominal tergites as wide as head ..... **Latrocimicinae** .... *Latrocimex*
Scent gland openings on abdominal tergites much narrower than width of head 9
9. Front femora with a row of short, stiff, comblike bristles on inner anterior face in addition to the longer bristles. Ecdysial lines evenly rounded, U-shaped ..... **Afrocimicinae** .... *Afrocimex*
Front femora without a row of short, stiff bristles. Ecdysial lines more-or-less sinuate 10
10. Tibiae straight, with small stiff spines as well as longer hairs ..... **Haematosiphoninae** 11
Tibiae bent inward, without small stiff spines between the longer hairs ..... **Cacodminae** 17
11. Sides of thorax with numerous bristles more-or-less equal in length. First and second abdominal tergites with transverse sclerotized areas .... *Hesperocimex*
Pronotum with 1 or 2 and mesonotum and metanotum each with 1 long bristle at posterolateral angles in addition to other shorter bristles. First

and second abdominal tergites completely membranous or with a single small sclerotized area at middle 12

12. Rostrum long, the first segment reaching base of head ..... ***Haematosiphon***
Rostrum shorter, the first segment not reaching base of head 13

13. Long bristles of posterolateral angles of pronotum short, less than ¼ length of pronotum 14
Long bristles of posterolateral angles of pronotum nearly ½ as long as pronotum 15

14. Pronotum ½ again as wide as head ..... ***Cimexopsis***
Pronotum more than ½ again as wide as head ..... ***Ornithocoris***

15. Sides of pronotum anteriorly with 1 or 2 bristles as long as humeral bristles. Pronotum widest in front of middle ..... ***Synxenoderus***
Sides of pronotum anteriorly with only shorter bristles. Pronotum widest at or behind middle 16

16. Second antennal segment as long as, or longer than, interocular space. Second tarsal segment without a pair of long, subapical bristles ..... ***Psitticimex***
Second antennal segment much shorter than interocular space. Second tarsal segment dorsally and subapically with a pair of long bristles ..... ***Caminicimex***

17. Dorsal abdominal scent gland openings wider than clypeus 18
Dorsal abdominal scent gland openings much narrower than clypeus 20

18. One or 2 long bristles at sides of each abdominal segment. Ecdysial lines abruptly angulately bent mesad of eyes in addition to bend at eyes ..... ***Loxaspis***
Three or more long bristles at sides of each abdominal segment. Ecdysial lines not abruptly bent as above 19

19. Eyes large, ¼ as wide as interocular space. Tibiae enlarged apically and with the suggestion of a pseudojoint (pale area) subapically on hind tibiae. Margins of abdominal segments each with 3 or 4 long bristles. Basal rostral segment with 2 pairs of long bristles ..... ***Aphrania***
Eyes smaller, ⅙ as wide as interocular space. Tibiae scarcely enlarged apically, the hind tibiae without a pale area subapically. Abdominal margins with many long bristles. Basal rostral segment with 1 pair of long bristles ..... ***Cacodmus***

20. Rostrum shorter than head, very wide, second segment wider than long ..... ***Crassicimex***
Rostrum reaching beyond base of head, more slender, second segment narrower than long 21

21. Third antennal segment as long as the other segments combined. Third segment of rostrum twice as long as second ..... ***Leptocimex***
Third antennal segment shorter than the other segments combined. Third segment of rostrum subequal to second ..... ***Stricticimex***

Primicimex cavernis Barber
(Fig. 13–6)

Egg.—Length 2.2 mm, width at middle 0.86 mm, across cap end, 0.53 mm. Shape elongate and bent at round cap end with flange briefly dilated. Surface finely longitudinally rugose, without hexagonal reticulations. Cap rather evenly convex (Fig. 13–4f).

Nymphs.—*First Instar.*—Elongate-oval, attenuated anteriorly, with a pattern of long bristles over entire body. Length (somewhat shriveled, slide-mounted) 2.48 mm. Head 0.5 mm wide, longer than wide, 22:18; eyes about ⅕ as wide as interocular space; clypeus with 4 long, erect bristles anteriorly; head also with a very long bristle on each jugum and slightly shorter ones behind each antennal insertion and at inner posterior corner of each eye. Ecdysial lines not sinuate except slightly at thickened area near

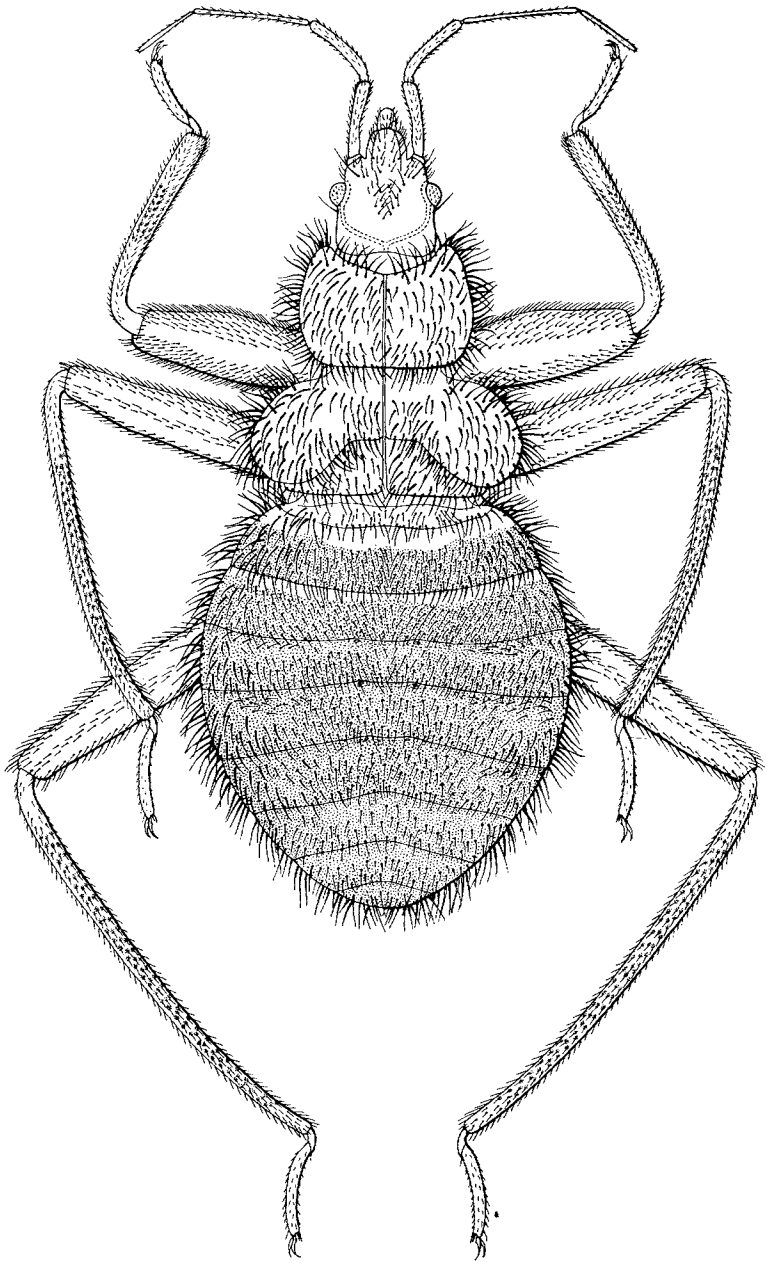

FIG. 13–6.—*Primicimex cavernis*. Last-instar nymph.

inner margins of eyes, U-shaped. Antennae 2 mm long; proportion of segments 13:16: 24:16. Rostrum reaching about to middle of front coxae; 0.77 mm long; proportion of segments 5:15:7.

Pronotum 0.71 mm wide; 3/5 as long as wide; long bristles at sides of pronotum about 0.3 mm; like those of sides of other segments; sides of pronotum with 4 long bristles; front and hind margins each with 8; center of disk naked. Mesonotum 0.8 mm wide, likewise with 4 long bristles on each side and 8 or 10 bristles of various lengths in front of posterior margin. Metanotum 0.9 mm wide, with 3 long bristles on each side and about 8 on posterior half.

Abdominal segments each with a very long lateral bristle posteriorly and each with a row of shorter but erect bristles across disk.

Legs very long; hind femora 1.66 mm long, 1/6 as wide as long; tibia 1/5 longer than femur; tarsi long and slender, with 2 stout spines at inner apex in apposition to claws.

Second Instar.—Generally larger and with more bristles, including several at side of each abdominal segment. Head width 0.66 mm, pronotum, 0.86 mm, mesonotum 1.0 mm, metanotum 1.06 mm. Antennae 2.6 mm long, proportion of segments 8:8:13:10.

Third Instar.—Head width 0.86 mm, pronotum 1.23 mm, mesonotum 1.6 mm, metanotum 1.66 mm. Antennae 2.93 mm long, proportion of segments 10:10:15:10.

Fourth Instar.—Head width 1.0 mm, pronotum 1.53 mm, mesonotum 2.13 mm, metanotum 2.06 mm. Antennae 3.2 mm long, proportion of segments 11:11:15:11.

Last Instar.—Differing from first instar by its much larger size, more bristles, and development of mesonotal pads. Sides and terga of thorax and abdomen densely beset with long bristles like those of adult, thus obscuring pattern of few long bristles seen in first instar.

Head 1.2 mm wide, longer than wide, 50:41. First antennal segment about as long as interocular space. Rostrum reaching about to base of head. Pronotum 1.8 mm wide, 2/3 as long as wide. Mesonotum 2.9 mm wide; very short at middle; 1/4 as long as wide, but nearly twice as long laterally at the full length of subrounded mesonotal lobes. Exposed part of metanotum densely covered with bristles. Width of metanotum 2.34 mm.

Abdomen with first tergite distinct at base but scarcely reaching sides. Second tergite about the same size as other tergites, sclerotized over its entire surface except narrowly along anterior margin, much like third segment.

Legs with tarsi bearing 3 stout spines at inner apex in apposition to claws.

Bucimex chilensis Usinger

(Fig. 13–3, 13–7)

EGG.—Length 1.26 mm, width at middle 0.53 mm, width at cap end 0.33 mm. Surface with minute spines arranged in a vaguely reticulate pattern. Cap cylindrical with a thickened areolate rim and feebly convex disk.

NYMPHS.—*First Instar.*—Body oval, dorsoventrally compressed, setose, amber in color except for brown head and thoracic nota; body length 2.3 mm.

Head subrectangular, length 0.4 mm, width 0.5 mm, ratio of length to width 4:5; eyes black, 0.07 mm wide. Clypeus not widened apically; short, fine setae on clypeus and dorsolateral angles of head, continuing dorsad with curved seta inserted above eye (longest on head), 1 stout seta arising on dorsolateral angle of head between eye and antennal insertion, 2 short setae on dorsolateral angle of head between antennal insertion and base of clypeus. Antennae 1.33 mm long, proportion of segments 7:23:28:22. Rostrum reaching to trochanters of first pair of legs, length 0.7 mm, proportion of segments 16:15:9.

Pronotum subrectangular, humeral angles rounded, disk bearing scattered short setae, lateral and anterolateral margins with single row of long, curved bristles, pronotal length at midline 0.4 mm, width 0.7 mm, ratio of length to width 4:7. Mesono-

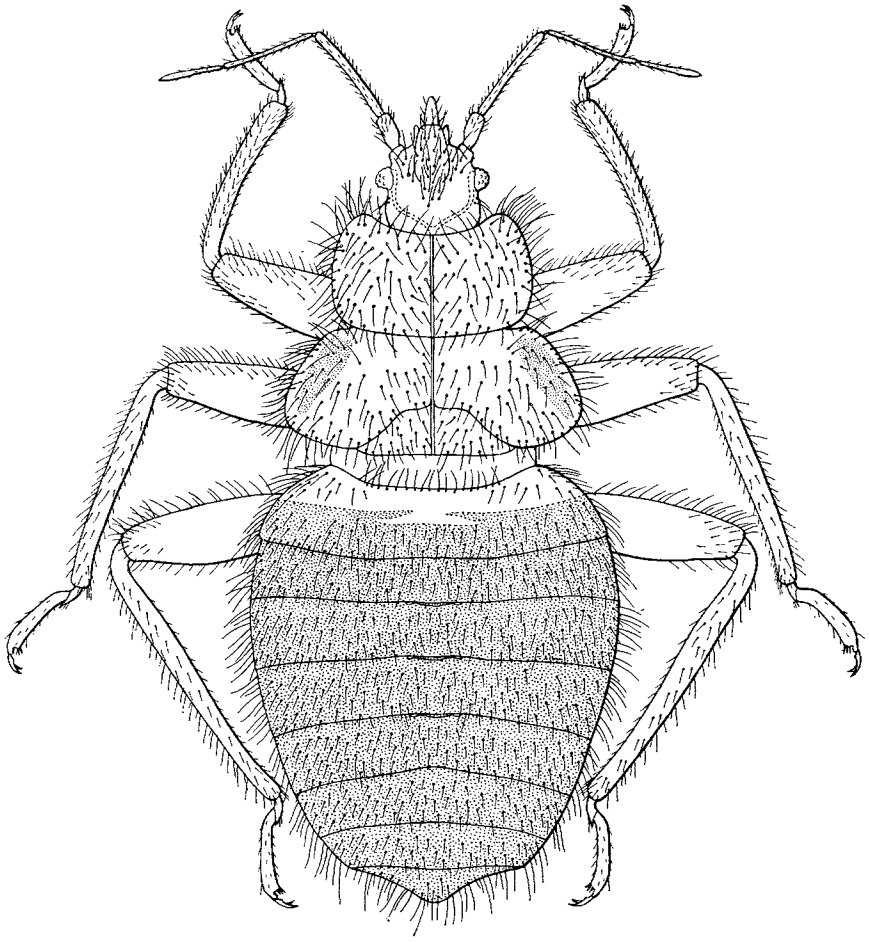

FIG. 13–7.—*Bucimex chilensis*. Last-instar nymph.

tum subrectangular, 0.55 mm. Metanotum also subrectangular but with posterior margin convex, 0.60 mm.

All legs setose, femora stout, flattened, tibiae with distal ventral "comb" consisting of 3 short spines; tarsi 2-segmented, second segment with bristles in apposition to simple claws. Abdomen at widest point 1.3 mm, a long seta at side of each segment.

Second Instar.—Differing from previous instar in the following respects: Body length 3.1 mm. Head length 0.5 mm, head width 0.6 mm, ratio of length to width approximately 1:1; eye width 0.08 mm; proportion of first and second antennal segments 13:30; length of rostrum 0.7 mm, proportion of segments 14:19:10; basal segment with fine setae. Pronotum length 0.5 mm, width 1.0 mm, ratio of length to width approximately 1:2. Tibial combs usually with 10 spines, fine setae on tarsi, apex with approximately 7 bristles. Abdomen at widest point 1.8 mm.

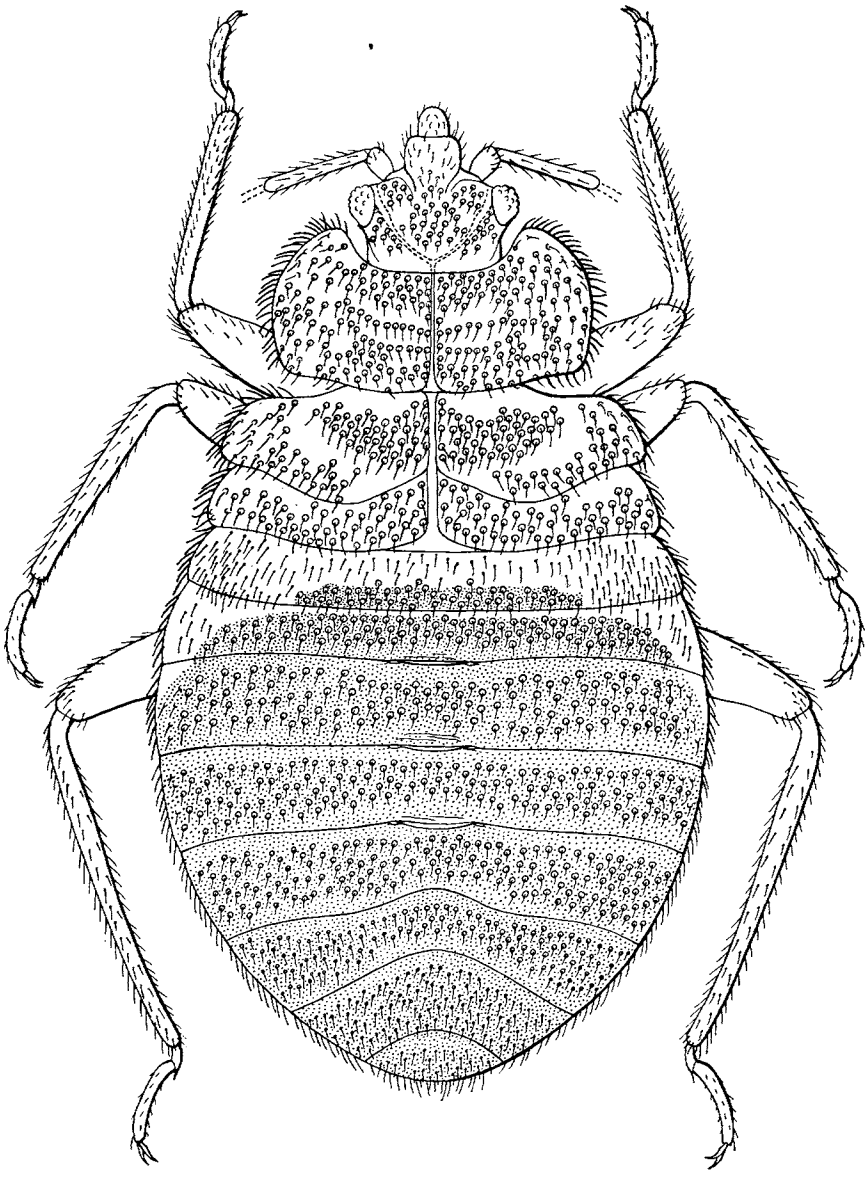

FIG. 13–8.—*Bertilia valdiviana*. Last-instar nymph.

Third Instar.—Differing from previous instar as follows: Body dark brown, except for amber membranous areas, setose, length 3.5 mm. Head length 0.6 mm, width 0.7 mm, ratio of length to width 5:7; eye width 0.08 mm; antennae 1.8 mm long, proportion of segments 12:30:35:31; rostrum length 0.8 mm, proportion of segments 12:7:6. Pronotum length 0.6 mm, width 1.0 mm, ratio of length to width 3:5. Mesonotum with no wing pads, lateral margin with single row of spines; mesonotum with similar row of less conspicuous setae. Tibial comb of about 10 spines, marginal spines longer than medial ones; tarsi with conspicuous setae. Abdomen at widest point 1.9 mm.

Fourth Instar.—Differing from previous instar as follows: Body length 4.7 mm. Head length 0.6 mm, width 0.9 mm, ratio of length to width 2:3; eye width 0.1 mm; proportion of first and second antennal segments 10:21, rostrum length 1.0 mm, proportion of segments 11:11:7. Pronotum length 0.7 mm, width 1.3 mm, ratio of length to width 1:2, pronotum with second row of spines on anterolateral margin. Wing pads at margins of mesonotum. Tibial combs with approximately 15 spines. Abdomen at widest point 2.8 mm.

Last Instar.—Differs from previous instar as follows: Body length 6.3 mm, sclerites dark, membranous areas brown. Head length 0.7 mm, width 1.0 mm, ratio of length to width 7:10; eye width 0.9 mm; antennae with stout bristles, proportion of first and second segments 20:43, rostrum length 1.1 mm, setose, long setae on basal segment, proportion of segments 24:31:15. Pronotum length 0.9 mm, width 1.8 mm, ratio of length to width 1:2, median line and integumental folds light brown. Wing pads relatively larger, extending to posterior edge of metanotum but their medial edges not meeting as in adult. Tibiae with short bristles. Abdomen at widest point 3.9 mm, dorsum of first segment covered with bristles.

Bertilia valdiviana (Philippi)

(Fig. 13–8)

NYMPH.—*Last Instar.*—Body suboval and flattened, with rather stiff serrate bristles set in conspicuous pits, the bristles often widened and truncate at tips, approximately 0.83 mm long.

Head 0.86 mm wide, about ⅓ wider than long, 13:10; eyes about ¼ as wide as interocular space. Setae numerous on vertex, juga, clypeus, and laterad of prominent ecdysial lines behind eyes. Ratio of first and second antennal segments 8:30, last 2 segments broken. Rostrum lacking.

Pronotum 1.6 mm wide, 2½ times as wide as long and nearly twice as wide as head, 24:13; sides broadly dilated, with about 40 bristles on each side. Mesonotum 2.1 mm wide, metanotum 2.2 mm wide, the sides of each lamellately expanded.

Abdomen with first segment completely membranous, second segment with a prominent transverse sclerotized area dorsally at middle, third segment sclerotized except at sides. Scent gland openings about 0.5 mm wide.

Hind femora about 4 times as wide as long. Tibiae straight, without pseudojoints or apical tufts.

Size.—Length 4.66 mm, width (pronotum) 1.6 mm, (abdomen) 2.6 mm.

Propicimex tucmatiani (Wygodzinsky)

(Fig. 13–9)

NYMPH.—*Last Instar.*—Body oval, with short serrate bristles, the longest at sides of body approximately 0.06 mm.

Head 0.8 mm wide, ⅔ as long as wide, eyes prominent, ¼ width of interocular space; clypeus more than ½ as wide as interocular space, 4.5:8; ecdysial lines sinuate laterally, bristles shorter than distance between bristles. Antennae somewhat shriveled but approximately 1.5 mm long, proportion of segments 3:7:7:5. Rostrum broken.

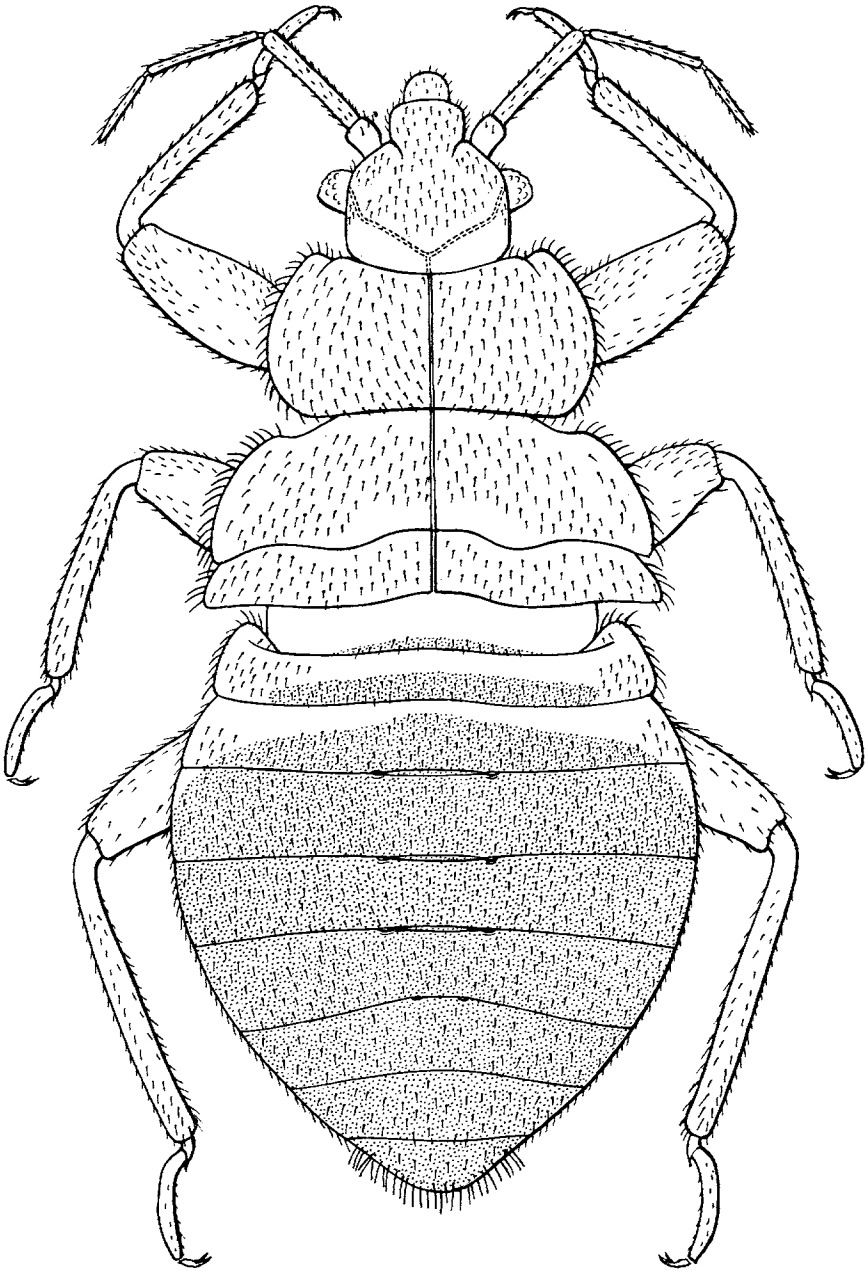

FIG. 13-9.—*Propicimex tucmatiani.* Last-instar nymph.

Pronotum 1.26 mm wide, more than twice as wide as long, 19:8, and ½ again as wide as head; disk convex, sides narrowly depressed and rather evenly arcuate, each with about 30 backwardly bent bristles. Mesonotum 1.7 mm wide, metanotum 1.8 mm wide, the sides lamellately expanded.

Abdomen with first segment membranous except for an ill-defined transverse pigmented area at middle of dorsal surface. Second segment with a distinct broad sclerotized area at middle dorsally. Scent gland openings prominent but less than 0.5 mm wide. Sides of abdominal segments with very short, inconspicuous bristles except for 1 or 2 somewhat longer ones, the last segment with a clump of prominent, erect bristles.

Hind femora more than 3 times as long as wide, 15:4.5; tibiae without pseudojoints.

Size.—Length about 3 mm, width (pronotum) 1.26 mm, (abdomen) 2 mm.

Cimex lectularius Linnaeus

(Fig. 13–5d, Fig. 13–10)

Egg.—With pink eye spots. Length 1.08 mm. Width 0.45 mm. Cap end diameter 0.3 mm. Cap diameter about 0.2 mm. Shape asymmetrical; ventral or short side ⅛ shorter than upper side; head or cap end thus directed obliquely. Posterior end larger and elongate-oval. Ring at cap end distinctly raised and a little reflexed. Cap round, convex, middle raised and coarsely granular. Outer edge of cap depressed a little below edge of ring, white. Surface of chorion shiny, minutely roughened by what appear to be scattered, superficial granules. Empty egg shells depressed on either side of convex middle of ventral (short) side.

For 100 newly laid eggs Jones (1930) found the average length to be 1.0178 mm (range 0.966–1.073 mm), the average width 0.434 mm (range 0.355–0.493 mm), and the weight 0.000158 g.

Nymphs.—*First Instar.*—Body elongate-oval, beset with erect bristles that are subequal in length at sides. Length 1.45 mm, greatest width (abdomen) 0.69 mm. Head subtriangular, slightly wider than long, 12.5:10.5; eyes ⅛ as wide as interocular space.

Head width across eyes 0.35 mm. Head bristles: 3 pairs on labrum, 2 on clypeus, 5 on either side of frons near base of clypeus, 2 on either side near eyes. Vertex behind ecdysial lines with 3 bristles on either side. Eyes each with 2 bristles. Under surface of head with a single bristle on either side near base of antennae. Antennae 0.77 mm long; proportion of segments 3:5:8:11; first segment with a subapical ring of several bristles; second segment with long bristles throughout, arranged in several rows; third and fourth segments with finer bristles, apex of fourth segment without bristles. Rostrum reaching hind margins of front coxae; total length 0.43 mm, proportion of segments 4:5:6.

Pronotum wider than head, 0.44 mm, and about 3 times as wide as long; front margin concave, sides and hind margin convexly rounded; sides with 4 long bristles; disk with a submarginal row of 6 bristles anteriorly and 8 posteriorly. Mesonotum wider than pronotum, 0.46 mm, with 3 lateral bristles on each side and 5 submarginal bristles on either side posteriorly. Metanotum still wider, 0.51 mm, with 3 lateral bristles, 1 posterior and sublateral, and 4 on each side submarginally behind.

Abdomen with first segment small, membranous, distinctly narrower than metanotum, 41:48, with a single long bristle on each side margin and about 6 bristles on either side along hind margin. Second abdominal segment wider and longer, partially membranous, with about 6 bristles on each side margin and 5 on either side along hind margin. Third abdominal segment membranous anteriorly, distinctly sclerotized posteriorly whence the abdominal disk continues backward in suboval form. Hind margins of third, fourth, and fifth segments each with a broad scent gland opening at middle. Lateral margins of all segments with 2 long bristles except seventh segment which has only 1 on each side. Disk of each segment with 3 or 4 bristles on each side.

