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 *Phlacogala*

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

Family Abrocomophagidae—Neotropical
  Genus: *Abrocomophaga*

Family Gyropidae—Neotropical
  Subfamily Protogyropinae
    Genus: *Protogyropus*
    Subfamily Gliricolinae
      Genera: *Gliricola*, *Monothoraxius*, and *Pitirufquenia*
    Subfamily Gyropinae
      Genera: *Aotilla*, *Gyropus*, *Macrogyropus*, and *Phlteropoius*

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Suborder ISCHNOCERA

Family Trichodectidae—Holarctic and/or Ethiopian

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:

<table>
<thead>
<tr>
<th>Order</th>
<th>Extinct</th>
<th>Living</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marsupialia</td>
<td>81</td>
<td>57</td>
</tr>
<tr>
<td>Primates</td>
<td>99</td>
<td>59</td>
</tr>
<tr>
<td>Edentata</td>
<td>113</td>
<td>19</td>
</tr>
<tr>
<td>Rodentia</td>
<td>275</td>
<td>344</td>
</tr>
<tr>
<td>Carnivora</td>
<td>261</td>
<td>144</td>
</tr>
<tr>
<td>Proboscidea</td>
<td>22</td>
<td>2</td>
</tr>
<tr>
<td>Hyracoidea</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>Perissodactyla</td>
<td>152</td>
<td>6</td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>333</td>
<td>86</td>
</tr>
</tbody>
</table>
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Of 14 families of the Primates, chewing lice are found on three prosimian families and one anthropoid family. They are as follows:

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of Living Species</th>
<th>Number of Species Known with Mallophaga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lemuridae</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Indridae</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Lorisiidae</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Cebidae</td>
<td>37</td>
<td>7</td>
</tr>
</tbody>
</table>

The philopterid species *Trichophiloterus babakotophilus* (Stobbe) has been recorded from two species of Lemuridae and two species of Indridae, 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 (Lorisiidae) of southeastern Asia has the ischnoceran species *Lorisicola mijobergi* (Stobbe) (Trichodectidae).

Within the Cebidae, dourcoucouli (*Aotus trivirgatus*) have the gyropid *Aotillia 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 (Ichnocera): *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:
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, Hellingthal, 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 Geomyoculus (Trichodectidae) are known, and there are undoubtedly others still to be described. The trichodectid Geomyoculus 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 Hellingthal 1975, 1976, 1979, 1980; Timm and Price 1980; and Hellingthal 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 Geomyoculus. 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.

Cummingisia inopinata Mendez (Trimenoponidae) has been recorded from the cricid Thomasaumys cinereiventris; it probably represents a relatively recent transfer from a Neotropical marsupial. Another cricid, Scaupeteromys gnambiquae, now has Gyropus riebei Wernec (Gyropidae), 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

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of Living Species</th>
<th>Number of Species Known with Mallophaga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geomyidae</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td>Cricetidae</td>
<td>623</td>
<td>2</td>
</tr>
<tr>
<td>Erethizontidae</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Caviidae</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>Dasyproctidae</td>
<td>17</td>
<td>8</td>
</tr>
<tr>
<td>Chinchillidae</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Capromyidae</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>Ctenomyidae</td>
<td>27</td>
<td>10</td>
</tr>
<tr>
<td>Abrocomidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Echimyidae</td>
<td>43</td>
<td>21</td>
</tr>
</tbody>
</table>

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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 taxonomy 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 Abrocomphagidae; 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 Echinophthiridiae. The major diversity of mallophagans is found on Mustelidae and Viveridae. The breakdown of this diversity is the following:

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of Living Species</th>
<th>Number of Species Known with Mallophaga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canidae</td>
<td>38</td>
<td>14</td>
</tr>
<tr>
<td>Ursidae</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Procynidae</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td>Mustelidae</td>
<td>68</td>
<td>36</td>
</tr>
<tr>
<td>Viveridae</td>
<td>82</td>
<td>36</td>
</tr>
<tr>
<td>Proteidae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Hyaenidae</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Felidae</td>
<td>37</td>
<td>13</td>
</tr>
</tbody>
</table>

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, Suriatocus (Trichodectidae) is the mallophagan normally found on foxes. Suriatocus species apparently are more host specific than are those of *Trichodectes or Heterodoxus*. In the future, more information...
fusing over the early records on *Genetta genetta* and *G. tigrina*. We need new material from properly identified hosts to clarify these records. The ischnoceran *Neofelis* and *Parafelis* are found only on species of Viverridae, while *Felis*, *Sarcastictes*, and *Trichodectes* are also found on other mammalian families. The water mongoose (*Attilax paludinosus*) has the distinction of having seven species of Mallophaga that are host specific to it.

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

*Felis* has been the only genus found to date on the cats (*Felidae*). Mallophaga have been examined from only a third of the species of *Felis*, 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 rhinocophithrinan 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.

**Hystricidae**

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

The ischnoceran genera *Dasodon*, *Euhyrachydoctes*, *Procapra*, and *Procapra* (*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 (*Geomyideae*) 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 Procapridae. Cooperation between mammalogists and Mallophaga taxonomists probably can produce a new and useful classification of the Procapridae.
**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:

<table>
<thead>
<tr>
<th>Family</th>
<th>Number of Living Species</th>
<th>Number of Species Known with Mallophaga</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suidae</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Tayassuidae</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Camelidae</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Tragulidae</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Cervidae</td>
<td>41</td>
<td>14</td>
</tr>
<tr>
<td>Bovidae</td>
<td>126</td>
<td>52</td>
</tr>
</tbody>
</table>

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

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

*Bovicola brevicauda* (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.

*Damaelina tragula* 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*, *Damaelina*, and *Tricholipurus* (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 *Tricholipurus lippeuroides* (Megin) and *T. paralleus* (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 jemlahica*) and the bharal (*Pseudois nayaur*). Three species of *Damaelina* 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 amblycerean Bopoidea, 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
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 Boopidae 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. *Therodaxus oereni* 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 Boopidae 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 Boopidae originated in Australia from a stock not found elsewhere and became parasitic as the marsupials evolved on that land mass. The family Boopidae 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).
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 Chinchilidae, 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, *Harrisionia* and *Hoplomophillus*, 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 *Harrisionia*, *Hoplomophillus*, *Philandesia*, *Chinchillophaga*, and *Trimenopon* had their origin from a common species of Caviomorpha that is now extinct. These taxa probably evolved later than *Cummingsia*, the genus found on South American marsupials.

*Abrocomphaga chilensis* Emerson and Price (Fig. 6.4), the only species in the amblyceran family Abrocomphagidae, 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 Gyropodidae (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-
thromboid Ceboidea. The species *Aotiella aotophila* (Ewing) found only on *Aotus trivirgatus* (Cebidae) and *Gyropus riebei* on *Scapteromys grumphiarae* (Cricetidae) are recent transfers from other hosts. All species of Gyropidae probably evolved from a common stock that became parasitic on early forms of Caviomorpha. 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 Mallophaga evolved was found only in South America. Differences in morphology and feeding habits between the gyropid species and those of Trimenoponidae and Afrotromphagidae 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 Caviomorpha.

**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, Procyonidae, 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
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 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 spine-like projections on the head such as those found elsewhere on mammal Mallophaga in the genus Cummingia and the family Boopidae, 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-
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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 babakotaphilus* 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.

REFERENCES


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