

Parallel Evolution, Cladistics, and Classification of Parasitic Psocodea¹

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ABSTRACT

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We recognized the three orders of Psocodea in 1978: Psocoptera, Mallophaga, and Anoplura. Objecting to our view, Haub (1980) maintained, without any new evidence, that all parasitic Psocodea constitute the order Phthiraptera, within which the Anoplura are placed as a suborder. We have reexamined the phylogenetic relationships and taxonomic rankings of parasitic Psocodea with new data and procedural precision. All the taxonomic characters previously considered by Haub, Kim and Ludwig, and others are reevaluated, and new characters discussed and added to the cladistic analyses. Five cladistic hypotheses are critically tested, and the most parsimonious cladogram is accepted as the basis for the classification of Psocodea. The classification is constructed from the phylogram by using subordination and phyletic sequencing. The phylogram is developed by revamping the accepted cladogram with other autapomorphic and plesiomorphic characters not used in searching and testing the nested pattern of synapomorphy. Diagnosis is made directly from the phylogram for each of the psocodean taxa recognized in the classification. In summary, our view is reaffirmed that the Anoplura are distinct from the Amblycera, Ischnocera, and Rhynchophthirina (order Mallophaga) and should be treated as a separate order.

We have proposed that the three primary taxa of the Psocodea are distinct and that they represent the separate orders Psocoptera, Mallophaga, and Anoplura (Kim and Ludwig 1978b). In response to our paper, Haub (1980) reiterated, without any new evidence, the view proposed by Königsmann (1960), and subsequently supported by Clay (1970). This view recognizes the equivalence of the Psocoptera and Phthiraptera (or Phthiriaptera), two separate orders of the Psocodea, and of the four higher taxa Amblycera, Ischnocera, Rhynchophthirina, and Anoplura as suborders within the Phthiraptera. Recently, Chin (1980) proposed a new suborder Protanoplura within the Phthiraptera for *Mirophthirus liae* Chin newly discovered from *Typhlomyces cinereus* Milne-Edwards in China. One of us (K.C.K.) has examined the type specimens of *M. liae*. The results show that *M. liae* is a highly specialized sucking louse related to the Polyplacidae and does not require the rank of a suborder.

Monophyly of the Psocodea is generally accepted by most workers (Königsmann 1960, Kim and Ludwig 1978b, Seeger 1979, Haub 1980). This does not suggest, however, the simultaneous origin of all parasitic psocodeans. The Mallophaga are considered a paraphyletic group (Königsmann 1960, Clay 1970, Kim and Ludwig 1978b). Recently, monophyly of the Psocoptera was suggested by Smither (1972) and Seeger (1979), and the Anoplura are also considered monophyletic (Kim and Ludwig 1978a,b).

Major controversy exists over the phylogenetic relationships and taxonomic rankings of three taxa within the order Mallophaga (Amblycera, Ischnocera, and Rhynchophthirina) and also over the relationship and ranking of the Anoplura. The main issue in the contro-

versy between the two principal views lies in: (1) evaluation and interpretation of character states and polarity, and (2) taxonomic approach to the categorical ranking of member taxa of the Psocodea.

The classification of the Psocodea proposed by Kim and Ludwig (1978b) was based on the result of a cladistic analysis, but imprecision in the formulation and testing of cladistic hypotheses and in the taxonomic approach to categorical ranking caused complication in interpreting our results. The purpose of this paper is to clarify some points raised by Haub (1980) and to affirm our view on the phylogenetic relationships and taxonomic rankings of parasitic Psocodea with procedural precision. All the taxonomic characters previously considered were reevaluated, and new characters were considered and added to the analysis. Cladistic hypotheses were tested by the procedure of Eldredge and Cracraft (1980), and on the basis of the most parsimonious cladogram, the classification for the Psocodea was developed. Here we accept the phylogenetic terms and concepts used by Wiley (1980), unless stated otherwise.

Evaluation of Taxonomic Characters

We considered 21 characters in the previous analysis (Kim and Ludwig 1978b), and Haub (1980) cited 20 characters used by Königsmann (1960). Essentially the same characters were considered in these studies, although some character states were interpreted somewhat differently. Approximately nine characters had loss or regressive character states, of the sort that Hecht and Edwards (1976) consider to contain the least information. Haub (1980) cited 11 synapomorphies for the parasitic members of the Psocodea, and 6 synapomorphies were recognized for the IIB Group A, including Anoplura, Ischnocera, and Rhynchophthirina. They include: (1) homonomous antennae, (2) presence of obturaculum, (3) presence of spiracular glands, (4) presence of symbiotes, (5) testis with two follicles, and (6) compound eyes with one ommatidium.

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All these characters were critically reevaluated and analyzed cladistically and anagenetically. The relevant new data on taxonomic characters used by Kim and Ludwig (1978) and Haub (1980) are also discussed. Comparative morphology of the character complexes discussed in Kim and Ludwig (1978b) is not repeated, unless new data and different interpretations have become available. The characters are numbered as treated in the following cladistic analyses (Table 2).

(1) *Head: Characters 1, 5*

Character 1.—Prognathy and the horizontal head in the parasitic Psocodea is related to flattening of the head, but the displacement and position of sclerites of the head differ significantly among these taxa. In the Amblycera and Ischnocera, the clypeus is bent ventrally in varying degrees, with the mouth located ventrally. In the Rhynchophthirina, the clypeus forms the dorsal part of the long rostrum with the mouth located at its anterior end (Mukerji and Sen-Sarma 1955). In the Anoplura, the clypeus is a dorsal plate with the mouth opening anteriorly through the haustellum.

The comparative morphology of the psocodean head suggests that, in the Amblycera and Ischnocera line, the clypeus was bent ventrally, leaving the mouth ventral as the head became flattened. However, in the Rhynchophthirina line, the clypeus formed the dorsal part of the rostrum as the forehead became prolonged. In the Anoplura line, the clypeus remained dorsal as the head became modified to accommodate the rapidly developing piercing-sucking mouthparts.

Character 5.—The tentorium of the Mallophaga lacks the distinct dorsal arms, but the Anoplura lack a tentorium altogether (Symmons 1952). Among the Mallophaga, there is a wide range of character polarity in tentorial structure; extreme reduction is found in the Rhynchophthirina, where only the posterior tentorial pits remain distinct. The fact that no intermediate form is found in the Anoplura suggests that the tentorium of the Protanoplura became reduced rapidly and eventually left no trace in the descendants as their head became flattened and the mouthparts modified for the blood-sucking habit.

