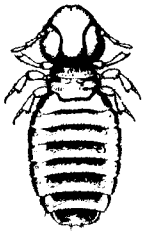
OFFPRINTS FROM COEVOLUTION OF PARASITIC ARTHROPODS AND MAMMALS
Edited by Professor Ke Chung Kim



Bovicola bovis (Linnaeus)

Chapter 6

Evolution of Mallophaga on Mammals

K. C. Emerson and Roger D. Price

INTRODUCTION

Mallophaga (chewing lice) are small wingless obligatory external parasites that live on certain species of land mammals and birds. Although they are more numerous in genera and species on birds than on mammals, this chapter discusses only the Mallophaga found on mammals.

Mallophaga spend the entire life cycle on the host. Their eggs are attached to the hair or fur of the host. Following hatching, there are three nymphal or preadult stages. Adults and nymphs, depending on the species, feed on fur, hair, blood, serum, and secretions of sebaceous glands. The microclimate, composition of food, and other ecological conditions found near the skin of the mammal and their tolerance of these factors likely are the greatest influences in determining host specificity of the Mallophaga. Most species of chewing lice cannot tolerate a temperature much higher than that of their normal host, however, they are more tolerant of a lower temperature. The humidity of the microclimate next to the skin appears to effect Mallophaga. Chewing lice depend on an intimate and continuous association with their host, living at most only a few days when deprived of their normal food.

A few species of Mallophaga are found on several species of related mammals, however, many are limited in distribution to a single species or subspecies of host. Therefore we believe that, as mammalian species evolved, their Mallophaga evolved too, but at a slower rate, because the host's environment sometimes changed more drastically than the microhabitat near the skin of the host where the Mallophaga live. When mammals could not adapt to changing ecological conditions, Mallophaga unique to those hosts probably became extinct with their hosts. To date, the remains of many extinct species of mammals are known, but no fossils of any Mallophaga have ever been found, or have any specimens been found in amber.

Hopkins (1949) has presented an excellent summary of mammal–louse associations, and Werneck (1948, 1950) has treated the taxonomy of mammalian Mallophaga described up to that time.

The classification and scientific names of mammals used in this chapter are those of Honacki et al. (1982). We published a host–parasite list of the Mallophaga on mammals (Emerson and Price 1981) and here follow taxonomic treatments and scientific names used in that list.

DIVERSITY AND HOST DISTRIBUTION OF MALLOPHAGA

The current classification, up to the generic level, of the Mallophaga found on living mammals and the probable faunal region of origin for each mallophagan family are listed as follows:

Suborder AMBLYCERA

Family Boopiidae—Australasian
Genera: *Boopia, Heterodoxus, Latumcephalum, Macropophila, Paraboopia, Paraheterodoxus,* and *Phacogalia*

Family Trimenoponidae—Neotropical
Genera: *Chinchillophaga, Cummingsia, Harrisonia, Hoplomyophilus, Philandesia,* and *Trimenopon*

Family Abrocomophagidae—Neotropical
Genus: *Abrocomophaga*

Family Gyropidae—Neotropical
Subfamily Protogyropinae
Genus: *Protogyropus*
Subfamily Gliricolinae
Genera: *Gliricola, Monothoracius,* and *Pitrufquenia*
Subfamily Gyropinae
Genera: *Aotiella, Gyropus, Macrogyropus,* and *Phtheiropoios*

Suborder ISCHNOCERA

Family Trichodectidae—Holarctic and/or Ethiopian
Genera: *Bovicola, Cebidicola, Damalinia, Dasyonyx, Eurytrichodectes, Eutrichophilus, Felicola, Geomydoecus, Lorisicola, Lutridia, Lymeon, Neofelicola, Neotrichodectes, Parafelicola, Procavicola, Procaviphilus, Stachiella, Suricatoecus, Trichodectes,* and *Tricholipeurus*

Family Philopteridae—Madagascar (for genus listed below)
Genus: *Trichophilopterus*

Suborder RHYNCHOPHTHIRINA

Family Haematomyzidae—Ethiopian and/or Oriental
Genus: *Haematomyzus*

Kim and Ludwig (1978) believe the suborder Amblycera developed in the late Cretaceous period and early Paleocene epoch, the suborder Ischnocera and Rhynchophthirina in the late Paleocene and early Eocene epochs. However, there are no fossil records to prove or disprove these conclusions. As we later discuss, species in the suborder Amblycera are found only on mammals considered to be the more primitive of the living mammals.

When Simpson completed the manuscript of *The Principles of Classification and a Classification of Mammals* in 1942 (published in 1945), he noted that 54% of the mammalian families and 67% of the genera were extinct. He also stated that ". . . of the 18 surviving orders, 15 include known extinct families." The numbers of extinct genera and species of mammals have increased significantly since 1942, while the number of new species of living mammals found has been almost nil. To date, Mallophaga have been found on only nine orders of living mammals. The number of extinct and living genera in these orders, as given by Simpson, are as follows:

	Genera	
Order	Extinct	Living
Marsupialia	81	57
Primates	99	59
Edentata	113	19
Rodentia	275	344
Carnivora	261	144
Proboscidea	22	2
Hyracoidea	10	3
Perissodactyla	152	6
Artiodactyla	333	86

We believe there are at least 4268 species of living mammals, and a majority of these (3400) do not normally have Mallophaga (Emerson and Price 1981). No chewing lice are known from Monotremata, Insectivora, Scandentia, Dermoptera, Chiroptera, Pholidota, Lagomorpha, Cetacea, Pinnipedia, Sirenia, and a majority of Rodentia. Of the remaining 868 species of living mammals, Mallophaga have been recorded from 356. So it is believed that, to date, less than half of the existing species of Mallophaga on living mammals have been found and described. Many of the endangered or rare and seldom-collected mammals have not been examined for Mallophaga; current laws protecting the larger mammals, especially the Carnivora, Perissodactyla, and Artiodactyla, have reduced opportunities to collect Mallophaga from wild hosts. We hope that, within the next 20 years, Mallophaga can be obtained from all known living species of Carnivora, Perissodactyla, and Artiodactyla.

Here, we summarize the Mallophaga recorded on species of each mammalian family. We omit the mammalian families in each order for which no species of Mallophaga have been recorded, even though the possibility exists of their having the parasites.

Marsupialia

Of 16 families of the Marsupialia, only six families have been recorded to harbor mallophagans.

Family	Number of Living Species	Number of Species Known with Mallophaga
Didelphidae	65	4
Dasyuridae	58	10
Peramelidae	19	3
Caenolestidae	7	1
Vombatidae	2	2
Macropodidae	54	23

One species of *Cummingsia* (Trimenoponidae) is found on the didelphid *Monodelphis*, another on the didelphid *Marmosa*, and a third on the caenolestid *Lestoros*. The other species of *Cummingsia* is found on a Neotropical rodent and probably was acquired from a Neotropical marsupial. All of the mallophagans recorded for the Boopiidae are found on the marsupials of Australia and New Guinea, except for one which originated there on the Dingo and is now found on *Canis* species worldwide. Recent work by Kéler (1971) and Clay (1976) provides excellent data on the Mallophaga found on marsupials of Australia and New Guinea. No comprehensive study of the Mallophaga found on marsupials of the Neotropics has been published.

