

## Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocodea: Phthiraptera)

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**ABSTRACT.** Apomorphies that have been proposed for the Psocodea, Psocoptera, Phthiraptera and superfamilial groups within the Phthiraptera are enumerated and evaluated. The Psocodea and Phthiraptera are considered to be holophyletic, but the sister-group of the Phthiraptera lies within the Psocoptera. Within the Phthiraptera the Anoplura and Rhyncophthirina form a holophyletic group whose sister-group is the Ischnocera, and the Amblycera is the sister-group of this assemblage. The common ancestor of the Phthiraptera is suggested to have been parasitic, and all lice are believed to have evolved under environmental constraints similar to those operating today. On the evidence provided by host relationships the origin of the lice is dated as the Cretaceous, but the host of the ancestor of the order is not identified. The lice of marsupials in South America and Australia are not considered to comprise a holophyletic group.

### Introduction

The superorder Psocodea comprises two orders: the Psocoptera (booklice, barklice) and the Phthiraptera (lice). This paper is concerned mainly with the latter order, although the holophyly of both the Psocodea and the Psocoptera is discussed. The cladistic relationships of the Psocodea to other insects, and the group names used in this study, are given in Fig. 1.

Psocoptera and Phthiraptera are in many respects morphologically similar, and the differences between them can probably be attributed to adaptations to their very different environments. The Psocoptera are free-living insects feeding on fungi or fragments of animal or vegetable matter. Some are associated with

mammals or birds through dwelling in their nests, but none are parasitic. Phthiraptera have no free-living stage and are all obligate ectoparasites of mammals and birds. They feed on skin, feathers, sebaceous exudates or blood.

The Phthiraptera are generally recognized as comprising four major groups: Anoplura, Rhyncophthirina, Ischnocera and Amblycera. The Anoplura are colloquially known as sucking lice, the others (sometimes grouped as the Mallophaga) as chewing lice. The phylogenetic relationships of these four groups and the way in which they should be classified are matters of some contention (Königsmann, 1960; Kim & Ludwig, 1978, 1982; Boudreaux, 1979; Haub, 1980). All these authors use cladistic methodology in their analyses, but they disagree on the results: for example, only Kim & Ludwig (1982) believe the Mallophaga to be holophyletic, the others identifying it as a

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paraphyletic group. Kim & Ludwig (1978, 1982) use the Mallophaga as an ordinal name in the traditional manner to include all three groups of chewing lice. Boudreaux (1979) retains Mallophaga as an ordinal name but restricts it to the Amblycera, and Königsman (1960) and Haub (1980) reject the use of Mallophaga and include all groups in the order Phthiraptera. Two areas of contention may therefore be identified: (1) the evaluation and polarity determination of character states, with consequent identification of holophyletic groups, and (2) the relationship between the results of a systematic analysis and the structure of the classification applied to the groups analysed. Details of the disagreements on particular points will be indicated below where appropriate.

The time of origin of the Phthiraptera is uncertain, and dates ranging from the late

Cretaceous (c. 64 m.y.b.p.) to the late Carboniferous (c. 280 m.y.b.p.) have been proposed. Most discussions of this problem have included the assumptions that (1) obligate parasitism and host specificity arose only after the evolution of the modern groups of lice (and hosts), and (2) that there was a more or less lengthy period of evolution of the order before the advent of birds and mammals. Both of these assumptions are open to challenge.

The objectives of this paper may be summarized as follows: (1) to re-evaluate the apomorphies proposed by previous authors for holophyletic groups within the Psocodea and to propose additional apomorphies; (2) to perform a cladistic analysis on the major groups of parasitic Psocodea (lice); (3) to provide a classification for the parasitic Psocodea; (4) to discuss the origin of the lice in the light of the cladistic analysis.

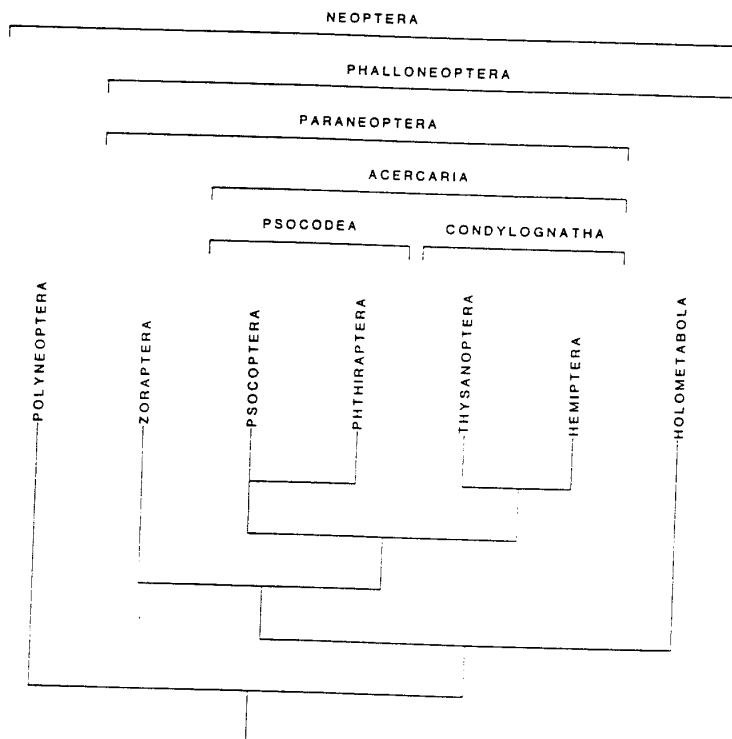


FIG. 1. Phylogeny and classification of the Neoptera showing the systematic position of the Phthiraptera.

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## Methods

The term 'holophyletic' is used below to refer to groups of taxa comprising a single ancestral species (known or inferred) and all of its descendants. The more familiar term 'monophyletic' is avoided because ambiguities in its use by some of the authors cited above have caused misunderstandings in the resolution of systematic problems in the Psocodea.

A cladistic analysis is only possible if the groups discussed are holophyletic; inclusion of paraphyletic or polyphyletic assemblages must invalidate hypotheses of cladistic relationships. The first step in any analysis must therefore be to determine, by the distribution of apomorphies, that all the groups included in the analysis are holophyletic. In this study hypotheses of holophyly are tested by (1) evaluation of 'supporting' apomorphies, both 'new' and proposed in the literature, and (2) search for and evaluation of 'falsifying' apomorphies. Evaluation is by consideration of four assumptions implicit in any hypothesis of apomorphy: (1) that the initial observations are correct; (2) that the polarity assignment is correct; (3) that the apomorphic state is homologous and not homoplastic in the taxa concerned; (4) that apomorphies considered separate should not more properly be considered 'linked' as aspects of a single complex character. If apomorphies listed below are considered 'justified' by the correctness of these four assumptions, no comment is made on them.

In this study there are seven taxa to be considered: the Anoplura, the Rhyncophthirina, the Ischnocera, the Amblycera, the Phthiraptera (comprising the previous four groups), the Psocoptera, and the Psocodea (comprising the Phthiraptera and the Psocoptera). Further groups within the Phthiraptera, comprising various combinations of the four constituent taxa, are also discussed. The polarity and relative apomorphy of character states are assessed by reference to an outgroup, the Condylognatha (comprising the orders Hemiptera and Thysanoptera). This group is identified as the sister-group of the Psocodea by a

number of authors (e.g. Hennig, 1981; Kristensen, 1975, 1981; Boudreaux, 1979). A cladogram of the section of the Insecta including the Psocoptera, the Neoptera, is given in Fig. 1.

## Apomorphies proposed for the Psocodea

(1) *Development of structural mechanism for rupturing the antennae* (Seeger, 1975; Seeger in Hennig, 1981).

(2) *Reduction of ovipositor* (Boudreaux, 1979).

(3) *Loss of cardo* (Matsuda, 1965; Kim & Ludwig, 1978). Kim & Ludwig (1978) consider that the cardo is fused to the stipes rather than lost, but this does not affect the validity of the apomorphy.

(4) *Loss of loral arm* (Matsuda, 1965).

