The family classification of the Anoplura

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ABSTRACT. Fifteen families of Anoplura are recognized and defined, one with two sub-families, 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 obligatory, 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 protrusible 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 Palaearctic region, fifty-two (13.3%) from the Oriental region, forty (10.2%) from the

Nearctic region, and forty-three (11.0%) from the Neotropical 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. Piotrowski (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 eutherian mammals except the Chiroptera, Edentata, Pholidota, Cetacea, Proboscidea and Sirenia. Those sucking lice which have moved on to new host groups have acquired additional specialized morphological and biological characteristics, e.g. *Sathrax* and *Docophthirus* on Insectivores.

Increase in the number of known species of Anoplura from Linnaeus to present.

486: Ludwig & Kim (1976)
454 Piotrowski (1973)
452: Ludwig (1974)
342: Ludwig (1968)
255: Ferris (1951)
223: Ferris (1935)
220: Fahrenholz (1936)
144: Fahrenholz (1919)
123: Ferris (1916)
64: Enderlein (1904)
29: Gervais (1844)
22: Burmeister (1838)
20: Nitzsch (1864)
37: Piaget (1885)
7: Nitzsch (1818)
33: Piaget (1880)
32: Giebel (1874)
6: Linnaeus (1758)
20: Denny (1842)

Number of known species

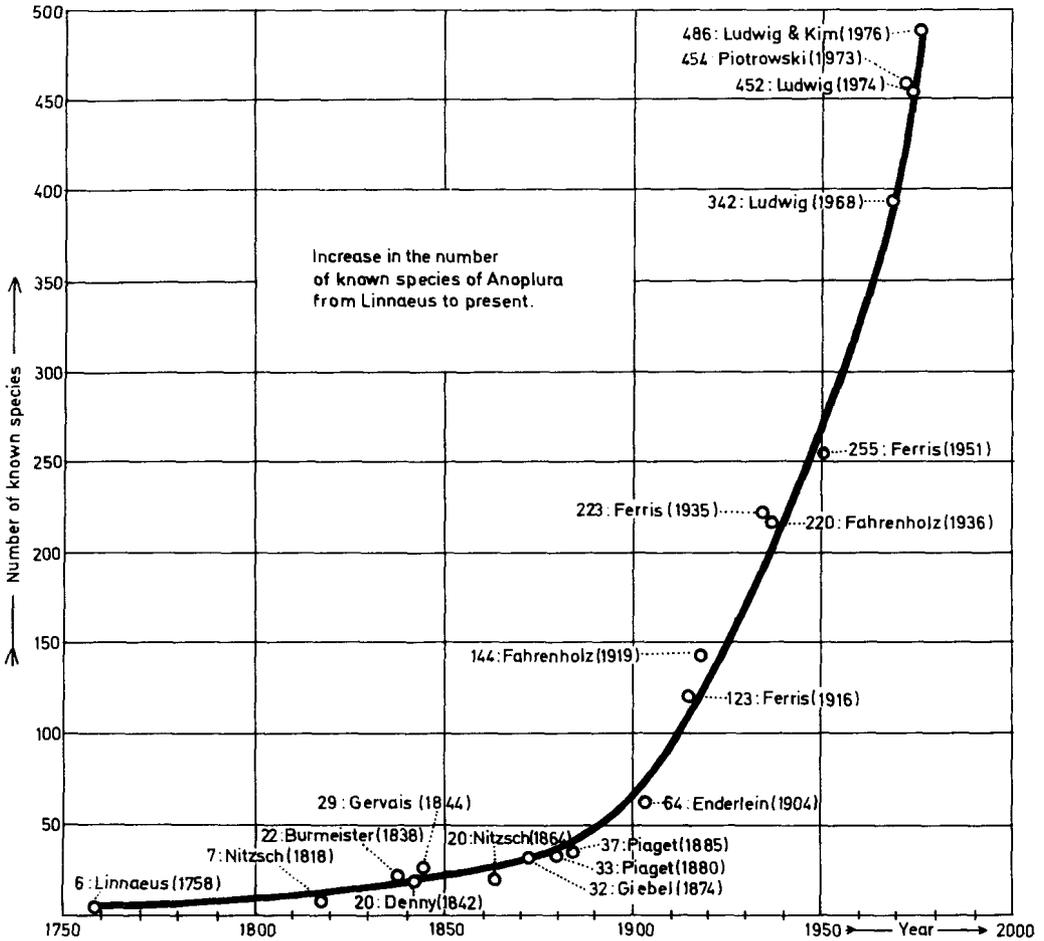1750   1800   1850   1900   1950 ►—— Year ——► 2000

FIG. 1

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 of the mammalian orders which are known 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, *Johnsonpthirus* and *Cuyana*, are not accepted here; six genera accepted are *Lemurpediculus, Sathrax, Latagophthirus, Atopophthirus, Phthirunculus* and *Alenapthirus*. Three of the genera recognized by Ferris are not accepted in this paper: *Symoca, Galeophthirus* and *Lagidiophthirus*. Accord-

ingly, 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 polyspecific 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 (1688) illustrated many chewing and sucking lice with considerable accuracy.

Linnaeus described the genus *Pediculus*, into which he put almost everything that could conceivably be called a 'louse', and placed this genus in the 'INSECTA APTERA'. *Pediculus* Linnaeus originally comprised an unlikely assortment of thirty-nine forms, including sucking lice, biting lice, booklice or psocids, a beetle triungulinid and a louse-fly or hippoboscid fly.

After Linnaeus, Fabricius (1775, 1805) placed *Pediculus* in the order ANTLIATA along with other miscellaneous assortments of forms. Latreille (1806) established the order PARASITA for two groups of lice, with the genera *Pediculus* for the sucking lice and *Ricinus* for the biting lice. Later, Latreille (1825) divided the order PARASITA into two

groups, SIPHUNCULATA for the sucking lice and MANDIBULATA for the biting lice in the 'ORTHOPTERA EPIZOICA'.

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 Burmeister (1835, 1838), in the order PHTHIRAPTERA for two groups of lice by Haeckel (1896), in the order PSEUDORHYNCHOTA by Cholodkovsky (1904), in the order ELLIPOPTERA by Shipley (1904) and in the LIPOGNATHA 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 PARASITA (Osborn, 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 Haeckel, 1896. However, these names have not been consistently applied or interpreted.

The ordinal name SIPHUNCULATA was used by Handlirsch (1908) for the sucking lice alone, but Mjöberg (1910) and Harrison (1916) included two suborders: ANOPLURA for the sucking lice and MALLOPHAGA for the biting lice. Dalla Torre (1908), followed by Ferris (1919–35, 1951) and many other workers, considered the sucking lice as an independent order ANOPLURA, but Fahrenholz (1936) included *Haematomyzus* in the ANOPLURA. Fahrenholz divided the order ANOPLURA into two suborders, RHYNCHO-PHTHIRINA, 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: ANOPLURA, MALLOPHAGA and RHYNCHOPHTHIRINA. Conversely, Ferris (1951) and many other workers, including ourselves, have treated the sucking lice as the order ANOPLURA, independent of the order MALLOPHAGA with its suborder Rhynchophthirina.

Until 1815 all the known sucking lice were included in the genus *Pediculus* (Fabricius, 1775; Latreille, 1806). Leach (1815, 1817) was the first to subdivide the sucking lice into *Pthirus, Haematopinus* and *Pediculus*; together with one genus of the biting lice, *Nirmus*, he placed these three genera in the order ANOPLURA, family Pediculidae.

During the period 1819–1903 little new information was obtained on ANOPLURA. Papers by Nitzsch (1818, 1864), Burmeister (1835, 1847), Denny (1842), Giebel (1871, 1874), Piaget (1880–85) and Osborn (1891, 1894, 1896) are the most significant from that era.

Nitzsch (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 (Nitzsch, 1864). Burmeister (1838) recognized two genera, *Phthirus* (one species) and *Pediculus* (twenty-one species) in the family Pediculina under the order RHYNCHOTA which included scales, aphids, leafhoppers, and other Homoptera. Denny (1842), in his *Monographia Anoplurorum Britanniae*, resorted the order ANOPLURA, dividing it into two suborders, RHYNCHOTA (Haustellata) 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 Denny's 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 *Echinophthirius* for a seal louse, *Pediculus phocae* Lucas. Thereafter, in his *Insecta Epizoa*, Giebel (1874) placed the sucking lice as the family PEDICULINA (corresponding to the family MALLOPHAGA for the biting lice) in the order HEMIPTERA, and called

the group HEMIPTERA EPIZOA. In a monumental work entitled *Les Pediculines*, Piaget (1880–85) recognized six genera, including the new genus *Haematomyzus* 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 *Haematopinoides* (Osborn, 1891) and then renamed it as the genus *Euhaematopinus* (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 ANOPLURA). About sixty of these species were included in the genus *Haematopinus*; the remainder were classified as *Echinophthirius, Haematopinoides, Pedicinus, Pediculus* and *Pthirus*. Up to this time there was little demand for a supra-generic classification of the sucking lice.

Enderlein (1904) commenced a series of papers on the sucking lice which provided the most comprehensive overview up 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 Haematomyzidae with *Haematomyzus* which is not now considered to be Anopluran. 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, *Hoplopleura* (1904), *Antarctophthirus* and *Lepidophthirus* (1906), and *Hybophthirus* (1909b).

When Dalla Torre (1908) published the first catalogue of the ANOPLURA 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 *Catalog 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 1909 (i.e. after the publi-

cations by Enderlein and Dalla Torre). Not surprisingly this catalogue contains some false synonymy and erroneous judgements on the systematic position of several taxa. However, in the period 1919–34, Ferris published a series of papers entitled 'Contributions toward 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 230 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 Blagoveshtchensky (1937–72), Sosnia (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 *Microphthirus uncinatus*, to more than 8 mm for *Pecaroecus javalii*. Although its adaptive significance is not readily assessed, the body length seems to characterize each genus. For example, species of *Haematopinus* are usually large lice of about 4 mm length but *Polyplax*, *Enderleinellus* and *Hoplopleura* (Hoplopleuridae 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 *Haematopinus, Pecaroecus, Pediculus* and *Microthoracius* have all legs similar in size and shape with acuminate claws, and paratergites either cap-like or tuberculiform if present. In the smaller taxa, the size and shape of legs differ considerably in various combinations; also the paratergites are plate-like with the apex free from the body as shown in Enderleinellidae, Hoplopleuridae and Polyplacidae. In Enderleinellidae the fore- and midlegs are similar in size and only the tibio-tarsus of the hind legs are highly modified for grasping hairs. The forelegs are

smallest in Hoplopleuridae 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 mere cap over the apex of lateral lobes of the abdomen. Furthermore, it is interesting to note that the small hoplopleurids 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 to serve different purposes. Some setae are modified into scales and spines as in *Antarctophthirus* and *Lepidophthirus* (Kim, 1971); others are enlarged and modified for perhaps mechanical or special sensory function (Figs. 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 *Microthoracius* (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 consistent among congeneric species. The basic pattern of the chaetotaxy of head, antennae, thorax and legs is remarkably constant among species of a higher taxon. The primary pattern of chaetotaxy of head, antennae and legs of the first nymphal instar does not change throughout the post-embryonic development. New setae 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. *Pedicinus*) the adult chaetotaxy is already developed in the second nymphal instar (Kuhn & Ludwig, 1967). The consistency and constancy of these setal patterns seem to suggest that the chaetotaxy must have been fixed by selection quite early in the evolution of the Anoplura.