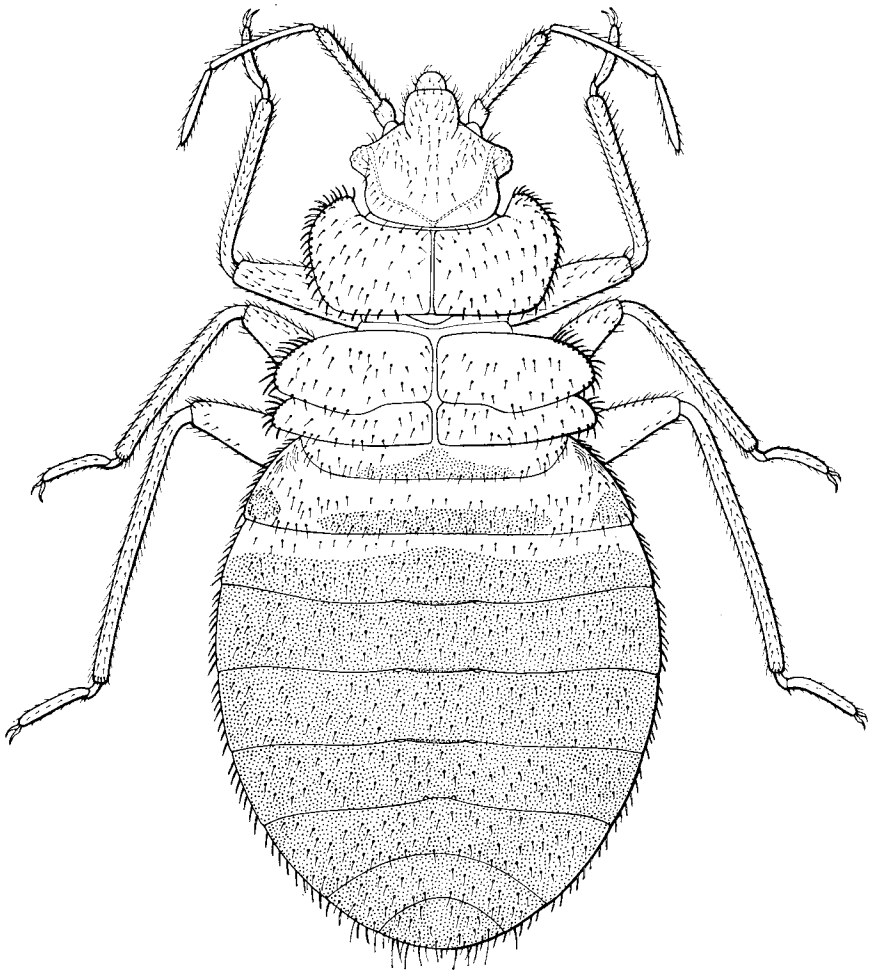

FIG. 13–10.—*Cimex lectularius*. Last-instar nymph.

Abdominal venter with prominent bristles laterally on each segment and a row of finer bristles medially.

Legs stout, with numerous bristles. Tibiae without apical tufts. Tarsi 2-segmented, basal segment short. Claws unequal. Color uniform pale fulvous.

Second Instar.—More robust and generally with an increase in number of bristles including an additional row on each abdominal tergite. Length 2.05 mm. Greatest width (abdomen) 1 mm. Head width 0.47 mm. Antennal length 0.88 mm; proportion of segments 3:7:10:11. Rostral length 0.51 mm; proportion of segments 5:5:8. Pronotal width 0.63 mm, mesonotum 0.67 mm, metanotum 0.77 mm. First abdominal segment nearly as wide as metanotum.

Third Instar.—Larger with more numerous bristles. Length 2.45 mm. Greatest width

(abdomen) 1.31 mm. Head width 0.59 mm. Antennal length 1.1 mm; proportion of segments 3.5:9:13:13. Rostral length 0.57 mm, proportion of segments 6:6:8. Pronotal width 0.74 mm, mesonotum 0.86 mm, metanotum 0.97 mm.

Fourth Instar.—Larger with bristles forming at least 3 rows on abdominal tergites. Length 3.03 mm. Greatest width (abdomen) 1.65 mm. Head width 0.68 mm. Antennal length 1.31 mm, proportion of segments 5:13:15:13. Rostrum reaching only to middle of fore coxae, length 0.65 mm; proportion of segments 7:7:9. Pronotal width 1 mm, mesonotum 1.18 mm, metanotum 1.31 mm.

Last Instar.—Larger, bristles on abdominal tergites forming 4 ill-defined transverse rows. Length 4.45 mm. Greatest width (abdomen) 2.2 mm. Head width 0.83 mm. Antennal length 1.58 mm, proportion of segments 6:17:18:14.5. Rostrum reaching only to anterior third of fore coxae, 0.88 mm long; proportion of segments 12:8:11. Pronotal width 1.27 mm, mesonotum 1.6 mm, metanotum 1.64 mm. Hind margin of mesonotum distinctly, broadly concave. Hind margin of metanotum sinuate sublaterally.

Mean head widths: 0.35 mm (first instar); 0.47 mm (second instar); 0.59 mm (third instar); 0.68 mm (fourth instar); and 0.83 mm (fifth instar). Growth ratios based on head widths: 1.27 from first to second instar, 1.15 from second to third, 1.21 from third to fourth, 1.22 from fourth to fifth, and 1.20 (males) and 1.21 (females) from fifth to adult.

The sexes may be distinguished in the fifth instar by means of a small transverse spot at the sinuate middle of the hind margin of the seventh ventral segment in the female. In the male there is no such spot and the margin is evenly arcuate. Also in the female there are 2 median pairs of small pale spots, 1 pair on either side of the suture separating the eighth and ninth ventrites. In the male there is only 1 pair of pale spots located near the anus.

KEY TO THE IMMATURE STAGES OF *CIMEX LECTULARIUS*

1. One row of spines on each abdominal tergite ..... **First instar**
   Two or more rows of spines on each abdominal tergite 2
2. Two rows of spines on each abdominal tergite ..... **Second instar**
   Three or more rows on each abdominal tergite, more-or-less distinct 3
3. Last 2 antennal segments subequal ..... **Third instar**
   Fourth segment distinctly shorter than third 4
4. Hind margin of mesonotum not or scarcely concave at middle ..... **Fourth instar**
   Hind margin of mesonotum distinctly, broadly concave at middle ..... **Fifth instar**

Oeciacus vicarius Horvath

(Fig. 13–4d, Fig. 13–11)

EGG.—Length 0.93 mm, greatest thickness 0.40 mm, diameter of cap end 0.20 mm. Cap end bent abruptly downward. Surface of chorion minutely, spinously granular, with irregular reticulations visible only when light is reflected through egg shell. With conspicuous areoles adjacent to outwardly flanged ring around cap. Cap slightly convex and distinctly areolate throughout, without a ringlike thickening on the periphery. Cap 0.86 mm in diameter.

NYMPHS.—*First Instar.*—Oval, flattened, sparsely bristled. Body length 1.1 mm.

Head subtriangular, convexly rounded posteriorly; length 0.2 mm, width 0.4 mm, ratio of length to width 1:2; eye width 0.05 mm, interocular space 0.3 mm, interocular space 6 times eye width. Proportion of antennal segments 5:7:8:10. Rostrum reaching slightly past end of front coxae, overall length 0.5 mm, proportion of segments 13:7:10.

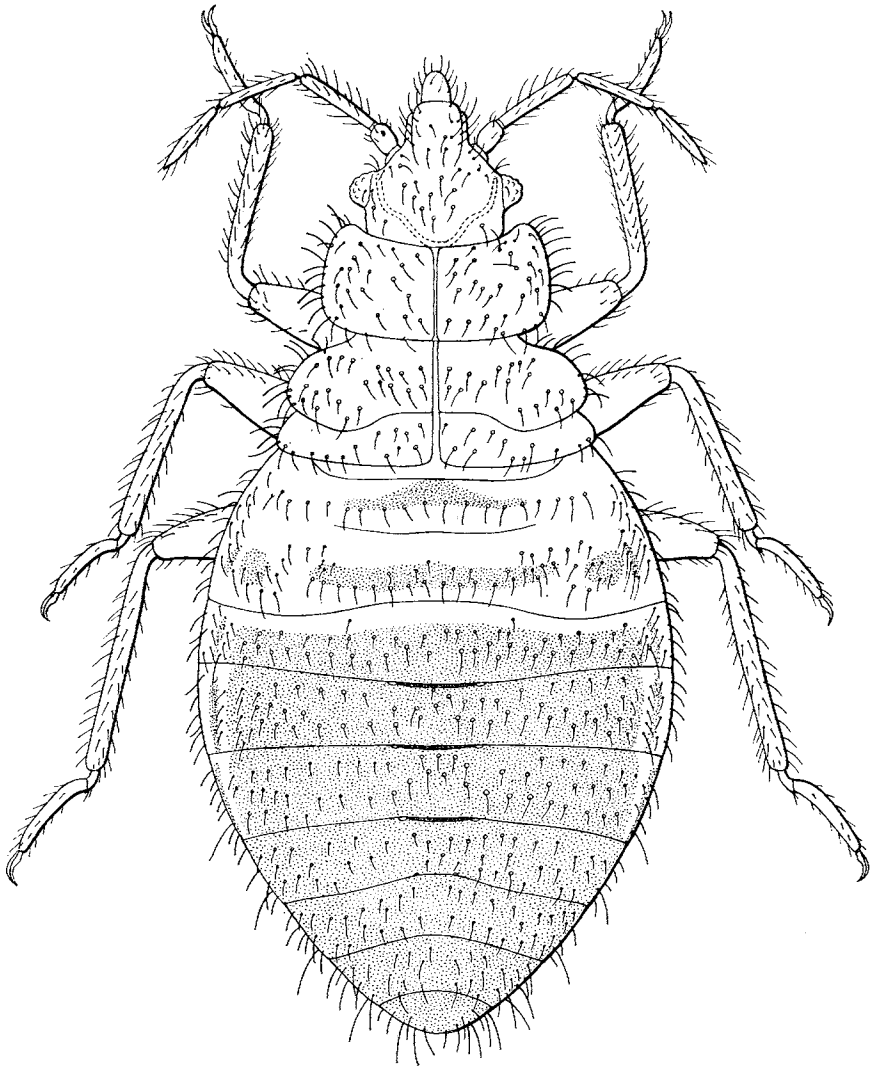

FIG. 13–11.—*Oeciacus vicarius*. Last-instar nymph.

Pronotum subrectangular, anterior margin concave, humeri rounded, lateral margins with a single row of strong spines subequal in length; pronotal length 0.17 mm, width 0.5 mm, ratio of length to width 17:50. Mesonotum and metanotum less rectangular in shape, shorter than pronotum, lateral margins also with strong spines.

Abdomen at widest point 0.5 mm, first abdominal segment with a posterior row of bristles extending from lateral margin to lateral margin.

Legs setose, claws simple, curved; a small pad at base of claws. Color uniformly pale amber; eyes ruby red.

Second Instar.—Differing from preceding instar as follows: Body length 2.1 mm. Head length 0.5 mm, width 0.5 mm, ratio of length to width 1:1; eye width 0.08 mm, interocular space 0.3 mm, approximately 3 times eye width; proportion of antennal segments 5:11:13:17; length of rostrum 0.5 mm, proportion of segments 15:9:9. Pronotum length 0.2 mm, width 0.6 mm, ratio of length to width 1:3. Abdomen width at widest point 1.1 mm.

Third Instar.—Differing from previous instar as follows: Body length 2.1 mm, body more densely clothed with long setae. Head length 0.5 mm, width 0.6 mm, ratio of length to width 5:6; eye width 0.08 mm, interocular space 0.4 mm, interocular space approximately 5 times eye width; proportion of antennal segments 8:15:17:18; length of rostrum 0.6 mm, proportion of segments 19:9:10. Pronotum length 0.32 mm, width 0.7 mm, ratio of length to width 32:70. Abdomen width at widest point 1.4 mm.

Fourth Instar.—Differing from preceding instar as follows: Body more densely clothed with long setae, larger, body length 2.8 mm, elongate oval. Head length 0.5 mm, width 0.6 mm, proportion of length to width 5:6; proportion of antennal segments 9:17:19:18; length of rostrum 0.7 mm, proportion of segments 21:9:12. Wingpads barely overlapping metanotum; pronotum length 0.37 mm, width 0.8 mm, ratio of length to width 37:80. Abdomen width at widest point 1.5 mm. Sclerotized areas of antennal segments, rostrum, head, thoracic nota, abdominal nota, legs, scent gland openings, pre-tarsal pads, and sternites slightly infuscated.

Last Instar.—Body with moderately long bristles of equal length at sides. Length 3.0 mm. Head 0.56 mm wide; ratio of length to width 18:22; eyes $1/6$ as wide as interocular space, 2.5:16; labrum, clypeus, and most of head in front of ecdysial lines with long bristles; 3 bristles on each side at and behind eyes along ecdysial lines. Antennae 1 mm long; proportion of segments 10:20:21:21. Rostrum 0.5 mm long; proportion of segments 5:6:5.

Pronotum 0.95 mm wide; ratio of length to width 13:30; bristles at sides approximately 0.1 mm.

Mesonotum 1.1 mm wide, with about 10 bristles on each side; disk with bristles about as long as those on pronotum and metanotum. Width across metanotum 1.2 mm.

Abdomen 1.8 mm wide, first and second segments sclerotized transversely at middle and sublaterally on second segment exactly as in *Cimex*. Sixth, seventh, and eighth segments each with a very long bristle on either side in addition to the more numerous shorter bristles. Tip of abdomen with the usual clump of somewhat longer bristles.

Legs with hind femora 3 times as long as wide. Tibiae and tarsi without unusual characters.

Paracimex capitatus Usinger

(Fig. 13–4g, Fig. 13–12)

Egg.—Length 0.93 mm, greatest thickness 0.36 mm. Cap end 0.26 mm in diameter, slightly bent downward, the edge of operculum narrowly reflexed. Cap 0.25 mm in diameter, moderately convex with edge thickened and a little reflexed, disk distinctly reticulate. Entire chorion distinctly reticulate.

Nymphs.—*First Instar.*—Length 1.20 mm; elongate-oval; sparsely beset with long bristles especially conspicuous along margins of body. Head 0.33 mm wide; nearly as long as wide, 11:12; eyes $1/10$ the width of interocular space. Antennae 0.61 mm long; proportion of segments 5:8:9:15. Rostrum 0.45 mm long; proportion of segments approximately 8:10:10.

Pronotum 0.43 mm wide; $1/2$ as long as wide, 8:15; disk with a few long bristles and sides each with 4 long bristles. Mesonotum 0.46 mm wide and metanotum 0.5 mm wide, each with 3 or 4 long bristles on either side.

Abdominal segments with several long bristles, one in particular on each side of each segment very long.

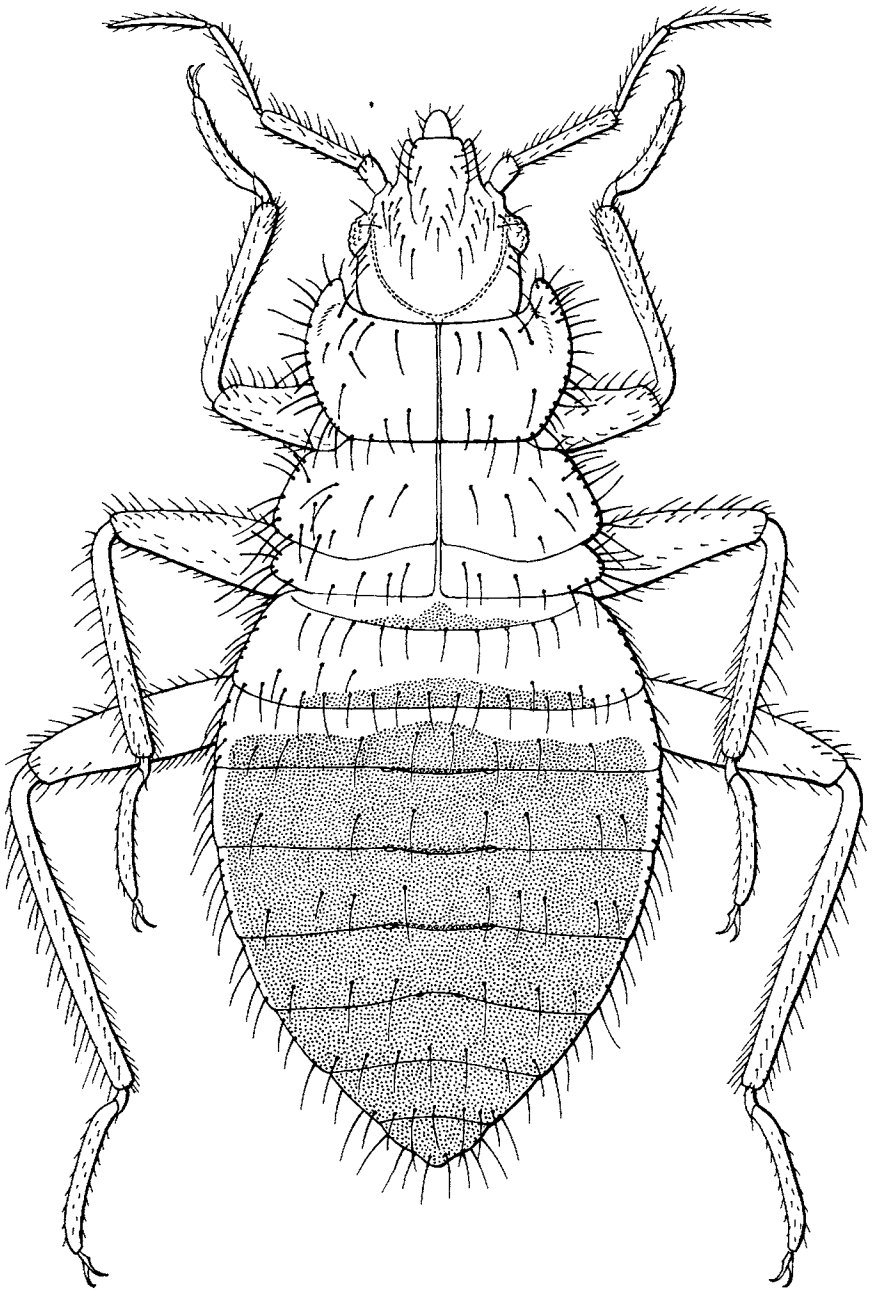

FIG. 13–12.—*Paracimex capitatus*. Last-instar nymph.

Legs relatively long; hind femora 3 times as long as greatest thickness; tibiae ¼ longer than femora. Tarsi simple, without unusual bristles or spines.

Second Instar.—Similar to first but with additional long bristles at sides of body (5 on pronotal margin). Head width 0.41 mm, pronotum 0.53 mm, meso- and metanota 0.55 mm. Antennae 0.78 mm long, proportion of segments 5:11:12:19.

Third Instar.—Sides of pronotum with about 10 bristles. Head width 0.53 mm, pronotum 0.68 mm, mesonotum 0.80 mm, metanotum 0.85 mm. Antennae about 1 mm long, proportion of segments 7:15:18:21.

Fourth Instar.—Sides of pronotum each with about 15 long bristles. Head width 0.65 mm, pronotum 0.9 mm, mesonotum 1.1 mm, metanotum 1.17 mm. Antennae 1.25 mm long, proportion of segments 10:20:22:23.

Last Instar.—Length 4.13 mm. Long bristles at sides of body of approximately equal length, 0.2 mm. Head 0.80 mm wide, about as long as wide; interocular space about 7 times as wide as an eye; numerous strong, fine bristles on labrum and clypeus, bristles on juga; eyes with a few short bristles and head just behind eyes along ecdysial lines with 3 bristles on each side. Antennae 1.7 mm long; proportion of segments 12:32:30:28. Rostrum approximately 0.86 mm long; proportion of segments 5:4:4.

Pronotum 1.2 mm wide; almost ½ as long as wide, with long discal bristles, especially anteriorly and posteriorly, and with about 25 lateral bristles. Mesonotum 1.5 mm wide and metanotum 1.56 mm wide, the former with about 15 and the latter with 6 lateral bristles.

Abdomen with membranous lateral margins of second segment densely beset with short bristles. Sclerotized areas of first and second segments short, simple and transverse, each of basal tergites with a transverse row of bristles. Remaining tergites each with 6 or 8 long bristles in a row and about 8 bristles at sides of each segment.

Legs moderately stout; hind femora more than 3 times as long as wide, 16:5; front and middle femora with a short dense row of bristles subapically like the "ctenidium" of adults. Tibiae with very fine, long (as long as thickness of tibiae) erect bristles on outer edges in addition to short, apically directed bristles.

Cacodmus vicinus Horvath

(Fig. 13–4a, Fig. 13–13)

NYMPH.—*Last Instar.*—Bristles very numerous and long, to 0.3 mm at sides.

Head 0.63 mm wide, less than ½ again as wide as long, 22:16; interocular space more than 3 times as wide as an eye, 14:4; ecdysial lines arched on either side to inner posterior corners of eyes and then bent forward along inner margins of eyes. Antennae 1.51 mm; proportion of segments 6:17:15:15. Rostrum (slide-mounted) reaching apex of prosternum; segments subequal, first segment with 1 pair of long bristles.

Pronotum 1.05 mm wide, twice as wide as long, 37:18; entirely surrounded by long bristles and with bristles on disk. Mesonotum 1.4 mm wide; metanotum 1.34 mm wide.

Basal abdominal tergites with a broad transverse sclerotized area, especially on second segment. Third segment narrowly membranous anteriorly and laterally. Anterior scent gland opening nearly twice as wide as clypeus. Abdominal tergites with many long bristles at sides and several ill-defined rows on disks.

Hind femora a little more than 2½ times as long as wide, 33:12.5; tibiae slightly enlarged and bent inward at tips, without subapical pseudojoints.

Size.—Length 3.77 mm, width (pronotum) 1.05 mm.

Aphrania vishnou Mathur

(Fig. 13–14)

NYMPH.—*Last Instar.*—Bristles long and often curved, the longest ones at sides of body about 0.28 mm.

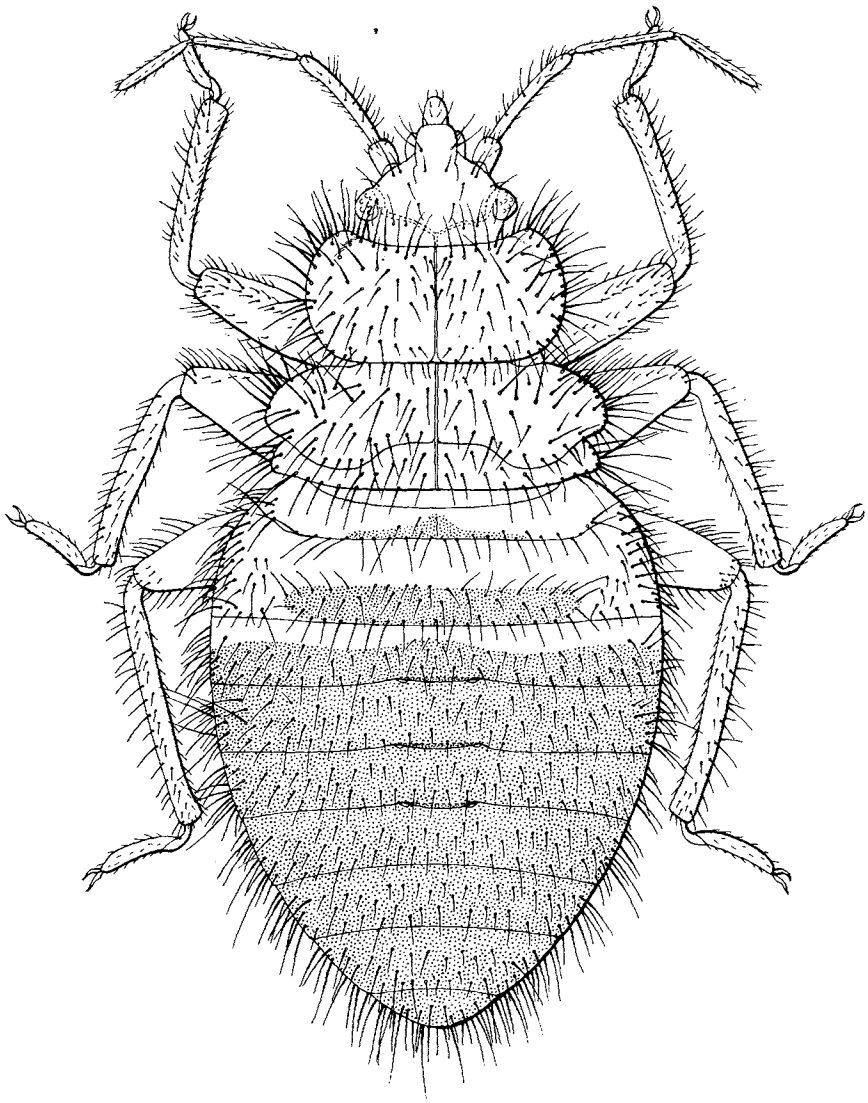

FIG. 13–13.—*Cacodmus vicinus*. Last-instar nymph.

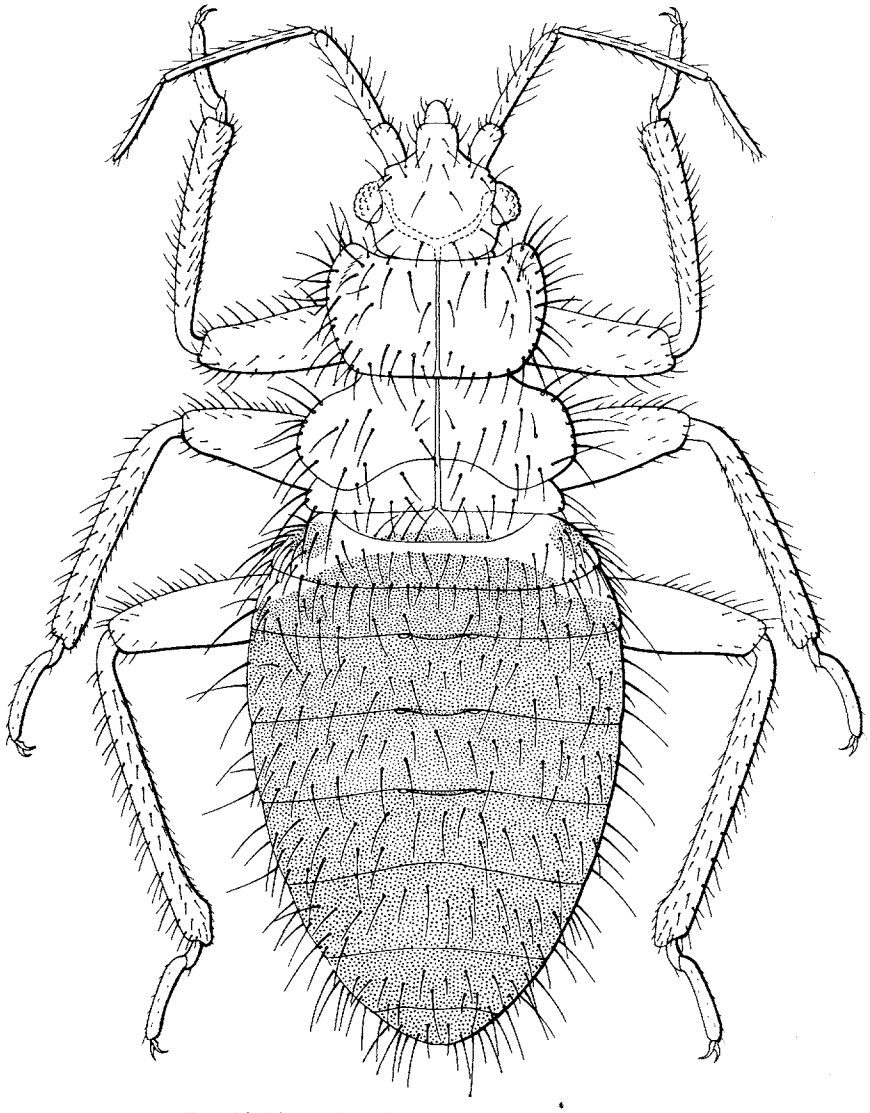

FIG. 13–14.—*Aphrania vishnou.* Last-instar nymph.

Head 0.71 mm wide, about 1/3 wider than long, 25:19, eyes large, 1/3 as wide as interocular space. Antennae 1.85 mm long, proportion of segments 7:22:21:15. Rostrum relatively short, reaching only to anterior margins of front coxal cavities (slide-mounted), approximately 0.54 mm; first segment with 2 pairs of long bristles; proportion of segments about 6:6:7. Ecdysial lines only feebly sinuate behind and mesad of eyes.

Pronotum 0.91 mm wide, nearly twice as wide as long, 32:17, widest in front of middle, shallowly concave on front margin, sides each with about 20 long bristles. Width across mesonotum 1.14 mm; across metanotum 1.08 mm.

Abdomen with first and second tergites visible as transverse sclerotized areas, third segment membranous only along anterior margin. Scent gland openings about twice as wide as clypeus. Sides of abdominal segments with 3 or 4 long bristles, tergites each with 2 rather irregular rows of bristles.

Legs with hind femora about 3 times as wide as long. Tibiae thickened at apices where apical tufts will be in adults, hind tibiae with a faint indication of a pseudojoint subapically.

Size.—Length 3.77 mm, width (pronotum) 0.91 mm.

Loxaspis spinosa Usinger
(Fig. 13–15)

NYMPH.—*Last Instar.*—Bristles at sides of body stiff, erect, the longest about 0.23 mm.

Head 0.8 mm wide, ratio of length to width 22:28. Interocular space 5 times as wide as an eye; ecdysial lines anteriorly divergent and then abruptly bent backward and sinuate to inner hind margin of eyes whence they follow the inner margins of eyes. Antennae 2.2 mm long; proportion of segments 7:28:24:20. Rostrum (slide-mounted) reaching nearly to apices of front coxae, about 1 mm long, ratio of segments 10:13:13.