Primates

Of 14 families of the Primates, chewing lice are found on three prosimian families and one anthropoid family. They are as follows:

Family	Number of Living Species	Number of Species Known with Mallophaga
Lemuridae	16	2
Indriidae	4	2
Lorisidae	11	1
Cebidae	37	7

The philopterid species *Trichophilopterus babakotophilus* (Stobbe) has been recorded from two species of Lemuridae and two species of Indriidae, both of these families found on the island of Madagascar. All records are from specimens taken from museum skins, so some host records are suspect. However, this species is unique, as are many organisms from Madagascar.

The slow loris (Lorisidae) of southeastern Asia has the ischnoceran species *Lorisicola mjobergi* (Stobbe) (Trichodectidae).

Within the Cebidae, douroucouli (*Aotus trivirgatus*) have the gyropid *Aotiella aotophilus* (Ewing). Gyropid Mallophaga are known only from Neotropical mammals. Howler monkeys (*Alouatta* sp.) have an ischnoceran species of *Cebidicola* (Trichodectidae), which has not been found on other hosts. Trichodectid Mallophaga are found worldwide on a variety of hosts, as discussed later.

Edentata

Of seven living species of Bradypodidae only two species harbor the trichodectid mallophagans (Ischnocera): *Lymeon cummingsi* Eichler on the three-toed sloth (*Bradypus tridactylus*) and *Lymeon gastrodes* (Cummings) on the two-toed sloth (*Choloepus didactylus*).

Rodentia

The occurrence of Mallophaga on rodents is sporadic, although the order Rodentia represents the largest diversity among living mammals. The following shows their diversity relationship:

Family	Number of Living Species	Number of Species Known with Mallophaga
Geomyidae	31	31
Cricetidae	623	2
Erethizontidae	9	8
Caviidae	15	10
Dasyproctidae	17	8
Chinchillidae	6	3
Capromyidae	11	4
Ctenomyidae	27	10
Abrocomidae	2	2
Echimyidae	43	21

During the last 35 years, mammalogists have conducted extensive research on the taxonomy and evolution of the pocket gophers (Geomyidae). In the last 12 years, Price and his co-workers, Emerson, Hellenthal, and Timm, have examined Mallophaga from all 31 species and more than 300 subspecies of Geomyidae. Before these studies began, only 11 specific taxa of Mallophaga were known from pocket gophers. Now 102 species and subspecies of *Geomydoecus* (Trichodectidae) are known, and there are undoubtedly others still to be described. The trichodectid *Geomydoecus* is confined to hosts of Geomyidae. Detailed results of these research efforts, dealing with each species of Geomyidae and their Mallophaga, have been published in a series of papers (e.g. Price 1972; Price and Emerson, 1971, 1972; Price and Hellenthal 1975, 1976, 1979, 1980a–c; Timm and Price 1980; and Hellenthal and Price 1976, 1980). This research is continuing; however, it already represents the most exhaustive study done to date of a family of mammals and their Mallophaga. These results indicate that the Mallophaga exhibit varying degrees of host specificity at the host generic, specific, and subspecific levels and that many hosts have more than one species of *Geomydoecus*. These studies are providing new clues to mammalogists on the taxonomy and evolution of the pocket gophers, and it is hoped that in the future comparable research efforts can be expended on other groups of mammals and their Mallophaga.

Cummingsia inopinata Mendez (Trimenoponidae) has been recorded from the cricetid *Thomasomys cinereiventer;* it probably represents a relatively recent transfer from a Neotropical marsupial. Another cricetid, *Scapteromys gnambiquarae*, now has *Gyropus ribeiroi* Werneck (Gryopidae), which it probably acquired from another Neotropical rodent, perhaps Echimyidae.

The ischnoceran *Eutrichophilus* (Trichodectidae) is found only on the New World porcupines (Erethizontidae). The number of *Eutrichophilus* species found on each species of porcupine varies from one to three, and they are host specific. *Eutrichophilus* is unique in that some species have asymmetrical heads, a condition not found in other mammalian

Five species of *Cavia* (Caviidae) have Mallophaga in the genera *Gliricola* and *Gyropus* (Gyropidae), and *Trimenopon* (Trimenoponidae). *Trimenopon hispidum* (Burmeister) has been found on guinea pigs. The species of *Gliricola* and *Gyropus* on guinea pigs do not appear to be host specific, but are found only on *Cavia*. Other species of each taxon are found on other Neotropical hosts.

Mallophaga found on rodent hosts in the Dasyproctidae, Chinchillidae, Capromyidae, Ctenomyidae, Abrocomidae, and Echimyidae are all in the families Trimenoponidae, Gyropidae, and Abrocomophagidae; all are restricted to Neotropical mammalian hosts. These mallophagan families originated in the Neotropical region and have not become established elsewhere on other hosts. Mammalogists seem to be having difficulty with the taxonomy of the spiny rats of the genus *Proechimys* (Echimyidae). To date, we (Emerson and Price 1975) have seen Mallophaga from 10 species of *Proechimys*, and, based on our studies of these specimens, the Mallophaga will provide clues to help separate the populations of *Proechimys*.

Carnivora

The Mallophaga occur exclusively on land carnivores (Fissipedia) and are completely absent on marine carnivores (Pinnipedia) and some aquatic fissipeds like river otters, which harbor the anopluran Echinophthiriidae. The major diversity of mallophagans is found on Mustelidae and Viverridae. The breakdown of this diversity is the following:

Family	Number of Living Species	Number of Species Known with Mallophaga
Canidae	38	14
Ursidae	7	3
Procyonidae	18	5
Mustelidae	68	36
Viverridae	82	36
Protelidae	1	1
Hyaenidae	3	1
Felidae	37	13

Trichodectes canis (De Geer) (Trichodectidae), the common mallophagan on the domestic dog, has now been collected from other wild hosts in the genus *Canis*. The other chewing louse found on these hosts is *Heterodoxus spiniger* (Enderlein) (Boopiidae), originally found only on the dingo. These two species of Mallophaga have been found occasionally on some of the foxes; however, *Suricatoecus* (Trichodectidae) is the mallophagan normally found on foxes. *Suricatoecus* species apparently are more host specific than are those of *Trichodectes* or *Heterodoxus*. In the future, with more intermin-

gling between domestic dogs and wild canids, the Mallophaga common on the dog may replace other species on wild foxes.