(2) *Mouthparts: Characters 2–4*

The mouthparts are located ventrally in the Amblycera and Ischnocera but anteriorly in the Rhynchophthirina. In the Anoplura, the piercing-sucking mouthparts are developed internally. All the mallophagan taxa have mandibles with different articulations: in the Amblycera, the mandibles lie parallel with the ventral surface of the head (horizontal or dorsal-ventral); in the Ischnocera, each mandible is inserted at right angles to the head (vertical or anterior-posterior); but in the Rhynchophthirina, the mandibles are articulated lateral to the head (moving outwards). The mandibles of the Anoplura are internally rudimentary or completely absent. Character states of all other structures related to the mouthparts, including the musculature, sitophore,

and hypopharynx, are influenced by the type, position, and function of the mouthparts.

(3) *Labial Glands: Character 16*

Two pairs of labial glands are found in the thorax of the Psocoptera (Weber 1938, Cope 1940a) and Anoplura (Snodgrass 1944, Ferris 1951), whereas, in the Mallophaga, a pair of labial glands is found beneath the subesophageal ganglion (Weber 1938, Cope 1940b, Risler 1951). In the Ischnocera (Cope 1940b, Risler 1951) and Rhynchophthirina (Mukerji and Sen-Sarma 1955), there is also a pair of salivary glands in the thorax (Richards and Davies 1977).

(4) *Antennae and Antennal Sense Organs: Characters 6–10*

Character 6.—Filiform antennae are found in all Psocodea except the Amblycera, whose capitate antennae are concealed in deep fossae. The parasitic Psocodea have five-segmented antennae that may be reduced to four or even to three segments. Reduction of the antennal segments is not unique to the Psocodea, often being related to the parasitic mode of life (Kim and Ludwig 1978b). This synapomorphy could have been developed by cladogenesis of a monophyletic taxon (e.g., Phthiraptera) or by anagenesis of paraphyletic taxa (e.g., Anoplura and Mallophaga).

Character 7.—Pedunculation of the third antennal segment is unique to the Amblycera (Königsmann 1960, Clay 1970, Haub 1980). However, pedunculation and modification of other antennal segments is relatively common in other parasitic Psocodea; for example, in the Polyplacidae (Anoplura), particularly males, the fourth antennal segment is often petiolated.

Characters 8–10.—Remarkable similarity in antennal sensilla of the parasitic Psocodea led Clay (1969) to conclude that the Mallophaga are not monophyletic and that the present classification of parasitic Psocodea does not reflect their true phylogenetic relationships. However, new data lead to a different conclusion. The characters of antennal organs are closely related to the shortening of antennae by fusion. Examination of antennal sense organs of over 80 species of Anoplura, Mallophaga, and Psocoptera representing 22 families revealed that many apomorphic character states of antennal sense organs were developed independently in different lineages of the parasitic Psocodea (Al-Abbasi 1981). The Psocoptera have six to seven sensilla coeloconica (SC-type A) on the antennae, two or three on the third segment, and one on each of the 4th, 6th, 8th, and 11th segments. In the parasitic Psocodea, antennal sensilla are aggregated on the fourth and fifth or terminal segments. They are reduced to four or fewer and variously modified; the sensilla basiconica are derived from the sensilla coeloconica, and likewise saucer-shaped pore organs are developed from large sense pegs often found in the cavity of sensilla coeloconica in the Amblycera.

Definite patterns of the shared homologs exist in the four characters of antennal sense organs of the Psocodea (Table 1). In the Amblycera, the number of sensilla

Table 1.—Distribution of four characters of antennal sense organs in Psocodea^a

| Taxa | No. of sense organs | Sensilla | | No. of pore organs | Arrangement type ^b |
|------------------|---------------------|----------|--------|--------------------|-------------------------------|
| | | No. | Type | | |
| Psocoptera | 6-7 | 6-7 | SC | 0 | I |
| Amblycera | | 4, 2 (3) | SC | 0 | I |
| Anoplura | 4, 2 | 4 (3) | SC, SB | 2 (0) | II (I) |
| Ischnocera | 5 | 2 | SC | 3 | II |
| Rhynchophthirina | 3 | 1 | SB | 2 | II |

^aSC, Sensilla coeloconica; SB, sensilla basiconica; S, sensilla; P, pore organs (modified from Al-Abbasi [1981]).

^bArrangement type I (fifth or terminal segment) = 1S (no P); type II = 1S + 2P.

coeloconica varies with four, two, or occasionally three; but in the Ischnocera and Rhynchophthirina, it is reduced to two and one, modified to the sensillum basiconicum, respectively. The Anoplura commonly have four and occasionally three antennal sensilla, either as sensilla coeloconica or sensilla basiconica. The number of antennal sensilla shows a definite morphocline but the sensilla basiconica appear to have developed independently in each lineage. Although the pore organs and the arrangement type II are found in the Anoplura, Ischnocera, and Rhynchophthirina, many Anoplura lack pore organs and still retain the arrangement type I. These patterns suggest that these character states were independently developed in each phyletic line.

(5) Eyes

The Psocoptera usually have three dorsal ocelli and a pair of normal compound (lateral) eyes. In apterous Liposcelidae, the compound eyes are vestigial and reduced to small groups of ommatidia, and in many apterous Psocoptera, the dorsal ocelli are completely lacking (Wundrig 1936, Richards and Davies 1977). Furthermore, the nymphs of Psocoptera usually lack ocelli (Smithers 1972). The Amblycera usually have two ommatidia on each side of the head, whereas the Ischnocera often possess lateral eyes (Wundrig 1936). They show a widely ranging morphocline from distinct lenses to ocular vestiges. Many Anoplura still retain lateral eyes represented by a single lens (Webb 1948). Absence of ocelli and reduction of lateral eyes are common among parasitic insects. Accordingly, these characters are not useful in phylogenetic analysis.

(6) Thorax: Characters 11, 12

In the Mallophaga, the prothorax is usually well developed and distinct. The meso- and metathorax are usually separate in the Amblycera, although there are various degrees of fusion of the thoracic segments; the meso- and metanotum may be fused (Laemobothriidae, Ricinidae), the meso- and pronotum fused (Trimenoponidae), or all three thoracic nota fused (Gyropidae) (Clay 1970, Kéler 1971). The mesonotum in the Ischnocera and Rhynchophthirina is completely fused with the metanotum. However, the prothorax is distinct from the pterothorax; even in the Rhynchophthirina (*Haematomyz*),

the prothoracic segment is membranous but distinguishable from the pteronotum (Mukerji and Sen-Sarma 1955). However, in the Anoplura, thoracic segments are completely fused without a trace of segmental suture.

