The family classification of the Anoplura

KE CHUNG KIM and HERBERT W. LUDWIG* From Entomological Museum, Pennsylvania State University, and *Zoologisches Institut der Universität Heidelberg, Germany

ABSTRACT. Fifteen families of Anoplura are recognized and defined, one with two subfamilies, and a key is provided for their identification. The included genera are listed for each family, together with the relevant type species as well as the mammalian hosts. Phylogenetic relationships between the families are discussed, and an extensive historical review and analysis of the available taxonomic characters is presented.

Introduction

The Anoplura (sucking lice) are obligate, permanent ectoparasites of mammals. Having adapted to the microenvironment of the host body surface, they have coevolved with the Mammalia. Sucking lice have many pronounced morphological adaptations, both structural and functional, suitable for their ectoparasitic way of life. For example, the body is more or less flattened dorsoventrally, the head is equipped with a piorotusible proboscis and sucking mouthparts, and the legs are fitted for clinging to hairs.

Anoplura are widely distributed around the world, the fauna being especially rich in the Ethiopian region. Ludwig (1968) recorded 135 species (34.4% of all Anoplura) from the Ethiopian region, seventy-two (18.3%) from the Oriental region, fifty-two (13.3%) from the Neartic region, and forty-three (11.0%) from the Neotropic region.

The diversity of the sucking lice is still not fully known. Their taxonomy was reviewed in detail by Fahrenholz (1936) and Ferris (1951), but no major study has been made since then on the higher classification. Ferris (1951) recognized six families, thirty-nine genera, and 255 species of Anoplura, but many new taxa have been discovered in the last 20 years. Ludwig (1968) reported forty-two genera and 392 species of Anoplura from forty-six families of mammals, based on Zoological Records until 1964 and part of 1965. Pietrowski (1973) reported 454 known species from 1356 host species and subspecies up to the end of 1971. In this paper we recognize 486 species of sucking lice from about 840 species (241 genera) of mammals (Fig. 1); this is about a 90% increase in the number of known species during the period of the last 25 years. We group the 486 species of Anoplura in forty-two genera and fifteen families.

The Anoplura are parasitic on all major groups of terrestrial mammals except the Chiroptera, Edentata, Pholidota, Cetacea, Probosciidae, and Sirenia. Those sucking lice which have moved on to new host groups have acquired additional specialized morphological and biological characteristics, e.g., Sarcoptes and Duplicithrix on Insectivores.
There are approximately 4060 species of mammals known in the world; they are referred to approximately 1004 genera and 122 families (Anderson & Jones, 1967). Although the sucking lice are parasitic on diverse groups of mammals, from shrews, seals to aardvarks, they are apparently absent from Monotremata, Marsupialia, most of the land Carnivora and those Eutheria already mentioned. Approximately 65%, or 2600 species, of the living mammals are suspected of harbouring sucking lice. This estimate is made by subtracting the number of species not to harbour Anoplura from the total number of mammalian species. The sucking lice have been recorded from only about 32% of the 2600 suspected host species. The discovery rate of new taxa and our knowledge of Anoplura suggests that the number of sucking lice will amount to more than 1000 species when all the recent mammals are examined.

The classification system of the Anoplura developed by Ferris (1951) has been commonly accepted. Since 1951, eight new genera and more than 230 new species have been discovered, and new data on ecology and hosts of many taxa have been gathered. Of eight new genera two, Johnsenothrips and Cuvana, are not accepted here; six genera accepted are Lernuripesculus, Sathras, Latagophthirus, Alopophthirus, Pithrunculus, and Alopophthirus. Three of the genera recognized by Ferris are not accepted in this paper: Symosia, Galeagnosthus and Lapidophthirus. Accordingly, Ferris' system is here updated and modified to accommodate all the available information in a new classification of the sucking lice, based on all the known biological attributes.

In the course of preparing this new higher classification of the Anoplura all of the nominal genera and type-species for each genus have been studied. For all polygeneric genera, one or more representative species has been studied in addition to the type-species. Taxonomic characters including those used as key characters were critically studied with light microscopy and, when necessary, with scanning electron microscopy (SEM).

This paper presents a revised higher classification of the Anoplura, with definitions of all suprageneric taxa and a key to fifteen families. Taxonomic techniques are discussed, the taxonomic characters used for the higher classification are described, and the relationships of all the recognized families of Anoplura are discussed.

**Historical review**

Since the time of Aristotle, the sucking lice have been known to be parasitic upon man and other animals. Prior to Linnaeus 'Systema Naturae' (1758), approximately thirty papers had been published dealing mainly with infestation, biology and anatomy of human lice and certain domestic animal lice. Redi (1668) illustrated many chewing and sucking lice with considerable accuracy.

Linnaeus described the genus Pediculium, into which he put almost everything that could conceivably be called a 'louse', and placed this genus in the 'Insecta Apera'. Pediculius Linnaeus originally comprised an unholy assortment of thirty-nine forms, including sucking lice, biting lice, booklice or psocids, a beetle tritoniid and a louse fly or hippocratic fly.

After Linnaeus, Fabricius (1775, 1803) placed Pediculius in the order ANTILIAA along with other miscellaneous assortments of forms. Latreille (1804) established the order PARASITI for two groups of lice, with the genera Pediculus for the sucking lice and Rumenius for the biting lice. Later, Latreille (1825) divided the order PARASITI into two groups, Siphunculata for the sucking lice and Mandibulata for the biting lice in the Orthoptera Epizoa.

The sucking lice were put with the fleas and some mites in the group RHINAPTERA by Dumeril (1823), with the Thysanura, the myriopods and various arachnids in the order APTERA by Kirby & Spence (1826), in the order RHYNCHOTA by Burneisiter (1835, 1838), in the order Phthiraptera for two groups of lice by Haackel (1896), in the order Pseuophylyctacea by Bohakovsky (1904), in the order ELLIPHOTA by Shipley (1904) and in the Lipoptenata by Börner (1904). During the latter part of the nineteenth century, the idea grew that the sucking lice are related to the Hemiptera. This concept was retained as late as 1913 by some workers, the sucking lice being placed in the Hemiptera as the suborder Prasita (oborn, 1891, 1896).

The problem of what name to employ for the sucking lice is still a contentious matter. The issue is both nomenclatural and zoological. On the basis of habit similarities, the sucking lice have been considered to be closely related to the chewing lice by many authors. This has led to the proposal of three ordinal names: ANOPLURA Leach, 1815, Siphunculata Latreille, 1825, and Phthiraptera Haackel, 1896. However, these names have not been consistently applied or interpreted.

The ordinal name Siphunculata was used by Handrich (1908) for the sucking lice alone, but Mjöberg (1910) and Harrison (1916) included two suborders: Anoploga for the sucking lice and Mallophaga for the biting lice. Dallar Thompson (1908) followed by Ferris (1914-1951) and many other workers, considered the sucking lice as an independent order Anoplura, but Fahrenheit (1936) included Haematomyzus in the Anoplura. Fahrenheit divided the order Anoplura into two suborders, Rhynchophthirina, a name previously proposed by Ferris as a suborder of the Mallophaga for inclusion of Haematomyzus, and the new suborder Inrostrata for the true sucking lice.

The last ordinal name, Phthiraptera, has been consistently used by British, German and other workers, notably Weber (1938).
Hopkins (1949, 1957), Königsmann (1960) and Clay (1970), for an ordinal taxon consisting of three suborders: ANOPLOLA, MALLOPHAGA and RHYNOCHOPTERINA. Conversely, Ferris (1951) and many other workers, including ourselves, have treated the sucking lice as the order ANOPLOLA, independent of the order MALLOPHAGA with its suborder Rhyynchopterina.

Until 1915 all the known sucking lice were included in the genus Pediculus (Fabricius, 1775; Latreille, 1806). Leach (1815, 1817) was the first to subdivided the sucking lice into Phthirius, Haematoptus and Pediculus; together with one genus of the biting lice, Niturus, he placed these three genera in the order ANOPLOLA, family Pediculidae. During the period 1819-1903 little new information was obtained on ANOPLOLA. Papers by Nitrous (1818, 1864), Burmeister (1835, 1847), Denys (1842), Giebel (1871, 1874), Piaget (1880–85) and Osborn (1891, 1894, 1896) are the most significant from that era.

Nitrous (1818) presented an excellent review of the families and genera ectoparasitic on birds and mammals. In Pediculus he originally recognized seven species of sucking lice, later increasing this to twenty species (1864). Burmeister (1838) recognized two genera, Phthirius (one species) and Pediculus (two species) in the family Pediculina under the order RHYNCHOTA which included scales, aphids, leafhoppers, and other Homoptera. Denys (1842), in his Monographie des Anophaga, divided it into two suborders, RHYNCHOTA (Hautella) for the sucking lice and MALLOPHAGA (Mandibulata) for the biting lice. He recognized three genera and twenty species of sucking lice in the family Pediculidae, as did Leach. In 1844 Gervais, following Denys' system, reviewed the known diversity and recognized four genera, one of which was the new genus Pedicinus with twenty-nine species.

In 1871 Giebel established a new genus Echinophaeus for a seal louse, Pediculus phoceae Lucas. Thereafter, in his Insecta Epitea, Giebel (1874) placed the sucking lice in the family PEDICULINA (corresponding to the family MALLOPHAGA) for the biting lice) in the order HEMIPtera, and called the group HEMIPtera EPIZOa. In a monamental work entitled Les Pediculides, Piaget (1880–85) recognized six genera, including the new genus Haematoptus for an elephant louse. All these genera he placed in the family Pediculidae without referring them to any ordinal name. In his work Piaget included keys to genera and species along with good descriptions of each taxon. In North America, the contemporary worker Osborn (1891, 1894, 1896) described many new species of sucking lice. He first recognized the genus Haematoptinosis (Osborn, 1891) and then renamed it as the genus Echthophaeus (Osborn, 1896).

By 1904 a total of sixty-five species of sucking lice were known (one of which was later shown not to belong to ANOPLOLA). About sixty of these species were included in the genus Haematoptus; the remainder were classified as Echinopthinus, Haematoptinosis, Pedicinidae, Pediculus and Phthirius. Up to this time there was little demand for a suprageneric classification of the sucking lice.