(5) *Development of atmospheric water-vapour uptake system*. The structural components of the water-vapour uptake system (the ovoid lingual sclerites connected by a Y-shaped filamentous duct to the cibarial sclerite) are identified as such by Rudolph (1982a, b, 1983). The mechanism is found only in Psocodea, and is accepted here as apomorphic for the group, although it is not present in the highly-modified Rhyncophthirina and Anoplura (the lingual sclerites were seen in the anopluran embryo by Seeger, 1979). Water vapour is condensed on the lingual sclerites and pumped through the duct by the action of the cibarial pump (the cup-shaped cibarial sclerite acting in conjunction with an epipharyngeal process). The two components of the cibarial pump are identified as apomorphic developments of the Psocodea by Königsmann (1960) and Kristensen (1975) respectively. A cibarial pump of very similar structure is present in the Thysanoptera (Matsuda, 1965; Heming, 1978), and thus the cibarial pump may be a plesiomorphic development within the Acercaria and lost in the Hemiptera.

A further component of the cibarial pump is probably to be found in the enlarged clypeus of the Psocoptera, which houses the cibarial dilator muscles. Smithers (1972) identifies this as an apomorphic development of the order and indicative of its holophyly. Some enlargement of the clypeus to house the cibarial dilator muscles is present in the Thysanoptera.

but the separate modifications of the head in both this order and the Phthiraptera may obscure any such enlargement. The form of the psocopteran clypeus cannot be used with confidence as an apomorphy of this group.

(6) *Lacinia protrusible and retractable, serving as 'pick'* (Boudreaux, 1979). Boudreaux (1979) includes in his formulation of this apomorphy the detachment of the lacinia from the rest of the maxilla, despite having already cited this development as apomorphic for the Acercaria. Heming (1978) notes that the lacinia of Thysanoptera is also protrusible and retractable, whilst Hennig (1981) suggests that some degree of lacinial transformation is characteristic of all Acercaria. Smithers (1972) holds a conflicting view, maintaining that this character state is an autapomorphy of the Psocoptera and is 'convergent in some Mallophaga'. The view of Hennig (1981) is held here, and the character state taken as a possible apomorphy of the Acercaria.

(7) *Ovarioles polytrophic* (Königsmann, 1960; Kristensen, 1975, 1981; Seeger in Hennig, 1981). Heming (1977) suggests that, as polytrophic or acrotrophic ovarioles (the latter being derived from the former) are found in the Psocodea, Hemiptera and throughout the Holometabola, the plesiomorphic panoistic ovariole was lost in the stem-group of the Acercaria plus Holometabola (he excludes Zoraptera from the Phalloneoptera) and secondarily regained only in the Thysanoptera. If the Zoraptera are placed as sister-group to the Acercaria (as suggested by Hennig, 1981, and Kristensen, 1975, 1981), reversal must be postulated to have occurred twice (once in the Zoraptera, once in the Thysanoptera). This is a more parsimonious proposal than postulating convergent gain of the polytrophic condition in the Psocodea, Hemiptera and Holometabola.

(8) *Failure of mesomeres to fuse and form aedeagus* (Boudreaux, 1979). Snodgrass (1935) defines the aedeagus as a tube comprising the fused mesomeres, through which the endophallus is everted. This structure is found only in the Phalloneoptera and may be an autapomorphy of this group, lost in the Diptera (Matsuda, 1976) and the Psocodea. If this is the case the Psocodea are characterized by a further apomorphy, the development of the permanently-everted endophallus (Lyal,

1985a). Two alternative hypotheses are available: (1) that the aedeagus is apomorphic for the Condylgnatha plus the Holometabola and the Psocodea is the sister-group of this assemblage, and (2) that the aedeagus is a convergent development in the Condylgnatha and the Holometabola. There is insufficient evidence at present to allow a decision to be made between the three hypotheses and, as the investigation of the problem is beyond the scope of the present paper, no apomorphy is proposed here.

It is pertinent to note that Smithers (1972) considers the male genitalia of Psocoptera and Phthiraptera totally different and supporting in their form the holophyly of the former group with respect to the latter. In this study, however, the male genitalia of the two groups are considered to be so similar that a specimen could not be placed with confidence in one group rather than the other by study of this structure alone and without knowledge of the species or genus concerned.

(9) *Parameres and mesomeres both clasping* (Boudreaux, 1979). This supposed apomorphy is not supported by observations of mating mechanics in lice, and is rejected.

Apomorphies 1-5 above suggest by their distribution the holophyly of the Psocodea, and no apomorphies are available which indicate the holophyly of any group within the Psocodea and some group presently excluded. The holophyly of the Psocodea is therefore accepted.

#### Apomorphies proposed for the Phthiraptera

(10) *Haploid reduction in primary spermatogonia* (White, 1957).

(11) *Development of hydropyle in egg*. The presence of a basal hydropyle of the egg has not previously been used as an apomorphy of the Phthiraptera. The hydropyle is not found elsewhere in the Acercaria.

(12) *Development of operculum in egg* (Königsmann, 1960; Haub, 1980).

(13) *Egg-cement vaginal, not anal* (Königsmann, 1960; Haub, 1980). The proposal of this character-state as apomorphic follows the observation that in Phthiraptera the cement is produced in accessory glands apparently ab-

sent from the Psocoptera (Florence, 1921; Weber, 1936; Mukerji & Sen-Sarma, 1955). There have been no observations of the actual source of the cement in Psocoptera or those lice which also lack the glands, however, and without these the proposal must be regarded as unfounded.

(14) *Dorsoventral compression of head* (Boudreaux, 1979). This apomorphy is variably expressed in lice, being most marked in the Amblycera and Ischnocera.

(15) *Development of prognathy* (Boudreaux, 1979). Among the lice only Anoplura and Rhyncophthirina are truly prognathous. In Amblycera the mouth, whilst anterior, is displaced onto the ventral surface of the head by the extension of the clypeus, a state similar to that in Ischnocera where the mouth is displaced even further posteriorly by the pulvinus. Prognathy may be apomorphic only for the Anoplura and Rhyncophthirina or (perhaps less likely) for the whole order but more or less lost in the Amblycera and Ischnocera.

(16) *Movement of suproesophageal ganglion posteriorly* (Königsmann, 1960; Boudreaux, 1979). This feature is probably linked to the alteration of head shape (character 14).

(17) *Loss of dorsal tentorial arms* (Symmons, 1952; Boudreaux, 1979). This apomorphy is probably linked to the alteration of head shape (character 14). See comment following character 70.

(18) *Virtual loss of discrete abdominal ganglia* (Königsmann, 1960). This incorporation of the abdominal and third thoracic ganglia into a composite ventral ganglion is an extreme of a transformation series, amalgamation of the abdominal ganglia being an apomorphy of the Acercaria.

(19) *Reduction of lacinial stylets* (Königsmann, 1960; Boudreaux, 1979). The stylets are lost in the Rhyncophthirina and Anoplura. See comment following character 22.

(20) *Development of lacinial gland* (Symmons, 1952; Boudreaux, 1979). The gland is not present in the highly-modified Rhyncophthirina and Anoplura, but whether or not this is a secondary absence cannot be directly determined. See comment following character 73.

(21) *Great reduction in maxillae* (Matsuda, 1965; Boudreaux, 1979). See comment following character 22.

(22) *Reduction of labial palpi* (Symmons, 1952; Boudreaux, 1979). In the Rhyncophthirina and Anoplura the labial palpi are lost. Apomorphies 19, 21 and 22 may all be aspects of a single apomorphy, the reduction of the mouthparts.

(23) *Reduction of antennal flagellum to three flagellomeres (plus pedicel)* (Königsmann, 1960; Boudreaux, 1979).

(24) *Loss of wings* (Boudreaux, 1979). See comment following character 26.

(25) *Loss of ocelli* (Königsmann, 1960; Boudreaux, 1979). Throughout the Acercaria the presence of wings and ocelli are linked, and therefore this character cannot be considered as independent from character 24. See comment following character 26.

(26) *Reduction of compound eye to two ommatidia* (Boudreaux, 1979). Further reduction, to one ommatidium or complete absence, takes place within the group (see character 85).

The three characters above may be the result of heterochronous development, perhaps associated with the reduction in number of nymphal stadia (see character 27) (Matsuda, 1976). Although these characters are presented as autapomorphies of the Phthiraptera, they are all found in at least some members of the Liposcelidae (Psocoptera).

(27) *Reduction to three nymphal stadia* (Königsmann, 1960; Boudreaux, 1979; Haub, 1980).

(28) *Loss of abdominal spiracles 1 and 11* (Königsmann, 1960; Boudreaux, 1979). Similar loss is found in some members of the Liposcelidae (Psocoptera); see discussion below on phthirapteran-liposcelid relationships.