Trichodectes ferrisi Werneck (Trichodectidae) is found on the spectacled bear (*Tremarctos ornatus*) of South America, *T. pinguis pinguis* Burmeister on the European brown bear (*Ursus arctos*), and *T. pinguis euarctidos* Hopkins on the North American black bear (*Ursus americanus*). No Mallophaga have been seen from the Asiatic black bear (*Selenarctos thibetanus*), the North American brown or grizzly bears (*Ursus arctos*), the polar bear (*Thalarctos maritimus*), the sun bear (*Helarctos malayanus*), or the sloth bear (*Melursus ursinus*). If Mallophaga from the bears just listed could be studied, relationships of the living species of bears might be answered.

The North American cacomistle, *Bassariscus astutus*, has the ischnoceran *Neotrichodectes thoracicus* (Osborn) (Trichodectidae). No Mallophaga have been examined from the other species of *Bassariscus*. The North American raccoon, *Procyon lotor*, has *Trichodectes octomaculatus* Paine (Trichodectidae); the crab-eating raccoon, *P. cancrivorus*, has *T. fallax* Werneck. No Mallophaga have been seen on the five insular species of *Procyon*, so it cannot be stated at this time whether or not they might be subspecies of the North American raccoon. The common coati, *Nasua nasua*, has another ischnoceran *Neotrichodectes pallidus* (Piaget); no Mallophaga have been examined from the other two species of coatis. The kinkajou, *Potos flavus*, has *Trichodectes potus* Werneck. No Mallophaga have been seen from the three species of olingos, *Bassaricyon* species. We hope that in the near future Mallophaga can be obtained from the two species of pandas, as they should prove to be interesting to study.

Mallophaga have been collected from slightly more than half of the living species of mustelids, from which the mallophagans collected are *Lutridia, Neotrichodectes, Stachiella,* and *Trichodectes* (Trichodectidae). The genus *Lutridia* has been found only on four species of otters (Lutrinae). No specimens have been seen to date on the North American or sea otters. The *Neotrichodectes* has been found on some New World species of Mustelinae, the American badger (*Taxidea taxus*), and New World skunks (*Mephitis, Spilogale,* and *Conepatus*), where they are mostly host specific. *Stachiella* has been found on mammalian species of *Mustela, Martes, Galictis, Ictonyx,* and *Poecilictis,* where they are host specific. The genus *Trichodectes* has been found on species of *Martes* (Asian), *Eira, Galictis, Grisonella, Mellivor, Meles,* and *Melogale.* The species of Mallophaga found on the mustelids are generically diverse. Perhaps, when Mallophaga from other species of mustelids are collected, a revision of the mallophagan species will be required.

Less than half of the species of the mammalian family Viverridae have been examined for Mallophaga; the genera found to date are *Felicola, Neofelicola, Parafelicola, Suricatoecus,* and *Trichodectes* (Trichodectidae). Most of the species of these Mallophaga are host specific, and several hosts have more than one species of louse. The species on *Genetta* ought to be reexamined when better identifications of the hosts are available; there is confusion over the early records off *Genetta genetta* and *G. tigrina.* We need new material from properly identified hosts to clarify these records. The ischnoceran *Neofelicola* and *Parafelicola* are found only on species of Viverridae, while *Felicola, Suricatoecus,* and *Trichodectes* are also found on other mammalian families. The water mongoose (*Atilax paludinosus*) has the distinction of having seven species of Mallophaga that are host specific to it.

The aardwolf (*Proteles cristatus*) has a *Felicola* species that is only subspecific from the form found on the brown hyaena (*Hyaena brunnea*). Mallophaga have not been examined from the other two species of hyaenas.

Felicola has been the only genus found to date on the cats (Felidae). Mallophaga have been examined from only a third of the species of Felidae, but those studied show a good degree of host specificity.

Proboscidea

There are two species of living elephants (Elephantidae); *Elephas maximus* and *Loxodonta africana.* The rhynchophthirinan species *Haematomyzus elephantis* Piaget (Haematomyzidae) has been recorded on both species of living elephants. We have seen specimens collected from wild Asian elephants but have not seen any from wild African elephants. The only other species of *Haematomyzus* known is a closely related species, *H. hopkinsi* Clay, found on wart hogs in Africa. There is little doubt that the original hosts for this genus were elephants.

Hyracoidea

The living hyraxes consist of three genera, *Dendrohyrax, Heterohyrax,* and *Procavia.* Three species each are recognized for *Dendrohyrax* and *Heterohyrax.* There is a controversy over the taxonomy of *Procavia:* previously six species were recognized for this group, but recently it was considered a single species (Honacki et al. 1982). Of the 11 species previously recognized, nine species of hyraxes are recorded to harbor mallophagans.

The ischnoceran genera *Dasyonyx, Eurytrichodectes, Procavicola,* and *Procaviphilus* (Trichodectidae) are found only on hyraxes. They exhibit host specificity ranging from host genus to host subspecies, and in many cases more than one species of a mallophagan genus will be found on a host subspecies. The host–parasite relationships are similar to those found on the pocket gophers (Geomyidae) and the spiny rats (Echimyidae: *Proechimys*). The present data show that the Mallophaga are specific to various hyrax populations (probably subspecies) and thus could be used to identify more accurately the host of Procaviidae. Cooperation between mammalogists and Mallophaga taxonomists probably can produce a new and useful classification of the Procaviidae.

Perissodactyla

Nine species of extant *Equus* (Equidae) are recognized at present, and most of these equids harbor chewing lice. Mallophagan species of the genus *Bovicola* (subgenus *Werneckiella*) (Trichodectidae) have been recorded from all living species of horses, asses, and zebras except Grevy's zebra (*Equus grevyi*). Moreby (1978) found one species of *Bovicola* on each of the other six species of Equidae, except for the common zebra (*Equus burchelli*) which has two species, one on the subspecies in southern Africa and one on the subspecies of central Africa.

Artiodactyla

Of the eight families of Artiodactyla recognized (Honacki et al. 1982), the following six families have infestation records of Mallophaga:

Family	Number of Living Species	Number of Species Known with Mallophaga
Suidae	8	1
Tayassuidae	2	2
Camelidae	6	3
Tragulidae	4	2
Cervidae	41	14
Bovidae	126	52

Haematomyzus hopkinsi Clay (Haematomyzidae), a close relative of the mallophagan from elephants, has been taken from wart hogs in Africa (Clay 1963).

Macrogyropus dicotylis (Macalister) (Gyropidae) has been recorded on both species of living peccaries. The genus *Macrogyropus*, as noted later, is restricted to larger Neotropical mammals.

Bovicola breviceps (Rudow) (Trichodectidae) has been recorded from the llama (*Lama glama*), the guanaco (*Lama guanicoe*), and the alpaca (*Lama pacos*) (Camelidae). No Mallophaga have been seen on the vicuna (*Vicugna vicugna*) or the camels.