Enderlein (1904) commenced a series of papers on the sucking lice which provided the most comprehensive account to that time. He recognized several new taxa and established a modern system of classification using the ordinal name RHYNCHOTA for the sucking lice. His system initially recognized four families and thirteen genera; this included the family Haematoptinoidae with Haematoptus which is now not considered to be Anoplura. Enderlein's system was followed in the Genera Insectorum by Dalla Torre (1908) and subsequently by Ferris (1916, 1951) with some modifications. Enderlein eventually described four additional genera, Holothephra (1904), Antarctophilus and Lepidophaeus (1906), and Homblophora (1908).

When Dalla Torre (1908) published the first catalogue of the ANOPLOLA he listed sixty-five species, but the work was done rather poorly due to inadequate overall knowledge of the sucking lice.

Ferris (1916) published a Catalogue and Host List of the Anoplura listing twenty-three genera and 123 species, of which approximately nine genera and sixty species had been described since 1899 (i.e., after the publication by Enderlein and Dalla Torre). Not surprisingly this catalogue contains some false synonyms and erroneous judgments on the systematic position of several taxa. However, in the period 1919–34, Ferris published a series of papers entitled 'Contributions towards a monograph of the sucking lice'. When fully re-published in monograph form (Ferris, 1951) these studies provided the foundation of modern taxonomic opinion on the Anoplura. Ferris (1951) recognized 255 species in thirty-nine genera and six families. Subsequently, eight new genera and more than 330 new species have been described, bringing the total to about 486 species by the end of 1975. Most of the recent contributions to our knowledge of the Anoplura have been by Biagiovinciketch (1937–72), Suggs (1951), Johnson (1957), Benoit (1959), Kaneko (1954), Kuhn (1963–70), Ludwig (1963–), Kim (1963–) and Werneck (1931–59).

Evaluation of taxonomic characters

1. Body size and general morphological trends. The sucking lice are usually small, with body length ranging from 0.35 mm in the male of Micropterus urinatus, to more than 8 mm for Pecoraecus jardini. Although its adaptive significance is not readily assessed, the body length seems to characterize each genus. For example, species of Haematoptus are usually large lice of about 4 mm length but Polyplexius, Enderleinellidae and Homblophora (Homblophoridae Ferris, 1951) are generally small to medium sized lice of 0.5–1.5 mm in length. It appears that the taxa of large body size are less specialized morphologically. The large lice Haematoptus, Pecoraecus, Pediculus and Microthoracoides have all legs similar in size and shape with acuminate claws, and parantergites either caplike or tuberculoform if present. In the smaller taxa, the size and shape of legs differ considerably in various combinations; also the parantergites are plate-like with the apex free from the body as shown in Enderleinellidae, Homblophoridae and Polyplacidae. In Enderleinellidae the fore- and midlegs are similar in size and only the tibio-tarsi of the hind legs are highly modified for grasping hairs. The forelegs are

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smallest in Homblophoridae and Polyplacidae. All of these taxa have distinct paratergites, always, partly at least, with an apical part free from the body and not forming a metacarp over the apex of lateral lobes of the abdomen. Furthermore, it is interesting to note that the remaining homplagids are primarily found on small mammals including rodents and insectivores.

2. Setae and chaetotaxy. The setae in the Anoplura are perhaps primarily sensory, being secondarily modified for the different purposes. Some setae are modified into scales and spines as in Antarctophilus and Lepidophaeus (Kim, 1971); others are enlarged and modified for perhaps mechanical or special sensory function (Fig. 7 and 13). The number of setae seems to be related to the size of the surface area of the structure concerned. It appears that more setae are present on membranous areas when the louse is devoid of abdominal sclerites, as shown in Microthoracoidae (Fig. 31). The type and number of setae are, of course, important taxonomic characters.

The primary chaetotaxy is rather constant within a higher taxon, and a certain setal pattern is typical of each taxon. The basic pattern of the chaetotaxy of head, antennae, thorax and legs is remarkably constant among species of a higher taxon. The primary chaetotaxy of head, antennae and legs of the first nymphal instar does not change throughout the post-embryonic development. Nymphal instars are added to the primary chaetotaxy as the nymph passes through each successive stage to the adult. This phenomenon can be experimentally enhanced by juvenile hormone (Boström, 1976). As far as is known, no setae of the primary chaetotaxy are lost during metamorphosis, although some nymphal setae are modified to another type or become greatly reduced in the adult. For some groups (e.g., Pediculus) the adult chaetotaxy is already developed in the second nymphal instar (Kuhn & Ludwig, 1967). The constancy and consistency of these setal patterns seem to suggest that the chaetotaxy must have been fixed by selective quite early in the evolution of the Anoplura.

It is rather unlikely that nymphal instars are subjected to special selection pressures,
since nymphs and adults occupy essentially the same habitat. As van Emden (1957) stated, the nymphs possess no character distinctions from the adults, except for the differential body size, ratio of the body length and head length, degree of chaetotactic development, the number of antennal segments, and the developmental state of the reproductive organs. However, in some closely related species the adults are quite similar and yet the nymphs are markedly different from each other, as shown in the *Hoplopleura intermedia* complex, *H. optiosa*, *H. intermedia*, *H. thoroumner* and *H. johnsonii* (Kim, 1966c; Johnson, 1972). In Procochinophorus, the nymphs have unusually pronounced spines and tubercles on the ventral side of the head, the thorax and the antennae, which are not found in the adults.

The chaetotaxy of the head (Fig. 2), thorax and abdomen (Fig. 3) is presented here to standardize the terminology and setae nomenclature. The chaetotactic nomenclature is based on the topographic position of setae.
with the following standard abbreviations: 
A = abdominal, Ac = accessory, An = anterior, 
Ap = apical, At = antennal, C = central, 
D = dorsal, G = genital, H = head, I = inner, 
If = infracaudal, Im = intermedian, In = inter- 
L = lateral, M = marginal, Md = median, Ms = mesothoracic, Mx = metathoracic, O = outer, 
Or = oral, P = principal, Pa = preantennal, 
P0 = posterior, Pt = paratergial, Pr = prothor- 
acic, S = seta, Sp = supra, St = sternal, 
Su = subtergal, T = thoracic, Te = tergal, 
V = ventral.

Head (Fig. 2): 1, 2: Dorsal anterior head setae (DANHS) (= OS of Kim, 1966b; Weiser & Kim, 1972); 3, 4: Apical head setae (ApHS) (= CS of Kim, 1966b; or of Weiser & Kim, 1972); 5, 6: Oral setae (OrS) (= OS or OrS of Kim, 1966a and subsequent use); 7, 8: Anterior marginal head setae (AnMHs) (= AMHS of Kim, 1966b); 9, 10: Dorsal preantennal lateral head setae (DPLHS) (= PaMHs and PaLHS of Weiser & Kim, 1962); 11, 12: Ventral preantennal head setae (VPfHS); 13: Dorsal preantennal head setae (DPfHS) (= PAS of Kim, 1966b); 14: Supraantennal head setae (SPaHS) (= AS of Kim, 1966b; Weiser & Kim, 1972); 15: Supraantennal central head setae (SPaCHS) (= DCHS of Weiser & Kim, 1972); 16, 17: Sutural head setae (SHS); 18: Ventral principal head setae (VPHS); 19, 20, 21, 22: Dorsal marginal head setae (DMHS); 23: Dorsal anterior central head setae (DAnCHS) (= ACHS of Kim, 1966b); 24: Dorsal posterior central head setae (DPfCHS) (= PCHS of Kim, 1966b); 25: Dorsal principal head setae (DPHS) (= PDHS of Kim, 1965); 26: Dorsal accessory head setae (DACHS) (= ADHS of Kim, 1966b); 27: Ventral lateral head setae (VLHS) (= VLMH of Weiser & Kim, 1972); 28: Ventral anterior marginal head setae (VAMHS); 29: Ventral posterior marginal head setae (VpMHs).

Thorax (Fig. 3): 30: Dorsal prothoracic setae (DPS); 31: Dorsal mesothoracic setae (DMs) (= DMS of Kim, 1966b); 32: Dorsal metathoracic setae (DMs); 33: Dorsal principal thoracic setae (DPTS).

Abdomen (Fig. 3): 34: Dorsal marginal abdominal seta (DMAS) = dorsal paratergal setae (DPs); 35: Ventral marginal abdominal seta (VMA) = ventral paratergal setae (VPS); 36: Dorsal lateral abdominal setae (DLAS); 37: Ventral lateral abdominal setae (VLAS); 38: Dorsal central abdominal setae (DCAS); 39: Ventral central abdominal setae (VCAS); 40: Tergal abdominal setae (TeAS); 41: Sternal abdominal setae (SAS); 42: Intertergal abdominal setae (InTeAS); 43: Intesternal abdominal setae (InStAS); 44: Transverse setal row; 45: Transverse setal field.

3. Head. The head is generally conical and may be divided into two parts, foreband and hindhead, by the presence of a transverse suture (clypeo-frontal suture) (Fig. 3). The head shape is generally characteristic of each taxon, but the head length varies considerably, even within a genus-taxon. The ocular points are well developed in Haematopinidae and Hystaphithini (apomorph) (Fig. 5) and the postantennal angles are generally evident in Ceratoneuridae, Hoplopleuridae, Polyplacidae, and somewhat in Limognathus. Ocular lenses are found in few taxa (Figs 4 and 9), namely Microthoracis, Pecaroeris, Pediculus, Pedicinus and Phinus (pleisiomophy). The occipital apophysis, a paired internal structure at the posterior end of the head, is only present in Haematopinidae (Figs 2 and 5) and Microthoracis (pleisiomophy).

The basic setal arrangement of the head is rather consistent within higher taxa. The head chaetotaxy is quite characteristic of species and genera, particularly in the Hoplopleuri- dae, but the position of certain setae varies between genera. Each VPHS is usually positioned next to the base of an antenna, e.g. in Hoplopleura, Polyplax; and many other genera of Polyplacidae, but may be moved posteriorly to a position far removed from the antenna, e.g. in Microthoracis and Haematopinidae.