Pronotum a little more than 1/2 again as wide as long, 39:24; 1.1 mm wide; anterior margin very shallowly concave, sides each with about 14 stiff bristles; disk with scattered, mostly smaller bristles; width across mesonotum 1.45 mm; across metanotum 1.4 mm.

First and second abdominal tergites each with a broad sclerotized plate, third segment sclerotized except on its anterior and extreme lateral borders. Each abdominal segment with one, and some with a shorter second, stiff bristle at sides and each tergite with a row of 8 very long bristles in addition to short ones. Scent gland openings 2/3 again as wide as clypeus, 18:11.

Legs rather stout, hind femora 3 times as long as wide. Tibiae relatively short and stout, bent subapically.

Size.—Length 4 mm, width (pronotum) 1.1 mm.

Stricticimex transversus Ferris and Usinger
(Fig. 13–16, *S. brevispinosus*)

NYMPH.—*Last Instar.*—Bristles stiff, straight, of intermediate length, the longest about 0.17 mm.

Head 0.6 mm wide; 1/2 again as wide as long, 21:14; interocular space 5 times as wide as an eye. Antennae 1.57 mm; proportion of segments 5:10:23:17. Rostrum reaching onto prosternum, apex of second segment reaching base of head (slide-mounted), segments subequal.

Pronotum 0.74 mm wide; nearly 2 1/2 times as wide as long, 26:11; about 12 prominent spines on each side and others on disk. Mesonotum 0.86 mm wide. Metanotum 0.94 mm. Mesonotum with about 8 and metanotum with about 4 prominent bristles at sides and each with a transverse row across middle.

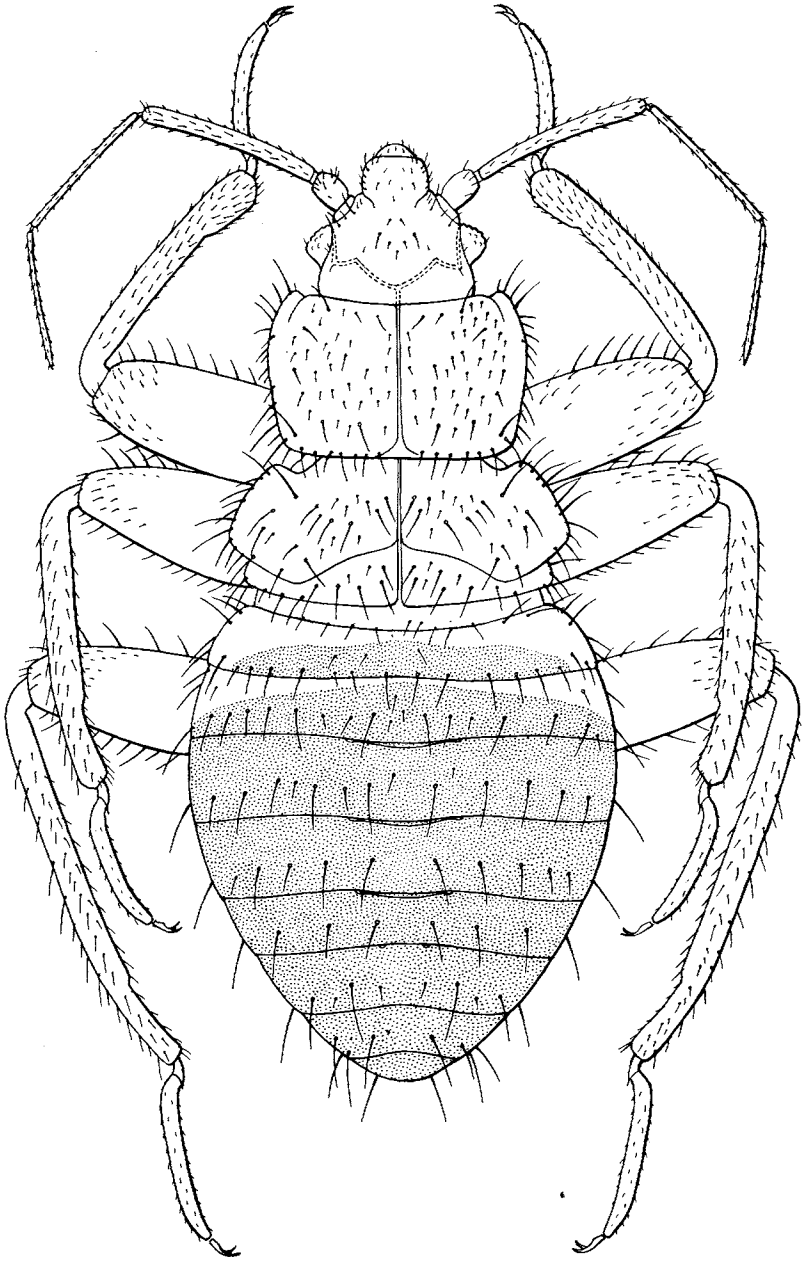

FIG. 13–15.—*Loxaspis spinosa*. Last-instar nymph.

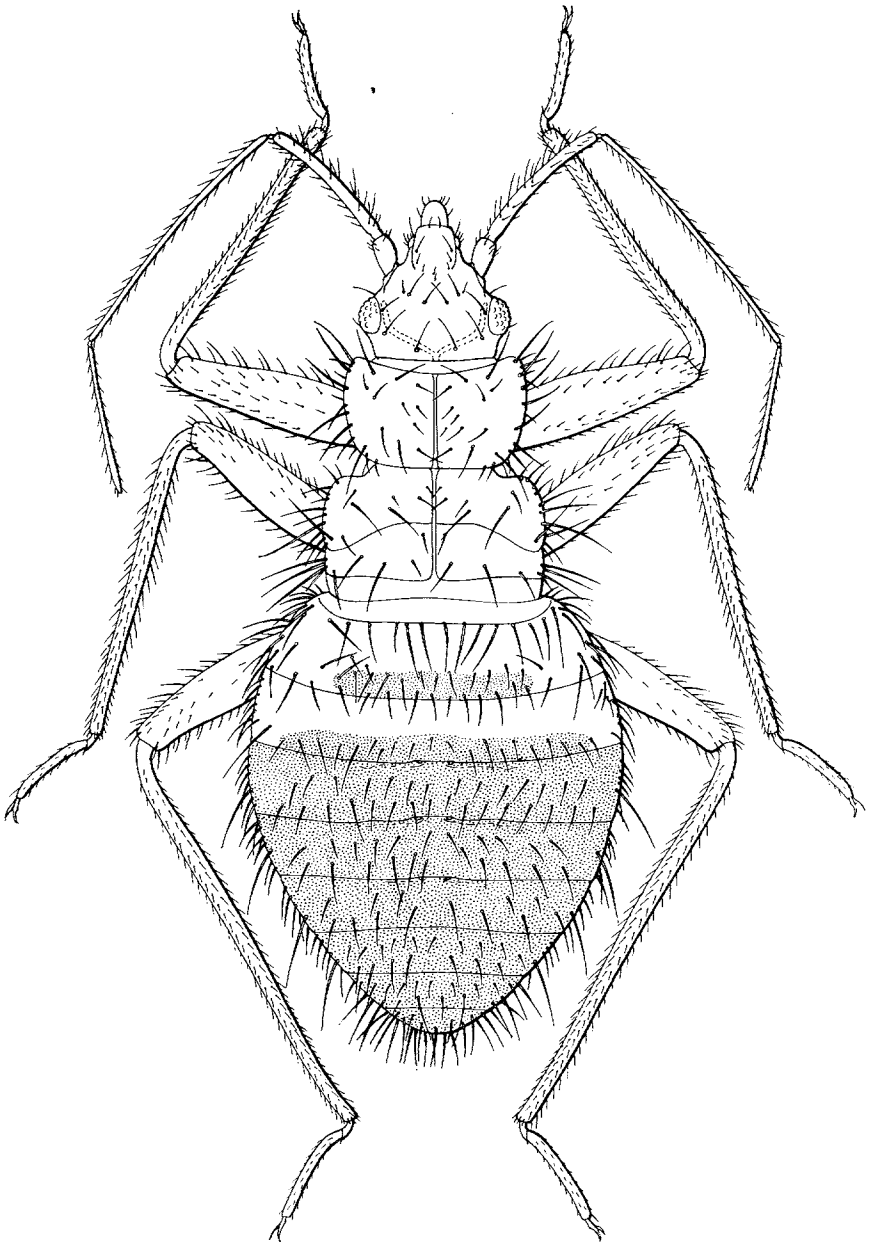

FIG. 13–16.—*Stricticimex brevispinosus*. Last-instar nymph.

First and second abdominal tergites represented by a narrow transverse sclerotized band bearing bristles. The rest of base and sides of abdomen membranous, with bristles. Third tergite sclerotized posteriorly and remaining segments fully sclerotized. Scent gland openings much narrower than width of clypeus.

Legs relatively stout for this group; hind femora 3½ times as long as wide. Tibiae tapering and bent subapically. Femora and tibiae with long bristles.

Size.—Length 2.91 mm, width (pronotum) 0.74 mm.

Leptocimex duplicatus Usinger

(Fig. 13–4c, 13–17)

Egg.—Length 0.93 mm, greatest width 0.46 mm, width across cap end 0.22 mm. Shape suboval, relatively short and thick, the cap end narrowed and briefly reflexed, strongly bent downward. Chorion whitish, the surface smooth or minutely granular. Cap but little convex, finely reticulate.

Nymphs.—*First Instar.*—Elongate oval, body with sparse bristles, little dorso-ventral compression; body length 1.02 mm, abdomen width 0.44 mm.

Head triangular, length 0.27 mm, width 0.29 mm, ratio of length to width 27:29; eyes consisting of 5–7 ommatidia, width 0.03 mm, interocular space 0.22 mm; labrum curved over base of beak, bristled; rostrum reaching to distal end of hind coxae, length 0.14 mm, proportion of segments 8:7:15; antennae longer than body, fourth segment no wider than third and not rounded distally, finely setose, third convexly curved, proportion of segments 6:7:26:22.

Thoracic nota subrectangular. Pronotum with reflex angled anterior margin, small anteriorly projecting process with parallel sides on each humeral angle; pronotum length 0.11 mm, width 0.29 mm; mesonotum length 0.15 mm, width 0.29 mm; metanotum length 0.05 mm, width 0.34 mm.

Appendages attenuate; legs uniformly setose, femora slightly dorsoventrally compressed; hind femora extending beyond tip of abdomen, length 0.37 mm; hind tibia 0.61 mm.

Second Instar.—Differing from previous instar as follows: Body length 1.2 mm, width of abdomen 0.7 mm.

Head length 0.3 mm, width 0.4 mm, ratio of length to width 3:4; eye width 0.1 mm, interocular space 0.2 mm, eyes with many ommatidia; beak reaching middle of hind coxae, basal segment with a bristle on either side of midline, ⅔ distance from base, proportion of segments 14:8:17; basal segment of antenna swollen apically, proportion of segments 7:10:39:25.

Pronotum with seta on tubercle at each angle, pronotum length 0.17 mm, width 0.4 mm; mesonotum with seta borne on tubercle at each posterior angle, posterior margin convexly sinuate, length 0.08 mm, width 0.4 mm; metanotum length 0.08 mm, width 0.4 mm.

Length of hind femur 0.6 mm, length of hind tibia 0.8 mm.

Third Instar.—Differing from previous instar as follows: Body length 1.8 mm, abdomen width 1.0 mm.

Head length 0.5 mm, width 0.5 mm; eye width 0.08 mm, interocular space 0.3 mm, eyes black; rostrum reaching proximal ends of hind coxae, proportion of segments 16:13:21; a seta borne on tubercle in anteocular space dorsad of each antennal insertion; fourth antennal segment bent, slightly rounded at tip, proportion of segments 9:13:62:28.

Pronotum length 0.2 mm, width 0.5 mm; posterior margin of mesonotum becoming more convex, length 0.1 mm, width 0.6 mm; posterior angles of metanotum each with a stout seta borne on tubercle; metanotum length 0.17 mm, width 0.6 mm; nota of first and second abdominal segments with a seta on a tubercle on each posterolateral angle.

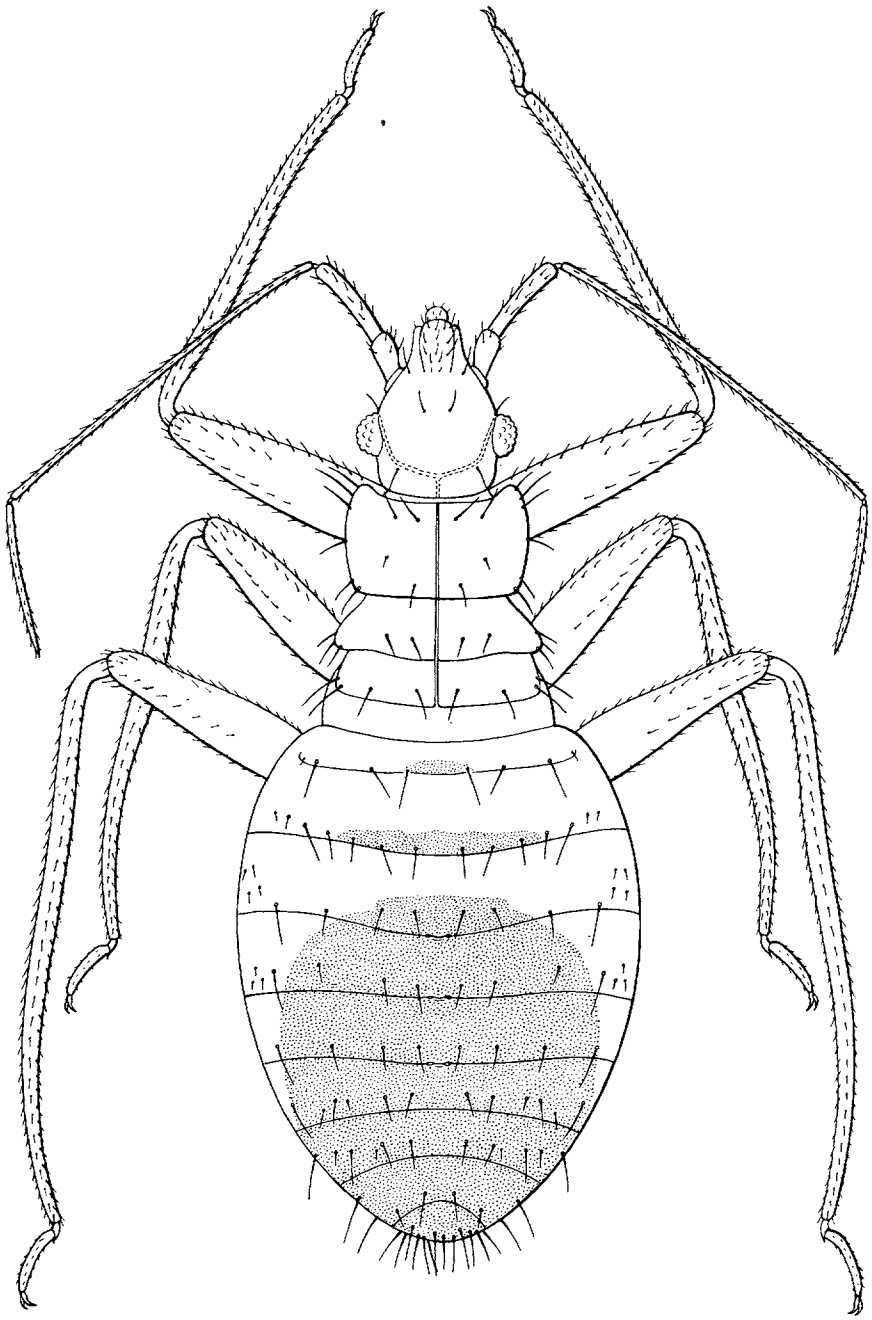

FIG. 13–17.—*Leptocimex duplicatus*. Last-instar nymph.

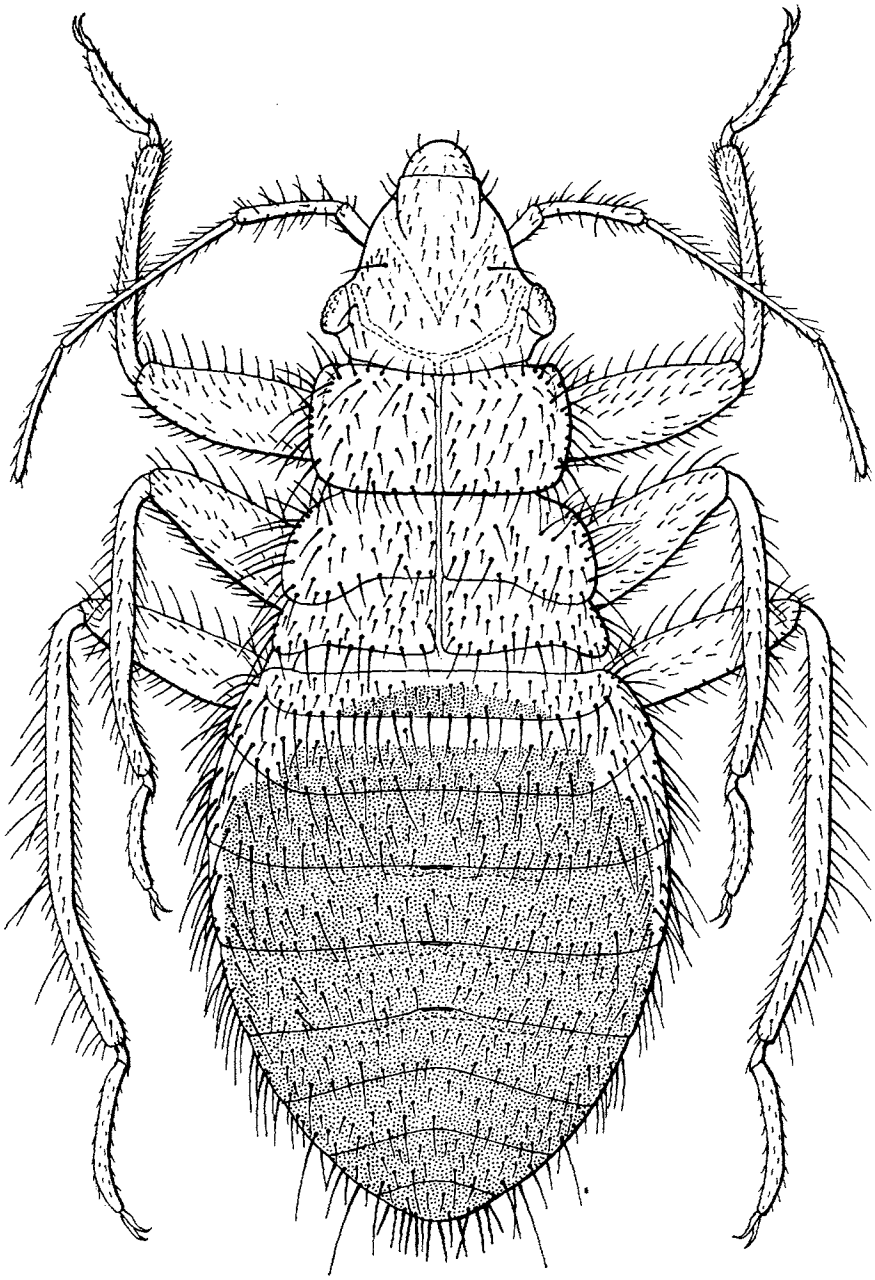

FIG. 13–18.—*Crassicimex pilosus*. Last-instar nymph.

Length of hind femur 0.8 mm; length of hind tibia 1.2 mm.

Fourth Instar.—Differing from previous instar as follows: Body length 2.0 mm, abdomen width 1.1 mm.

Head length 0.4 mm, width 0.5 mm, ratio of length to width 4:5; a pigmented convex sclerite in front of each eye; eye width 0.08 mm, interocular space 0.3 mm; proportion of rostral segments 15:12:24.

Length of pronotum 0.3 mm, width 0.6 mm; length of mesonotum 0.1 mm, width 0.6 mm; metanotal length 0.15 mm, width 0.66 mm; second abdominal notum with a spine on each anterolateral angle.

Length of hind femur 1.0 mm; length of hind tibia 1.2 mm.

Last Instar.—Differs from previous instar as follows: Body length 2.7 mm, abdomen width 1.5 mm.

Head length 0.7 mm, width 0.6 mm, ratio of length to width 7:6, eye width 0.1 mm, interocular space 0.36 mm, proportion of rostral segments 21:15:34, proportion of antennal segments 13:19:96:36.

Nota of thorax and first abdominal segment carinate on anterior margins; length of pronotum 0.36 mm, width 0.6 mm; mesonotal length 0.15 mm, width 0.6 mm; metanotum with lateral tubercles bearing clavate setae, metanotal length 0.2 mm, width 0.7 mm. Length of hind femur 1.5 mm.

Crassicimex pilosus Ferris and Usinger
(Fig. 13–18)

NYMPH.—*Last Instar.*—Bristles long, those at sides of pronotum to 0.28 mm.

Head unique in shape, 0.94 mm wide; about 1/4 wider than long, 33:26; eyes relatively small, 1/6 as wide as interocular space, 4:25; sides of head strongly convex above bases of antennae; ecdysial lines forming almost an even arc to front margins of eyes; labrum about twice as wide as long. Antennae about 2.25 mm long; proportion of segments 7:21:30:21. Rostrum very short, not reaching base of head; total length 0.48 mm; proportion of segments about 8:7:5; second segment wider than long.

Pronotum 1.05 mm wide; almost twice as wide as long, 37:19; about 15 stout bristles on each side and numerous bristles elsewhere. Mesonotum 1.25 mm wide; metanotum 1.37 mm. First and second abdominal tergites very broadly and completely sclerotized and bearing numerous rows of bristles. Anterior scent gland orifice only 1/3 as wide as clypeus.

Hind femora 4 times as long as wide. Tibiae long and bent inward beyond middle. Tarsi with a small hump on upper side subapically.

Size.—Length 4.1 mm, width (pronotum) 1.05 mm.

Afrocimex constrictus Ferris and Usinger
(Fig. 13–19)

NYMPHS.—*First Instar.*—Similar to the last but smaller with the following proportions: Head 0.67 mm wide, slightly wider than long. Pronotum 0.85 mm. Mesonotum 1 mm. Metanotum 1.12 mm. Antennae approximately 2 mm long; proportion of segments 7:24:22:20.

Size.—Length 3.58 mm; width (pronotum) 0.85 mm.

Last Instar.—Relatively large with long legs and very long, fine bristles, the longest bristles nearly 1 mm and not stiff.

Head 1 mm wide, as long as wide; interocular space 5 times as wide as an eye; ecdysial lines evenly rounded backward and inward behind eyes, not sinuate; clypeus 2/5 as wide as interocular space. Antennae 3.51 mm long; proportion of segments 9:48:40:26. Rostrum reaching well onto prosternum; second segment just reaching base of

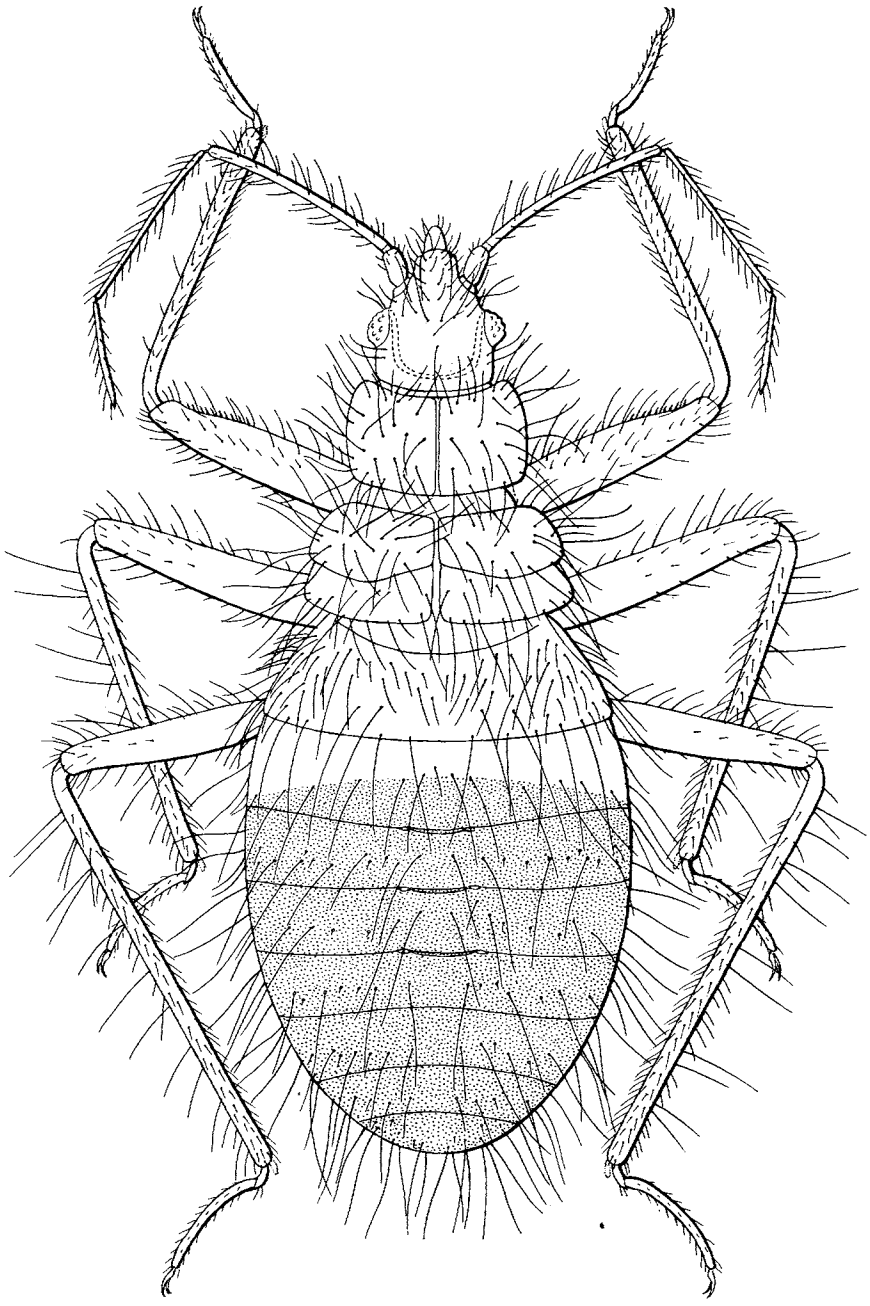

FIG. 13-19.—*Afrocimex constrictus*. Last-instar nymph.

head (slide-mounted); length about 1.1 mm; proportion of segments approximately 12:14:14.

Pronotum 1.3 mm wide; ¾ as long as wide; about 12 very long bristles on lateral margins and others anteriorly, posteriorly and on disk.

Mesonotum 1.61 mm wide, 2½ times as wide as long. Metanotum 1.7 mm wide.

Abdomen with basal segment membranous and third segment membranous anteriorly and sclerotized posteriorly. All tergites pale at extreme edges, bearing 3 or 4 very long bristles at edges and a row of very long bristles across middle. Scent gland openings twice as wide as clypeus.

Legs long and slender; hind femora 5 times as long as wide. Femora and tibiae with very long erect bristles as well as shorter bristles. Fore femora with a fine pecten as in adults. All tibiae with incipient apical tufts at apices.

Size.—Length 6 mm, width (pronotum) 1.3 mm.

Latrocimex spectans Lent
(Fig. 13–20)

NYMPHS.—*First Instar.*—Elongate-oval, with long, erect bristles. Length 2.43 mm. Head 0.43 mm wide, wider than long, 15:12. Eyes small, ⅛ as wide as interocular space. Head above with 2 fine bristles on labrum, 2 fine and 2 prominent bristles on clypeus, and 1 longer bristle on each jugum. Antennae 1.2 mm long, proportion of segments 4:11:11:16. Rostrum 0.54 mm long; proportion of segments 4:6:9.

Pronotum 0.63 mm wide; less than twice as wide as long, sides with about 6 intermediate to long bristles, the longest at humeri being 0.2 mm; disk with 4 long bristles anteriorly and 4 posteriorly.

Mesonotum 0.77 mm wide, 3 times as wide as long, 27:9; with smaller bristles anteriorly at sides, 2 long bristles posterolaterally, 6 discal bristles posteriorly.

Metanotum 0.86 mm wide, with 8 or 10 prominent bristles posteriorly.

First abdominal segment with 4 long bristles posteriorly and only 1 or 2 short ones laterally. Second segment with 1 long bristle on each side and 4 posteriorly on disk, the remaining segments following this same pattern. First and second segments broadly sclerotized but surrounded with membrane, third segment membranous anteriorly and laterally. Remaining segments only narrowly pale laterally. Scent gland openings very broad, wider than distance from outer opening to lateral margin.

Under surface with more numerous long bristles on abdomen. Second antennal segment with several very long bristles, front coxae each with 1 very long bristle at middle. Femora and tibiae with long bristles, tarsi without distinctive bristles.

Abdominal spiracles relatively large, 0.03 mm in diameter.