(29) *Loss of metathoracic spiracle* (Königsmann, 1960; Boudreaux, 1979).

(30) *Loss of trochantin* (Boudreaux, 1979).

(31) *Reduction of ovipositor*. Boudreaux (1979) suggests that the ovipositor is completely lost in the Phthiraptera, but gonapophysis VIII has been retained in the Trichodectidae, Rhyncophthirina, Anoplura and some Amblycera and Ischnocera. See discussion following character 89.

(32) *Reduction of testicular follicle number to three* (Boudreaux, 1979). Further reduction to two follicles occurs in the Phthiraptera, the polarity of the transformation series being supported by histological evidence (Schmutz,

1955) (see character 86). The status of the reduction to three as an apomorphy of the Phthiraptera is doubtful, however. Reduction has certainly occurred in the Psocodea, as more follicles are present in other Acercaria and some Polyneoptera (Matsuda, 1976). However, within the Psocoptera the number is either one or three (rarely four), the Liposcelidae for example having three. This pattern of variation indicates a considerable degree of homoplasy, and there is disagreement over the plesiomorphic state for the order (Wong & Thornton, 1968; Matsuda, 1976). In view of this, character 32 cannot be used as an apomorphy for the Phthiraptera.

(33) *Adoption of ectoparasitic habit on vertebrate hosts* (Boudreaux, 1979). Kim & Ludwig (1978, 1982) argue that the ectoparasitic habit was attained separately in the Anoplura and the 'Mallophaga', although they present no evidence supporting this view. As some of the apomorphies listed above are probably adaptations to ectoparasitism, treating the habit as an apomorphy in the same analysis would add undue weight.

Although a number of the supposed apomorphies listed above are rejected, the distribution of those accepted supports the holophyly of the Phthiraptera. A supposed apomorphy not mentioned above, the 'closure of the posterior border of the sitophore sclerite' (Haub, 1973) links all Psocodea except the Rhyncophthirina (in which the sclerite is absent) and the Ischnocera: Trichodectidae. This supposed apomorphy is not supported by any others and is rejected. The significance of those apomorphies apparently shared with the Psocoptera: Liposcelidae will be discussed below.

#### Apomorphies proposed for the Psocoptera

(34) *Reduction in thickness of chorion* (Seeger, 1979; Seeger in Hennig, 1981). The very thin chorion is offset by a thick serosal cuticle (suborder Trogiomorpha) or added suprachorionic layers such as coverings of silk, encrustations from anal secretions and other debris (suborders Troctomorpha and Psocomorpha) (Seeger, 1979).

(35) *Loss of micropyles* (Seeger, 1979; Seeger in Hennig, 1981). Königsmann (1960) and

Haub (1980) contend that the absence of micropyles is plesiomorphic within the Acercaria and their presence in the Phthiraptera is apomorphic. As micropyles are also present in the Condylognatha this is unlikely, and their absence in the Psocoptera must be considered apomorphic. Absence of micropyles may be connected with the thinness of the chorion (character 34).

(36) *Loss of aeropyles* (Seeger, 1979; Seeger in Hennig, 1981). The absence of aeropyles may be associated with the thinness of the chorion, and perhaps should not be considered as distinct from this apomorphy.

(37) *Loss of chorionic sculpturing*. Smithers (1972) proposes this as an apomorphy of the psocopteran suborders Troctomorpha and Psocomorpha, as sculpturing is present on the eggs of the third suborder, Trogiomorpha. Seeger (1979) points out that the sculpturing of trogiomorph eggs is derived from serosal cuticle, not the chorion. Loss of chorionic sculpturing is therefore a synapomorphy of all three suborders. The loss may be a consequence of the thinness of the chorion, and perhaps should not be considered separately.

(38) *Adoption of unusual (dorsal) position in egg by embryo, with no rotation of egg and embryo* (Seeger, 1979; Seeger in Hennig, 1981).

(39) *Adoption of unusual manner of folding of embryonic appendages* (Seeger, 1979; Seeger in Hennig, 1981).

(40) *Insertion of dorsal longitudinal muscles on strongly-arched mesoscutum* (Boudreaux, 1979).

(41) *Suppression or reduction of prophragma and mesophragma* (Boudreaux, 1979). The phragmata are reduced in the Phthiraptera, so reduction in the Psocoptera does not provide an apomorphy precluding paraphyly of this group with respect to the lice. The reduction of the prophragma is related to the transfer of the insertion of the longitudinal mesothoracic muscles to the mesoscutum (character 40), and should not be considered as distinct from this. The mesophragma, contrary to Boudreaux' assertion, is present and not reduced in the Psocoptera (Badonnel, 1934).

(42) *Reduction of prothorax* (Smithers, 1972; Boudreaux, 1979: 226). Boudreaux (1979: 280) lists 'Metathorax small'—presumably an error for prothorax. The char-

acter was limited by Smithers (1972) to winged forms only and does not apply to apterous members of the group, in which the apomorphy is presumed to be reversed. The apomorphy does not provide evidence precluding paraphyly of the Psocoptera with respect to the apterous Phthiraptera.

(43) *Spermatozoa biflagellate and uni-flagellate in each sperm bundle* (Boudreaux, 1979). The extent of this character state and the state in the Phthiraptera is not known, as published information is very limited.

(44) *Media of forewing three-branched* (Boudreaux, 1979). This feature is not found in some Permopsocida (Hennig, 1981), an absence probably due to the nature of the group which, according to Hennig (1981), comprises members of the stem-groups of the Acercaria, Psocoptera, and possibly other acercarian orders. See comment following character 47.

(45) *Cu and Mp united at base* (Boudreaux, 1979). See comment following character 47.

(46) *Rs forked* (Boudreaux, 1979). Hennig (1981) refers to this as a plesiomorphic character state for the Psocodea. See comment following character 47.

(47) *Wings coupled at rest by blunt projection of stigma of forewing* (Boudreaux, 1979; Seeger, 1979). This character state is rather more variable than implied by Boudreaux (1979) but is unlikely to have arisen more than once.

Although the four character states 45–47 are suggested as apomorphies for the Psocoptera it is clear, despite the assertions of Smithers (1972) and Boudreaux (1979), that they do not provide evidence precluding paraphyly of the group with respect to the secondarily apterous Phthiraptera.

(48) *Antennal flagellum slender and setiform* (Boudreaux, 1979). The form of the psocopteran antenna does not preclude reduction to the phthirapteran condition and does not therefore provide evidence against paraphyly of the Psocoptera.

(49) *Form of the female genitalia* (Smithers, 1972). Smithers (1972) is not precise about the nature of this supposed apomorphy, but there seems no reason to suppose that the very reduced form of the female external genitalia of the Phthiraptera (Lyal, 1985a) could not have been derived from the psocopteran type.

A hypothesis of holophyly of the Psocoptera is supported by the distribution of five apomorphies (34–39), but refuted by the distribution of five others (24–26, 28 and 32) that indicate the holophyly of a group comprising the Phthiraptera and the Psocoptera: Liposcelidae. Smithers (1972) suggests that the Liposcelidae are 'highly derived', but most of the derived features cited are those in which the Liposcelidae approach the Phthiraptera. Apomorphies proposed by Smithers (1972) for the establishment of the phylogenetic position of the Liposcelidae, with the exception of those pertaining to the wings, are listed and discussed below. The distribution of these character states, together with others listed above and below and pertinent to the holophyly of the Psocoptera, is presented in Table 1.

TABLE 1. Distribution of apomorphies within the Psocodea. 'Gain' states are indicated by 'g', 'loss' states by 'l', and states not present in all members of a taxon by '(g)' and '(l)' respectively. For explanation of characters see text.

TAXON	PSOCOPTERA						
	PHTHIRAPTERA	LIPOSCELIDAE	SPHAEROPSOCIDAE	AMPHITENOMETAE	PACHYTROCTIDAE	PSOCOMORPHA	TROGLOMORPHA
CHARACTER							
34		g	g	g	g	g	g
35		l	l	l	l	l	l
36		l	l	l	l	l	l
37		l	l	l	l	l	l
38		g	g	g	g	g	g
39		g	g	g	g	g	g
50	(g)	(g)	g	g	g		
54		l	l	l	l	l	
55		l	l	l	l		
56		l	l	l	l		
22		l	l	l	l		
24		l	(l)	(l)	(l)		
25		l	(l)	(l)	(l)		
84		(g)	(g)	(g)			
14		l	l				
26		l	l				
57		l	l				
28		l	(l)				

(50) *Development of T-shaped sclerite in female subgenital plate.* This sclerite is absent in some members of the Liposcelidae (Smithers, 1972), and probably from all Phthiraptera, although the subgenital plate in the latter group frequently bears a sclerite of some form.