It is rather unlikely that nymphal instars are subjected to special selection pressures,
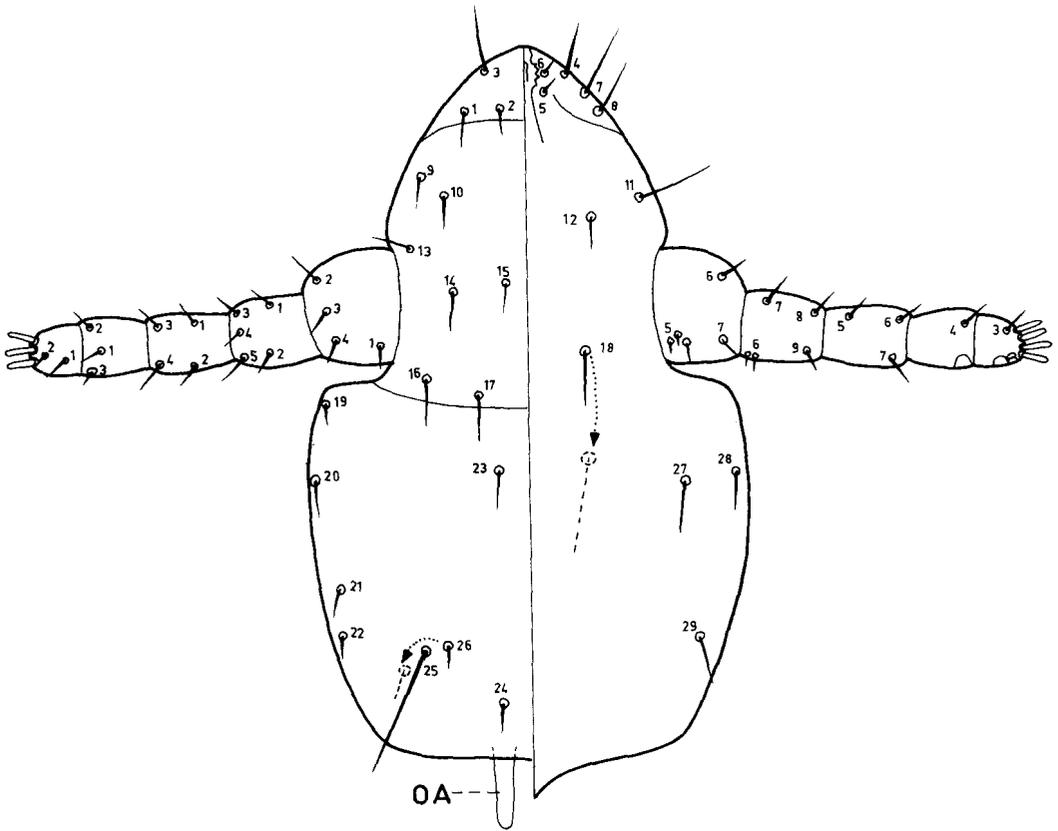
FIG. 2. Standardized chaetotaxy of Anoplura (generalized), head; left side shows the dorsal half and right side is venter; setae on head, thorax and abdomen are continuously numbered and setae on each antennal segment are separately numbered without specific positional designation; 1, 2: dorsal anterior head setae (DAnHS); 3, 4: apical head setae (ApHS); 5, 6: oral setae (OrS); 7, 8: anterior marginal head setae (AnMHS); 9, 10: dorsal preantennal lateral head setae (DPaLHS); 11, 12: ventral preantennal head setae (VPaHS); 13: dorsal preantennal head setae (DPaHS); 14: supraantennal head setae (SpAtHS); 15: supraantennal central head setae (SpAtCHS); 16, 17: sutural head setae (SHS); 18: ventral principal head seta (VPHS); 19, 20, 21, 22: dorsal marginal head setae (DMHS); 23: dorsal anterior central head setae (DAnCHS); 24: dorsal posterior central head setae (DPoCHS); 25: dorsal principal head setae (DPHS); 26: dorsal accessory head setae (DAcHS); 27: ventral lateral head setae (VLHS); 28: ventral anterior marginal head setae (VAnMHS); 29: ventral posterior marginal head setae (VPoMHS); OA: occipital apophysis.

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.captiosa*, *H.intermedia*, *H.thurmonae* and *H.johnsonae* (Kim, 1966c; Johnson, 1972). In *Proechinophthirus*, 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 setal nomenclature. The chaetotactic nomenclature is based on the topographic position of setae
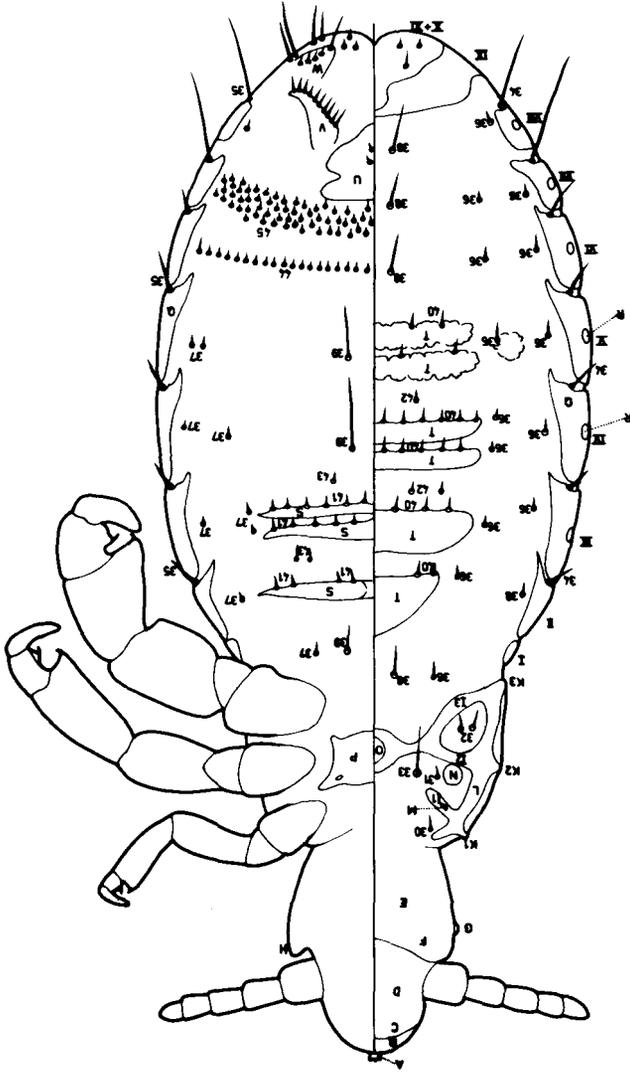
FIG. 3. Anatomy and standardized chaetotaxy of Anoplura ♀ (generalized). Anatomy: A — haustellum; B — labrum; C — clypeus; D — forehead; E — hindhead; F — clypeo-frontal suture; G — eye lens; H — ocular point; I_1 — prothoracic pleural apophysis; I_2 — mesothoracic pleural apophysis; I_3 — meta-thoracic pleural apophysis; K_1 — prothoracic coxal process; K_2 — mesothoracic coxal process; K_3 — metathoracic coxal process; L — longitudinal pleural bar; M — pleural apophysial pit; N — mesothoracic spiracle; O — notal pit; P — thoracic sternal plate with apophysial pit; Q — paratergite; R — spiracles; T — tergites; S — sternite; U — subgenital plate; V — gonopod VIII; W — gonopod IX; Cx 1, 2, 3 = coxae 1, 2, 3; I — X + XI — number of abdominal segments. Chaetotaxy: 30 — dorsal prothoracic setae (DPTS); 31 — dorsal mesothoracic setae (DMsS); 32 — dorsal metathoracic setae (DMtS); 33 — dorsal principal thoracic setae (DPTS); 34 — dorsal marginal abdominal seta (DMAS) = dorsal paratergal setae (DPrS); 35 — ventral marginal abdominal seta (VMAS) = ventral paratergal setae (VPrS); 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 (StAS); 42 — intertergal abdominal setae (InTeAs); 43 — intersternal abdominal setae (InStAS); 44 — transverse setae row; 45 — transverse setal field.

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- = infra-, Im = intermedian, In- = inter-, L = lateral, M = marginal, Md = median, Ms = mesothoracic, Mt = metathoracic, O = outer, Or = oral, P = principal, Pa = preantennal, Po = posterior, Pr = paratergal, Pt = prothoracic, S = seta, Sp- = supra-, St = sternal, Su = sutural, T = thoracic, Te = tergal, V = ventral.

Head (Fig. 2): 1, 2: Dorsal anterior head setae (DAnHS) (= OS of Kim, 1966b; Weisser & Kim, 1972); 3, 4: Apical head setae (ApHS) (= CS of Kim, 1966b; or of Weisser & Kim, 1972); 5, 6: Oral setae (OrS) (*not* 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 (DPaLHS) (= PaMHS and PaLHS of Weisser & Kim, 1962); 11, 12: Ventral preantennal head setae (VPaHS); 13: Dorsal preantennal head setae (DPaHS) (= PAS of Kim, 1966b); 14: Supraantennal head setae (SpAtHS) (= AS of Kim, 1966b; Weisser & Kim, 1972); 15: Supraantennal central head setae (SpAtCHS) (= DCHS of Weisser & Kim, 1972); 16, 17: Sutural head setae (SHS); 18: Ventral principal head seta (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 (DPoCHS) (= 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 Weisser & Kim, 1972); 28: Ventral anterior marginal head setae (VAnMHS); 29: Ventral posterior marginal head setae (VPoMHS).

Thorax (Fig. 3): 30: Dorsal prothoracic setae (DPtS); 31: Dorsal mesothoracic setae (DMsS) (= DMtS of Kim, 1966b); 32: Dorsal mesothoracic setae (DMtS); 33: Dorsal principal thoracic setae (DPTS).

Abdomen (Fig. 3): 34: Dorsal marginal abdominal seta (DMAS) = dorsal paratergal setae (DPrS); 35: Ventral marginal abdominal seta (VMAS) = ventral paratergal setae (VPrS); 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 (StAS); 42: Intertergal abdominal setae (InTeAS); 43: Intersternal 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, forehead 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 *Hybophthirus* (apomorphy) (Fig. 5) and the postantennal angles are generally evident in Enderleinellidae, Hoplopleuridae, Polyplacidae, and somewhat in *Linognathus*. Ocular lenses are found in few taxa (Figs. 4 and 9), namely *Microthoracius, Pecaroecus, Pediculus, Pedicinus* and *Pthirus* (plesiomorphy). The occipital apophysis, a paired internal structure at the posterior end of the head, is only present in *Haematopinus* (Figs. 2 and 5) and *Microthoracius* (plesiomorphy).

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 Hoplopleuridae, 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 *Microphthirus* and *Haematopinus.*