The size of DPHS and DPCHS varies among different taxa. DPHS is long in Hoplopleura and Polyplax (apomorph) but is very small in Haematopinidae (pleisiomorph). At the same time, most of the dorsal setae on the head are equally short in a taxon like Haematopinidae, and yet the head setae are equally long and stout for Solenopotes.

4. Antennae. The antennae of the sucking lice are primarily five-segmented with two distinct sensillae (Figs. 2 and 13), each on the fourth and the fifth segment (pleisiomophy). The number of the antennal seg-
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ments varies within a family-taxon (Fig. 14), and is constant within a genus-taxon. In Echinosiphonidae, the primary number of five antennal segments is found only in Antarctophthirius, whose nymphs, however, have four antennal segments. Other genera in this family have four-segmented antennae. Latagophthirius even has three segments (apomorphy). The number of the antennal segments and the number and position of sensilla are good taxonomic characters at the generic level. The size and shape of the basal segments are good characters at the species level. The third antennal segment in Polypilidae is often sexually dimorphic (Fig. 13).

5. Thorax. The thorax consists largely of pleural and subcoxal structures. The tegmma is greatly reduced and often invaginated to form a notal apophysis shown externally by a notal pit. The notal pit is not evident in Enderleinellidae, Hoplopilidae and Polypilidae (apomorphy), but is quite distinct in Echinosiphonidae, Microthoraxus, Ratteneus, Pecicius and Haeomatopinus (plesiomorphy) (Figs. 3 and 9). The thoracic segments are fused dorsally. Each segment can be identified by strong pleural apophyses or phragmata and coxal processes (Fig. 3). The coxal process articulates with the corresponding coxa, and the pleural apophyses of the meso- and metathorax are often fused to form a transverse ridge as in Antarctophthirius and Haeomatopinus (plesiomorphy).

The sternal plate is developed in many taxa and variously shaped within a given genus-taxon (plesiomorphy) (Figs. 22-25). The sternal plate is an important character in Enderleinellidae. Haematopinidae, Hoplopilidae, Polypilidae and Solenopotes at generic and species levels, but is lacking in groups such as Peciciidae, Phipidae, Pe- rocosus and Haeomatopinus.

The thoracic chaetotaxy is rather constant within a family-taxon. DPS, DMS and DITS are usually singular setae, one on each side (plesiomorphy). DMS are usually missing in most Anoplura (apomorphy), but number two or more on each side of the thorax in Echinosiphonidae, Haeematopinus, and Haeomatopinus (plesiomorphy).

6. Abdomen. The abdomen provides the majority of taxonomic characters, and shows striking sexual dimorphism within each species, especially in terminalia. The abdomen consists of nine rather distinct segments with the tenth segment and perhaps eleventh segment obscure (Fig. 3). The abdomen is primarily membranous, devoid of sclerites in most Anoplura (apomorphy) (Figs. 26-32), although tergites and sternites are highly developed in Hoplopilidae and Polypilidae (Fig. 19) (plesiomorphy). In these taxa the abdominal sclerites may be divided longitudinally or transversely (Figs. 20 and 21), and sometimes fused to form a synterite as in Echinosiphonidae and Ctenosphinae or a synterite (apomorphy). The genital plates for both male and female are usually syntenites. In Enderleinellidae the sternal plate of the abdominal segment 2 is divided into peculiar plates. When sclerotized plates are present, the abdominal setae are usually associated with each plate (Fig. 3). There is a tendency to have more setae on membranous areas when the abdomen is devoid of sclerites. These setae sometimes form a transverse setal field (45 in Fig. 3).

7. Paratergites and spiracles. The number, size and shape of the paratergites provide good taxonomic characters at generic and species levels when present (Figs. 16-18 and 26-30). The paratergites in Hoplopilidae and Polypilidae are plate-like with the distal margin free from the body (apomorphy) (Figs. 16-18, 26 and 29) and in Haematopinidae and Peciciidae are caplike without a free distal margin (plesiomorphy) (Fig. 26). They are tuberculous in Peococetidae (Fig. 27) and Haeomatopinidae (Fig. 30). In Hoplopilidae the number of the paratergites ranges from six to eight on each side, one on each of the abdominal segments 2 to 9. The reduction in number is apomorphy. Each paratergite usually has a pair of setae, one on the dorsal side (DMS = DPS) and the other on the ventral side (VM = VPS). The size of these setae and the shape of the lateral lobes of the paratergites is specific characters in Hoplo- pilidae and Polypilidae (Figs. 17 and 18).

The abdominal spiracles are usually associated with paratergites (Figs. 3, 16 and 17). The basic number of functional spiracles is six pairs (plesiomorphy), one pair on each of the abdominal segments 3 to 8. The number of the abdominal spiracles is generally rather constant within each higher taxon. However,
In *Enderleinellus* the majority have six pairs of abdominal spiracles and yet many species have less than five pairs (apomorph): four pairs in *E. menenetus*, three pairs in *E. nitens*, and two pairs in *E. platyspicatus*. *Neoliniogasterus elephantus* has only one pair of large spiracles on the eighth abdominal segment. The spiracle generally consists of the subabdominal atrium constricted at its inner end and an oval or circular opening at its outer end (Fig. 34).

In some groups like the Echinophthiriiidae the atrium is highly modified (Fig. 33).

8. **Male genitalia**. The male genitalia consist of four primary parts: basal apodeme, a pair of parameres, andedeus with gonopore and pseudopenis (Figs. 37–41). In addition there are endomerites in some taxa. The *basal apodeme* (= basal plate or bp of Ferris, 1919; Ewing, 1932) is a long, rodlike sclerite (pleiomorph). The length and thickness

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**FIGS. 35–41.** (35–36) Female genitalia. (35) *Enderleinellus venezuelae*. (A) Spermatheca. (36) *Haematopterus neurogri*; (37–38) subgenital plate; Va = valvula; GS = genital seta; GVIII = gonopod VIII; GIX = gonopod IX; VI = valvular lamellae. (37–41) Male genitalia. (38) *Hoplitisura acanthopus*; (39) *Enderleinellus longiceps*; (40) *Microthoraxus camelli*; (41) *Pediculina humanus*; BA = basal apodeme; Pa = paramere; G = gonopore; Ps = pseudopenis; Ae = Aedeagus; AE = Anterior endomerite; ME = Middle endomerite; PE = posterior endomerite; DB = dorsal endomerite; Ed = endosheca or internal sac.
of the basal apodeme is specifically distinct. Sometimes, the basal apodeme becomes widened to form a plate with thickened lateral sides as in *Enderleinellus* (Fig. 38), and also may take the shape of inverted V or Y as in *Enderleinellus nitidus* (Kim, 1966b) and *Neolimniogongrus elephantidi*.

As shown in *Enderleinellus* there are components of the endomecral dorsal to the basal apodeme. They are variously shaped. The elaborate structures of the endomecrers are found in *Enderleinellus longipes* group (Kim, 1966b).

The parameters are paired elongate sclerites which articulate anteriorly with the basal apodeme (pleosomophy). The parameters may be extremely reduced as in *Haematopinoides* (Weisser, 1974) (apomorphically). The shape, length and thickness of the parameters are of taxonomic importance at generic and specific levels.

The *analogus* or *penis* (= penis or p of Ferris, 1919; Ewing, 1932) is usually membranous (apomorphically) or a weakly sclerotized tube located within the genital sac (= "peripatular sack" of Möberg, 1910); mesosome of Cunnings, 1916; = vesica penis of Nuttall, 1917; = internal sac of Ewing, 1932, and Kim, 1966b; = vesicula penis of Ferris, 1919; = endotheca of Weisser, 1974) (pleosomophy) or the frame of the endomecrers as in *Enderleinellus* (Fig. 38).

The *pseudopenis* (= pseudopenis or pp of Ferris, 1919, 1951; = ventral apodeme of Ewing, 1932) is a Y- or V-shaped sclerite between the parameters (pleosomophy). The pseudopenis is sometimes separated at the apex as in *Lepidopinoides* (apomorphically). The subgenital plate is a systemite of abdominal segments 7, 8 and perhaps 9. The shape of the subgenital plate is an important taxonomic character at species level.

The *female genitalia*. The principal parts of the female genitalia are the subgenital plate, gonopods and spermatheca (Figs. 3, 35 and 36). The subgenital plate is the sternal plate of abdominal segment 8 (= genital plate of Kim, 1965, 1966b; Ferris, 1951) and sometimes involves also the ventral of segment 7. It is variously shaped and usually bears a definite number of setae.

The gonopods are paired, sclerotized, flattened lobes or plates on abdominal segments 8 and 9. The gonopods of segment 8 bear a row of marginal setae with typical infraspecific variation; e.g. an apical cluster of three rather strong setae on each side in *Hoplopleura hesperomysis* complex (Kim, 1965). The gonopods of abdominal segment 9 have been referred to as genital lobes by several workers (Kim, 1965, 1966b). They are a pair of more or less distinct lobes near the lateral margin of the ninth abdominal segment bearing a tuft or a row of setae. The gonopods of segment 9 often bear an enlarged seta which is generally referred to as the genital seta (Kim, 1965). The shape and the number of setae of the gonopods are of taxonomic importance at species level.

A very delicately sclerotized spermatheca is present but not conspicuous in many Anopluran genera, although certain taxa such as *Enderleinellus* have a well sclerotized spermatheca. The spermatheca seems to be lacking in *Pediculida* and *Haematopinoides*. In many taxa there is an unsclerotized or only partially sclerotized plate called the *valvula* between the gonopods of segment 8 (Kim, 1966b) (Fig. 35). The valvula is variously shaped, it may be tapered, serrated, or even blunted at the apex, its posterior border is often serrated, forming the valvula *finibraria* in *Enderleinellidae* and *Hoplopleuridae*. In *Enderleinellidae* there is ventrally a short, wide, sclerotized plate referred to as the *intercalculus*.

The spermatheca, valvula and intercalulus sometimes are of taxonomic importance at species level.

The suprageneric classification of Anoplura

The higher classification of Anoplura by Ferris has been widely used by subsequent workers throughout the world. However, Ferris' system has become rather outdated, and is no longer adequate for the known diversity of the Anoplura fauna. Since 1951 eight new genera and about 230 new species of Anoplura have been described, and new information on ecology and hosts of many more sucking lice have been obtained.