Damalinia traguli Werneck (Trichodectidae) has been taken from the larger Malay chevrotain (*Tragulus napu*) and the lesser Malay chevrotain (*Tragulus javanicus*) (Tragulidae).

Mallophaga have been recorded on only about a third of the species of living Cervidae, those being in the genera *Bovicola*, *Damalinia*, and *Tricholipeurus* (Trichodectidae). The red deer (*Cervus elaphus*) of Europe and Asia and the wapiti (*Cervus canadensis*) of North America have the same mallophagan species, *Bovicola longicornis* (Nitzsch) and *B. concavifrons* (Hopkins). The mule deer (*Odocoileus hemionus*) and the white-tail deer (*Odocoileus virginianus*), both found in North America, have *Tricholipeurus lipeuroides* (Megnin) and *T. parallelus* (Osborn). Since so many of the other species of Cervidae have not been examined for Mallophaga, what the host specificity of their lice is not known.

The situation concerning Mallophaga on species of Bovidae is not much different from that of the Cervidae, with the same three genera of Mallophaga found to date on less than half of the known living species of hosts. A few hosts have two species of Mallophaga, and a few species of hosts in the same genus share the same mallophagan species. There are, however, some unique examples. The aoudad (*Ammotragus lervia*) has two species of *Bovicola*, subgenus *Werneckiella*, which are not typical of the species of *Bovicola* found on other species of Cervidae or Bovidae; they are typical of the type found on horses, asses, and zebras. Furthermore, the domestic Angora goat has *Bovicola crassipes* (Rudow), not found on domestic short-haired goats. This species is closely related to the species found on the Himalayan tahr (*Hemitragus jemlaica*) and the bharal (*Pseudois nayaur*). Three species of *Damalinia* have been recorded from the brindled gnu (*Connochaetes taurinus*), which constitutes the only record we have of three species of Mallophaga from a species of Bovidae. As in the Cervidae, Mallophaga from the hosts that have no present collection records would be very interesting to study.

The foregoing brief discussion provides some data on the presently known distribution of Mallophaga on living land mammals. A complete list of mammals and their mallophagan parasites has recently been published (Emerson and Price 1981). The classification of Mallophaga currently used has, for several reasons, not been accepted by some entomologists. It is based upon a few morphological similarities and a belief that all Mallophaga, including those found on birds, evolved from a common ancestral stock. Also, it does not recognize the fact that many recent mammals, now extinct, probably also had chewing lice and that Mallophaga have been examined from less than half of the living mammals that probably have these parasites. Although there are no known fossil records of Mallophaga, it is postulated that the evolution of Mallophaga must have occurred later and more slowly than that of their hosts. The following discussion concerns all of these factors and their impact upon the present classification of Mallophaga.

EVOLUTION OF MAMMALIAN MALLOPHAGA

Amblycera

The amblyceran Boopiidae, commonly found on marsupials of New Guinea and Australia, most likely originated in Australia. Marsupials are known from fossils in the Cretaceous period in both South and North

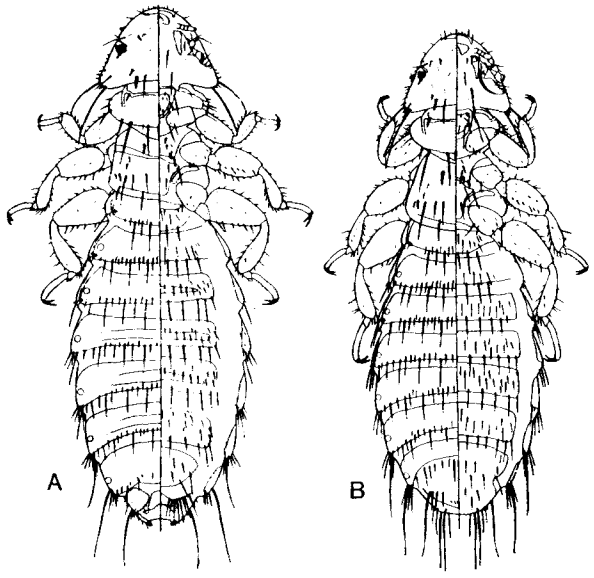


Figure 6.1 *Heterodoxus spiniger* (Enderlein), from *Canis familiaris*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1975. Mallophaga of Venezuelan mammals. *Brigham Young Univ. Sci. Bull., Biol. Sci.* **20**:1–77. By permission of the Brigham Young University Press.)

America, but not in Australia. They probably were in Australia in the late Cretaceous period, even though no fossils have been found. Those three continents have not been part of a single land mass since mammals evolved (Kurtén 1969; Simpson 1980). Only two species of Boopiidae are not found on marsupials. *Heterodoxus spiniger* (Fig. 6.1) is found on the dingo and has spread in modern times to canids worldwide. This louse is similar to other *Heterodoxus* found on marsupials and must have evolved recently from one of those species as it became established on the feral or semidomesticated dogs introduced by the aborigines. *Therodoxus oweni* Clay is a monotypic species recently described from specimens collected from a cassowary (Casuariiformes) in New Guinea (Clay 1971). This species is properly placed in the Boopiidae and probably originated from a form found on marsupials in the area. Because no other species of this genus, or any closely related to it, have been found on other species of cassowaries, it may be assumed that the species did not evolve from another avian mallophagan form. We believe the Boopiidae originated in Australia from a stock not found elsewhere and became parasitic as the marsupials evolved on that land mass. The family Boopiidae is a logical grouping of related genera and species.

The Trimenoponidae, found only on certain land mammals in the Neotropics, contains diverse genera of Mallophaga (Ferris 1922; Mendez 1967).

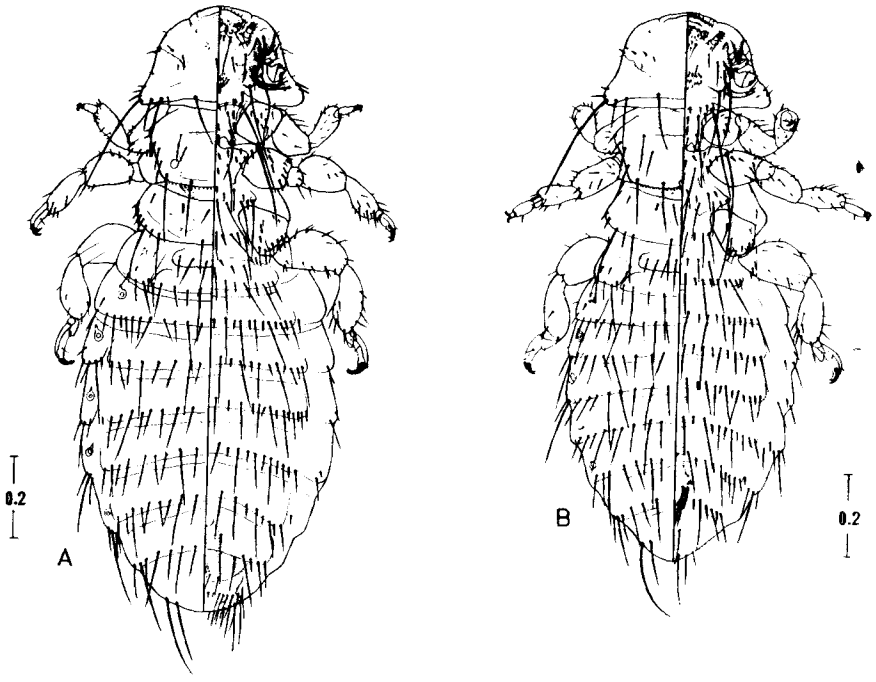


Figure 6.2 *Cummingsia peramydis* Ferris, from *Monodelphis brevicaudata*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1975. Mallophaga of Venezuelan mammals. *Brigham Young Univ. Sci. Bull., Biol. Sci.* **20**:1–77. By permission of the Brigham Young University Press.)