The size of DPHS and DPoCHS varies among different taxa. DPHS is long in *Hoplopleura* and *Polyplax* (apomorphy) but is very small in *Haematopinus* (plesiomorphy). At the same time, most of the dorsal setae on the head are equally short in a taxon like *Haematopinus*, 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 sensoria (Figs. 2 and 13), each on the fourth and the fifth segment (plesiomorphy). The number of the antennal seg-
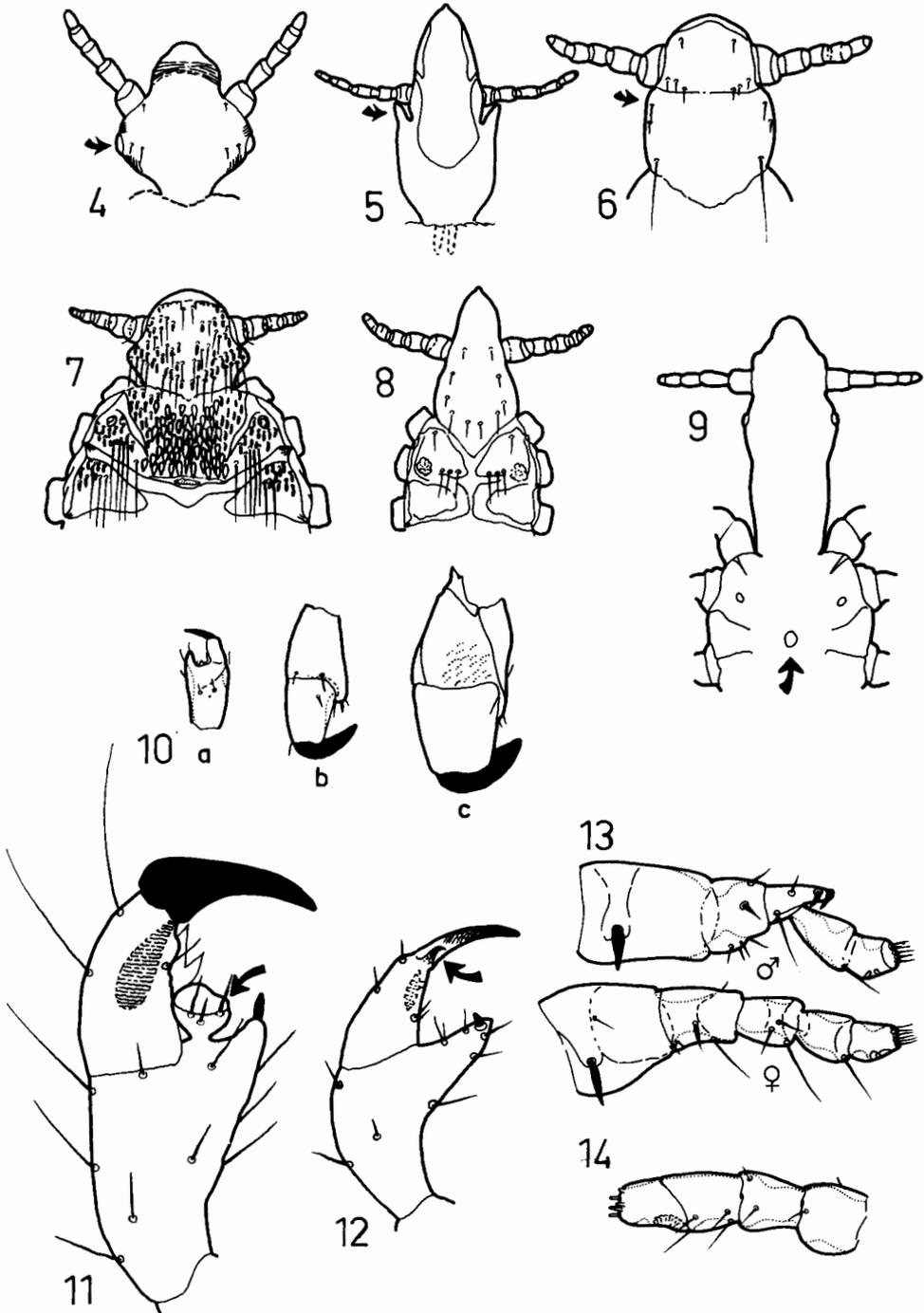
FIGS. 4–14. (4) Generalized head of *Pediculus*; (5) Generalized head of *Haematopinus*; (6) Generalized head of *Hoplopleura*; (7) Head and thorax (generalized) of *Antarctophthirus*; (8) Head and thorax (generalized) of *Linognathus*; (9) Head and thorax of *Pecaroecus*; (10) Legs of *Hoplopleura ancanthopus*: a, foreleg; b, midleg; c, hindleg; (11) Leg of *Haematopinus*; (12) Foreleg of *Hybophthirus notophallus*; (13) Antennae of *Neohaematopinus sciuropteri*, sexual dimorphism; (14) Antenna of *Ancistroplax crocidurae*.
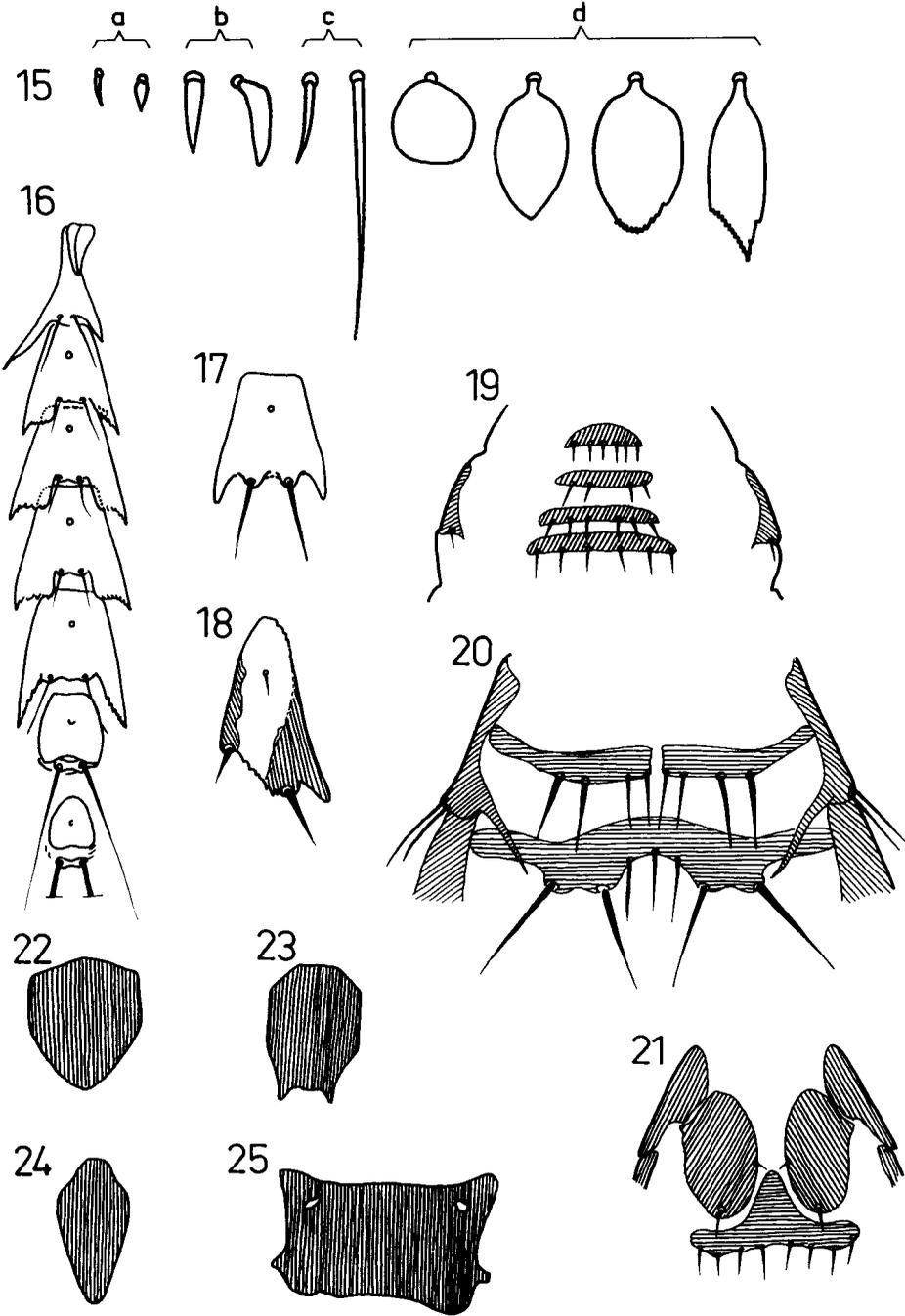
FIGS. 15–25. (15) Various setae of Echinophthiriidae; (16) Paratergites of *Hoplopleura acanthopus*; (17) Paratergite of *Neohaematopinus sciuropteri*; (18) Paratergite of abdominal segment 2, *Polyplax spinulosa*; (19) Venter of abdominal segments 1–3, *Polyplax spinulosa*; (20) Venter of abdominal segments 2–3, *Hoplopleura acanthopus*; (21) Venter of abdominal segments 2–3, *Ancistroplax crocidurae*; (22) Thoracic sternal plate of *Polyplax spinulosa*; (23) Thoracic sternal plate of *Neohaematopinus sciuropteri*; (24) Thoracic sternal plate of *Ancistroplax crocidurae*; (25) Thoracic sternal plate of *Haematopinus suis*.

ments varies within a family-taxon (Fig. 14), and is constant within a genus-taxon. In Echinophthiriidae, the primary number of five antennal segments is found only in *Antarctophthirus*, whose nymphs, however, have four antennal segments. Other genera in this family have four-segmented antennae. *Latagophthirus* even has three segments (apomorphy). The number of the antennal segments and the number and position of sensoria 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 Polyplacidae is often sexually dimorphic (Fig. 13).

5. *Thorax*. The thorax consists largely of pleural and subcoxal structures. The tergum 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, Hoplopleuridae and Polyplacidae (apomorphy), but is quite distinct in Echinophthiriidae, *Microthoracius, Ratemia, Pediculus* and *Haematopinus* (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 *Antarctophthirus* and *Haematopinus* (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, Hoplopleuridae, Polyplacidae and *Solenopotes* at generic and species levels, but is lacking in groups such as Pedicinidae, Pthiridae, *Pecaroecus* and *Hybophthirus*.

The thoracic chaetotaxy is rather constant within a family-taxon. DPtS, DMsS and DPTS are usually singular setae, one on each side (plesiomorphy). DMtS are usually missing in most Anoplura (apomorphy), but number two or more on each side of the thorax in Echinophthiriidae, *Haematopinus*, and *Hamophthirius* (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 Hoplopleuridae and Polyplacidae (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 syntergite as in *Schizophthirus* and *Ctenophthirus* or a synsternite (apomorphy). The genital plates for both male and female are usually synsternites. In *Enderleinellus* 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 level when present (Figs. 16–18 and 26–30). The paratergites in Hoplopleuridae and Polyplacidae are platelike with the distal margin free from the body (apomorphy) (Figs. 16–18, 28 and 29) and in *Haematopinus* and *Pediculus* are caplike without a free distal margin (plesiomorphy) (Fig. 26). They are tuberculiform in *Pecaroecus* (Fig. 27) and *Haemodipsus* (Fig. 30). In *Hoplopleura* the number of the paratergites ranges from six to eight on each side, one on each of the abdominal segments 2–9. The reduction in number is apomorphic. Each paratergite usually has a pair of setae, one on the dorsal side (DMAS = DPrS) and the other on the ventral side (VMAS–VPrS). The size of these setae and the shape of the lateral lobes of the paratergites are specific characters in *Hoplopleura* and *Polyplax* (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 3–8. The number of the abdominal spiracles is generally rather constant within each higher taxon. However,
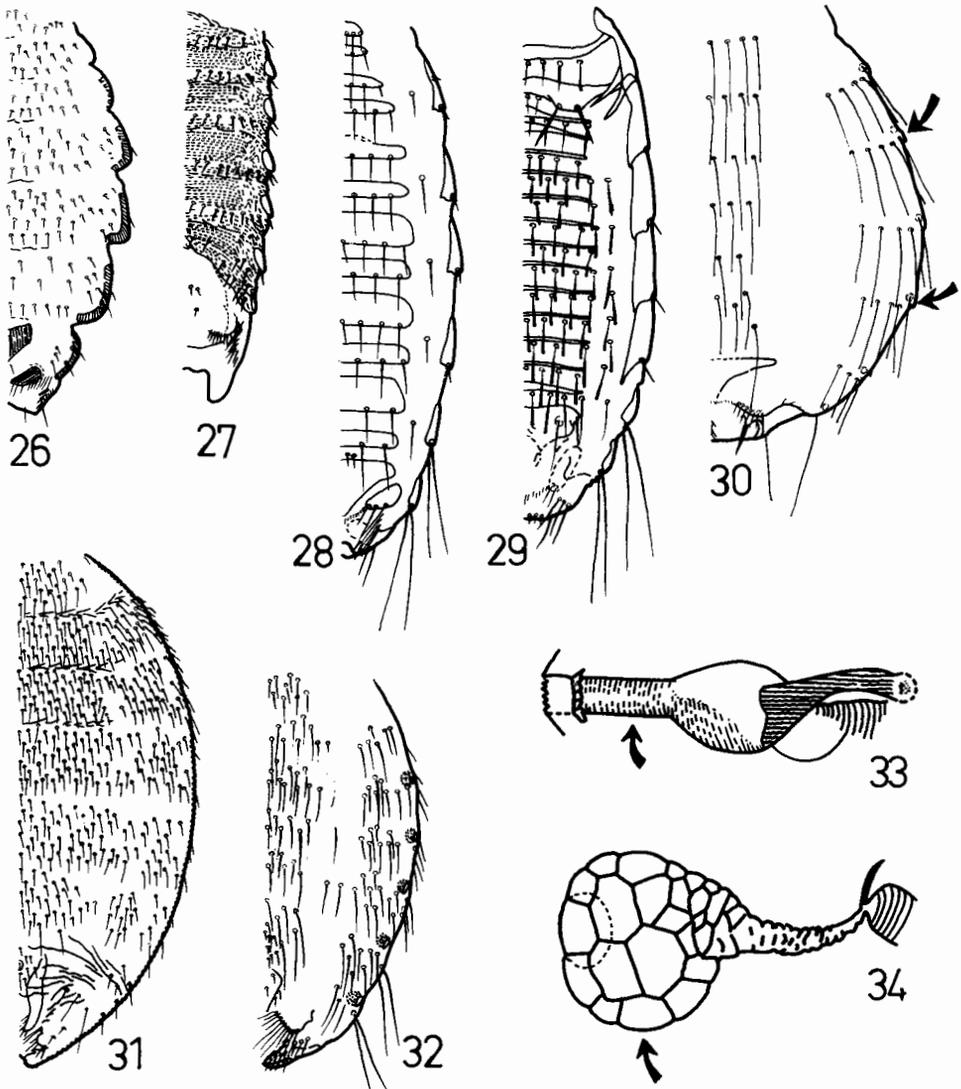
FIGS. 26–34. (26–32) Venter of female abdomen (right side); (26) *Pediculus humanus*; (27) *Pecaroecus javalii*; (28) *Polyplax spinulosa*; (29) *Hoplopleura acanthopus*; (30) *Haemodipsus ventricosus*; (31) *Microthoracius cameli*; (32) *Linognathus setosus*; (33) Abdominal spiracle of *Antarctophthirus callorhini*; (34) Abdominal spiracle of *Linognathus setosus*.

in *Enderleinellus* the majority have six pairs of abdominal spiracles and yet many species have less than five pairs (apomorphy): four pairs in *E.menetensis*, three pairs in *E.nitzschi*, and two pairs in *E.platyspicatus*. *Neolinognathus elephantuli* has only one pair of large spiracles on the eighth abdominal segment. The spiracle generally consists of the subglobular atrium constricted at its inner end and an oval or circular opening at its outer end (Fig. 34).