The modern classification of Anoplura has grown from Enderlein's system. Enderlein (1904, 1909) recognized four families: *Pediculidae* (with subfamilies *Pediculinae* and *Pedi culinae*); *Haematopinoides* (with subfamilies *Haematopininae*, *Linognathinae* and *Eubradypinae*); *Echionophilidae* (with subfamilies *Echionophilinae*, *Microphilinae* and *Haematopininae*); *Pediculinae* (with subfamilies *Pediculinae* and *Pediculinae*).

**TABLE 1. Comparison of two classification systems of Anoplura. Asterisk (*) indicates the taxon whose taxonomic status has been changed.**

<table>
<thead>
<tr>
<th>Old system (Ferris, 1951)</th>
<th>New system (Kim &amp; Ludwig)</th>
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<tbody>
<tr>
<td><em>Echionophilidae</em></td>
<td><em>Echionophilidae</em></td>
</tr>
<tr>
<td><em>Linognathidae</em></td>
<td><em>Linognathidae</em></td>
</tr>
<tr>
<td><em>Microphilinae</em></td>
<td><em>Microphilinae</em>, n.fam.</td>
</tr>
<tr>
<td><em>Haematopinidae</em></td>
<td><em>Haematopinidae</em>, n.fam.</td>
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<tr>
<td><em>Haematopinidae</em></td>
<td><em>Haematopinidae</em>, n.fam.</td>
</tr>
<tr>
<td><em>Hoplopleuridae</em></td>
<td><em>Hoplopleuridae</em></td>
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<tr>
<td><em>Subfam. Enderleinellinae</em></td>
<td><em>Subfam. Enderleinellinae</em></td>
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<tr>
<td><em>Subfam. Hoplopleurinae</em></td>
<td><em>Subfam. Hoplopleurinae</em></td>
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<tr>
<td><em>Pediculinae</em></td>
<td><em>Pediculinae</em></td>
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<tr>
<td><em>Subfam. Pediculinae</em></td>
<td><em>Subfam. Pediculinae</em></td>
</tr>
<tr>
<td><em>Neolimniogongridae</em></td>
<td><em>Neolimniogongridae</em></td>
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<tr>
<td><em>Pediculina</em></td>
<td><em>Pediculina</em>, n.fam.</td>
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<tr>
<td><em>Pediculina</em></td>
<td><em>Pediculina</em>, n.fam.</td>
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<tr>
<td><em>Pediculina</em></td>
<td><em>Pediculina</em>, n.fam.</td>
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</tbody>
</table>

*Hoplopleuridae* and *Echionophilidae* were removed from *Haematopinidae* and placed in the *Hoplopleuridae* with two genera *Hybophthirius* and *Scipo*, which are considered to be a clade based on the true claw on the front tarsi. *Pediculina* was no longer regarded as part of the *Pediculinae*; instead it was treated as a monobasic subfamily, the *Pediculinae*.

Animal classification is the scientific theory that animals are arranged into taxa on the basis of inferences concerning their genetic and evolutionary relationships. A meaningful classification should be based, as Hennig (1966) emphasized, on all homomorphie characters and their environmental relationships. Thus, all biological traits of the taxa under study (e.g. structures, functions, homeostasis, habitats, host associations) should be used for taxonomic inference in deciding classification and phylogeny. A good classification of organisms is based on the relative merit of five major considerations: distinctness (size of gap); nature of adaptive zone; degree of differences; size of taxon; equivalence of ranking in related taxa (Mayr, 1969).

In developing this higher classification of the sucking lice the distinctness of each taxon was first established on morphological
grounds; then other biological attributes such as the host association were considered to augment the morphological evidence. All taxonomic characters used in the classification of family, subfamily, and genus-taxon were standardized, and then considered together. Taxonomic decisions on the ranking of each taxon were based on the states of morphological characters judged to be of the greatest importance. Morphological characters shared by adults and nymphs were considered primarily. Adaptations to microhabitats on the host were studied secondarily; for example, scales and coloration were considered, if available. Taxonomic distance was also estimated in terms of the degree of morphological difference or discontinuity. The uniqueness of each new adaptive zone was expressed by the host association of the suckinglice. The distinctness of a taxon was further considered in the light of the known fossil history of the host groups.

In Paucometabolous insects, nymphs and adults are very much alike and occupy the same habitat. Although none of the instars are normally threatened by predators, there is no constant threat to nymphs and adults alike caused by the grooming of the host. Due to the probable lack of differential selection, nymphal instars usually do not possess acquired characters significantly different from the adults. In many instances nymphal morphology is more conservative and generalized, and yet certain characters are unique in nymphal forms and used as defining criteria between taxa which are almost indistinguishable in adults (Kim, 1966c; Johnson, 1972).

Mammalian hosts provide unique specific niches and microenvironments for the sucking lice. The host association is therefore of great significance in taxonomic inference concerning classification and phylogeny. However, as pointed out by Ferris (1951) when the host associations are used to infer phylogeny of the sucking lice, and then the relationships of lice are employed to make quasicyclophylactic inferences about mammalian evolution, the reasoning becomes circular. Nevertheless, host information, such as that concerning habitat, behaviour, diversity, distribution, and fossil history of mammalian hosts, is an integral part of the biological data on species of sucking lice and should be employed judiciously in developing the classification of the Anoplura.

Survival of the sucking lice as obligate ectoparasites depends largely upon the well-being of the host animals and the microenvironment they provide. Anoplura are uniquely adapted to mammals and habitats on the mammalian skin surface. Mammals provide the most acceptable ecological settings for their survival, and sucking lice live and propagate successfully on most of the eutherian mammals. The life cycle and transmission of the sucking lice is to a large extent determined by the biology and social behaviour of the host (Kim, 1972, 1975). Likewise, the mammalian hosts have evolved with sucking lice. Thus, the present diversity and distribution of Anoplura is the result of long co-evolutionary processes. Undoubtedly, large sections of once very successful groups of Anoplura disappeared along with the extinction of the host group. Some of the monotypic taxa perhaps represent something of a remnant of what was once a large group. At the same time, certain groups of Anoplura may have speared rapidly by invading a new host taxon, or radiated along with rapidly diversifying mammalian groups such as Rodentia. Further, being a very small and highly specialized group, for the processionally connecting links have been left in the present array of Anoplura, and evolution of the sucking lice has modified the original form-function complex by reduction or loss of certain characters leaving reduced complements of characters available for study.

Microthoracidae is exclusively parasitic on camels (Camelidae, Artiodactyla) and Pecora on pecorines (Tayassuidae, Artiodactyla). Yet Microthoracidae with four known species and the monotypic Peccarco must be considered as the remnants of formerly much larger taxa, in view of their clear morphological affinity and the far greater host species diversity that existed in the late Tertiary. Camels and camelid relatives were then abundant (twenty-five genera in five subfamilies), although only two genera, Lama and Camelus, are now extant. Likewise, Tayassuidae were once a much larger group comprising eleven genera. From the early Oligocene to the Pleistocene most of the known taxa became extinct, and Tayassus (pecorine) is the sole surviving genus, with two species in the New World (Simpson, 1945; Anderson & Jones, 1967).

Ratelina (12 spp.) is known only from Equidae (Perissodactyla). Perissodactyla flourished in the Tertiary and were abundantly represented in almost all faunal regions (Anderson & Jones, 1967). The superfamly Equoidea once consisted of two families with at least twenty-six genera, but the only genus now extant is Equus (Simpson, 1945). The taxonomic position of Microthoracidae is difficult to assess correctly. It has certain characters in common with Haematopinidae and also shows some similarity to Linognathidae to which Ferris (1951) assigned it. Microthoracidae retains several plesiomorphic characters such as eyes and natal pit, and yet has many apomorphous characters; for example, lack of paratergites and abdominal tergites, and highly modified genitalia. Peccarco was placed in Haematopinae by Ferris (1951); a few characters are similar to Haematopinae, but the differences far exceed the similarity among many characters such as the female genitalia. Ratelina is similar to Linognathidae with some polypiloid characters. Ferris (1951) placed Ratelina in the subfamily Polyplacinae on the basis of plate-like paratergites with apical margin free from the body and the presence of a thoracic sternal plate. However, Ratelina has many unique characters, and is similar to linognathids, such as the female genitalia and abdominal chaetotaxy. With their uniqueness and relative merits of morphological characters and the geological history of their hosts Microthoracidae, Peccary and Ratelina are considered the remnants of once much larger taxa, and thus each taxon is treated here as a monotypic family.

Hybosphinae is a very distinctive louse parasite on the highly specialized antelopes, Orycteropus afer (Orycteropodidae, Tubulidentata). Ferris (1951) recognized the subfamily Hybosphininae with the two included genera, Hybosphina and Scipio, characterized by the common presence of a peculiar claw-like structure alongside the true claw. Hybosphina has probably coevolved with its host over a long period of time, and is here assigned to the monotypic family Hybosphinae. But Scipio is undoubtedly a polyplacid louse, considering the form of such characters as the paratergites, genitalia, abdominal sclerites and natal pit; thus Scipio is here assigned to the Polycladidae.
during their evolution, although they are at present mostly large animals far removed from the range and habitat of hyraxes.

The Echinophthiridae are exclusively parasitic on the suborder carnivores of the Phalangida and Mustelidae. These lice are highly specialized and have unique morphological traits not found in other groups of Anoplura. Five genera are recognized: Prochinophthirus on the Acanthocidae, Echinophthirus and Echinophthirius on Phalangida, Antarctophilus on a wide range of pinniped hosts, and Echinophthirius on the river otter, Lutra canadensis. Their highly specialized morphology, host distribution and transmission strongly suggests that the echinophthirids must have evolved with the pinnipeds and aquatic fissipeds after the ancestral carnivores ventured into aquatic habitats (Kim, 1975; Kim et al., 1975). This further suggests that the absence of the sucking lice on terrestrial carnivores is secondary, as was speculated by Hopkins (1949).