In the Mallophaga, the pleural and sternal components of the thoracic segment are usually distinct from the tergum, whereas, in the Anoplura, the pleuron is completely fused with the notum, and the sternum is largely membranous with a small occasional sternal plate. The dorsal part of the anopluran thorax is largely pleural, and the tergal component is confined to the center of the thorax or the notal pit as apophyses; it is well shown in *Haematopinus* and *Solenopotes* (Ferris 1951) and *Antarctophthirus* (Al-Abbasi 1978).

In the winged Psocoptera, the prothorax is reduced and the pterothorax well developed, whereas the prothorax of apterous forms is well developed and the meso- and metanotum sometimes fused. The sterna are reduced in winged forms but broad in flattened, apterous forms (Smithers 1972).

In view of these facts, we must conclude that the Amblycera, Ischnocera, and Rhynchophthirina were derived from a common ancestor and form a distinct holophyletic group. The degree of similarity in the thorax between the Anoplura and the mallophagans was developed independently without direct morphological correspondence.

(7) Legs

All Mallophaga lack pulvilli and empodia; all have one or two tarsal segments and two claws, except for the mammal-infesting Gyropidae (Amblycera), Trichodectidae (Ischnocera), and Haematomyzidae (Rhynchophthirina), which have a single claw. The Psocoptera have two to three tarsal segments with two claws and pulvilli. The Anoplura have one-segmented tarsi with a single claw and no pulvilli.

(8) Spiracles: Characters 13-15

The hypopneustic respiratory system is not uncommon among parasitic and phytophagous insects, including Anoplura, Mallophaga, Thysanoptera, Hemiptera, and Homoptera (Richards and Davies 1977). In the parasitic Psocodea, there are a pair of thoracic and six pairs of abdominal spiracles which are often further reduced

in the Amblycera and Anoplura. The mesothoracic spiracles are often displaced and located on the prothorax in the Amblycera and some Ischnocera; Webb (1946) referred to them as the prothoracic spiracles. In the Rhynchophthirina, the thoracic spiracles are located on the mesothorax as in the Anoplura. They are ventrally (or ventrolaterally) located in the Mallophaga but dorsal in the Anoplura. The spiracular gland is commonly found in the Anoplura, Ischnocera, and Rhynchophthirina, but is lacking in the Amblycera (Webb 1946); however, information on the Psocoptera and Amblycera is meager. In the parasitic Psocodea, the first two abdominal segments lack spiracles.

(9) Brain and Ganglia

In the parasitic Psocodea, the brain is placed directly above or posterodorsal to the subesophageal ganglion. This trend is related to the prognathy and general shape of the head. The fusion of the metathoracic and abdominal ganglia is not unique to the parasitic Psocodea; it is rather common in all five orders of Hemipteroidea (Matsumura 1976) and many orthopteroid insects.

(10) Testicular Follicles: Character 17

The testes are usually composed of three follicles in the Amblycera and two in the Ischnocera, Rhynchophthirina (Mukerji and Sen-Sarma 1955), and Anoplura. However, some Amblycera also have two testicular follicles (e.g., *Myrsidea*) (Blagoveshtchensky 1956, Clay 1970). The Psocoptera usually have three testicular follicles; some species even have a single one. Thus, this character is not useful in phylogenetic inference.

(11) Symbiotes and Obturaculum

The parasitic Psocodea have acquired symbiotes independently as their dietary requirements changed (Kim and Ludwig 1978b).

In Anoplura, a mass of connective tissue forms a plug which fills the occipital foramen in the posterior part of the head (Stojanovich 1945, Ferris 1951). An enlargement of the connective tissue surrounding the head ganglia is also found in the Ischnocera and Rhynchophthirina. Similarity has been noted and homology inferred between the obturaculum of Anoplura and the fibrous mass of the Mallophaga (Symmons 1952, Pipa and Cook 1958). Because the obturaculum and similar tissues appear to have developed independently among the parasitic Psocodea and information on structure and distribution of fibrous masses is not yet sufficient to make any reasonable phylogenetic judgment, it is best not to use this character state at this time.

(12) Eggs and Nymphs: Character 18

In the parasitic Psocodea, the egg is provided with a chorionic hypopyle (= Eistigma) at or near the posterior pole, an operculum (= lid of egg), and the micropyles which open through the operculum. The presence of chorionic hypopyle, operculum, and micropyles is not unique to the parasitic Psocodea; they are also found

in many other insects, such as Embioptera, Hemiptera, and Homoptera (Hinton 1981) and thus are not useful in phylogenetic inference.

The Mallophaga and Anoplura have three nymphal instars, and the Psocoptera have six. The number of instars was reduced as the primitive psocodeans entered a parasitic mode of life (Kim and Ludwig 1978b). Nevertheless, this synapomorphy is included in the analysis because of its probable phylogenetic implication, although convergence or parallel evolution cannot be ruled out completely.

Taxonomic Characters and Shared Character States

Of all of the character complexes evaluated, 18 characters are considered important and useful in phylogenetic analysis (Table 2). These characters and character states are as follows (1) Head: hypognathous (p), horizontal (a), prognathous (b). (2) Mouthparts: chewing (or biting) type (p), piercing-sucking (a). (3) Mouth: ventral (p), anterior (a). (4) Mandibles: horizontal (p), vertical (a), lateral (b), internal (or lacking?) (c). (5) Tentorium: present (p), absent (a). (6) Antennae: 10-segmented (p), five or fewer segments (a). (7) Third antennal segment: filiform (p), penduculate (a). (8) Arrangement type of antennal sense organs: I (p), II (a). (9) Number of antennal sensilla: 6-7 (p), 4-3 (a), 2-1 (b). (10) Number of antennal pore organs: 0 (p), 2 (a), 3 (b). (11) Prothorax: distinct (p), indistinct (a). (12) Meso- and metanotum: separate (p), fused (a). (13) Thoracic spiracles: lateral (p), ventral (a), dorsal (b); (14) Spiracles: 2 thorax + 8 abdomen (p), 2 + 6 or less (a). (15) Spiracular gland: absent (p), present (a). (16) Cephalic labial glands: absent (p), present (a). (17) Testicular follicles: 3 (p), 2 (a). (18) Nymphal instars: 6 (p), 3 (a).

In summary, the parasitic members of the Psocodea share three synapomorphies: (6) antennae with five or fewer segments, (14) one thoracic and six or fewer abdominal spiracles; and (18) three nymphal instars. The Psocoptera and the Mallophaga share three symplesiomorphies: (2) biting-chewing mouthparts; (5) presence of tentorium; and (11) prothorax distinct. The Psocoptera and Anoplura share one symplesiomorphous state: (16) two pairs of labial glands in the thorax without cephalic labial gland.