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

8. *Male genitalia.* The male genitalia consist of four primary parts: basal apodeme, a pair of parameres, aedeagus with gonopore and pseudopenis (Figs. 37–41). In addition there are endomeres in some taxa. The *basal apodeme* (= basal plate or bp of Ferris, 1919; Ewing, 1932) is a long, rodlike sclerite (plesiomorphy). The length and thickness
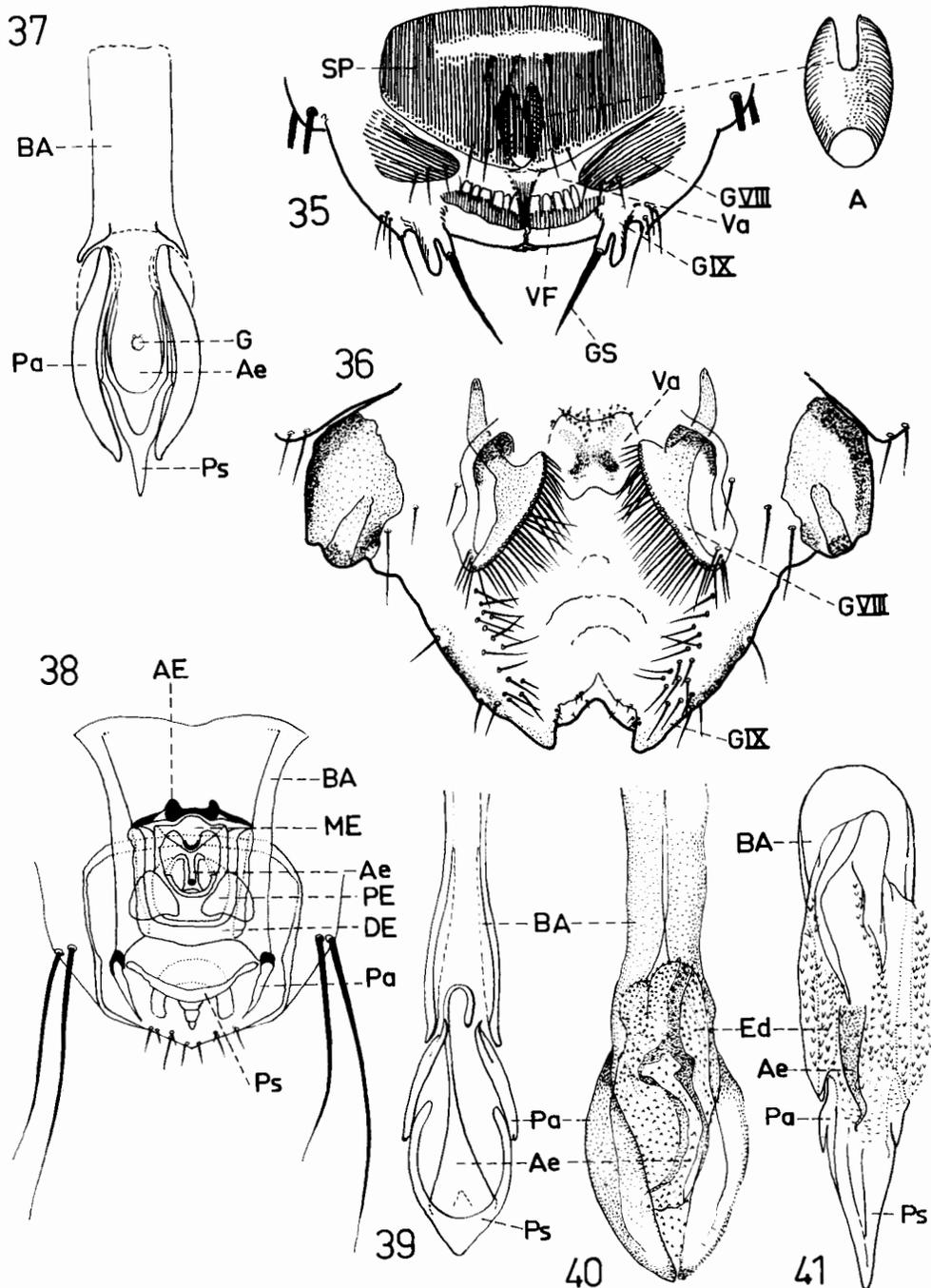
FIGS. 35–41. (35–36) Female genitalia; (35) *Enderleinellus venezuelae*, (A) Spermatheca; (36) *Haematopinus taurotragi*; SP — subgenital plate; Va — valvula; GS — genital seta; GVIII — gonopod VIII; GIX — gonopod IX; VF — valvular fimbriae. (37–41) Male genitalia; (37) *Hoplopleura acanthopus*; (38) *Enderleinellus longiceps*; (39) *Microthoracius cameli*; (40) *Haematopinus apri*; (41) *Pediculus humanus*; BA — basal apodeme; Pa — paramere; G — gonopore; Ps — pseudopenis; Ae — Aedeagus; AE — Anterior endomere; ME — Middle endomere; PE — posterior endomere; DE — dorsal endomere; Ed — endotheca 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 nitzschi* (Kim, 1966b) and *Neolinognathus elephantuli.*

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

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

The *aedeagus* or penis (= penis or p of Ferris, 1919; Ewing, 1932) is usually membranous (apomorphy) or a weakly sclerotized tube located within the genital sac (= 'perputial sack' of Mjöberg, 1910; = mesosome of Cummings, 1916; = vesica penis of Nuttall, 1917; = internal sac of Ewing, 1932, and Kim, 1966b; = vesicula penis of Ferris, 1919; = endotheca of Weisser, 1974) (plesiomorphy) or the frame of the endomere 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 parameres (plesiomorphy). The pseudopenis is sometimes separated at the apex as in *Lepidophthirus* (apomorphy).

The *subgenital plate* is a synsternite of abdominal segments 7, 8 and perhaps 9. The shape of the subgenital plate is an important taxonomic character at species level.

9. *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 venter 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 hesperomydis* 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 *Pediculus* and *Haematopinus*. 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 blunt at the apex. Its posterior border is often serrated, forming the *valvula fimbriae* in Enderleinellidae and Hoplopleuridae. In *Enderleinellus* there is ventrally a short, wide, sclerotized plate referred to as the *intervalvula.* The spermatheca, valvula, intervalvula and valvula fimbriae 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

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

'Ferris' system (1951)	New system (Kim & Ludwig)
Echinophthiriidae	Echinophthiriidae
Linognathidae (*Linognathus, Solenopotes,*	Linognathidae
*Prolinognathus, *Microthoracius*)	Microthoraciidae, n.fam.
Haematopinidae (*Haematopinus, *Pecaroecus*)	Haematopinidae
	Pecaroecidae
Hoplopleuridae	
*Subfam. Enderleinellinae	Enderleinellidae
Subfam. Hoplopleurinae (*Hoplopleura,*	Hoplopleuridae
Pterophthirus, Schizopthirus,	Subfam. Hoplopleurinae
Ancistroplax, Haematopinoides)	Subfam. Haematopinoidinae
	(*Schizophthirus, Ancistroplax,*
	Haematopinoides)
*Subfam. Polyplacinae (*Polyplax* and	Polyplacidae
other genera, *Hamophthirius,*	Hamophthiriidae
Ratemia)	Ratemiidae, n.fam.
*Subfam. Hybophthirinae	Hybophthiridae
*Subfam. Pedicininae	Pedicinidae
Neolinognathidae	Neolinognathidae
Pediculidae (*Pediculus,*	Pediculidae
Pthirus)	Pthiridae

Pedicininae); Haematopinidae (with sub-families Haematopininae, Linognathinae and Euhaematopininae); Echinophthiriidae (with subfamilies Echinophthiriinae and Antarcto-phthirinae), and Haematomyzidae which was transferred from the Anoplura to the Order Mallophaga by Ferris (1951).

In developing the recent classification of the Anoplura, Ferris primarily considered external adult morphology and used information on the host association only to supplement the morphological evidence. The importance of this approach is worth emphasizing, since it is certainly unjustified to rely on host evidence when this disagrees with inferences based on morphological evidence.

Table 1 compares Ferris' classification of Anoplura with that proposed in this paper. Ferris recognized six families, by far the largest being the Hoplopleuridae. *Microthoracius* was placed in Linognathidae, and *Pecaroecus* in Haematopinidae. The family Hoplopleuridae contained five subfamilies (Enderleinellinae, Hoplopleurinae, Poly-placinae, Hybophthirinae and Pedicininae). Many aberrant genera including *Hamophthirius* and *Ratemia*, along with the large genera *Polyplax* and *Neohaematopinus*, were put in the subfamily Polyplacinae. The

Hybophthirinae were removed from Haemato-pinidae and placed in the Hoplopleuridae with two genera *Hybophthirus* and *Scipio*, both possessing a claw-like structure alongside the true claw on the front tarsi. *Pedicinus* was no longer regarded as part of the Pediculidae; instead it was treated as a monobasic sub-family, the Pedicininae.

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 holomor-phic semaphoronts and their environmental relationships. Thus, all biological traits of the taxon 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 merits 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-taxa were assessed 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 microhabitat preferences (Kim, 1972). Host associations and ecological parameters were also 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 sucking lice. The distinctness of a taxon was further considered in the light of the known fossil history of the host-group.

In Paurometabolous 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 a 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 nymphs and markedly distinct 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 quasiphylogenetic 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 only 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 speciated 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, few or none of the evolutionarily 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.

Microthoracius is exclusively parasitic on camels (Camelidae, Artiodactyla) and *Pecaroecus* on peccaries (Tayassuidae, Artiodactyla). Yet *Microthoracius* with four known species and the monotypic *Pecaroecus* 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 *Tayassu* (peccaries) is the sole surviving genus, with two species in the New World (Simpson, 1945; Anderson & Jones, 1967).

Ratemia (2 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 superfamily 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 *Microthoracius* 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. *Microthoracius* retains several plesiomorphic characters such as eyes and notal pit, and yet has many apomorphic characters; for example, lack of paratergites and abdominal tergites, and highly modified genitalia. *Pecaroecus* was placed in Haematopinidae by Ferris (1951); a few characters are similar to *Haematopinus*, but the differences far exceed the similarity among many characters such as the male and female genitalia. *Ratemia* is similar to Linognathidae with some polyplacid characters. Ferris (1951) placed *Ratemia* in the subfamily Polyplacinae on the basis of plate-like paratergites with the apical margin free from the body and the presence of a thoracic sternal plate. However, *Ratemia* has many unique characters, but others 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 *Microthoracius, Pecaroecus* and *Ratemia* are considered the remnants of once much larger taxa, and thus each taxon is treated here as a monotypic family.

Hybophthirus is a very distinctive louse parasitic on the highly specialized aardvark, *Orycteropus afer* (Orycteropodidae, Tubulidentata). Ferris (1951) recognized the subfamily Hybophthirinae with the two included genera, *Hybophthirus* and *Scipio*, characterized by the common presence of a peculiar claw-like structure alongside the true claw. *Hybophthirus* has probably coevolved with its host over a long period of time, and is here assigned to the monotypic family Hybophthiridae. But *Scipio* is undoubtedly a polyplacid louse, considering the form of such characters as its paratergites, genitalia, abdominal sclerites and the type of nymphs; thus *Scipio* is here assigned to the Polyplacidae.

Hamophthirius and *Neolinognathus* are highly specialized taxa, parasitic on colugos (Cynocephalidae, Dermoptera) and elephant shrews (Macroscelidae, Insectivora) respectively. The affinities of both taxa are obscure. *Hamophthirius* retains some primitive characters, such as thoracic apophyses (or phragmata) and notal pit, but generally departs radically from other taxa in major characters, e.g. in the form of the legs, the head, the male genitalia and others (Johnson, 1969). The nymphs seem to be primarily of polyplacid type. *Hamophthirius* must have been separated from the other Anoplura for a very long time; with its distinct morphological characters, coupled with the fact that the association with *Cynocephalus* seems to be primary, it is now placed in the monotypic family Hamophthiriidae as recognized by Johnson (1969). Likewise, the family Neolinognathidae is recognized for *Neolinognathus*.

The family Linognathidae seems to be a rather homogeneous group of Anoplura, closely related to Ratemiidae and perhaps to Hoplopleuridae and Polyplacidae. *Linognathus, Solenopotes* and *Prolinognathus* are assigned to this family. *Linognathus* is primarily parasitic on Bovidae and Giraffidae (Artiodactyla), and has expanded its distribution to Canidae (Carnivora). *Solenopotes* is parasitic upon Bovidae and Cervidae (Artiodactyla), while *Prolinognathus* is found exclusively on Procaviidae (Hyracoidea). After extensive study of Linognathidae, Weisser (1975) concluded that *Prolinognathus* is a close ally of the two other genera, the three genera probably having monophyletic origin despite the remote relationships of their hosts. Weisser (1975) has suggested that protolinognathids might have colonized hyraxes secondarily through physical contact, since Artiodactyla used to be mostly small forms which were likely to have been in frequent close contact with the Procaviidae

during their evolution, although they are at present mostly large animals far removed from the range and habitat of hyraxes.