The genus *Cummingsia* (Fig. 6.2) contains four species at present; three are known from South American marsupials and a fourth is found on a rodent (*Thomasomys cinereiventer:* Cricetidae). These four species are closely related, each having prominent spinelike projections on the ventral side of the head. These structures differ in shape and size from those found on species of Boopiidae, but they are an indication that the species are very old. The species found on the rodent apparently represents a recent transfer from a marsupial. Despite many specimens examined, no Mallophaga have been found to date on the common opossum (*Didelphis marsupialis*); we can offer no explanation for this. We predict that, with better collecting, more species of *Cummingsia* will be discovered. The genus *Cummingsia* is not found outside the Neotropics, so it is likely to have evolved there. It has morphological structures that suggest that it could have originated on marsupials or some early form of Cavimorpha, but we believe the prominent ventral spinelike projections on the head (Fig. 6.2) indicate that it may have originated on the marsupials. We believe it would be logical to remove the genus *Cummingsia* from Trimenoponidae and place it in a new monotypic family.

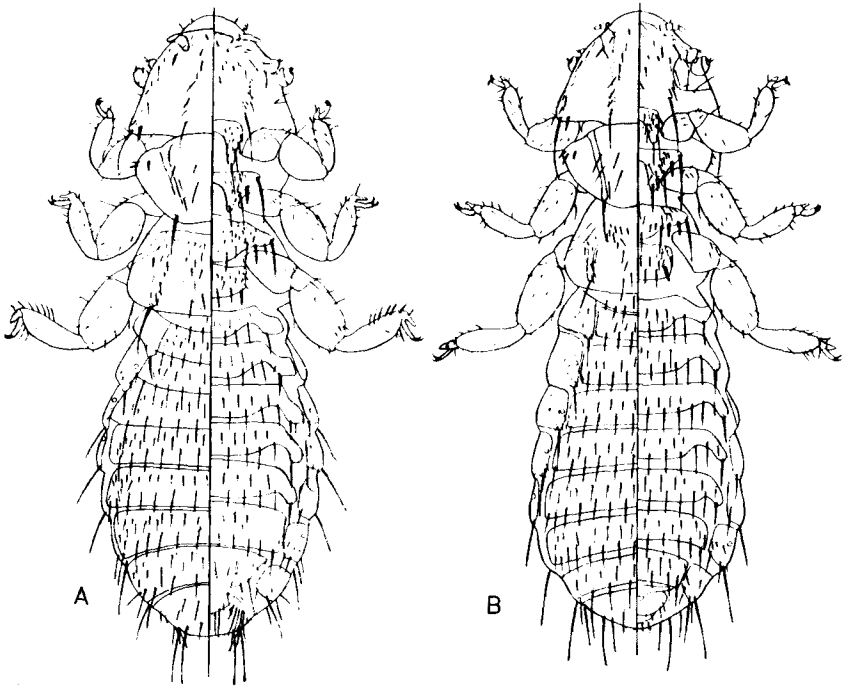


Figure 6.3 *Trimenopon hispidum* (Burmeister), from *Cavia porcellus*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1975. Mallophaga of Venezuelan mammals. *Brigham Young Univ. Sci. Bull., Biol. Sci.* **20**:1–77. By permission of the Brigham Young University Press.)

The earliest rodents in South America were the Caviomorpha, descendants of some early stock which reached South America from Africa or North America before the early Oligocene epoch (Simpson 1980). The mallophagan genus *Philandesia* is restricted to hosts of the family Chinchillidae, so it probably evolved in South America. The genus *Chinchillophaga* is found only on the mara (*Dolichotis patagonum*), which is probably improperly placed in the family Caviidae. It, too, likely had its origin in South America. *Trimenopon* (Fig. 6.3) is found only on guinea pigs (*Cavia:* Caviidae) and is another of probable South American origin. These genera, we believe, are properly placed in the family Trimenoponidae. The other two genera now in the family Trimenoponidae, *Harrisonia* and *Hoplomyophilus*, are found only on spiny rats (*Proechimys* and *Hoplomys:* Echimyidae) in the Neotropics, so their origin may also have been in South America. It is possible that *Harrisonia, Hoplomyophilus, Philandesia, Chinchillophaga,* and *Trimenopon* had their origin from a common stock that was originally parasitic on an early species of Caviomorpha that is now extinct. These taxa probably evolved later than *Cummingsia,* the genus found on South American marsupials.