Last Instar.—Similar to first instar but larger and differing chiefly in the reduction in size of certain characteristic bristles. Widths of head, pronotum, mesonotum, and metanotum: 0.57 mm, 0.93 mm, 1.25 mm, and 1.34 mm, respectively. Length of body 3.8 mm. Antennae 1.85 mm long, proportion of segments 6:19:18:22. Proportion of rostral segments 7:10:14.

Bristles basically as in first instar but all on mesonotum, metanotum, and abdomen greatly reduced to less than half: 0.17 mm in first instar for long bristles at sides of abdomen in contrast to 0.086 mm for last instar.

Ornithocoris pallidus Usinger
(Fig. 13–21)

NYMPH.—*Last Instar.*—Elongate-oval. Surface with very fine, short bristles except at sides of thorax, tip of abdomen, and on appendages.

Head 0.63 mm wide; ⅔ as long as wide, 15:22; interocular space 5 times as wide as

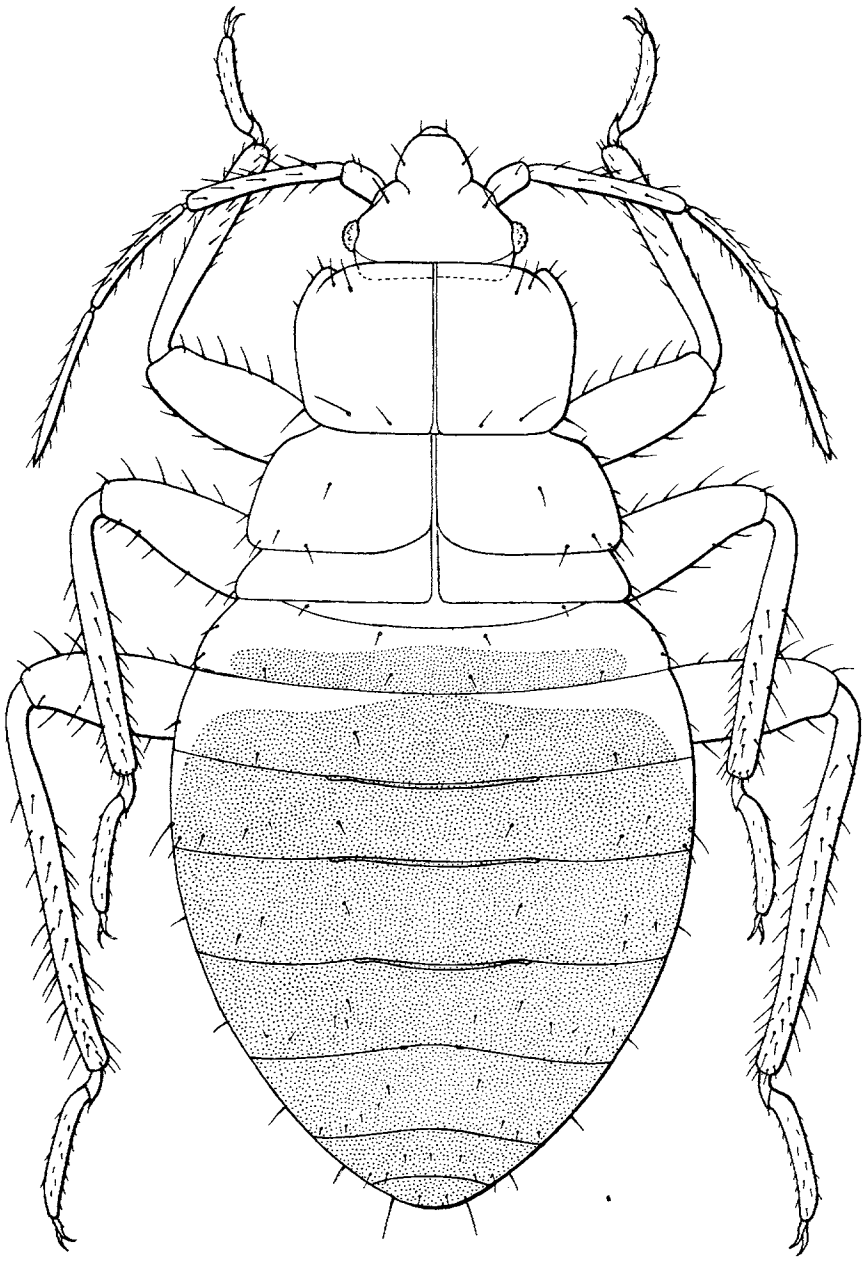

FIG. 13–20.—*Latrocimex spectans*. Last-instar nymph.

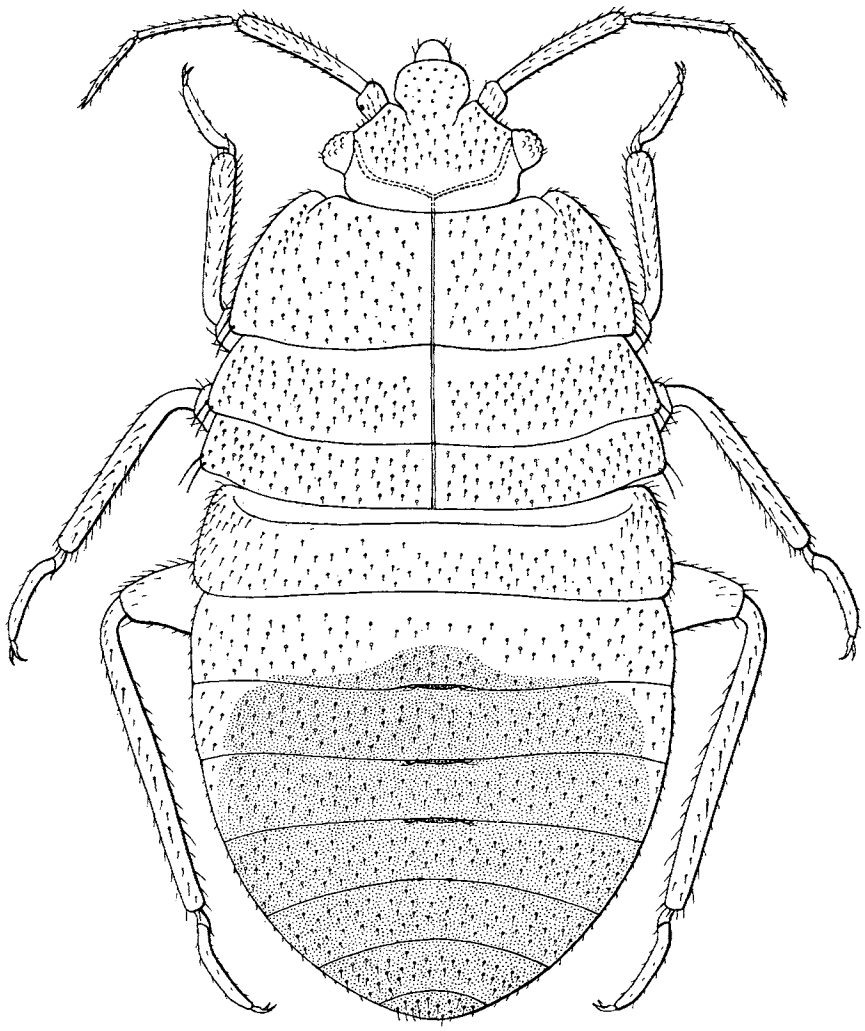

FIG. 13–21.—*Ornithocoris pallidus*. Last-instar nymph.

an eye, 16:3. Antennae 1.06 mm long; proportion of segments 5:12:10:10; second segment much shorter than interocular space, 12:16. Rostrum 0.63 mm long, not nearly reaching level of apices of front coxae (slide-mounted); proportion of segments 7:7:8.

Pronotum 1.23 mm wide; nearly 3 times as wide as long, 43:15, and almost twice as wide as head, 43:22; bristles very small at sides except for 2 at each humerus which measure 0.17 mm and are less than ½ as long as pronotum.

Mesonotum 1.34 mm wide, with 1 long and 1 slightly shorter bristle posterolaterally; hind margin feebly concave at middle as is that of pronotum.

Abdomen with base and sides broadly membranous; second and basal parts of third

tergite and sides of fourth and fifth membranous around abdomen. Abdomen apparently without long bristles, at least in this instar.

Legs stout, without trace of tibial tufts. Hind femora 3 times as long as broad, 25:9; hind tibiae 1/3 longer than femora. Middle and hind tibiae with short stout bristles as well as finer ones.

Caminicimex furnarii (Cordero and Vogelsang)

(Fig. 13–22)

EGG.—Length 0.73 mm, greatest width 0.32 mm, width across cap end 0.22 mm. Shape oval with cap end bent downward, the cap flange prominent and rather strongly reflexed. Cap. 0.2 mm across, convex. Chorion appearing smooth and polished, minutely granular under high magnification.

NYMPHS.—*First Instar.*—Body elongate oval, sparsely beset with minute bristles and 4 long bristles on each side. Length 1.1 mm. Head subtriangular, wider than long, 28:22, interocular space 6 times as wide as an eye; width across eyes 0.33 mm; labrum with 2 pairs of long bristles, clypeus with 1 pair. Antennae about 0.49 mm; proportion of segments 5:10:11:19. Rostrum 0.34 mm in length, reaching nearly to apices of front coxae; proportion of segments 12:7:12.

Pronotum twice as wide as long, 13:6, and a little wider than head, 13:11, with 1 long bristle on each side just in front of humeral angle; front margin concave; sides and hind margin arcuately rounded. Mesonotum scarcely wider than pronotum, 3½ times as wide as long, with a prominent bristle on each side. Metanotum slightly wider than pronotum, 15:13, 5 times as wide as long, also with a long bristle on each side.

Abdomen with first segment almost completely membranous, its limits difficult to define; second segment slightly wider than metanotum, with many fine bristles at sides and a long bristle sublaterally on each side; remaining tergites with very sparse, inconspicuous hairs until eighth segment, which has 1 long bristle on each side, and ninth, which has 2 on each side; ventral surface with numerous longer bristles.

Legs stout, with rows of prominent bristles; tarsi each with a subapical pair of very long bristles.

Second Instar.—More robust and with small marginal bristles more conspicuous, the most significant difference being a second long bristle at each humeral angle. Length 1.48 mm. Width of head 0.4 mm. Length of antennae 0.6 mm, proportion of segments 3:5.5:5:7. Rostrum reaching middle of front coxae; proportion of segments 5:4:4. Width of pronotum 0.5 mm, mesonotum 0.53 mm, metanotum 0.6 mm.

Third Instar.—Relatively broader with bristles of dorsal surface still inconspicuous but marginal bristles prominent. Length 1.74 mm, width of head 0.46 mm. Antennae 0.68 mm long; proportion of segments 3:7:6:8. Rostrum 0.4 mm long, proportion of segments 5:4:6. Pronotal width 0.63 mm, mesonotum 0.7 mm, metanotum 0.77 mm.

Fourth (Last) Instar.—Marginal bristles of pronotum approximately 12 in number in addition to very long pair at humeri. Eight stiff marginal bristles on mesonotum in addition to a long pair (unequal length, the hind one shorter as with humeral pair). Metanotum with 4 bristles in addition to long one posterolaterally. Body surface above with very inconspicuous bristles, practically wanting. Sides of abdomen, especially basally, with numerous bristles, under surface with many bristles. Second abdominal segment with single very long bristle on each side. First, second, and basal part of third tergite membranous except for a small pigmented area at middle of second. Tibiae with numerous very short spines in addition to fine bristles. Length of body 2.7 mm, width of head 0.57 mm. Length of antennae 0.83 mm; proportion of segments 3:10:7:9. Rostrum reaching only to front part of fore coxae, 0.5 mm long; proportion of segments 6:5:6. Width of pronotum 0.8 mm; mesonotum 0.94 mm; metanotum 1.03 mm. Hind margins of pro-, meso-, and metanota not sinuate, straight, or arcuate.

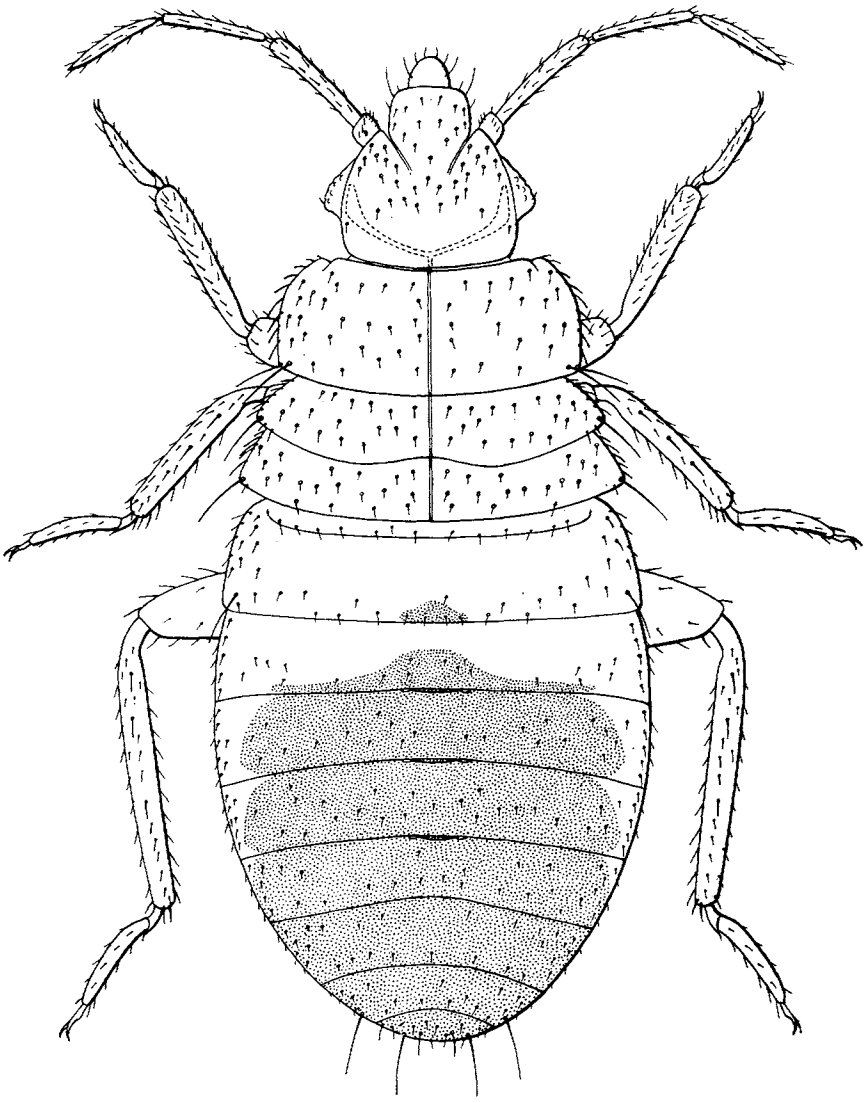

FIG. 13–22.—*Caminicimex furnarii*. Last-instar nymph.

KEY TO THE IMMATURE STAGES OF *CAMINICIMEX FURNARII*

1. Humeri with only 1 long bristle ..... **First instar**
   Humeri each with a pair of long bristles 2
2. Sides of pronotum with approximately 6 small bristles ..... **Second instar**
   Sides of pronotum with more than 6 small bristles 3
3. Sides of pronotum with 9 small bristles ..... **Third instar**
   Sides of pronotum with 12 small bristles ..... **Fourth instar**

According to rearing records, there are only 4 nymphal instars. This agrees with the nearly related *Haematosiphon*. However, later nymphs have head widths that form a continuous series, so growth ratios are not decisive.

Psitticimex uritui (Lent and Abalos)
(Fig. 13–23)

NYMPH.—*Last Instar.*—Body suboval, with very short bristles except as noted below.

Head 0.73 mm wide, less than ½ again as wide as long, 11:8; ratio of eye width to interocular space 2:7; clypeus broadly truncate at apex. Antennae 1.43 mm long, proportion of segments 7:33:25:20. Rostrum approximately 0.58 mm long, proportion of segments 10:10:15.

Pronotum 1.13 mm wide, 2½ times as wide as long and ½ again as wide as head, 17:11; sides with some short bristles and 1 long bristle at each humeral angle; mesonotum 1.3 mm wide, metanotum 1.4 mm wide, each with an erect bristle at posterolateral angles.

Abdomen with first and second segments broadly and completely membranous, the tergites of remaining segments sclerotized broadly at middle but leaving a wide area of third segment membranous. Ratio of scent gland width to clypeus width 10:17. A few long bristles at tip of abdomen.

Hind femora 3 times as long as wide. Tibiae straight, without pseudojoints, beset with a few short, stiff bristles.

Size.—Length 3.8 mm, width (pronotum) 1.13 mm.

Haematosiphon inodorus (Dugés)
(Fig. 13–4b, 13–24)

EGG.—Chorion white, unhatched egg colored light brown because of contents. Fine irregular pattern imprinted on chorion; unlike regular hexagonal reticulations on *C. lectularius*. Length 0.883 mm; width at widest part 0.441 mm; diameter of ring 0.261 mm. Cap moderately smooth.

NYMPHS.—*First Instar.*—Elongate-oval, flattened, sparsely bristled, overall body length 1.14 mm; abdomen, width 0.517 mm.

Head triangular, somewhat rounded, proportion of width to length 25:16.5, head width 0.382 mm. Eyes about ⅙ as wide as interocular space, 3:17. Antennae inserted slightly behind middle of anteocular space on ventrolateral aspect of head; fourth segment pointed apically. Proportion of antennal segments 6:11:11:16.5. Proportion of rostral segments 15.5:12.5:13; rostrum extending to beyond middle coxae; overall length 0.619 mm.

Pronotum subrectangular, anterior margin concave, posterior margin convex, humeri rounded, width 0.441 mm, ratio of length to width 12.5:30, bearing a single long bristle on each posterior angle. Mesonotum and metanotum less rectangular in shape, shorter than pronotum, also bearing single long bristle on each posterior angle.

No indication of wing pads. First abdominal segment bearing single long bristle on posterior angle similar to those on thoracic segments. Scattered bristles on venter, very few on dorsum, 6 long bristles extending beyond tip of abdomen; spicules present on legs. Tarsi 2-segmented; claws simple, curved. Small pads situated at bases of claws.

Second Instar.—Differing from preceding as follows: More robust than first-instar nymph. Head width 0.450 mm, proportion of width to length 31:21. Proportion of antennal segments 7:16:15:19.5. Proportion of rostral segments, 19:17:18, overall length 0.727 mm.

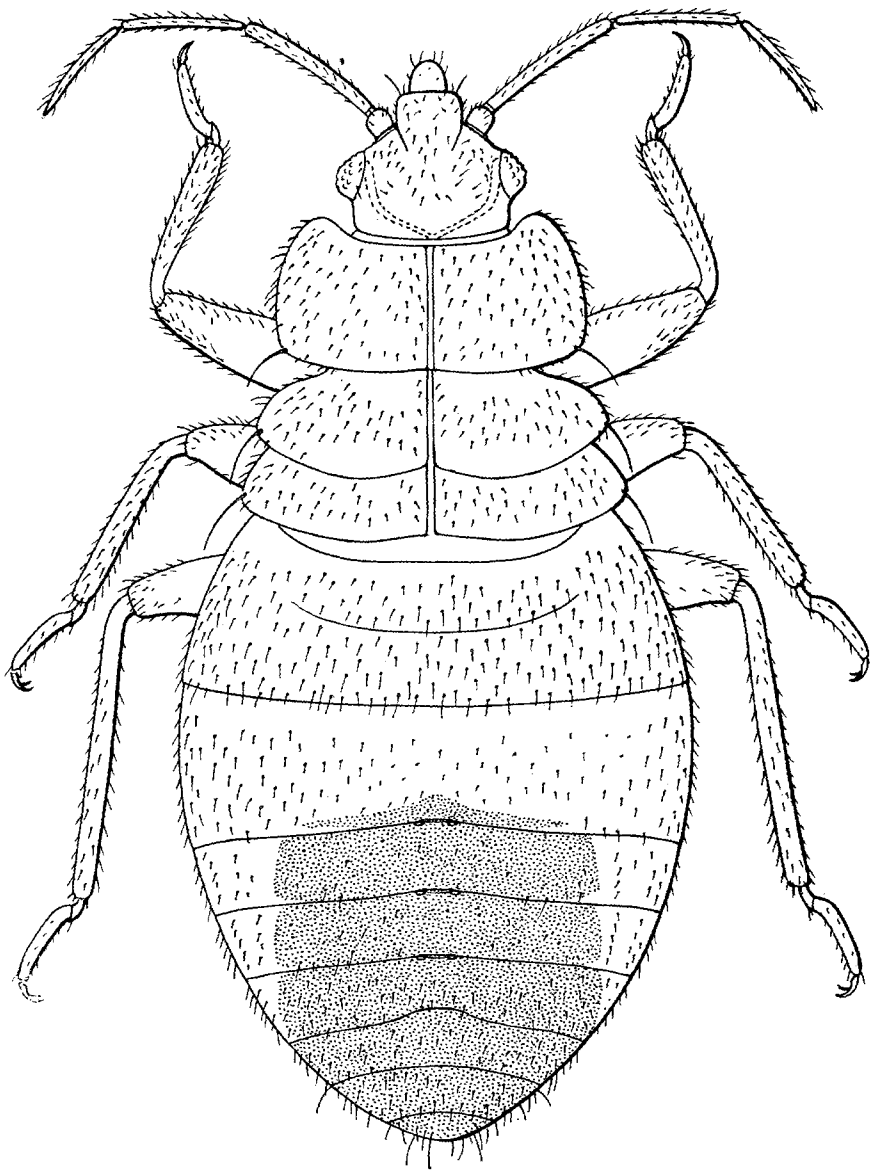

FIG. 13-23.—*Psitticimex uritui*. Last-instar nymph.

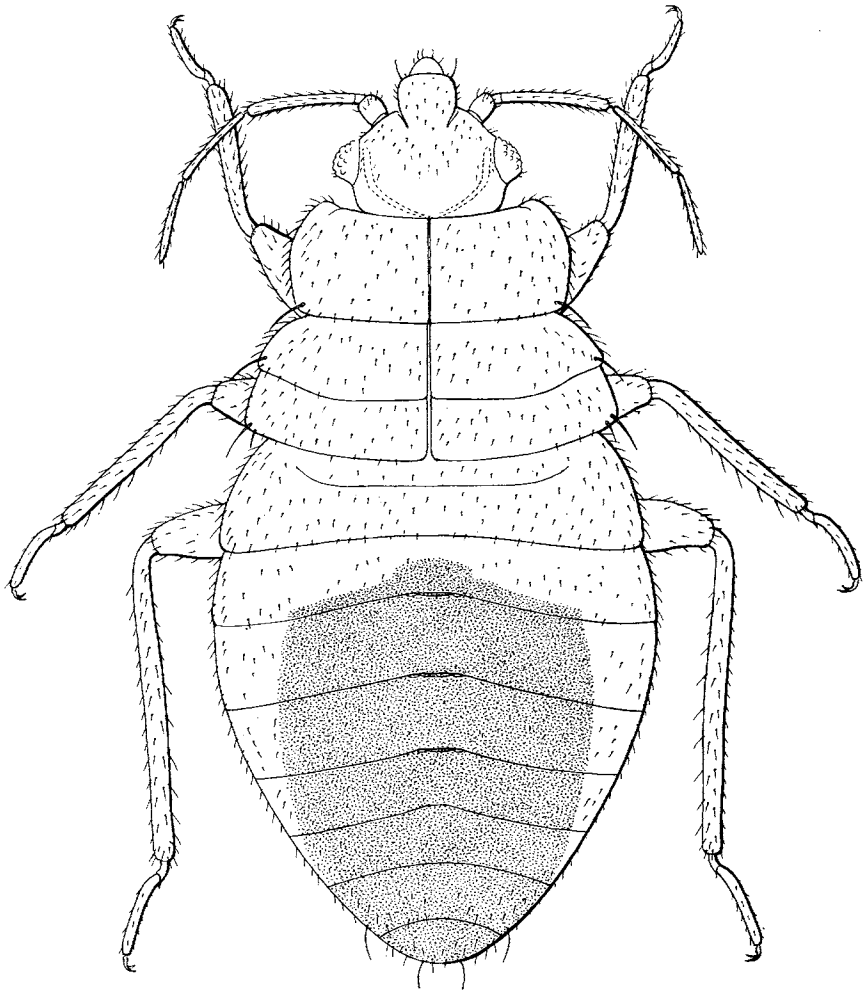

FIG. 13–24.—*Haematosiphon inodorus*. Last-instar nymph.

Apparent first abdominal segment not bearing long bristle on posterior angles. Overall body length 1.45 mm; abdomen width 0.770 mm; prothorax width 0.564 mm.

Third Instar.—Differing from preceding in following respects: Proportionately larger than previous instars. Head width 0.582 mm; proportion of width to length, 11:8. Proportion of antennal segments, 10:25.5:21.5:23.5. Proportion of rostral segments, 26.5:21.5:24, overall length 0.983 mm. Prothorax width 0.775 mm; abdomen width 1.11 mm; overall body length 2.14 mm.

Fourth (Last) Instar.—Differing from preceding in following respects: Proportionately larger than previous instars. Head width 0.741 mm; proportion of width to length,

24.5:17.5. Proportion of antennal segments 13:34.5:24.5:25. Proportion of rostral segments, 15:13:14.5, overall length 1.28 mm. Prothorax width 1.01 mm; abdomen width 1.51 mm; overall body length 2.94 mm.

The unusual feature of only 4 nymphal stages was verified by repeated rearings and by calculating growth ratios of head widths (Table 13–1).

Cimexopsis nyctalis List
(Fig. 13–25)

NYMPH.—*Last Instar.*—Head 0.63 mm wide; about ¼ broader than long, 22:17; eyes ⅕ as wide as interocular space. Antennae 1.12 mm long; proportion of segments 4:12:12:12. Rostrum approximately 0.5 mm long; proportion of segments about 7:5:6.

Pronotum 0.91 mm wide; a little more than 2½ times as wide as long, 32:12, widest anteriorly; sides with numerous short bristles and 2 longer stiff bristles at humeri, the longer of the two almost ½ as long as pronotum, 5:12. Mesonotum 1.05 mm wide; nearly 4 times as wide as long at middle, 37:10; hind margin concave at middle; sides with numerous small bristles and 1 longer bristle at each posterolateral angle. Metanotum 1.2 mm wide; 5 times as wide as long, 42:8, with a long bristle at each posterolateral angle; long bristles of meso- and metanota as long as longest of the pair on pronotum.

Abdomen with second segment totally membranous, third segment sclerotized posteriorly, the remaining segments sclerotized for their entire length but with abdomen clear and membranous along sides, broadly at first and more narrowly toward apex. Scent gland openings about as wide as clypeus.

Legs rather stout; hind femora 3 times as long as broad; tibiae with rows of fine, short, stiff bristles.

Size.—Length 3.31 mm, width (pronotum) 0.91 mm.

Synxenoderus comosus List
(Fig. 13–4e, 13–26)

NYMPH.—*Last Instar.*—Head 0.63 mm wide; slightly wider than long, 22:19; eyes $^1/_7$ as wide as interocular space. First and second antennal segments in the ratio of 5:13; remaining segments broken. Rostrum long, exceeding apices of front coxae; 0.8 mm long; proportion of segments about 8:7:11. Gula scarcely convex but prosternum thickened along anterior margin and a little sinuate at middle.

Pronotum 0.93 mm wide; 2½ times as wide as long; widest in front of middle; sides with bristles of various lengths, at least 2 on each side being very long like 2 humeral spines (broken in the specimens at hand).

Table 13–1.—Measurements of head widths and study of the progressive development in size from instar to instar in *Haematosiphon inodorus* (Lee 1955b).