The Echinophthiriidae are exclusively parasitic on the aquatic carnivores of the Pinnipedia and Mustelidae. These lice are highly specialized and have unique morphological traits not found in other groups of Anoplura. Five genera are recognized: *Proechinophthirus* on the Arctocephalinae, *Echinophthirius* and *Lepidophthirus* on Phocidae, *Antarctophthirus* on a wide range of pinniped hosts, and *Latogophthirus* on the river otter, *Lutra canadensis*. Their highly specialized morphology, host distribution and transmission strongly suggests that the echinophthiriids 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 has rather generalized or primitive character states in paratergites, thoracic apophyses, thoracic sternal plate, notal pit, legs and genitalia, and is widely distributed on the Ungulata, Artiodactyla and Perissodactyla. The present distribution and relatively unspecialized 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 once much larger group. Although Ferris (1951) included two genera, *Haematopinus* and *Pecaroecus* in the family Haematopinidae, we restrict the family to the single genus *Haematopinus*.

Pediculus, Pthirus and *Pedicinus* are found on anthropoid primates. *Pedicinus* is exclusively parasitic on Cercopithecidae or Old World monkeys, *Pediculus* is found on Hominidae, Pongidae and Cebidae, and *Pthirus* on Hominidae and Pongidae. Because of these host relationships, the three taxa had been grouped in the family Pediculidae until Ferris (1951) removed *Pedicinus* from the Pediculidae. *Pedicinus* is morphologically distinct from *Pediculus* and *Pthirus*, but in some respects similar to forms of the Hoplopleuridae. Ferris treated *Pedicinus* as a subfamily of the Hoplopleuridae. Considering all

the morphological characters of adults and nymphs, we have decided to recognize a family for *Pedicinus*. *Pthirus* is peculiar and has been recognized to constitute either a subfamily (Ferris, 1951) or a family (Ewing, 1929). *Pediculus* and *Pthirus* are basically very different taxa, apart from a few plesiomorphic characters such as a pair of distinctive lens and five-segmented antennae. Morphological details distinguishing these two taxa include the structure of the head, thorax, legs, paratergites and genitalia. On the basis of this morphological evidence, *Pediculus* and *Pthirus* are considered to represent two well-separated lineages and thus are treated here as constituting two families, Pediculidae and Pthiridae.

Ferris (1951) recognized the largest family Hoplopleuridae to include the majority of Anoplura subdivided into five subfamilies: Enderleinellinae, Hoplopleurinae, Polyplacinae, Hybophthirinae and Pedicininae. This family is a 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 paratergites. Consistent morphological patterns are usually found within each subfamily, but practically no morphological character is consistent throughout the family. For example, the paratergal plates of the abdomen are usually highly developed with the apical point free from the body, but these are completely lacking in *Phthirunculus* (Enderleinellinae) and some *Haemodipsus* (Polyplacinae) or much reduced in *Lemurphthirus* (Polyplacinae). 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 Hoplopleuridae are primarily found on Rodentia but they are also found on Lagomorpha, Insectivora and even Prosimian Primates. This family, as interpreted by Ferris, included more than 70% of the known species of Anoplura. Sucking lice assigned to the Hoplopleuridae are generally highly specialized, particularly in the head, the thoracic apophyses, tibio-tarsus complex of the hindlegs, paratergites, sternite of abdominal segment 2, and genitalic armatures. The known distribution of the Hoplopleuridae suggests that the evolution of these sucking

lice must have centred in Rodentia, and that the invasion of other host groups, such as Insectivores, Lagomorpha and Prosimian Primates, is secondary. The establishment of *Sathrax* and *Docophthirus* on Tupaiidae and *Lemurphthirus, Lemurpediculus* and *Phthirpediculus* on Prosimian Primates must have occurred in more recent evolutionary times. After considering the differential characters for each subfamily of the Hoplopleuridae 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 Enderleinellidae are a homogeneous group exclusively parasitic on Sciuridae (Rodentia). Five genera and forty-nine species are currently recognized. *Enderleinellus* is widely distributed throughout the Sciuridae, and *Werneckia* is found on African squirrels. The remaining three genera, *Microphthirus, Phthirunculus* and *Atopophthirus*, are highly specialized lice parasitic on flying squirrels; *Microphthirus* on the North American flying squirrel (*Glaucomys*), the others on the giant flying squirrels (*Petaurista*) of South-east Asia.

The Hoplopleuridae is the second largest family of Anoplura, having five genera and 132 species parasitic upon rodents, pikas (Ochotonidae, Lagomorpha), moles (Talpidae, Insectivora) and shrews (Soricidae, Insectivores). *Hoplopleura* and *Pterophthirus* are linked by having the sternal plate of abdominal segment 2 prolonged laterally on each side to articulate with the corresponding paratergites, and by the similar ventral tubercles on the head and antennae of the nymphs. Thus, they are here recognized as a monophyletic taxon, the subfamily Hoplopleurinae. The remaining three aberrant taxa, *Haematopinoides, Schizophthirus* and *Ancistroplax*, constitute a rather homogeneous group, recognizable by the presence of the distinctly divided sternal plates of the abdominal segment 2, each side of which is prolonged laterally to articulate with the corresponding paratergite, and also by the paratergites and the aberrant nymphs. For this group, the

subfamily Haematopinoidinae is recognized here.

The taxonomic status of the Polyplacidae, the largest family, having fourteen genera and 175 species, is still confusing, and phylogenetic relationships of the included genera are extremely difficult to assess. Apparently, several taxa such as *Sathrax* and *Docophthirus*, successfully established on the tree shrews, are neotonously 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 neotonous evolution. This resulted in extreme specialization of the numerous form—function complexes. Several aberrant taxa such as *Hamophthirius* and *Ratemia* are here removed from the family as previously discussed. And yet taxonomic relationships of *Ctenophthirus, Eulinognathus, Scipio* and *Haemodipsus*, along with three genera parasitic on Prosimian Primates, *Lemurphthirus, Lemurpediculus* and *Phthirpediculus*, are tenuous and require further study. The summary of the system of the Anoplura classification adopted here is presented in Table 1.

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 fibrillar layer of connective tissue and an outer layer of modified epidermal cells (Pipa & Cook, 1958); tentorium absent; mouthparts highly modified for piercing and sucking blood; proboscis small, snout-like, armed with small denticles and two stylets of hypopharyngeal and labial origin retracted within the trophic pouch (Ramcke, 1965); mouth usually prognathous but sometimes shifted slightly ventrad; 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 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 fused, 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 largely of 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 unisegmented, 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 (gonapophyses) 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 parameres, aedeagus with dorsal gonopore, and a pseudopenis (Figs. 37–41).

Internal anatomy poorly known (the following description is based on *Pediculus* and *Haematopinus*): *alimentary canal* with modified cibarium and pharynx forming a powerful sucking pump armed with dilator muscles; large stomach with caeca at its anterior end; hindgut with moderate convolution receiving four Malpighian tubules; rectum swollen anteriorly and with a whorl of six sclerotized papillae; *dorsal vessel* long, slender aorta with a bulbous heart located in abdominal segments 7 and 8; *nervous sytem* highly concentrated, ganglia congregated into closely associated masses covered with connective tissues, one in thorax and another containing metathoracic and abdominal ganglia (Haefner, 1971).

Female reproductive organs with five polytrophic ovarioles per ovary and a pair of accessory glands; spermatheca not always present or distinct. *Male reproductive system* with a pair of compact bilobed testes and vasa deferentia issuing from the constricted portion of each testis. Mycetome variable, on or in the midgut. Eggs narrowly oval with operculum and micropyles; attached to host

hair with cement (an exception is *Pediculus humanus humanus* which attaches its eggs to projecting fibres of clothing).

After hatching from the egg, the louse passes through a simple metamorphosis with three nymphal instars. Under normal conditions the nymphal development takes 2–3 weeks. The instars differ in size or proportion of parts, in the degree of sclerotization and in the development of the reproductive apparatus. Each instar usually has a distinct chaetotaxy and setal density.

Key to families

1 Head with distinct eyes (Fig. 4) or subacute ocular points (Fig. 5) on lateral margins posterior to antennae 2
– Head without external evidence of eyes or prominent ocular points (Fig. 6). 8
2 Head with prominent ocular points but without eyes (Fig. 5) 3
– Head with eyes having distinct lens but without ocular points (Fig. 4). 4
3 Thoracic sternal plate well developed (Fig. 25); abdomen with paratergites on segments 2–8 or 3–8 as sclerotized caps over apex of each lateral lobe, not at all free from body; all legs subequal in size and shape, each with distotibial process (Fig. 11); on even-toed ungulates (Bovidae, Cervidae and Suidae; Artiodactyla) and horses and zebras (Equidae; Perissodactyla)
HAEMATOPINIDAE
– 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 acuminate true claw (Fig. 12); forelegs much smaller than mid- and hindlegs; on aardvarks (Orycteropodidae; Tubulidentata) . . . . HYBOPHTHIRIDAE
4 Abdomen without paratergites and dorsoventrally densely covered with fine setae (Fig. 31); head attached to thorax dorsally; on camels and llamas (Camelidae, Artiodactyla)
MICROTHORACIIDAE
– Abdomen with paratergites as tubercles, caps or lobes and sparsely covered with setae (Figs. 26 and 27); head attached to thorax in the same plane 5
5 Head long and slender, much longer than thorax (Fig. 9); abdomen narrowly elliptic, with small tuberculiform paratergites on segments 3–8 (Fig. 27); on peccaries (Tayassuidae; Artiodactyla) . . . . PECAROECIDAE
– Head about as long as thorax (Fig. 3); abdomen oval or elliptic, with paratergites as sclerotized caps or lobes (Fig. 26); on anthropoid Primates. . 6

6 Compact Anoplura 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 hindlegs very stout, each with a stout claw; on man (Hominidae) and gorilla (Pongidae) . . . . PTHIRIDAE

– Slender Anoplura with body more than twice as long as wide; abdomen long, wider than thorax with paratergites as sclerotized caps or lobes 7

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) PEDICULIDAE

– Paratergites present on abdominal segments 4—6 or 5—6 each with apical angles free from body; abdomen with a single row of setae on each segment; on Old World monkeys (Cercopithecidae). . . . . .PEDICINIDAE

8 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. 33); on seals, sea-lions and walrus (Pinnipedia), and river otter (Mustelidae; Carnivora) ECHINOPHTHIRIIDAE

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

9 Abdomen almost devoid of distinct setae except for two at each lateral lobe of segment 8 and few setae on genital area, with spiracles present only on segment 8; abdominal cuticle scaly, with numerous minute sclerotized points arranged in transverse rows; on elephant shrews (Macroscelididae; Insectivora) . NEOLINOGNATHIDAE

– Abdomen with numerous distinct setae and with spiracles present on more than one segment, usually on segments 3—7 or 3—8 (Figs. 3, 16 and 32); abdominal cuticle without minute sclerotized points 10

10 Antennae distinctly three-segmented, with basal segment unusually enlarged as long as the last two segments combined; forehead and basal antennal segment, each ventrally with a posteriorly-directed stout hook on each side; head and thorax heavily sclerotized; on 'flying' lemurs (colugos) (Cynocephalidae; Dermoptera) HAMOPHTHIRIIDAE

– Antennae four- or five-segmented, with basal segment not unusually enlarged, less than one-half as long as the remaining apical segments combined (Figs. 13 and 14); head and basal antennal segment without such stout hook . . 11

11 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 larger and stouter claw; second ab-

dominal 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 tergal and sternal plate or basal segment of antennae ventrally with a heavily sclerotized plate bearing three to five large thorn-like structures; on squirrels (Sciuridae; Rodentia) ENDERLEINELLIDAE

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

– Abdomen without distinct paratergites (Fig. 32) or at most with small tubercles posterior to each spiracle (Fig. 30); forecoxae widely separated from each other; on even-toed ungulates (Bovidae, Cervidae and Giraffidae; Artiodactyla), canids (Canidae; Carnivora), and hyraxes (Procaviidae; Hyracoidea) . . . . LINOGNATHIDAE

13 Thorax with distinct notal pit (Fig. 9); mesothoracic pleural apophyses highly developed and fused medially (Fig. 3); abdomen membranous, with paratergites on segments 4—6; on donkeys and zebras (Equidae; Perissodactyla) RATEMIIDAE

– Thorax without distinct notal pit (Fig. 8); mesothoracic pleural apophyses poorly developed and usually separated medially; abdomen usually with highly developed tergal and/or sternal plates, paratergites present in any arrangement other than segments 4—6 14

14 Sternite of abdominal segment 2 extended laterally on each side to articulate with the corresponding paratergal plates (Figs. 20 and 21); hindlegs largest of the three pairs, stout, each with a stout and blunt claw (Fig. 10c); on rodents (Rodentia), pikas (Ochotonidae; Lagomorpha), and moles and shrews (Talpidae and Soricidae; Insectivora) . . . HOPLOPLEURIDAE

– Sternites of abdominal segment 2 narrow, not 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

ECHINOPHTHIRIIDAE Enderlein

Echinophthiriidae Enderlein, 1904: 136. Type-genus *Echinophthirius* Giebel, by original designation; Enderlein, 1906: 601; Dalla Torre 1908: 7, 17; Enderlein, 1909a: 505—507; Ferris, 1916: 133, 180; Freund, 1928: 2, 5; Ass, 1934: 89, 92; Séguy, 1944: 452; Ferris, 1951: 71, 72; Blagov-

eshtchensky, 1964: 326 (1967 in English: 406–407).