(51) *Development of secondary annulations on antennal flagellomeres distal to flagellomere IV.* The absence of flagellomeres distal to flagellomere III in the Phthiraptera renders this character state irrelevant to any discussion of paraphyly or holophyly of the Psocoptera. The flagellomeres of some Amblycera (Phthiraptera) do possess secondary annulations.

(52) *Loss of pilosity on external lobe of gonapophyses.* The absence of gonapophyses in most Phthiraptera, and the considerable degree of modification of these structures when they are present, renders this character state irrelevant to any discussion of paraphyly or holophyly of the Psocoptera.

(53) *Anterior closure of male basal apodeme.* The ontogeny of this structure is such that the anterior end is always 'closed', whilst the degree of sclerotization and of anterior divergence of the lateral margins is very variable in the Phthiraptera.

(54) *Absence of paraproct spine.* This character state is also found in the Phthiraptera, but may be plesiomorphic for that group.

(55) *Absence or reduction of Pearman's organ.* Pearman's organ is absent in the Phthiraptera, but absence may be plesiomorphic for the group.

(56) *Absence of trichobothrial field.*

(57) *Shortening of legs.*

### The sister-group of the Phthiraptera

From Table 1 it can be seen that the holophyly of the Psocoptera is supported by the distribution of six apomorphies, of which 34, 35, 36 and 37 are aspects of a single apomorphy and 38 and 39 are probably linked in a similar way. The holophyly of the Liposcelidae plus Phthiraptera (and thus the paraphyly of the Psocoptera) is supported by the distribution of twelve apomorphies, of which 24 and 25 are linked and 50 and 84 are of very dubious validity. If the Psocoptera are holophyletic there has been convergence of seven or nine 'loss' character

states and two (dubious) 'gain' character states; if they are paraphyletic there has been secondary loss of four 'gain' character states (one of which is anyway lost in some Liposcelidae) and, linked with one of these, reversal of three loss states. The majority of apomorphies therefore supports holophyly of the Liposcelidae plus Phthiraptera, but all these apomorphies are loss character states which can be given low (or no) phylogenetic 'weight'. Waage (1979) suggests that the Phthiraptera arose from a nidicolous ancestor much like some modern Liposcelidae in habit, and the holophyly of the Psocoptera implies that this ancestor was itself derived from a winged insect similar to the Psocoptera (with the possible exceptions of apomorphies 34-39). The selective pressures acting on this ancestor would, by reason of its habitat, have been very similar to those acting on modern (and ancestral) Liposcelidae, and may be presumed to have favoured the same set of adaptations. These adaptations include not only the 'loss' character states mentioned above, but also behavioural and physiological adaptations that must be accounted 'gains'. If allowance is made for these 'gain' synapomorphies of the ancestors of the Liposcelidae and the Phthiraptera, the hypothesis that these ancestors were the same becomes more parsimonious than that they were different. Because of this the Liposcelidae and the Phthiraptera are here accepted as sister-groups and the Psocoptera is postulated to be paraphyletic with respect to the Phthiraptera. It is presumed that the adoption of the ectoparasitic habit by the ancestor of the phthiraptera imposed a new set of environmental pressures on the egg, which reverted to the plesiomorphic thick-chorion form but developed an operculum, maintaining easy egress for the nymph. Embryonic orientation within the egg also reverted to the plesiomorphic state.

An alternative hypothesis is presented by Kim & Ludwig (1982). They suggest that the Mallophaga (Amblycera, Ischnocera and Rhyncophthirina) arose from the Permopsocida: Dichentomidae and the Anoplura from the Permopsocida: Lophioneuridae. They also state that both the Psocoptera (including the Permopsocida) and the Phthiraptera are monophyletic (i.e. holophyletic, given the context). These statements are clearly contra-



dictory. The evidence supporting the proposed ancestry of the Mallophaga is that the Dichtenomidae have both a short rostrum and antennae placed in pits, these being apomorphies associated with the Rhyncophthirina and Amblycera respectively. No evidence is given for the relationship proposed between the Anoplura and the Lophioneuridae, although the lophioneurids are described as having 'a broad head, a character state found among the mallophagans'. The Dichtenomidae and the Lophioneuridae do not form a holophyletic group (Smithers, 1972), and it is shown below that the Mallophaga as defined by Kim & Ludwig (1982) are not holophyletic either. The hypothesis proposed by Kim & Ludwig (1982) demands that the Psocoptera (s.lat.), the Phthiraptera and the Mallophaga are all paraphyletic, a fact which their cladistic analysis purports to disprove. No evidence has been found in this study to support their hypothesis, which is rejected.

#### Apomorphies proposed for the Amblycera

(58) *Development of pedunculate first flagellar 'segment'* (Clay, 1970; Boudreaux, 1979; Kim & Ludwig, 1982). Haub (1980) refers to the presence of a 'peduncle-like part between the scape and the flagellum', presumably the pedicel, as being a plesiomorphic character state within the Psocodea, its loss being a synapomorphy of the Ischnocera, Rhyncophthirina and Anoplura. However, the pedicel is not pedunculate in any of the Psocodea and the first flagellomere is pedunculate only in the Amblycera, an autapomorphy of this group. See comment following character 88.

(59) *Development of antennal fossa concealing antennae* (Boudreaux, 1979).

Apomorphies 58 and 59 indicate the holophyly of the Amblycera. Paraphyly of the group is indicated by the distribution of apomorphy 84 (see Table 2), but this hypothesis is rejected as less parsimonious.

#### Apomorphies proposed for the Rhyncophthirina

(60) *Prolongation of head anteriorly into rostrum with mandibles terminal and rotated through 180 degrees; suppression of tibiotarsal*

*muscles; extension of pretarsal apodeme into femur without tibial muscle bundle* (Boudreaux, 1979).

(61) *Reduction of posterior tentorial arms and loss of tentorial bridge* (Boudreaux, 1979). The tentorium is absent from all Anoplura, so character 61 is apomorphic for both Rhyncophthirina and Anoplura. See character 70.

A further apomorphy of the Rhyncophthirina, the migration of one pair of labial glands from the thorax to the head, is discussed below (character 94) as it was initially (mistakenly) proposed for the Mallophaga. There is no doubt that the two species of Rhyncophthirina together form a holophyletic group.

#### Apomorphies proposed for the Anoplura

(62) *Development of piercing stylets from hypopharynx and labium; great development of connective tissue septum (obturaculum—see character 78); fusion of pronotum to mesonotum; reduction of mesothoracic and metathoracic terga, with dorsal extension to thoracic pleura* (Kim & Ludwig, 1978; Boudreaux, 1979).

(63) *Thoracic spiracles on dorsal part of the pleurum* (Boudreaux, 1979). This condition is found throughout the Phthiraptera (Matsuda, 1970), and thus is not an autapomorphy of the Anoplura. The dorsal position of the spiracle on the anopluran thorax is a result of the autapomorphic dorsal extension of the pleura (character 62, in part).

(64) *Tibia modified for grasping hair of host* (Boudreaux, 1979). This character state is also found in the Ischnocera, particularly the Trichodectidae.

The apomorphies listed under character 62 strongly indicate the holophyly of the Anoplura.

#### Apomorphies proposed for the Ischnocera

(65) *Rotation of mandibles to operate about a vertical axis* (Boudreaux, 1979). The autapomorphic modifications of the mouthparts of the Rhyncophthirina and Anoplura do not preclude this form of mandibular articulation being ancestral. This character state, therefore, whilst apomorphic, cannot be used as an apomorphy of the Ischnocera.

(66) *Development of pulvinus*. Although restricted to the Ischnocera and plainly apomorphic, this character state cannot be used to demonstrate the holophyly of the group for the same reasons as outlined for character 65.

(67) *Separation of small rhombic sclerite from anterior pronotal margin*. This sclerite is present in all Ischnocera except some Philopteridae, and occurs in no other group. In some species of *Anatoecus* (Philopteridae) the sclerite is present but not detached from the pronotal margin. The distribution of the apomorphy suggests the paraphyly of the Philopteridae with respect to the other Ischnocera.