Age group	Number measured	Range in size, mm	Mean, mm	Standard deviation	Growth quotient
First instar	25	0.356–0.403	0.382	±0.0117	—
Second instar	25	.425– .477	.450	± .0156	1.18
Third instar	25	.548– .616	.583	± .0183	1.30
Fourth instar	25	.682– .806	.741	± .0311	1.27
Adult male	25	.775– .884	.825	± .0298	1.11
Adult female	25	.791– .930	.874	± .0326	1.18
Average					1.21

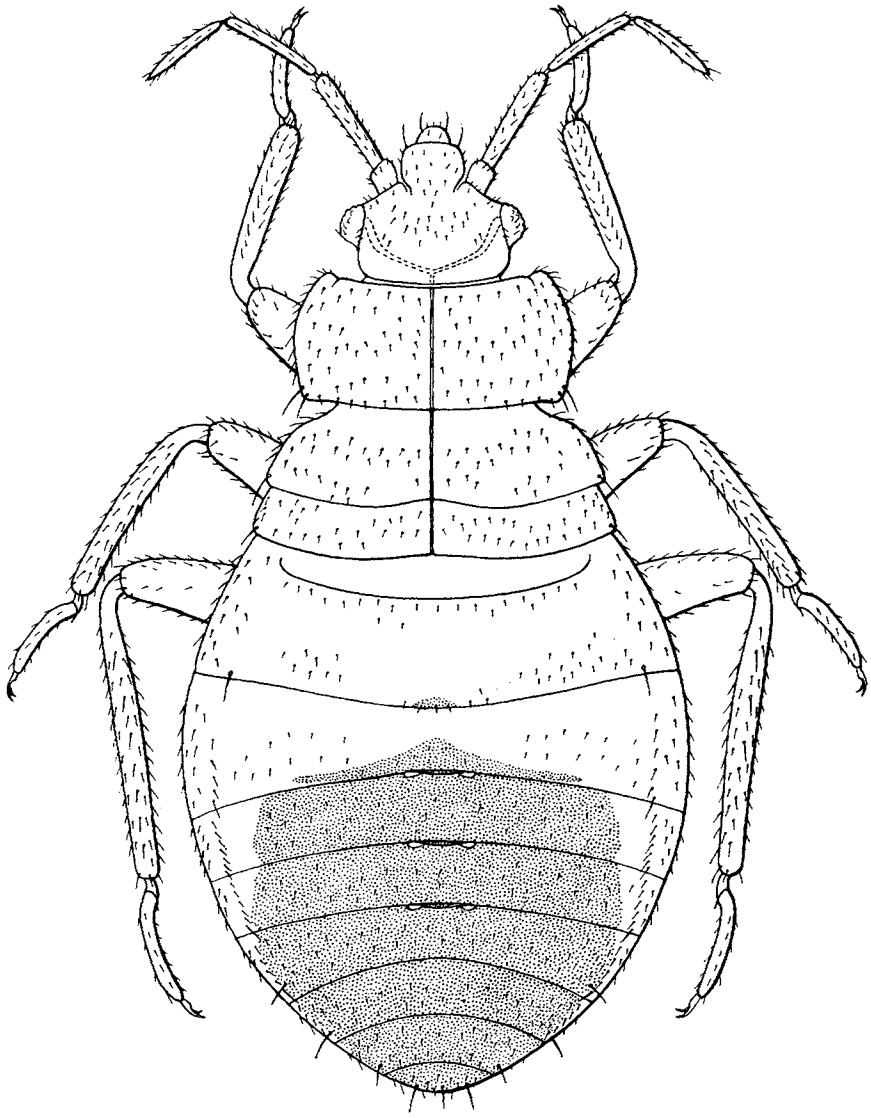

FIG. 13–25.—*Cimexopsis nyctalis*. Last-instar nymph.

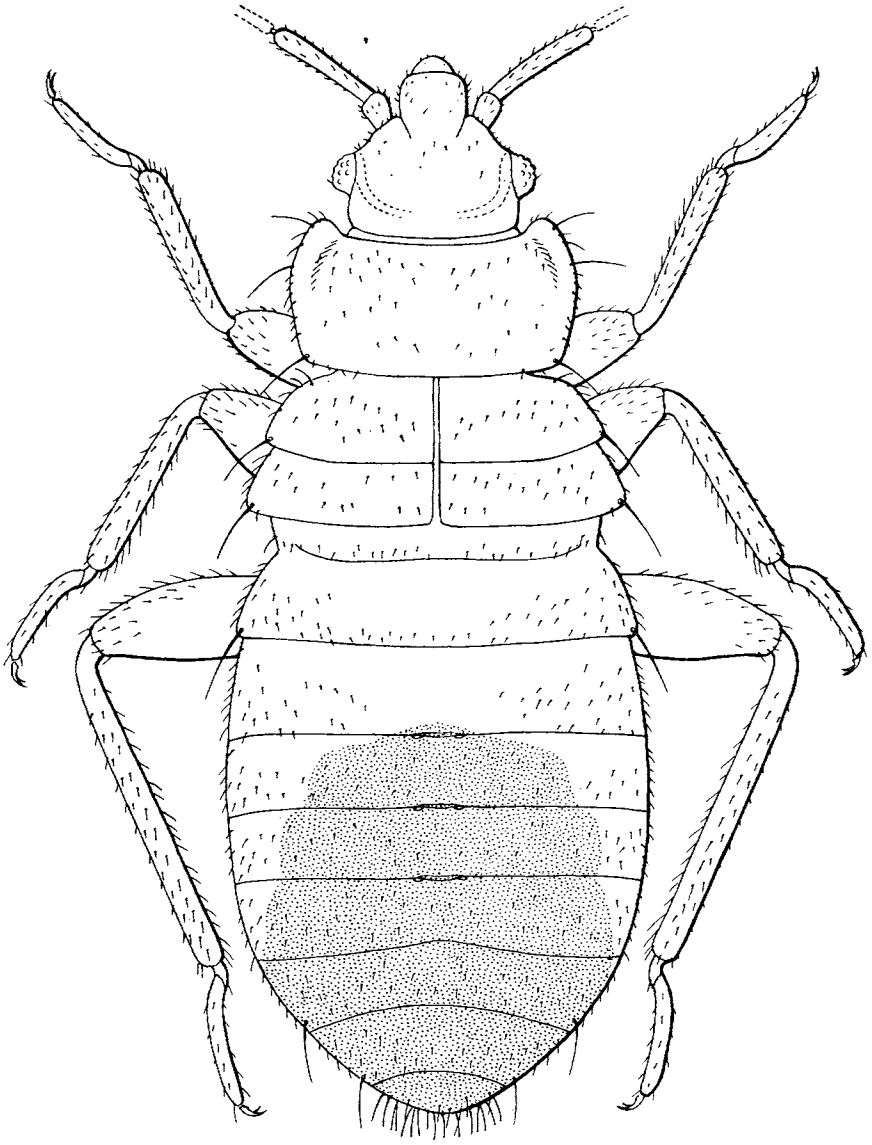

FIG. 13–26.—*Synxenoderus comosus*. Last-instar nymph.

Mesonotum 1 mm wide and 3½ times as wide as long; sides with short bristles and posterior angles each presumably with a long bristle (broken).

Metanotum about 1.2 mm wide and 5 times as wide as long, with a long bristle at each posterolateral angle approximately 0.25 mm long.

Second abdominal segment membranous and with an equally long bristle on each posterolateral angle. Sclerotized part of abdominal tergum as in *Cimexopsis* but scent gland openings narrower than width of clypeus, 5.5:8.

Legs essentially as in *Cimexopsis* with the same proportions of hind femora.

Size.—Length 3.3 mm, width (pronotum) 0.93 mm.

Hesperocimex sonorensis Ryckman

(Fig. 13–27)

Eggs (eye spot stage).—Length 0.97 mm; width 0.43 mm; the ring 0.24 mm; the cap 0.23 mm. Shorter and wider than *C. lectularius*, with the anterior end much more oblique. Ventral length to ring, ⅕ shorter than dorsal length. Cap convex and coarsely punctate, the punctures more elongate near the edges. Surface of chorion shining and minutely roughened by granules, without hexagonal reticulations. Egg shells depressed on either side of middle of ventral face. Eggs glued to substrate in a completely random manner as to direction of head or posterior end, but always with ventral (short) side up or more or less lateral.

Nymphs.—*First Instar.*—Elongate-oval, with several long bristles on each side. Length 1.14 mm. Head subtriangular, 0.33 mm wide. Eyes about ⅙ as wide as interocular space. Labrum with 4 prominent bristles, clypeus with two, one on each side anterolaterally. Prominent bristles on each side near bases of antennae. Antennae about 0.5 mm long; proportion of segments 5:9:10:17. Rostrum reaching apices of front coxae; proportion of segments approximately 10:8:12. Pronotum 0.43 mm wide and ⅓ as long as wide; 3 long bristles on each side, the posterior bristle longest; also with a long bristle anterolaterally on disk approximately behind each eye; other smaller bristles inconspicuous. Mesonotum slightly wider, 15.5:15 and distinctly shorter, 4:5, than pronotum; 3 bristles on each side, the posterior one the longest and disk with a long bristle sublaterally. Metanotum still wider, 0.5 mm, and shorter, 0.09 mm, with bristles as above but posterolateral ones double. First abdominal segment membranous and difficult to see. Second and third each with a prominent posterolateral bristle and smaller discal and lateral bristles. The remaining abdominal segments each with a prominent posterolateral bristle and smaller lateral and discal bristles. Legs with a few bristles in addition to short ones on tibiae. Tarsi with subapical bristles reaching about to apex.

Second Instar.—Larger, 1.6 mm long, with many additional bristles, the number of prominent ones approximately doubled, forming ill-defined transverse rows on the disks of segments.

Head broader, 0.4 mm. Pronotum 0.51 mm, mesonotum 0.57 mm, metanotum 0.65 mm. Antennae 0.57 mm long; proportion of segments approximately 3:5:5:7. Rostrum about 0.38 mm long; proportion of segments 5:3.5:5.

Third Instar.—Larger with more long bristles, especially along the sides. Length 1.65 mm. Head, 0.43 mm. Antennae as in previous instar. Rostrum, 0.44 mm; proportion of segments about 5:4:6. Pronotum 0.57 mm. Mesonotum 0.66 mm. Metanotum 0.71 mm. Longest bristles at sides still recognizable as one to a segment on each side posterolaterally.

Fourth Instar.—Larger, with bristles numerous over body but basically in the same pattern as to longest bristles. Length 2.28 mm. Head 0.54 mm. Antennae somewhat shriveled but approximately 0.63 mm, proportion of segments about 5:6:6:6. Rostrum reaching only to middle of fore coxae; proportion of segments about 6:5:8. Pronotal width 0.74 mm. Mesonotum 0.89 mm. Metanotum 1 mm.

Last Instar.—With short or long bristles throughout, numerous at sides, thus obscur-

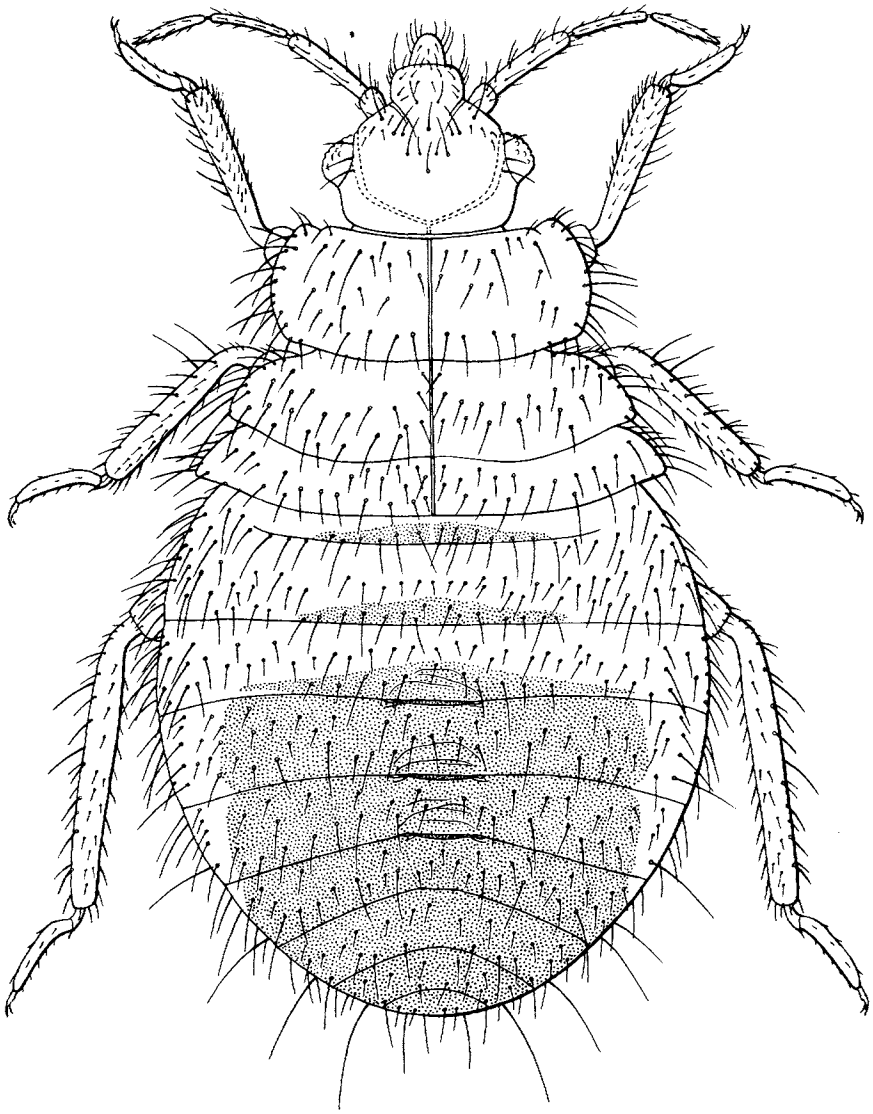

FIG. 13–27.—*Hesperocimex sonorensis*. Last-instar nymph.

ing the longest bristles of previous instars. Membranous area at base of abdomen extensive, expanded laterally and extending backward on either side of sclerotized tergites at least to sixth segment. Length 3.2 mm. Head width 0.71 mm. Antennae 0.94 mm long; proportion of segments 4:10:10:9. Rostrum reaching middle of fore coxae; proportion of segments approximately 8:6:10. Pronotal width 1.09 mm, mesonotum 1.33 mm, metanotum 1.57 mm.

Ryckman (1958) gives a table of measurements based on 21 nymphs. As might be expected, his averaged figures differ in small degree from those given above.

14 References Cited

Abalos, J. W., and P. Wygodzinsky. 1951. Las Triatominae Argentinas (Reduviidae, Hemiptera). Monogr. no. 2, Pub. no. 601, Min. Educ., de la Educ. Nac., Univ. Nac. Tucumán, Inst. Med. Reg. (Tucumán, Argentina), 178 p., 318 fig.

Abraham, R. 1934. Das Verhalten der Spermien in der weiblichen Bettwanze (*Cimex lectularius* L.) und der Verbleib der überschüssigern Spermamasse. Z. Parasitenk. 6: 559–91.

Acloque, A. 1897. Faune de France. III. J.-B. Baillière et Fils, Paris. viii + 516 p., 219 fig. (Cimicidae, p. 392, fig. 158C).

Adams, R. M. 1960. The origin of cities. Sci. Amer. 203: 153–68.

Adkins, T. R., Jr., and F. S. Arant. 1959. A technique for the maintenance of a laboratory colony of *Cimex lectularius* L. on rabbits. J. Econ. Entomol. 52 (4) : 685–6.

Aldrovandi, U. 1638. De animalibus insectis libri septum cum singulorum iconibus ad vivum expressis. 2nd ed. Clementem Ferronium, Bononiae. Vol. IV. 767 p. (De Cimice, p. 534). (Edit I, Bononiae, 1602.)

Allen, A. A. 1920. Banding bats. J. Mammalogy 2: 53–57, 4 fig.

Allen, G. M. 1939. Bats. Harvard Univ. Press, Boston, Mass. x + 368 p., 57 fig. (Dover reprint, 1962) (Cimicidae, p. 306–7).

Amyot, C. J. B., and A. Serville. 1843. Histoire naturelle des insectes. Hémiptères (In "Suites à Buffon") Paris. lxv + 675 p., 12 pl. (Cimicidae, p. 311–13).

Anciaux de Faveaux, F. 1959. La Voix de l'Orycterope. Bull. Sect. Speleologique du Cercle de la Panda. Jadotville, Congo Belg. 1: 1–42, 3 pl., 3 maps.

Andre, Ch. 1912. Recherches anatomiques et experimentales sur la punaise des lits. J. Phys. Path. Gén. 14 (3) : 600–75.

Anonymous. 1828. Moyens surs et faciles de detruire les punaises. 3rd ed., G. Mathot, Paris. 33 p.

1959. How to control bedbugs. U. S. Dep. Agr., Entomol. Res. Div., Leaflet no. 453, 6 p., 4 fig.

Aristotle. 1949. Historia Animalium. Vol. IV, The Works of Aristotle. D'Arcy W. Thompson, translator, under the supervison of J. A. Smith and W. D. Ross. Reprint of 1910 first ed. Clarendon Press, Oxford. Sections 486–633 + xv, appendix and index (Cimicidae, section 556).

Arkwright, J. A., E. E. Atkin, and A. Bacot. 1921. An hereditary rickettsia-like parasite of the bedbug (*Cimex lectularius*). Parasitology 13: 27–36.

Ashmore, S. A. 1938. Discussion on recent advances in methods of bedbug disinfestation. J. Roy. Sanit. Inst. 58: 536–44.

Bacot, A. W. 1914. The influence of temperature, submersion and burial on the survival of eggs and larvae of *Cimex lectularius*. Bull. Entomol. Res. 5: 111–17.

1921. Bionomics of *Cimex hirundinis*. Proc. Ent. Soc. London 69: ii.

Balfour, A. 1912. *Cimex rotundatus* in the Anglo-Egyptian Sudan. Bull. Entomol. Res. 2 (2) : 179–80.

Banks, N. 1910. Catalogue of the Nearctic Hemiptera-Heteroptera. Philadelphia. viii + 103 p. (Cimicidae, p. 25).

Bannerman, D. A. 1953. The Birds of the British Isles. Oliver and Boyd, London. Vol. 2, viii + 301 p., 41 pl. (Pied flycatcher, p. 268).

Barber, H. G. 1934. The first type fixation for *Cimex* Linnaeus. Bull. Brooklyn Entomol. Soc. 29: 106.

1939a. Insects of Porto Rico and the Virgin Islands. Hemiptera-Heteroptera (excepting the Miridae and Corixidae). Sci. Surv. Porto Rico, Virgin Islands. New York Acad. Sci. 14(3): 263–441, 36 fig. (Cimicidae, p. 397–8).

1939b. A new bat bug from the eastern United States. Proc. Entomol. Soc. Wash. 41: 243–6, 2 fig.

1941. Description of a new bat bug (Hemiptera-Heteroptera: Cimicidae). J. Wash. Acad. Sci. 31(7): 315–7, 1 fig.

Barnes, S. 1946. The influence of certain biological factors on the resistance of bedbugs (*Cimex lectularius,* L.) to DDT. Bull. Entomol. Res. 36 (4) : 419–22.

Beaucournu, J.-C. 1961. Ectoparasites des Chiroptères de l'ouest de la France. 1re partie. Ixodoidés, Cimicidés et Nycteribiidés. Bull. Soc. Sci. Bretagne 36: 315–38.

Beck, D. E. 1953. A study of some consortes found at a nesting site of the Northern Cliff Swallow, *Petrochelidon albifrons albifrons* (Rafinesque). Proc. Utah Acad. Sci., Arts, Lett. 30: 39–42.

Bedford, G. A. H. 1932. A synoptic check-list and host list of the ectoparasites found on South African Mammalia, Aves and Reptilia. 2nd ed. Rep. Vet. Res. S. Afr. 18: 223–523, 26 fig.

Benjamini, E., B. F. Feingold, and L. Kartman. 1960a. Allergy to flea bites. III. The experimental induction of flea bite sensitivity in

guinea pigs by exposure to flea bites and by antigen prepared from whole flea extracts of *Ctenocephalides felis felis*. Exp. Parasitol. 10: 214–22.

1960b. Antigenic property of the oral secretion of fleas. Nature 188: 959–60.

Bequaert, J. 1926. Medical Report of the Hamilton Rice Seventh Expedition to the Amazon, in conjunction with the Department of Tropical Medicine of Harvard University, 1924–1925. Part II. Medical and Economic Entomology. Contr. Harvard Inst. Trop. Biol. Med. no. 4, p. 157–360 (Cimicidae, p. 184–7).

1930. Medical and economic entomology. *In* The African Republic of Liberia and the Belgian Congo. Harvard African Exped. 1926–1927. Contributions from the Dep. Trop. Med. and Inst. Trop. Biol. Med., no. V. Harvard Univ. Press, Cambridge. Vol. II (3), ix + 569–1063 p., 476 illus., 28 text fig. (Cimicidae, p. 823–4).

Berghe, L. van den, M. Chardome, and E. Peel. 1959. Decouverte du cycle de transmission par un Cimicidae d'un trypanosome de chauve-souris insectivore. Folia Sci. Africae Centr. 5: 36–37.

Bergroth, E. 1892. Does *Acanthia pipistrelli* occur in North America? Entomol. News 3: 154–5.

Berlese, A. 1898. Fenomeni che accompagnano la fecondazione in taluni insetti. I, II. Riv. Patol. Veg. 6(3): 1–16; 7 (1): 1–18.

1903. Gli Insetti. Milano Sociéta Editrice Libraria. Vol. I, x + 1004 p., 1290 fig., 10 pl. (Cimicidae, p. 955–7).

Biester, H. E., and L. H. Schwarte. 1952. Diseases of poultry. 3rd ed., Iowa State College Press, Ames, xiii + 1245 p.

Blanford, W. T. 1903. Sokotra. Nature 69: 199–201, 2 fig. (*Clinophilus*, p. 200).

1904. The type species of *Cimex*. Nature 69: 464–5.

1905. The type species of *Cimex*. Entomologist 38: 110.

Blatchley, W. S. 1926. Heteroptera or True Bugs of Eastern North America. The Nature Publishing Co., Indianapolis, Ind. 1116 p., 2 pl., 215 fig. (Cimicidae, p. 616–20, fig. 154–6).

1928. The Mexican chicken bug in Florida. Florida Entomol. 12: 43–44.

Bodenheimer, F. S. 1928–1929. Materialien zur Geschichte der Entomologie bis Linné. Vols. I, II. W. Junk, Berlin. Vol. I (1928): x + 498 p., 155 fig. Vol. II (1929): vi + 486 p., 98 fig.

1960. Animals and Man in Bible Lands. Collection de Traveaux de l'Académie Internationale d'Histoire des Sciences, no. 10. E. J. Brill, Leiden. 232 p., frontisp. (Cimicidae, p. 73).

Bonhag, P. F. 1958. Ovarian structure and vitellogenesis in insects. Annu. Rev. Entomol. 3: 137–60.

Bonhag, P. F., and W. J. Arnold. 1961. Histology, histochemistry and

tracheation of the ovariole sheaths in the American cock-roach *Periplaneta americana* (L.). J. Morphol. 108 (1): 107–18.

Bonhag, P. F., and J. R. Wick. 1953. The functional anatomy of the male and female reproductive systems of the milkweed bug, *Oncopeltis fasciatus* (Dallas) (Heter. Lygaeidae). J. Morphol. 93 (2): 177–284.

Bonhote, J. L. 1901. On the birds collected during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. Proc. Zool. Soc. London 1: 57–81.

Börner, C. 1934. Ueber System und Stammesgeschichte der Schnabelkerfe. Entomol. Beihefte 1: 138–44. (Cimicidae, p. 144).

1935. Die Tierwelt Mitteleuropas, Insekten, 1 Teil. 4 (3) x. Quelle & Meyer, Leipzig. 113 p., 181 fig. (Cimicidae, p. 9, 11, 15, 18, 36, fig. 27).

Bowhill, T. 1906. Note on Haematozoa observed in a bat and the occurrence of *Acanthia pipistrelli* Jenyns in South Africa. J. Hyg. 6: 246–7, 1 pl.

Bradshaw, G. V. R., and A. Ross. 1961. Ectoparasites on Arizona bats. J. Ariz. Acad. Sci. 1 (4): 109–12 (Cimicidae, p. 109–12).

Braidwood, R. J. 1960. The agricultural revolution. Sci. Amer. 203: 130–48.

Brindley, M. D. H. 1930. On the metasternal scent-glands of certain Heteroptera. Trans. Entomol. Soc. London 78: 199–207, 1 pl.

Britten, H. 1916. *Cimex pipistrelli* Jenyns, in Oxfordshire. Entomol. Mon. Mag. 52: 142.

Britton, W. E. 1923. Guide to the insects of Connecticut. Part IV. The Hemiptera or sucking insects of Connecticut. State Geol. Nat. Hist. Surv. Bull. 34: 1–805, 169 fig., 20 pl.

Brown, S. W. 1961. Fracture and fusion of coccid chromosomes. Nature 191(4796): 1419–20.

Brumpt, E. 1910. Précis de Parasitologie. 1st ed., Masson et C^ie^., Paris. xxvi + 915 p., 4 pl., 683 fig.

Büchner, P. 1921. Ueber ein neues, symbiotisches Organ der Bettwanze. Biol. Zentralbl. 41: 570–4.

1923. Studien an intracellularen Symbionten. IV. Die Bakteriensymbiose der Bettwanze. Arch. Protistenk. 46: 225–63, 3 pl., 2 fig. (*Cimex* embryol., fig. on p. 238).

1953. Endosymbiose der Tiere mit pflanzlichen Mikroorganismen. Birkhäuser Verlag, Stuttgart. 771 p., 3 pl., 366 fig. (Cimicidae, p. 209, 409–17, 570, 577, 599, 600, 635, 683, 716, 4 fig.).

Buffon, G. L. L. de. 1808. Histoire Naturelle des Insectes, etc. Deterville, Paris. Vol. II, 306 p. (Cimicidae, p. 201–2, 204).

Burton, G. J. 1963. Bedbugs in relation to transmission of human diseases. Pub. Health Rep. 78: 513–24.

Busvine, J. R. 1959. Insecticide-resistance in bed-bugs. Bull. World Health Organ. 19: 1041–52.

Butler, E. A. 1893. Our household insects. Longmans, Green and Co., London. vii + 344 p., 27 pl., 113 fig. (Cimicidae, p. 273–303, pl. vi, fig. 85–98).

1923. A Biology of the British Hemiptera-Heteroptera. H. F. and G. Witherby, London. viii + 682 p., 6 pl.

Buxton, P. A., and C. G. Johnson. 1942. Ecology of the bed-bug: Summary of new knowledge. *in* Report of the Committee on Bed-Bug Infestation, 1935–1940. Med. Res. Counc., London, Special Report Series no. 245, p. 6–17.

Carayon, J. 1946. Pénétration et dispersion des spermatozoïdes dans l'organisme des femelles de certains Hémiptères. Compt. Rend. Acad. Sci. 222: 107–9 (Cimicidae, p. 107–9).

1952a. Existence chez certains Hémiptères Anthocoridae d'un organe analogue à l'organe de Ribaga. Bull. Mus., 2e ser., 24 (1): 89–97.

1952b. Existence d'un double orifice génital et d'un tissu conducteur du genre *Alleorhynchus*. Compt. Rend. Acad. Sci. 234: 751–3.

1953a. Organe de Ribaga et fécondation chez un Hémiptère Cimicidée du Cambodge; *Aphraniola orientalis* Ferris et Usinger. Rev. franç. Entomol. 20 (2): 139–46, 3 fig.

1953b. Existence d'un double orifice génital et d'un tissu conducteur des spermatozoïdes chez les Anthocorinae (Hémipt. Anthocoridae). Compt. Rend. Acad. Sci. 236: 1206–8.

1954a. Organes assumant les fonctions de la spermathèque chez divers Hétéroptères. Bull. Soc. Zool. France 79 (2–3): 189–97.

1954b. Fécondation hémocoelienne chez un Hémiptère Cimicidé dépourvu d'organe de Ribaga. Compt. Rend. Acad. Sci. 239: 1542–4, 2 fig.

1957. Introduction à l'étude des Anthocoridae omphalophores (Hemiptera-Heteroptera). Ann. Soc. Entomol. France 126: 159–97.

1959. Insémination par "spermalège" et cordon conducteur de spermatozoïdes chez *Stricticimex brevispinosus* Usinger (Heteroptera, Cimicidae). Rev. Zool. Bot. Afr. 60 (1–2): 81–104, 5 fig.

1964. Les aberrations sexuelles "Normalisées" de certains Hémiptères Cimicoidea. *in* Brion, A., et Henri Ey. "Psychiatrie animale". Bibliothèque neuro-psychiatrique de langue Française, p. 283–94.

Carayon, J., and R. L. Usinger. 1965. A new genus of Neotropical Anthocoridae that resembles the bed bug. Pan-Pacific Entomol. 41: 200–4.

Carazzi, D. 1902. La borsa di Berlese nella dei letti. Int. Monatsschr. Anat. Phys. 19: 337.

Carvalho, J. C. M. 1939. Sobre a biologia do *Ornithocoris toledoi*

Pinto, 1927, percevejo dos galinheiros em Minas Gerais (Hemiptera, Cimicidae). Ceres 1: 128–40.

Castellani, A., and A. J. Chalmers. 1913. Manual of Tropical Medicine. 2nd ed. Baillière, Tindall, and Cox, London. xxxii + 1744 p., 630 fig. (Clinocoridae, p. 636–40).

1919. Manual of Tropical Medicine. William Wood and Co., New York. x + 2436 p., 909 fig., 16 pl.

Champion, G. C. 1900. Biologia Centrali-Americana. Insecta-Rhynchota, Hemiptera-Heteroptera. Vol. II. Taylor and Francis, London. xvi + 416 p., 22 pl. (Cimicidae, p. 336–7).

Chandler, A. C. 1961. Introduction to Parasitology with Special Reference to the Parasites of Man. 10th ed. John Wiley and Sons, New York. xii + 822 p., 273 fig.

Chatton, E., and G. Blanc. 1918. Large éclectisme parasitaire de la paunaise des lits. Son entretien aux dépens des reptiles. Culture du trypanosome du gecko chez la punaise des lits. Bull. Soc. Path. Exot. 11 (5): 382.

Chickering, A., and B. Bacorn. 1933. Spermatogenesis in the Belostomatidae. IV. Multiple chromosomes in *Lethocerus*. Pap. Mich. Acad. Sci. 17: 529–533.

China, W. E. 1930. Insects of Samoa. Part II. Hemiptera. p. 81–162.

1938. From letter, *in* W. Stichel, Illustrierte Bestimmungstabellen der deutschen Wanzen (Hemiptera-Heteroptera). Geographische Verbreitung III. Ergänzungen und Berichtigungen I. Lief. 15. Naturwissenschaftl. Publik., Berlin-Hermsdorf. p. 403–58, 8 fig. (Cimicidae, p. 456).