Lepidophthiriidae Mjöberg, 1910: 177. Type-genus *Lepidophthirus* Enderlein 1904, by tautonomy; Ferris, 1916: 180 rejected Lepidophthiriidae as a synonym.

Phocaphthiriidae Ass, 1962: 55. Type-genus *Echinophthirius* Giebel, by original designation. Syn.n.

Description. Medium-sized 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; mesothorathic phragmata connected across the dorsum, usually enclosing notal pit; no sternal plate present; sternal apophyses and apophyseal pit indistinct. *Legs:* Mid- and hindlegs large and similar in size and shape, with blunt claw; tibial thumb elaborate, with several short, blade- or peg-like apical setae; forelegs small and slender, with acuminate claw except in *Echinophthirius* which has large forelegs similar to midlegs. *Abdomen* completely membranous or leathery, with no sclerotized plates and usually with various types of setae including pegs and scales (Fig. 15); six spiracles small and of distinctive type, each with a long, slender atrial chamber and a long chitinous rod (Fig. 33). *Genitalia:* Male with large basal apodeme and well-developed parameres; pseudopenis U- or V-shaped or apically open; subgenital plate weakly developed. Female without gonopods and genital lobe; subgenital plate poorly developed; spermatheca absent; vagina surrounded by thick patches of long setae.

Host: Aquatic carnivores (Pinnipedia and Mustelidae).

Antarctophthirus Enderlein, 1906 (6 spp.). Type-species: *Antarctophthirus ogmorhini* Enderlein, by original designation. Host: Various groups of Pinnipedia.

Echinophthirius Giebel, 1871 (1 sp.). Type-species: *Pediculus phocae* Lucas = *Pediculus horridus* von Olfers, by monotypy. Host: Phocidae.

Lepidophthirus Enderlein, 1904 (2 spp.). Type-species: *Lepidophthirus macrorhini*

Enderlein, by original designation. Host: Phocidae.

Proechinophthirus **Ewing**, 1923 (2 spp.). Type-species: *Echinophthirius fluctus* Ferris, by original designation. Host: Otariidae.

Latagophthirus **Kim & Emerson**, 1974 (1 sp.). Type-species: *Latagophthirus rauschi* Kim & Emerson, by monotypy. Host: Mustelidae (*Lutra canadensis*).

ENDERLEINELLIDAE Ewing

Enderleinellinae Ewing, 1929: 132. Type-genus *Enderleinellus* Fahrenholz, by original designation; Ferris, 1951: 101–118.

Enderleinellidae Kéler, 1963: 6.

Description. Small lice. *Head* with postantennal angle not developed; antennae usually five-segmented or if four-segmented, the terminal segment with two sensoria. *Thorax* with phragmata poorly developed; sternal plate usually well developed but if weakly developed or not present, coxae of each pair widely separated from each other. *Legs:* Forelegs subequal to midlegs in size and shape, both small and slender; each with a slender claw; hindlegs stout, with tibia–tarsus complex highly developed and large stout claw. *Abdomen:* Paratergites present on segments 2–4, 2–5, or 2–6, or if absent, the entire abdomen membranous; sternal and tergal plates usually poorly developed or completely lacking; functional spiracles variable in number, on segments 3–4, 3–5, 3–6 or at times 3–8. *Genitalia:* Male as in Fig. 38, female as in Fig. 35. Nymphs without ventral tubercles on the head.

Host and distribution: Sciuridae, world-wide except for Australian region, Madagascar, Southern South America, polar regions, and certain desert regions.

Enderleinellus Fahrenholz, 1912 (43 spp.). Type-species: *Pediculus sphaerocephalus* Nitzsch (preoccup.) = *E.nitzschi* Fahrenholz, by monotypy. Host: Sciuridae.

Werneckia Ferris, 1951 (3 spp.). Type-species: *Enderleinellus minutus* Werneck, by original designation. Host: Sciurinae (Funambulini).

Microphthirus Ferris, 1919 (1 sp.). Type-

species: *Enderleinellus uncinatus* Ferris, by monotypy. Host: Petauristinae (*Glaucomys*).

Phthirunculus Kuhn & Ludwig, 1965 (1 sp.). Type-species: *P.sumatranus* Kuhn & Ludwig, by monotypy. Host: Petauristinae (*Petaurista*).

Atopophthirus Kim, 1977 (1 sp.). Type-species: *A.emersoni* Kim, by monotypy. Host: Petauristinae (*Petaurista*).

HAEMATOPINIDAE Enderlein

Haematopinidae Enderlein, 1904: 136. Type-genus *Haematopinus* Leach, by original designation (restricted to *Haematopinus*); Dalla Torre, 1908: 5; Mjöberg, 1910: 156; Ferris, 1916: 133, 142; Séguy, 1944: 424; Ferris, 1951: 68.

Haematopina Murray (*partim*), 1877: 384 (restricted to *Haematopinus*).

Description. Intermediate to large Anoplura. *Head* without external evidence of eyes, but with prominent ocular lobes posterior to the antennae; antennae five-segmented; a pair of occipital apophyses elongated. *Thorax* with distinct notal pit, a pair of small sternal apophyseal pits, and strongly sclerotized sternal plate (Fig. 25); mesothoracic phragmata continuous across the entire thoracic dorsum enclosing notal pit; dorsum with a posterior lobe at each posterolateral angle. All *legs* subequal in size and shape; each tibia with a flap-like tibial lobe bearing few spiniform setae; tibial thumbs well developed, each with an apical spiniform seta. *Abdomen* with strongly sclerotized cap-like paratergites on prominent lateral lobes on segment 2 or 3–8; paratergites not free from the body wall; abdominal cuticula leathery, minutely wrinkled, dorsally with weakly sclerotized areas; segmental setae short, arranged in simple transverse rows; segments 3–8 each with a spiracle on each side. *Genitalia:* Male with parameres reduced and pseudopenis apparently fused to form a large V-shaped structure or separated at apex; subgenital plate strongly sclerotized; aedeagus asymmetrical; basal apodeme thick and about as long as pseudopenis (Fig. 40). Female with gonopods of segments 8 and 9 well developed; gonopods each with an inner marginal

row of long and strong setae; valvula lightly sclerotized with a cluster of small setae; gonopod IX developed (Fig. 36).

Host: Artiodactyla (Suidae, Bovidae and Cervidae), and Perissodactyla (Equidae). Recorded in two cases from Camelidae (Artiodactyla) which are obviously contamination.

Haematopinus Leach, 1815 (22 spp.). Type-species: *Pediculus suis* Linnaeus, by original designation. Host: Suidae, some Bovidae, Cervidae (Artiodactyla) and Equidae (Perissodactyla).

HAMOPHTHIRIIDAE Ewing

Hamophthiriinae Ewing, 1929: 140. Type-genus *Hamophthirius* Mjöberg, by original designation.

Hamophthiriidae Johnson, 1969: 420.

Description. Medium to intermediate Anoplura with head and thorax heavily sclerotized. *Head* without external evidence of eyes but ventrally with strong lateral hook at antero-distal angle; dorsally antennal-ocular segment strongly broadened, with a postero-lateral lobe on each side; clypeus short and truncate anteriorly; antennae three-segmented, with basal segment strongly enlarged and bearing stout, posteriorly directed hook at antero-distal angle, and terminal segment bearing two sensoria; apophyses strongly developed, undivided at occipital end. *Thorax* with a large syntergite and well-defined notal pit; phragmata developed; prothoracic tergal and sternal apophyses and indication of pit also present; sternal plate enlarged, posterioapically free from body wall. All *legs* subequal in size; tibiotarsal separation evident; tarsal claw with rounded protuberance basally to the side of the true claw; tibial thumb with several short, blunt, blade-like apical setae. *Abdomen* without tergal and sternal plates except for segment 2 and genitalic segments; segment 2 with one large sternal plate; cuticula scalloped or reticulate; segments 2–8 each with a pair of paratergites; segments 3–8 each with a pair of spiracles. *Genitalia:* Male with basal apodeme large; subgenital plate entire; parameres long, separated; pseudopenis long, narrow V-shaped. Female with definite

gonopods VIII and IX; subgenital plate and spermatheca not evidently developed.

Host: Dermoptera (Cynocephalidae).

Hamophthirius Mjöberg, 1925 (1 sp.). Type-species: *Hamophthirius galeopitheci* Mjöberg, by monotypy. Host: *Cynocephalus* (Cynocephalidae).

HOPLOPLEURIDAE Ewing

Hoplopleurinae Ewing, 1929: 133. Type-genus *Hoplopleura* Enderlein, by original designation.

Hoplopleuridae Ferris, 1951: 98. Blagoveshtchensky, 1964: 329.

Euhaematopininae Enderlein, 1904: 138. Type-genus *Euhaematopinus.*

Haematopinoididae Ewing, 1929: 131, 140. Type-genus *Haematopinoides* Osborn.

Docophthiridae Webb, 1946: 107. Type-genus *Docophthirus* Webb.

Eulinognathidae Webb, 1946: 107. Type-genus *Eulinognathus* Webb.

Description. Small to medium Anoplura. *Head* without external indication of eyes; postantennal angles variably developed, but no prominent ocular lobes present; antennae usually five-segmented; no occipital apophysis present. *Thorax* without notal pit and sternal apophyseal pit; phragmata weakly developed; mesothoracic phragmata variable; sternal plate usually developed, with its posterior apex free (Fig. 24). *Legs:* forelegs always small, each with an acuminate claw; midlegs usually larger than forelegs, although similar in shape; hindlegs usually largest, each with a stout claw; tibial thumbs highly developed on hindlegs. *Abdomen* usually with tergal, sternal and paratergal plates highly developed; paratergites each with its apex free from the body wall and overlapping that of the succeeding segment; segments 3–8 each with a pair of spiracles; sternal plates of segment 2 prolonged laterally on each side to articulate with the corresponding paratergites; each segment usually with one (or rarely two) transversal row of setae. *Genitalia:* Male with large basal apodeme; parameres well developed; pseudopenis usually well developed (Fig. 37). Female with large subgenital plate; gonopods VIII

usually developed; gonopods IX usually short; spermatheca usually absent.

Host: Rodentia, Insectivora, Lagomorpha and Prosimian Primates.

Key to subfamilies of Hoplopleuridae

1   Sternite of abdominal segment 2 entire or if divided, two plates separated by a membranous area and not expanded into definite plates (Fig. 20); nymphs with ventral tubercles on head and antennae; on rodents (Rodentia) and pikas (Ochotonidae, Lagomorpha)
                              Hoplopleurinae Ewing
–   Sternite of abdominal segment 2 completely divided longitudinally into two separate, expanded plates (Fig. 21); nymphs without ventral tubercles on head and antennae; on moles and shrews (Talpidae and Soricidae; Insectivora) and myomorph rodents (Gliridae and Zapodidae; Rodentia) . . . . Haematopinoidinae Ewing

Subfamily Hoplopleurinae Ewing

Hoplopleurinae Ewing, 1929: 133. Type-genus *Hoplopleura* Enderlein; Ferris, 1951: 119 (not *Ancistroplax, Schizophthirus,* and *Haematopinoides*).

Description. Head with postantennal angles developed; antennae five-segmented. *Thorax:* Phragmata weakly developed; sternal plate highly developed, with its apex free from the body wall. *Legs:* Forelegs always small, with acuminate claw; midlegs similar to forelegs but larger; hindlegs much larger, generally flattened, each with very 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. 20). Nymphs with ventral tubercles on head and antennae.

Host: Rodentia and Lagomorpha.

Hoplopleura Enderlein, 1904 (117 spp.). Type-species: *Pediculus acanthopus* Burmeister, by original designation. Host: Rodentia and Lagomorpha.

Pterophthirus Ewing, 1923 (5 spp.). Type-species: *Hoplopleura alata* Ferris, by original designation. Host: Hystricomorpha–Rodentia.

Subfamily Haematopinoidinae Ewing

Haematopinoidinae Ewing, 1929: 140. Type-genus *Haematopinoides* Osborn.
Euhaematopininae Enderlein, 1904: 136; Dalla Torre, 1908: 15.

Description. Small Hoplopleuridae. *Head* with antennae four- or five-segmented; postantennal angle moderately developed. *Thorax* with mesothoracic phragmata distinct; sternal plate well developed, with its apex free from body wall. *Legs* with forelegs always small and slender, each with acuminate claw; midlegs larger than forelegs, each with stouter claws; hindlegs still larger, generally flattened, each with very broad claw. *Abdomen* with seven or eight highly developed paratergites on segments 2–9 on each side, each with a pair of distinct posterior setae; each spiracle with short atrium and no sclerotized rod; tergal and sternal plates variously developed; segment 2 with a pair of sternal plates which are completely divided and laterally extended to articulate with corresponding paratergite (Fig. 21).