The three mallophagan taxa share three character states: (9) antennae with two or one sensillum; (13) thoracic spiracles ventrally located; and (16) presence of cephalic labial glands. Three character states are common to the Anoplura and Rhynchophthirina: (1) prognathous head; (3) mouth opening anteriorly; and (10) antennae with two pore organs. The Ischnocera share two character states with the Rhynchophthirina: (4) mandibles articulated not horizontally but either vertically or laterally; and (9) antennae with two or one sensillum. Some of the shared characters listed here are synapomorphies, some symplesiomorphies, and some a mixture of the two. The structural organization and morphoclines of characters associated with the head, mouthparts, and thorax are quite similar in many aspects among the Amblycera, Ischnocera, and Rhynchophthirina. Many char-

Table 2.—Distribution of character states of 18 characters in the Psocodea^a

| Characters | PSO | AMB | ISC | RHY | ANO |
|------------|------|------|-----|-----|------|
| 1 | p | a | a | b | b |
| 2 | p | p | p | p | a |
| 3 | p | p | p | a | a |
| 4 | p | p | a | b | c |
| 5 | p | p | p | p | a |
| 6 | p | a | a | a | a |
| 7 | p | a | p | p | p |
| 8 | p | p | a | a | a(p) |
| 9 | p | a,b | b | b | a |
| 10 | p | p | b | a | a(p) |
| 11 | p | p | p | p | a |
| 12 | p(a) | p(a) | a | a | a |
| 13 | p | a | a | a | b |
| 14 | p | a | a | a | a |
| 15 | p | p | a | a | a |
| 16 | p | a | a | a | p |
| 17 | p | p(a) | a | a | a |
| 18 | p | a | a | a | a |

^aPSO, Psocoptera; AMB, Amblycera; ISC, Ischnocera; RHY, Rhynchophthirina; ANO, Anoplura; P, plesiomorphy; a, b, c, apomorphy, morphocline series. Parentheses indicate minor occurrence. Character states: (1) head: hypognathous (p), horizontal (a), prognathous (b); (2) mouthparts: chewing (or biting) type (p), piercing-sucking type (a); (3) mouth: ventral (p), anterior (a); (4) mandibles: horizontal (p), vertical (a), lateral (b), internal (or lacking?) (c); (5) tentorium: present (p), absent (a); (6) antennae: 10 segmented (p), five or less segmented (a); (7) third antennal segment: filiform (p), pedunculate (a); (8) arrangement type of antennal sense organs: I (p), II (a); (9) number of antennal sensilla: 6–7 (p), 4–3 (a), 2–1 (b); (10) number of antennal pore organs: 0 (p), 2 (a), 3 (b); (11) prothorax: distinct (p), indistinct (a); (12) meso- and metanotum: separate (p), fused (a); (13) thoracic spiracles: lateral (p), ventral (a), dorsal (b); (14) spiracles: 2 thorax + 8 abdomen (p), 2 + 6 or less (a); (15) spiracular gland: absent (p), present (a); (16) cephalic labial glands: absent (p), present (a); (17) testicular follicles: 3 (p), 2 (a); (18) nymphal instars: 6 (p), 3 (a).

acters shared by the parasitic members of the Psocodea appear to have developed independently along each phyletic line and probably evolved more than once during the psocodean evolution.

Cladistic Analysis

Cladistic Hypotheses

Five alternative hypotheses were formulated to test cladistic relationships of the five higher taxa of the Psocodea (Fig. 1–5). These hypotheses were erected on the basis of prior systematic work (Königsmann 1960, Kim and Ludwig 1978b) and general similarities.

Hypothesis 1 (Fig. 1).—The Ischnocera and Rhynchophthirina form a monophyletic group which is the sister group of the Anoplura. The cladograms by Königsmann (1960) and Kim and Ludwig (1978b) are essentially alike, but the Königsmann cladogram differs from that of Kim and Ludwig by the terminal placement of the two-taxon set Ischnocera + Rhynchophthirina. This difference led to different interpretation and application of cladograms and was reflected in their classifications. The three-taxon set Ischnocera + Rhynchophthirina + Anoplura ("Group A" of Königsmann) is a sister group of the Amblycera.

Hypothesis 2 (Fig. 2).—The Rhynchophthirina and Anoplura form a monophyletic group which is the sister group of the Ischnocera.

Hypothesis 3 (Fig. 3).—The Anoplura and Amblycera form a monophyletic group which is the sister group of the Ischnocera. The Rhynchophthirina diverged from

the main phyletic line much earlier (Mukerji and Sen-Sarma 1955).

Hypothesis 4 (Fig. 4).—The Ischnocera and Amblycera are a monophyletic group which is the sister group of the Rhynchophthirina. The Anoplura diverged from the main phyletic line quite early.

Hypothesis 5 (Fig. 5).—The Ischnocera and Rhynchophthirina form a monophyletic group and the Amblycera are its sister group.

Analysis of Synapomorphy

Of 18 characters evaluated, three synapomorphies (characters 6, 14, and 18) were recognized for the parasitic members of the Psocodea, and four characters (2, 5, 7, and 11) are involved in autapomorphy (Table 2). Among the parasitic Psocodea five characters (1, 4, 9, 10, and 13) show varying degrees of variability, and seven other characters (3, 8, 12, 15, 16, and 17) represent simple, primitive-derived states.

Character 1: Head.—The head is horizontal in the Amblycera and Ischnocera but prognathous in the Rhynchophthirina and Anoplura; the anopluran head has entirely different structural organization. It is not a true synapomorphy.

Character 3: Mouth.—The orientation of the mouth is determined by anagenetic modification of the head and mouthparts. The anterior opening of the mouth is a derived character state but the shared homolog between the Anoplura and Rhynchophthirina is a result of convergence.