China, W. E., and N. C. E. Miller. 1955. Check-list of family and subfamily names in Hemiptera-Heteroptera. Ann. Mag. Nat. Hist. (12) 8: 257–67 (Cimicidae, p. 263).

China, W. E., and J. G. Myers. 1929. A reconsideration of the classification of the cimicoid families (Heteroptera) with the description of two new spider-web bugs. Ann. Mag. Nat. Hist. (10) 3: 97–125, 5 fig. (Cimicidae, p. 116, 118).

Chittenden, F. H. 1898. The European bat bug in America. U. S. Dep. Agr., Div. Entomol., Bull. (N. S.) 18: 97.

Chow, C. Y., T. C. Huang, and T. F. Yue. 1950. Bibliography of Chinese arthropods of medical and veterinary importance. Quart. J. Taiwan Mus. 3 (3): 157–85 (Cimicidae, p. 182–3).

Christophers, S. R., and F. W. Cragg. 1922. On the so-called "penis" of the bed-bug (*Cimex lectularius* L.) and on the homologies generally of the male and female genitalia of this insect. Indian J. Med. Res. 9: 445–63, 3 pl.

Clay, T., and G. H. E. Hopkins. 1950–1960. The early literature on Mallophaga (4 pt.) 155 p., 13 pl., 270 fig. Bull. Brit. Mus. [Nat.

Hist.], (Entomol.) Vol. 1, no. 3; Vol. 2, no. 1; Vol. 3, no. 6; Vol. 9, no. 1).

Cloudsley-Thompson, J. L. 1958. Spiders, scorpions, centipedes and mites. Pergamon Press, N. Y. xiv + 228 p., 40 fig., 17 pl.

Comstock, J. H. 1888. An Introduction to Entomology. Publ. by author, Ithaca, N. Y. iv + 234 p., 4 pl., 201 fig. (Cimicidae, p. 204–5).

Cordero, E. H., and E. G. Vogelsang. 1928. Dos nuevas especies del género *Cimex* parásitas de aves. Bol. Inst. Clin. Quir. 4 (28–31): 671–6, 4 fig. (Also in Cuarta Reunión Soc. Argent. Pat. Reg. del Norte, Santiago del Estero, same pagination).

Cornwall, J. W. 1923. Note on the salivary glands and sucking apparatus of *Cimex rotundatus*. Indian J. Med. Res. 10: 687–91, 11 fig.

Cornwall, J. W., and W. S. Patton. 1914. Some observations on the salivary secretion of the commoner blood-sucking insects and ticks. Indian J. Med. Res. 2: 569–93 (Cimicidae, p. 581–2).

Costa, A. 1843–1860. Cimicum Regni Neapolitani Centuriae. Napoli. 2:16 (1843). 3 (7):160 (1847). 4:67 (1852). Additamenta ad Centurias Cimicum Regni Neapolitani. Napoli. 1, fig. 2 (1860).

Costa Leite, J. 1948. *Cimex hemipterus* (Hemiptera, Cimicidae). An. Acad. Brasil. Cienc. 20 (3): 273–6, 4 fig.

Cowan, F. 1865. Curious Facts in the History of Insects. J. B. Lippincott & Co., Philadelphia. 396 p.

Cowdry, E. V. 1923. The distribution of Rickettsia in the tissues of insects and arachnids. J. Exp. Med. 37: 431–56.

Cragg, F. W. 1915. A preliminary note on fertilization in *Cimex*. Indian J. Med. Res. 2: 698–705.

1920. Further observations on the reproductive system of *Cimex* with special reference to the behaviour of the spermatozoa. Indian J. Med. Res. 8: 32–79, pl. 5–12, fig. 1–4.

1923. Observations on the bionomics of the bed-bug (*Cimex lectularius* L.), with special reference to the relations of the sexes. Indian J. Med. Res. 11 (2): 449–73.

1925. Observation on the reproductive system of *Cimex:* impregnation. Indian J. Med. Res. 12: 451–5.

Cummings, B. F. 1918. The bed-bug, its habits and life history and how to deal with it. 2nd ed. Brit. Mus. (Nat. Hist.), Econ. Series no. 5, 20 p., 7 fig.

Curtis, J. 1835. British Entomology. London (*Cimex lectularius,* XII, p. 569, pl. 569, fig. 9).

Darlington, C. D. 1939. The genetical and mechanical properties of the sex chromosomes. V. *Cimex* and the Heteroptera. J. Genet. 39 (1): 101–37.

Dasgupta, B., and H. N. Ray. 1955. Studies on the follicle cells of bed bug. Proc. Zool. Soc. Calcutta 8: 1–7, 1 pl.

1956. Observations on the "Corpus luteum" and the "NR bodies" in the female gonads of bed-bug. Proc. Zool. Soc. Calcutta 9(2): 55–63.

Davis, N. T. 1956. The morphology and functional anatomy of the male and female reproductive systems of *Cimex lectularius* L. (Heteroptera, Cimicidae). Ann. Entomol. Soc. Amer. 49 (5) : 466–93.

1964. Studies of the reproductive physiology of Cimicidae (Hemiptera)—I. Fecundation and egg maturation. J. Insect Physiol. 10: 947–63, 5 fig.

1965a. Studies of the reproductive physiology of Cimicidae (Hemiptera). II. Artificial insemination and the function of the seminal fluid. J. Insect Physiol. 11: 355–66.

1965b. Studies of the reproductive physiology of Cimicidae (Hemiptera). III. The seminal stimulus. J. Insect Physiol. 11: 1199–1211.

De Bomare, V. 1764. La punaise de lit, *Cimex domesticus.* Dictionnaire raisonné universal d'histoire naturelle; contenant l'histoire des animaux, des végétaux et des minéraux, et celle, etc., etc. Paris. 4: 519–22.

DeGeer, C. 1773. Punaise des lits. Mémoires pour servir a l'histoire des insects. Stockholm. 3: 296–305, pl. 17, fig. 9–15.

1780. Abhandlungen zur Geschichte der Insekten. G. B. Raspe, Nürnberg. 3: 1–454, index, 44 pl. (Cimicidae p. 195–200, pl. 17, fig. 9, 10).

D'Herculais, J. K. 1886. La punaise de lit et ses appareils odoriférants. —Des glandes abdominales dorsale de la larve et de la nymphe; des glandes thoraciques sternales de l'adulte. Compt. Rend. Acad. Sci. 103: 81–84. Separate, Paris, 5 July 1886, 4 p.

Dickerson, G., and M. M. J. Lavoipierre. 1959. Studies on the methods of feeding of blood-sucking arthropods. II. The method of feeding adopted by the bed-bug (*Cimex lectularius*) when obtaining a blood-meal from the mammalian host. Ann. Trop. Med. Parasitol. 53: 347–57, 5 fig.

Dioscorides. 1959. The Greek Herbal of Dioscorides, illustrated by a Byzantine, A. D. 512, Englished by John Goodyear, A. D. 1655, Edited and first printed A. D. 1933 by Robert T. Gunther. Hafner Publ. Co., New York. p. ix + 701, fig. (Bk. II, 36 Koreis; Bed Bugs, p. 101).

Distant, W. L. 1904. The Fauna of British India, including Ceylon and Burma. Rhynchota, vol. II. (Heteroptera). Taylor and Francis, London. xvii + 503 p., 319 fig. (Cimicidae, p. 410–11).

1910. The Fauna of British India, including Ceylon and Burma. Rhynchota, vol. V, Heteroptera: Appendix. Taylor and Francis, London. xii + 362 p., 214 fig.

Djonic, S. 1937. Ueber die Möglichkeit der Verbreitung der Bettwanze

[*Cimex (Acanthia) lectularia* L.] durch die Schwalbe (*Hirundo urbica* L.). Zool. Anz. 119 (1–2): 46–48.

Dohrn, A. 1859. Catalogus Hemipterorum. Entomol. Verein Stettin. vii + 112 p.

Doner, M. H. 1945. Biology and identification of bedbugs. Pests 13 (7): 5–7.

Douglas, J. W. 1867. True bugs. Entomol. Mon. Mag. 4: 20–21 (Cimicidae, p. 20–21).

1871. Insects in birds' nests. Entomol. Mon. Mag. 8: 64–65.

1883. *Cimex* or *Acanthia*. Entomol. Mon. Mag. 19: 202–3.

1897. Cimices in birds' nests? Entomol. Mon. Mag. (Ser. 2) 8(33): 212.

1897. Query respecting *Acanthia ciliata* Eversmann. Entomol. Mon. Mag. (Ser. 2) 8 (33): 236–7.

Douglas, J. W., and J. Scott. 1865. The British Hemiptera. Vol. I. Hemiptera-Heteroptera. Ray Society, R. Hardwicke, London. xii + 628 p., 21 pl. (Cimicidae, p. 509–12).

Downes, W. 1927. A preliminary list of the Heteroptera and Homoptera of British Columbia. Proc. Entomol. Soc. Brit. Columbia 23: 1–22 (Cimicidae, p. 11).

Drenski, P. 1928. Die in Bulgarien lebenden Wanzenarten (Fam. Cimicidae) und die Mittel zur Bekämpfung derselben (Russian with German summary, p. 94–95). Trav. Soc. Bulg. Sci. Nat. 13: 63–93, 3 fig.

Dubinin, V. B. 1947. Ekologicheskie nabludeniya nad krovososushchimi klopami sem. Cimicidae Daurskoi stepi. Entomol. Oboz. 29: 232–46.

Dufour, L. 1833. Recherches anatomiques et physiologiques sur les Hémiptères, accompagnées de considérations relatives à l'histoire naturelle et à la classification de ces insectes. Mémoire des Savants étrangers à l'Acad. de Science. IV. Paris. Separate, Paris, 1833 (*Cimex*, p. 343–4, fig. 174).

Dugés, A. 1892. *Acanthia inodora,* A. Dug. (Chinches de gallos). La Naturaleza II (1891–1896), Ser. 2, p. 169–70, pl. VIII, fig. 1–7.

Dunn, L. H. 1924. Life history of the tropical bedbug, *Cimex rotundatus,* in Panama. Amer. J. Trop. Med. 4 (1): 77–83.

Dupuis, C. 1955. Les génitalia des Hémiptères Hétéroptères. Mém. Mus. nat. d'Hist. nat., A. Zool. Nouv. Sér. 6 (4): 183–278, 17 fig. (Cimicidae, p. 203, 205, 207, 210, 211, 230, 242, 250, 251).

Eddy, P. F. 1931. Insects in English poetry. Sci. Mon. 33: 53–77, 148–63 (Cimicidae, p. 3, 4).

Eichler, W. 1935. Die Vogelparasiten. Eine Uebersicht über die verschiedenen Gruppen. I. Die Vogelwanzen. Orn. Mschr. 60 (5–6): 90–96.

1937. Ueber die bei europäischen Vögeln vorkommenden Wanzenarten. Zool. Anz., 120 (11–12): 267–71.

1942. *Oeciacus gerdheinrichi* nov. spec., eine Salanganenwanze (Heteroptera, Cimicidae) von *Collocalia spodiopygia sororum* Stresemann 1931 aus Celebes. Mitt. Zool. Mus. Berlin 25: 292–9, 1 fig.

Essig, E. O. 1942. College Entomology. Macmillan, New York. vii + 900 p., 308 fig.

Eversmann, E. 1841. Quaedam insectorum species novae. Bull. Soc. Imp. Nat. Moscou 14: 351–60.

Fabricius, J. C. 1775. Systema entomologiae sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae (Cimicidae, p. 693–4).

1776. Genera insectorum eorumque characteres naturales secondum numerum, figuram, situm et proportionem omnium partium oris adiecta mantissa specierum nuper detectarum. Chilonii (Cimicidae, p. 180, 181).

1787. Mantissa insectorum sistens species nuper detectas adiectis synonymis, observationibus, descriptionibus, emendationibus. Hafniae. Vol. II, 374 p. (Cimicidae, p. 278).

1794. Entomologia systematica emendata et aucta. Hafniae. Vol. IV, 472 p. (Cimicidae, p. 67–8).

1803. Systema rhyngotorum secundum ordines, genera, species, adiectis synonymis, locis, observationibus, descriptionibus. Brunsvigae. 314 p. (Cimicidae, p. 1, 112).

Fallén, C. F. 1829. Hemiptera Sueciae. Berlingiana. London. 186 p. (*Acanthia,* p. 140–42).

Ferris, G. F., and R. L. Usinger. 1953. A new species of *Aphraniola* from Cambodia (Hemiptera, Cimicidae). Rev. Franç. Entomol. 20 (2): 138–9.

1957a. Notes and descriptions of Cimicidae. Microentomology 22: 1–37.

1957b. Hemiptera Heteroptera: Cimicidae. A new genus and species from South Africa. *In* Hanström, Brinck, and Rudebeck, South African Animal Life. 4: 374–6, 1 fig.

1959. A new species of *Stricticimex* from Kenya (Hemiptera: Cimicidae). Ann. Entomol. Soc. Amer. 52 (1): 81–82, 2 fig.

Fieber, F. X. 1851. Genera Hydrocoridum. Abhandl. König. Böhmisch. Ges. Wiss. Prag 5 (7): 181–212.

1860–1861. Die europäischen Hemiptera. Halbflügler (Rhynchota Heteroptera). C. Gerold's Sohn, Wien. vi + 112 p., 1860; 113–444 p., 2 pl., 1861 (Cimicidae, p. 24, 37, 135, 402).

Flor, G. 1860. Die Rhynchoten Livlands in systematischer Folge beschrieben. Dorpat. Vol. I, 825 p. (*Acanthia lectularia,* p. 672–5).

Frickinger, H. W. 1920. *Chelifer cancroides* als Feind der Bettwanze (*Cimex lectularius* L.). Z. Angew. Entomol. 6: 170–1.

Gaillard, H. 1934. Rôle de la mue embryonnaire des Reduvides héma-

tophages dans le processus d'éclosion. Ann. Parasitol. Hum. Comp. 12: 345–9, 2 fig.

Galli-Valerio, B. 1927. Notes de parasitologie et de technique parasitologique. C) Observations sur quelques parasites animaux. 13. Invasion d'une habitation par *Acanthia pipistrelli* Jenyns. Zentralbl. Bakt. 103: 177–82.

Geisthardt, G. 1937. Ueber die ökologische Valenz zweier Wanzenarten mit verschiedenen Verbreitungsgebiet. Z. Parasitol. 9: 150–202.

Geoffroy, E. L. 1762. Histoire abrégée des insectes qui se trouvent aux environs de Paris, etc. Paris. Vol. I, xxviii + 556 p., 10 pl. (Cimicidae, p. 434–5).

George, J. E., and R. W. Strandtmann. 1960. New records of ectoparasites on bats in West Texas. Southwestern Natur. 5 (4) : 228–9.

Gillette, C. P. 1890. *Acanthia pipistrella* in nests of the barn swallow. Entomol. News 1: 26–27.

Gillette, C. P., and C. F. Baker. 1895. A preliminary list of Hemiptera of Colorado. Colorado Agr. Exp. Sta., Bull. no. 31 (no. I, Tech. Ser.) (Cimicidae, p. 56).

Girault, A. A. 1905. The bedbug, *Clinocoris* (= *Cimex* = *Acanthia* = *Klinophilos*) *lectularia* Linnaeus. Part I. Life-history at Paris, Texas, with biological notes, and some considerations on the present state of our knowledge concerning it. Psyche 12: 61–74. Reviewed, Editors (1906).

1906a. The bedbug, *Cimex lectularius* Linnaeus. Part II. Critical remarks on its literature, with a history and bibliography of pathogenic relations. Psyche 13: 42–58. Idem, p. 107.

1906b. A bibliography of the bedbug, *Cimex lectularius* Linnaeus. Zool. Ann. 2 :143–201.

1908. Notes on the feeding habits of *Cimex lectularius* Linnaeus. Psyche 15: 85–87.

1910. Preliminary studies on the biology of the bedbug (*Cimex lectularius*). I. The effect of quantitatively controlled food supply on development. J. Econ. Biol. 5: 88–91.

1912. Preliminary studies on the biology of the bedbug, *Cimex lectularius*. II. Facts obtained concerning the duration of its different stages. J. Econ. Biol. 7: 163–88.

1913. Fragments on North American insects. VI. 9. The fowl bug, *Cimex columbarius* Jenyns (Hemip.). Entomol. News 24: 341–2.

1914. Preliminary studies on the biology of the bed-bug, *Cimex lectularius*, Linn. J. Econ. Biol. 9: 25–45.

Girault, A. A., and J. F. Strauss. 1905. The bedbug, *Clinocoris lectularius* (Linnaeus), and the fowl bug, *Clinocoris columbarius* (Jenyns) : host relations. Psyche 12: 117–23.

Glover, B. T. J. 1938. Demonstration of apparatus used in bed-bug disinfestation. J. Roy. Sanit. Inst. 58: 545–55.

1939. The use of heavy Naphtha in bed-bug disinfestation. J. Roy. Sanit. Inst. 59: 671–81.

Glover, T. 1876. Manuscript notes from my journal, or illustrations of insects, native and foreign. Order Hemiptera, suborder Heteroptera. Washington (Cimicidae, p. 18–19, pl. III, fig. 9).

Goidanich, A. 1947. *Oeciacus hirundinis* Jenyns versus Dryobatem: allotrophia aut allotopia? (Hemiptera, Cimicidae). Boll. Ist. Entomol. Univ. Stud. Bologna 16: 1–22, 11 fig.

Gordon, R. M., and W. Crewe. 1948. The mechanisms by which mosquitoes and tsetse-flies obtain their blood-meal, the histology of the lesions produced, and the subsequent reactions of the mammalian host; together with some observations on the feeding of *Chrysops* and *Cimex*. Ann. Trop. Med. Parasitol. 42 (3–4): 334–56.

Gregson, J. D. 1949. Notes on the occurrence of *Ornithodoros hermsi* in British Columbia, and its probable relation to relapsing fever (Argasidae, Ixodoidae). Proc. Entomol. Soc. Brit. Columbia 45: 15–16.

Gulde, Johannes. 1941. Die Wanzen Mitteleuropas. Hemiptera Heteroptera. Otto H. Wrede, Frankfurt, VIII Teil, p. 117–131.

Gunther, R. T. 1933. (See Dioscorides)

Halbert, J. N. 1935. A list of the Irish Hemiptera (Heteroptera and Cicadina). Proc. Roy. Irish Acad. (B) 42 (8): 211–318.

Hall, M. C. 1937. The bedbug, its relation to public health, its habits and life history, and methods of control. Public Health Reports, Suppl. 129, Public Health Service. ii + 7 p.

Harrisson, T. 1958. Fauna of the Great Cave, Niah, Borneo. Cent. Bicent. Congr. Univ. Malaya, Singapore. Abstracts of papers, p. 27.

Hartnack, H. 1939. 202 Common Household Pests of North America. Hartnack Publ. Co., Chicago, Ill. 319 p. (Cimicidae, p. 234–61).

Hase, A. 1917. Die Bettwanze (*Cimex lectularius* L.) ihr Leben und ihre Bekämpfung. Monogr. Angew. Entomol. No. 1. Z. Angew. Entomol. IV, Beiheft I, vi + 144 p., 6 pl., 131 text fig.

1918. Beobachtungen über den Kopulationsvorgang bei der Bettwanze, *Cimex lectularius* L. S. B. Ges. Naturf. Freunde 8: 311–21.

1930. Weitere Versuche zur Kenntnis der Bettwanzen *Cimex lectularius* L. und *Cimex rotundatus* Sign. (Hem.-Rhynch.). Beitr. Exper. Parasitol. 4. Z. Parasitenk. 2: 368–418, 9 fig.

1931. Ueber Lebensbedingungen, Verhalten und Fruchtbarkeit der tropischen Hauswanze *Cimex rotundatus* Sign. (Hem. Rhynch.) in Venezuela. Z. Parasitenk. 3: 837–93, 11 fig.

1933. Bekämpfung der Bettwanze durch die Spinne *Thanatos flavidus*. Naturwissenschaften 21: 285.

1934. Ueber eine erfolgreiche biologische Wanzenbekämpfung durch die Spinne: *Thanatos flavidus*. Naturwissenschaften 22: 649–50.

1938. Zur hygienischen Bedeutung der parasitären Haus- und Vogelwanzen sowie über Wanzenpopulationen und Wanzenkreuzungen. Z. Parasitenk. 10 (1): 1–30.

Heal, R. E., E. F. Rogers, R. T. Wallace, and O. Starnes. 1950. A survey of plants for insecticidal activity. Lloydia 13: 89–162.

Hecht, O. 1930. Die Hautreaktion auf Insektenstiche als allergische Erscheinung. Zool. Anz. 87: 94–109, 145–57, 231–46.

Hedicke, H. 1935. 1. Unterordnung: Ungleichflügler, Wanzen, Heteroptera. *in* C. Börner, Die Tierwelt Mitteleuropas, Insekten, 1. Teil. 4 (3) Quelle & Meyer, Leipzig. p. 15–111; fig. 15–181 (Cimicidae, p. 15, 18, 36, fig. 27).

Hemming, F., and D. Noakes. 1958a.Official list of generic names in zoology. First installment: Names 1–1274. Int. Trust for Zool. Nomencl. London. xxxvi + 200 p. (Cimicidae, p. 28, opinion 81: name no. 275).

1958b. Official index of rejected and invalid generic names in zoology. Int. Trust for Zool. Nomencl., London. p. 93–94.

Henrici, H. 1940. Die Hautdrüsen der Landwanzen (Geocorisae), ihre mikroskopische Anatomie, ihre Histologie, und Entwicklung. Teil II. Die thorakalen Stinkdrüsen. Zool. Jahrb., Anat. 66: 371–402.

Herms, W. B. 1939. Medical Entomology, 3rd ed. Macmillan Co., New York. xix + 582 p., 196 fig. (Cimicidae, p. 92).

Herrich-Schäffer, G. A. W. 1853. Alphabetisch synonymisches Verzeichniss der wanzenartigen Insekten nebst historischer Uebersicht der einschlägigen Literatur. J. L. Lotzbeck, Nürnberg (Cimicidae, p. 54).

Hertig, M., and S. B. Wolbach. 1924. Studies on rickettsia-like microorganisms in insects. J. Med. Res. 44: 329–74.

Hicks, E. A. 1959. Check list and bibliography on the occurrence of insects in birds' nests. The Iowa State Coll. Press, Ames. 681 p. (Cimicidae, p. 239–49).

1962. Check-list and bibliography on the occurrence of insects in birds' nests. Supplement I. Iowa State J. Sci. 36 (3): 233–344, 2 p. index.

Hinton, H. E. 1964. Sperm transfer in insects and the evolution of haemocoelic insemination. *in* K. G. Highnam, Insect Reproduction, Symposium no. 2, Roy. Entomol. Soc. London, p. 95–107.

Hiregaudar, L. S., and D. V. Bal. 1956. Some ectoparasites of bats from India. Agra Univ. J. Res. (Sci.) 5: 1–134 (Cimicidae, p. 81–84).

Hixson, H. 1943. The tropical bedbug established in Florida. Florida Entomol. 26 (3): 47.

Hoberlandt, L. 1942. De nova specie generis *Cimex* L. Časopis Č. Spol. Entomol. 39: 130–1, 1 fig.

1944. Heteroptera Bohemiae 3. Sb. Entomol. Odd. Národní Mus. Pragae 21–22 (1943–1944) : 276–83.

Hoeppli, R., and I-hung Ch'iang. 1940. The louse, crab-louse and bed-bug in old Chinese medical literature, with special consideration of phthiriasis. Chinese Med. J. 58: 338–62.

Horvath, G. 1909. Adnotationes synonymicae de Hemipteris nonnullis extra-europaeis. Ann. Mus. Nat. Hung. 7: 631–2 (Cimicidae, p. 632).

1910a. Description of a new bat bug from British Columbia. Entomol. Mon. Mag. (2) 21 (46) : 12–13, fig.

1910b. Species nova Europaea cimicum sanguisugarum. Ann. Mus. Nat. Hung. 8: 361–3, 1 fig.

1911. Nomenclature des familles des Hemipteres. Ann. Mus. Nat. Hung. 9: 1–34 (Cimicidae, p. 17–18).

1912. Revision of the American Cimicidae. Ann. Mus. Nat. Hung. 10: 251–62.

1913a. A propos de deux Cimicidés du Soudan Français. Bull. Soc. Entomol. France (1913) : 370–2, 1 fig.

1913b. Die Entdeckung der Wanze *Cimex dissimilis* Horv. in Böhmen. Časopis, Acta Soc. Entomol. Bohemiae 10: 141–2.

1913c. Rectification synonymique. Bull. Soc. Entomol. France, observations diverses, p. 131 (*Aphraniola*).

1913d. Hemipteren aus Java. Tijdschr. Entomol. 55: 338–46, 3 fig.

1914a. Miscellanea Hemipterologica XIII–XVII. Ann. Mus. Nat. Hung. 12: 623–60, 9 fig. (Cimicidae, p. 660).

1914b. La distribution géographique des Cimicidés et l'origine des punaises des lits. IXe Int. Congr. Zool., Monaco (1913) : 294–9.

1925. Description of a new batbug from India. Rec. Indian Mus. 27 (3) : 191–2, 1 fig.

1934. Description de deux Cimicidés nouveaux des Chauves-souris (Hem.). Bull. Soc. Entomol. France 39 (2) : 22–23, 2 fig.

1935. Eine neue Fledermauswanze aus dem Spessart. Mitt. Deut. Entomol. Ges. 6: 14–15.

Howard, L. O., and C. L. Marlatt. 1896. The principal household insects of the United States. U. S. Dep. Agr., Div. Entomol., Bull. 4 (N.S.), 130 p., 64 fig.

Hüeber, T. 1893. Fauna Germanica. Die Wanzen (Hemiptera Heteroptera). Systematisches Verzeichnis der bis jetzt in Deutschland gefundenen Wanzen nebst Angabe ihrer Fundorte, Benennungen und Beschreibungen. Jh. Ver. Math. Naturw., Ulm (1892) (3) : 9–240.

Hughes-Schrader, S., and F. Schrader. 1961. The kinetochore of the Hemiptera. Chromosoma 12: 327–50.

Hutchinson, C. M. 1925. Micro-anatomy of *Cimex* with special refer-

ence to the technique of insect histology. Indian J. Med. Res. 12: 487–98, 1 pl.

Illiger, J. K. W. 1802. Namen der Insekten-Gattungen, ihr Genetiv, ihr grammatisches Geschlect, ihr Silbenmass, ihre Herleitung; zugleich mit den deutschen Bennennungen. Mag. f. Insektenk. herausg. v. Karl Illiger, Braunschweig, 1: 125–62 (Cimicidae, p. 125, 132).

International Commission of Zoological Nomenclature. 1924. Opinion 81: The genotype of *Cimex, Acanthia, Clinocoris,* and *Klinophilos.* Opinions 78–81. Smiths. Misc. Coll. 73 (2): 19–32 (Opinion by C. W. Stiles).

Jabłońska, J. 1964. The species of the family Cimicidae occurring in Poland. Bull. Entomol. Pologne 34: 185–7.

Jaczewski, T. 1962. Family-group names in Heteroptera proposed for the official list and official index. (Class Insecta, Order Hemiptera). Z. N. (S) 958. Bull. Zool. Nomencl. 19 (1): 15–22 (Cimicidae, p. 15, 16, 17).

James, M. R. (Transl.) 1924. The Apocryphal New Testament. Oxford Univ. Press, London. xxxi + 594 p.

Jameson, D. K. 1959. A survey of the parasites of five species of bats. The Southwestern Natur. 4 (2): 61–65.

Janisch, E. 1933. Beobachtungen bei der Aufzucht von Bettwanzen. 1. Ueber das Verhalten von Populationen bei verschiedenen Zuchtbedingungen. Z. Parasitenk. 5: 460–514, 23 fig.

1935. Ueber die Vermehrung der Bettwanze *Cimex lectularius* in verschiedenen Temperaturen. (Beobachtungen bei der Aufzucht von Bettwanzen 2.) Z. Parasitenk. 7: 408–39, 18 fig.

Jarocki, P. 1838. Zoologija czyli zwierzetopismo ogólne. VI. Warszawa. [4] + 699 + [40] p., 27 tt.

Jenyns. L. 1839. On three undescribed species of the genus *Cimex,* closely allied to the common bed-bug. Ann. Nat. Hist. 3: 241–4, 1 pl.

Johnson, C. G. 1937. The relative values of man, mouse, and domestic fowl as experimental hosts for the bed-bug, *Cimex lectularius* L. Proc. Zool. Soc. London, (A) 107 (1): 107–26.

1939. Taxonomic characters, variability and relative growth in *Cimex lectularius* L. and *C. columbarius* Jenyns (Heteropt. Cimicidae). Trans. Roy. Entomol. Soc. London 89 (2): 543–68, 1 pl., 8 fig.

1940. Development, hatching and mortality of the eggs of *Cimex lectularius* L. (Hemiptera) in relation to climate, with observations on the effects of preconditioning to temperature. Parasitology 32 (2): 127–173, 13 fig.

1942. The ecology of the bed-bug, *Cimex lectularius* L., in Britain. J. Hyg. 41 (4): 345–61.

1952. The bed bug. New Biol. 13: 80–97.

1960. The relation of weight of food ingested to increase in body

weight during growth in the bed-bug, *Cimex lectularius* L. (Hemiptera). Ent. Exp. Appl. 3 (3): 238–40.