Host: Insectivora (Talpidae and Soricidae) and Myomorpha–Rodentia.
   Haematopinoides Osborn, 1891 (1 sp.). Type-species: *Haematopinoides squamosus* Osborn, by monotypy. Host: Talpidae (Insectivora).
   Ancistroplax Waterston, 1929 (2 spp.). Type-species: *Ancistroplax crocidurae* Waterston, by original designation. Host: Soricidae (Insectivora).
   Schizophthirus Ferris, 1922 (7 spp.). Type-species: *Pediculus pleurophaeus* Burmeister, by original designation. Host: Myomorpha–Rodentia.

an appearance of triangular head; clypeus short; postantennal angle strongly prolonged, forming definite ocular points; antennae five-segmented; no external evidence of eyes present; apophyses at occipital end pointed. *Thorax* with meso- and metathoracic phragmata well developed; mesothoracic phragmata connected across the dorsum; metanotum with a distinct lateral lobe at posterolateral angle; notal pit distinct; no sternal plate present; sternal apophysis and apophyseal pit indistinct. *Legs:* Forelegs slender and small, with acuminate claw and a short claw-like structure at the base of true claw (Fig. 12); mid- and hindlegs large, stout and subequal in size and shape, with stout claw; tibial thumbs strongly developed, each with a single apical seta. *Abdomen* almost circular or broadly elliptical and without tergal and sternal plates except for genital and terminal segments; segments 2–8 each with a pair of paratergites with dorsal lobe prolonged and rounded; segmental setae arranged in transverse rows; segments 3–8 each with a pair of small spiracles. *Genitalia:* Male with large basal apodeme; parameres elongate, with terminal hook; endomere sclerotized and prolonged; pseudopenis small and sclerotized; subgenital plate not sclerotized. Female with large subgenital plate; gonopods VIII rounded; gonopods IX prolonged, without distinct setae; spermatheca indistinct.

Host: Tubulidentata (Orycteropodidae).
   Hybophthirus Enderlein, 1909 (1 sp.). Type-species: *Hybophthirus orycteropodis* Enderlein, 1909b (= *Haematopinus notophallus* Neumann, 1909), by monotypy. Host: Aardvark, *Orycteropus* (Orycteropodidae, Tubulidentata).

HYBOPHTHIRIDAE Ewing

Hybophthirinae Ewing, 1929: 133. Type-genus *Hybophthirus* Enderlein, by monotypy; Ferris, 1951: 148.
Hybophthiridae Kéler, 1963: 5.

Description. Large Anoplura with short and compact body. *Head* short and broad, with antennal-ocular segment strongly broadened and then constricted sharply at apex, giving

LINOGNATHIDAE Enderlein

Trichaulinae Enderlein, 1904: 138. Type-genus *Trichaulus* Enderlein, by original designation, pre-occupied by *Trichaulus* Mayr, 1885 (Chalcidoidea: Hymenoptera).
Linognathinae Enderlein, 1906: 194. Type-genus *Linognathus* Enderlein, replacement name; Dalla Torre, 1908: 5; Ferris, 1916: 47; Séguy, 1944: 425.

Linognathidae Webb, 1946: 107; Blagovesh-
tchensky, 1964: 322 (1967 in English:
415); Ferris, 1951: 220; Blagoveshtchensky,
1960: 64.

Description. Medium to intermediate Ano-
plura. *Head* without external evidence of eyes;
postantennal angles variously developed;
occipital apophyses not developed; antennae
five-segmented or if four-segmented the ter-
minal segment compound. *Thorax* with meso-
and metathoracic phragmata well developed
and notal pit distinct or occasionally obscure;
sternal plate absent, at most narrow, pig-
mented longitudinal band, or if present, its
apex not free from the body. *Legs:* Forelegs
small and slender, with acuminate claw; mid-
legs and hindlegs subequal, and larger than
forelegs, each with stout claw, and tibial
thumbs developed, each with a single spini-
form seta. *Abdomen* membranous, with no
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 of each on
segments 3–8; spiracles with distinct internal
ledges (Fig. 34). *Genitalia:* Male with basal
apodeme slender and pseudopenis elongate or
poorly sclerotized; parameres well developed,
free at apex; subgenital plate strongly devel-
oped; endomere sclerotized, with distinct
aedeagus. Female with subgenital plate
variously shaped, sometimes lacking; gono-
pods VIII well developed; gonopod IX well
developed and prolonged posteriorly, with
either a spiniform genital seta or pointed
apical process; spermatheca not strongly
sclerotized.

Host: Artiodactyla (Bovidae, Cervidae, and
Giraffidae), Perissodactyla (Equiidae), Car-
nivora (Canidae), and Hyracoidea (Pro-
caviidae).
   Linognathus Enderlein, 1904 (51 spp.).
Type-species: *Pediculus setosus* von Olfers
(= *Pediculus piliferus* Burmeister), by origi-
nal designation. Host: Bovidae, Giraffidae
(Artiodactyla) and Canidae (Carnivora).
   Solenopotes Enderlein, 1904 (10 spp.).
Type-species: *Solenopotes capillatus* Ender-

lein, by original designation. Host: Cervidae
and Bovidae (Artiodactyla).
   Prolinognathus Ewing, 1929 (8 spp.).
Type-species: *Pediculus caviaecapensis* Pallas,
by original designation. Host: Procaviidae
(Hyracoidea).

MICROTHORACIIDAE Kim & Ludwig, new family

Type-genus – *Microthoracius* Fahrenholz, by
   monotypy.

Description. Medium to large Anoplura 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 sensoria; head setae crowded on the
lateral side; occipital apophyses present; head
attached to thorax dorsally. *Thorax* small and
short, with distinct notal 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); cuticula
minutely wrinkled; no sclerotized tergal,
sternal and paratergal plates developed; seg-
ments 3–8 each with a pair of spiracles.
Genitalia: Male with moderately developed
basal apodeme; parameres thin and short;
pseudopenis well developed, either U- or
V-shaped; subgenital plate very weakly devel-
oped (Fig. 39). Female with subgenital plate
weakly developed; gonopods VIII rounded;
gonopods IX usually prolonged.

Host: Artiodactyla (Camelidae).
   Microthoracius Fahrenholz, 1916 (4 spp.).
Type-species: *Haematopinus (Linognathus)
praelongiceps* Neumann, by original desig-
nation. Host: Camelidae.

NEOLINOGNATHIDAE Ewing

Neolinognathinae Ewing, 1929: 133. Type-
   genus *Neolinognathus* Bedford, by mono-
   typy.

Neolinognathidae Fahrenholz, 1936: 56; Ferris, 1951: 257.

Description. Small to medium Anoplura. *Head* elongated, without external evidence of eyes; postantennal angle not developed; antennae five-segmented; no occipital apophyses present. *Thorax* with phragmata poorly developed; sternal plate divided into two longitudinal plates; distinct notal pit, sternal apophysis and apophyseal pit absent. *Legs:* Forelegs small, slender, with acuminate claw; mid- and hindlegs subequal in size and shape, each with a stout claw, and much longer than forelegs; tibial thumbs highly developed, with a single apical spiniform seta. *Abdomen* membranous, except for genital and terminal segments, with at times minute sclerotized points; no sternal, tergal and paratergal plates present; setae minute, except for a pair at each lateral angle of segment 8 and in the genital area; only a single pair of spiracles present on segment 8. *Genitalia:* Male with genital apodeme small and inverted Y-shaped; parameres completely fused at apex; pseudopenis poorly sclerotized and obtriangular; subgenital plate well developed. Female with gonopods VIII short and gonopods IX not prolonged; genital plate obovate tapering and pointed at apex.

Host: Insectivora (Macroscelididae).

Neolinognathus Bedford, 1920 (2 spp.). Type-species: *Neolinognathus elephantulis* Bedford, by original designation. Host: Elephant shrews, Macroscelididae (Insectivora).

PECAROECIDAE Kéler

Pecaroecidae Kéler, 1963: 4. Type-genus *Pecaroecus* Babcock & Ewing, by monotypy.

Description. Large Anoplura 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 notal pit and a pair of small sternal apophyseal pits; sternal plate very narrow and long (it may appear indis-

tinct in the cleared specimens); meso- and metathoracic phragmata distinct (Fig. 9). All *legs* subequal in size and shape. *Abdomen* long and narrowly elliptical, with six paratergites, six spiracles and the derm 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 spiracle 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.

Host: Artiodactyla (Tayassuidae).

Pecaroecus **Babcock & Ewing,** 1938 (1 sp.). Type-species: *P.javalii* Babcock & Ewing, 1938, by monotypy. Host: Peccaries, Tayassuidae.

PEDICINIDAE Enderlein

Pedicininae Enderlein, 1904: 136. Type-genus *Pedicinus* Gervais, by monotypy; Dalla Torre, 1908: 4; Fahrenholz, 1912: 28; Séguy, 1944: 454; Ferris, 1951: 69; Hopkins, 1957: 109; Kuhn & Ludwig, 1967: 270.
Pedicinidae Kéler, 1963: 4.

Description. Medium to intermediate Anoplura. *Head* oval to narrowly oval, without prominent postantennal angle; distinct eyes present with lens and pigments; antenna 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 notal 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 paratergites 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 apodeme deeply emarginate at apex; parameres well developed, not fused distally; pseudopenis pentagonal, not heavily sclerotized; aedeagus and endomeres sclerotized; subgenital plate developed. Female with small genital plate; gonopods poorly developed; gonopod IX indistinct.

Host: Primates (Cercopithecidae).

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

PEDICULIDAE Leach

Pediculidae Leach, 1817: 64. Type-genus *Pediculus* Linnaeus, by monotypy.
Pediculina Burmeister, 1835: 56; Giebel, 1874: 21, 27–32.
Haematopina Murray, 1877: 384.
Pediculidae Stephens, 1829: 329. Type-genus *Pediculus* Linnaeus, by monotypy. Denny, 1842: 3; Gervais, 1844: 293; Piaget, 1880: 615–619; Osborn, 1891: 7; Osborn, 1896: 164; Enderlein, 1904: 136; Dalla Torre, 1908: 4; Mjöberg, 1910: 167; Blagoveshtchensky, 1964: 326 (1967 in English: 406–409. Ferris (1951) included *Pediculus* and *Pthirus* in this family.

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 apophyseal pit lacking. All *legs* subequal in shape and size and each leg with a long acuminate claw; tibial thumbs 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 Hominidae (man).

POLYPLACIDAE Fahrenholz

Polyplacinae Fahrenholz, 1912: 58. Type-genus *Polyplax* Enderlein, by original designation. Ferris, 1951: 101; Hopkins, 1957: 109; Johnson, 1960: 6.
Polyplacidae Kéler, 1963: 6.
Lemurphthirinae Fahrenholz, 1936: 56. Type-genus *Lemurphthirus* Bedford, by monotypy.
Docophthiridae Webb, 1946: 107. Type-genus *Docophthirus* Waterston, by original designation.
Eulinognathidae Webb, 1946: 107. Type-genus *Eulinognathus* Cummings, by original designation.
Phthirpediculinae Ewing, 1929: 141. Type-genus *Phthirpediculus* Ewing, by monotypy.
Scipionidae Kéler, 1963: 5. Type-genus *Scipio* Cummings, by monotypy.

Haemodipsidae Kéler, 1963: 6. Type-genus
Haemodipsus Enderlein, by monotypy.

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 hind-
legs larger than midlegs. *Abdomen* with para-
tergites usually highly developed (Fig. 28) and
occasionally represented by small sclerites or
completely lacking; six spiracles present;
tergal and sternal plates usually highly devel-
oped 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, para-
meres 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 (76 spp.). Type-
species: *Pediculus spinulosa* Burmeister, by
original designation. Host: Rodentia and
Insectivora.

Proenderleinellus **Ewing,** 1923 (1 sp.).
Type-species: *Proenderleinellus africanus*
Ewing (= *Polyplax calva* Waterston), by
monotypy. Host: Muridae (Rodentia).

Fahrenholzia **Kellogg & Ferris,** 1915 (13
spp.). Type-species: *Fahrenholzia pinnata* Kel-
logg & Ferris, by original designation. Host:
Sciuromorpha–Rodentia.

Alenapthirus **Benoit,** 1969 (1 sp.). Type-
species: *Alenapthirus spinosissimus* Benoit,
1969, by monotypy. Host: Sciuridae.

Neohaematopinus **Mjöberg,** 1910 (41 spp.)
(including *Johnsonpthirus*). Type-species:
Haematopinus sciuropteri Osborn, by original
designation. Host: Sciuridae, other Rodentia,
and Insectivora.

Sathrax **Johnson,** 1964 (1 sp.). Type-
species: *Sathrax durus* Johnson, by mono-
typy. Host: Tupaiidae (Primates).

Docophthirus **Waterston,** 1923 (1 sp.).
Type-species: *Docophthirus acinetus* Water-

ston, by monotypy. Host: Tupaiidae (Pri-
mates).