(68) *Absence of mandibulo-hypopharyngeal muscle* (Symmons, 1952; Haub, 1973). This loss is proposed as an apomorphy of all Ischnocera except Trichodectidae, in which the muscle is reduced, but relatively few ischnoceran genera have so far been examined. The loss of the muscle in Rhyncophthirina is possibly homoplastic and connected with the extensive modifications to the mouthparts of this group.

None of the apomorphies above support directly the holophyly of the Ischnocera. Not only is it not possible to demonstrate the holophyly of the group, but it is also impossible to subdivide it into holophyletic units. The number of families making up the Ischnocera is a matter of contention. Eichler (1963) recognizing 21 and Hopkins & Clay (1952) recognizing only three. In this study five families are recognized: Gonioididae, Heptapsogasteridae, Trichophilopteridae, Trichodectidae (*sensu* Hopkins & Clay, 1952; Trichodectiformia of Eichler, 1963) and Philopteridae. Of these only two are demonstrably holophyletic: Trichophilopteridae (by definition, as it comprises only one species) and Trichodectidae (Lyal, 1985b). Of the other three families, Heptapsogasteridae and Gonioididae are each phenetically-recognizable groups and may be holophyletic, whilst the Philopteridae is a miscellaneous collection of genera and is almost certainly paraphyletic or polyphyletic.

#### Apomorphies proposed for the Rhyncophthirina plus the Anoplura

(69) *Head 'fixed' in relation to thorax* (Kim & Ludwig, 1978). This feature may be linked

to the feeding mechanisms of the two groups, both of which have led to the development of prognathy. These feeding mechanisms are quite different, and the loss of free articulation of the head may therefore be homoplastic in the two groups.

(70) *Loss of anterior tentorial pits* (Symmons, 1952). There is a transformation series of tentorial reduction running Psocoptera – Amblycera – Ischnocera – Rhyncophthirina – Anoplura (Symmons, 1952; see characters 17 and 61). Kim & Ludwig (1982) regard the virtual loss of the tentorium in the Rhyncophthirina and the complete loss in the Anoplura as independent apomorphies, but there is no evidence to support this *a priori* assumption.

(71) *Loss of articulation between pronotum and forecoxae* (Kim & Ludwig, 1978). This loss has also occurred in some Amblycera (Matsuda, 1970), but the holophyly of the Amblycera, demonstrated above, indicates this loss to be homoplastic.

(72) *Suppression of lateral cervical sclerites* (Boudreaux, 1979). Mayer (1954) considers these sclerites absent from *Bovicola caprae* (Trichodectidae), but examination has shown that they are present in this and all other species of the family.

(73) *Absence of lacinial gland* (Kim & Ludwig, 1978). This absence may be primary or secondary in either of the two groups, depending on whether the development of the gland is postulated as an apomorphy of the Amblycera plus Ischnocera or of the Phthiraptera (see comment following character 20).

(74) *Loss of lacinia* (Boudreaux, 1979). The loss of the lacinia in these two groups is in each case associated with considerable modifications to the mouthparts. These modifications being separate autapomorphies, there must be a high probability that the loss of the lacinia is homoplastic in these two groups.

(75) *Reduction in number of tarsal claws to one* (Kim & Ludwig, 1978; Boudreaux, 1979). Kim & Ludwig (1978) consider this character state autapomorphic for the Anoplura, although admitting some homoplasy in the Amblycera and Ischnocera. Boudreaux (1979) correctly points out that the Rhyncophthirina also have only a single tarsal claw, and proposes the reduction as a synapomorphy of the Rhyncophthirina and the Anoplura. The reduction to a single tarsal claw occurs in the

Gyropidae and Abrocomophagidae (Amblycera), Trichodectidae, Rhyncophthirina and Anoplura, all groups ectoparasitic on mammals. A similar reduction has taken place in those Hippoboscidae (Diptera) ectoparasitic on mammals, indicating the high probability of homoplasy in this feature.

In their discussion on the legs of lice, Kim & Ludwig (1978, 1982) maintain that the pulvinus and empodium do not occur in the group. Clay (1969), however, demonstrates the presence of the empodium in Menoponidae (Amblycera) and Clay (1970) figures structures in *Boopia* (Amblycera) that almost certainly are pulvilli, although she follows Kéler (no reference given) in terming them plantulae of the second tarsomere.

(76) *Development of large cibarial and pharyngeal pumps* (Boudreaux, 1979). The cibarial pump is present in all other Acercaria, and is not an autapomorphy of the Anoplura plus Rhyncophthirina. The pharynx does not act as a separate pump, but contributes to the action of the cibarial pump (Mukerji & Sen-Sarma, 1955; Kim & Ludwig, 1978).

The distribution of those apomorphies listed above that are acceptable is presented in Table 2 and discussed below.

### Apomorphies proposed for the Ischnocera plus the Rhyncophthirina plus the Anoplura

(77) *Development of saucer-shaped antennal sensilla* (Clay, 1970; Kim & Ludwig, 1978; Boudreaux, 1979). Kim & Ludwig maintain that the development of these sensilla ('pore organs') is convergent in the Anoplura and the other two groups. They base this assumption on the absence of the sensilla from some Anoplura, apparently rejecting the possibility of secondary loss. The presence of the sensilla is believed here to be plesiomorphic within the Anoplura. See comment following character 90.

(78) *Development of connective tissue septum nearly occluding occipital foramen* (Symmons, 1952; Kim & Ludwig, 1978; Boudreaux, 1979). The development of this feature may be allied to the reduction of the tentorial bridge, and is carried to a far greater degree in the Anoplura than in the Rhyncophthirina and

Ischnocera. A transformation series thus exists, but the use of an intermediate state in this series as an autapomorphy of the Ischnocera and Rhyncophthirina (Kim & Ludwig, 1978) is not justified. Kim & Ludwig (1982) do not use the apomorphy because 'the obturaculum and similar tissues appear to have developed independently among the parasitic Psocodea'. They do not indicate why such independent development is postulated.

(79) *Development of spiracular glands* (Königsmann, 1960; Kim & Ludwig, 1978; Haub, 1980). Kim & Ludwig (1982) attempt to minimize the reliability of this proposed apomorphy by stating that 'information on the Psocoptera and Amblycera is meager'. This view is not maintained here, and the apomorphy is accepted.

(80) *Development of tensory ligament muscle* (Symmons, 1952).

(81) *Development of occipital apodeme extending into thorax* (Boudreaux, 1979). The occipital apodeme has not been detected in Trichodectidae, Goniididae, some Philopteridae and some Anoplura, and the degree of sclerotization of the apodeme where it has been seen is variable. The possible presence of the apodeme in the first two families mentioned above is obscured by the apomorphic development of the occipital ring, so the presence of the apodeme cannot be used as an apomorphy for any group excluding these two. The absence of the apodeme in some Anoplura is interpreted by Kim & Ludwig (1982) as apomorphic.

(82) *Transfer of attachment site of antennal muscles to dorsum of head, at least in part*. This apomorphy is clearly linked in the Rhyncophthirina and Anoplura to the loss of the anterior tentorial arms, on which the muscles attach in other Phthiraptera. The anterior arm is present in Ischnocera, so the cause of the transfer in Goniididae and Philopteridae is not known. The muscles are attached to the anterior arms in Trichodectidae, and the state in Heptapso-gasteridae and Trichophilopteridae is not known (Symmons, 1952).

(83) *Presence of symbionts* (Königsmann, 1960; Haub, 1980). Ries (1930, 1931) records symbiotic bacteria or Rickettsia-like organisms in Rhyncophthirina, Anoplura, seven species of Philopteridae, four out of five species of Goniididae and one species of Amblycera. He

failed to find them in four species of Trichodectidae and species of eight genera of Amblycera: he did not examine any Heptapso-gasteridae or Trichophlopteridae. The loca-tion of the symbionts and the form of the mycetocytes or mycetomes differ considerably in Amblycera, Ischnocera, Rhyncophthirina and Anoplura (Buchner, 1965). Kim & Ludwig (1978) suggest a number of separate acqui-sitions of endosymbionts in the Phthiraptera connected with changes in diet, and Buchner (1965) notes that symbiotic bacteria are pre-sent chiefly in blood- and keratin-feeding in-sects. The absence of symbionts in one of the Goniodidae studied by Ries (1930, 1931) sug-gests either independent acquisition in the other Goniodidae or secondary loss. In view of the high probability of homoplasy and the paucity of information regarding the full dis-tribution of endosymbionts within the Phthir-aptera, the apomorphy is not given great weight in this study.