Haematopinus is rather generalized or primitive characters states in paruteretes, thoracic apophyses, thoracic sternal plate, natal pit, legs and genitalia, and is widely distributed on the ungulates, Artiodactyla and Perissodactyla. The present distribution and relatively unspecified morphological traits of Haematopinus suggest that haematopinids were widely distributed on the ungulates during the Tertiary period, so that the present diversity perhaps represents the remnants of a much larger group. Although Ferris (1951) included two genera, Haematopinus and Proctovacuna in the family Haematopinidae, we restrict the family to the single genus Haematopinus.

Pediculus, Phthirus and Pediculinae are found on anthropoid primates. Pediculinae is exclusively parasitic on Cercopithecidea or Old World monkeys. Pediculus is found on Hominiidae, Pongidae and Cebidae, and Phthirus on Hominiidae and Pongidae. Because of these host relationships, the three taxa had been grouped in the family Pediculidae until Ferris (1951) removed Pediculinae from the Pediculidae. Pediculinae is morphologically distinct from Pediculus and Phthirus, but in some respects similar to the Hoplophoridea. Ferris treated Pediculinae as a subfamily of the Hoplophoridae. Considering that the morphological characters of adults and nymphs, we have decided to recognize a family for Pediculus. Phthirus is peculiar and has been recognized to constitute either a subfamily (Ferris, 1951) or a family (Ewing, 1939). Pediculinae and Pediculus are basically very different taxa, apart from a few plecoomorphic characters such as a pair of distinctive claws and five-segmented antennae. Morphological details distinguishing these two taxa include the structure of the head, thorax, legs, parateretes and genitalia. On the basis of this morphological evidence, Pediculinae and Phthirus are considered to represent two well-separated lineages and thus are treated here as constituting two families, Pediculidae and Phthiridae.

Ferris (1951) recognized the largest family Hoplophoridae to include the majority of Anoplura subdivided into five subfamilies: Enderleinellinae, Hoplophorinae, Pollyphilinae, Hyphophthirinae and Pediculinae. This family is rather heterogeneous group and at best unwieldy, although the genera included are well defined and linked by certain morphological patterns, especially by the development of the parateretes. Consistent morphological patterns are unequally found in a subfamily, but practically no morphological character is consistent throughout the family. For example, the paratergal plates of the adults are usually highly developed with the apical point free from the body, but these are completely lacking in Phthiriculinae (Enderleinellinae) and some Haematopinus (Pollyphilinae) or much reduced in Leuropo- phthirus (Pollyphilinae). Similar patterns are repeated in the number of antennal segments, thoracic sternal plate, abdominal chaetotaxy, size and shape of legs, and male and female genitalia. The Hoplophoridae are primarily found on Rodentia but they are also found on Lagomorpha, Insectivora and even Primates. This family, as interpreted by Ferris, included more than 70% of the known species of Anoplura. Sucking lice assigned to the Hoplophoridae are particularly highly specialized, particularly in the head, the thoracic apophyses, chitinous complex of the hindlegs, parateretes, sternite of abdominal segment 2, and genitalia. The known distribution of the Hoplophoridae suggests that the evolution of these sucking lice must have centred in Rodentia, and that the invasion of other host groups, such as Insectivora, Lagomorpha, and Primates, is secondary. The establishment of Sathrus and Doxophthirus on Tupaiidae and Lemuriformes, Lemuripalaeus and Phthir- phthirus on Prosimian Primates must have occurred in more recent evolutionary times.

After considering the differential characteristics for each subfamily of the Hoplophoridae in the sense of Ferris, and the suite of morphological characters for adults and nymphs of each subfamily, we here elevate each of them to the rank of a family. This system deals more effectively with this unwieldy group, and will better allow the growth of each family-group taxon in the light of future research.

The Enderleinellinae are a homogenous group exclusive parasitic on Sciuridae (Rodentia). Five genera and forty-nine species are currently recognized. Enderleinella is widely distributed throughout the Sciuridae, and Mesocricetus is found on African squirrels. The remaining thirteen genera, Microphthirius, Phthirius, Phterippus and Atophthirus, are highly specialized lice parasitic on flying squirrels. Microphthirius on the North American flying squirrel (Glauconurus), the others on the giant flying squirrel (Petaurista) of Southeast Asia.

The Hoplophorinae is the second largest family of Anoplura, having five genera and 13 species parasitic upon rodents, pikas (Ochotomys, Lagomorpha), moles (Elidae, Insectivora) and shrews (Soricidae, Insecti- voridae). Hoplophorus and Phthirius are limited to the family of abdo- minal segment 2 prolonged laterally on each side to articulate with the corresponding parateretes, and by the similar ventral tubercles at the head and antennae of the nymphs. Thus, they are here recognized as a mono- phylectic group, the subfamily Hoplophoridae. The remaining three aberrant taxa, Haematopinus, Schizophthirus and Anistroscapheus, constitute a rather homogeneous group, recognizable by the presence of the distinctly divided cephalic plates of the abdominal seg- ment 2, each side of which is prolonged laterally to articulate with the corresponding paratergite, and also by the paratergites and the alternate nymphs. For this group, the subfamily Haematopinidae is recognized here.

The taxonomic status of the Pollyphilidae, the largest family, having fourteen genera and 175 species, is still confusing, and phylo- genetic relationships of the included genera are extremely difficult to assess. Apparently, several taxa such as Sathrus and Doxophthirus, successfully established on the tree shrews, are neoteniouly derived groups. Although their invasion of this host group seems to be rather recent, they must have adapted to the new host-habitat very rapidly by neotenic evolution. This resulted in extreme specializa- tion of the numerous form-function complexes. Several aberrant taxa such as Hamop- phthirus and Ratt Rocks are here removed from the family as previously discussed. And yet taxonomic relationships of Ctenophthirus, Balanognathus, Scepio and Haemoptopus, are removed from the family as previously discussed. And yet taxonomic relationships of Ctenophthirus, Balanognathus, Scepio and Haemoptopus, are recognized here as new families. The remaining subfamilies are presented here.

Definition of the Anoplura

Small wingless insects; obligate blood-sucking permanent ectoparasites of eutherian mammals.

Body dorso-ventrally flattened. Head conical; obturaculum composed of an inner flabellum of connective tissue and an outer layer of modified epidermal cells (Pipa & Cook, 1969). Antennae highly modified for piercing and sucking blood; proboscis small, snout-like, armed with small denticles and two styles of hypopharynges and labial organ retracted within the trophic pouch (Ramcke, 1965); mouthparts usually prognathous but sometimes shifted slightly ventrally; antennae short, filiform, usually five-segmented (occasionally only three- or four-segmented), fourth and fifth segments each with sensillum coeloconicum (may be absent when these segments are reduced), fifth segment with a pair of pore organs and a number of peg organs distally; compound eyes reduced, usually absent; ocelli absent.

Thorax relatively small and fuscous, one pair
of spiracles on mesothorax. Notum strongly reduced to narrow median area, usually unsclerotized but occasionally with distinct notal apodeme forming a median pit. Dorsum composed of two subcoxal or pleural components. Venter generally membranous, usually with median sternal plate. Legs strongly developed, with delicate modification of tibia and tarsus for effective grip (Figs. 10-12), tarsus unsclerotized, with a strong claw, trochanter with five sensilla campaniformia, two anterior and three posterior.

**Abdomen** with nine visible segments, terga and sterna usually weakly sclerotized, paratergites usually strongly developed; six pairs of spiracles usually present, opening laterally on segments 3-8; external genitalia well developed in both sexes: female with two pairs of gonopods (gonopophyses) those on segment 8 usually with a cluster of setae, those on segment 9 with tufts of setae or slight lobes (Figs. 35 and 36), sternal plate of segment 8 lobe-shaped, forming a sclerotized genital plate; male genitalia with basal apodeme, a pair of paraeresomes, aedeagus with dorsal gonocoxa, and a pseudopenis (Figs. 37-41).

Internal anatomy poorly known (the following description is based on Pediculus and Haematoptusia): alimentary canal with muscular walls, forming a powerful sucking pump armed with dilator muscles; large stomach with caeca at its anterior end; hindgut with moderate con- 


**Key to families**

1. Head with distinct eyes (Fig. 4) or subcuticular occipital points (Fig. 5) on lateral margins posterior to antennae
   - Head without external evidence of eyes or prominent occipital points (Fig. 6) .............................................. 8

2. Head with prominent occipital points but without eyes (Fig. 3) ................................................................. 4

3. Thoracic sternal plate well developed (Fig. 25); abdomen with paratergites on segments 2-8, each with 3-8 asclerotized caps over apex of each lateral lobe, not at all fused; each seta counts as less sub- 

   inature in shape and size, each with papilla on its flat surface (Fig. 11); on even-tined ungulates (Bovidae, 

   Cervidae and Suidae; Artiodactyla) and horses and zebras (Equidae; Perissodactyla).

**HEMATOPTIINAE**

- Thoracic sternal plate lacking; abdomen with paratergites on segments 2-8, each with posterior apex free from body; forelegs with claw-like structure at base of acuminated true claw (Fig. 12); forelegs much smaller than hind legs; and hind legs on sarcoptes (Sarcoptes, 

   Tubulidentata). ................................................................. HYPOPTINAE

4. Abdomen without paratergites and dorso- 

   ventrally densely covered with fine setae (Fig. 1); head attached to thorax dorsally, on camels and 

   llamas (Camelidae; Artiodactyla).

**MICOPTERINAE**

- Abdomen with paratergites as tubercles, caps or lobes and sparsely covered with setae (Figs. 26 and 27); hind legs attached to thorax in the same plane ................................................................. 5

5. Head long and slender, much longer than thorax (Fig. 9); abdomen narrowly eliptic, with small tuberciform paratergites on segments 3-8 (Fig. 27); on pecorines (Tayassuidae; Artio-

   daeta). ................................................................. PECARINAE

- Head about as long as thorax (Fig. 3), abdomen ovate or elliptic, with paratergites as sclerotized caps or lobes (Fig. 26); on antropodous Primates ........................................ 6

6. Compact Anophila with body less than twice as 

   long as wide; thorax very wide; abdomen short, as wide as thorax at base, and narrower toward apex with prominent, tubercular lateral lobes, forelegs slender, mid and hind legs very stout, each with a stout claw; on man (Hominidae) and gorilla (Pongidae) ........................................ 7

   - slender Anophila with body more than twice as long as wide, as long as wide as thorax with paratergites as sclerotized caps or oval, ochreous, each 

   paratergite as long as the body; on New World monkeys (Cebidae) .................................................. P. D. U. B. I. A. D. I. 7

   - paratergites present on abdominal segments 3-8, at least last three as sclerotized caps over apex of each lateral lobe, not free from body (Fig. 26); abdomen with setae not arranged in distinct rows; on man (Hominidae), chimpanzee (Pongidae) and New World monkeys (Cebidae). .................................................. PEDICINAE

7. Head and thorax thickly covered with setae (Fig. 7); abdomen thickly covered with setae of various shape and size including scales and spines (Fig. 15); spiracular atrium tubular (Fig. 23); on seals, sea lions and walruses (Pinnipedia), and river otter (Mustelidae; Carnivora).