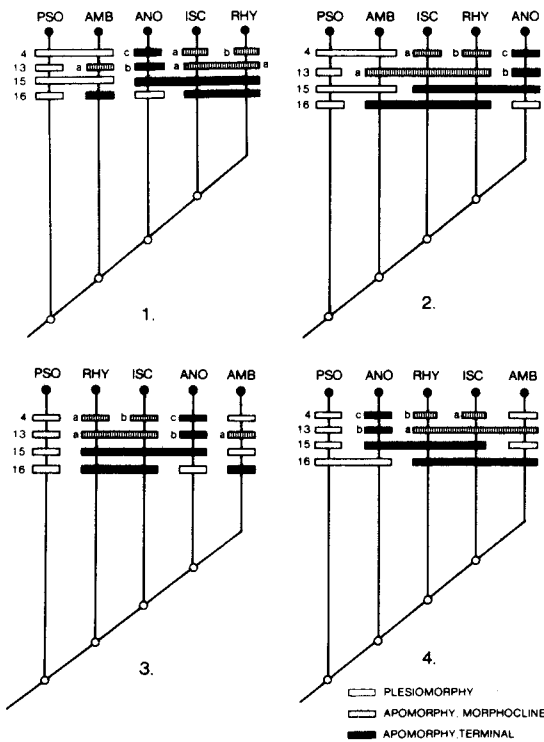


FIG. 1-4.—Alternative cladistic hypotheses (4) with postulated synapomorphies. Shaded rectangles indicate synapomorphies; open rectangles represent the primitive conditions. Numerals indicate characters. (1) Hypothesis 1; (2) hypothesis 2; (3) hypothesis 3; (4) hypothesis 4.

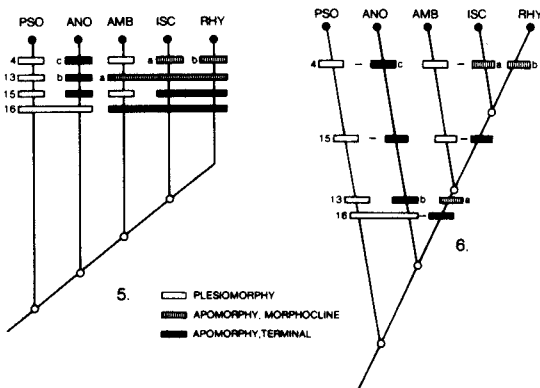


FIG. 5-6.—The fifth alternative cladistic hypothesis with postulated synapomorphies and the accepted cladogram for the Psocodea. Numerals indicate characters. PSO, Psocoptera; ANO, Anoplura; AMB, Amblycera; ISC, Ischnocera; RHY, Rhynchophthirina; a, b, c, apomorphy, morphocline.

Character 4: Mandibles.—In the Anoplura, the mandibles are completely lacking or internally rudimentary.

Distinct mandibles are found among the Psocoptera and the mallophagan taxa. However, the Psocoptera retain a generalized type of mouthparts, whereas the mandibles and their associated structures are highly modified and variable within the Amblycera, Ischnocera, and Rhynchophthirina. The articulation and movement of the mandibles are determined by the shape and structural organization of the head and other mouthparts. This series of character states does not reflect a linear relationship, and each apomorphy shows the result of independent development within each phyletic line.

Character 5: Tentorium.—The lack of the tentorium is a derived character state and represents an autapomorphy for the Anoplura.

Character 7: Third Antennal Segment.—The pedunculation of the third antennal segment is a derived character state and represents an autapomorphy for the Amblycera.

Character 8: Arrangement Type of Antennal Sense Organs.—The type II arrangement appears to be a synapomorphy for the Ischnocera, Rhynchophthirina, and part of the Anoplura (the remainder still possess the type I arrangement); if this represents a true synapomorphy, the Anoplura cannot be holophyletic (*sensu* Ashlock 1979).

Character 9: Number of Antennal Sensilla.—The reduction in the number of antennal sensilla is a derived character state. The Amblycera and Anoplura have two character states of the morphocline polarity, indicating convergence.

Character 10: Number of Pore Organs.—The development of pore organs is a derived character state, but the synapomorphy is the result of convergence. Some Anoplura have the plesiomorphic character state.

Character 11: Prothorax.—The complete fusion of the thoracic segments without any trace of segmental sutures in the Anoplura is an autapomorphy. The thorax of the Amblycera, Ischnocera, and Rhynchophthirina shows distinct segmental boundaries; even in the Gyropidae (Amblycera) and *Haematomyzus* (Rhynchophthirina), the prothorax is distinctly identifiable.

Character 12: Meso- and Metanotum.—The shared homolog (the fusion of meso- and metanotum, even with pronotum) is found among the Ischnocera, Rhynchophthirina, and Anoplura, but some of the Psocoptera and Amblycera also show this apomorphy. This suggests that the sharing of this character state is the result of parallel evolution or convergence and does not represent a true synapomorphy.

Character 13: Thoracic Spiracles.—The position of the mesothoracic spiracles is determined by the structural organization of the thoracic segments. The transformation sequence of the character states is not linear, and each character state reflects the anagenesis of the thorax in each lineage.

Character 15: Spiracular Glands.—The presence of the spiracular glands is a derived character state (Webb 1946), but the data for the Amblycera and Psocoptera are insufficient to make any reasonable inference. Nevertheless, the data now available for the parasitic Psocodea are considered useful.

Character 17: Testicular Follicles.—The reduction in the number of testicular follicles is a derived condition and some Amblycera have both apomorphic and plesiomorphic states.

Accordingly, five shared character states (characters 3, 8, 9, 10, and 12) are considered the results of parallelism or convergence (*sensu* Eldredge and Cracraft 1980).

Test of Cladistic Hypotheses

Four synapomorphies (characters 4, 13, 15, and 16) were used to test the five cladistic hypotheses (Fig. 1–5). Two postulated synapomorphies (13 and 16) exclusively define the three-taxon set Ischnocera + Rhynchophthirina + Amblycera (Fig. 4 and 5), and one synapomorphy (15) defines the set Anoplura + Ischnocera + Rhynchophthirina (Fig. 1 and 2). No postulated synapomorphy defines the two-taxon set Amblycera + Anoplura (Fig. 3), and no synapomorphy exclusively defines the following sets: Ischnocera + Amblycera (Fig. 4), Rhynchophthirina + Ischnocera (Figs. 1, 5), and Anoplura + Rhynchophthirina (Fig. 2). On the basis of these test results, hypothesis 3 is the most thoroughly rejected hypothesis (Fig. 3).

Of the four remaining hypotheses, hypotheses 1 (Fig. 1) and 2 (Fig. 2) should be rejected because no synapomorphy exclusively unites the two-taxon sets, Rhynchophthirina + Ischnocera and Anoplura + Rhynchophthirina, and only one synapomorphy unites the three-taxon set. Accordingly, hypotheses 4 (Fig. 4) and 5 (Fig. 5) are acceptable, but hypothesis 5 is more parsimonious because one synapomorphy (15) unites the two-taxon set Ischnocera + Rhynchophthirina (Fig. 5).

In other words, the three cladistic hypotheses proposed by Königsmann (1960) and Haub (1980, Fig. 1a), Kim and Ludwig (1978b), and Mukerji and Sen-Sarma (1955) (Fig. 3) must be rejected on the basis of the preceding cladistic tests. Furthermore, it must be concluded that the parasitic taxa of Psocodea evolved independently along each phyletic line (Fig. 6), and many of those synapomorphies and similarities were developed by parallel evolution.