(84) *Fusion of mesonotum and metanotum* (Kim & Ludwig, 1978, 1982). This apomorphy is also exhibited by some Amblycera (Clay, 1970) and Liposcelidae (Smithers, 1972). Kim & Ludwig (1982) cite this as evidence that the fusion is homoplastic in the Anoplura and other Phthiraptera, but propose the fusion to be homologous in Ischnocera and Rhyncoph-thirina. This decision reflects their *a priori* assessment of the Mallophaga as a holophyletic group, and is not justified on the evidence. In the Anoplura the pronotum is fused to the meso-metanotum (character 62), but the propo-sal of Kim & Ludwig (1978) of the 'fusion of mesonotum and metanotum (but not pro-notum)' as a synapomorphy of the Ischnocera and Rhyncophthirina is not justified.

(85) *Reduction of eye to a single ommati-dium (or complete loss)* (Boudreaux, 1979). See comment following character 26.

(86) *Reduction in number of testicular folli-cles to two pairs* (Königsmann, 1960; Kim & Ludwig, 1978; Boudreaux, 1979; Haub, 1980). Some Amblycera also have only two pairs of follicles (Kim & Ludwig, 1982). See comment following character 32.

(87) *Loss of maxillary palpi* (Boudreaux, 1979). The loss of the palpi in the three groups may be homoplastic. See comment following character 74.

(88) *Antennae homonomous* (Königsmann,

1960; Haub, 1980). This state is contrasted with the supposed plesiomorphic heterono-mous condition in Psocoptera and Amblycera. Haub (1980) misinterprets the morphology of the amblyceran antenna (see discussion follow-ing character 58), and his postulated similarity of the Psocoptera and Amblycera is rejected. Moreover, the scape and pedicel are of greater diameter than the flagellomeres not only in Psocoptera but also in Rhyncophthirina, most Anoplura and most Ischnocera, although not in Amblycera. The degree to which the Ischnocera, Rhyncophthirina and Anoplura exhibit the heteronomous condition is not as great as the Psocoptera, but the antennae in these groups cannot be considered homono-mous.

The distribution of those apomorphies listed above that are acceptable is given in Table 2 and discussed below.

#### **Apomorphies proposed for the Rhyncophthirina plus the Anoplura plus the Trichodectidae**

(89) *Presence of gonapophyses* (Symmons, 1952). Gonapophyses are present in a number of Amblycera and Ischnocera other than Trichodectidae, and are remnants of the great-ly reduced ovipositor. The retention of the gonapophyses cannot be used as a synapomor-phy. See comment following character 31.

No other apomorphies have been proposed for this group.

#### **Apomorphies proposed for the Rhyncophthirina plus the Ischnocera**

(90) *Increase in number of antennal pore organs from two to three*. Kim & Ludwig (1982) state incorrectly that the Rhyncophthir-ina have only two pore organs, not three as shown by Clay (1970). The plesiomorphic number of pore organs may be two, in which case the apomorphy is valid, or three, in which case the reduction to two is apomorphic for the Anoplura. Some Anoplura have lost the pore organs entirely. See comment following char-acter 77.

(91) *Mouthparts of modified chewing type* (Kim & Ludwig, 1978); *mandibles articulating*

not horizontally but either vertically or laterally (Kim & Ludwig, 1982). The mandibular modifications are totally different in the two groups, and cannot be considered as synapomorphic. The proposal also neglects the unknown type of mandibular articulation of the ancestor of the Anoplura.

(92) *Reduction in the number of antennal sensilla coeloconica and basiconica* (Kim & Ludwig, 1982). Kim & Ludwig (1982) note that the number of these sensilla is 6–7 in the Psocoptera, 2–4 in the Amblycera, 3–4 in the Anoplura, 2 in the Ischnocera and 1 in the Rhyncophthirina (data from Al-Abbasi, 1981). The data are slightly incorrect in that the Rhyncophthirina have two such sensilla. The greater reduction in numbers in the Ischnocera and the Rhyncophthirina are, as 'loss' character states, of little or no value in cladistic analysis, and may well be homoplastically derived in the two groups.

In addition to these three supposed apomorphies another four have been discussed above: the loss of the anterior tentorial pits (character 70); the development of the pore organs (see character 77); the partial development of the obturaculum (see character 78); and the fusion of the mesonotum and metanotum but not pronotum (see character 84). Each of these has been rejected. See Table 2.

#### Apomorphies proposed for the Rhyncophthirina plus the Ischnocera plus the Amblycera

(93) *Reduction from two to one pair of labial glands* (Kim & Ludwig, 1978, attrib. Königs- mann, 1960). All three groups have two pairs of labial glands, and the apomorphy must be rejected. See comment following character 94.

(94) *Presence of cephalic labial gland* (Kim & Ludwig, 1982). This character state is contrasted with the thoracic placement of both pairs of labial glands in Psocoptera and Anoplura, and is the chief supporting apomorphy used for the Mallophaga by Kim & Ludwig (1982). The use of both character 93 and character 94 is based on the misconceptions that: (a) the lingual sclerites are labial salivary glands (Snodgrass, 1899; Cope, 1940a, b, 1941), and (b) the thoracic glands are connected to the alimentary canal not the salivar-

ium (Snodgrass, 1899; Imms, 1925; Richards & Davies, 1977). Paired thoracic labial glands, with a duct opening into the salivarium, are present in the Psocoptera (Weber, 1938). Anoplura (Snodgrass, 1944; Haug, 1952). Amblycera (Haug, 1952; Buckup, 1959) and Ischnocera (Risler, 1951; Haug, 1952). In the Rhyncophthirina the dorsal labial glands have migrated to the head (Mukerji & Sen-Sarma, 1955), and character 94 is apomorphic for this group.

No other apomorphies have been proposed for this group.

TABLE 2. Distribution of apomorphies within the Phthiraptera. 'Gain' states are indicated by 'g', 'loss' states by 'l', and states not present in all members of a taxon by '(g)' and '(l)' respectively. For explanation of characters see text.

TAXON	ISCHNOCERA							
	PSOCOPTERA	AMBLYCERA	TRICHOECTIDAE	CONTIDAE	HEPTASOGASTERIDAE	PHILOPTERIDAE	TRICHOPTILOPTERIDAE	RHYNCOPTHIRINA
CHARACTER								ANOPLURA
69							g	g
70							l	l
71							l	l
72							l	l
73							l	l
90		g	g	g	g	?	g	
68			l	l	l	?	l	
82			g	?	g	?	g	g
83			(g)	?	g	?	g	g
81				g	(g)	?	g	g
67		g	g	g	(g)	g		
77		g	g	g	g	g	g	g
78		g	g	g	g	g	g	g
79		g	g	g	g	g	g	g
80		g	g	g	g	?	g	g
84	(g)	(g)	g	g	g	g	g	g
85			l	l	l	l	l	l
86			l	l	l	?	l	l
87			l	l	l	?	l	l

### Cladistic relationships within the Phthiraptera

The distribution of 'acceptable' apomorphies within the Phthiraptera is summarized in Table 2. The hypothesis of holophyly of a sister-group to the Amblycera comprising the Ischnocera, the Rhyncophthirina and the Anoplura is supported by the distribution of eight apomorphies, five of them 'gain' states, and is consistent with a further eleven. An alternative hypothesis, the holophyly of a group comprising the Amblycera and the Ischnocera, is supported by the distribution of a single apomorphy (character 20), and is consequently rejected as less parsimonious.