**ECHINOPTERINAE**

- Head and thorax with few setae (Fig. 8); abdomen without scales; spiracular atrium bulbous (Fig. 34); on terrestrial mammals ... 9

8. Anterior distal segments of thorax and abdomen distinctly delimited on each side, each with a distinct cuticle; on elephants (Elephantidae; Proboscidea).

**LONINGNATHIDAE**

- Anterior distal segments of thorax and abdomen distinctly delimited on each side, each with a distinct cuticle; on elephants (Elephantidae; Proboscidea).

**THORACICA**

- Thorax without distinct notal pit (Fig. 9); thoracic pleural apodemes poorly developed and usually separated medially, abdomen usually with slender developed tegula and/or sternal plates, paratergites present on small extensions of body other than segments 3-8 ........................................ 10

9. Stereome of abdominal segment 2 extended laterally on each side to articulate with the corresponding paratergals (Figs. 20 and 21); hindlegs largest of the three pairs, stout, each with a stout and blunt claw (Fig. 16); on rodents (Rodentia), pikas (Ochotonidae; Lagomorpha), and moles and shrews (Talpidae and Soricidae; Insectivora).  

**HOPLOLOBIDAE**

- Stereome of abdominal segment 2 narrow, and extending laterally (Fig. 19); midlegs usually subequal to hindlegs in size and shape; very diverse group on rodents (Rodentia), rabbits and hares (Lagomorpha), insectivores (Insectivora), and Prosimian Primates .................................................. POLYPLACIDAE

**ECHINOPTERINAE**

- Antennae four- or five-segmented, with baso 

   segment strongly developed, head and head internal segment without such stout hook; on 

   forelegs smallest of the three pairs (Fig. 10); midlegs usually subequal to hindlegs in size and shape or at least somewhat larger than forelegs, each with a longer and stouter claw; second abdominal segment without detached ventral plate .................................................. 12

- Forelegs subequal to midlegs in size and shape, both more slender and smaller than hindlegs, and with acuminate claw; second abdominal segment usually with a pair of small, sclerotized, detached ventral plates or, if these plates lacking, either antennae less than five-segmented and abdomen without tegula and sternal plate or basal segment of antennae ventrally with a heavily sclerotized plate bearing the characteristic joint-like structures; on squirrels (Sciuridae; Rodentia).  

**ELLENDELIIDAE**

12 Abdomen with distinct paratergites, apically free from the body (Figs. 16, 28 and 29); forecoxae mesially close together ................................................................. 13

- Abdomen without distinct paratergites (Fig. 32) or at most with very small tubercules posterior to each 

   spine (Fig. 30); forecoxae widely separated from each other; on even-tined ungulates (Bovidae, 

   Cervidae and Giraffidae; Artiodactyla), canids (Canidae; Carnivora), and hyraxes (Procaviidae; 

   Hyracoidea) ................................................................. LONINGNATHIDAE

13 Thorax with distinct notal pit (Fig. 9); meso-

   thoracic pleural apodemes highly developed and fused medially (Fig. 31); abdomen membranous, with paratergites on segments 4-8; on donkeys and zebras (Equidae; Perissodactyla).  

**RATINAE**

- Thorax without distinct notal pit (Fig. 8); thoracic pleural apodemes poorly developed and usually separated medially, abdomen usually with slender developed tegula and/or sternal plates, paratergites present on small extensions of body other than segments 3-8 ........................................ 14

- Stereome of abdominal segment 2 extended laterally on each side to articulate with the corresponding paratergals (Figs. 20 and 21); hindlegs largest of the three pairs, stout, each with a stout and blunt claw (Fig. 16); on rodents (Rodentia), pikas (Ochotonidae; Lagomorpha), and moles and shrews (Talpidae and Soricidae; Insectivora).  

**HOPLOLOBIDAE**

- Stereome of abdominal segment 2 narrow, and extending laterally (Fig. 19); midlegs usually subequal to hindlegs in size and shape; very diverse group on rodents (Rodentia), rabbits and hares (Lagomorpha), insectivores (Insectivora), and Prosimian Primates .................................................. POLYPLACIDAE

**ECHINOPTERINAE**

Echinopterinae Endlener, 1904: 136. Type-genus Echinopterus Giebel, by original designation later vide Endlener, 1900: 7, 17; Endlener, 1909a: 505-507; Ferris, 1916: 133, 180; Freund, 1928: 2, 5; Ass. 1934: 89, 92; Ségy, 1949: 452; Ferris, 1951: 71, 72; Hågav-
Enderlein, by original designation. Host: Pholcidae.


Lagotrupes Enderlein & Emerson, 1924 (1 sp). Type-species: Lagotrupes ramosus Kim & Emerson, by monotypy. Host: Mustelidae (Mustela species).

**ENDELLELLIDAE**


**HAEMATOPOCAINAE**


Haematothorax Murray (partim), 1877: 384 (restricted to Haematothorax).

**HAPTOPHTHIRIDAE**


**Description.** Medium to large Anoplura; body thickly beset with various setae, spiniform setae, scales and pegs, in addition to the regular setae (Figs. 5 and 15). Head without distinct external lens and long setae; antennae three, four or five-segmented; occipital apophyses elongated, either divided or entire. Thorax with well-developed phragmata; mesothoracic phragmata connected across the dorsum, usually enclosing notal pit; no sternal plate present; sternal apophyses and apophyses pit indistinct. Legs: Mid-and hindlegs large and similar in size and shape, with blunt claws; tibial thumb elaborated, with several short, blade-like spines; forelegs small and slender, with acuminate claw except in Echinophthirus which has large forelegs similar to midlegs. Abdomen completely membranous or leathery, with no sclerotized plates at any of the segment types of setae including pegs and scales (Fig. 15); six sparses small and of distinctive type, each with a long, slender atrial chamber and a long cuticular rod (Fig. 33). Genitalia: Male with large, basally apodematous and well-developed parameres; pseudopenis U- or V-shaped or apically open; subgenital plate weakly developed. Female without gonopods and genital labium; subgenital plate poorly developed; spermathecal tubes surrounded by thick patches of long setae.
Subfamily Haematopinidae Ewing

Haematopinidae Ewing, 1929: 140. Type-genus Haematopinus. Osborn, 1891. Type-species H. anatipestis (Ewing, 1919).

Description. Small Hoplopleuridae. Head with antennae four—five segmented; post—antennal angle moderately developed. Thorax with mesothoracic phragmatogastriae distinct; sternal plate well developed, with its apex free from body wall. Legs forelegs always small and slender, each with a stout clavus, hindlegs much larger, generally flattened, each with a broad flattened claw. Abdomen Paratergites highly developed, those of segments 4—6 enclosing sides of the abdomen and each to some extent overlapping the succeeding paratergites; tergal and sternal plates well developed but variable, segment 2 with sternal plate extended laterally to articulate with the corresponding paratergite (Fig. 21). Nymphs with ventral tubercles on head and antennae.

Host: Rodentia and Lacomorpha.

Notes: This subfamily is characterized by the presence of a distinct lateral lobe at posterior lateral angle, post—sternal plate distinct; sternal apophysis and apophyseal pit indistinct. Legs: Forelegs slender and small, with a distinct cuticle on the tibia and femur. Thorax: Mesothoracic phragmatogastriae connected across the dorsum; metanotum with a distinct lateral lobe at posterior lateral angle, post—sternal plate distinct; sternal apophysis and apophyseal pit indistinct. Legs: Forelegs slender and small, with a distinct cuticle on the tibia and femur.

Description. Medium to intermediate Anopla. Head without external evidence of eyes; postantennal angles variously developed; occipital apophyses not developed; antennae five-segmented or if four-segmented the terminal segment compound. Thorax with meso- and metasternal phragmata well developed and natal pit distinct or occasionally obscure; sternal plate absent, at most narrow, pigmented longitudinal band, or if present, its apex not free from the body. Legs: Forelegs small and slender, with acuminate claw; midlegs and hindlegs subequal, and larger than forelegs; each with stout claw, and tibial thumbs developed, each with a single spiniform seta. Abdomen membranous, without trace of sternal and tergal plates except for those associated with genital and terminal segments (Fig. 32); paratergites absent or at most represented by small tubercles anterior to each spiracle; dorsally and ventrally with two or more longitudinal rows of CAS; six pairs of spiracles present, a pair on each segment; 5-8 spines with distinct internal teeth (Fig. 34). Genitalia: Male with basal apodeme slender and pseudopenis elongate or poorly sclerotized; parameres well developed, free at apex; subgenital plate strongly developed; cerci also sclerotized, with distinct aedeagus. Female: With subgenital plate variously shaped, sometimes lacking; gonopods VIII well developed; gonopod IX well developed and prolonged posteriorly, with either a spiniform genital seta or pointed apical process; spermheca not strongly sclerotized.

Hosts: Artiodactyla (Bovidae, Cervidae, and Giraffidae), Perissodactyla (Equidae), Carnivora (Canidae), and Hyaenidae (Procyonidae).

Linognathus Enderlein, 1904 (51 spp.). Type-species: Pediculus setulosus von Ollers (=Pediculus piliferus Burmeister), by original designation. Host: Bovidae, Giraffidae (Artiodactyla) and Canidae (Carnivora).

Solenopotes Enderlein, 1904 (10 spp.). Type-species: Solenopotes capitatus Enderlein, by original designation. Host: Cervidae and Bovidae (Artiodactyla).