Origin of Parasitic Psocodea

The Psocodea date back to the Carboniferous (Smithers 1972) or at the latest to the early Permian (Hennig 1969), as indicated by the presence of numerous fossils recognizable as the Psocoptera (Permpsocida) in the Permian. The Psocoptera are a monophyletic group (Seeger 1979); two suborders, Trogiomorpha with Trogioformia and Psyllipsociformia and Psocomorpha with Amphientomiformia and Psociformia, are recognized in addition to the fossil Permpsocida (Smithers 1972).

Significant morphological features of the fossils Permpsocida of the Lower Permian (United States) and Upper Permian (Australia, U.S.S.R) and extant Psocoptera are relevant to the discussion on the origin of the parasitic Psocodea. The fossil Dichentomidae have the head prolonged into a short rostrum, the antennal socket placed in a pit with adjacent ridges, the prothorax short

and collarlike, and the meso- and metathorax large without clear evidence of division (Smithers 1972). The Lophioneuridae have a broad head with the antennae reaching only to the midwing; in *Lophiocypha* of the Upper Permian, the meso- and metathorax are fused, and the compound eyes are round and wide apart (Smithers 1972).

In the Psocoptera, the number of segments in serial structures (the antennae, maxillary, and labial palps) tends to be reduced in modern forms. Fusion of the meso- and metathorax is rather common. The apterous and nymphal psocids have much shorter antennae, two-segmented tarsi, small or no compound eyes, and no ocelli. Many of these characters, including the fusion of thoracic segments and the number of tarsal segments, are variable, and the maxillary and labial palps are reduced among the mallophagan taxa. Furthermore, the association of different psocids with the fur of mammals (Pearman 1960) and plumage of birds (Hicks 1959, Rapp 1961, Mockford 1967) is long standing, and found even today.

Although it seems clear that the parasitic members of the Psocodea are derived from common psocodean stock, perhaps the Permpsocida, there is no evidence to indicate that all of the parasitic Psocodea are descendants of any single group of the permpsocidan ancestors, such as the Permpsocidae of the Lower Permian (United States). The Dichentomidae also possess those apomorphies found in the Amblycera and Rhynchophthirina, these being the antennae in pits and head with rostrum, respectively. The Lophioneuridae have a broad head, a character-state found among the mallophagans. Furthermore, the nymphs and apterous forms of the extant Psocoptera show a dynamic structural plasticity in many character complexes (Smithers 1972). The associations of psocids with birds and mammals have been frequent and are common (Pearman 1960, Rapp 1961, Mockford 1967).

These facts lead to the conclusions that all extant Psocodea are derived from common ancestral psocodeans, perhaps the Permpsocida or their relatives, during the Carboniferous, but each of the parasitic members of the Psocodea may have originated from different specific preparasitic stocks; for example, the mallophagan taxa (Amblycera, Ischnocera, and Rhynchophthirina) arose perhaps from a dichentomid ancestor, whereas the Anoplura arose from a lophioneurid ancestor. Nevertheless, the forerunners of the parasitic psocodeans must have been common in the early Triassic Period, and associated with ancestral birds and mammals during the Jurassic Period. Later, they further exploited their associations by invading new habitats and niches, the skin surface and dermal derivatives of primitive birds and mammals, perhaps during the Cretaceous or late Jurassic Period (Kim and Ludwig 1978b), irrespective of what models may be applicable to the origin of higher taxa (Bock 1965, Van Valen 1971, 1974, Schaefer 1976).

Phylogram and Classification of Psocodea

The classification of the Psocodea by Kim and Ludwig (1978b) differs from that of Königsmann (1960), Clay (1970), and Haub (1980) in the grouping and cat-

egorical ranking of the mallophagan taxa with regard to the Anoplura, although both classifications are based on the results of similar cladistic analysis. Incongruence between the two classifications reflects the different interpretation of character states of some character complexes and conflicting approaches to classification.

Approaches to biological classification have been a focal point in systematic biology throughout its history and are well documented (Simpson 1961, Hennig 1966, Hull 1965, Sneath and Sokal 1973, Ross 1974, Eldredge and Cracraft 1980, Mayr 1981). Thus, various theoretical views of biological classification are not discussed here except those related to the procedural details relevant to the classification of the Psocodea.

Cladistic Classification

Cladistic analysis specifically searches for the nested pattern of synapomorphy and the cladogram is the only basis for classification. In the analysis, a synapomorphy combines taxa into sets and subsets, but neither symplesiomorphy nor autapomorphy is used for that purpose (Eldredge and Cracraft 1980). Accordingly, cladistic classification is relatively objective and testable if the synapomorphies are correctly postulated, as the following procedure will show. However, this classification is less useful to biologists as a general reference system to provide biological information on phylogenetic relationships of organisms (Mayr 1969, Ashlock 1979, Weygoldt 1979).

By phyletic sequencing, the cladogram (Fig. 6) depicting the accepted hypothesis is transformed into the following classification:

- Group 1: Psocoptera
- Group 2: Anoplura
- Group 3: Amblycera
- Group 4: Ischnocera
- Group 5: Rhynchophthirina

This classification signifies that each taxon (e.g., Psocoptera) is the sister group of the remaining taxa listed below it. Here, no rank is specified, and one rank is sufficient to specify relationships.

However, if the cladogram is transformed into a hierarchic classification by subordination, five ranks are required. When Linnean categorial ranks are specified for the group and each of the subgroups in the hierarchic classification by strictly adhering to the hierarchic logic of subordination (Simpson 1961, Hennig 1966, Eldredge and Cracraft 1980), the following cladistic classification will result for the Psocodea:

- Group: PSO, ANO, AMB, ISC, RHY
- Subgroup 1a: PSO
- Subgroup 1b: ANO, AMB, ISC, RHY
- Subgroup 2a: ANO
- Subgroup 2b: AMB, ISC, RHY
- Subgroup 3a: AMB
- Subgroup 3b: ISC, RHY
- Subgroup 4a: ISC
- Subgroup 4b: RHY

A similar cladistic classification was proposed with much larger number of categories and ranks by Boudreaux (1979).