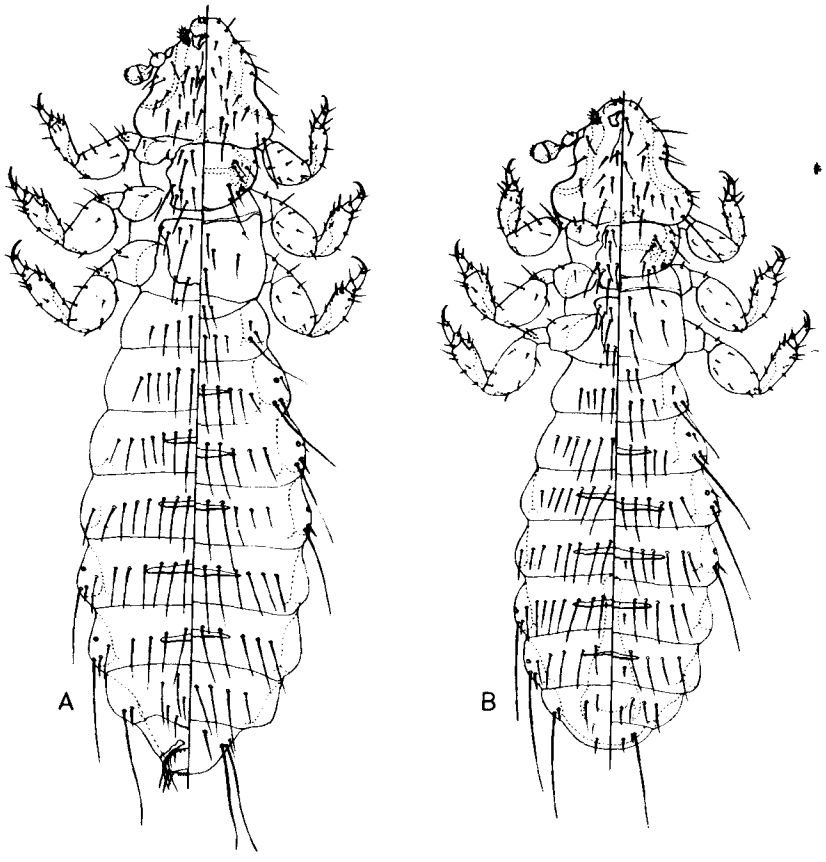


Figure 6.4 *Abrocomophaga chilensis* Emerson and Price, from *Abrocoma bennetti*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1976. Abrocomophagidae (Mallophaga), a new family from Chile. *Fla. Entomol.* **59**:425–428. By permission of the Florida Entomological Society.)

Abrocomophaga chilensis Emerson and Price (Fig. 6.4), the only species in the amblyceran family Abrocomophagidae, has been found only on the rat chinchilla (*Abrocoma bennetti:* Abrocomidae) in Chile (Emerson and Price 1976). This taxon also is likely to have originated in South America and probably evolved early from the ancestor that produced most of the taxa in the family Trimenoponidae.

The family Gyropidae (Figs. 6.5, 6.6), containing three subfamilies and eight genera, is found only on Neotropical mammals. Diversity within the family is properly represented by this classification. Species of Gyropidae are found on hosts of the rodent Caviidae, Dasyproctidae, Capromyidae, Ctenomyidae, Abrocomidae, Echimyidae, and Cricetidae, and the an-

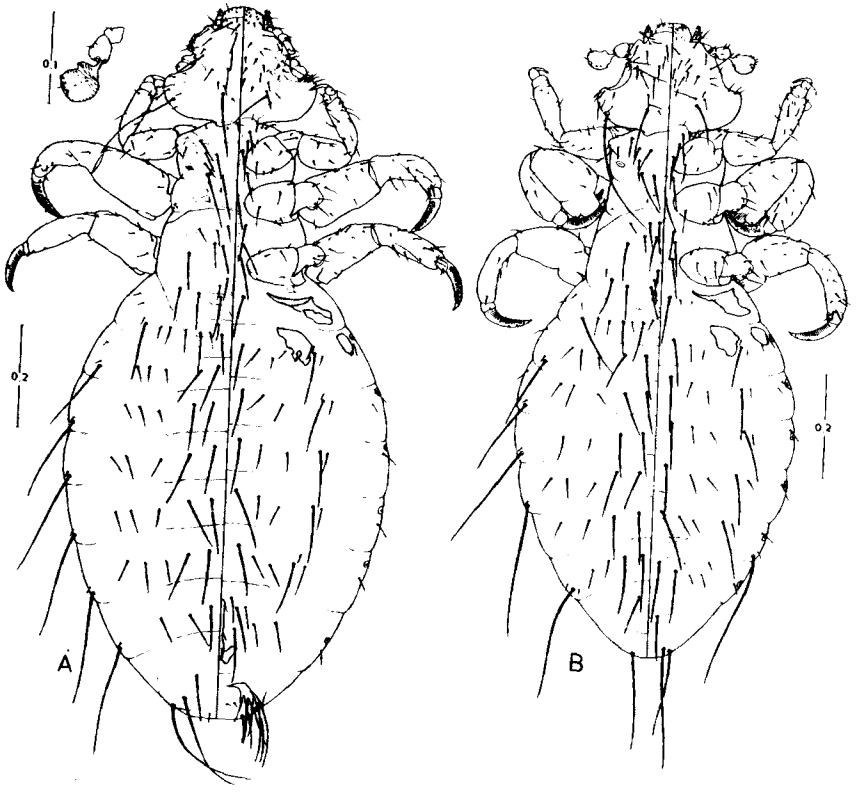


Figure 6.5 *Gyropus wernecki* Emerson and Price, from *Proechimys semispinosus*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1975. Mallophaga of Venezuelan mammals. *Brigham Young Univ. Sci. Bull., Biol. Sci.* **20**:1–77. By permission of the Brigham Young University Press.)

thropoid Cebidae. The species *Aotiella aotophilus* (Ewing) found only on *Aotus trivirgatus* (Cebidae) and *Gyropus ribeiroi* on *Scapteromys gnambiquarae* (Cricetidae) are recent transfers from other hosts. All species of Gyropidae probably evolved from a common stock that became parasitic on early forms of Cavimorpha. Since no species of Gyropidae are known from Recent native mammals in North America or Africa, it might be assumed the common stock from which these Mallophaga evolved was found only in South America. Differences in morphology and feeding habits between the gyropid species and those of Trimenoponidae and Abrocomophagidae are great enough to suggest that the gyropids evolved from an ancestral form different from those of the other two families and that the evolution of Gyropidae occurred at a later period. The common stock from which the gyropids evolved probably became parasitic on one or more species of Cavimorpha.

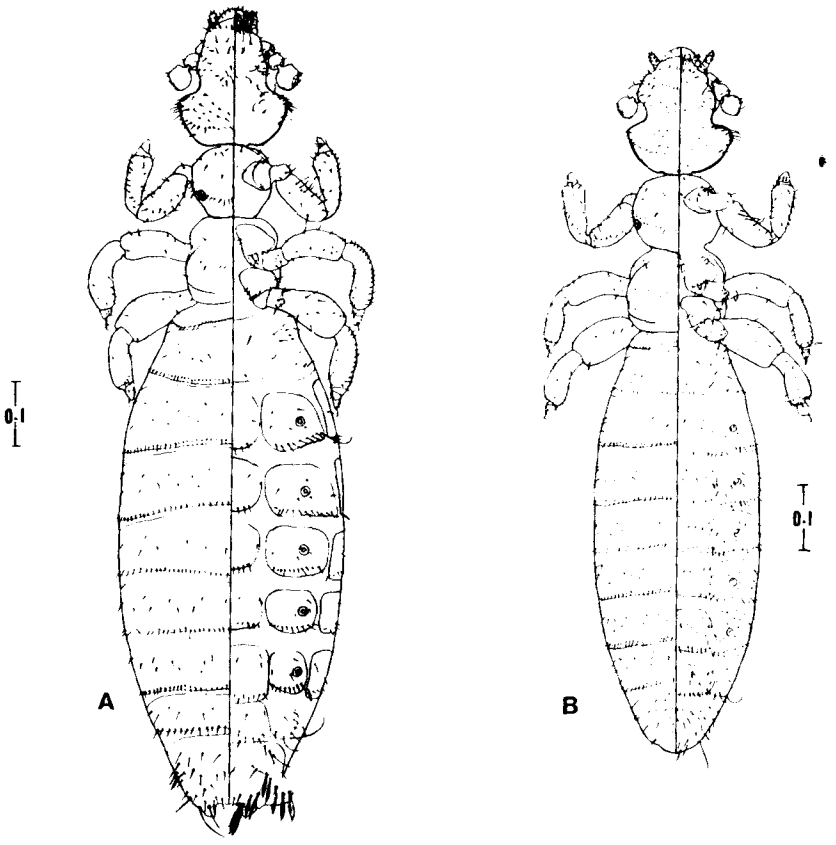


Figure 6.6 *Gliricola porcelli* (Schrank) and *Cavia porcellus*. (*A*) Female; (*B*) male. (From K. C. Emerson and R. D. Price. 1975. Mallophaga of Venezuelan mammals. *Brigham Young Univ. Sci. Bull., Biol. Sci.* **20**:1–77. By permission of the Brigham Young University Press.)