Johnson, C. G., and K. Mellanby. 1939. Bed-bugs and cockroaches. Proc. Roy. Entomol. Soc. London (A) 14 (2–3): 50.

Johnson, C. W. 1925. Insects that infest birds. Bull. Northeastern Bird-Banding Ass. 1 (4): 51–53.

Johnson, M. S., and A. J. Hill. 1948. Partial resistance of a strain of bedbugs to DDT residual. Med. News Letter 12 (1): 26–28.

Jones, R. M. 1930. Some effects of temperature and humidity as factors in the biology of the bedbug (*Cimex lectularius* Linn.). Ann. Entomol. Soc. Amer. 23: 105–19.

Jordan, K. 1922. Note on the distribution of the organ of Berlese in Clinocoridae. Ectoparasites 1: 284–6, fig. 276–80.

Jordan, K., and N. C. Rothschild. 1912. Notes on Clinocoridae, a family of Rhynchota, with descriptions of a new genus and species. Novitates Zool. 19: 352–6, fig. 1–4.

Jördens, J. H. 1801. Entomologie und Helminthologie des menschlichen Körpers, oder Beschreibung und Abbildung der Bewohner und Feinde desselben unter den Insekten und Würmern. Hof, G. A. Grau. Bd. I, xxviii + 319 p., 15 pl. (Die Bettwanze, Abt. 2, Abschn. I, p. v, 32–40, pl. 1, fig. 16–25).

Joyeux, C. 1913. Biologie de *Cimex boueti.* Arch. Parasitol. 1913: 140–6.

Kassianoff, L. 1937. Etude morphologique et biologique de la famille des Cimicidés. Ann. Parasitol. Hum. Comp. 15 (2): 97–124, fig. 1–7; (3): 193–217, fig. 8–20; (4): 289–319, fig. 21–42; (5): 385–408, fig. 43–46.

Kellogg, V. L. 1905. American Insects, New York (Cimicidae, p. 195, 203, 205–6, 616, 634, fig. 285).

Kemper, H. 1929a. Untersuchungen über die Sinnesorgane und die Sinnesphysiologie der Bettwanze. Z. Desinfektion 21 (12): 1–13, 5 fig.

1929b. Beitrag zur Kenntnis des Stinkapparates von *Cimex lectularius* L. Z. Morphol. Oekol. Tiere 15: 524–46.

1930. Beiträge zur Biologie der Bettwanze (*Cimex lectularius* L.). I. Ueber den Einfluss des Nahrungsmangels. Z. Morphol. Oekol. Tiere 19 (1): 160–83, 4 fig.

1932. Beiträge zur Biologie der Bettwanze (*Cimex lectularius* L.). III. Ueber den Mechanismus des Stech-Saugaktes. Z. Morphol. Oekol. Tiere 24 (3–4): 491–517, 16 fig.

1936. Die Bettwanze und ihre Bekämpfung. Z. Kleintierk., Pelztierk. 12 (3): 1–107, 18 Abb. (Band 4 der Schr. Hyg. Zool.).

1959. Die tierischen Schädlinge im Sprachgebrauch. Duncker und Humblot, Berlin. 401 p., 66 fig. (Cimicidae, 72–76, 152, 206, 367).

Khalifa, A. 1952. A contribution to the study of reproduction in the

bed-bug (*Cimex lectularius* L.) Bull. Soc. Fouad 1er Entomol. 36: 311–36.

Kirby, W., and W. Spence. 1816. An Introduction to Entomology; or Elements of the Natural History of Insects. 2nd ed. London. Vol. I, xxiii + 517 p., 3 pl. (Cimicidae, p. 107–9).

Kirby, W. F. 1894. Catalogue of the described Hemiptera, Heteroptera and Homoptera of Ceylon, based on the collection formed (chiefly at Pundaloya) by Mr. E. Ernest Green. J. Linn. Soc. London, Zool. 24: 72–176, pl. 4–6 (Cimicidae, p. 111).

Kiritshenko, A. N. 1913. Ad cognitionem fam. Cimicidae (Latr.) (=Clinocoridae Kirk.) (Hemiptera-Heteroptera). Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg 18: 542–4.

1951. True bugs of the European part of the U.S.S.R. Moscow. Zool. Inst., Acad. Sci., USSR., 423 p. (Cimicidae, p. 36).

1952. Novye i maloizvestnye poluzhestkokrylye Tadzhikistana. Trudy Zool. Inst. Akad. Nauk SSSR. 10: 140–98.

Kirkaldy, G. W. 1899a. On the nomenclature of the Rhynchota. Part I. Entomologist 32: 217–221.

1899b. The expedition to Sokotra. Descriptions of ten new species of Hemiptera. Bull. Liverpool Mus. 2: 45–47.

1902. Fauna Hawaiiensis. Vol. 3, pt. 2., Hemiptera. Cambridge Univ. Press. p. 79–174, pl. 4, 5 (Cimicidae, p. 129).

1904a. Zoological nomenclature. Nature 69: 464.

1904b. Note on the Coruco, *Haematosiphon inodora* (Dugés). Entomol. News 15: 307–8.

1905. Bibliographical notes on the Hemiptera. No. 4. Entomologist 38: 76–79.

1906. List of the genera of the pagiopodous Hemiptera-Heteroptera, with their type species, from 1758 to 1904, and also the aquatic and semi-aquatic Trochalopoda. Trans. Amer. Entomol. Soc. 32 (2): 117–56 (Cimicidae, p. 147).

Klein-Krautheim, F. 1932. Beitrag zur Kenntnis der Staubwanze (*Reduvius personatus* L.) Ber. Oberhess. Ges. Natur Heilk. (N. F.) 15: 103–7.

Kohls, G. M., and W. L. Jellison. 1948. Ectoparasites and other arthropods occurring in Texas bat caves. Nat. Speleol. Soc. Bull. 10: 116–17.

Kolenati, F. A. 1857. Die Parasiten der Chiropteren. Kuntze, Dresden. p. 51, 4 pl.

Krieg, A. 1961. Grundlagen der Insektenpathologie. Dr. Dietrich Steinkopff Verlag, Darmstadt. xviii + 304 p.

1963. Rickettsiae and Rickettsioses. Chap. 17, p. 577–617, *in* E. A. Steinhaus, Insect Pathology, an Advanced Treatise. Vol. 1. Academic Press, New York. xvii + 661 p., illus.

Kunhikannan, K. 1912. No. xxxi. The bed bug (*Cimex rotundatus*) on the common yellow bat (*Scotophilus kuhli*). J. Bombay Nat. Hist. Soc. 21 (4) : 1342.

Lahaye, J. 1931. Traitement des maladies parasitaires des volailles. Reports for Sectional Meetings, XIth Int. Vet. Congr., (1930), London 3: 801–13.

Lamarck, J. B. P. 1816. Histoire Naturelle des Animaux sans vertèbres. Paris, Verdière. 3: 1–586 (Cimicidae, p. 501–3).

Landois, L. 1868–1869. Anatomie der Bettwanze (*Cimex lectularius* L.) mit Berücksichtigung verwandter Hemipterengeschlechter. Z. wiss. Zool. 18: 206–24, taf. 11–12 (1868). Ibid. 19: 206–33, taf. 18–19, fig. 1–25 (1869).

Lansbury, I. 1961. Comments on the genus *Cimex* (Hem. Het. Cimicidae) in the British Isles. Entomologist 94: 133–4.

Laporte, F. L. 1833. Essai d'une classification systématique de l'ordre des Hémiptères (Hémiptères Hétéroptères, Latr.) Guérin's Mag. de Zool., 81 p., 5 pl. (Cimicidae, p. 51).

Latreille, P. A. 1796. Précis des caractères génériques des insectes, disposés dans un ordre naturel par le citoyen Latreille. Brive. p. III, XII, 83–92 (Cimicidae, p. 83).

1802. Histoire naturelle des crustacés et des insectes. F. Dufart, Paris. Vol. 3, xii + 467 p. (Cimicides, p. 240–251).

1804. Histoire naturelle, genérale et particulière, des crustacés et des insectes. F. Dufart, Paris. Vol. 12, 424 p., pl. xciv-xcvii (Cimicidae, p. 235).

1807. Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Paris. Vol. III, 258 p. (Cimicidae, p. 36–37).

1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes. F. Schoell, Paris. 445 p. (Cimicidae, p. 257).

1829. *In* Cuvier, Le Règne Animal, n. ed. Paris. Vol. V, xxiv + 556 p. (Cimicidae, p. 201).

Lattin, J. D., and J. Schuh. 1959. *Hesperocimex coloradensis* List in Oregon. (Hemiptera, Cimicidae). Pan-Pacific Entomol. 35 (4) : 175–76.

Lavoipierre, M. M. J., G. Dickerson, and R. M. Gordon. 1959. Studies on the methods of feeding of blood sucking arthropods. I. The manner in which triatomine bugs obtain their bloodmeal, as observed in the tissues of the living rodent, with some remarks on the effects of the bite on human volunteers. Ann. Trop. Med. Parasitol. 53 (2) : 235–50, 7 fig., 2 pl. (Cimicidae, p. 236, 238).

Leach, W. E. 1815. *in* Brewster's Edinburgh Encycl. 9 (1) : 57–172 (Cimicidae, p. 112).

Lederer, G. 1950. Auftreten von *Cimex hemipterus* Fabricius 1803 (= *C. rotundatus* Sign.) sowie anderer *Cimex*arten in Hessen (Heteropt. Cimicidae). Anz. Schädlingsk. 23 (3): 44–46, 4 fig.

Lee, R. D. 1954a. The absence of negative phototropism in the Mexican chicken bug, *Haematosiphon inodorus* (Dugés) (Hemiptera: Cimicidae). Pan-Pacific Entomol. 30 (2): 159–60.

1954b. Oviposition by the poultry bug. J. Econ. Entomol. 47: 224–6.

1954c. First report of the poultry bug from a Golden Eagle's nest, with new locality records. J. Econ. Entomol. 47 (6): 1144.

1955a. New locality records for *Cimexopsis nyctalis* List, the chimney swift bug (Hemiptera: Cimicidae). Bull. Brooklyn Entomol. Soc. 50 (2): 51–52, 1 fig.

1955b. The biology of the Mexican chicken bug, *Haematosiphon inodorus* (Dugés) (Hemiptera: Cimicidae). Pan-Pacific Entomol. 31: 47–61, 3 fig., 1 pl.

Lee, R. D., and R. E. Ryckman. 1955. First precise locality record of *Hesperocimex coloradensis* List from Mexico (Hemiptera, Cimicidae). Proc. Entomol. Soc. Wash. 57 (4): 164.

Lefevre, G., and U. B. Jonsson. 1962. Sperm transfer, storage, displacement and utilization in *Drosophila melanogaster*. Genetics 47: 1719–36.

Lent, H. 1939. Lista does artropodos infestados experimentalmente pelo *Schizotrypanum cruzi*. Mem. Inst. Oswaldo Cruz 34: 595–7.

1941. *"Latrocimex spectans"* n. gen., n. sp., Parasito de morcegos no Brasil. Rev. Brasil. Biol. 1 (1): 41–46, 4 fig.

Lent, H., and J. W. Abalos. 1946. Un neuvo Cimicidae encontrado en nidos de *Myiopsitta monacha cottora* (Vieillot). An. Inst. Med. region, Tucumán (Pub. no. 406) 1 (3): 337–48, 17 fig.

Lent, H., and M. Cavalcanti Proença. 1937. *Cimex limai* Pinto, 1927, parasito de morcegos no Brasil. Mem. Inst. Oswaldo Cruz 32: 211–15, 2 pl.

Le Peletier de Saint-Fargeau and A. Serville. 1825. *in* Encyclopedie methodique. Historie naturelle. Entomologie, ou histoire naturelle des crustacés, des arachnides et des insectes, par M. Latreille, etc. Paris. 10: 1–828, index (Cimicidae, p. 251, pl. 122, fig. 1–3).

Leston, D., J. G. Pendergrast, and T. R. E. Southwood. 1954. Classification of the terrestrial Heteroptera (Geocorisae). Nature 174: 91 (Cimicidae, p. 91).

Lethierry, L., and G. Severin. 1896. Catalogue général des Hémiptères (Mus. Roy. Hist. Nat. Belgique, Bruxelles). Berlin. 3: 1–275. (Cimicidae, p. 235).

Levi, W. L. 1941. The Pigeon. R. L. Bryan Co., Columbia, S. C. xxxii + 512 p., 785 illus.

Lewis, D. T. 1949. The distribution of Cimicidae (Hemiptera) in the Anglo-Egyptian Sudan. Parasitology 39: 295–9, 4 fig.

Lima, A. da Costa. 1940. Insetos do Brasil. 2º Tomo, Capitulo XXII. Hemipteros. Escola Nac. Agron. Série Didatica No. 3, Rio de Janeiro, 351 p., fig. 219–446 (Cimicidae, p. 244–60, 5 fig.).

Lindquist, A. W., A. H. Madden, and H. O. Schroeder. 1946. Effect of temperature on knock-down and kill of mosquitoes and bedbugs exposed to DDT. J. Kans. Entomol. Soc. 19: 13–15.

Linnaeus, C. 1746. Fauna Svecica . . . Laurentii Salvii, Stockholmiae, xxvi + 411 p., 2 pl. (*Cimex apterus,* p. 203).

1750. Plantae camtschatcenses rariores (J. P. Halenius). Amoenitates Academicae (Schreber ed.). J. Palm, 1787, Erlangae. 2: 332–64 (*Actaea cimicifuga,* p. 354–5).

1752. Noxa insectorum (M. A. Baeckner). Amoenitates Academicae (Schreber ed). J. Palm, 1787, Erlangae. 3: 335–62 (*Cimex,* p. 343).

1753. Species Plantarum. Vol. I. 1957 facsim. ed. Roy. Soc., London. xiv + 560 p., index (*Cimicifuga,* p. 504).

1758. Systema Naturae per regni tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th ed., revised. Laurentii Salvii, Holmiae. 823 p. (Cimicidae, p. 441).

1761. Fauna Svecicae sistens animalia Svecicae regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes, distributa per classes et ordines, genera et species, cum differentiis specierum, etc. Edito altera, auctior. Laurentii Salvii, Stockholmiae. xlvi + 578 p., 2 pl., frontisp. (*Cimex lectularius apterus,* p. 245).

1767. Systema Naturae, Editio duodecima reformata, Laurentii Salvii, Holmiae. Tom I, Pars II, p. 1–1327, indices (*Cimex,* p. 715).

Linnavuori, R. 1964. Hemiptera of Egypt, with remarks on some species of the adjacent Eremian region. Ann. Zool. Fenn. 1: 306–56 (Cimicidae, p. 321–322).

List, G. M. 1925. Three new genera and three new species of Cimicidae from North America. Proc. Biol. Soc. Wash. 38: 103–10.

Lofgren, C. S., J. C. Keller, and G. S. Burden. 1958. Resistance tests with the bedbug and evaluation of insecticides for its control. J. Econ. Entomol. 51: 241–4.

Lorando, N. T. 1929. A biological method for destroying bedbugs. Sci. Mon. 29: 265–8.

Ludwig, W. 1937. Ueber die Genese der Asymmetrieform bei Bettwanzen. Arch. Entwicklungsmech. Organismen 136 (2–3): 294–312, 7 fig.

Ludwig, W., and H. Zwanzig. 1937. Ueber normalen und abnormalen (inversen, derdoppelten, sterilen, intersexuellen) Kopulationsapparat der Bettwanze. Z. Naturw. 89: 136–48.

Lugger, O. 1900a. Hemiptera or bugs destructive in Minnesota. 2nd Annu. Rep. Entomol., Minn. Agr. Exp. Sta. Bull. 6: 1–245.

1900b. *Acanthia lectularia* Linn. (The common bedbug). 6th Annu. Rep. Entomol., Minn. Agr. Exp. Sta. Bull. 69: 48–53, fig. 3c, 40–43.

MacMillan, J. 1938. Demonstration of apparatus used in bed-bug disinfestation with heavy coal tar naphtha. J. Roy. Sanit. Inst. 58: 555–60, 4 fig.

Mail, G. A. 1940. Infestation of a high school by *Oeciacus vicarius* Horv. J. Econ. Entomol. 33 (6) : 949.

Makino, S. 1951. An atlas of the chromosome numbers in animals. 2nd ed. Iowa State Coll. Press, Ames. xxviii + 290 p.

Mallis, A. 1960. Handbook of Pest Control. 3rd ed. MacNair-Dorland Co., New York. 1132 p., 238 fig. (Cimicidae, p. 392–418).

Mallis, A., and A. C. Miller. 1964. Prolonged resistance in the house fly and bed bug. J. Econ. Entomol. 57: 608–9.

Manna, G. K. 1951. A study of the chromosome during meiosis in forty-three species of Indian Heteroptera. Proc. Zool. Soc. Bengal 4: 1–116.

Marlatt, C. L. 1896. The bedbug (*Cimex lectularius* Linn.). U. S. Dep. Agr., Div. Entomol., Bull. no. 4 (n. s.), p. 32–38, fig. 7–9. Revised ed., 1902.

Martini, E. 1952. Lehrbuch der medizinischen Entomologie. 4th ed., rev. G. Fischer, Jena. xii + 694 p., 318 fig. (Cimicidae, p. 147–58, 9 fig.).

Marx, R. 1955. Ueber die Wirtsfindung und die Bedeutung des artsspezifischen Duftstoffes bei *Cimex lectularius* Linné. Z. Parasitenk. 17: 41–72.

Massee, A. M. 1955. The county distribution of the British Heteroptera-Hemiptera. 2nd ed. Entomol. Mon. Mag. 91: 7–27 (Cimicidae, p. 14, 15).

Matheson, C. 1941. The distribution of *Cimex lectularius* in towns in England and Wales. Bull. Entomol. Res. 32: 165–71.

Matheson, R. 1950. Medical Entomology. 2nd ed. Comstock Pub. Co. Inc., Ithaca. vi + 612 p; 4 pl., 242 fig. (Cimicidae, p. 171–80, 356, 3 fig.).

Mathur, R. N. 1953. A new species of bat-bug—*Aphraniola*—from Dehra Dun (Cimicidae: Hemiptera). Indian J. Entomol. 14: 257–61, 4 fig. (Dec., 1952).

Matthioli, A. 1568. Discorsi Dim. Pietro Andrea Matthioli . . . . Di Pedacio Dioscoride Anazarbeo della materia Medicinale. Vincenzo Valgrisi, Venetia. Vol. 1, 672 p., illus. (Cimicidae, p. 362–3; fig. p. 363).

Mayr, E. 1937. Birds collected during the Whitney South Sea Expedi-

tion. XXXIII. Notes on New Guinea Birds. I. Amer. Mus. Novitates 915: 1–19.

Mazzotti, L. 1941. Experimental infection of *Haematosiphon inodora* (Dugés) with *Trypanosoma cruzi* Chagas. Bull. Brooklyn Entomol. Soc. 36 (2): 67–68.

Medway, Lord. 1958. 300,000 bats. Sarawak Mus. J. 8: 667–79.

Meillon, B. de, and F. Hardy. 1951. Fate of *Cimex lectularius* on adult and on baby mice. Nature 167: 151.

Mellanby, K. 1932. Effects of temperature and humidity on the metabolism of the fasting bed bug (*Cimex lectularius*). Parasitology 24: 419–28, 3 fig.

1935. A comparison of the physiology of the two species of bed-bug which attack man. Parasitology 27: 111–22, 3 fig.

1939a. Fertilization and egg production in the bed-bug, *Cimex lectularius* L. Parasitology 31: 193–9.

1939b. The physiology and activity of the bed-bug (*Cimex lectularius* L.) in a natural infestation. Parasitology 31: 200–11.

Metschnikoff, E. 1887. Ueber den Phagocytenkampf beim Rückfalltyphus. Virchow's Archiv Path. Anat. Physiol. Klin. Med. 109: 176–92.

Michalk, O. 1938. Die Wanzen (Hemiptera heteroptera) der Leipziger Tieflandsbucht und der angrenzenden Gebiete. Sitzungsber. Naturforsch. Ges. Leipzig 63–64: 15–188 (Cimicidae, p. 101–2).

Miller, N. C. E. 1956. The biology of the Heteroptera. Leonard Hill, Ltd., London. x + 162 p., frontisp., 5 pl., 64 fig. (Cimicidae, p. viii, 8, 36, 66, 119–20, fig. 42).

Moufet, T. 1634. Insectorum sive Minimorum Animalium Theatrum. Thom. Cotes, London. 18 + 326 p., 4 pl. (Transl. by E. Topsel, 1658, in "The History of Four-footed Beasts, Serpents and Insects." E. Cotes., London. p. 10, 889–1130, + 6) (Chap. XXV on Wall lice, p. 1096–8).

Murray, C. H. 1914. Notes on the anatomy of the bed bug (*Acanthia lectularia* L.). Parasitology 7: 278–321, pl. 22–23, fig. 1–40.

Myers, L. E. 1928. The American swallow bug, *Oeciacus vicarius* Horvath (Hemiptera, Cimicidae). Parasitology 20 (2): 159–172, 4 pls.

Negi, P. S. 1933. The small red ant, *Solenopsis geminata* subsp. *rufa* Jerdon, and its usefulness to man. J. Bombay Nat. Hist. Soc. 36: 1018–20.

Newman, E. 1834. Attempted division of British insects into natural orders. Entomol. Mag. 2: 379–431 (Cimicidae, p. 427).

1855. A word for the cockroach. Trans. Entomol. Soc. London 3: 77 (Cimicidae, p. 77).

Nordenskiöld, H. 1961. Tetrad analysis and the course of meiosis in three hybrids of *Luzula campestris*. Hereditas 47: 203–38.

Nuttall, G. H. F. 1900. On the role of insects, arachnids and myriapods, as carriers in the spread of bacterial and parasitic diseases of man and animals. A critical and historical study. Johns Hopkins Hospital Reports, Baltimore, VIII (Cimicidae, p. 13–14, 17, 18, 20, 22–23, 24–25, 32–33, 39, 120).

Oakley, K. P. 1956. Fire as a paleolithic tool and weapon. Proc. Prehistoric Soc. 21: 36–48.

Omori, N. 1939. Experimental studies on the cohabitation and crossing of two species of bedbugs, *Cimex lectularius* and *Cimex hemipterus*. Preliminary report. VII Int. Kongr. Entomol. (Berlin) Weimar, G. Uschmann, 2: 895–915.

1939. Experimental studies on the cohabitation and crossing of two species of bed-bugs (*Cimex lectularius* L. and *C. hemipterus* F.) and on the effects of interchanging males of one species for the other, every alternate day, upon the fecundity and longevity of females of each species. Acta Jap. Med. Trop. 1: 127–54.

1941. Comparative studies on the ecology and physiology of common and tropical bed bugs, with special references to the reactions to temperature and moisture. J. Med. Ass. Formosa 60 (4) no. 433: 555–729, 19 fig., 55 + 113 tables.

Osborn, H. 1892a. Catalogue of the Hemiptera of Iowa. Proc. Iowa Acad. Sci. (1890–91) 1 (2): 120–131.

1892b. Note on the species of *Acanthia*. Can. Entomol. 24: 262–5.

1896. Insects affecting domestic animals: an account of the species of importance in North America, with mention of related forms occurring on other animals. U. S. Dep. Agr., Div. Entomol., (n. s.) Bull. no. 5, 1–302 p., 170 fig. (Acanthiidae, p. 157–63).

Oshanin, B. F. 1909. Verzeichnis der palaearktischen Hemipteren, etc. Vol. I, St. Petersburg. lxxiv + 1087 p. (Cimicidae, p. 609–11).

1912. Katalog der paläarktischen Hemipteren. R. Friedländer u. Sohn, Berlin. x + 187 p. (Cimicidae, p. 56).

Oxford English Dictionary. 1933. The Clarendon Press, Oxford. Vol. I (Bug, p. 1159).

Parshad, R. 1957. Cytological studies in Heteroptera, III. A comparative study of the chromosomes in the male germ cells of eleven species of the subfamily Pentatominae. Res. Bull. Punjab Univ. (Zool.) 122: 401–20.

Parshley, H. M. 1914. List of the Hemiptera-Heteroptera of Maine. Psyche 21: 139–49 (Clinocoridae, p. 143).

1917. Fauna of New England, 14. List of the Hemiptera-Heteroptera. Occas. Papers Boston Soc. Nat. Hist. 7 (14): 1–125 (Cimicidae, p. 8, 10, 67).

1923. Cimicidae. *In* W. E. Britton, Guide to the insects of Connecticut, Part IV. The Hemiptera or sucking insects of Connecticut. Hartford, State of Conn. Pub. Doc. no. 47, Bull. 34, 807 p., 20 pl., 167 fig. (Cimicidae, p. 668–70, pl. 16:32).

Patton, W. S. 1907. Notes on the distribution of the two species of bed-bug. Indian Med. Gaz. 42: 41.

1908. XVI—*Cimex rotundatus* Signoret. Rec. Indian Mus. 2 (2): 153–5, 5 fig.

Patton, W. S., and F. W. Cragg. 1913. A Textbook of Medical Entomology. Christian Lit. Soc. for India, London. xxxiv + 768 p., 78 pl. (Cimicidae, p. 479, 483, 498–524, illus. p. 498).

Payne, F. 1910. The chromosomes of *Acholla multispinosa*. Biol. Bull. 18: 174–9.

1912. A further study of the chromosomes of the Reduviidae, II. The nucleolus in the young oöcytes and the origin of the ova in *Gelastocoris*. J. Morphol. 23: 331–47.

Peters, J. L. 1940. Check-list of birds of the world. Vol. IV. Harvard Univ. Press, Cambridge. xii + 291 p.

Pfeiffer, H. 1931. Beiträge zu der Bakteriensymbiose der Bettwanze (*Cimex lectularius*) und der Schwalbenwanze (*Oeciacus hirundinis*). Zentralbl. Bakteriol., Parasitenk., Infektionskr. 123 (3–4): 151–71, 13 fig.

Philip, C. B. 1956. Comments on the classification of the order Rickettsiales. Can. J. Microbiol. 2: 261–270.

Philippi, R. A. 1865. *Acanthia valdiviana* und *Bacteria unifoliata*. Stett. Entomol. Z. 26: 63–64.

Picaglia, L. 1884. Nuova specie di *Acanthia*. Atti Soc. Nat. Modena. Rendic. adunanze. Serie III, 2: 44.

Pinto, C. 1927a. *Ornithocoris toledoi,* novo genero e nova especie de percevejo de ave (Hemiptera—Fam. Cimicidae). Rev. Biol. Hyg. 1 (2): 17–22.

1927b. *Cimex limai,* n. sp., parasite of bats in Brasil. Bol. Biol. 10: 186–93.

1928. Sobre a presença do *Cimex foedus* (Stål, 1854) no Brasil. Bol. Biol. 13: 85–91, 7 fig.

1930. Tratado de parasitologia. Vol. IV. Arthropodes parasitos e transmissores de doencas, Tomo I. Bibliotheca Scientifica Brasileira, n. CXVII. Pimenta de Mello & C., Rio de Janeiro. xvi + 395 p., 185 fig., 4 pl.

1938. Zoo-parasitos de interêsse medico e veterinário. Pimenta de Mello & C., Rio de Janeiro. vii + 376 p., 162 fig., 105 black and white plates, 1 colored plate.

1945. Zoo-parasitos de interêsse medico e veterinário. Editora Sci-

entifica, Rio. xv + 461 p., 102 pl., 160 fig. (Cimicidae, p. 115–19, 3 fig.).

Poppius, B. 1912. *Cimex vespertilionis* n. sp. Medd. Soc. Fauna Flora Fenn. 38: 56–58.

Populus, Dr. 1880. Catalogue des Hémiptères du Département de l'Yonne. Bull. Soc. Sci. hist. nat. l'Yonne, Auxerre. (1880): 1–49 (Cimicaria, p. 24).

Povolný, D. 1957. Kritická studie o štěnicovitých (Het. Cimicidae) v Československu. Zool. Listy, Folia Zool. VI (XX): 59–80, 8 pl. with 45 fig.

1962. Die wahrscheinlichen Richtungen und Wege der Entstehung des Parasitismus bei den Bettwanzen (Cimicidae) und die Frage der Eusynanthropie von *Cimex lectularius* als Menschenschmarotzer. Z. angew. Zool. 49 (1): 53–59, 1 fig.

Priesner, H., and A. Alfieri. 1953. A review of the Hemiptera Heteroptera known to us from Egypt. Bull. Soc. Fouad 1er Entomol. 37: 1–119 (Cimicidae, p. 81).

Pringault, E. 1914. *Cimex pipistrelli* Jen., agent de la transmission de la trypanosomiase des Chauves-Souris. Compt. Rend. Soc. Biol. 76: 881–88.

Puri, I. M. 1924. Studies on the anatomy of *Cimex lectularius* L. I, II. Parasitology 16: 84–97, 269–278, 1 pl., 18 fig.

Puton, A. 1886. Catalogue des Hémiptères (Hétéroptères, Cicadines et Psyllides) de la faune paleárctique. Troisième édition. Caen. 100 p. (Cimicidae, p. 42).

Rao, T. R., and A. V. Halgeri. 1956. A note on resistance of bed bugs to DDT in Bombay State. Indian J. Malariol. 10 (2): 149–54.

Ray, H. N., and B. Dasgupta. 1955. Role of the nuclei of the follicle cells in the formation of the chorion in *Cimex lectularius columbarius* Jen. Nature 175: 216–17.