The sister-group of the Rhyncophthirina is either the Anoplura (hypothesis supported by apomorphies 69–73), the Ischnocera (hypothesis supported by apomorphy 90), or some part of the Ischnocera (hypothesis supported by apomorphy 68). If, as recommended by Hecht & Edwards (1976, 1977), apomorphic 'loss' states are not used in cladistic analysis because of the impossibility of detecting homoplasy directly, the first two hypotheses are seen to be each supported by a single apomorphy (69 and 90 respectively) and the third by none. The third hypothesis is therefore rejected. Unfortunately, neither of the 'gain' apomorphies supporting the first two hypotheses are particularly reliable (see comments following their proposal above), and further evidence must be sought. Apomorphies 81–83 indicate by their distribution the paraphyly of the Ischnocera with respect to the Rhyncophthirina and Anoplura, the Trichodectidae (and possibly the Trichophlebotomidae) being excluded from the holophyletic group so formed. A consequence of this hypothesis is a refutation of the hypothesis supported by apomorphy 90 – the holophyly of the Rhyncophthirina plus the Ischnocera. These apomorphies can therefore be taken as supporting evidence for the holophyly of the Rhyncophthirina plus the Anoplura. However, as can be seen from the comments following their proposal above, none are considered sound. The hypothesis of paraphyly of the Ischnocera (including Trichodectidae) supported by apomorphies 81–83 is refuted by apomorphy 67, which supports the holophyly of a group comprising the Trichodectidae and most of the other Ischnocera. This apomorphy

is deemed more reliable than apomorphies 81–83, and the Trichodectidae are considered here as part of a holophyletic group including most if not all Ischnocera. This rejection of the evidence from characters 81–83 removes their support for the sister-group relationship of the Rhyncophthirina and the Anoplura, although it does not refute this hypothesis.

Although 'loss' apomorphies are not weighted as heavily as 'gain' apomorphies, the evidence provided by their distribution is the only indication of the sister-group of the Rhyncophthirina. As noted above, the hypothesis of sister-group relationship supported by the greatest number of apomorphies is that the Rhyncophthirina and the Anoplura are sister-groups. The sister-group of this assemblage must therefore be all or some of the Ischnocera, the holophyly of this latter group not being demonstrable at present.

### Ranking and classification

Following production of a cladistic scheme of relationships for the groups of lice (Fig. 2), a scheme of ranking and nomenclature for these groups must be adopted. Several such schemes have been proposed, and these are summarized in Fig. 3. Clay (1970) and Haub (1980) consider the Amblycera, Ischnocera, Rhyncophthirina and Anoplura to be of equal hierarchical rank as suborders of the order Phthiraptera. Boudreaux (1979) considers Phthiraptera (Phthirapterida) as a subcohort comprising two orders: Mallophaga, which he restricts to the Amblycera, and Anoplura. Two suborders of Anoplura are proposed: Ischnocera and Lipognatha, the latter comprising two infraorders, Rhyncophthirina and Siphunculata (Anoplura *sensu* Clay, 1970). Kim & Ludwig (1978) imply subordinal status for the Amblycera, Ischnocera and Rhyncophthirina, combining these into the order Mallophaga, and elevate the Anoplura to ordinal status. The same proposal is made by Kim & Ludwig (1982), although based on the premise (rejected here) that the 'Mallophaga' are a holophyletic group; this will not be discussed further.

The three schemes, of Clay (1970), Kim & Ludwig (1978) and Boudreaux (1979), reflect different approaches to systematic decision-

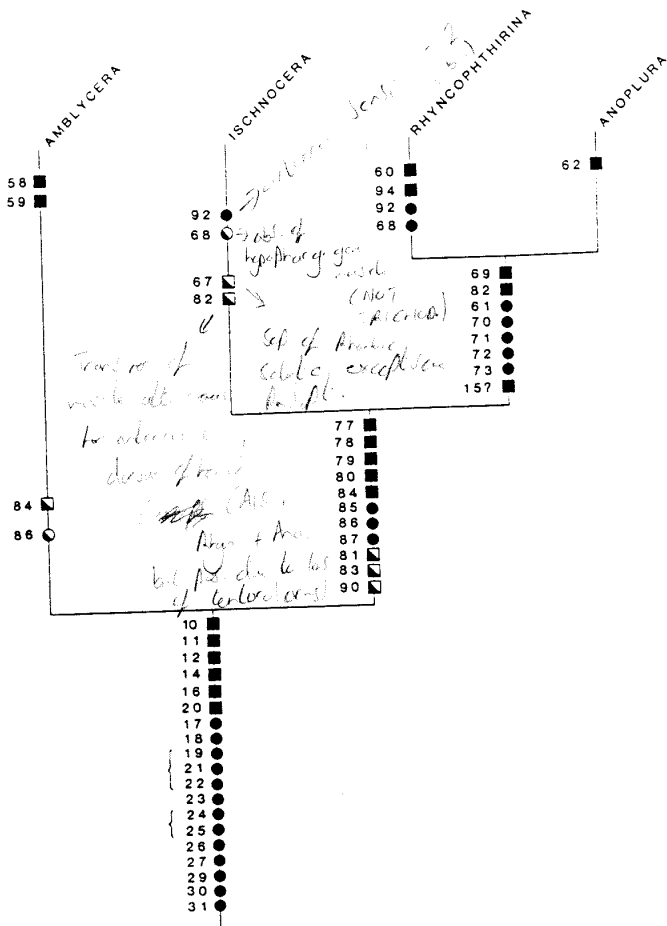


FIG. 2. Cladogram of the major groups of Phthiraptera. 'Gain' apomorphic states are indicated by solid squares, 'loss' states by solid discs, and states not present in all members of a taxon by half-solid squares and discs respectively. For explanation of apomorphies see text.

making. Boudreaux (1979), employing a strict cladistic methodology, accepts only holophyletic groups as true systematic entities and applies names in rank order to each group so produced. Kim & Ludwig (1978) represent the phylist approach, accepting paraphyletic groups as systematic entities and using the 'amount' of morphological difference between groups as a criterion in assessment of rank. Clay (1970) follows cladistic procedure in not accepting paraphyletic groups, and specifically rejects 'Mallophaga' as proposed by Kim &

Ludwig (1978). She does not feel obliged, however, to produce a series of names covering each presumed holophyletic group, as does Boudreaux (1979).

The paraphyletic group 'Mallophaga' *sensu* Kim & Ludwig (1978) is not accepted here, and only holophyletic groups are utilized. The plethora of names employed by Boudreaux (1979) is also rejected, because the alteration from the traditional usage of Mallophaga and Anoplura will, far from clarifying systematic discussion, serve only to increase confusion. It

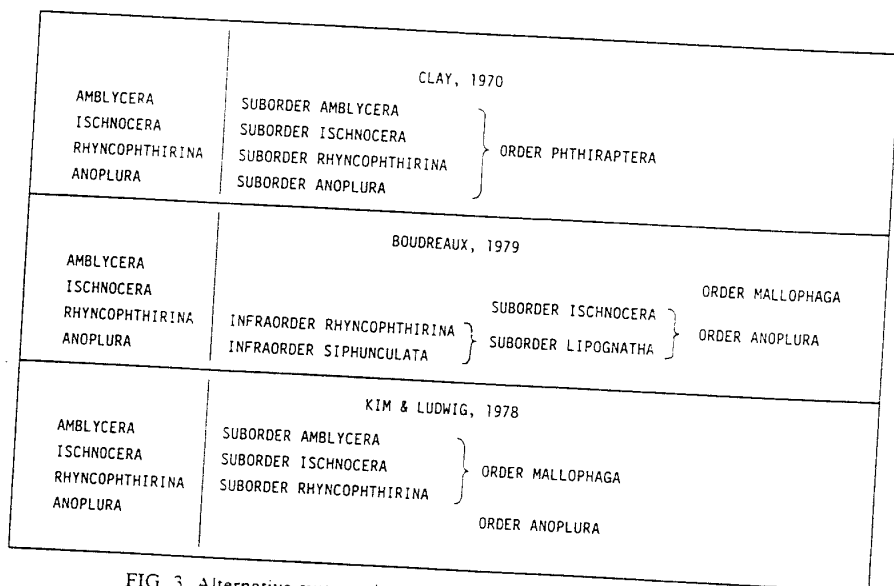


FIG. 3. Alternative systematic arrangements of the major groups of lice.

is possible for a classification to reflect cladistic relationships without including names for all holophyletic groups (Nelson, 1972, 1974; Cracraft, 1974; Wiley, 1979, 1981), and this system, known as 'phyletic sequencing', will be employed here. The classification is therefore represented:

- Order Phthiraptera
  - Suborder Amblycera
  - Suborder Ischnocera
  - Suborder Rhyncophthirina
  - Suborder Anoplura

#### The development of parasitism and the origin of the major groups of lice

As already noted, the Phthiraptera probably developed from a nidicolous ancestor (Hopkins, 1949; Rothschild & Clay, 1952; Kéler, 1957; Stenram, 1964; Waage, 1979), which in this study is identified as the common ancestor of the Phthiraptera and Liposcelidae. The association of modern Psocoptera (mostly Liposcelidae) with birds (Rapp, 1961; Mockford, 1967) and mammals (Pearman, 1960; Mockford, 1971) is not uncommon, and a similar phoretic association on the part of the

ancestor of the lice is likely to have led to the more permanent relationship now found. The generally-accepted scenario for the subsequent development of parasitism in the Phthiraptera is stated in the next paragraph.