Evolutionary Classification

Strict application of cladistic formalism forbids for biological classification the provision of biological similarity that takes into account anagenetic data and uniquely evolved characters including autapomorphy (Hull 1970, Bock 1973, Ashlock 1979, Mayr 1981). To overcome this shortcoming, Ashlock (1979) proposed the phylogram as the basis of biological classification that results from both cladistic and anagenetic analyses. Similarly, Weygoldt (1979) proposed that cladistic and evolutionary classifications be superimposed to maximize the phylogenetic information about organisms in a classification. In our view, biological classification must provide a maximum of biological information about organisms and their evolutionary history as a general reference system. Additionally, higher taxa at all taxonomic categories recognized in a classification system must be clearly delimited by definite gaps so that they can subsequently be identified with such taxonomic gaps. The concept of higher taxa defined by Ashlock (1979) could provide the means to meet such goals in biological classification: "A higher taxon is a monophyletic group of species (or a single species) separated from each phylogenetically adjacent taxon of the same rank by a gap greater than any found within these groups."

The inherent problems in Hennig's approach by strict subordination have been well reviewed by Eldredge and Cracraft (1980). To alleviate the difficulties of Hennig's approach, they proposed the use of subordination and phyletic sequencing for constructing sound biological classification. This approach reduces the number of categories and ranks, improves practicality, and warrants the stability of categorial and rank names in biological classification.

The accepted cladogram (Fig. 5 and 6) does not show the patterns of morphological convergence and differentiation of plesiomorphous structures among the mallophagan taxa, such as the cibarial sclerites and the cibarium (Haub 1972, 1973), tentorium (Symmons 1952), mandibles and thoracic segments. Thus, this cladogram is revamped by incorporating other character states which were not used in searching and testing the nested pattern of synapomorphy; this diagram is called the phylogenetic diagram or phylogram (Fig. 7). The phylogram shows character distributions and the nested sets of taxa, as well as their distinctness by symplesiomorphy, autapomorphy, and shared character states of convergence and parallelism. The nested sets of taxa can be accu-

- Superorder PSOCODEA
- Order PSOCOPTERA
- Order PHTHIRAPTERA
- Suborder ANOPLURA
- Suborder MALLOPHAGA
- Infraorder AMBLYCERA
- Infraorder ISCHNOCERA
- Superfamily ISCHNOCERA
- Superfamily RHYNCHOPHTHIRINA

rately depicted in the classification. The gaps clearly define each taxon, by which subsequent identification of members of such taxa can be made.

From the phylogram (Fig. 7), the following classification may be constructed by using subordination and phyletic sequencing (Eldredge and Cracraft 1980):

Superorder PSOCODEA

Order PSOCOPTERA

Order ANOPLURA

Order MALLOPHAGA

Suborder AMBLYCERA

Suborder ISCHNOCERA

Suborder RHYNCHOPHTHIRINA

This classification states that the Psocoptera are the sister group of the four following taxa, the Anoplura are the sister group of the three mallophagan taxa, and the Amblycera are the sister group of the Ischnocera-Rhynchophthirina.

The following diagnosis is made from the phylogram for each of the psocodean taxa recognized in the classification.

Order PSOCOPTERA—Winged psocodeans with hypognathous head; antennae filiform, with 12-50 segments; biting-chewing mouthparts with mandibles, maxillary palps four-segmented, and labial palps one to two segmented; three dorsal ocelli and compound eyes distinct; tentorium complete; prothorax distinct; tarsi two to three segmented, with two claws and pulvilli; thorax with two pairs labial glands in thorax; in apterous forms and nymphs, eyes reduced or vestigial and pterothorax fused; free living.

Order ANOPLURA—Apterous psocodeans with prognathous head; antennae filiform, with three to five segments; piercing-sucking mouthparts internal, without visible mandibles, maxillary and labial palps; ocelli lacking and compound eyes reduced or lacking; tentorium completely lacking; thoracic segments completely fused; tarsi one segmented, with one claw and no puvilli; thorax completely fused, with one pair dorsal spiracles and abdomen with six or fewer pairs lateral spiracles; 2 pairs labial glands in thorax; hosts—mammals.

Order MALLOPHAGA—Apterous psocodeans with horizontal and rarely prognathous head; antennae filiform or capitate, with three to five segments; chewing mouthparts modified, with mandibles; ocelli lacking and compound eyes reduced or completely lacking; tentorium reduced, without dorsal arms; prothorax distinct; tarsi one or two segmented, with one or two claws and no puvilli; thorax with one pair ventral or lateroventral spiracles and abdomen with six or fewer pairs lateral spiracles; one pair labial glands in head and often additional pair on thorax; hosts—birds and mammals.

Suborder AMBLYCERA—Head wide and horizontal, with capitate antennae inserted in fossae and third antennal segment pedunculate; mandibles with dorsal and ventral articulations; maxillary palps two to five segmented; labial palps one segmented or absent; hosts—birds and mammals.

Suborder ISCHNOCERA—Head wide and horizontal, with filiform antennae exposed; mandibles with anterior and posterior articulations; maxillary palps absent; labial palps one segmented; hosts—birds and mammals.

Suborder RHYNCHOPHTHIRINA—Head prognathous, prolonged into rostrum, with filiform antennae exposed; mandibles laterally articulated at apex of rostrum; maxillary and labial palps vestigial; hosts—mammals.

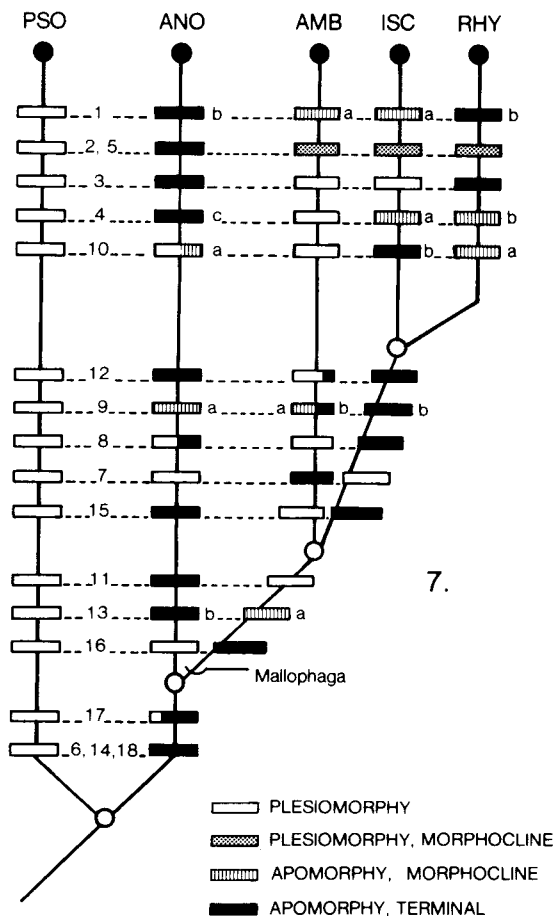


FIG. 7.—Phylogram showing phylogenetic relationships of the Psocodea and similarities by synapomorphy, symplesiomorphy, and autapomorphy. Numerals indicate characters. PSO, Psocoptera; ANO, Anoplura; AMB, Amblycera; ISC, Ischnocera; RHY, Rhynchophthirina; a, b, c, apomorphy, morphocline.