Ischnocera

Species of the ischnoceran family Trichodectidae (Fig. 6.7) are now found on the following mammalian hosts: Primates (Lorisidae and Cebidae), Edentata (Bradypodidae), Rodentia (Geomyidae and Erethizontidae), Carnivora (Canidae, Ursidae, Procyonidae, Mustelidae, Viverridae, Protelidae, Hyaenidae, and Felidae), Hyracoidea (Procaviidae), Perissodactyla (Equidae), and Artiodactyla (Camelidae, Tragulidae, Cervidae, and Bovidae). The Trichodectidae do not occur on any native wild land mammals of Australia or on mammals of North or South America, except those which appeared after the "great American interchange" which started in the early Pliocene (Vanzolini and Guimaraes 1955). This means the taxon evolved from a stock found in Africa, Asia, Europe, or North America. We

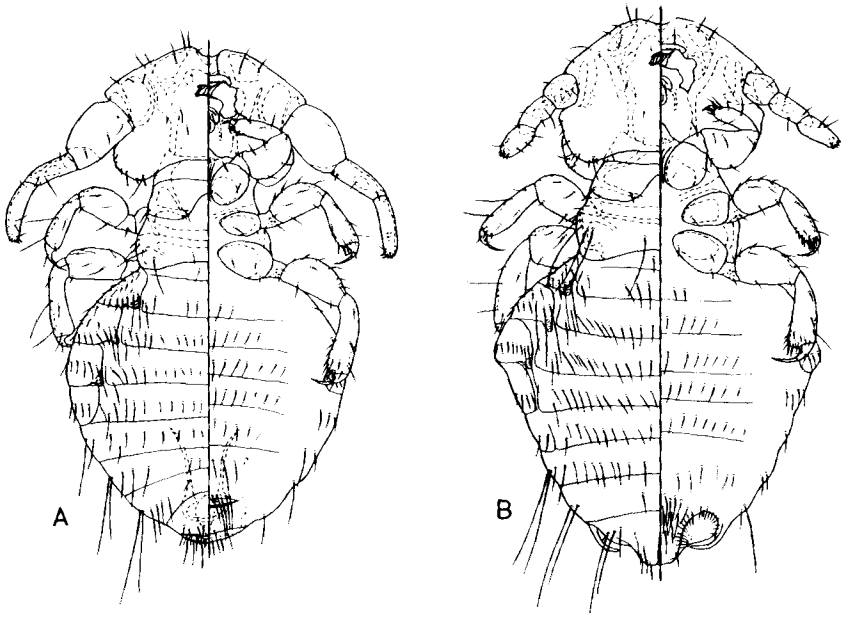


Figure 6.7 *Geomydoecus mexicanus* Price and Emerson, from *Pappogeomys merriami saccharalis*. (*A*) Male; (*B*) female. (From R. D. Price and C. Emerson. 1971. A revision of the genus Geomydoecus (Mallophaga: Trichodectidae) of the New World pocket gophers (Rodentia: Geomidae). (*J. Med. Entomol. Bishop Mus.* **8**:228–257. By permission of the Bernice D. Bishop Museum.)

believe it occurred after Gondwanaland divided into the various future continental land masses and before Laurasia was completely divided into future continental land masses. By the time the "great American interchange" occurred, Mallophaga in the suborder Amblycera were well established in South America. Species of the mallophagan suborder Ischnocera, which include those of Trichodectidae, are obviously of more recent origin than those of Amblycera. This means that species of Trichodectidae now found in South America were obtained during the "great American interchange" and, in so doing, may have displaced some species of the suborder Amblycera on the native mammalian species. The mammals introduced to South America during this interchange took their mallophagan parasites with them. This suggests that the mallophagan family evolved from stock in Africa (less Madagascar) or Europe and Asia. We believe it was probably on the Europe-Asia landmass.

Trichophilopterus babakotophilus (Fig. 6.8) is a philopteran parasite found only on certain primates (Lemuridae and Indriidae) restricted to the island of Madagascar. Currently this species is placed in the family Philopteridae even though all other philopterids occur only on birds. When the species and genus were described by Stobbe (1913), they were placed in the family

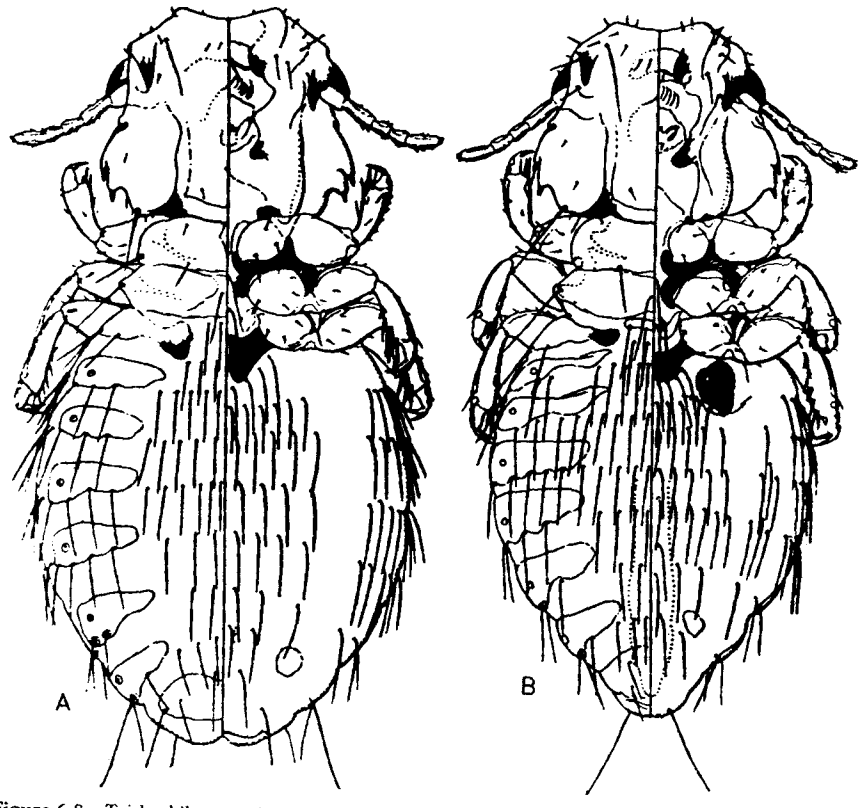


Figure 6.8 *Trichophilopterus babakotophilus* Stobbe, from *Lemur cronatus*. (*A*) Female; (*B*) male (from Ferris 1933).