The ancestor(s) of the Phthiraptera were only facultatively parasitic, and much less host-specific than modern lice (Hopkins, 1949, 1957; Kéler, 1957; Königsmann, 1960). During this early period the major divisions of the modern Phthiraptera evolved, to become fixed with the development of obligate parasitism and divergence of the hosts (Hopkins, 1949; Kéler, 1957). With the shift to obligate parasitism host-specificity developed also, and since then the lice have, in their phylogenetic development, broadly followed the evolution of their hosts, with very little transfer taking place between unrelated hosts (Bedford, 1939; Hopkins, 1941; Kéler, 1957; Kim & Ludwig, 1978).

The suppositions upon which the latter part of this scenario is based will be examined in future publications, but here the temporal relationship of the development of obligate parasitism, host specificity and the division of the Phthiraptera into groups will be discussed. It is suggested above that the major groups of



Phthiraptera arose before the development of obligate parasitism, a proposal also made by Mukerji & Sen-Sarma (1955) and Kim & Ludwig (1978, 1982). The development of obligate parasitism must have involved the development of several adaptive features, primarily involving the ovipositor, the structure of the egg, oviposition, and other modifications to behavioural patterns. The most parsimonious hypothesis, and one for which there is no refuting evidence, is that these adaptive features developed only once, and hence that obligate parasitism arose only once, in the common ancestor of all Phthiraptera. The ecological factors affecting the development of host-specificity (Lyal, 1985c) consequently must have applied to this ancestor, and all divisions of the order arose under their constraints (with the proviso that the ecological relationships of the early hosts may have differed from those of the present hosts). The evolution of the Phthiraptera must therefore be viewed not in two parts, but as a single process, subject always to the same constraints.

### The time of origin of the Phthiraptera

The Phthiraptera have been suggested as originating in the late Mesozoic (Harrison, 1914), the late Jurassic or Cretaceous (Harrison, 1916), the Jurassic (Harrison, 1928), the late Triassic or early Jurassic (Kéler, 1957; Kim & Ludwig, 1978), the late Triassic (Hopkins, 1949), the Triassic (Stenram, 1964) and the Upper Carboniferous or Lower Permian (Kim & Ludwig, 1982). The very early date proposed by Kim & Ludwig (1982) results from their belief that the lice are derived from Permopsocida (Dichentomidae and Lophioneuridae), an hypothesis rejected in this study. The assumption that Phthiraptera and Psocoptera are sister-groups has led workers to suggest an earlier date than is perhaps justified by the evidence, as an early date is believed necessary for the emergence of an order, and many millions of years presumed to be required for the development of the nidicolous habit in the ancestor of the lice. If, as is suggested here, the sister-group of the lice is the Liposcelidae, this great length of time would not have been required.

The absence of a fossil record for lice forces any decisions on their age to be based on comparative phylogeny with the hosts (Hopkins, 1949; Hennig, 1966) and geographical distribution. The mammalian environment (i.e. the habitat provided by a nest-building hair-covered homoiotherm) was probably available in the mid to late Triassic (Patterson, 1957), and the birds (as represented by *Archaeopteryx*) appeared in the mid to late Jurassic. The Metatheria and Eutheria appeared in the first half of the Cretaceous, but the modern orders of Eutheria and of birds do not appear in the fossil record until the Palaeocene (although this probably represents a deficiency in the record rather than a true absence) (Patterson, 1957; Romer, 1962).

The Anoplura are confined to mammals, and it is reasonable to assume that they arose on this group. Traub (1980) examines the geographical and host distribution of the suborder, and concludes that it was present on rodents in the Palaeocene and probably arose on this group, although an earlier Cretaceous origin (as suggested by Hopkins, 1949) on ungulates or multituberculates is not ruled out. He suggests that the suborder arose in North America.

The time of origin of the Anoplura and the Rhyncophthirina must be the same, as they are sister-groups. The host of the ancestor of the Rhyncophthirina was probably a mammal, as both of the modern species parasitize members of this group, and the Proboscidea (the probable primary hosts of *Haematomyzus*) have a fossil record extending back to the Eocene (Patterson, 1957). The evidence suggests that the common ancestor of the Rhyncophthirina and the Anoplura was present on an ancestor of all or part of the Eutheria in the late Cretaceous or early Tertiary.

In the Ischnocera two families parasitize mammals: Trichophlopteridae on lemurs and Trichodectidae on a number of Eutheria. Trichophlopteridae almost certainly have a comparatively recent ancestry among the bird lice, and Trichodectidae are unlikely to have been present on the ancestor of the Eutheria (Lyal, 1985d). Other Ischnocera are present on most if not all bird orders. If the association with mammals of Ischnocera post-dates that of Anoplura and Rhyncophthirina, the ancestor of the former suborder must have been a

parasite of a bird. However, the absence of a phylogenetic analysis of the Ischnocera precludes any hypothesis of the identity of this host. The common ancestor of the Ischnocera, Rhyncophthirina and Anoplura may have been a parasite of a bird or a mammal, and there is no evidence to suggest a date for this ancestor much earlier than that of the ancestor of the Anoplura and the Rhyncophthirina.

Amblycera parasitize mammals and birds, the three bird-infesting families being world-wide in distribution and the four mammal-infesting families being confined to South America and the Australian Region (other than *Heterodoxus spiniger*, which was derived from a wallaby louse and now infests dogs all round the world). The Australian mammal parasites (Boopiidæ) are primary parasites of marsupials, secondarily infesting some canids and the cassowary. The South American families of mammal lice are the Abrocomophagidæ parasitic on a caviomorph rodent, the Gyropidæ, also parasitic on caviomorphs, and the Trimenoponidæ, parasitic on caviomorphs and marsupials. Harrison (1924, 1926), Hopkins (1949, 1957), Vanzolini & Guimarães (1955a, b) and Traub (1980) suggest that the Trimenoponidæ and Boopiidæ are descended from a single marsupial-infesting ancestor. If this is the case then marsupials must have been infested with Amblycera before the break-up of Gondwanaland, so the infestation must date to at least the Lower Cretaceous (Traub, 1980). Several points of this hypothesis are open to challenge. Clay (1970) suggests that the Trimenoponidæ and Gyropidæ form a monophyletic group and, although the phylogenetic position of the Abrocomophagidæ is not yet certain, it probably shares an ancestry with these families. In this group over seventy species parasitize members of eight caviomorph families and two species parasitize four species (in two genera) of one family of marsupials (Emerson & Price, 1981). The most parsimonious hypothesis of host relationships is that the ancestor of the South American mammal-infesting Amblycera parasitized a rodent and subsequently marsupials were colonized once or twice; the association with marsupials in South America is very unlikely to be ancient. Secondly, the relationship proposed between Trimenoponidæ and Boopiidæ is not based on apomorphic character states,

and is very questionable. Harrison (1924, 1926) and Hopkins (1949, 1957) are able to cite only one character supporting the relationship, and this (the presence of the posterior tracheal commisure) is plesiomorphic for the lice. Vanzolini & Guimarães (1955a) cite Hopkins (1949) as an authority, and Traub (1980) advocates the relationship solely on the basis of the common ancestry of the hosts. Traub (1980) goes on to cite this relationship of the lice as evidence for the common ancestry of the American and Australian marsupials, a purely circular argument that must be discarded. Clay (1970) derives the Boopiidæ directly from a bird-infesting ancestor, and cites apomorphies to demonstrate the sister-group relationship between the Boopiidæ and the Menoponidæ. There is no basis for assuming that the Trimenoponidæ and the Boopiidæ (or the Trimenoponidæ plus Gyropidæ and the Boopiidæ) are sister-groups, and thus that the infestation of marsupials dates to the Lower Cretaceous. Data presented by Clay (1970) suggest a sister-group relationship between the South American mammal-infesting Amblycera and all other members of the suborder. The common ancestor of the Amblycera may therefore have parasitized a bird or a South American rodent.

The identity of the host of the common ancestor of the Phthiraptera is still in doubt, and may have been a bird or a mammal. However, there is no evidence to suggest that lice were present on any but the Recent orders of mammals and birds, and there seems no reason to suppose that the development of the lice took place any earlier than the Cretaceous.

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