Lemurphthirus **Bedford,** 1927 (3 spp.).
Type-species: *Lemurphthirus galagus* Bedford,
by original designation. Host: Lorisidae
(Primates).

Lemurpediculus **Paulian,** 1958 (2 spp.).
Type-species: *Lemurpediculus petterorum*
Paulian, by original designation. Host: Lemuri-
dae (Primates).

Phthirpediculus **Ewing,** 1923(2 spp.).
Type-species: *Phthirpediculus propitheci*
Ewing, by original designation. Host: Indri-
idae (Primates).

Eulinognathus **Cummings,** 1916 (23 spp.)
(including *Cuyana, Lagidiophthirus, Galeo-
phthirus*). Type-species: *Eulinognathus denti-
culatus* Cummings, by original designation.
Host: Rodentia.

Ctenophthirus **Ferris,** 1922 (1 sp.). Type-
species: *Ctenophthirus cercomydis* Ferris, by
monotypy. Host: Echimyidae (Hystrico-
morpha–Rodentia).

Scipio **Cummings,** 1912 (4 spp.). Type-
species: *Haematopinus aulacodi* Neumann, by
original designation. Host: Hystricomorpha–
Rodentia.

Haemodipsus **Enderlein,** 1904 (6 spp.).
Type-species: *Pediculus lyriocephalus* Bur-
meister, by original designation. Host: Lepor-
idae (Lagomorpha).

PTHIRIDAE Ewing

Phthiridae Ewing, 1929: 132. Type-genus
Phthirus = Pthirus Leach, by monotypy.
Phthirinae Schröder, 1925: 519; Ferris,
1951: 281.

Description. Medium, compact Anoplura.
Head short, much narrower than thorax, never
constricted into a next; definite eyes present
externally as a pair of distinct lenses on large
lateral protuberances; antennae five-
segmented, not sexually dimorphic; no occi-
pital 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

margins, each with a large tubercle; tibial thumbs well developed, each with a spiniform apical seta. *Abdomen* relatively small, as broad basally as the posterior part of the thorax, and membranous, except for genitalic segments and lateral lobes, without tergal and sternal plates; segments 5—8, each with prominent, heavily sclerotized paratergal lobes, the last being very prolonged; six pairs of spiracles present, the first three being crowded together and the first two being displaced toward the dorsal meson; segmental setae arranged in transverse rows. *Genitalia:* Male with parameres thick and pointed and a pair of small sclerotized, pointed structures ('pseudo-penis'?); endomere and aedeagus sclerotized; subgenital plate large. Female with well-developed gonopods and large spermatheca; subgenital plate wide and obtriangular.

Host: Hominidae and Pongidae (Primates).

Pthirus Leach, 1815 (2 spp.). Type-species: *Pediculus pubis* Linnaeus, by original designation. Host: Man (Hominidae) and *Gorilla* (Pongidae).

RATEMIIDAE Kim & Ludwig, new family

Type-genus: *Ratemia* Fahrenholz, by mono-typy.

Description. Medium Anoplura. *Head* without external evidence of eyes; antennal-ocular segment much wider than clypeus; post-antennal angles not developed; antennae five-segmented; occipital apophyses indistinct. *Thorax* with meso- and metathoracic phragmata distinct; mesothoracic phragmata connected across the dorsum; sternal plate short and wide; sternal apophysis and apophyseal pit absent; notal pit small and usually distinct. *Legs:* Forelegs small, slender, with acuminate claw; mid- and hindlegs subequal in size and shape, each with stout claw; tibial thumbs developed, each with apical spiniform seta. *Abdomen* without tergal and sternal plates except for genital area; short setae scattered in eight or more irregular transverse rows; segments 4—6 each with a pair of well-developed paratergites which are posteriorly free from the body wall; segments 3—8 each with a pair of spiracles. *Genitalia:* Male with distinct

basal apodeme and highly developed parameres; pseudopenis mostly membranous except for sclerotized apical end; subgenital plate lyre-shaped. Female with a pair of short gonopods and no distinct spermatheca; gonopods IX prolonged, each with a spiniform seta at apex; subgenital plate T-shaped.

Host: Perissodactyla (Equidae).

Ratemia Fahrenholz, 1916 (2 spp.). Type-species: *Haematopinus (Linognathus) squamulatus* 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 gives an insight to Anopluran phylogeny.

When considering phylogenetic relationships, the retention or the complete loss of a primitive character obscures true evolutionary relationship. 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 analysing the distribution and patterns of the derived characters. On the other hand, symplesiomorphy 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.) Presumed evolutionary sequence: 1−2, 1−4, or 1−7, where 1 is the most primitive state (plesiomorphy), 2 and larger number are alternative intermediate derived states, and the largest number is the most specialized state (apomorphy).

Char-acters	HAE	MIC	ECH	PEC	PED	LIN	HYB	RAT	PTH	PEI	HAM	NEO	END	HOP	POL
1. BS	1−2	1−2	1−2	1	1−2	2−3	1	3	3	2−3	3	3−4	4	3−4	2−3
2. EYE	2	1	2	1	1	2	2	2	1	1	2	2	2	2	2
3. OP	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1
4. NAS	1	1	1−3	1	1	1−2	1	1	1	1	3	1	1−2	1	1
5. OA	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1
6. DPHS	1	1	2	1	1	2	2	2	1	2	1	1	1	2	2
7. NP	1	1	1	1	1	1, 2	1	1	2	2	1	2	2	2	2
8. MsPA	1	1	1	2	2	1, 2	1	1	2	2	2	2	1	1	1, 2
9. MtPA	2	1	1	1	1	1, 2	1	1	1	1	1	1	1	1	1
10. TSP	1	3	3	2	2	1−3	1	1	3	3	1	4	1	1	1
11. DMtS	1	2	1	2	2	2	2	2	2	2	1	2	2	2	2
12. FL	2	2	1, 2	2	2	1	1	1	1	1, 2	2	1	2	1	1
13. HL	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1, 2
14. AC	2	3	3, 4	2	1	1, 2	2	1	2	1	1	3, 4	1	1	1
15. AST	4	4	4	4	2, 4	4	4	4	4	4	3	4	2, 3, 4	1	1, 2, 4
16. PT	1	5	5	3	2	3, 5	4	4	3	4	4	5	4, 5	4	4, 5
17. NPT	3	7	7	3	3	3−7	2	6	5	6	2	7	2−7	1−3	2−7
18. NSP	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
19. PA	3	3	1	1	2	1	1	1	1	1	1	2	1	1	1
20. PS	1, 3	1	1, 3	1	1	1, 2	2	2	3	2	1	2	1, 2	1	1
21. G8	1	1	2	1	2	1	2	1	1	2	2	1	1, 2	1	1
22. G9	1	1	2	2	1	1	1	1	1	2	1	2	1	1	1

Abbreviations and codes: Family-taxa: HAE − Haematopinidae, MIC − Microthoraciidae, ECH − Echinophthiriidae, PEC − Pecaroecidae, PED − Pediculidae, LIN − Linognathidae, HYB − Hybophthiridae, RAT − Ratemiidae, PTH − Pthiridae, PEI − Pedicinidae, HAM − Hamophthiriidae, NEO − Neolinognathidae, END − Enderleinellidae, HOP − Hoplopleuridae, POL − Polyplacidae.
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 apophysis (OA): 1, absent; 2, present. (6) Dorsal principal head setae (DPHS): 1, short; 2, strong. (7) Notal pit (NP): distinctly present; 2, indistinct or absent. (8) Mesothoracic pleural apophyses (MsPA): 1, fused medially; 2, separated. (9) Metathoracic pleural apophyses (MtPA): 1, separated from MsPA; 2, fused to MsPA. (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 acuminate 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, cap-shaped; 2, lobe-shaped; 3, tuberculiform; 4, plate-shaped with its apex free from body; 5, absent. (17) Number of paratergites (NPT): 1, 2, 3, 4, 5, 6, 7. (18) Number of abdominal spiracles (NSP): 1, six spiracles; 2, less than five spiracles. (19) Parameres (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.

'Evaluation of Taxonomic Characters'). Presumed evolutionary sequence was enumerated for each character: e.g. 1 to 2, 1 to 4, or 1 to 7, where 1 is the most primitive state (plesiomorphy), 2 and larger numbers are alternative derived states, and the largest number is the most specialized state (apomorphy). The characters and character states used in this matrix are the following:

(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 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 (MtPA): 1, separated from MsPA; 2, fused to MsPA.

(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 acuminate 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, cap-shaped; 2, lobe-shaped; 3, tuberculiform; 4, plate-shaped with its apex free from body; 5, absent.

(17) Number of paratergites (NPT): 1, 2, 3, 4, 5, 6, 7.

(18) Number of abdominal spiracles (NSP): 1, six spiracles; 2, less than five spiracles.

(19) Parameres (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 infested with closely related parasites belonging to a particular taxon. Accordingly, the secondary infestations comprise those infestations originating after divergence of a

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

	HAE	PEC	MIC	PED	PTH	ECH	LIN	NEO	PEI	POL	END	HYB	RAT	HOP	HAM
HAE	0														
PEC	4	0													
MIC	5	3	0												
PED	4	6	4	0											
PTH	3	5	3	3	0										
ECH	5	3	7	4	3	0									
LIN	6	7	6	6	9	8	0								
NEO	2	4	5	4	5	6	9	0							
PEI	3	5	5	6	6	7	9	7	0						
POL	4	4	5	5	6	6	9	8	8	0					
END	4	4	5	5	4	6	8	8	8	7	0				
HYB	4	3	2	3	3	4	6	4	6	6	7	0			
RAT	2	2	2	2	3	3	7	5	7	7	6	6	0		
HOP	2	2	1	2	3	2	6	4	5	8	7	5	5	0	
HAM	2	2	1	3	2	4	3	3	5	5	6	4	3	4	0

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 Neolinognathidae, and parts of the Hoplopleuridae and Polyplacidae. The evolutionary fate of each taxon of lice must have followed the evolutionary path of the mammalian hosts. However, the infestations of Hoplopleuridae and Polyplacidae on Insectivora and Primates are secondary, and the establishment of *Neolinognathus* on Macroscelidae (Insectivora) seems to be secondary. *Neolinognathus* shares many characters with Polyplacidae and is considered here as a taxon broken off from the Polyplacid 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 Polyplacidae, Hoplopleuridae, Pedicinidae, Pthiridae and Enderleinellidae, although they themselves are highly specialized. The Linognathidae colonized primarily the ungulates and secondarily the Carnivora, while the Polyplacidae, Hoplopleuridae and Enderleinellidae invaded and coevolved with rodents. These families are considered here to be the major phylogenetic line from which the Pedicinidae, Neolinognathidae and Ratemiidae have branched off. The Echinophthiriidae, along with Pediculidae, Pecaroecidae, Haematopinidae and Microthoracidae, are highly specialized and yet retain may primitive characters. Perhaps this suggests that they diverged from the main phylogenetic line much earlier. *Hybophthirus*, *Hamophthirus* and *Pthirus* 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.
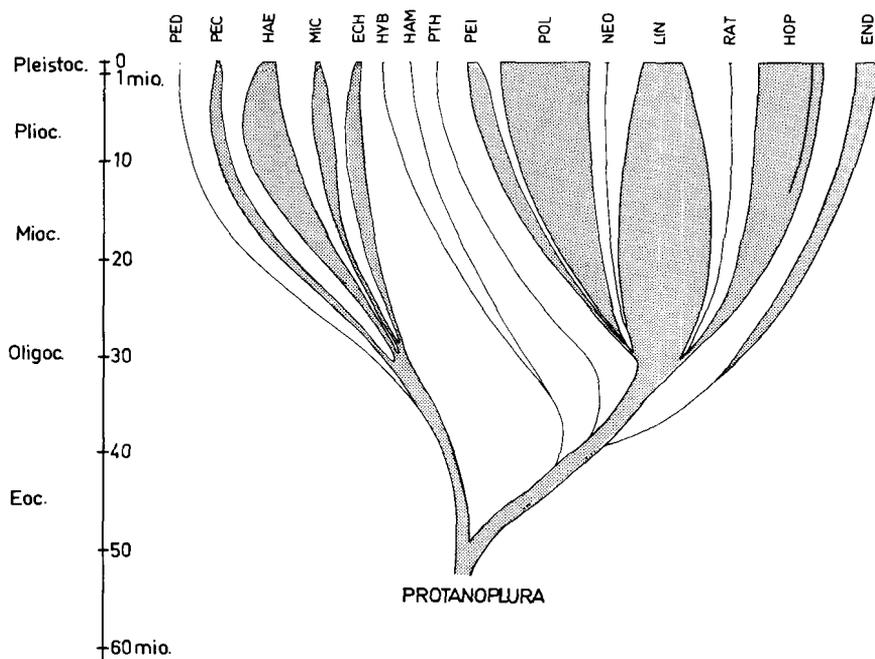

FIG. 42. Inferred phylogeny of the Anoplura.

Acknowledgments

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