Ray, J. 1710. Historia insectorum. A. and J. Churchill, London. p. xv + 400 (*Cimex*, p. 7).

Reed, E. C. 1901. Sinopsis de los Hemípteros de Chile. Rev. Chil. Hist. Nat. 5: 1–107, 1 pl. (Cimicidae, p. 92).

Rendtorff, R. C. 1938. A method of rearing the bedbug, *Cimex lectularius* L., for studies in toxicology and medical entomology. J. Econ. Entomol. 31 (6): 781, 1 fig.

Reuter, O. M. 1871. Skandinaviens och Finlands Acanthiider. Öfv. Sven. Vet.-Akad. Förh. 28 (3): 403–29 (Cimicidae, p. 407–9).

1880. Remarks on some British Hemiptera-Heteroptera (Cont'd). Entomol. Mon. Mag. 16: 12–15, 172–5 (Cimicidae, p. 172–3).

1881. Remarks on some British Hemiptera-Heteroptera (Concluded). Entomol. Mon. Mag. 17: 10–15 (Cimicidae, p. 14).

1882a. Ueber die Gattungsnamen *Cimex* und *Acanthia*. Wien. Entomol. Zeitung 1: 301–6.

1882b. Eine neue *Cimex*-Art aus der Wiener-Gegend. Wien. Entomol. Zeitung 1: 306–7.

1888. Revisio Synonymica Heteropterorum palaearcticorum quae descripserunt auctores vetustiores (Linnaeus 1758—Latreille 1806). Acta Soc. Sci. Fenn. Part I, 15: 241–313; Part II, 15: 443–812 (*Cimex lectularius* full synonymy, p. 267, 273, 689–90).

1908. On the nomenclature of some (British) Hemiptera-Heteroptera. Entomol. Mon. Mag. 44: 22–29 (Cimicidae, p. 27).

1910. Neue Beiträge zur Phylogenie und Systematik der Miriden. Acta Soc. Sci. Fenn. 37 (3): 1–171. 1 pl., 3 fig. (Cimicidae, p. 2, 6, 14, 15, 16, 19, 20, 21, 39, 40, 49, 57, 71, 72).

1912. Bemerkungen über mein neues Heteropterensystem. Öfv. Finska Vet.-Soc. Förh. 54 (A) 6: 1–62 (Cimicoideae, p. 19–21, 48, 53).

1913a. Ueber *Cimex valdivianus* Phil. Wien. Entomol. Zeitung 32 (10): 237–8.

1913b. Die Familie der Bett- oder Hauswanzen (Cimicidae), Phylogenie, Systematik, Oekologie und Verbreitung. Z. Wiss. Insektenbiol. 9 (18): 251–5; 303–6; 325–9; 360–4. Ann. Soc. Linn. Lyon, (N.S.) 30: 423–4.

1913c. Vagglusfamiljen (Cimicidae), dess fylogeni, systematik, ekologi och utteredning. Entomol. Tidskr. 34 (1): 1–21.

Ribaga, C. 1897. Sopra un organo particolare delle cimici dei letti. Riv. Patol. Veg. 5: 223–6.

Riley, C. V. 1889. Some insect pests of the household. III. Bedbugs and red ants. Insect Life 2 (4): 104–108, 3 fig. (Cimicidae, p. 104–5, 1 fig.).

Riley, C. V., and L. O. Howard. 1891. A curious bedbug find. Insect Life 3 (7–8): 336–7.

Riley, W. A., and O. A. Johannsen. 1932. Medical Entomology, a Survey of Insects and Allied Forms which Affect the Health of Man and Animals. McGraw Hill, N. Y. xi + 476 p., 184 fig.

Rivnay, E. 1930. Host selection and cannibalism in the bed bug *Cimex lectularius* L. Ann. Entomol. Soc. Amer. 23: 758–64.

1932a. Studies in tropisms of the bed bug *Cimex lectularius* L. Parasitology 24 (1): 121–36, 9 fig.

1932b. The influence of relative humidity upon the rate of development of the bed bug *C. lectularius* L. Bull. Soc. Roy. Entomol. Egypte 16: 13–16.

1933. The tropisms effecting copulation in the bed bug. Psyche 40: 115–20.

Rondani, C. 1842. Nota sopra una specie di *Cimex* trovata nei con-

torni di Parma vivente ne nidi della *Hirundo urbica*. Bol. Accad. Aspir. Nat. Napoli 1: 98–99.

Ronderos, R. A. 1961. Cimicidae argentinos. Notas sobre su distribución geográfica y descripción del alotipo macho de *Cimex tucmatiani* (♂) Wygod., 1951 (Hemiptera). Notas Mus. La Plata 20 (Zool.) no. 190: 29–37, 11 fig.

Rothschild, M., and T. Clay. 1952. Fleas, flukes and cuckoos. A study of bird parasites. The New Naturalist. Collins, London. xiv + 304 p., 5 text fig. 40 pl. (Cimicidae, fig. 36a, 36b).

Rothschild, N. C. 1912a. A new Indian bed-bug: *Clinocoris peristerae*, sp. nov. Entomol. Mon. Mag. (2) 23: 87.

1912b. Notes on the structure of the sexually modified segments of the Cimicidae (= Clinocoridae), with special reference to *Clinocoris columbarius* (Jenyns). Novitates Zool. 19: 93–96, 9 fig.

1912c. A new form of bed-bug: *Cacodmus ignotus* sp. nov. Entomol. Mon. Mag. (2) 23 (48): 85–86.

1912d. On a new genus and species of Clinocoridae (Cimicidae) from Uganda. Bull. Entomol. Res. 1: 363–4. 1 fig.

1913. On the genus *Cacodmus*. Entomol. Mon. Mag. (2) 24 (49): 102–3.

1914a. The tropical bed-bug *Clinocoris hemiptera* Fabr. Bull. Entomol. Res. 4: 345.

1914b. Siphonaptera and Clinocoridae. Suppl. Entomol. 3: 117–18, 1 fig. (Cimicidae, p. 118).

1915. On some species of *Cacodmus*, a genus of bedbugs (Clinocoridae). Bull. Entomol. Res. 5: 41–42, 5 fig.

1916. The President's Address: Convergent Development among Certain Ectoparasites. Proc. Entomol. Soc. London (1916): cxli–clvi.

1922. The occurrence in England of a species of *Clinocoris* unrecorded from the United Kingdom. Ectoparasites 1 (4): 216.

Roubal, J. 1913. Oekologicke črty o broucich—Koleopterologisch-oekologische skizzen. Časopis, Acta Soc. Entomol. Bohemiae 10: 121–23.

1917. Einige addenda über Cavernicola. Arch. Naturgesch., Abt. A, 83 (3): 22–25.

Roubaud, E. 1913. Cimicides du Soudan francais. Bull. Soc. Entomol. France 1913: 348–51, 2 fig.

Ruscart, J. B. 1951. Les homas du mont Hoyo, Ituri-Congo Belge. Pub. Dir. Agr. l'Elevage, Bruxelles. 66 p., 32 fig.

Ryckman, R. E. 1952. Laboratory culture of Triatominae with observations on behavior and a new feeding device. J. Parasitol. 38: 210–14.

1956. Parasitic and some nonparasitic arthropods from bat caves in Texas and Mexico. Amer. Midland Nat. 56: 186–90.

1958. Description and biology of *Hesperocimex sonorensis*, new spe-

cies, an ectoparasite of the purple martin (Hemiptera Cimicidae). Ann. Entomol. Soc. Amer. 51 (1): 33–47, 7 fig.

Ryckman, R. E., and N. Ueshima. 1963. *Hesperocimex cochimiensis* new sp., from Baja California, Mexico (Hemiptera: Cimicidae). Proc. Entomol. Soc. Wash. 65 (3): 247–9, 1 fig.

1964. Biosystematics of the *Hesperocimex* complex (Hemiptera: Cimicidae) and avian hosts (Piciformes: Picidae; Passeriformes: Hirundinidae). Ann. Entomol. Soc. Amer. 57 (5): 624–38, 16 fig.

Sailer, R. I. 1950. The second record for *Primicimex cavernis* Barber (Heteroptera, Cimicidae). Proc. Entomol. Soc. Wash. 52 (6): 308.

1952. The bedbug. An old bedfellow that's still with us. Pest Control 20 (10): 22, 24, 70, 72. 4 fig.

Samouelle, G. 1819. The Entomologist's Useful Compendium. T. Boys, London. 496 p., 12 pl. (Cimicidae, p. 223).

Saunders, E. 1892. The Hemiptera-Heteroptera of the British Islands. L. Reeve & Co., London. vi + 349 p., 32 pl. (Cimicidae, p. 186–8, pl. xvii, fig. 5–7).

Schenk, A. 1877. Die Arten der Gattung *Acanthia* F. (*Cimex* L.). Entomol. Nachr. 2 (11): 182–3.

Schildknecht, H. 1964. Defensive substances of the arthropods, their isolation and identification. Angew. Chemie (Int. Ed.) 3: 73–82.

Schouteden, H. 1932. Les deux punaises de lits, *Cimex lectularius* et *Cimex rotundatus* du Congo Belge. Rev. Zool. Bot. Afr. 23 (1): 70.

1951. Un genre nouveaux de Cimicide du Katanga (Hemipt. Cimic.) Rev. Zool. Bot. Afr. (44): 278–80.

Schrader, F. 1940. The formation of tetrads in the meiotic mitoses in the male of *Rhytidolomia serialis* Say. (Hemiptera, Heteroptera). J. Morphol. 67: 123–42.

1947. The role of the kinetochore in the chromosomal evolution of the Heteroptera and Homoptera. Evolution 1: 134–42.

Schrader, F., and S. Hughes-Schrader. 1956. Polyploidy and fragmentation in the chromosomal evolution of various species of *Thyanta* (Hemiptera). Chromosoma 7: 469–96.

Schummel, T. E. 1832. Bericht der entomologischen Section in der schlesischen Gesellschaft für vaterländische Kultur, am Ende des Jahres 1831. Arb. schles. Ges. vaterl. Kultur, Breslau (1832): 73–74.

Scott, H. 1928. Occurrence of the bat-bug, *Loxaspis mirandus,* in Portuguese East Africa, and note on the association of some Coleoptera with bats. Entomol. Mon. Mag. 64: 108–9.

Scudder, G. G. E. 1957. Additions to the county distribution tables of the British Hemiptera Heteroptera. Entomol. Mon. Mag. (4) 207: 49–51 (Cimicidae, p. 50).

1959. The female genitalia of the Heteroptera: morphology and bear-

ing on classification. Trans. Roy. Entomol. Soc. Lond. 3 (14) : 405–7, 103 fig. (Cimicidae, p. 430, 431, 432).

Sherborn, C. D. 1927. Index Animalium. 1801–1850. Oxford Univ. Press, London. Part XII: *haani–implicatus,* p. 2281–3136 (Cimicidae, p. 3010).

Shih-chen, Li. 1590. Pen ts'ao kang mu (A system of Pharmacopeia), 40: 28–29; Suppl. 10: 66–69.

Siebold, C. Th. v. 1839 (December). Beiträge zur Fauna der wirbellosen Thiere Preussens. Preuss. Provinzialbl. 22: 552.

Signoret, V. 1852. *Acanthia rotundata,* mihi. Notice sur quelques Hémiptères nouveaux ou peu connus. Ann. Soc. Entomol. France (2) 10: 540–1, pl. 16, fig. 2, 2a.

Sikes, E. K., and V. B. Wigglesworth. 1931. The hatching of insects from the egg, and the appearance of air in the tracheal system. Quart. J. Microscop. Sci. 14: 165–92, 8 fig. (Cimicidae, p. 175–8).

Singh-Pruthi, H. 1925. V. The morphology of the male genitalia in Rhynchota. Trans. Entomol. Soc. London I, II, p. 127–267, 26 pl., 3 fig. (Cimicidae, p. 170, 1 pl.).

Sioli, H. 1937. Thermotaxis und Perzeption von Wärmestrahlen bei der Bettwanze (*Cimex lectularius* L.). Zool. Jahrb., Jena, Allg. Zool. 58: 284–96, 2 fig.

Skeat, W. W. 1901. List of place-names in the Siamese Malay States visited by members of the "Skeat Expedition." Proc. Zool. Soc. London 2: 583–6.

Slack, H. D. 1937. Note on Scottish Hemiptera-Heteroptera. Scot. Nat., no. 225, p. 91.

1938. Chromosome numbers in *Cimex.* Nature 142: 358.

1939a. Chromosomes in *Cimex.* Nature 143: 78.

1939b. Structural hybridity in *Cimex.* Chromosoma 1: 104.

Smart, J. 1942. Appendix A: Selected bibliography of the bed-bug. Report of the Committee on bed-bug infestation, 1935–1940. Privy Council Medical Research Council, special report Series no. 245, London. P. 58–63. (Bibliography through 1941; continuation of Rep. Publ. Health Med. Subj. no. 72, 1934. (bibliography to 1933.)

Snipes, T., J. C. M. Carvalho, and O. E. Tauber. 1940. Biological studies of *Ornithocoris toledoi* Pinto, The Brazilian chicken bedbug. Iowa State Coll. J. Sci. 15: 27–36, 1 pl.

Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., Inc., New York. ix + 667 p., 319 fig.

1944. The feeding apparatus of biting and sucking insects affecting man and animals. Smiths. Misc. Pub. 104 (7) (no. 3373) : 1–112, 39 fig.

Southall, John. 1730. A treatise of buggs: shewing when and how they were first brought into England. How they are brought into and in-

fect houses. Their nature, several foods, times and manner of spawning and propagating in this climate. Their great increase accounted for, by proof of the numbers each pair produce in a season, etc. J. Roberts, London. v–xii, 44 p., frontisp. of 16 fig.

Southwood, T. R. E. 1954. The production of fertile eggs by *Cimex pipistrelli* Jenyns when fed on human blood. Entomol. Mon. Mag. 90: 35.

Southwood, T. R. E., and D. Leston. 1959. Land and water bugs of the British Isles. Fr. Warne &Co. Ltd., London and New York. xi + 436 p., 31 pl., 32 col. pl., 153 fig. (Cimicidae, p. 169–70, 187–92, pl. 26: 2, 3; pl. 5: 12 fig.).

Spencer, G. I. 1930. The status of the barn swallow bug, *Oeciacus vicarius* Horvath. Can. Entomol. 62 (1) : 20–21.

1935. The bedbugs of British Columbia. Proc. Entomol. Soc. Brit. Columbia 31: 43–45.

Spinola, M. M. 1840. Essai sur les Insectes Hémiptères, Rhyngotes ou Hétéroptères. Baillière, Paris. Extract from Ann. Sci. Nat. Paris 12, ser. 2, 1839, 381 p. (Cimicidae, p. 170–3).

1850. Tavola Sinottica. R. D. Camera, Modena, 138 p. (Cimicoideae, p. 39) (*From* Mem. di Matem. e di Fis. Soc. Ital. Modena 25, 1852).

Stål, C. 1854. Nya Hemiptera. Öfv. Vet.-Akad. Förh. (1854) : 230–55.

1865. Hemiptera Africana. Vol. III. Holmiae. 200 p. (Cimicidae, p. 24–25).

1868. Hemiptera Fabriciana. Fabricianska Hemipterarter, efter di i Köpenhamn och Kiel förvarade typexemplaren granskade och beskrifne af, etc. Vol. 1. Kongl. Sven. Vet.-Akad. Handl. 7 (11) : 1–148.

1855. Hemiptera från Cafferlandet. Öfv. Svenska Vet.-Akad. Förh. 12: 27–47.

1873. Enumeratio Hemipterorum III. *in* Kongl. Sven. Vet.-Akad. Handl. 11 (2) : 1–163 (Cimicidae, p. 104).

Stalker, H. D. 1942. Sexual isolation studies in the species complex *Drosophila viridis*. Genetics 27: 238–57.

Steinhaus, E. A. 1941. A study of the bacteria associated with thirty species of insects. J. Bacteriol. 42: 757–90.

Stichel, W. 1926. Illustrierte Bestimmungstabellen der deutschen Wanzen (Hemiptera-Heteroptera). Lief. 4. Naturwiss. Publ., Berlin. P. 91–120, fig. 249–317 (Cimicidae, p. 119–20, fig. 316).

1937. Illustrierte Bestimmungstabellen der deutschen Wanzen (Hemiptera-Heteroptera). Geographische Verbreitung I. Lief. 13. Naturwiss. Publ., Berlin. P. 363–94 (Cimicidae, p. 376–7).

1938. Illustrierte Bestimmungstabellen der deutschen Wanzen (Hemiptera-Heteroptera). Geographische Verbreitung. III. Ergänzungen und Berichtigungen I. Lief. 15. Naturwiss. Publ., Berlin-Hermsdorf. P. 403–58, 8 fig. (Cimicidae, p. 456).

1959. Illustrierte Bestimmungstabellen der Wanzen, II. Europa (Hemiptera-Heteroptera Europae), 3 (3), Cimicomorpha: Microphysidae, Cimicidae, Reduviidae (1): 65–96, 68 fig. (Cimicidae, p. 76–80, fig. 230–47).

Stiles, C. W. 1924. International Commission on Zoological Nomenclature. Opinion 81. Smiths. Misc. Coll. 73 (2): 19–32.

Stiles, C. W., and M. O. Nolan. 1930. Key catalogue of parasites reported from Chiroptera (bats) with their possible public health importance. Nat. Inst. Health, Bull. no. 155, p. 603–742 (Cimicidae, p. 641–2).

Syms, E. E. 1953. (Exhibit Note) *C. pipistrelli* Jenyns, a bug parasite on bats, found on a fallen elm in Wanstead Park, Essex, Nov. 10, 1952. Proc. S. London Entomol. Soc. 1952: 53–57.

Thompson, D. W. (See Aristotle)

Titschack, E. 1930. Untersuchungen über das Wachstum, den Nahrungsverbrauch und die Eierzeugung. 3. *Cimex lectularius* L. Z. Morphol. Oekol. Tiere 17: 471–551, 5 fig.

1949. Die Bettwanze und die Taubenwanze. Verhandl. deut. Ges. angew. Entomol. 11: 71–77.

Torre Bueno, J. R. de la. 1914. European Heteroptera alleged to occur in the United States. Entomol. News 25 (5): 230 (Cimicidae, p. 230).

1915. The *Cimex* on American Bats. (Hemipt., Heter.) Entomol. News 26 (1): 16.

1931. What is the type of the genus *Cimex* Linné? Editorial. Bull. Brooklyn Entomol. Soc. 26 (1): 49.

Townsend, C. H. T. 1894. Note on the coruco, a hemipterous insect which infests poultry in southern New Mexico. Proc. Entomol. Soc. Wash. 3 (1): 40–41.

Troedsson, P. H. 1944. The behavior of the compound sex chromosomes in the females of certain Hemiptera Heteroptera. J. Morphol. 75: 103–47.

Twinn, C. R. 1953. The bedbug and its control. Canada Dep. Agr., Sci. Serv., 3 p.

Ueshima, N. 1962. Cytotaxonomy of the genus *Cimex*. Unpublished thesis, Univ. of Calif., Berkeley.

1963a. Chromosome behavior of the *Cimex pilosellus* complex (Cimicidae: Heteroptera). Chromosoma 14: 511–21, 31 fig.

1963b. New techniques in cytotaxonomy. Chromosome Information Service, no. 4, p. 17–18.

1964. Experiments on reproductive isolation in *Cimex lectularius* and *Cimex columbarius* (Hemiptera: Cimicidae). Pan-Pacific Entomol. 40 (1): 47–53.

Uhler, P. R. 1884. Natural History of Arthropods: Order VI—Hemip-

tera. Standard Natural History 2: 204–96, fig. 286–343 (Cimicidae, p. 285, fig. 328).

1886. Checklist of the Hemiptera Heteroptera of North America. Brooklyn Entomol. Soc., 32 p. (Cimicidae, p. 21).

Usinger, R. L. 1939. Key to the North American Cimicidae, *in* W. B. Herms, Medical Entomology, 3rd ed. Macmillan Co., New York. xxx + 582 p., 196 fig. (Cimicidae, p. 92).

1947. Native hosts of the Mexican chicken bug, *Haematosiphon inodora* (Dugés) (Hemiptera, Cimicidae). Pan-Pacific Entomol. 23 (3): 140.

1950. Key to North American Cimicidae, *in* W. B. Herms, Medical Entomology, 4th ed. Macmillan Co., New York. xvi + 643 p., 191 fig. (Cimicidae, p. 99–100).

1959a. A new species of *Stricticimex* from Ruanda-Urundi (Hemiptera: Cimicidae). Rev. Zool. Bot. Afr. 60 (1–2): 61–64, 1 fig.

1959b. New species of Cimicidae (Hemiptera). Entomologist 92: 218–22.

1960. The Cimicidae of Egypt (Hemiptera). J. Egypt. Pub. Health Ass. 35 (2): 81–89, 4 pl.

1963. A new bat bug from southern Chile (Hemiptera: Cimicidae). Pan-Pacific Entomol. 39 (1): 51–55, 1 fig.

Usinger, R. L., and G. F. Ferris. 1960. Heteroptera. Insects of Micronesia 7 (5): 219–86, 32 fig. Bishop Mus. (Cimicidae, p. 285–6, 1 fig.).

Usinger, R. L., and D. Povolný. 1966. The discovery of a possibily aboriginal population of the bed bug (*Cimex lectularius* Linnaeus, 1758) Acta Mus. Moraviae, Sci. Nat. 51 (in press).

Usinger, R. L., and N. Ueshima. 1965. New species of bat bugs of the *Cimex pilosellus* complex. Pan-Pacific Entomol. 41: 114–17.

Van Duzee, E. P. 1916. Check list of the Hemiptera (Excepting the Aphididae, Aleurodidae, and Coccidae) of America, North of Mexico. New York Entomol. Soc., N. Y. xi + 111 p. (Cimicidae, p. 33–34).

1917. Catalogue of the Hemiptera of America North of Mexico. Univ. of Calif. Pub. Ent. (Tech. Bull.), Vol. 2, xiv + 902 p. (Cimicidae, p. 284–7).

Vaurie, C. 1959. The birds of the Palearctic fauna, a systematic reference: Order Passeriformes. H. F. and G. Witherby, Ltd., London. xii + 762 p.

Venkatachalam, P. S., and B. Belavadi. 1962. Loss of haemoglobin iron due to excessive biting by bedbugs. Trans. Roy. Soc. Trop. Med. Hyg. 56: 218–21.

Vlassov, J. P. 1929. Sur la biolgie de *Phlebotomus sergenti* Parrot. Russ. J. Trop. Med. 7 (10): 688–92, 1 fig. (Cimicidae, p. 692).

Walkden, H. 1963. Common names of plants composed in part of in-

sect names or insect products. Bull. Entomol. Soc. Amer. 9 (1) : 17–23 (Cimicidae, p. 17, 18).

Waterhouse, D. F., D. A. Forss, and R. H. Hackman. 1961. Characteristic odour components of the scent of stink bugs. J. Insect Physiol. 6 (2) : 113–21.

Wattal, B. L., and N. L. Kalra. 1961. New methods for the maintenance of a laboratory colony of bed-bug *Cimex hemipterus* Fabricius, with observations on its biology. Indian J. Malariol. 15 (2) : 157–71.

Webster, W. H. B. 1834. Narrative of a voyage to the southern Atlantic ocean, in the years 1828, 29, 30, performed in H. M. Sloop Chanticleer, under the command of the late Captain Henry Foster, F.R.S., etc. R. Bentley, London. 2 vols. (Cockroaches and bedbugs, vol. 1, p. 373).

Weidner, H. 1958. Die auf Fledermäusen parasitierenden Insekten mit besonderer Berücksichtigung der in Deutschland vorkommenden Arten. Nachr. naturwiss. Mus. Aschaffenburg 59: 1–88, 21 pl. (Cimicidae, p. 16–26).

Weitz, B. 1956. Identification of blood-meals of blood-sucking arthropods. Bull. World Health Organ. 15 (3/4/5) : 473–90.

Weitz, B., and P. A. Buxton. 1953. The rate of digestion of blood-meals of various haematophagous arthropods as determined by the precipitin test. Bull. Entomol. Res. 44: 445–50.

Wendt, A. 1937. 35. Beitrag zur mecklenburgischen Heteropterenfauna (Zur Kenntnis der mecklenburgischen Fauna X). Arch. Ver. Naturgesch. Mecklenburg (N. F.) 12: 41–58.

1939a. 46. Beitrag zur Kenntnis der Verbreitung und Lebensweise der Schwalbenwanze (*Oeciacus hirundinis* Jen.) in Mecklenburg (Zur Kenntnis der mecklenburgischen Fauna XII). Arch. Ver. Naturg. Mecklenb. (N. F.) 14: 71–94.

1939b. *Cimex hemipterus* f. *flavifusca* form. nov. (Hex., Rhynchota). Z. Parasitenk. 11 (2–3) : 199–201, 3 fig.

1941a. Familie Cimicidae Latreille 1804. *In* J. Gulde, Die Wanzen Mitteleuropas. Hemiptera Heteroptera Mitteleuropas. VIII Teil. O. H. Wrede, Frankfurt a m. P. 119–265, 61 fig. (Cimicidae, p. 119–31, 10 fig.).

1941b. Ueber *Cimex pipistrelli* Jenyns und seine Formen (Hex. Rhynchota). Z. Parasitenk. 12 (2) : 259–72, 13 fig.

White, M. J. D. 1954. Animal Cytology and Evolution. 2nd ed. Cambridge Univ. Press, London. xiv + 454 p., 147 fig.

Whitfield, F. G. S. 1939. Air transport, insects and disease. Bull. Entomol. Res. 30 (3) : 365–442 (Cimicidae, p. 418).

Wigglesworth, V. B. 1931. Effect of desiccation on the bed-bug (*Cimex lectularius*). Nature 127: 307–8, 2 fig. Also Proc. Entomol. Soc. London 6: 25–26.

1936. The function of the corpus allatum in the growth and reproduction of *Rhodnius prolixus* (Hemiptera). Quart. J. Microscop. Sci. 79: 91–121.

1937. Wound healing in an insect (*Rhodnius prolixus*-Hemiptera). J. Exp. Biol. 14 (3): 364–81.

1955. The role of the haemocytes in the growth and moulting of an insect, *Rhodnius prolixus* (Hemiptera). J. Exp. Biol. 32: 649–63, 8 fig.

1956a. The functions of the amoebocytes during moulting in *Rhodnius*. Ann. Sci. Nat. Zool., 11e ser., XVIII, 10: 139–44.

1956b. The haemocytes and connective tissue formation in an insect, *Rhodnius prolixus* (Hemiptera). Quart. J. Microscop. Sci. 97 (1): 89–98.

Wilson, E. B. 1907. Notes on the chromosome groups of *Metapodius* and *Banasa*. Biol. Bull. 12: 303–13.

1909. Studies on chromosomes. V. The chromosomes of *Metapodius*, a contribution to the hypothesis of the genetic continuity of chromosomes. J. Exp. Zool. 6: 147–205.

1910. Studies on chromosomes. VI. A new type of chromosome combination in *Metapodius*. J. Exp. Zool. 9: 53–78.

1913. A chromatid body simulating an accessory chromosome in *Pentatoma*. Biol. Bull. 24: 392–411.

Wilson, E. O., and W. H. Bossert. 1963. Chemical communication among animals. Recent progress, 19. Acad. Press, Inc., New York. P. 673–716, 10 fig.

Wiltberger, P. B. 1916. A note on the anatomy and bionomics of the bedbug (*Cimex lectularius* L.). Biologist 1: 1–2.

Wolff, J. F. 1800. Die Bettblutwanze (*Acanthia lectularia*). Abbildungen der Wanzen. Erlangen 4: 127–28, Table 13, fig. 121, a, b.

Woodroffe, G. E. 1956. Some insects and mites associated with batroosts, with a discussion of the feeding habits of the cheyletids (Acarina). Entomol. Mon. Mag. 92: 138–41.

Wright, W. H. 1944. The bedbug—its habits and life history and methods of control. Public Health Reports, Suppl. no. 175, 9 p., 2 fig.

Wygodzinsky, P. 1950. Sobre *Bertilia valdiviana* (Philippi, 1865) (Cimicidae, Hemiptera). An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (1): 119–22, 2 fig.

1951. Notas sobre Cimicidae de la Republica Argentina. (Hemiptera). An. Inst. Med. Reg. Mus. Nac. Tucumán 3 (2): 185–97, 50 fig.

1952. Los insectos de las islas Juan Fernandez. 2. Reduviidae y Cimicidae (Hemiptera). Rev. Chil. Entomol. 2: 15–19, 6 fig. (Cimicidae, p. 19).

Zetterstedt, J. W. 1828. Coleoptera, Orthoptera et Hemiptera, Faunae

Insectorum Lapponicae. Hammone, Libraria Schulziana, xx + 563 p. (Cimicidae p. 485).

Zimmer, J. T. 1914. Cimex pipistrelli Jenyns in North America? Entomol. News 25: 418–19.

Zumpt, F. 1940. Über neuere Untersuchungen zur Rolle der Bettwanzen als Krankheitsüberträger. Zbl. Bakteriol. Abt. 1 Ref. 136 (19–20): 401–14.

1942. Medizinisch wichtige Insekten. Merkblatt 2. Bettwanzen. Merkblätter des Institut für Schiffs- und Tropenkrankheiten, Hamburg. 8 p., 6 fig.