Conclusions

The Psocodea are a monophyletic group whose origin dates from the Carboniferous to the early Permian. The Psocoptera including the fossil Permopsocida are monophyletic. The Anoplura are a higher taxon distinct from the remainder of parasitic Psocodea and must have evolved independently from the main line for a long period of time, perhaps as early as the Jurassic. The Mallophaga, including Amblycera, Ischnocera, and Rhynchophthirina, represent a diverse group, perhaps paraphyletic, but are distinct as a higher taxon from the Psocoptera and Anoplura (Fig. 8).

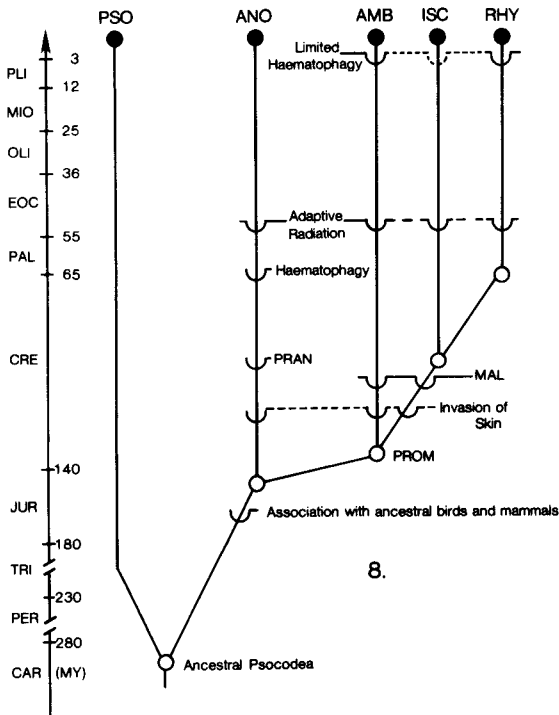


FIG. 8.—Phylogenetic tree of the Psocodea. PSO, Psocoptera; ANO, Anoplura; AMB, Amblycera; ISC, Ischnocera; RHY, Rhynchophthirina; MAL, Mallophaga; PRAN, Protanoplura; PROM, Protomallophaga; CAR, Carboniferous; PER, Permian; TRI, Triassic; JUR, Jurassic; CRE, Cretaceous; PAL, Paleocene; EOC, Eocene; OLI, Oligocene; MIO, Miocene; PLI, Pliocene.

All the parasitic Psocodea are descended from a common psocodean stock but each higher taxon within the Psocodea may be traced back to a specific preparasitic psocodean ancestor. Each of the phyletic lines independently developed many similar morphological and ontogenetic characters related to a parasitic mode of life. The following characters developed by the parasitic mode of life are commonly found among parasitic members of the Psocodea: (1) dorsoventral flattening and prognathy of head, (2) reduction of the antennal segments, (3) development and arrangement of the antennal sensilla, (4) reorganization of the thoracic segments, (5) reduction in the number of thoracic and abdominal spiracles, (6) reduction of the tarsal segments and loss of pulvilli, (7) presence of symbionts and obturaculum, and (8) three nymphal stages.

The phylogram and the classification proposed here differ from those postulated by Kim and Ludwig (1978b) in the following: (1) the classification directly depicts the phylogram; (2) the set Ischnocera + Rhynchophthirina forms the terminal sister group of the Amblycera; and (3) the three-taxon set Amblycera + Ischnocera + Rhynchophthirina is the sister group of the Anoplura.

The Anoplura are not directly related to either the Ischnocera or the Rhynchophthirina. Many similarities among Ischnocera, Rhynchophthirina, and Anoplura are the result of parallel evolution (Fig. 7). Thus, the contention of Haub (1980) is not supported, and the classification by Königsmann (1960) is rejected.

All the facts suggest that the higher taxa of the parasitic Psocodea have evolved independently and satisfy the conditions set up for parallel evolution by Eldredge and Cracraft (1980). Thus, the concept of parallelism should be retained, contrary to the view presented by many cladists.

Some primitive psocodeans made the first evolutionary breakthrough by associating themselves with ancestral birds and mammals (warm-blooded vertebrates) perhaps during the late Triassic or Jurassic Period as Proaves and Panthotheria began to appear (Romer 1966). Later, perhaps as early as the late Jurassic or the early Cretaceous, they made a major evolutionary shift into a new habitat—the body surface and dermal products (feathers and furs) of birds and mammals—in the early Cretaceous (Fig. 8). The invasion and exploitation of this new adaptive zone resulted in considerable modification of several major character complexes, such as the head, thorax, legs, sensory organs, life cycles, and reproduction.

The mammalian Mallophaga are commonly considered to have derived from bird-infesting mallophagans (Harrison 1916, Webb 1946), and a primitive psocodean ancestor became parasitic first on birds (Clay 1949). The fact that the Gyropidae, Boopidae, and Trimenoponidae among Amblycera, Trichodectidae among Ischnocera, and Haematomyzidae (Rhynchophthirina) infest mammals perhaps supports the avian origin of the mammalian Mallophaga. However, if this view is accepted, the mammal-infesting Amblycera and Ischnocera must have diverged from the avian mallophaga quite early and evolved independently along with other lice. The mallophagan infestations of both birds and mammals could also support the argument that primitive psocodean ancestors had invaded ancestral birds and mammals simultaneously considering the geological age of both host groups.

Some specialized Amblycera (*Trimenopon* and *Trochiloecetes*) and Rhynchophthirina (*Haematomyzus*) made another evolutionary shift to blood feeding (Clay 1949) very late in the mallophagan evolution (Fig. 8), as evidenced by the retention of the principal organization and structures of the chewing mouthparts (Kim and Ludwig 1978b).

The Protanoplura made two major evolutionary shifts, the invasion of a new habitat (the body surface and fur) on mammals perhaps between the Jurassic and Cretaceous, and the exploitation of a new food source (blood) after they were well established in the first shift, perhaps during the late Cretaceous or the early Paleocene (Fig. 8). Once the Anoplura were established in their adaptive zone, rapid radiation must have taken place without changing much of the primary characters which were involved in the breakthrough to their adaptive zone.

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