Prolophus Ewing, 1929 (8 spp.). Type-species: Pediculus capricornis Pallas, by original designation. Host: Procaviidae (Hyracoidea).

MICROTHERACIDAE Kim & Ludwig, new family

Type-genus: Microthetaerus Fahrenholz, by monotypy.

Description. Medium to large Anopla with clearly evident eyes. Head generally elongated greatly and fusiform, at times being almost as long as abdomen; antennal-ocular segment much longer than clypeus; clearly evident eyes represented by a lens on each postantennal angle; antennae usually five-segmented, or if four-segmented, terminal segment compound with two sensillia; head setae crowded on the lateral side; occipital apophyses present; head attached to thorax dorsally. Thorax small and short, with distinct natal pit; mesothoracic phragmata connected across the dorsum; ventrally with sternal apophyseal pits and with poorly developed sternal plate. All legs similar in size and shape, each with acuminate claw; tibial thumbs weakly developed, each with an apical seta. Abdomen densely covered with small, fine setae (Fig. 31). Cuculla minutely wrinkled. In the sclerotized tegal, sternal and paratergal plates developed segments 3-8 each with a pair of spines. Genitalia: Male with moderately developed basal apodeme; parameres thin and short; pseudopenis well developed, either U- or V-shaped; subgenital plate very weakly developed (Fig. 39). Female with subgenital plate weakly developed; gonopods VIII rounded; gonopods IX usually prolonged.

Hosts: Cimicidae (Macroscelidae).


Description. Large Anopla with long and slender body. Head long and slender, with clearly evident eyes represented by a lens, antennal-ocular segment about four times longer than clypeus; antennae five-segmented, with basal segment much broader than the others. Thorax relatively short, and heavily sclerotized, with distinct natal pit and a pair of small sternal apophyseal pits; sternal plate very narrow and long (it may appear indistinct in the cleared specimens); meso- and metasternal phragmata distinct (Fig. 9). All legs subequal in size and shape. Abdomen long and narrowly elliptical, with six paratergites, six spines and the sternum finely wrinkled; paratergites small, rounded, tuberculiform (Fig. 27); no distinct tergal and sternal plate present; segmental setae short and arranged in transverse rows; segments 3-8 each with a spine and paratergite on each side. Genitalia: Male with basal apodeme thick; parameres strongly developed and laterally enlarged, with apical end pointed and curved outward; pseudopenis V-shaped; subgenital plate not developed. Female with a pair of gonopods IX pronounced and widely separated; gonopods VIII short; subgenital plate trapezoid.

Hosts: Artiodactyla (Tayassuidae).


Description. Medium to intermediate Anopla. Head oval to narrowly oval, without prominent postantennal angle; distinct eyes present with lens and pigments; antennae five-segmented, occasionally the last three segments partially fused, and sexually dimorphic, the male having a short and very stout seta dorsally on each of the last three segments; occipital apophyses lacking. Thorax with phragmata well developed and united in a weakly sclerotized median area surrounding the poorly developed natal pit; median longitudinal ridge articulating with occipital sclerotization of the head; sternal plate, sternal apophyses and apophyseal pit lacking. Legs variable in shape, either all legs subequal in size and shape, slender, each with acuminate claw or only the forelegs slender.
with acuminate claw and mid- and hindlegs large and stout, each with stout claw; tibial thumbs developed each with a single spiniform apical seta. Abdomen membranous, with no traces of sternal and tergal plates except for genital and terminal segments; segments 4 (or 5) to 6 each with a pair of triangular paragents which are marginally free from body wall; segments 3–8 each with a pair of spiracles, dorsal and ventral setae always very small, arranged in segmental rows (one row per segment). Genitalia: Male with genital aperture developed at apex; parameres well developed, not fused distally; pseudopenis pentagonal, not heavily sclerotized; aedeagus and endomerites sclerotized; subgenital plate developed. Female with small genital plate, gonopods poorly developed, gonopod IX indistinct.

Host: Primates (Cercopithecidae).

*Pediculus* *Gervais*, 1844 (16 spp.). Type-species: *Pediculus erythroderma* Burmeister, 1838, by original designation. Host: Old World monkeys, Cercopithecidae (Primates).

**PEDICULIDAE Leach**

Pediculidae Leach, 1817: 64. Type-genus *Pediculus* Linnaeus, by monotypy.


Haematopina Murray, 1877: 384.


Description. Large Anoplura, head relatively short, abruptly constricted posteriorly into a short neck, with eyes externally represented by a pair of distinct lenses and pigmentation on lateral lobes; postantennal angle not developed; antennae five-segmented, not sexually dimorphic; no occipital apophyses. Thorax with well-developed phragmata, not connected across the dorsum; notal pit small, longitudinal; sternal plate slightly sclerotized or completely lacking; sternal apophyses and apophysis of pit lacking. All legs subequal in shape and size and each with a long acuminate claw; tibial thumb developed, each with a spiniform seta. Abdomen usually membranous except for the usual genital and terminal segments and small tergites in the male; the lateral margins more or less strongly lobed, the lobes covered by the sclerotized paratergal plates which are not free from the body wall (Fig. 26): segments 3–8 each with a pair of spiracles, which are usually borne on paratergites or in sclerites; segmented setae distinct, arranged in transverse fields. Genitalia: Male with basal apodeme large; paramere very short and articulated to V-shaped pseudopenis, statum penis and aedeagus sclerotized, connected to internal sac which bears conspicuous teeth (Fig. 41); subgenital plate not developed. Female with subgenital plate large, transverse; gonopods VIII and IX strongly developed; spermatheca indistinct.

Host: Anthropoidea (Primates).

*Pediculus* Linnaeus, 1758 (2 spp.). Type-species: *Pediculus humanus* Linnaeus, 1758, by original designation. Host: Cebidae (New World monkeys), Pongidae (gibbons and great apes), and Homoidea (man).

**POLYPLACIDAE**


Description. Medium to small Anoplura. Head with antennae five-segmented, usually sexually dimorphic; postantennal angles variable. Thorax with mesothoracic phragmata usually evident; sternal plate usually well developed (Figs. 22 and 23) and rarely absent, no notal pit. Legs: Forelegs always small and slender, each with acuminate claw; mid- and hindlegs subequal in size and shape or hindlegs larger than midlegs. Abdomen with paratergites usually highly developed (Fig. 28) and occasionally represented by small sclerites or completely lacking; six spiracles present, tergal and sternal plates usually highly developed and at times reduced or lacking; sternal plate of segment 2 not extending laterally to articulate with the corresponding paratergites (Fig. 19). Genitalia: Male with well-developed but variously shaped basal apodeme, parameres and pseudopenis. Female with well-developed subgenital plate and gonopods VIII and IX; spermatheca usually indistinct.

Host: Rodentia, Lagomorpha, Insectivora and Prosimian Primates.

Polyplax Enderlein, 1904 (17 spp.). Type-species: *Pediculus spinulosa* Burmeister, by original designation. Host: Rodentia and Insectivora.

Prenoderneina Ewing, 1923 (1 sp.). Type-species: *Prenoderneinina aequorea* Ewing (= *Polyplax calva* Waterton), by monotypy. Host: Muridae (Rodentia).


Neohematopinae Möbius, 1910 (41 spp.) including *Jokohemaphora*. Type-species: *Hematopinae scutiferi* Osborn, by original designation. Host: Sciuroidae Rodentia, and Insectivora.


Docothepus Waterton, 1923 (1 sp.). Type-species: *Docothepus scintus* Water-

**PHTHIRIDAE Ewing**


Description. Medium, compact Anoplura. Head short, much narrower than thorax, never constricted into a next, definite eye present externally as a pair of distinct lenses on large lateral protuberances; antennae five-segmented, not sexually dimorphic; no occipital apophyses developed. Thorax short and very wide, and the sclerotization of the apparent notum confined to the lateral areas; no sternal plate and apophyses present; no apparent notal pit present. Legs: Forelegs very slender, with acuminate claw; mid- and hindlegs very large and stout, with stout claw; all the coxae set at the extreme thoracic
basal apodeme and highly developed parameres; pseudopes mostly membranous except for sclerotized apical end; subgenital plate lyre-shaped. Female with a pair of short gonopods and no distinct spermatica; gonopods IX prolonged, each with a spiniform seta at apex; subgenital plate T-shaped.

**Host:** Perissodactyla (Equidae).

**Ratanaia Fahrenholz, 1916 (2 spp.).** Type-species: Hecematopinus (Linognathus) squamatus Neumann, by original designation. Host: Zebras and asses (Equidae).

**Phylogenetic relationships**

The present state of knowledge on the diversity and evolutionary parameters of Anoplura is still too scanty for us accurately to interpret the phylogenetic relationships of all the various genera. Yet available information on morphological characters of nymphs and adults, diversity patterns, and host associations give an insight to Anopluran phylogeny.

When considering phylogenetic relationships, the retention or complete loss of a primitive character obscures true evolutionary relationships. According to Hennig (1966), phylogenetic inferences should be based on synapomorphy or shared derived characters. Synapomorphy is usually the result of close phylogenetic relationship; synapomorphy due to convergence is usually revealed by carefully analyzing the distribution and patterns of the derived characters. On the other hand, synapomorphy with respect to a particular character occurs when taxa have not yet lost the primitive or ancestral character state in their separate evolutionary pathways. At best it may indicate the original state of that character as probably present in ancestral forms.