Philopteridae because each leg had two tarsal claws. Mjöberg (1919) and Ewing (1929) considered the species to be sufficiently different so that it should be placed in a monotypic family—Trichophilopteridae. Ferris (1933) moved the genus and species back to the family Philopteridae. Opinions are still divided as to which family it should be assigned. We believe that we have now examined more species of mammalian and avian Mallophaga than any other workers in the field and herewith offer our opinion on the matter. The head, thorax, and abdomen of *T. babakotophilus* are similar to species of trichodectids with these exceptions: (1) both sexes possess spinelike projections on the head such as those found elsewhere on mammal Mallophaga in the genus *Cummingsia* and the family Boopiidae, this suggesting that it is as old as the Mallophaga found on marsupials; (2) the female does not have gonopophyses on the terminal abdominal segment; and (3) each leg has two tarsal claws. It should be noted that the mouth-

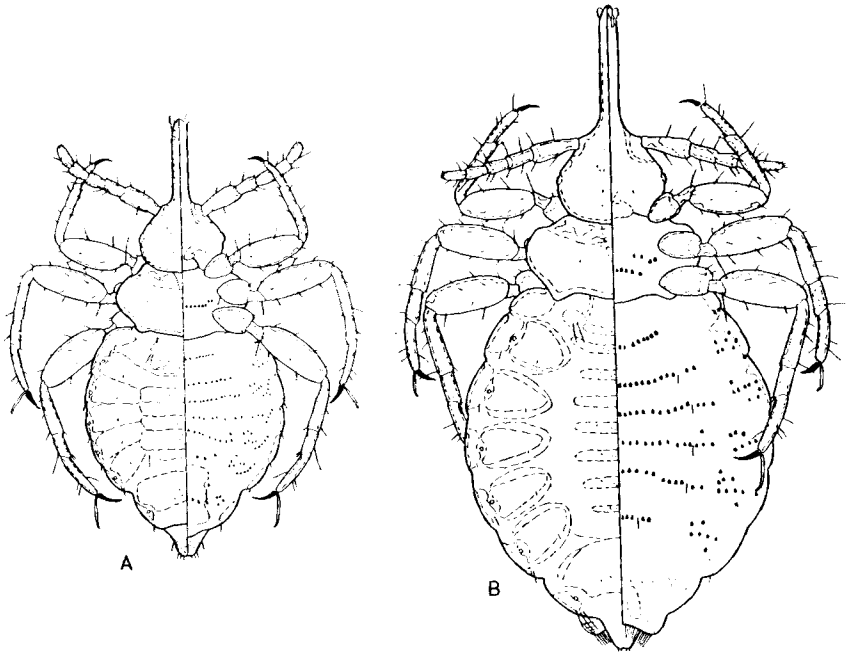


Figure 6.9 *Haematomyzus elephantis* Piaget, from *Elephas maximus*. (*A*) Male; (*B*) female. (From Werneck 1950.)

parts are typical of those found in trichodectid species. The absence of gonopophyses (used to hold the egg while it is being cemented to the hair of the host) and the presence of two claws on each leg are the only features typical of philopterid species. Shape and size of the head, thorax, and abdomen and their chaetotaxy are essentially the same as those found on both trichodectids and philopterids. The male genitalia are unique, differing considerably from any found on trichodectids and philopterids. We believe *Trichophilopterus babakotophilus* is older than any living species of Trichodectidae or Philopteridae, that it evolved from a stock found only on Madagascar, and that it is sufficiently unique to warrant assignment to the monotypic family Trichophilopteridae.

Rhynchophthirina

The mallophagan species *Haematomyzus elephantis* Piaget (Haematomyzidae) (Fig. 6.9) has been found on both species of living elephants (Ferris 1931). It is common on the hairy ears of young elephants. The second species in this family, *H. hopkinsi*, is found on the wart hog. Distinctions between the two species of *Haematomyzus* are so slight that they may prove

to be only of a subspecific nature. Since the wart hog and the African elephant share common watering and wallowing sites, it is probable that the species (or subspecies) on the wart hog evolved recently from the species found on the elephant. The Haematomyzidae is the only family in the suborder Rhynchophthirina, and it differs greatly from members of the other two suborders, Amblycera and Ischnocera. Some workers have considered it to represent a link between the Mallophaga and Anoplura (sucking lice); however, it is assigned to the Mallophaga because the mouthparts are mandibulate rather than piercing. We agree with that assignment. The Haematomyzidae probably evolved from stock found in the Old World tropics—either the Ethiopian or Oriental region, or both.

CONCLUSION AND SUMMARY

1. Mallophaga (chewing lice) are obligatory parasitic insects which live on birds and some mammals.
2. Mallophaga have evolved from several stocks after Laurasia and Gondwanaland broke up into the present continents. As the birds and mammals evolved, mallophagan species evolved also, but at a slower rate.
3. The more species and genera of Mallophaga found on a living host, the better the data will be concerning evolution of the host and its relationships with other hosts.
4. There are no fossil records of Mallophaga.
5. Birds have more species and genera of Mallophaga than do mammals.
6. In two groups of mammals—pocket gophers (Geomyidae) and hyraxes (Procaviidae)—each host species has almost as many species of Mallophaga as do species of birds. Extensive research on the Mallophaga found on pocket gophers has contributed greatly to the understanding of the taxonomy and distribution of pocket gophers. For other groups, the degree of assistance to mammalogists may not be as great.
7. Mallophaga have been collected to date from less than half of the living mammals that are expected to have these parasites. Collections of Mallophaga from these hosts would help our understanding of the relationships within the Mallophaga and the mammals.

There are insects, other than Mallophaga, that are ectoparasites on mammals. The Anoplura (sucking lice) are also wingless obligatory external parasites and exhibit varying degrees of host specificity. Some mammals have both Anoplura and Mallophaga, some may have only one of the orders, and some may have neither (Kim and Adler, Chapter 4; Kim,

Chapters 5, 7). Since the Mallophaga and Anoplura developed in different geological periods, the host specificity of each parasite should be considered by mammalogists in their reviews of mammal relationships. There are parasitic mites, ticks, and insects in other orders, each with varying degrees of specificity, that can also assist the mammalogists. We believe that some mammalogists are overlooking very useful data—Mammal–Mallophaga relationships—in their research.

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