A character matrix was constructed to show the trends of morphological characters among fifteen family-group taxa in the Anoplura (Table 2). After the overall analysis of taxonomic characters twenty-two characters were selected for detailed assessment. The character state, either plesiomorphy (primitive state) or apomorphy (derived state), was determined for each character (see Table 2). Character matrix for family taxa of the Anoplura. (For abbreviations and codes, see the legends.)

| Character | HAE | MIC | ECH | PEC | FED | LIN | HYB | RAT | PTH | FEL | HAM | NEO | END | HOP | POL |
|-----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Basal spine | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Paramere | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Subgenital plate | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

**Abbreviations and codes:**
- **HAT:** Haematosiphonidae
- **MIC:** Microthoracidae
- **ECH:** Echinothripidae
- **PEC:** Paraceratidae
- **FED:** Pediculidae
- **LIN:** Linognathidae
- **HYB:** Hyobothridae
- **RAT:** Riteniidae
- **PTH:** Ptiliphilaena
- **FEL:** Feliphilaena
- **HAM:** Hamaphilidae
- **NEO:** Neodincipitidae
- **HOP:** Hoptoeididae
- **POL:** Polypplacidae

**Characters:**
- **1.** Body size (BS): 1, large (more than 3 mm); 2, intermediate (2–3 mm); 3, medium (1–2 mm); 4, small (less than 1 mm) (2 Eyes (EYE): 1, present; 2, absent; (3) Ocular points (OP): 1, absent; 2, present; (4) Number of antennal segments (NAS): 1, five-segmented; 2, four-segmented; 3, three-segmented. (5) Occipital apophyses (OA): 1, absent; 2, present. (6) Dorsal principal head setae (DPS): 1, short; 2, strong. (7) Notal pit (NP): 1, present; 2, absent. (8) Mesothoracic pleural apophyses (MPA): 1, fused medially; 2, separated. (9) Metathoracic pleural apophyses (MPA): 1, separated from MPA; 2, fused to MPA. (10) Thoracic sternal plate (TSP): 1, well developed; 2, poorly developed; 3, absent; 4, divided. (11) Dorsal metathoracic setae (DMTs): 1, present; 2, absent. (12) Forelegs (FL): 1, smallest of the three pairs of legs, with scutum claw; 2, subequal to midlegs. (13) Hindlegs (HL): 1, subequal to midlegs; 2, highly enlarged and modified. (14) Abdominal chaetotaxy (AC): 1, moderately covered with setae; 2, sparsely covered with setae; 3, densely covered with fine setae; 4, setae highly modified. (15) Abdominal sternites and tergites (AST): 1, highly developed; 2, poorly developed; 3, modified; 4, absent. (16) Paratergites (PT): 1, capsule-shaped; 2, lobate-shaped; 3, tuberculariform; 4, plate-shaped with its apex free from body. (17) Number of paratergites (NPT): 1, 2, 3, 4, 5, 6, 7. (18) Number of abdominal spiracles (NAS): 1, six spiracles; 2, less than six spiracles. (19) Parameres (PA): 1, highly developed; 2, fused at apex; 3, reduced. (20) Pseudopes (P): 1, fully developed; 2, V-shaped; 3, poorly developed; 4, separated at apex. (21) Gonopods IX (G9): 1, highly developed; 2, poorly developed; (22) Gonopods IX (G9): 1, highly developed; 2, poorly developed.

**Evaluation of Taxonomic Characters:**

- **Basal spine:** 1, large (more than 3 mm); 2, intermediate (2–3 mm); 3, medium (1–2 mm); 4, small (less than 1 mm).
- **Paramere:** 1, present; 2, absent.
- **Subgenital plate:** 1, present; 2, absent.
- **Ocular points (OP):** 1, absent; 2, present.
- **Number of antennal segments (NAS):** 1, five-segmented; 2, four-segmented; 3, three-segmented.
(5) Occipital apophysis (OA): 1, absent; 2, present.
(6) Dorsal principal head setae (DPHS): 1, short; 2, strong.
(7) Notal pit (NP): 1, distinctly present; 2, indistinct or absent.
(8) Mesothoracic pleural apophyses (MSPA): 1, fused medially; 2, separated.
(9) Metathoracic pleural apophyses (MPA): 1, separated from MPA; 2, fused to MPA.
(10) Thoracic sternal plate (TSP): 1, well developed; 2, poorly developed; 3, absent; 4, divided.
(11) Dorsal metathoracic setae (DMSS): 1, present; 2, absent.
(12) Forelegs (FL): 1, smallest of the three pairs of legs, with acuminate claw; 2, subequal to middle legs.
(13) Hindlegs (HL): 1, subequal to middle legs; 2, highly enlarged and modified.
(14) Abdominal chaetotaxy (AC): 1, moderately covered with setae; 2, sparsely covered, with setae; 3, densely covered with fine setae; 4, setae highly modified.
(15) Abdominal sternite and tergites (AST): 1, highly developed; 2, poorly developed; 3, modified; 4, absent.
(16) Parategites (PT): 1, cap-shaped; 2, lobe-shaped; 3, tuberculiform; 4, plate-shaped with its apex free from body; 5, absent.
(17) Number of parategites (NPT): 1, 2, 3, 4, 5, 6, 7.
(18) Number of abdominal spiracles (NSP): 1, six spiracles; 2, less than five spiracles.

(19) Paramera (PA): 1, highly developed; 2, fused at apex; 3, reduced.
(20) Pseudopenis (PS): 1, highly developed; U- or V-shaped; 2, poorly developed; 3, separated at apex.
(21) Gonopods VIII (G8): 1, highly developed; 2, poorly developed.
(22) Gonopods IX (G9): 1, highly developed; 2, poorly developed.

To summarize the character matrix in Table 2 a triangular matrix was made for synapomorphy of fifteen family-group taxa of the Anoplura (Table 3). The number in each square represents the number of derived characters (apomorphy) shared by two taxa. In scoring synapomorphy only those characters having identical character state were counted.

Endemism of the sucking lice on a particular mammalian taxon is important in discussing Anopluran phylogeny, and accurate data on the host distribution of the sucking lice provide invaluable correlates of mammalian evolution (Hopkins, 1957; Patterson, 1957; Kim et al., 1975). Primary infestation is defined by Hopkins (1949) as the presence of a parasite taxon dating back at least to the time when its host group diverged from the ancestral stock. Thus, in primary infestation, almost all members of a given host taxon are infected with closely related parasites belonging to a particular taxon. Accordingly, the secondary infestations comprise those infestations originating after divergence of a host group from its parental stock. The type of infestation is usually determined by studying the distribution of the sucking lice on the host groups, and further confirmed by findings in ecology, behaviour, and biology of the species.

Occurrence of the families of Anoplura on their respective mammalian groups appears to be mostly primary, except for the Neolothognatidae, and parts of the Hoplopleuridae and Polypelidae. The evolutionary fate of each taxon of lice must have followed the evolutionary path of the mammalian hosts. However, the infestations of Hoplopleuridae and Polypelidae on insectivora and Primates are secondary, and the establishment of Neolothognatidae on Macroscelidea (Heterocephalidae) seems to be secondary. Neolothognatidae shares many characters with Polypelidae and is considered here as a taxon broken off from the Polypelidae line rather early in its evolutionary time. By considering the mammalian diversity in the Tertiary period, phylogenetic relationships of fifteen families of the Anoplura were evaluated and a 'preliminary' phylogeny of the Order constructed (Fig. 42).

The Linognathidae share the most apomorphic states with other taxa, particularly Polypelidae, Hoplopleuridae, Pediculidae, Phthiridae and Enderleinellidae, although they themselves are highly specialized. The Linognathidae colonized primarily the ungulates and secondarily the Carnivora, while the Polypelidae, Hoplopleuridae and Enderleinellidae invaded and coevolved with rodents. These families are considered here to be the major phylogenetic line from which the Pediculidae, Neolothognatidae and Ratermiidae have branched off. The Echinothripidae, along with Pediculidae, Pecaryoceridae, Haematoptea and Microthoracidae, are highly specialized and yet retain many primitive characters. Perhaps this suggests that they diverged from the main phylogenetic line much earlier. Hybosphirinae, Hamosphirinae and Phthirinae are considered to have diverged early from the major phylogenetic line, and thus to have coevolved with their respective host-groups for a long time. While there is some evidence supporting each of these hypotheses the phylogenetic inferences made in this paper are at best preliminary and should be considered as a starting point for future research.

TABLE 3. Matrix for synapomorphy of fifteen family taxa of the Anoplura (for abbreviations, see the legends of Table 2)

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FIG. 42. Inferred phylogeny of the Anoplura.
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The New World species of the water-beetle genus Notomerus (Noteridae)*

FRANK N. YOUNG
Indiana University, Bloomington

ABSTRACT. Eight species of Notomerus Sharp are recognized and described partially redescribed with figures of dorsal outlines and external male genitalia: brevicomis Sharp, gracilipes Sharp, bifrons sp., mallei sp., navillus (LeConte), reticulatus Zimmermann, sp. Balfour-Browne, trailli Sharp. A key for identification is given, but the main reliance for recognition of the species is on the external male genitalia. New distribution records are given for all species.

Introduction

The genus Notomerus Sharp contains some of the smallest of all aquatic beetles. Most of the species range between 1.2 to just over 1.6 mm in total length, but some individuals of N. brevicornis Sharp scarcely attain 1.0 mm in length.

The genus is readily distinguished from other Noteridae by the small size of the species, the lack of a curved hook or spur on the fore tibia, and the slender hind legs which seem unmodified for swimming but have the tarsus longer than the tibia. The ventral platform, formed by the conjointed prosternal process, metasternum, and inner lamina of the hind coxal base is distinct but not bordered or margined on the metasternum and the sutures between the inner coxal laminae and the metasternum cannot be detected except in some species by a difference in colour. The posterior end of the inner lamina is feebly excised and is separated along the sutures. The cavities in which the trochanters articulate (coxal cavities) are very narrowly separated, and the coxal lines are unmarked by a raised border or margin. Except for the mating and dispersal flight, these small beetles spend their lives in debris or root mats along the edges of standing or slowly running water. They may sometimes be collected by examining sticks or roots along the margins of ponds or streams but are seldom taken in the collecting net. The best way of collecting series is to place masses of debris or sections cut out of root mats on the screen of a Berlese funnel. Many specimens in collections have been taken at light. The black light trap (ultraviolet light trap) seems to attract most of the American species in numbers except Notomerus navillus (LeConte).

Abbreviations

Abbreviations of museums in which material is deposited or will be deposited as follows: AMNH: The American Museum of Natural History, New York, New York, U.S.A.; BMNH: British Museum (Natural History), London, U.K.; CAS: California Academy of Sciences, San Francisco, California, U.S.A.; DZ: Deutsches Zentrum für Zoologie, Berlin; FM: Field Museum, Chicago, Illinois, U.S.A.; FSCA: