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A morphological phylogeny for four families of amblyceran lice (Phthiraptera: Amblycera: Menoponidae, Boopiidae, Laemobothriidae, Ricinidae)

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The suborder Amblycera (Insecta: Phthiraptera) comprises seven recognized families of parasitic lice. Three of these families (the Menoponidae, Laemobothriidae and Ricinidae) are present on a wide range of avian hosts. The four remaining families are restricted to a small section of mammals (the Boopiidae are parasites of Australian and New Guinean marsupials, and the Gyropidae, Trimenoponidae and Abrocomophagidae parasitize South and Central American rodents). This study uses a morphological approach to examine the evolutionary relationships between the genera from four amblyceran families: the Menoponidae, Boopiidae, Laemobothriidae and Ricinidae. Genera are represented by exemplars and a total of 44 louse taxa and one outgroup taxon were included. A cladistic analysis of 147 unordered characters recovered six equally parsimonious trees. Bootstrap, jackknife and Bremer support analyses were undertaken to assess the level of support for each resolved node in the strict consensus topology. Strong support was found for deep branch relationships between the families and in some cases for supra-generic groupings within families. The clades present in the strict consensus tree are discussed with reference to supra-generic and inter-family relationships, character choice, morphological convergence and host distribution. This study is the first phylogeny presented solely for amblyceran genera. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **138**, 39–82.

ADDITIONAL KEYWORDS: cladistics – coevolution – cospeciation – host–parasite systems – insect phylogeny – louse – morphology.

INTRODUCTION

Members of the order Phthiraptera (lice) are wingless insects, parasitic on most orders of birds and mammals. There are four recognized suborders: Amblycera, Ischnocera, Anoplura and Rhynchophthirina, of which the Amblycera are considered the most primitive (Königsmann, 1960; Clay, 1970; Lyal, 1985). The Amblycera contains seven families: the Menoponidae, Laemobothriidae and Ricinidae are distributed across a wide range of avian host orders, whilst the four remaining families are confined to a small selection of mammals. The Boopiidae are found on Australian and New Guinean marsupials, with the exception of *Therodoxus oweni* Clay on the Cassowary and *Heterodoxus spiniger* Enderlein which is thought to have secondarily parasitized the domestic dog. The Gyropidae, Trimenoponidae and Abrocomophagidae are parasites of South and Central American rodents, although *Macrogyropus dycotylis* MacAlister (Gyropidae) is also found on peccaries. The size of families varies greatly, with almost 70 genera in the Menoponidae compared to just a single genus in the Abrocomophagidae.

Most amblyceran genera were erected sometime between 1800 and 1950. In an age of high production of taxonomic descriptions, the Amblycera suffered the same fate as many other groups during this period: the literature became littered with duplicated descriptions, resulting in many generic and specific synonyms. Hopkins & Clay (1952, 1953, 1955) reviewed this situation, placing many taxa in synonymy, and recognized 69 distinct amblyceran genera in their checklist of Mallophaga. To date, there are over 90

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amblyceran genera recognized as valid, containing some 1350 valid species and subspecies (Price *et al*., in press). Most work has focused on the production of detailed taxonomic reviews and new species descriptions (e.g. Carriker, 1954; Price & Emerson, 1977), identification keys to a particular genus (Clay, 1962; Price & Beer, 1965b; Price, 1970) or to the Amblycera of a defined geographical area (Uchida, 1926; Ledger, 1980). A small number of workers have published works proposing species groups within genera (e.g. Price, 1970, 1971; Scharf & Price, 1977) and some have begun addressing phylogeny within individual genera, employing both morphological (e.g. Nelson, 1972) and molecular methods (e.g. Barker, Briscoe & Close 1992).

Very few authors have considered the broader relationships between amblyceran lice. In an attempt to address this question, Clay (1970) tabulated the distribution of 19 morphological characters across the suborder. There was no explicit phylogenetic analysis in this paper but Clay presented a detailed discussion on what she considered to be the evolutionary relationships of the six amblyceran families (the monogeneric Abrocomophagidae was as yet undescribed). She suggested that the establishment of parasitism by an avian louse on the marsupials gave rise to the Boopiidae and that the mammalian Amblycera were the therefore the result of two major host colonizations. In Clay's (1970) study, the Gyropidae were represented as three independent subfamilies (Gyropinae, Protogyropinae and Grilicolinae) as she had considered that the Gyropidae may not be a monophyletic group. Figure 1 shows the results of a preliminary cladistic analysis of Clay's (1970) data matrix of 19 characters, with the addition of the outgroup taxon to be used in this present study, the psocopteran (or free-living booklouse) *Liposcelis bostrychophilus* Badonnel. The tree presented (see Fig. 1) displays strong bootstrap support for only two general clades of lice ('A' and 'B'). Clade 'A' contains the avian-infesting families Menoponidae, Laemobothriidae, Ricinidae and also the mainly marsupial-infesting Boopiidae. Clade 'B' contains the rodent-infesting genera Trimenoponidae and the gyropid subfamilies (Protogyropinae, Gyropinae and Grilicolinae). Clay's (1970) proposal for two independent colonizations of mammals by amblyceran lice is not supported by the analysis of her data (Fig. 1) and in fact, given the low resolution of the tree presented, a more parsimonious interpretation of evolutionary events could be explained as the single colonization of birds from mammals. Clay (1970) also proposed that the Menoponidae and Boopiidae were sister taxa, which the cladistic analysis of her data (see Fig. 1) does not resolve.

There have been few studies which have examined the supra-generic relationships within amblyceran families. Symmons (1952), in an investigation primarily aimed at establishing some main types within the Amblycera, compared the tentorium (an endoskeleton of the head) across 14 louse genera with the condition found in the Psocoptera (or free-living booklice). She described four distinct forms of amblyceran tentorium, differing mainly in their degree of reduction and schematization. Symmons (1952) then placed the genera, on the basis of their tentorial type, into four groups: the Laemobothriidae, Gyropidae and Trimenoponidae constituted a single group; the Boopiidae were the second group and two supra-generic groups of Menoponidae were presented as groups three and four. In a much more in-depth work and entirely on the morphology of the Menoponidae, Clay (1969) indicated which characters she considered to define genera and supra-generic groups and discussed the stability of the character states. Clay (1969) also suggested that there were two distinct groups of menoponid genera (which contradicted those identified by Symmons, 1952) – the '*Colpocephalum* complex' and the '*Menacanthus* complex' (see Table 1). These two complexes both possess a large number of distinct, exclusive, characteristics but the groups contain only six and five genera, respectively, a very small proportion of the menoponid family. Clay (1969) gave no indication towards any ideas she may have had regarding phylogeny within these 'complexes' or of how they might be related to other menoponid taxa. Eichler (1963) took a much less conservative approach to this problem. He produced a very detailed classification of amblyceran genera, where previously recognized families were elevated to interfamily status and created a series of nested sets of taxa down to subfamily level (see Table 2). However, Eichler gave little justification for these hierarchical subdivisions and so most louse taxonomists still follow the more conservative classifications of Hopkins & Clay (1952) and Clay (1970), recognizing family groups but with no consensus of opinion on the evolutionary relationships of taxa below this rank.

The cladistic analysis of Clay's (1970) data on the morphology of the Amblycera segregates the avian and marsupial lice from the rodent lice (Fig. 1). The Amblycera are a large group (with over 90 genera) and as a consequence only genera from the families in clade 'A' (see Fig. 1) were included in this analysis.

This study set out to construct a morphologically based phylogeny for genera selected from four amblyceran families (Menoponidae, Boopiidae, Laemobothriidae and Ricinidae) using the exemplar approach, evaluate the monophyly and stability of families, evaluate the hypothesis that the Boopiidae and Menoponidae are sister taxa, and discuss any support for the alternative supra-generic groups proposed by Clay (1969) and Eichler (1963).

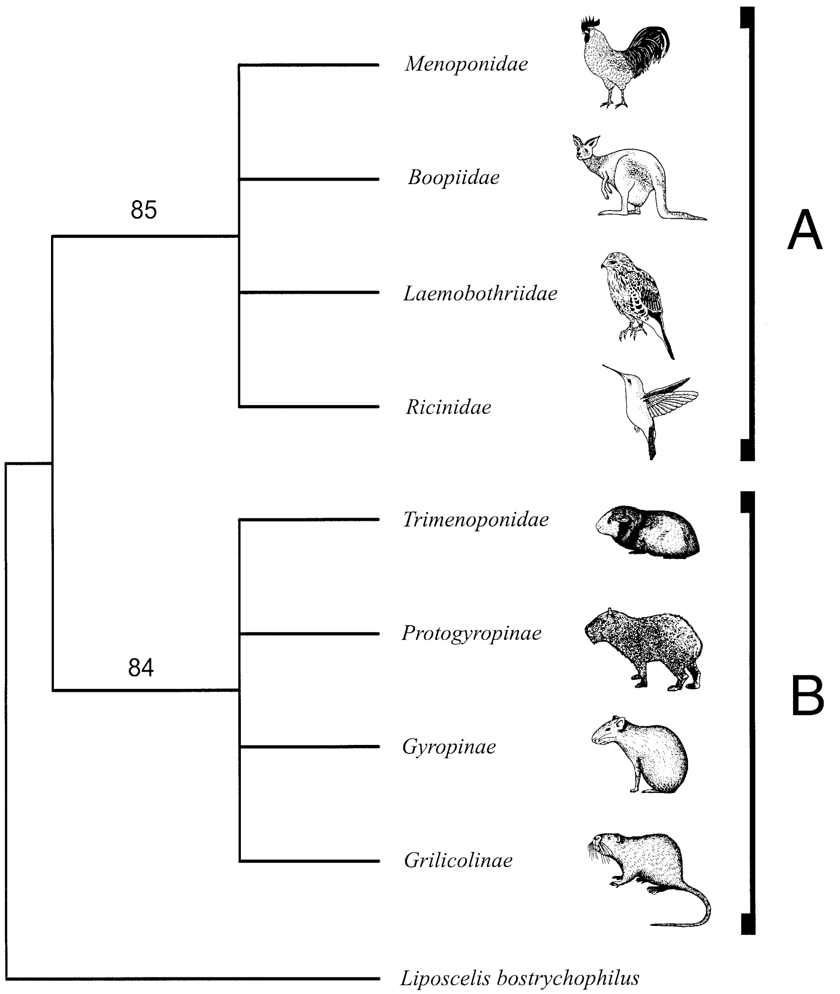

Figure 1. Strict consensus of the 24 most-parsimonious trees recovered from a cladistic analysis (1000 random addition replicates) of a morphological data matrix by Clay (1970). (Length = 24 steps, CI = 0.833, RI = 0.833, HI = 0.167.) Data for an outgroup taxon *Liposcelis bostrychophilus* were added to the original matrix. Bootstrap support (> 50%, 100 replicates) for two main clades of lice ('A' and 'B') is shown. A representative host for each louse family is also indicated.

MATERIAL AND METHODS

Four hundred and twenty-nine specimens representing 44 genera (in four families) of the suborder Amblycera were obtained for study from the slide-mounted Phthiraptera collection at The Natural History Museum (NHM), London. Since the four families in question comprise a large number of genera, specimens were chosen from a subset, which reflected both the Eichler (1963) and Clay (1969) classifications. This approach to taxa selection also offered an opportunity for comparing the different classifications of these two authors. Due to the large number of species in some genera (e.g. *Colpocephalum* Nitzsch contains in excess of 70 species) exemplars were selected, using the type species for the genus where possible. To assess a type species as a suitable typical representative, original taxonomic descriptions and generic review papers were employed and specimens of the type species were compared to other species within the genus before the final selection. In the few genera where types were rare or absent from the collection, the species morphologically most similar to the type species were included, either to increase the sample size or, in some cases, as a substitute for the type species. Adult male and female specimens were favoured over juveniles, as some features present in adults have been shown to appear at different instar developmental stages in the Ischnocera (Clay, 1951). For one genus (*Neomenopon* Bedford) only 3rd instar juveniles were available and additional information on the morphology of the adult was obtained from the literature. A final limiting fac-

Table 1. Suprageneric classification of the Menoponidae *sensu* Clay (1969). *Colpocephalum* and *Menacanthus* 'complexes'. Parentheses indicate those genera which Clay felt should possibly be included in these groups. * indicates three genera later considered to be subgenera of *Amyrsidea*. Taxa included in this study are highlighted in bold type

'*Colpocephalum* complex'	'*Menacanthus* complex'
Colpocephalum	***Menacanthus***
Comatomenopon	***Amyrsidea***
Ardeiphilus	*Argimenopon**
Ciconiphilus	*Cracimenopon**
Osborniella	*Desumenopon**
Psittacomenopon	
(***Odoriphila***)	(***Menopon***)
	(***Somaphantus***)
	(*Clayia*)
not	
Cuculiphilus	
Piagetiella	

tor in selection was specimen condition and only the clearest and best-mounted material was included. A list of study specimens is shown in Appendix 1.

OUTGROUP

Outgroup selection was influenced by two major factors. Firstly, the Amblycera are remarkably character-rich in contrast to the other three recognized suborders of the Phthiraptera. There are numerous structures and characteristics largely absent in the more specialized Ischnocera, Anoplura and Rhynchophthirina, making strong character homologies with other suborders difficult to determine. The second major factor is the finding of Lyal (1985), who in a morphological analysis of the Psocodea compared the phthirapteran groups to the Psocoptera (booklice). Lyal (1985) determined that the Amblycera formed the basal element in the Phthiraptera and that a single psocopteran family, the Liposcelididae, were the sister group to the lice. Comparisons of a range of specimens indicated that good homologies would be more easily established between the Liposcelididae and the Amblycera than between the Amblycera and other Phthiraptera, and consequently specimens of the booklouse *Liposcelis bostrychophilus* were chosen as the outgroup taxon for this study.

SEM

The amblyceran genera present in the NHM spirit collection were sampled for use in scanning electron micrography (SEM). Specimens were critical-point dried, mounted on stubs and coated with a gold–palladium mixture. Observation was via a Philips 500 scanning electron microscope set at 6–12 kV. Due to the age of the specimens in the spirit collection (commonly in excess of 75 years old) many of the images obtained were unable to be used for character development. However, as semi-transparent whole mounted material (such as the lice) appear layered using light microscopy, dorsal and ventral features were difficult to discern and the SEMs became an invaluable aid in the initial interpretation of the external morphology.

CHARACTER DEVELOPMENT

Characters were developed both by extensive observation and adaptation of descriptions from a number of taxonomic and review papers. Synonyms have accumulated in the literature for a number of amblyceran morphological structures and Lakshminarayana's (1985) glossary of taxonomic characters for the study of chewing-lice was found to be an invaluable aid in highlighting many such examples. The source of the terminology for characters developed for this study is indicated where appropriate.

CHARACTER RECORDING AND CODING

All character state data and associated notes were recorded using Nexus Data Editor (NDE) Version 0.4.8 (Page, 2000). The specimens were thoroughly sampled and 147 characters (113 binary and 34 multistate) suitable for phylogenetic analysis were collated. A descriptive list of characters and comments was prepared during this study and is presented as Appendix 2.

In this study a mixture of reductive and composite character-coding methods were used, both of which methods have positive and negative aspects. The reductive coding method consists of an initial delimiting character and any number of dependent characters which are scored as inapplicable where appropriate (e.g. character 17: *Dorsal head seta* (*DHS*) *24*: (0) absent; (1) present . . . character 18: *DHS 24* (*where present*): (0) macroseta; (1) microseta; (–) inapplicable). Taxa which do not possess DHS 24 are scored as inapplicable for the setal development character. This method maintains the hierarchy between the presence or absence of a morphological 'part' and any variability in the 'condition' of that part. It also allows separate primary homology statements and transformational independence, so each character can diagnose clades at the appropriate level in the tree (Lee & Bryant, 1999). Thus, reductive coding allows character information to be partitioned more effec-

Table 2. Suprageneric classification of the Amblycera (part) *sensu* Eichler (1963). Taxa included in this study for the four families: Menoponidae (M), Boopiidae (B), Laemobothriidae (L) and Ricinidae (R) are highlighted in bold type. The conservative familial classification of Clay (1970) is indicated on the right. *Microctenia* (in parentheses) was not included due to poor specimen quality and is presented only to illustrate the presence of the family *sensu* Eichler. Additionally, only currently recognized genera from this classification have been listed

Superfamily	Interfamily	Family	Subfamily	Genus	Clay (1970)
Laemobothrioidea	Laemobothriformia	Laemobothriidae	–	***Laemobothrion***	L
	Riciniformia	Ricinidae	–	***Ricinus***	R
		Trochiloecetidae	–	***Trochiloecetes***	R
Gyropoidea	Boopiformia	Boopiidae	Heterodoxinae	*Heterodoxus*	B
				Paraheterodoxus	B
			Boopinae	***Boopia***	B
				Paraboopia	B
		Latumcephalidae	–	***Latumcephalum***	B
Menoponoidea	Menoponiformia	Somaphantidae	Somaphantinae	***Amyrsidea***	M
				Clayia	M
				Rediella	M
				Somaphantus	M
			Bonomiellinae	***Bonomiella***	M
		Menoponidae	Menoponinae	***Menopon***	M
				Numidicola	M
			Menacanthinae	***Hohorstiella***	M
				Menacanthus	M
				Nosopon	M
			Machaerilaeminae	***Colimenopon***	M
				Eureum	M
				Machaerilaemus	M
				Neomenopon	M
			Dennyinae	***Dennyus***	M
				Myrsidea	M
		Ancistronidae	Ancistroninae	***Ancistrona***	M
			Austromenoponinae	***Austromenopon***	M
				Eidmanniella	M
				Holomenopon	M
				Plegadiphilus	M
			Actornithophilinae	***Actornithophilus***	M
				Chapinia	M
				Gruimenopon	M
				Longimenopon	M
				Meromenopon	M
			Hoazineinae	***Eomenopon***	M
				Hoazineus	M
		Pseudomenoponidae	–	***Pseudomenopon***	M
		Trinotonidae	–	***Trinoton***	M
	Colpocephaliformia	Colpocephalidae	Colpocephalinae	***Colpocephalum***	M
				Comatomenopon	M
			Anserphilinae	***Ardeiphilus***	M
				Ciconiphilus	M
				Dicteisia	M
			Cuculiphilinae	***Cuculiphilus***	M
				Carrikeria	M
				Odoriphila	M
				Osborniella	M
			Psittacomenoponinae	***Psittacomenopon***	M
			Microcteniinae	(*Microctenia*)	M
		Piagetiellidae	–	***Piagetiella***	M

tively. However, this method can also be potentially problematic for computational software as the inapplicable character states (–) are treated as missing values (?) and therefore homologous to truly applicable states. Globally parsimonious trees can therefore contain local suboptimal solutions (if homoplastic gains are separated by regions of primitive absence) and clades supported exclusively by homoplasies may need to be optimized by hand (Strong & Lipscomb, 1999).

In the composite coding method the presence of a part and any variability in its condition are combined within a single character (e.g. character 35: *Preocular feature of the dorsolateral head margin*: (0) no feature, unbroken margin; (1) notch; (2) slit). In this method transformations in part and condition are not independent, homology statements are not separate and essentially there is much less phylogenetic information (Lee & Bryant, 1999). There is also the added problem of how to construct composite characters, which contain the part and a number of related condition variables (e.g. the number, position and development of setae on part 'X').

In this study the reductive coding method was favoured, where feasible, to maintain as much phylogenetic information as possible and avoid overly complex characters. Composite coding was only used in those situations where a confident proposal of homology was not possible. The full data matrix for the 147 characters is presented as Appendix 3.

PHYLOGENETIC ANALYSIS

A heuristic search was completed using PAUP* 4.0b (Swofford, 1999) with stepwise addition and tree bisection reconstruction (TBR) branch swapping. All trees were held for inclusion into the branch swapping process and in this second stage of analysis multi-parsimonious trees were also held. This approach allows for the possibility that additional branch swapping on equally and even less-parsimonious trees may result in obtaining the shortest tree length. 10000 random addition sequence replicates were employed to increase the probability of finding all the most-parsimonious trees. All characters were treated as unordered and of equal weight. Where taxa had been coded as having multiple states, PAUP* was set to interpret these data as 'variable' (the respect '()' vs. '{ }' option), in order that a distinction would be made between uncertainty and polymorphism. Branch support statistics were determined by three types of analysis: bootstrap (1000 replicates with TBR branch swapping; Felsenstein, 1985), parsimony jackknife (33% character deletion, 1000 replicates with TBR branch swapping; Farris *et al*., 1996) and Bremer support (Bremer, 1988). Bremer support values were obtained using AutoDecay (Eriksson, 1997) and PAUP*. Character state distributions were interpreted using MacClade 4.0 (Maddison & Maddison, 2000) and unambiguous state changes mapped onto the trees using Winclada 0.9.9 (BETA; Nixon, 1999).

RESULTS

The analysis found six maximum-parsimony (MP) trees (on one island) with a length of 650 steps (CI: 0.326; RI: 0.585). The strict consensus of these trees is presented in Figure 2. Jackknife (bold type) and bootstrap values (regular type) above 50% are shown above their respective nodes. Bremer support values are shown below each node.

The strict consensus tree is fully resolved at all but two nodes, with disagreement only within two subgroups of the large clade containing the Menoponidae. In one unresolved group three of the six MP trees support *Cuculiphilus* Uchida as the sister taxon to the clade containing *Colpocephalum* and *Ardeiphilus* Bedford, whilst in two of the six arrangements *Ciconiphilus* Bedford has this relationship. In one tree *Cuculiphilus* and *Ciconiphilus* form a sister group to the *Ardeiphilus* clade. In the second unresolved group, *Dennyus* Neumann and *Myrsidea* Waterston are always sister taxa, but there are two conflicting arrangements for the other genera. Three trees define a sister group to the *Dennyus*–*Myrsidea* clade where *Ancistrona* Westwood is placed basal to *Pseudomenopon* Mjöberg and *Bonomiella* Conci. The remaining three trees suggest *Ancistrona* and *Pseudomenopon* are sister taxa with *Bonomiella* as the sister taxon to the *Dennyus*–*Myrsidea* clade.

CLADISTIC ANALYSIS

The tree presented in Figure 2 and the support obtained, for particular clades, from the jackknife, bootstrap and Bremer support statistical analyses are discussed below. Unambiguous character state changes were plotted onto the strict consensus tree and are presented as Figures 3–5. For each character discussed, the character number and corresponding state variable are indicated in parentheses.

In the strict consensus tree (Fig. 2), there is strong support for the deep branch relationships between the families and in many cases for supra-generic groupings within the families. Rooted on the outgroup taxon *Liposcelis*, the Boopiidae, Menoponidae and Ricinidae each form monophyletic groups (the Laemobothriidae is monogeneric).

At the base of the tree, the Ricinidae are very strongly supported by jackknife and bootstrap values of 100% and a Bremer support value of 12 (Fig. 2). *Trochiloecetes* Paine & Mann is the sister taxon to a clade containing *Ricinus* De Geer and *Trochiliphagus* Car-

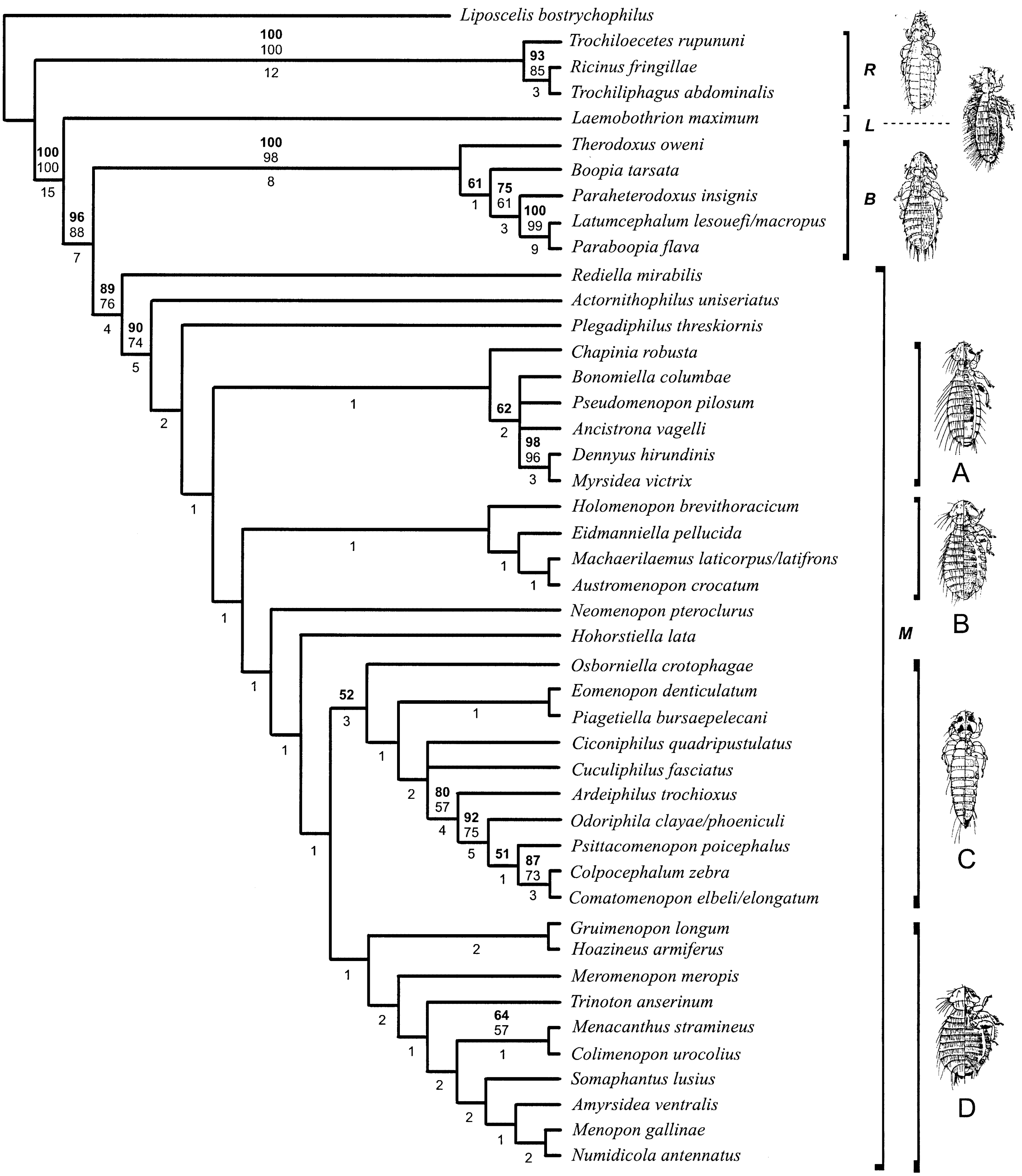

Figure 2. Strict consensus of six equally parsimonious trees recovered from a cladistic analysis using 10 000 random addition replicates. (Length = 650 steps, CI = 0.326, RI = 0.585, HI = 0.683.) Jackknife (33% deletion, bold type) and bootstrap values (> 50%, regular type), each based on 1000 replicates, are shown above the nodes, with Bremer support values (decay indices) shown below. Louse families and major clades within the Menoponidae are indicated.

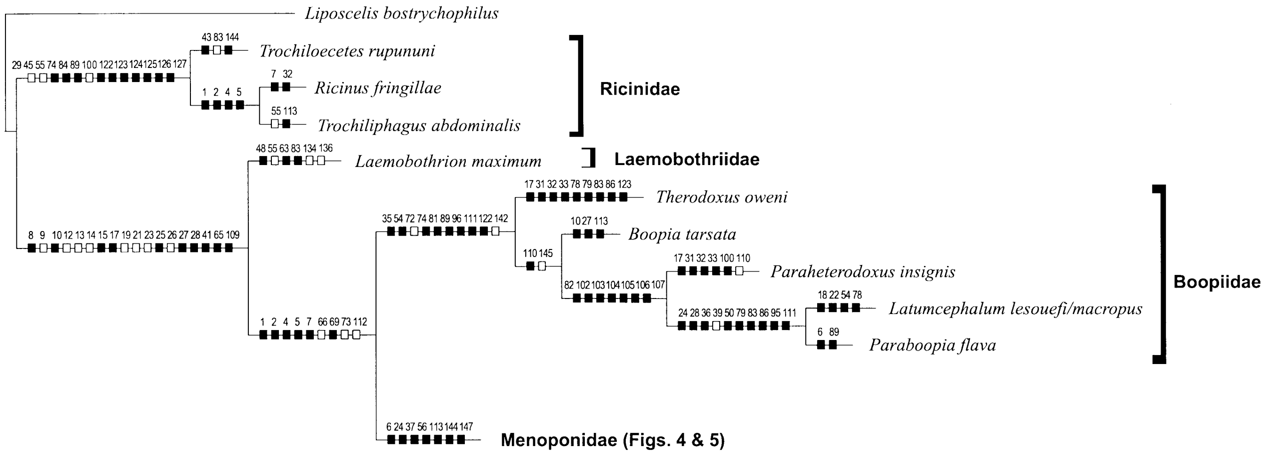

Figure 3. Character state evolution within the Ricinidae, Laemobothriidae and Boopiidae. Characters which change unambiguously are shown mapped onto the strict consensus tree. Unique changes = □. For character state descriptions, see Appendix 2.

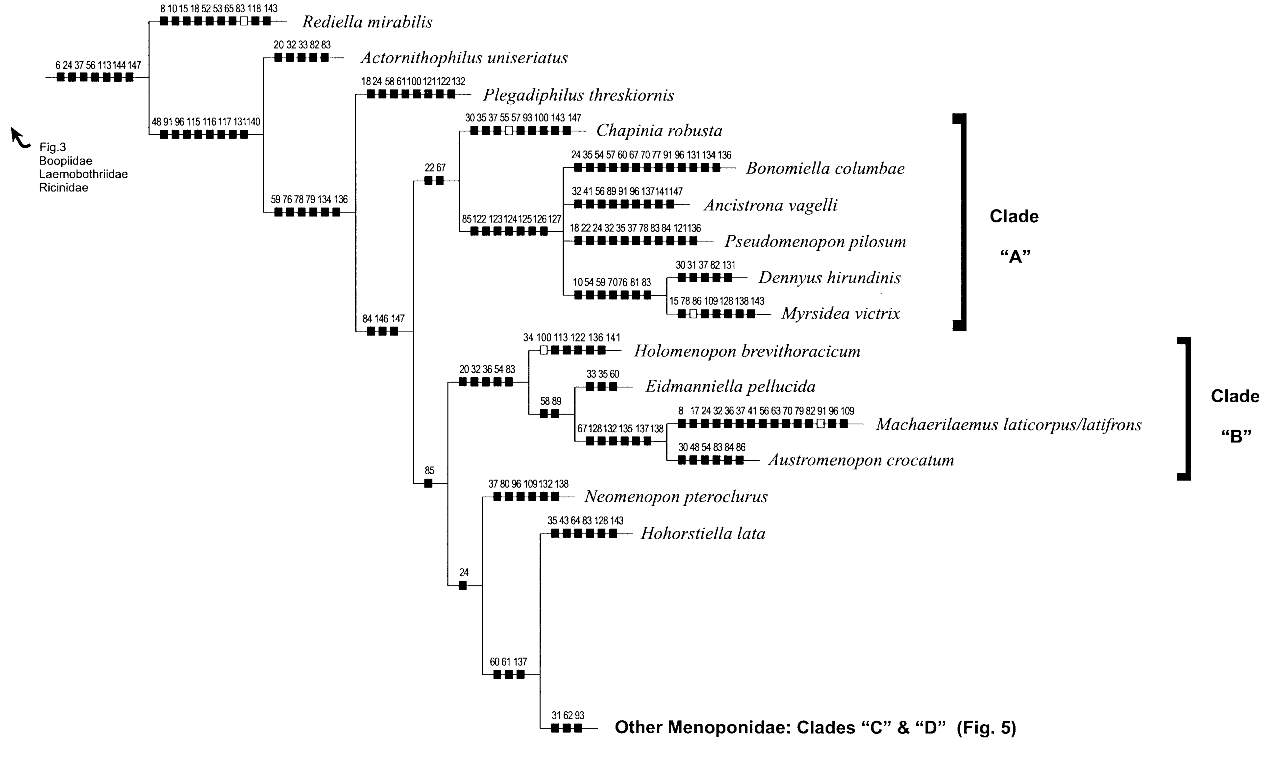

Figure 4. Character state evolution within the Menoponidae (clades 'A' and 'B'). Characters which change unambiguously are shown mapped onto the strict consensus tree. Unique changes = □. For character state descriptions, see Appendix 2.

riker. Three synapomorphies identify this small family. All ricinds have three pairs of dorsal head setae down the midline of the head (character 29: 1), lack the labial palps present in other amblycerans (45: 0) and have a poorly developed tergal setal row (100: 0) (Fig. 3).

A clade containing the other three families (Laemobothriidae, Boopiidae and Menoponidae) also has very strong support (Fig. 2). Character state synapomorphies for this clade are all dorsal head setae (DHS): the mid-dorsal head seta DHS 17 (9: 1), ocular seta DHS 20 (12: 1), occipital setae DHS 21 (13: 1), DHS 22

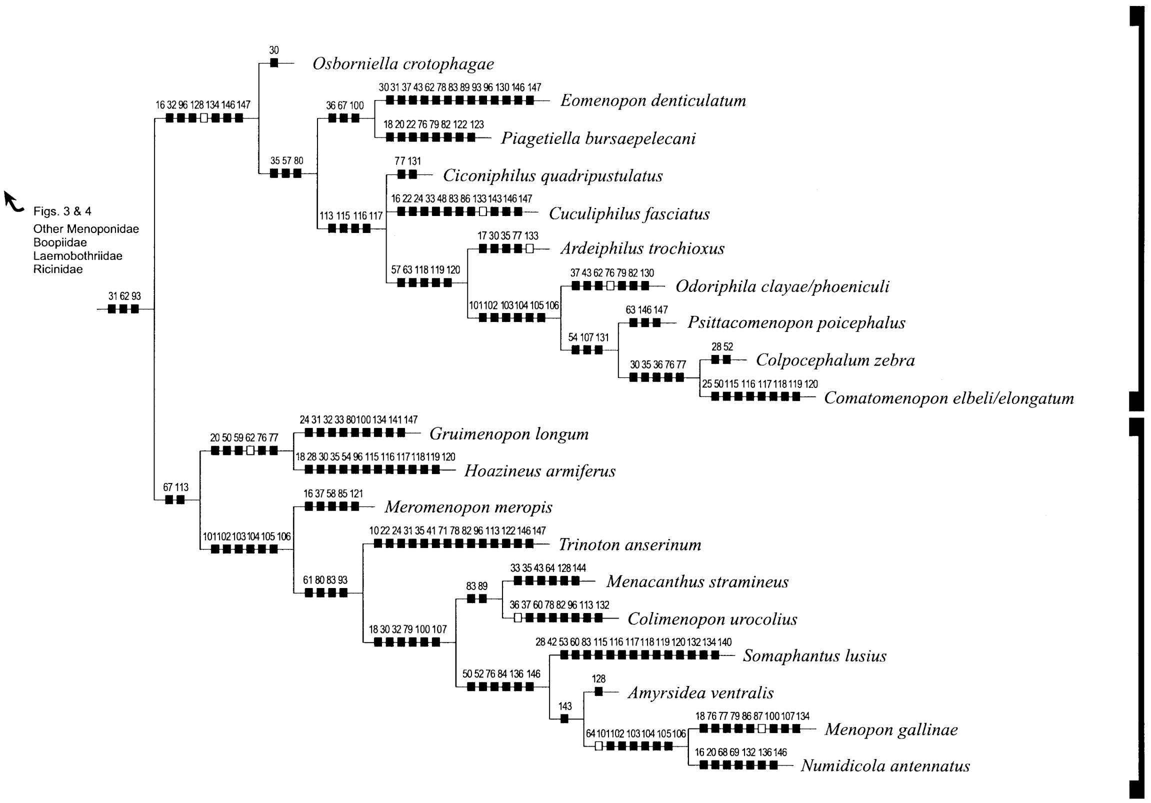

Figure 5. Character state evolution with the Menoponidae (clades 'C' and 'D'). Characters which change unambiguously are shown mapped onto the strict consensus tree. Unique changes = □. For character state descriptions, see Appendix 2.

(14: 1) and temple setae DHS 25 (19: 1), DHS 26 (21: 1), DHS 27 (23: 1) and DHS 29 (26: 1) (Fig. 3). All genera within the Laemobothriidae, Boopiidae and Menoponidae have the transverse pronotal carina (65: 1), except the menoponid *Rediella* Hopkins (65: 0) (Fig. 4). The small seta at each anterior end of tergite 2 (see Fig. 15C) termed '*a*' by Clay (1969) is usually present in these families (109: 1) as is a pair of isolated subterminal setae on the distal segment of the maxillary palp (41: 1) (but see Figs 4,5). These three characters are not present in members of the Ricinidae.

The Laemobothriidae is a monogeneric family, which is strongly supported as the sister taxon to the clade containing the Menoponidae and Boopiidae (Fig. 2). *Laemobothrion* Nitzsch has three short setae at the anterior ventrolateral head margin (55: 2) and, unusually, the setal patches on sternites 5 (134: 2) and 6 (136: 2) are composed of microcombs (Fig. 3) rather than regular setae, as in some Menoponidae. The clade containing the Boopiidae and Menoponidae is also very strongly supported (Fig. 2). This finding supports Clay (1970) who proposed a sister relationship for these two families. Both the Boopiidae and Menoponidae have a complete setal row across the edge of the dorsal prothorax (66: 2), which is always less developed in the Ricinidae and Laemobothriidae (Fig. 3). The mesonotum and metanotum are always separate (73: 0) and on each tergite the postspiracular setae are generally posterior to the spiracle (112: 0), whereas in the other families they are laterally placed (112: 1) (Fig. 3). All taxa, with the exception of the menoponid *Numidicola* Ewing, have the anterior mesonotal setae (69: 1) usually clustered around the postnotum (Fig. 3).

The monophyly of the Boopiidae is very strongly supported (Fig. 2). Synapomorphies for this clade are a seta on a rounded protuberance each side of the mesonotum (72: 1) and gonapophyses in the female (142: 1) (Fig. 3). The euplantula of the first tarsus is normally present in the Amblycera but has been lost in *Latumcephalum* Le Souëf and *Paraboopia* Werneck & Thomson. Where present in the Boopiidae, the euplantula has an unusual serrated and globular appearance (96: 2) (Fig. 3). At the base of the boopiid clade, the avian infesting *Therodoxus* Clay is the sister taxon to a reasonably supported clade containing all of the marsupial parasites. The male genitalia of the marsupial lice has a bulbous, well defined mesosomal arch (145: 1) and, with the exception of *Paraheterodoxus* Harrison & Johnston, the abdominal spiracles open onto the lateral plates instead of the usual amblyceran site on the tergites (110: 1) (Fig. 3). In *Paraheterodoxus*, the lateral plate is only partially divided (110: 2) (Fig. 3). *Latumcephalum* and *Paraboopia* are very strongly supported as sister taxa within the boopiid clade and have less than the normal four segments in the maxillary palp (39: 1) (Fig. 3).

The monophyly of the largest family, the Menoponidae, has good support (Fig. 2). A setal comb row lining the antennal margin (56: 1) is characteristic of this family and is undeveloped only in *Machaerilaemus* Harrison and *Ancistrona* (56: 0) (Figs 4,5). At the base of this large group, *Rediella* is the sister taxon to a clade containing the rest of the Menoponidae. All menoponid taxa have a setal fringe around the female terminalia (140: 1), except *Somaphantus* Paine (140: 0) and they usually have a brush (91: 2) or combs (91: 3) of setae on the ventral aspect of the third femur (Figs 4,5).

Within the Menoponidae, there are four main suprageneric groups (clades 'A–D') (Figs 2,4,5). Within clade 'A' (Figs 2,4), *Chapinia* Ewing is the sister taxon to a clade containing five genera, which has only moderate support (Fig. 2). These five genera have a complete marginal border encircling the prosternal plate (85: 2) (Fig. 4). Also within clade 'A', there is very strong support for *Dennyus* and *Myrsidea* (Dennyinae *sensu* Eichler, 1963) as sister taxa.

Clade 'B' (Figs 2,4) contains three genera from the Austromenoponinae (*sensu* Eichler, 1963) and *Machaerilaemus* (Machaerilaeminae). Support for clade 'B' is poor (Fig. 2). These genera share a well-developed temple seta, DHS 25 (20: 0) (Fig. 4) and, with the exception of *Machaerilaemus*, all have the dorsal head sensillum '*c*' (see Fig. 6A) *sensu* Clay (1969) (32: 1) and a smooth junction of the dorsolateral head and temple margins (36: 0) (Fig. 4).

Suprageneric clades 'C' and 'D' (Figs 2,5) are sister groups in this analysis, but this relationship is poorly supported (Fig. 2). Most of the genera in clades 'C' and 'D' have an additional submarginal row of short setae on the tibia of legs two and three (93: 1) (Fig. 5) but this trait is later lost within clade 'D'. The taxa in clade 'C' (Figs 2,5) generally represent the '*Colpocephalum* complex' (*sensu* Clay, 1969) (see Table 1) and Colpocephalidae (*sensu* Eichler, 1963) (see Table 2) but the monophyly of this clade is weakly supported (Fig. 2). Some of the internal branches in clade 'C' have good support, e.g. the clade containing *Colpocephalum* and *Comatomenopon* Uchida (Colpocephalinae *sensu* Eichler, 1963). There is, however, some difficulty in resolving the position of *Ciconiphilus* and *Cuculiphilus* (Fig. 2). Only genera in clade 'C' have setal combs on the third ventral sternite (St 3) (128: 2) and combs are also present on the ventral aspect of the third femur (91: 3) with the exception of *Eomenopon* Harrison (91: 2) (Fig. 5). *Osborniella* Thompson is sister taxon to a clade containing the remainder of the *Colpocephalum*-like genera and *Eomenopon*, which groups with *Piagetiella* Neumann.

The last suprageneric group, clade 'D' (Figs 2,5) is very poorly supported (Fig. 2). At the base of this clade *Gruimenopon* Clay & Meinertzhagen and *Hoazineus* Guimarães form a sister group to the other genera. These taxa are the only genera which have robust submarginal temporal setae (62: 2) (Fig. 5). Clade 'D' also contains the two genera (*Amyrsidea* Ewing and *Menacanthus* Neumann) included in the '*Menacanthus* complex' (*sensu* Clay, 1969) but these not sister taxa in this analysis (Figs 2,5). There is some support for the grouping of *Menacanthus* and *Colimenopon* Clay & Meinertzhagen as sister taxa. These two genera have more setae on the posterior aspect of the first coxa (89: 1) (Fig. 5) than the usual four or five setae commonly found in the Menoponidae. *Menopon* Nitzsch and *Numidicola* (Menoponinae *sensu* Eichler, 1963) are sister taxa in clade 'D' (Figs 2,5). Exclusive to these taxa, is the form of the sculpturing on the ventral submargin of the temple, which is composed of multi-tipped spikes (64: 1) and in place of the usual wide female anal fringe, these genera have a small rounded protruding anal margin with a short fine fringe (141: 2) (Fig. 5).

DISCUSSION

Clay (1970) considered the Menoponidae, Boopiidae and Ricinidae to be monophyletic groups. The tree derived from the cladistic analysis (Fig. 2) corroborates this view and the stability of each family is strongly supported. Clay (1970) also believed that the Menoponidae would hold the basal position in an amblyceran phylogeny, which has not been found by this study. The placing of the Ricinidae and Laemobothriidae at the base of the tree (see Fig. 2) may, however, only be an artefact of ingroup and outgroup selection. Both these families and the chosen outgroup taxon *Liposcelis* lack a number of characters and the arrangement may change with the addition of genera of other amblyceran families or different outgroup taxa. Clay (1970) wrote that the close morphological similarity of the Menoponidae and Boopiidae was indicative of a sister taxa relationship, which has been strongly supported in this analysis.

The suprageneric groups defined here only agree in part with the classifications of both Eichler (1963) and Clay (1969). Overall, there is little support for the intricate amblyceran classification of Eichler (1963; see Table 2). In his treatment of the Ricinidae, Eichler placed *Ricinus* and *Trochiloecetes* in two monogeneric families and in turn included the Ricinidae and *Laemobothrion* under the superfamily Laemobothrioidea, which is strongly paraphyletic in this study (Fig. 2). He regarded the Boopiidae as sharing more similarities with the Gyropidae and Trimenoponidae (rather than with the Menoponidae), placing these families under the superfamily Gyropoidea (see Table 2). The Boopiidae (*sensu* Eichler, 1963) are also strongly paraphyletic in this analysis with respect to his monogeneric Latumcephalidae (Fig. 2). Within the largest family, the Menoponidae, some of Eichler's generic groupings are unusual and, in comparison with the tree presented in Figure 2, most of his subdivisions are paraphyletic or polyphyletic. The tree found here supports the historical view that Eichler's groups were sometimes little more than arbitrary. Clay (1947), when discussing the preliminary classification of Eichler (1941), wrote of his groups '. . . that in many cases they bear little relationship to the facts'. None of the seven new families he proposed within the Menoponidae are monophyletic in this current analysis. Nevertheless, a few of Eichler's subfamilies are supported. The Menoponinae (*Menopon* and *Numidicola*), Colpocephalinae (*Colpocephalum* and *Comatomenopon*) and Dennyinae (*Dennyus* and *Myrsidea*) are all monophyletic, with the last two subfamilies having high levels of branch support (Fig. 2). *Dennyus* and *Myrsidea* were also presented as sister taxa by Cruickshank *et al*. (2001) in a molecular study using the *EF1α* gene, although with a poorer level of branch support than presented here.

Clade 'C' (Figs 2,5) contains the superfamily Colpocephaliformia (*sensu* Eichler, 1963) and the six taxa considered as part of the '*Colpocephalum* complex' (*sensu* Clay, 1969; see Table 1). *Eomenopon* has combs on some of the ventral sternites, which are more robust but generally similar to the combs found in the other genera in clade 'C', but both Eichler (1963) and Clay (1969) overlooked this similarity when constructing their classifications. Clade 'C' is more reflective of the Eichler (1963) classification than that of Clay (1969). With the exception of *Osborniella*, all of Eichler's Colpocephalidae are included in a single clade and his monogeneric Piagetiellidae is the sister taxon of *Eomenopon*. Eichler's Anserphilinae is paraphyletic and his monogeneric Psittacomenoponinae is the sister taxon to the Colpocephalinae. The Cuculiphilinae (*sensu* Eichler, 1963) is polyphyletic. Clay (1969) defined her '*Colpocephalum* complex' as '. . . all those genera with ctenidia (setal combs) on the venter of the third femur, with the exception of *Cuculiphilus s. l.*, *Bucerocolpocephalum*, *Piagetiella*, *Turacoeca* and *Odoriphila*', although she did consider that possibly the last genus should be included in the '*Colpocephalum* complex'. The tree presented in this analysis (Fig. 2) suggests that this group should be extended to include *Odoriphila* Clay & Meinertzhagen, *Cuculiphilus* and *Piagetiella*.

Within clade 'D' (Figs 2,5), *Amyrsidea* and *Menacanthus*, the two genera included from the '*Menacanthus* complex' (*sensu* Clay, 1969) do not group together. There is strong branch support (Fig. 2) for the clade containing *Menacanthus* and *Colimenopon* with *Amyrsidea* grouped with *Menopon* and *Numidicola*. However Clay (1969) did suggest that *Menopon* and *Somaphantus* should also possibly be included in the '*Menacanthus* complex'. The tree presented in Figure 2 suggests they should be included, but there is also some support for *Numidicola* and *Colimenopon* to be considered as part of the 'complex'.

EVIDENCE FOR HOST–PARASITE COEVOLUTION

Lice are considered to be very host-specific parasites and are widely assumed to be good models for coevolutionary analyses. The extent of host–parasite cospeciation has been investigated in the gopher lice (Ischnocera: Trichodectidae) by, for example, Hafner *et al*. (1994) and Hafner & Page (1995). These studies found that within genera, parasite and host phylogenies were almost completely congruent with one another, whilst the relationships between genera have been found to be only partially so (Page, Price & Hellenthal, 1995). Within the Amblycera, and specifically within the menoponid genus *Dennyus*, there have also been tests of host–parasite cospeciation. Clayton, Price & Page (1996) compared louse phenetic trees with a molecular cytochrome *b* (cyt *b*) phylogeny for their swift and swiftlet hosts, but the topologies were mostly incongruent. In a later publication, some evidence was found for cospeciation when molecular cyt *b* phylogenies for *Dennyus* (*Collodennyus*) species and their hosts were compared (Page *et al*., 1998).

The association between most louse species and their hosts is not necessarily an exclusive one-to-one relationship. A host may harbour more than one louse species, and a louse species may also be found on a limited number of hosts. This pattern also extends to louse genera. Some louse species are parasitic only on hosts of a particular order, sometimes even a single family, but many are distributed across multiple host orders and families, indicating a complex history of parasitism. Therefore, it may be very difficult, or even futile, in this study to investigate the extent of coevolution, when the phylogeny presented in Figure 2 contains only single representatives of genera.

However, where there are louse genera which are only present on a particular closely related group of hosts, some limited inference may be made. Smith (2000), for example, found that louse species which were present only on certain hosts were confined to single clades in his morphological analysis of the Goniodidae and Heptapsogasteridae (Ischnocera). In this study of amblyceran lice, the tree presented in

Figure 2 reveals similar results. Within the Boopiidae (Fig. 2), the clade containing *Boopia* Piaget, *Paraheterodoxus*, *Paraboopia* and *Latumcephalum* has genera which parasitize the marsupial order Diprotodontia (Kangaroos, wombats, etc.). Aside from *Boopia*, which has a wider distribution, the other three genera are exclusive to this host group. Similarly, within the menoponid clade 'D' (Figs 2,5), *Amyrsidea*, *Menopon*, *Numidicola*, *Somaphantus* and *Menacanthus* are grouped with *Colimenopon*. Excepting the latter genus, these taxa are all parasitic on the avian Galliformes (pheasants, fowl, etc.). Notably, the first four genera are contained within a single clade and their distribution is restricted to only two avian host families (Phasianidae and Numididae) which have been shown to be sister taxa (e.g. Sibley & Ahlquist, 1990). Such a result suggests that a cospeciation analysis of host and parasite using specific exemplars from some or all of the genera outlined above may bear interesting results. Some clades in the phylogeny presented here may enable more detailed coevolutionary analyses of the Amblycera and thus contribute to our presently limited understanding of the complicated history of parasitism in these lice.

The complete data matrix and all trees presented in this paper are accessible through TreeBASE (http://herbaria.harvard.edu.treebase) as study accession number S739.

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APPENDIX 1

Taxa included in the cladistic analysis. Type species for the genera examined and their type host species are denoted by a superscript^{T}, with species authority given for each taxon studied. Abbreviations: Brit. Mus. = British Museum of Natural History accession number; coll. = collection.

Taxon	Host taxon	Material examined
Actornithophilus uniseriatus^{T} (Piaget, 1880)	ex- *Recurvirostra avosetta*	9 adult ♀, 2 adult ♂ (Brit. Mus. 1962 – 127 [2 slides], Meinertzhagen coll. #4391, #8024, #11011).
Amyrsidea ventralis^{T} (Nitzsch, 1866)	ex- *Argusianus argus*^{T}	6 adult ♀, 4 adult ♂ (Brit. Mus. #1970 – 224 [2 slides], #1964 – 163, Meinertzhagen coll. #10889).
Ancistrona vagelli^{T} (Fabricius, 1787)	ex- *Fulmarus glacialis*^{T}	7 adult ♀ (Brit. Mus. #1959 – 419, Meinertzhagen coll. #11402).
	ex- *Daption capense*	2 adult ♀, 1 adult ♂ (Brit. Mus. #1970 – 208, #1974 – 278 & 1 slide unnumbered).
Ardeiphilus trochioxus^{T} (Burmeister, 1838)	ex- *Botaurus stellarus*^{T}	9 adult ♀, 5 adult ♂ (Brit. Mus. #1960 – 265, Meinertzhagen coll. #3832, Hopkins coll. [unnumbered] & 1 slide unnumbered).
Austromenopon crocatum^{T} (Nitzsch, 1866)	ex- *Numenius a. arquata*^{T}	12 adult ♀, 2 adult ♂ (Meinertzhagen coll. #289 [2 slides], #16685, Hopkins coll. [unnumbered], Waterston coll. [BM 1930 –232, 2 slides]).
Bonomiella columbae Emerson, 1957 Type species: *B. insolitungui-colata* (Conci, 1942)	ex- *Columba livia*^{T}	7 adult ♀ (Brit. Mus. #1981 – 171 [7 slides], #1966 – 653).
Boopia tarsata^{T} Piaget, 1880	ex- *Vombatus ursinus*^{T}	4 adult ♀, 2 adult ♂ (Brit. Mus. #1971 – 470, #1976 – 469).
Chapinia robusta^{T} Ewing, 1927	ex- *Ceratogymna atrata*^{T}	5 adult ♀, 3 adult ♂, 1 ⊙ (3 slides unnumbered).
Ciconiphilus quadripustulatus^{T} (Burmeister, 1838)	ex- *Ciconia c. ciconia*^{T}	11 adult ♀, 8 adult ♂. Brit. Mus. #1957 – 434, Meinertzhagen coll. #1122, #7857, #20514).
Colimenopon urocolius^{T} (Bedford, 1930)	ex- *Colius indicus*^{T}	2 adult ♀, 3 adult ♂, 4 ⊙ (Brit. Mus. #1954 – 474, # 1958 – 76 [3 slides], Meinertzhagen coll. #3872).
Colpocephalum zebra (Burmeister, 1838) Type species: *sub judice*	ex- *Ciconia ciconia*^{T}	4 adult ♀, 7 adult ♂ (Brit. Mus. 1954 – 474, Meinertzhagen coll. #14820, #20184 [BM 1953 – 225]).
Comatomenopon elbeli Emerson, 1958	ex- *Ardea p. purpurea*^{T}	2 adult ♀, 2 adult ♂ (Meinertzhagen coll. #7581/7582 [2 slides – paratypes]).
Comatomenopon elongatum^{T} Uchida, 1920	ex- *Egretta garzetta gularis* Type host: *Sterna sinensis*	2 adult ♀ (unnumbered).
Cuculiphilus fasciatus^{T} (Scopoli, 1763)	ex- *Cuculus c. canorus*^{T}	5 adult ♀, 2 adult ♂ (Brit. Mus. #1954 – 137, #1964 – 126, #1971 – 257, Hopkins coll. [unnumbered]).
Dennyus hirundinis^{T} (Linnaeus, 1761)	ex- *Apus apus*^{T}	4 adult ♀, 2 adult ♂ (Brit. Mus. #1955 – 735, #1957 – 571 & 2 slides unnumbered).
Eidmanniella pellucida^{T} (Rudow, 1869)	ex- *Phalacrocorax carbo*^{T}	5 adult ♀, 2 adult ♂ (Meinertzhagen coll. #1325, #11581, #20552, Waterston coll. [BM 1930 – 232], Morison coll. [unnumbered]).
Eomenopon denticulatum^{T} Harrison, 1915	ex- *Trichoglossus haematodus*^{T}	5 adult ♀, 4 adult ♂ (Brit. Mus. #1972 – 578 [2 slides], Thomson coll. [5 slides unnumbered]).
Gruimenopon longum^{T} (Giebel, 1874)	ex- *Grus grus*^{T}	8 adult ♀, 4 adult ♂ (Meinertzhagen coll. #1164 [4 slides – neoparatypes]).

APPENDIX 1 (*continued*)

Taxon	Host taxon	Material examined
Hoazineus armiferus^{T} (Kellogg, 1909)	ex- *Opisthocomus hoazin*^{T}	5 adult ♀, 6 adult ♂ (Brit. Mus. #1961 – 188 [3 slides], #1975 – 308, Meinertzhagen coll. #12612).
Hohorstiella lata^{T} (Piaget, 1880)	ex- *Columba liva*^{T}	5 adult ♀, 1 adult ♂ (Brit. Mus. #1968 – 384, Hopkins coll. [unnumbered]).
Holomenopon brevithoracicum (Piaget, 1880) Type species: *H. albofasciatum* (Piaget, 1880)	ex- *Cygnus melancoriphus*^{T}	17 adult ♀, 9 adult ♂ (Meinertzhagen coll. #13436).
Laemobothrion maximum^{T} (Scopoli, 1763)	ex- *Buteo buteo*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1959 – 234, Meinertzhagen coll. #19743).
Latumcephalum lesouefi Harrison & Johnston, 1916	ex- *Wallabia bicolor*^{T}	1 adult ♀, 2 adult ♂ (Brit. Mus. #1962 – 186 [2 slides]).
	ex- *Macropus ualabatus*	1 adult ♀ [unnumbered].
Latumcephalum macropus^{T} (LeSoëuf, 1902)	ex- *Wallabia bicolor* Type host: *Macropus dorsalis*	1 adult ♀ (Brit. Mus. #1962 – 677).
Machaerilaemus laticorpus (Carriker, 1903)	ex- *Euphagus carolinus* Type host: *Thamnophilus doliatus*	2 adult ♀ (Brit. Mus. # 1933 – 615 [2 slides]).
Machaerilaemus latifrons^{T} Harrison, 1915	ex- *Poephila gouldiae*^{T}	1 adult ♂ (Brit. Mus. #1980 – 40).
	ex- *Poephila mirabilis*	3 adult ♀ (Brit. Mus. #1980 – 40 [3 slides]).
Menacanthus stramineus (Nitzsch, 1818) Type species: *M. robustus* (Kellogg, 1896)	ex- *Gallus domesticus*^{T}	5 adult ♀, 4 adult ♂ (Brit. Mus. #1955 – 351, Thomson coll. [5 slides unnumbered], & 2 slides [unnumbered]).
Menopon gallinae^{T} (Linnaeus, 1758)	ex- *Gallus domesticus*^{T}	5 adult ♀, 4 adult ♂ (Brit. Mus. #1956 – 117, #1958 – 660, #1967 – 739, #1980 – 40).
Meromenopon meropis^{T} Clay & Meinertzhagen, 1941	ex- *Merops apiaster*^{T}	5 adult ♀, 5 adult ♂ (Brit. Mus. #1950 – 389, #1966 – 241, Hopkins coll. [unnumbered]).
Myrsidea victrix^{T} Waterston, 1915	ex- *Ramphastos tocard*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1914 – 535 [2 slides – paratypes], Hopkins coll. [unnumbered – paratype]).
	ex- *Ramphastos ambiguus*	1 adult ♀, 1 adult ♂ (Brit. Mus. #1968 – 86).
Neomenopon pteroclurus^{T} Bedford, 1920	ex- *Pterocles alchata* Type host: *P. namaqua*	4 ⊙ (Brit. Mus. #1928 – 327 [4 slides]).
Numidicola antennatus^{T} (Kellogg & Paine, 1911)	ex- *Numida meleagris*^{T}	5 adult ♀, 2 adult ♂ (Brit. Mus. #1953 – 89 [2 slides], #1955 – 229 [5 slides]).
Odoriphila clayae Tendeiro, 1960	ex- *Phoeniculus purpureus*^{T}	1 adult ♀ (unnumbered).
Odoriphila phoeniculi^{T} Clay & Meinertzhagen, 1941	ex- *Phoeniculus bollei jacksoni*^{T}	13 adult ♀, 9 adult ♂ (c).
Osborniella crotophagae^{T} (Stafford, 1943)	ex- *Crotophaga ani*^{T}	6 adult ♀, 6 adult ♂ (Brit. Mus. #1961 – 188 [2 slides], #1975 – 308, Hopkins coll. [unnumbered]).
Paraboopia flava^{T} Werneck & Thompson, 1940	ex- *Macropus robustus*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1962 – 677 [3 slides – paratype, lecotype], #1981 – 142).
Paraheterodoxus insignis^{T} Harrison & Johnston, 1916	ex- *Aepyrymnus rufescens*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1962 – 186 [2 slides]).
Piagetiella bursaepelecani^{T} (Perry, 1876)	ex- *Pelecanus occidentalis*^{T}	8 adult ♀, 7 adult ♂ (Brit. Mus. #1953 – 63, #1963 – 351, #1973 – 270, Meinertzhagen coll. #12850).

APPENDIX 1 (*continued*)

Taxon	Host taxon	Material examined
Plegadiphilus threskiornis^{T} Bedford, 1939	ex- *Threskiornis aethiopicus*^{T}	10 adult ♀, 12 adult ♂ (Brit. Mus. #1965 – 526, Meinertzhagen coll. #7218.7219, Hopkins coll. [unnumbered]).
Pseudomenopon pilosum^{T} (Scopoli, 1763)	ex- *Fulica atra*^{T}	6 adult ♀, 5 adult ♂ (Brit. Mus. #1969 – 595 [2 slides], #1980 – 40, Meinertzhagen coll. #2942, #10510 [neoparatypes]).
Psittacomenopon poicephalus^{T} (Bedford, 1920)	ex- *Poicephalus meyeri*^{T}	16 adult ♀, 11 adult ♂, 1 ⊙ (Brit. Mus. #1954 – 507, # 1957 – 219, Hopkins coll. [unnumbered]).
Rediella mirabilis^{T} Hopkins, 1948	ex- *Glareola ocularis*^{T}	1 adult ♀, 2 adult ♂ (Meinertzhagen. coll. #16660, Hopkins coll. #paratype '6').
Ricinus fringillae^{T} (De Geer, 1778)	ex- *Emberiza schoeniclus* Type host: *Emberiza citrinella*	2 adult ♀, 1 adult ♂ [3 slides unnumbered].
Somaphantus lusius^{T} Paine, 1914	ex- *Numida meleagris*^{T}	5 adult ♀, 7 adult ♂ (Brit. Mus. #1955 – 229 [2 slides], #1954 – 474, #1980 – 40, Hopkins coll. [unnumbered]).
Therodoxus oweni^{T} Clay, 1971	ex- *Casuarius casuarius*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1972 – 222 [2 slides]).
Trinoton anserinum^{T} (Fabricius, 1805)	ex- *Anser anser*^{T}	2 adult ♀, 1 adult ♂ (Meinertzhagen coll. #19758 (BM #1952 – 143), #20222 (BM 1953 – 658) & 1 slide unnumbered).
	ex- *Cygnus olor*	1 adult ♀, 2 adult ♂ (Brit. Mus. #1965 – 223, #1972 – 221 [2 slides]).
	ex- *Plectropterus gambiensis*	2 adult ♀ (Brit. Mus. #1980 – 40 [2 slides]).
Trochiloecetes rupununi Carriker, 1963 Type species: *T. prominens* (Kellogg & Chapman, 1899)	ex- *Phaethornis superciliosis*^{T}	2 adult ♀, 2 adult ♂ (Brit. Mus. #1970 – 726 [2 slides]).
Trochiliphagus abdominalis^{T} Carriker, 1960	ex- *Anthracothorax nigricollis*^{T}	2 adult ♀, 1 adult ♂, 3 ⊙ (Brit. Mus. #1961 – 606 [3 slides]).
Liposcelis bostrychophilus Badonnel, 1931	ex- *jar of rice, London* ex- *'household', Cornwall, England*	12 adult ♀ (Ref: 16/81). 9 adult ♀ (Ref: 83/83).

APPENDIX 2
CHARACTERS AND COMMENTS

Characters of the head

Dorsal head setae

The dorsal head setae (DHS, *sensu* Clay, 1969) are paired setae of the mid- and posterior dorsal head (Fig. 6). They are numbered DHS 8–31 and extend from the preocular margin, down through the midline of the head to the posterior occipital margin and around the temple. Most genera within the Menoponidae have the full complement of setae, but some setal subgroups are absent within other families. The most anterior head setae are not included in this analysis as they can be present or absent between species of the same genus and even sexually dimorphic (Clay, 1969). Setal development is also variable at different taxonomic levels and is not easily grouped into a number of developmental types. For this analysis, they can only be divided into macro- and microsetae.

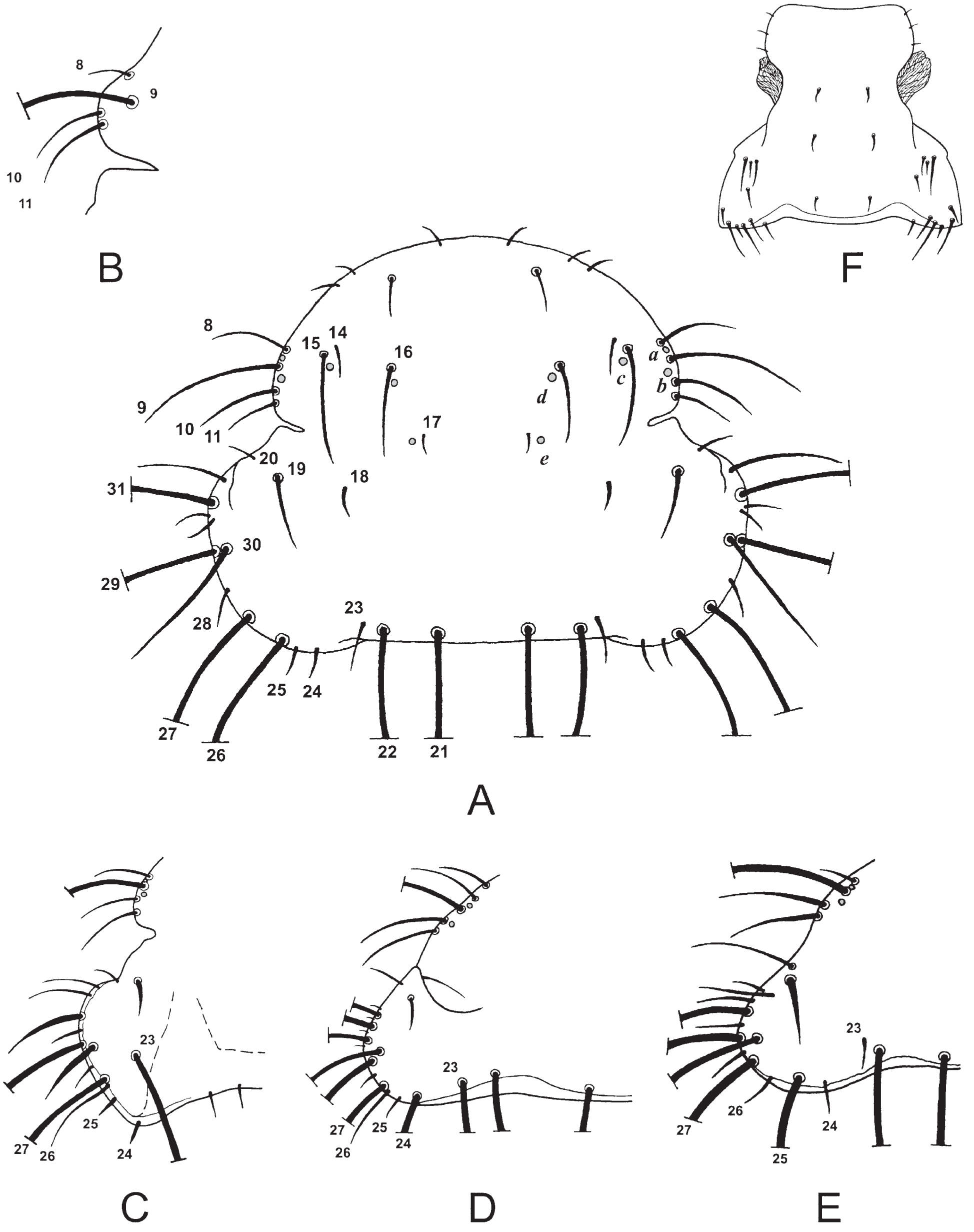

Figure 6. Characters of the dorsal head, the dorsal head setae (DHS 8–31) and sensilla (a–e) *sensu* Clay (1969) from (A) a typical menoponid head, (B) *Paraboopia*, (C) *Colpocephalum*, (D) *Colimenopon*, (E) *Austromenopon*, and (F) *Trochiloecetes*.

(a) Preocular setae (sensu Clay, 1969): DHS 8–11.

There are four setae in this group, which are located on the preocular margin. These setae are absent in *Trochiloecetes* (Ricinidae) and *Laemobothrion* (Laemobothriidae). *Laemobothrion* has 8–10 very robust setae on the anterior of the preocular margin in place of DHS 8 & 9 and a patch of 4–5 setae where DHS 10 & 11 might be expected.

1. DHS 8: (0) absent (Fig. 6F); (1) present (Fig. 6A–E).

This seta is usually quite poorly developed but it is long and quite robust in *Somaphantus* and *Numidicola* (Menoponidae).

2. DHS 9: (0) absent (Fig. 6F); (1) present (Fig. 6A–E).

This is usually the most developed seta of this group and easily identified. It may sometimes be as long as some of the more developed temple setae.

3. Position of DHS 9 (where present): (0) marginal (Fig. 6A,C–E); (1) submarginal and separate from other preocular setae (Fig. 6B).

In the most of the taxa studied, this seta is marginally located (in line with the other preocular setae) but in some boopiid genera (*Boopia*, *Latumcephalum* and *Paraboopia*) it is noticeably submarginal.

4. DHS 10: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

5. DHS 11: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

Meromenopon Clay and Meinertzhagen (Menoponidae) is unusual in that it has two copies of this seta on either side of the head.

(b) Dorsal setae (sensu Price & Beer, 1963), or setal complex (sensu Clay, 1969) DHS 14–16.

DHS 14 & 15 are usually grouped closely together with DHS 16 lying medially to this pair. DHS 14 is usually less developed and its position in relation to DHS 15 varies from directly anterior (e.g. *Dennyus*) to medial (e.g. *Chapinia*), with most taxa somewhere in between, making this unsuitable as a character state. DHS 16 may be closely associated with DHS 14 & 15 as in *Pseudomenopon* or situated far towards the midline of the head (e.g. *Amyrsidea*). Within the Ricinidae this setal group is absent in the hummingbird (Trochilidae) lice, *Trochiliphagus* and *Trochiloecetes*, although DHS 15 is present in the passeriform-infesting *Ricinus*.

6. DHS 14: (0) absent (Fig. 6F); (1) present (Fig. 6A).

7. DHS 15: (0) absent (Fig. 6F); (1) present (Fig. 6A).

8. DHS 16: (0) absent (Fig. 6F); (1) present (Fig. 6A).

(c) Mid-dorsal head setae (sensu Clay, 1969): DHS 17–18.

These setae are found in a part of the dorsal head, which tends to be over the site of the internal tentorium. DHS 18 is lateral to DHS 17, and its position usually corresponds to the width of the tentorial bridge. These setae may be widely spaced and one (or both) may be very small, which means they can be difficult to see in some genera (e.g. *Psittacomenopon* Bedford, *Gruimenopon,* and *Ancistrona*).

9. DHS 17: (0) absent (Fig. 6F); (1) present (Fig. 6A).

10. DHS 18: (0) absent (Fig. 6F); (1) present (Fig. 6A).

(d) Ocular setae (sensu Clay, 1969): DHS 19–20.

DHS 19 marks the division (or former site of the division) of the two ommatidia on each side of the head (Clay, 1969). Kéler (1971) also figured this setae for the Boopiidae. There is extensive variation in the development of the amblyceran eye (Wundrig, 1936) and the condition ranges from ommatidia with well-developed biconvex lenses (e.g. *Plegadiphilus* Bedford) to those with no lens at all (e.g. *Amyrsidea*).

DHS 20 is located on the ocular margin, either marginal or slightly submarginal. It is usually much smaller than DHS 19 and may be difficult to see, although it is quite developed in *Austromenopon* Bedford. *Trochiloecetes* (Ricinidae) has a patch of setae at this site.

11. DHS 19: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

12. DHS 20: (0) absent (Fig. 6F); (1) present (Figs 6A,C–E).

(e) Occipital setae (sensu Clay, 1969): DHS 21–22. These setae are normally long, well-developed, setae which emanate from the posterior head margin. They are unusually small and fine in *Colpocephalum* and absent in the Ricinidae. Kéler (1971; p112: fig. 100) labels the dorsal head 'frontal setae' of *Boopia tarsata* Piaget as 1–2. In my opinion these setae represent DHS 21 and DHS 22, respectively, the reasons for which are discussed below.

13. DHS 21: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

14. DHS 22: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

(f) Temple setae (sensu Clay, 1969): DHS 23–31.

These setae continue on from the occipital setae, running towards the anterior temples.

Kéler (1971; p112: fig. 100) numbers some of the temple setae in *Boopia tarsata*. However, I have found that the setal pattern in the Boopiidae almost mirrors that of the Menoponidae, allowing the confident proposal of homologies using the more extensive numbering system set out by Clay (1969). Kéler's (1971) 'frontal setae 3′ therefore represents DHS 23. The identity of his remaining temple is as follows: Seta 2 = DHS 25, Seta 1 = DHS 29, Seta 3 = DHS 30. Clay (1981) has since used this numbering system in the description of new species from this family.

Absent in the Ricinidae, *Trochiloecetes* has a patch of approximately six setae around the area of the posterior lateral temple margin while *Ricinus* and *Trochiliphagus* have about three to four setae.

15. DHS 23: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

This seta is absent in *Myrsidea* and *Rediella* (Menoponidae).

16. Position of DHS 23 (where present): (0) near DHS 22 (Fig. 6A,D–E); (1) sited far across the temple into the parietal area (Fig. 6C).

Clay (1969) states that DHS 23 may be anterior to DHS 22 (e.g. *Gruimenopon*), lateroanterior (e.g. *Cuculiphilus*) or in a straight line (e.g. *Psittacomenopon*). However, in many of the taxa where DHS 23 is far removed from DHS 22, it is very difficult to assign such character states. This is especially the case regarding taxa where the line of the temples has the tendency to run slightly backwards. Proximity to the occipital seta is a more conservative coding for the position of DHS 23.

17. DHS 24: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

18. Development of DHS 24 (where present): (0) macroseta. Well developed with distinct large alveoli, usually very robust and if long becomes finer distally until a very fine point, often reaching to the transverse pronotal carina (Fig. 6D); (1) microseta. Noticeably less developed than other head seta. May appear as fine and short, small and peg-like or so small as to appear as a micro dot setae (Fig. 6A,C,E).

19. DHS 25: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

20. Development of DHS 25 (where present): (0) macroseta. Well developed with distinct large alveoli, usually quite robust and if long becomes finer distally until a very fine point, often reaching to the transverse pronotal carina (Fig. 6E); (1) microseta. Noticeably less developed than other head setae. Fine and short, small and peg-like or micro dot seta (Fig. 6A,C,D).

21. DHS 26: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

22. Development of DHS 26 (where present): (0) macroseta. Moderately to well developed with distinct large alveoli, robust and if long becomes finer distally until a very fine point (Fig. 6A); (1) microseta. Noticeably less developed than other head setae. Fine and short, small and peg-like or micro dot seta (Fig. 6C–E).

23. DHS 27: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

Where present, this is always a large, well-developed setae which is easily identified. The position of DHS 27 aids in the identification of other temple setae.

24. Alveoli of DHS 26 & 27 (where present): (0) alveoli separate (Fig. 6A,E); (1) alveoli contiguous (Fig. 6C,D).

Clay (1969) discusses the alveoli of these setae in conjunction with the condition of DHS 26 (Character 22). Commonly, when the alveoli are separate, both DHS 26 and DHS 27 setae are long and robust. When the alveoli are contiguous, DHS 26 is reduced (with varying extent) towards a fine microseta, a condition which is generally (although not always) the case. In some taxa the alveoli are separate but DHS 26 is poorly developed.

25. DHS 28: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

Where present this seta is always somewhat reduced in comparison with the macrosetae of the temple. It is usually a small microseta.

26. DHS 29: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

As in DHS 27, this seta is always well-developed setae and easily identified. Its position aids in the identification of DHS 30.

27. DHS 30: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

This seta is usually associated with DHS 29, either directly medially submarginal (e.g. *Somaphantus*), anteriorly submarginal (e.g. *Pseudomenopon*) or directly anterior on the temple margin (e.g. *Amyrsidea*). However, due to a high level of grading between these suggested states for setal position, I am unable to explore this character further.

28. DHS 31: (0) absent (Fig. 6F); (1) present (Fig. 6A,C–E).

Clay (1969) wrote, '. . . one of the setae anterior to DHS 30 (here called DHS 31) may be long and stout'. As there is always at least one short setae (commonly two), between DHS 30 and the next macroseta, DHS 31 is interpreted as being the first macroseta after the DHS 29 and DHS 30 group.

29. Six setae (three pairs) down the midline of the dorsal head: (0) absent (Fig. 6A); (1) present (Fig. 6F).

These setae are peculiar to members of the Ricinidae. Nelson (1972) assigned a large number of chateotaxic labels in his revision of *Ricinus*, in a work that mirrored Clay's (1969) treatment of the Menoponidae. Nelson called these central dorsal head setae the 'd series' (d1, d2 and d3) and laid down terminology later followed by workers describing species from other ricinid genera (e.g. Oniki, 1995).

Dorsal head sensilla (sensu Clay, 1969)

Previously numbered as 1–5 (Clay, 1961), the dorsal head sensilla were re-labelled when a numerical system was applied to the dorsal head setae.

30. Sensillum 'a': (0) absent (Fig. 6B,F); (1) present (Fig. 6A,C–E).

This sensillum can be difficult to find as it is located between DHS 8 and DHS 9, which are often very close and can also be marginal. It is present only in some of the Menoponidae, including, in particular, all those genera that are restricted to galliform hosts.

31. Sensillum 'b': (0) absent (Fig. 6B,F); (1) present (Fig. 6A,C–E).

This sensillum is usually just posterior to DHS 9, but in some cases (e.g. *Somaphantus*) it appears more associated with DHS 10.

32. Sensillum 'c': (0) absent (Fig. 6F); (1) present (Fig. 6A).

Sensillum 'c' is associated with DHS 14 & 15. In most instances it is situated posterior, or lateroposterior, to DHS 15, although in *Menopon* and *Numidicola* it appears more associated with DHS 14.

33. Sensillum 'd': (0) absent (Fig. 6F); (1) present (Fig. 6A).

Where present this sensillum is found close to DHS 16.

34. Sensillum 'e': (0) absent (Fig. 6F); (1) present (Fig. 6A).

Sensillum 'e' is associated with DHS 17. In this assemblage of taxa, it was present only in *Holomenopon* Eichler.

Dorsal head shape

35. Preocular feature of dorsolateral head margin: (0) no feature, unbroken margin (Fig. 6D–F); (1) notch (Fig. 6C); (2) slit (Fig. 6A,B).

This character is first described by Clay (1947), in her preliminary key for the Menoponidae, with some reservation regarding consistency within some isolated genera but later proposed as a useful generic character in the later, revised publication (Clay, 1969). Occasionally, it is difficult to discern a wide slit from a notch, so I have followed the definitions set out by Clay (1947) and consulted the original generic alpha-taxonomic publications where appropriate. I have observed no consistency in the form of the preocular feature, within either the *Colpocephalum* or *Menacanthus* generic complexes. Notably, members of the Boopiidae, all posses a preocular slit.

36. Dorsolateral head junction with temple margin: (0) smooth line junction from dorsolateral margin through ocular margin to anterior temple margin (Fig. 6E,F); (1) ocular margin pronounced, but does not overlap anterior temple margin (Fig. 6C); (2) ocular margin overlaps anterior temple margin (Fig. 6A); (3) ocular margin and temple margin overlap dorsolateral margin (Fig. 6D).

Colimenopon is an unusual genus in that the ocular and temple margins overlap the dorsolateral margin.

Internal head

37. Form of the Tentorial bridge: (0) thick or with little reduction (Fig. 7A); (1) reduced and narrow (Fig. 7D); (2) reduced and wide (Fig. 7C); (3) reduced to a fine ligament (Fig. 7B).

The tentorium is a chitinous endoskeleton of the head, for the attachment of muscles for the mouthparts, antennae and oesophagus. In the Amblycera, it comprises of a pair of anterior arms linked by a bridge of hollow chitin. Nelson (1972) refers to the tentorial 'bar' in his review of *Ricinus* (Ricinidae).

Symmons (1952) described four forms of amblyceran tentorium: a generalized robust shape similar to that in the Psocoptera and three forms of reduced bridge ranging down to a fine membranous ligament. She conceded from her groupings that there may be a degree of parallel reduction in bridge sclerotization between some menoponid genera and those of other families. Most menoponids have a thick or partially reduced bridge (Symmon's groups 1 & 2). In other menoponid genera this is reduced to a rod like shape which is either narrow or wide relative to the width of the head. It is represented only as a fine ligament in the Boopiidae, Ricinidae (Nelson, 1972) and Laemobothriidae (Symmon's groups 3a and 4).

Mouthparts

38. Mouthparts: (0) developed chewing mandibles (Fig. 8A,B); (1) mandibles reduced with mouthpart structures modified into hollow stylets for piercing (Fig. 8D).

The mandibles are generally similar in the Amblycera, but within the Ricinidae genera exhibit varying degrees of modification. *Trochiloecetes* and *Trochiliphagus*, on hummingbirds (Trochilidae), show the most structural change. Although *Trochiloecetes* had been described by Paine & Mann (1913), no references to differences in the mouthparts were made until Clay (1949). The modifications consist of three structures of hypopharyngeal origin: a middle needle-like sucking tube originating from the sitophore sclerite, lying within a two-portioned sheath apparatus. The mandibles are minute and reduced to small cones Carriker (1960). *Ricinus* species parasitic on Passerines have 'regular' mandibles but they are less sclerotized and more elongate than in other Amblycera. *Ricinus* species on hummingbirds show similar changes to the mandibles and hypopharynx but they are not so modified Clay (1949).

39. Maxillary palp: (0) 4 segmented (Fig. 8A,B,F–H); (1) less than 4 segments (Fig. 8E).

There are generally four segments in the maxillary palp, although this has been reduced to two in *Latumcephalum* and three in *Paraboopia* (Boopiidae).

For a long period of time the amblyceran maxillary palp was misidentified. Kellogg (1896) stated quite clearly that he did not understand the maxillae and wrote there were no terminal free lobes, just a large basal part (labium) articulating with a conspicuous 4-segmented palpi. Kellogg repeatedly labelled ambly-

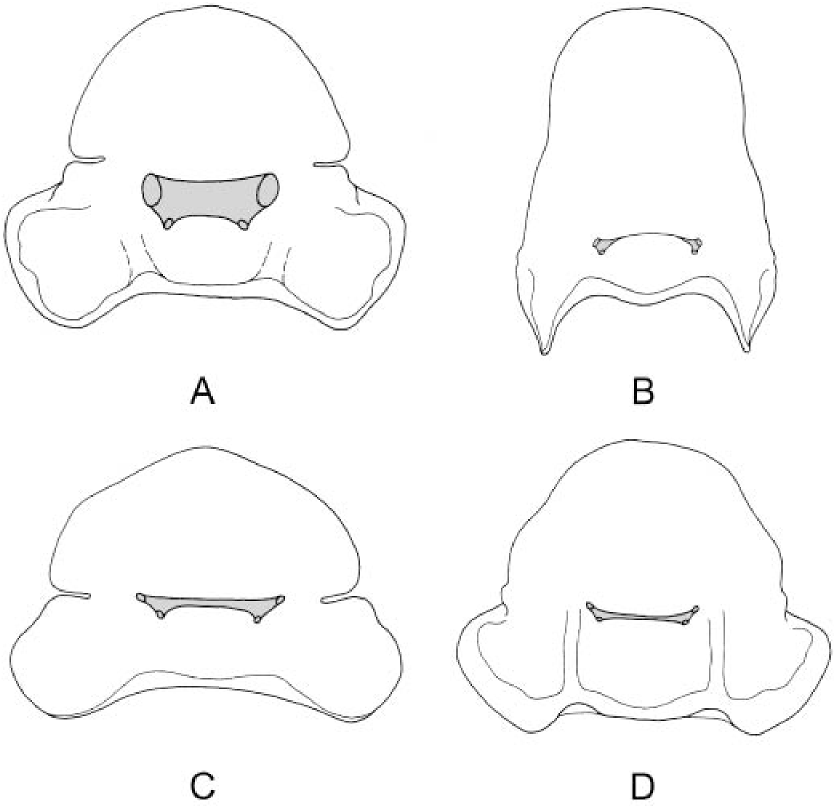

Figure 7. Forms of the tentorial bridge in (A) *Actornithophilus*, (B) *Ricinus*, (C) *Odoriphila*, and (D) *Dennyus*.

ceran maxillary palps as labial palps, but in some psocopterans, he labelled them correctly. Snodgrass (1899) also assigned labial origin to these structures. However, in a later publication, Snodgrass (1944) re-examined the mouthparts and wrote '. . . because of the close connections of the maxillae with the labium some writers have regarded the palpi as labial organs, but a comparison with the Corrodentia leaves little question that the mallophagan palpi are maxillary'.

40. Maxillary palp segmentation: (0) alternately short and long (Fig. 8B); (1) first few segments similar in length (Fig. 8A,E–H).

All the amblyceran families presented here have segments of similar length in the maxillary palp.

41. Isolated subterminal setae on the distal segment of the maxillary palp: (0) absent (Fig. 8B); (1) present (Fig. 8A,E–H).

All taxa scored as present have a pair of subterminal setae, one of which is usually peg-like. *Cuculiphilus*, is unusual in that it has three setae in this group.

42. Alveoli of maxillary palp subterminal setae (where present): (0) margins separate (Fig. 8F); (1) margins contiguous (Fig. 8A,E,G,H).

Clay (1966, 1968) illustrated the contiguous alveoli of the subterminal setae in *Myrsidea*. Only three taxa, *Laemobothrion* (Laemobothriidae), *Therodoxus* (Boopiidae) and *Somaphantus* (Menoponidae) have separate alveoli in this assemblage of taxa.

43. Ventral postpalpal processes: (0) absent (Fig. 8A,B); (1) present (Fig. 8G,H).

These arise just posterior to the base of the maxillary palps and have the appearance of loose flaps. They were extensively figured at species level for *Menacanthus* by Zlotorzycka (1965) and termed 'facial hooks'. Uchida (1926) and Price (1975, 1977) referred to them as 'ventral spinous head processes'. Clay (1961, 1962, 1966) called them 'sclerotized processes' or 'oral spines'.

44. Number of postpalpal processes (where present): (0) one (Fig. 8G); (1) two (Fig. 8H).

45. Labial palps: (0) absent; (1) present (Fig. 8A,B).

These are present as small lobes in the Amblycera. Notably, they are absent only in genera from the Ricinidae. Clay (1962) illustrates the labial palp of *Actornithophilus* Ferris.

46. Number of terminal setae on labial palpus (where present): (0) 5 (Fig. 8A,C); (1) more than 10 (Fig. 8B).

There are five terminal setae on the labial palps of all these amblyceran genera, although there may be

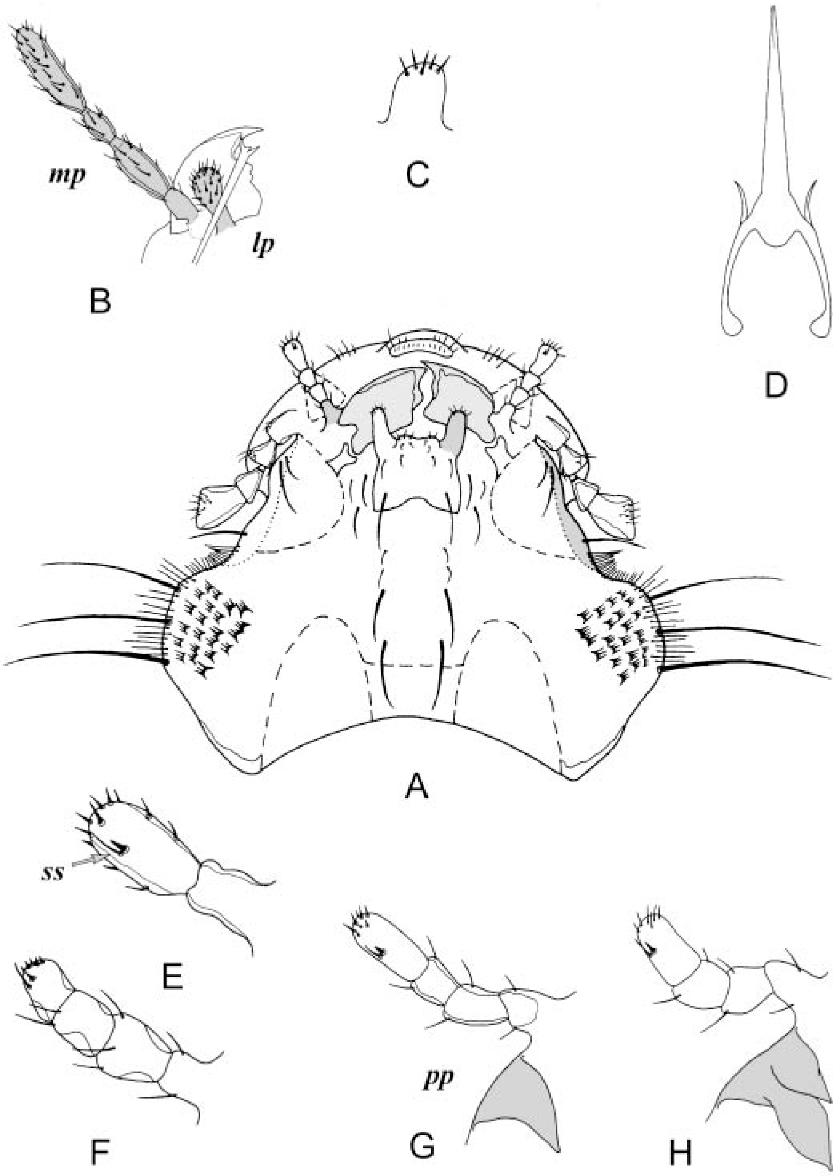

Figure 8. Characters of the ventral head and mouthparts in (A) *Colpocephalum* with maxillary palp, labial palp, antennal fossae (darker shading) and mandibles (lighter shading), (B) outgroup taxon *Liposcelis* with maxillary palp (*mp*) and labial palp (*lp*) (shaded), (C) amblyceran labial palp (detail), and (D) *Trochiloecetes*, piercing mouthparts. (E–H) Maxillary palps with postpalpal processes (*pp*) (shaded), in (E) *Latumcephalum* with subterminal setae (*ss*) indicated by arrow, (F) *Laemobothrion*, (G) *Menacanthus*, and (H) *Odoriphila*.

four in other genera of Boopiidae (Clay, 1970) not included in this study.

Antennal characters

47. Antennal length: (0) long (Fig. 9H); (1) much reduced (Figs 8A, 9A–G).

The amblyceran antennae are very short (4–5 segments) in comparison with those of *Liposcelis* (15 segments).

48. Number of flagellar segments (in the short antennae): (0) two segmented (Figs 8A, 9B,C,F); (1) three segmented (Fig. 9A,D,E,G).

The amblyceran antennae comprises of a basal scape, pedicel and a flagellum of two or three segments, the terminal segment in some taxa being subdivided (Clay, 1969). The majority of the Menoponidae examined here have two flagellomeres, although *Rediella*, *Austromenopon* and *Cuculiphilus* have three.

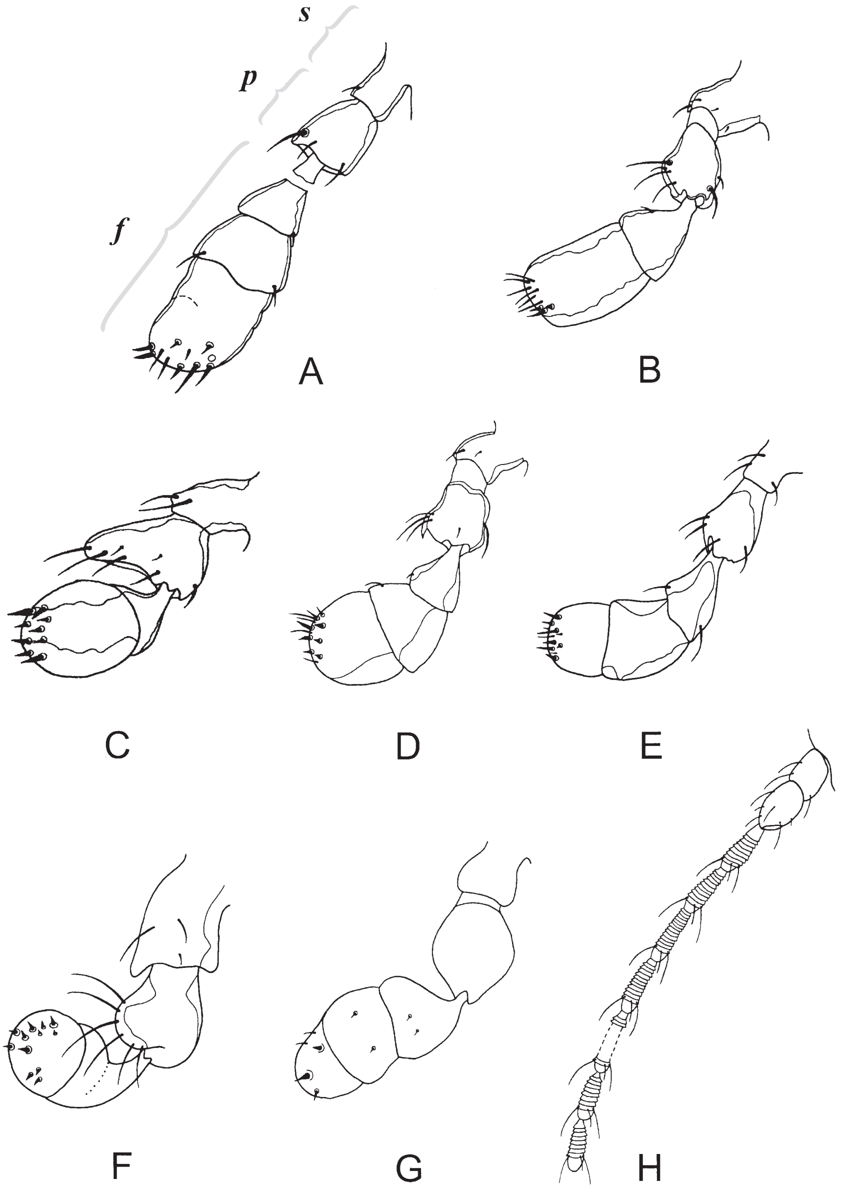

Figure 9. Form of the antennae in (A) *Rediella*, with scape (*s*), pedicel (*p*) and flagellum (*f*) components defined, (B) *Gruimenopon*, (C) *Hohorstiella*, (D) *Cuculiphilus*, (E) *Paraheterodoxus*, (F) *Laemobothrion*, (G) *Trochiliphagus*, and (H) outgroup taxon *Liposcelis*, with segments 1–4 and 12–13 of antenna shown.

There are also three flagellomeres in the Ricinidae and Boopiidae.

49. Secondary annulation of flagellar segments: (0) absent (Figs 8A, 9A–G); (1) present (Fig. 9H).

No annulation is present in the amblyceran taxa.

50. Flagellum shape: (0) filliform (Figs 8A, 9A,B,E,H); (1) globular (Fig. 9C,D,F,G).

The antennae may have a long slender look, with a filiform shaped flagellum. This feature is found in some boopiid and menoponid genera and is particularly a characteristic of the galliform-infesting taxa (*Amyrsidea*, *Somaphantus*, *Menopon* and *Numidicola*).

51. Shape of the first flagellar segment: (0) cylindrical (Fig. 9H); (1) pedunculate (Figs 8A, 9A–G).

The first flagellomere of the amblyceran antenna is always pedunculate or wine-glass shaped (Clay, 1969).

52. Sclerotization of the first flagellar segment: (0) regular and complete sclerotization (Fig. 9B–H); (1) irregularly sclerotized (Figs 8A, 9A).

It has previously been suggested (Tendeiro, 1967) that, in some Menoponidae, the pedunculate first

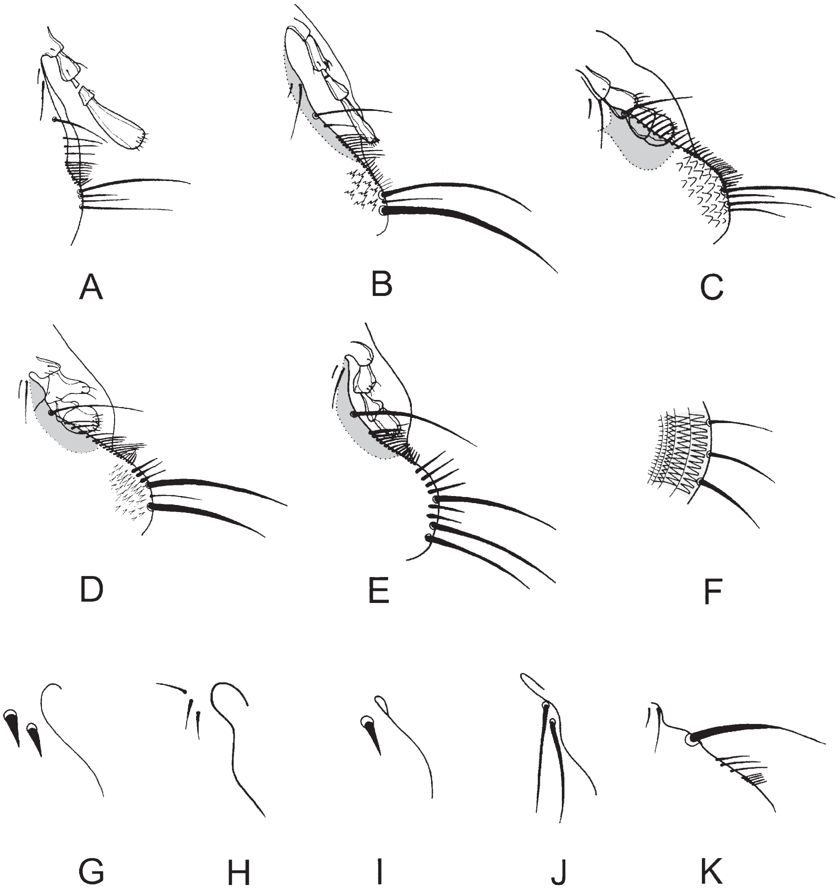

Figure 10. Characters of the ventrolateral head with the antennal fossae (shaded), in (A) *Somaphantus*, (B) *Numidicola*, (C) *Colimenopon*, (D) *Hohorstiella*, and (E) *Gruimenopon*. (F) *Laemobothrion* with fringe-like temple sculpturing (detail). (G–K): setae at the anterior termination of the ventrolateral head margin, in (G) *Ricinus*, (H) *Laemobothrion*, (I) *Trochiliphagus*, (J) *Chapinia*, and (K) *Plegadiphilus*.

flagellar segment may be divided in two, due to a darker pigmentation of the segmental 'stalk'. However, this has been refuted by Clay's (1969) scanning electron micrographs which show no line of division. Character 52 is only concerned with the degree of sclerotization down the flagellomere and does not consider any colour difference. A number of the taxa (e.g. *Chapinia*) do have a darker stalk, but sclerotization is still complete along the segment. However, in some genera this is not the case, giving the impression of a wide gap between stalk and 'bowl'. This is apparent in, e.g. *Rediella* and *Somaphantus*, however Paine (1914) did not mention this in his description of the latter genus.

Ventrolateral head

53. Antennal fossae: (0) absent or poorly developed (Fig. 10A); (1) present (Figs 8A, 10B–E).

The antennal fossae, where present, are located behind the ventrolateral head margin. They are absent in *Rediella* and *Somaphantus*.

54. Form of the antennal fossae (where present): (0) long and shallow (Fig. 10B); (1) short, very deep and pouch-like (Fig. 10C); (2) short and shallow (Fig. 8A); (3) short and deep, capable of containing the antennae (Fig. 10D,E).

Most commonly, the antennal fossae are short and shallow or short and deep, although the long and shallow state is found in both the Menoponidae and Boopiidae. In a few menoponids (e.g. *Colimenopon*), it has the appearance of a deep pouch.

55. Setae at the anterior termination of the ventrolateral head margin: (0) one long, one short (Figs 8A, 10A–E,K); (1) two short and stout (Fig. 10G); (2) three all short (Fig. 10H); (3) one short and stout (Fig. 10I); (4) two long (Fig. 10J).

The Boopiidae and Menoponidae have two setae (one long, one short) at this site (Clay, 1969), however, both setae are well developed in *Chapinia*. *Laemobothrion* has three, all short. In the Ricinidae, there may be one or two very stout setae.

56. Presence of a well-developed and compact setal comb row lining the subocular head margin: (0) absent; (1) present at least posteriorly (Figs 8A, 10A–E,K).

In most of the Menoponidae, the comb row is present, running posteriorly down the subocular margin towards the junction with the ventral temple margin. In *Machaerilaemus* (Harrison, 1915) and *Ancistrona* there are just a few setae spaced out along this edge. In *Ancistrona* there is also a row of fine setae on the underside of the dorsolateral head which should not be confused with the comb row (Clay, 1969).

57. Isolated subocular setae anterior to the comb row (where present): (0) subocular seta not isolated from comb row or anterior setae (where present) (Fig. 10C); (1) present (Figs 8A, 10A,B,D,E,K).

The comb row setae have their alveoli very close together. Anterior to this, along the margin is the subocular seta, which is quite well developed and usually isolated. Between the subocular seta and the comb row, there may be some additional widely spaced setae, which (Clay, 1969) termed group 's' setae (additional subocular setae) but are referred to here as anterior setae.

58. Subocular seta (where present): (0) normal seta (Figs 8A, 10A–E); (1) flattened (Fig. 10K).

The flattened condition is peculiar to four menoponids: *Eidmanniella* Kéler, *Austromenopon*, *Plegadiphilus* and *Meromenopon* (in which the seta is also flanged; Clay, 1969).

59. Anterior setae of comb row (where present): (0) absent (Figs 8A, 10E); (1) present (Fig. 10A–D,K).

60. Continuity between the setae of the subocular comb row and the anterior marginal temporal setae: (0) setal groups are continuous (Fig. 10A,C); (1) not continuous, distinctly separate or separated by the inclusion of a section of differing setae, unlike either the comb row or the marginal temporal setae (Figs 8A, 10B,D,E).

61. Submarginal ventral temporal setae: (0) absent (Fig. 10A–C); (1) present (Figs 8A, 10D,E).

On the ventral anterior temple between the posterior end of the comb row and the anterior marginal temple setae there is often a submarginal patch or line of setae of a differing type (Clay, 1969). This is very noticeable as they are usually finer and spikier than the setae of the comb row and markedly shorter and less developed than the anterior marginal temporal setae.

62. Sub-marginal temporal setae (where present): (0) patch or irregular row of setae. Much finer than comb row, usually extending halfway around temple (Fig. 8A); (1) weakly developed, short single row of fine setae, usually widely spaced and small in number. Does not extend far into the anterior marginal temporal setae (Fig. 10D); (2) compact, single row of quite robust setae, extending halfway around the temple (Fig. 10E).

In *Odoriphila* and *Osborniella* it is not as developed: being less compact, less deep and also extending less into the anterior temple setae.

63. Area of sculpturing on ventral submargin of the temple: (0) absent (Fig. 10A,E); (1) present (Figs 8A, 10B–D,F).

Many taxa, when viewed using phase contrast microscopy, have a soft scale-like topology over the entire the ventral temple. This character does not describe this condition, but relates only to the anterior of the ventral temple, around the point of the antennal fossae posterior margin.

64. Form of sculpturing on ventral submargin of the temple (where present): (0) single spikes (Fig. 10D); (1) multi-tipped spikes (Fig. 10B); (2) fringe-like (Fig. 10F); (3) simple scales (Fig. 10C); (4) spike tipped scales (Fig. 8A).

The sculpturing present on the temple of *Laemobothrion* is a sort of comb-like, flat fringe. Perez, Granados & Ruiz (1995) in SEMs of *Laemobothrion maximum* Scopoli, referred to this sculpturing as 'cephalic ctenidia'.

CHARACTERS OF THE THORAX

Dorsal thorax

65. Transverse pronotal carina: (0) absent (Fig. 11A,B); (1) present (Fig. 11C–E).

This feature is found running across, through the pronotum, at around the mid-point or less down the length of the segment. Harrison (1915) refers to the 'shoulders' of *Eomenopon* and *Machaerilaemus* and an 'interscapular bar' joining the 'scapular bands', which I assume represents the lobing of the prothorax, the extent of which is variable in amblyceran genera. Bedford (1920) also termed it as an 'interscapular bar' running between the 'scapulars'. It is only absent in the Ricinidae and in *Rediella* (Menoponidae).

66. Posterior pronotal setal row: (0) absent; (1) incomplete (Fig. 11A); (2) complete, across the posterior prothorax (Fig. 11B–E).

In the Menoponidae and Boopiidae there is a posterior row of setae on the dorsal prothorax. *Sensu* Clay (1962) these setae are included in the 'marginal prothoracic setae' (mps) which she labelled 1 . . . 2 . . ., etc. starting from the most anterior humeral seta. There are usually three humeral setae located at the lateroanterior angles of the segment, then a small gap followed by an evenly spaced posterior row. The Ricinidae have small patches of setae in the lateroposterior region, but the row is incomplete. In *Laemobothrion* the condition is very similar.

67. Setae medial to the lateral seta of the dorsal prothorax: (0) short (Fig. 11B,D); (1) well developed (Fig. 11C–E).

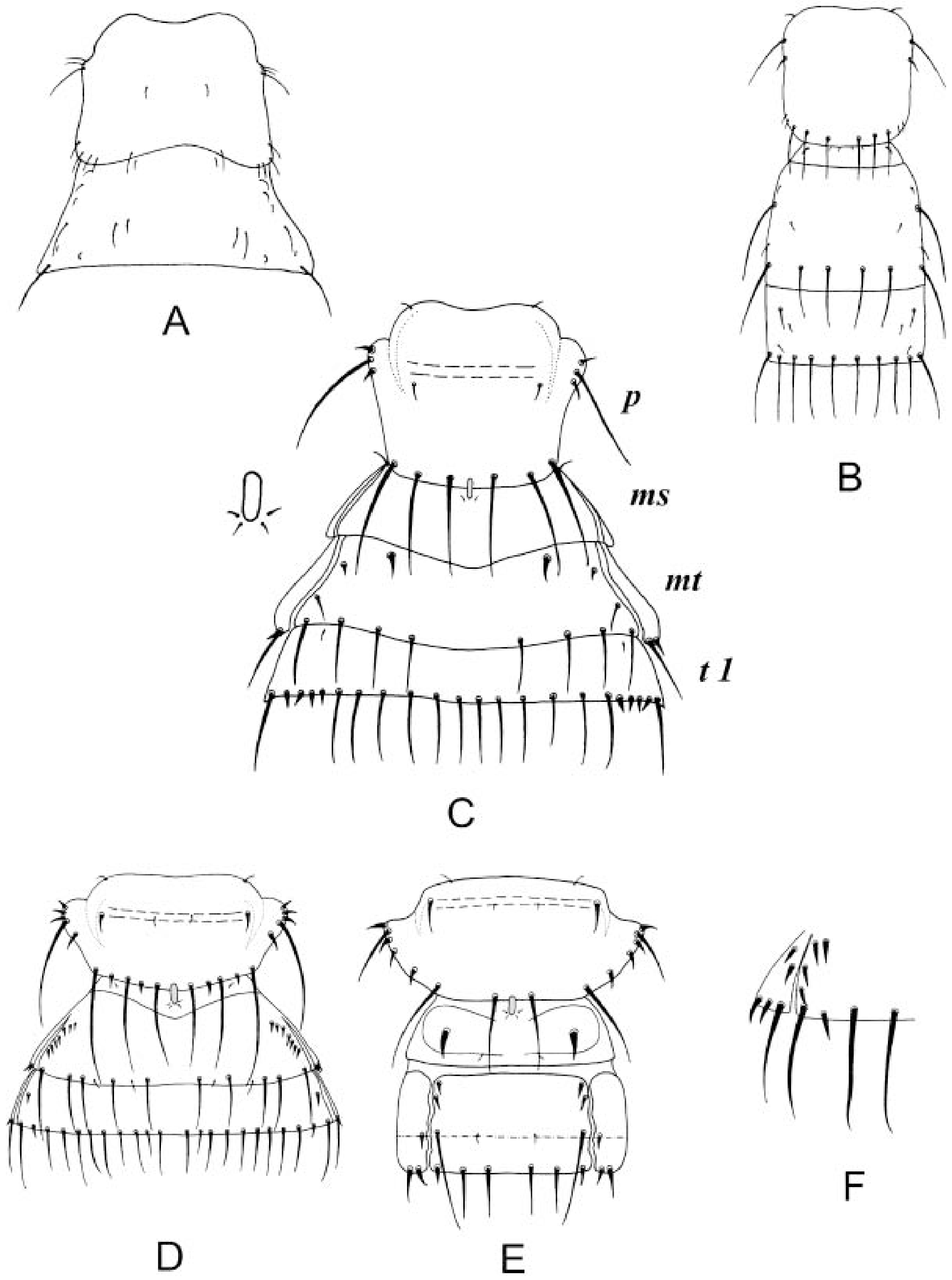

Figure 11. Characters of the dorsal thorax, in (A) *Trochiliphagus*, (B) *Rediella*, (C) *Dennyus*, with the thoracic segments, pronotum (*p*), mesonotum (*ms*) and metanotum (*mt*) and the first abdominal tergal segment (*t 1*) indicated. Postnotum (shaded) with postnotum (detail, with four setae) shown alongside part (C), (D) *Odoriphila*, (E) *Therodoxus*, showing metanotum fused with *t 1* indicated by dashed line, and (F) *Machaerilaemus*, metanotum (detail).

The lateral seta is a large well-developed seta roughly at the lateroposterior angles of the prothorax and is easily identified. In most genera, the lateral seta mps 4 (*sensu* Clay, 1962) is the first seta after the humeral setae. Clay's numbering system cannot be used here for two reasons: some genera have more than three humeral setae present and in a few cases the long lateral seta need not be the first seta after the humeral group. Nelson (1972) labelled the two seta at the posterolateral corners of *Ricinus* as L8 and L9. In *Comatomenopon* the lateral seta appears to be absent.

68. Postnotum at the posterior pronotum: (0) absent (Fig. 11A,B); (1) present (Fig. 11C–E).

This small, usually rectangular sclerite is found behind the pronotum, projecting over the mesonotum. It was previously termed 'median button' by Cope (1941) who assumed it to be the vestiges of a reduced mesonotum. In the Menoponidae, it is absent only in *Rediella* and *Numidicola* (Clay, 1969).

69. Anterior mesonotal setae: (0) absent (Fig. 11A); (1) present (Fig. 11C–E).

These are a small group of microsetae on the anterior mesonotum, around the base of the postnotum (where present).

70. Number of anterior mesonotal setae (where present): (0) 2 (Fig. 11C); (1) 4 (Fig. 11B,D,E).

There are normally four setae at this position. However, it should be noted that in some cases the setae may be very close to each other, giving a false appearance of only two setae on first observation. This is the case in *Odoriphila* (Clay, 1969).

71. Position of anterior mesonotal setae: (0) clustered around the postnotum (Fig. 11C–E); (1) widely spaced (Fig. 11B).

Commonly the setae are arranged in a tight cluster formation on either side of the sclerite. They are widely spaced out in *Trinoton* Nitzsch, *Actornithophilus* and *Rediella*.

72. Setae borne on a rounded protuberance each side of the mesonotum: (0) absent (Fig. 11A–D); (1) present (Fig. 11E).

This character is exclusive to the Boopiidae. Omitted from the original, unillustrated description of *Heterodoxus* (Boopiidae) by LeSoëuf, 1902), this feature was later figured by Paine (1912). They were also termed 'elevated warts' by Kéler (1971) and 'mesonotal warts' by Clay (1981).

73. Fusion of mesonotum and metanotum: (0) independent (Fig. 11B–E); (1) fused to metanotum (Fig. 11A).

In the Boopiidae and Menoponidae the mesonotum and metanotum are independent, although the former may be much reduced (Ferris, 1916). In the Laemobothriidae and Ricinidae they are fused (Clay & Price, 1970). Nelson (1972) also describes the abdominal lateral thickening which extends up to the mesothorax in *Ricinus* (and all Ricinidae) as pleural nodi.

74. Fusion of metanotum and tergum 1: (0) independent (Fig. 11B–D); (1) metanotum fused to tergum 1 (Figs 11A,E).

In the Ricinidae, a pterothorax exists of fused mesothorax, metathorax and first abdominal segment (Clay & Price, 1970; Nelson, 1972). Members of the Boopiidae have a free mesonotum but the metanotum is always fused to the first abdominal tergite (Clay, 1970).

75. Terminal metanotal row: (0) absent (Figs 11A,E); (1) present (Figs 11B–D,F).

Clay (1962) termed these setae the 'marginal metanotal setae' (mms) and numbered them 1 . . . 2 . . . etc. inwards from the lateral margin, but this system cannot be applied to all of the taxa in this study. Although the metanotum and tergum 1 are fused in the Boopiidae and Ricinidae, there are a few isolated setae (but not a row) around the area where the terminal metanotal setae might be expected. Nelson (1972) refers to the sparse ricinid setae as C3 and C4.

76. Second seta of the metanotal row (where present): (0) much shorter than outer metanotal seta, often peglike (Fig. 11F); (1) as developed as outer metanotal seta (Fig. 11B,C); (2) absent (Fig. 11D).

This is the seta next to the outer metanotal seta. It is probably absent in *Odoriphila* as here there is a gap in the row.

Ventral thorax

(a) prosternal plate.

77. Development of the prosternal plate: (0) absent or too undeveloped to figure (Fig. 12A); (1) present at least posteriorly (Figs 12B–L, 13A).

78. Marginal position of anterior setae on prosternal plate: (0) absent (Fig. 12C); (1) at or near the most anterior point of the lateral margins (Figs 12A,B,E,F,L, 13A); (2) at or near the mid point of the anterior margin (Fig. 12D,G–K).

These are very small setae found in either of two sites on the prosternal plate. They may be sited at the lateroanterior angles or close together on the anterior margin near the midline of the plate. They are absent only in *Myrsidea*.

79. Anterior setae on prosternal plate: (0) on main body of plate (Fig. 12B,G–K); (1) detached and anterior to main body of plate (Figs 12A,D–F,L, 13A).

Always found on the main plate in within the Laemobothriidae and Ricinidae, but in the other families the condition varies.

80. Anterior setae on prosternal plate (if detached): (0) situated on small islands of sclerotization (Fig. 12E,F); (1) on unsclerotized areas of sternal prothorax (Figs 12A,D,L, 13A).

In the Boopiidae the detached anterior setae are always on unsclerotized areas. Within the Menoponidae both conditions are found.

81. Anterolateral setae on prosternal plate: (0) absent (Figs 12A,D–J, 13A); (1) present (Fig. 12B,C,K,L).

In addition to the small anterior setae there is often a pair of well-developed setae present. These are situated on the main body of the plate submarginal to the anterolateral angles. They are always present in

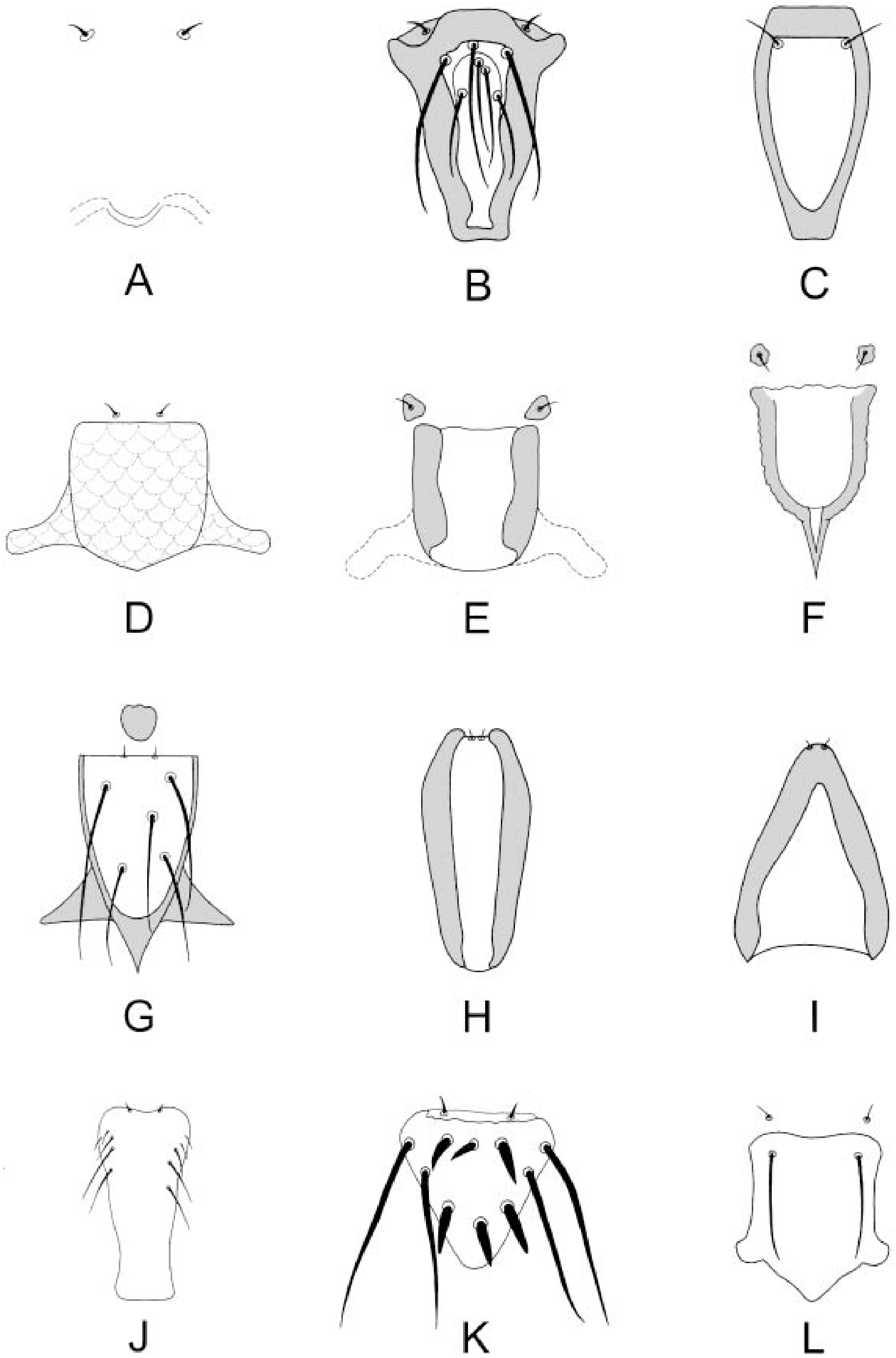

Figure 12. Thoracic prosternal plates with marginal border (shaded), in (A) *Colpocephalum*, (B) *Dennyus*, (C) *Myrsidea*, (D) *Eomenopon*, (E) *Chapinia*, (F) *Eidmanniella*, (G) *Colimenopon*, (H) *Ricinus*, (I) *Trochiloecetes*, (J) *Laemobothrion*, (K) *Paraheterodoxus*, and (L) *Therodoxus*.

the Boopiidae and are also found in *Dennyus* and *Myrsidea* (Menoponidae).

82. Additional setae on prosternal plate aside from the anterior setae and the anterolateral setae (where present): (0) absent (Figs 12A,C–F,H,I,L, 13A); (1) present (Fig. 12B,G,J,K).

83. Posterior margin of prosternal plate: (0) rounded (Fig. 12E,H,K); (1) angular (Fig. 12D,L); (2) long pointed spine (Fig. 12F,G, 13A); (3) pedestal (Fig. 12B,C,J); (4) flat and square; (5) concave (Fig. 12I); (6) posterior margin absent.

Clay (1969) described state two as a 'posterior process of the prosternal plate' for *Eidmanniella*. *Rediella* is unusual in that the posterior margin of the plate appears absent.

84. Well defined marginal border of prosternal plate: (0) absent (Fig. 12D,J–L); (1) present (Figs 12B,C,E–I, 13A).

A sclerotized border around the prosternal plate is found in all the Ricinidae and the majority of the Menoponidae, which possess a defined plate.

85. Marginal border of prosternal plate (where present): (0) only lateral or lateral and anterior (Fig. 12E,H,I); (1) lateral and posterior but not anterior (Figs 12F,G, 13A); (2) complete, encircling the plate (Fig. 12B,C).

The marginal border is only lateral or lateral and anterior in the Ricinidae. It is termed 'lateral nodi' by Nelson (1972) in his review of *Ricinus*. Where present in the Menoponidae, the border is usually just lateral and posterior but in *Dennyus*, *Myrsidea* and *Ancistrona* the border is complete.

(b) mesosternum and metasternum

86. Mesosternum type: (0) articulation of leg separated from the other side by an area without a plate (Figs 13A, 15A); (1) articulation of leg separated from the other side by a plate; (2) mesonotum, pleura and sternum fused in a sclerotized ring around the body (Fig. 13B).

Clay (1969) highlights three forms of mesosternum. There may be a distinct mesosternal plate or an area without a plate separating the points where the legs articulate, or the mesosternum, pleura and mesonotum can be fused, forming a ring of sclerotization around the body. *Cuculiphilus* and *Myrsidea* (Clay, 1966) have the sclerotized ring and although there has been a degree of fusion between the meso and metasternal plates of *Trinoton*, the legs are still separated.

87. Metasternal plate: (0) absent; (1) present (Figs 13A,B, 15A).

A metasternal plate is normally present but appears to be absent in *Menopon*.

(c) legs

88. Shape of the first coxa: (0) roughly spherical; (1) anteroposteriorly extended (Fig. 13A–C).

Mayer (1954) describes the antero-posteriorly extended coxa as an 'elongate bladder' lying flat on the body. The first coxa is almost V-shaped with a rounded posterior margin and the medial superior lobe lying a bit to the right over the lateral inferior one. Although *Trinoton* shows some antero-posterior extension to the coxa, extent of modification is noticeably less than for other genera.

89. Posterior setae of first coxa: (0) four or five setae (Fig. 13A); (1) more than five (Fig. 13C); (2) two or three (Fig. 13B).

Within the Menoponidae, there are usually four or five setae around the posterior of the first coxa. In some isolated groups of genera there may be more (Clay, 1969). This is apparent in, e.g. *Ancistrona*, *Austromenopon*, and *Eidmanniella*.

90. Shape of the third femur: (0) hugely inflated compared to femora 1 & 2 (Fig. 13H); (1) femora 3 not inflated (Figs 13A,B, 15A).

91. Pattern of setae on the venter of the third femur: (0) many small setae dotted all over (Fig. 13H); (1) many setae above and below, but absent from the venter of the third femur (Fig. 13F); (2) many setae arranged into a central discrete patch (Figs 13A, 15A); (3) many setae arranged into central discrete combs (Fig. 13I); (4) large patch of microtrichia (Fig. 13G); (5) fewer setae but with no evident pattern (Fig. 13D); (6) femur almost devoid of setae (Fig. 13E).

In the outgroup taxon *Liposcelis* there are many small setae evenly distributed over the ventral aspect of the third femur. All amblyceran taxa show some form of setal aggregation. The setal patch of the Menoponidae is usually quite well developed, e.g. in *Dennyus* (Emerson, 1956) and *Austromenopon* (Price & Clay, 1972) but in some taxa, e.g. *Holomenopon* the setae are quite loosely packed. *Machaerilaemus* is unusual in that setae are absent from the area in question (Bedford, 1920). Setal combs are interpreted as described by Clay (1947) as a 'row of short, stout setae, with the alveoli lying close together and approximately in a straight line'. *Laemobothrion* has a patch but it is not composed of regular setae. It is a patch of small combs (microtrichia), which under SEM photography (Perez *et al*., 1995) bears little resemblance to the condition found in the menoponid comb-bearing genera.

92. Number of combs on venter of the third femur: (0) two; (1) three (Fig. 13I); (2) four.

93. Dorsal tibial setae. Additional submarginal row of short setae on legs two and three: (0) absent (Figs 13A,H, 15A); (1) present (Fig. 13I).

Some genera within the Menoponidae have a developed submarginal row of setae on the dorsal aspect, whilst the legs of others are quite bare (Clay, 1969).

94. Number of tarsal segments: (0) three (Fig. 13H); (1) two (Figs 13A,I,J, 15A).

The tarsus is always two-segmented in the Amblycera.

95. Euplantula 1: (0) absent (Fig. 13H); (1) present (Figs 13A,I,J, 15A).

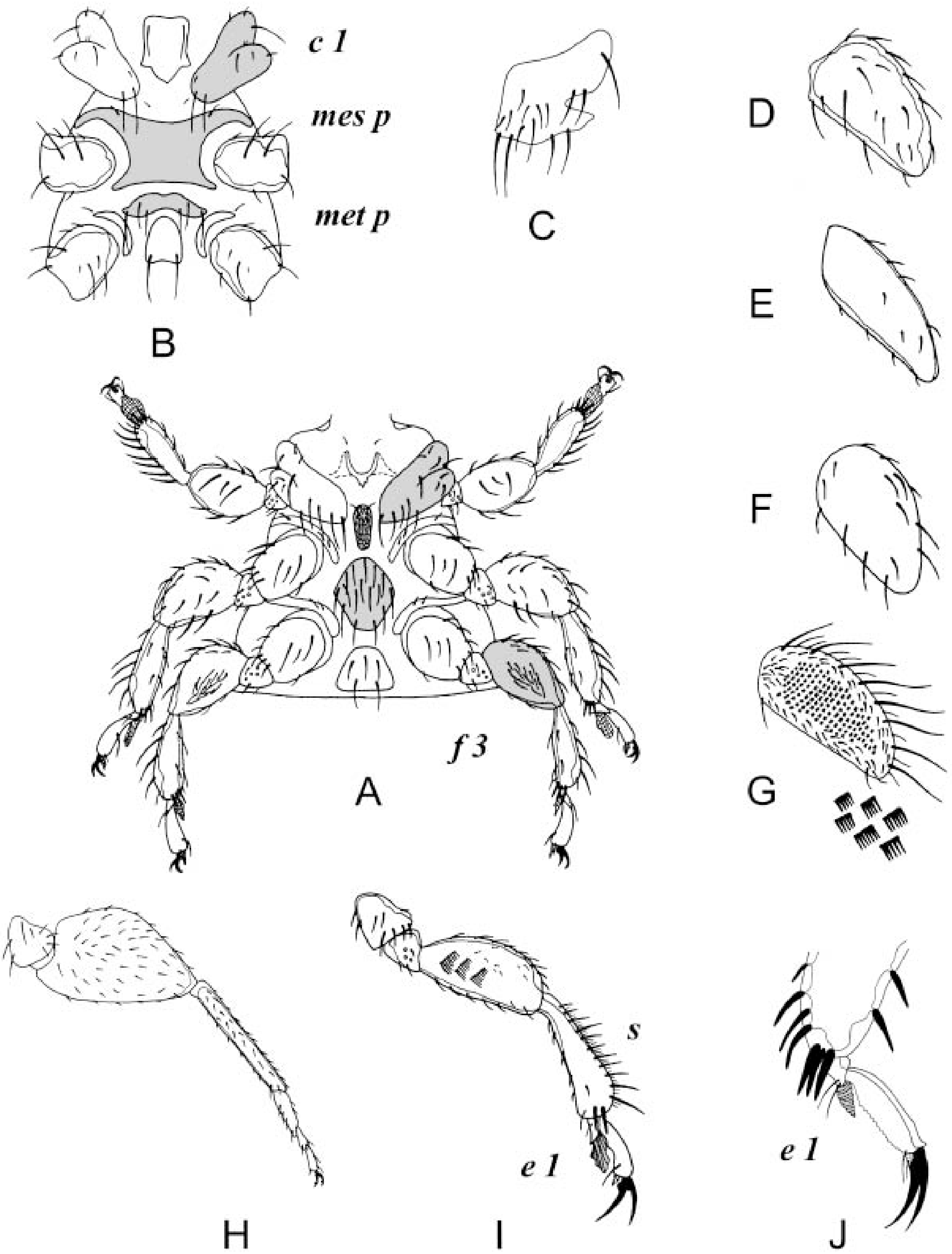

Figure 13. Characters of the ventral thorax, in (A) *Holomenopon*, with mesosternal and metasternal plates, first coxa and third femur (*f 3*) (all shaded), (B) *Therodoxus*, with first coxa (*c 1*), mesosternal plate (*mes p*) and metasternal plate (*met p*) (shaded), and (C) *Menacanthus*, first coxa. (D–G): Ventral aspect of the third femur, in (D) *Boopia*, (E) *Ricinus*, (F) *Machaerilaemus*, and (G) *Laemobothrion*, showing large patch of microtrichia (with detail). (H–J): Metanotal legs of (H) outgroup taxon *Liposcelis*, (I) *Comatomenopon*, with euplantula of first tarsus (*e 1*) and submarginal tibial setal row (*s*) indicated, and (J) *Paraheterodoxus*.

The smaller first tarsus is identified due to the possession of a pair of setae close to its distal margin. Distal to this is a pad-like lobe called the euplantula (Clay, 1969). Mjöberg (1910), described the first joint of the tarsus as short and bearing a large flap-like appendage on the inner side, whilst the second tarsus was longer with a small finger-like process, which collapsed in balsam mounts (euplantula 2). The variable condition of this latter structure excludes its inclusion in this analysis.

96. Form of Euplantula 1: (0) horizontal and vertical banding (Figs 13A, 15A); (1) vertical banding only (Fig. 13I); (2) serrated and globular (Fig. 13J).

Mjöberg (1910) observed the distinct horizontal and vertical banding in *Holomenopon albofasciatum* Piaget and the serrated sculpturing on *Boopia grandis* Piaget.

97. Claw shape: (0) claws have a protuberance proximally and are not serrated (Figs 13A,I,J, 15A); (1) claws have one sharp tooth distally and are serrated proximally (Fig. 13H).

CHARACTERS OF THE ABDOMEN

Dorsal abdomen

98. Lateral tergal thickening: (0) absent (Fig. 15A,B,E–G); (1) present (Fig. 14).

Exclusive to the Ricinidae and Laemobothriidae, are two conspicuous lateral bands of sclerotization running posteriorly through the abdomen. These may vary in degree of pigmentation but are generally darker than the regular colour of the abdomen. They are composed of segmental parts separated by diagonal sutures (Kellogg, 1896; Nelson, 1972) and are sited midway between the lateral aspect of the tergites and the lateral plates. This feature has been variously described by a number of authors. Paine & Mann (1913) refer to two pale 'submarginal bands' in *Trochiloecetes*, whilst Nelson (1972) and Oniki (1995) term them 'pleural nodi'. Clay (1969) describes the condition as a 'continuous lateral buttress of internal tergal thickening each side'.

Kellogg (1896) also described two new species of menoponids as having 'angular lateral bands on segments 3–8' (*Colpocephalum*) and 'broad lateral bands projecting inwards'(*Menopon*). I have found no later works (neither review papers nor alpha taxonomic descriptions) to corroborate his observations. It seems he may have been referring to the increased sclerotization seen around the spiracle in some menoponid genera.

99. Female tergites: (0) composed of one plate (Figs 14, 15A,E–G); (1) tripartite with narrow central plate (Fig. 15B).

This rare condition is exclusive to the Menoponidae and is present only in *Colpocephalum* (Mjöberg, 1910; Bedford, 1940; Price & Beer, 1965a) and *Psittacomenopon* where it is apparent in tergites 4–8 (Price & Beer, 1966).

100. Tergal posterior setal rows: (0) absent or very sparse (Fig. 14); (1) regular row of setae reaches across the tergite (Fig. 15E,F); (2) very well developed and compact row (Fig. 15A,B,G).

The term *posterior* is adopted here rather than marginal, as the setal rows in the Amblycera are not always on the posterior margin of the tergite (e.g. *Latumcephalum*, Fig. 15F).

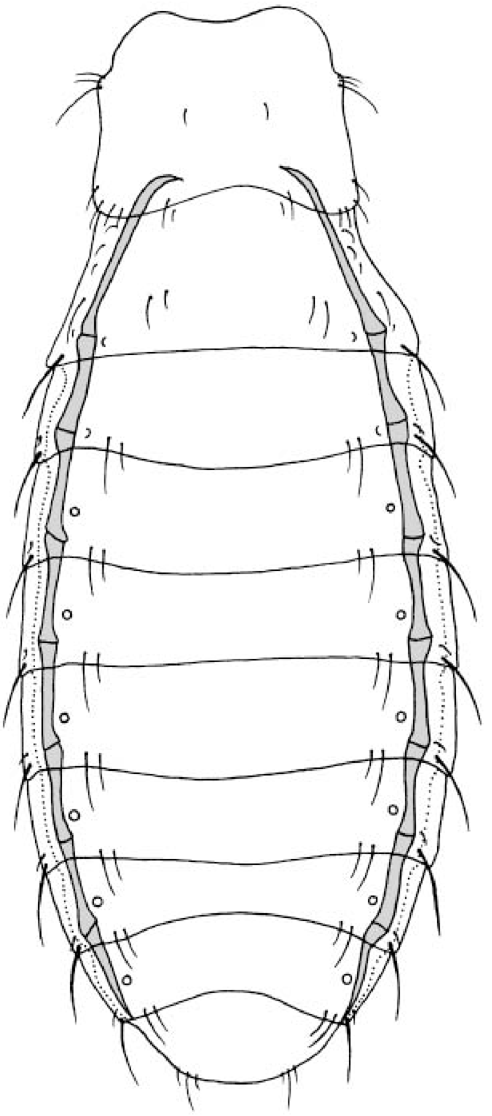

Figure 14. The dorsal abdomen of *Trochiliphagus* showing lateral tergal thickening (shaded).

101. Additional anterior setae on tergite 2 (T2), at least in females (*sensu* Clay, 1962; Price & Beer, 1966): (0) absent (Fig. 14); (1) present (Fig. 15A).

In many of the Menoponidae and Boopiidae there are additional rows or clusters of setae anterior to the posterior tergal row. In some genera, this is more apparent in females and there appears to be some clearly distinct patterns of anterior setal distribution. Condensing these patterns into one character for the whole abdomen would result in a loss of phylogenetic information and thus I have chosen the more conservative approach of scoring each tergite separately.

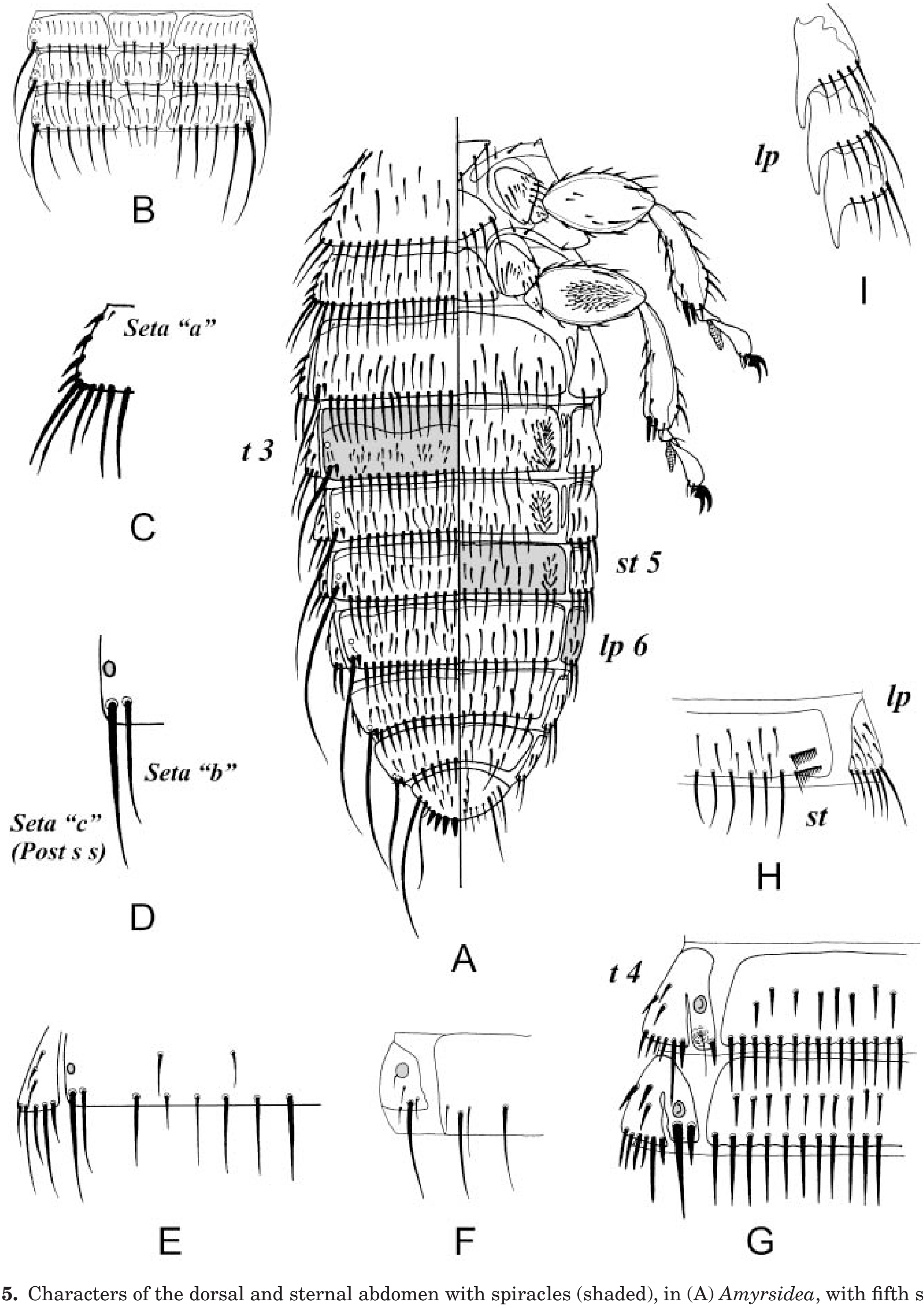

Figure 15. Characters of the dorsal and sternal abdomen with spiracles (shaded), in (A) *Amyrsidea*, with fifth sternite (*st 5*), sixth lateral plate (*lp 6*) and third tergite (*t 3*) (all shaded), (B) *Psittacomenopon*, tergites 4–6, (C) position of seta 'a', commonly found on tergites 1–2, (D) relationship between postspiracular seta 'c' and lateral seta 'b', (E) *Meromenopon*, fourth tergite, (F) *Latumcephalum*, fourth tergite, (G) *Paraheterodoxus*, third and fourth tergite, with *t 4* indicated, (H) *Ciconiphilus*, third sternite and lateral plate, and (I) *Pseudomenopon*, lateral plates (*lp*) 2–4.

102. Additional anterior setae on T3, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A).
103. Additional anterior setae on T4, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A,B,E,G).
104. Additional anterior setae on T5, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A,B,G).
105. Additional anterior setae on T6, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A,B).
106. Additional anterior setae on T7, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A).
107. Additional anterior setae on T8, at least in females: (0) absent (Fig. 14); (1) present (Fig. 15A).
108. Tergite 1, seta 'a': (0) absent; (1) present (Fig. 15A,C).

At each end of tergite 1 and 2 in the Menoponidae there is a small anterolateral setae (Clay, 1969).

109. Tergite 2, seta 'a': (0) absent (Fig. 14); (1) present (Fig. 15A).
110. Spiracle position: (0) open onto tergites (Figs 14, 15A,B,E); (1) open onto lateral plates (Fig. 15F); (2) on the middle part of a partially divided lateral plate (Fig. 15G).

In these amblyceran families, the abdominal spiracles are present on T3–8 (Clay, 1969). In the marsupial-infesting Boopiidae they are normally present on the lateral plate, but *Paraheterodoxus* is unusual in that they are on a partially divided lateral plate.

111. Distribution of postspiracular seta 'c' (where present): (0) absent; (1) present on T2–8 (Figs 14, 15A,B,E,F); (2) modified as trichobothria on T2–4 and present as normal setae on T5–8 (Fig. 15G).

The postspiracular setae, labelled 'c' (see Fig. 15D) *sensu* Clay (1970) are found near the lateral margins of T1–8. On T2–8 they are easily identified due to the presence of two small associated setae, the alveoli of which are contiguous with that of the well-developed postspiracular seta (Clay, 1954).

112. Position of postspiracular seta 'c' on T3–8 (where present): (0) generally posterior to spiracle, sometimes slightly lateral or medial (Fig. 15A,B,D,E,G); (1) extremely lateroposterior to spiracle (Fig. 14).

The postspiracular seta is usually found behind the spiracles but in the Laemobothriidae and Ricinidae they are laterally displaced. Nelson (1972) wrote in his review of *Ricinus* that the postspiracular setae were 'on the dorsal halves of the pleurites, somewhat removed from the spiracles'.

113. Position of postspiracular setae 'c' to the posterior tergal setae on T2–8: (0) marginal (Fig. 14); (1) submarginal (Fig. 15A,B,E–G).

In some taxa the postspiracular seta may merge with the posterior tergal row, but in others, e.g. *Somaphantus* it is found between the spiracle and posterior tergal setae (Clay, 1954).

114. Abdominal tergal seta 'b': (0) absent; (1) present (Figs 14, 15A–G).

Medial to the postspiracular seta and the two small setae, is a small seta called the associated postspiracular seta (Clay, 1966), or seta 'b' (see Fig. 15D) *sensu* Clay (1969). Together these four setae make up the postspiracular setal complex. Seta 'b' is absent only in *Laemobothrion*.

115. Position of seta 'b' to postspiracular setae 'c' (T2): (0) directly anterior (Fig. 14); (1) submarginal; (2) marginal (Fig. 15A); (3) posterior.

There appears to be some clearly distinct patterns in the changing position of seta 'b' down the abdomen. However, as in character 101, condensing these patterns into one would result in a loss of information and each tergite is scored separately. T8 is not scored due to the difficulty in seeing this small setae in all the specimens.

116. Position of seta 'b' to postspiracular setae 'c' (T3): (0) directly anterior (Fig. 14); (1) submarginal; (2) marginal (Fig. 15A); (3) posterior.
117. Position of lateral seta 'b' to postspiracular setae 'c' (T4): (0) directly anterior (Fig. 14); (1) submarginal (Fig. 15F); (2) marginal (Fig. 15A,D,E); (3) posterior (Fig. 15B,G).
118. Position of seta 'b' to postspiracular setae 'c' (T5): (0) directly anterior (Fig. 14); (1) submarginal; (2) marginal (Fig. 15A,G); (3) posterior (Fig. 15B).
119. Position of seta 'b' to postspiracular setae 'c' (T6): (0) directly anterior (Fig. 14); (1) submarginal; (2) marginal (Fig. 15A); (3) posterior (Fig. 15B).
120. Position of seta 'b' to postspiracular setae 'c' (T7): (0) directly anterior (Fig. 14); (1) submarginal; (2) marginal (Fig. 15A); (3) posterior.

Ventral abdomen

121. Lateral plate shape: (0) normal and squared-off (Fig. 15A,F–H); (1) ventral posterior margin developed into a medially posterior running protuberance (Fig. 15I).

Normally, the inner posterior angle of the lateral plate looks quite square when viewed from the ventral aspect but in some taxa the plate is more developed at this site. This unusual condition is present in only a few menoponids: *Gruimenopon*, *Pseudomenopon* (Mjöberg, 1910; Price, 1974) and *Plegadiphilus* (Bedford (1940).

122. Additional setae on the anterior of the second lateral plate (LP2), at least in females: (0) absent (Fig. 15I); (1) present (Fig. 15A).

For reasons outlined above in characters 101 and 115, the presence of these setae are scored separately for each abdominal segment. Again, LP8 is not scored due to the difficulty of seeing the plate properly in all the mounts.

123. Additional setae on the anterior of LP3, at least in females: (0) absent (Fig. 15I); (1) present (Fig. 15A,H).

124. Additional setae on the anterior of LP4, at least in females: (0) absent (Fig. 15I); (1) present (Fig. 15A,E–G).

125. Additional setae on the anterior of LP5, at least in females: (0) absent; (1) present (Fig. 15A,G).

126. Additional setae on the anterior of LP6, at least in females: (0) absent; (1) present (Fig. 15A).

127. Additional setae on the anterior of LP7, at least in females: (0) absent; (1) present (Fig. 15A).

128. Pattern of setae on sternite 3 (St 3): (0) regularly spaced, non-aggregated; (1) setal patch (Fig. 15A); (2) setal combs (Fig. 15H).

In some genera there is a distinct aggregation of setae on the lateral aspects of the sternal plates. Both patches and combs of setae (ctenidia) are found and these usually mirror the condition seen on the venter of the third femur. There are complex patterns, down the length of the abdomen, of presence and degree of development, so for the reasons outlined above (characters 101, 115, 122) each sternite is treated independently. The sternal patches and combs are conspicuous and are usually fully described by previous authors (e.g. Harrison, 1915; Clay & Meinertzhagen, 1941; Price & Beer, 1965b). Clay (1962) photographed the sternal patches in *Actornithophilus*.

129. Development of St 3 patch: (0) well developed (Fig. 15A); (1) weakly developed.

130. Number of combs on St 3: (0) one; (1) two (Fig. 15H).

131. Pattern of setae on St 4: (0) regularly spaced, nonaggregated; (1) setal patch (Fig. 15A); (2) setal combs.

132. Development of St 4 patch: (0) well developed (Fig. 15A); (1) weakly developed.

133. Number of combs on St 4: (0) one; (1) two; (2) three or more.

134. Pattern of setae on St 5: (0) regularly spaced, nonaggregated; (1) setal patch (Fig. 15A); (2) patch of microcombs.

On close observation the apparent setal patch of *Laemobothrion* is markedly different from that present in other taxa. Perez *et al*. (1995) presented a photograph of this area using scanning electron microscopy and demonstrated that the 'patch' was not composed of regular setae but small combs (microtrichia) which, as described above in character 91, are quite different from the combs found in some menoponid genera.

135. Development of St 5 patch: (0) well developed; (1) weakly developed (Fig. 15A).

136. Pattern of setae on St 6: (0) regularly spaced, non-aggregated (Fig. 15A); (1) setal patch; (2) patch of microcombs.

137. Development of St 6 patch: (0) well developed; (1) weakly developed.

138. Pattern of setae on St 7: (0) regularly spaced, nonaggregated (Fig. 15A); (1) setal patch.

139. Development of St 7 patch: (0) well developed; (1) weakly developed.

Female terminalia

140. Presence of a setal fringe around the female anal margin: (0) absent (Fig. 16A); (1) present (Figs 15A, 16B–D).

Rediella and *Somaphantus* are unusual in the Menoponidae in that the typical anal corona of setae is absent.

141. Form of the female anal corona (where present): (0) wide anal margin with, a usually obvious, thick fringe of setae (Fig. 16B); (1) as above, but fringe very short and fine (Fig. 16C); (2) small rounded protruding anal margin with short fine fringe (Fig. 16D); (3) anal fringe composed of short stout spine-like setae (Fig. 15A).

142. Presence of gonapophyses in the female: (0) absent (Figs 15A, 16B–D); (1) present (Fig. 16A).

The gonapophyses are characteristic of the Boopiidae and are described by Kéler (1971) as 'sickle-shaped bluntly or sharply pointed appendages'. They are found on each side of the postgenital sternum, behind the vulval margin. There is usually a single fine seta on the tip of each one. Clay (1970) observed some structure in *Chapinia* (Menoponidae) that she believed may be homologous with gonapophyses of the Boopiidae, however, no such structure was viewed in these specimens of *Chapinia*.

Male genitalia

The components of the male genitalia are perhaps the most difficult structures to identify confidently in the Amblycera. Clay (1956) wrote that the sclerites of the male genitalia 'may be fused in such a way as to make their homologies obscure and it is not always possible to homologize the parts even between species of the same genus'. Both Harrison (1915) and Carriker (1963) wrote that they were not confident in their observations of menoponid genitalia. Others have avoided the issue either providing figures with no descriptions or making statements akin to 'male genitalia as in fig. 4', whilst Ewing (1927) gave some description but with no illustration.

There has also been some variation in the descriptive terminology ascribed to some structures. Snodgrass (1899) described and illustrated the lateral parameres as 'processes' and 'lateral prongs', whilst

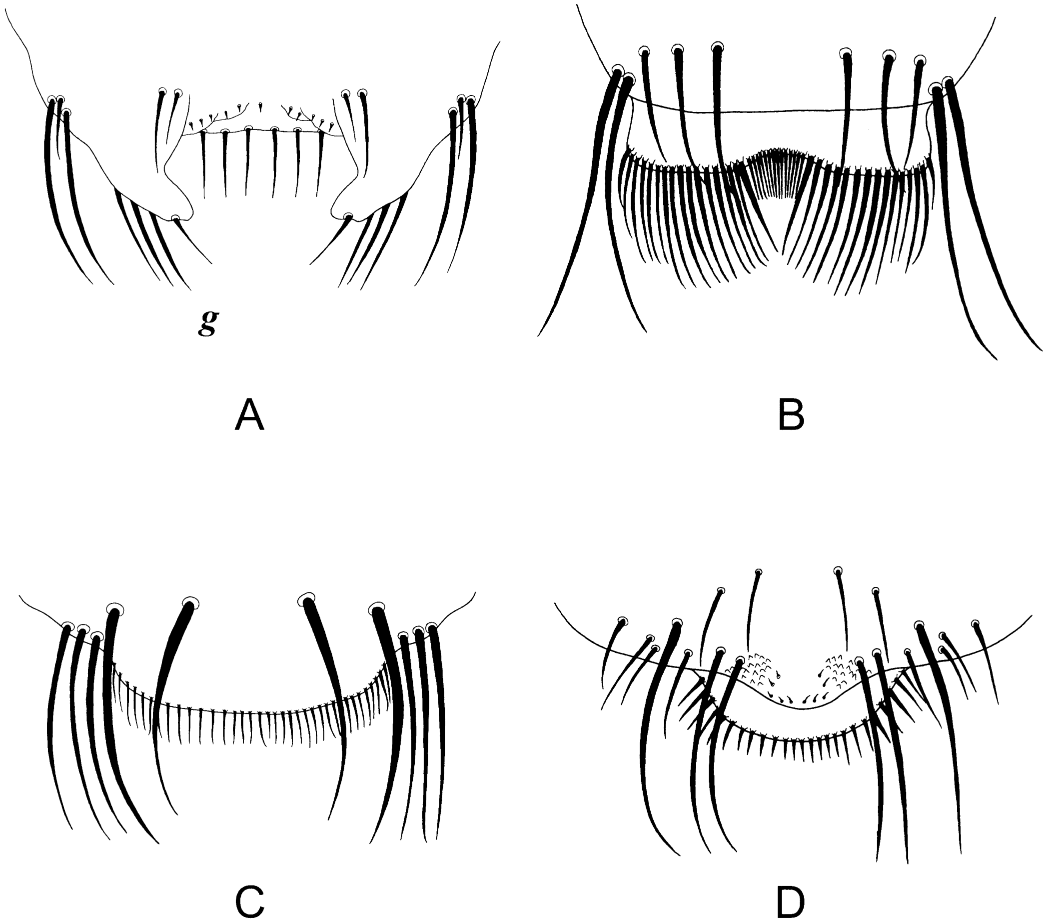

Figure 16. Female terminalia of (A) *Boopia*, with gonapophyses (g), (B) *Osborniella*, (C) *Ancistrona*, and (D) *Numidicola*.

Price (1967) and Price & Beer (1965a) termed them 'lateroposterior projections' and 'points'. More recently most authors have been consistent in following the terminology originally laid out by Clay (1956) and Blagoveshtchensky (1964) and a few have provided quite comprehensive and detailed accounts. The male genitalia are described with labelled illustrations for the Boopiidae (Kéler, 1971), Ricinidae (Nelson, 1972) and *Amyrsidea* (Menoponidae) (Scharf & Price, 1977).

I was able to use these key papers and other illustrated publications (e.g. Waterston, 1915; Price & Beer, 1965a; Price, 1975) to confirm the identification of the parameres, basal plate, endomeral plate, genital sclerite, mesosomal arch and in some cases endomeres and epimeres. In *Eomenopon*, however, the identification of component structures is difficult (Price, 1966). I believe this is because the genitalia appears to be turned on its side, so what is viewed is actually the lateral aspect.

143. Paramere shape: (0) outwardly curved (Fig. 17A,D); (1) straight or inwardly curved (Fig. 17B,C,E,F).

144. Paramere position: (0) parameres arise from around half way down the body of the aedeagus (Fig. 17A–D); (1) parameres arise near the posterior of the aedeagus (Fig. 17E,F).

145. Mesosomal arch: (0) indistinct (Fig. 17A–D,F); (1) bulbous well-defined arch (Fig. 17E).

Kéler (1971) describes the boopiid mesosome as 'membranous, stiffened dorsally by a chitinous arch'.

146. Basal apodome: (0) unsclerotized, largely absent (Fig. 17D); (1) very thin, stick-like rod (Fig. 17B,C); (2) medium to wide tapering rod (Fig. 17A,F); (3) bulbous, paddle-like rod (Fig. 17E).

147. Basal apodome apex shape: (0) unsclerotized (Fig. 17E); (1) rounded tip (Fig. 17F); (2) hooked tip (Fig. 17B); (3) pointed tip (Fig. 17C); (4) wide-squared apex (Fig. 17A).

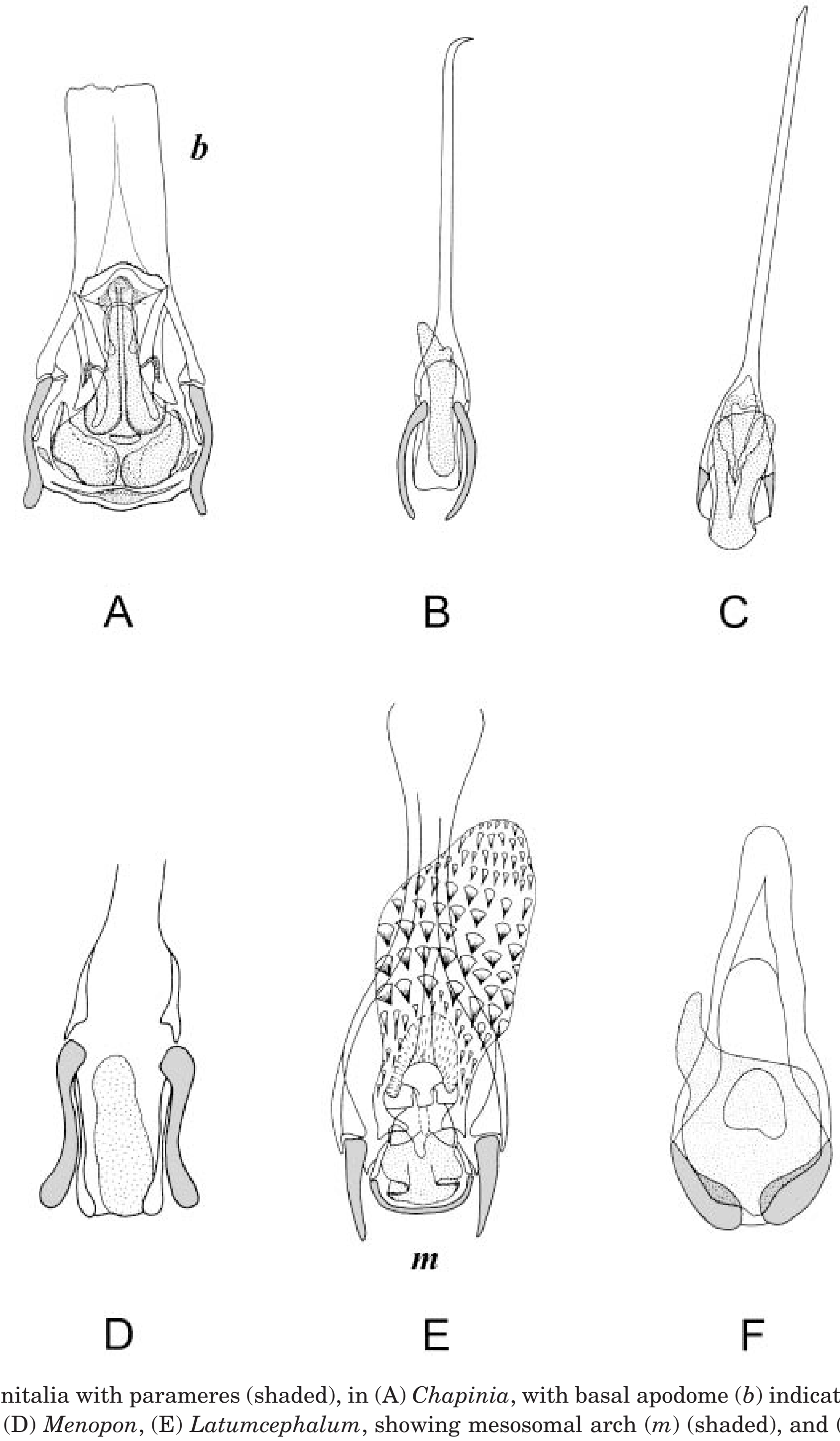

Figure 17. Male genitalia with parameres (shaded), in (A) *Chapinia*, with basal apodome (*b*) indicated, (B) *Plegadiphilus*, (C) *Colpocephalum*, (D) *Menopon*, (E) *Latumcephalum*, showing mesosomal arch (*m*) (shaded), and (F) *Ricinus*.

APPENDIX 3
DATA MATRIX FOR 147 MORPHOLOGICAL CHARACTERS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Liposcelis bostrychophilus	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	-	0	-	0	-
Laemobothrion maximum	0	0	-	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ricinus fringillae	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	-	0	-	0	-	0	-	0	-
Trochiloecetes rupununi	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	-	0	-	0	-
Trochiliphagus abdominalis	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	-	0	-	0	-	0	-	0	-
Therodoxus oweni	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	-	1	1	1	1	1	1
Paraheterodoxus insignis	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	-	1	1	1	1	1	1
Boopia tarsata	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Latumcephalum lesouefi/macropus	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	0
Paraboopia flava	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0
Amyrsidea ventralis	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Rediella mirabilis	1	1	0	1	1	1	1	0	1	0	1	1	1	1	0	-	1	0	1	1	1	1	1	0
Somaphantus lusius	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Bonomiella columbae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0/1	1	1
Menopon gallinae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Numidicola antennatus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1
Hohorstiella lata	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Menacanthus stramineus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Colimenopon urocolius	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Machaerilaemus laticorpus/latifrons	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	-	1	0	1	1	1	1
Neomenopon pteroclurus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Dennyus hirundinis	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0
Myrsidea victrix	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	-	1	1	1	1	1	0	1	0
Ancistrona vagelli	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0/1	1	0/1	1	0	1	0
Austromenopon crocatum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
Eidmanniella pellucida	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
Holomenopon brevithoracicum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
Plegadiphilus threskiornis	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Actornithophilus uniseriatus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
Chapinia robusta	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0
Gruimenopon longum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0
Meromenopon meropis	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Eomenopon denticulatum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hoazineus armiferus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1
Pseudomenopon pilosum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Trinoton anserinum	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0
Colpocephalum zebra	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Comatomenopon elbeli/elongatum	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ardeiphilus trochioxus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	-	1	1	1	1	1	1
Ciconiphilus quadripustulatus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cuculiphilus fasciatus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0
Odoriphila clayae/phoeniculi	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Osborniella crotophagae	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Psittacomenopon poicephalus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Piagetiella bursaepelecani	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Liposcelis bostrychophilus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	1	1	0	-
Laemobothrion maximum	1	1	1	1	0	0	0	0	0	0	0	1	3	0	0	1	1	0	0	-	1	0	1	0
Ricinus fringillae	0	0	0	0	1	0	0	1	0	0	0	0	3	0	0	1	0	-	0	-	0	-	1	1
Trochiloecetes rupununi	0	0	0	0	1	0	0	0	0	0	0	0	?	1	0	1	0	-	1	0	0	-	1	1
Trochiliphagus abdominalis	0	0	0	0	1	0	0	0	0	0	0	0	3	1	0	1	0	-	0	-	0	-	1	1
Therodoxus oweni	1	1	1	1	0	0	1	1	1	0	2	1	3	0	0	1	1	0	1	0	1	0	1	1
Paraheterodoxus insignis	1	1	1	1	0	0	1	1	1	0	2	1	3	0	0	1	1	1	0	-	1	0	1	1
Boopia tarsata	1	1	0	1	0	0	0	0	0	0	2	1	3	0	0	1	1	1	1	0	1	0	1	1
Latumcephalum lesouefi/macropus	1	1	1	0	0	0	0	0	0	0	2	2	3	0	1	1	1	1	1	1	1	0	1	1
Paraboopia flava	1	1	1	0	0	0	0	0	0	0	2	2	3	0	1	1	1	1	0	-	1	0	1	1
Amyrsidea ventralis	1	1	1	1	0	1	1	1	0	0	2	0	0	0	0	1	1	1	0	-	1	0	1	0
Rediella mirabilis	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	-	1	0	1	1
Somaphantus lusius	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	1	1	0	0	-	1	0	1	0
Bonomiella columbae	1	1	1	1	0	0	0	0	0	0	1	2	0	0	0	1	1	1	0	-	1	0	1	0
Menopon gallinae	1	1	1	1	0	1	1	1	0	0	2	0	0	0	0	1	1	1	0	-	1	0	1	0
Numidicola antennatus	1	1	1	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	-	1	0	1	0
Hohorstiella lata	1	1	1	1	0	0	0	0	0	0	2	2	0	0	0	1	1	1	1	0	1	0	1	0
Menacanthus stramineus	1	1	1	1	0	1	1	1	1	0	2	2	0	0	0	1	1	1	1	0	1	0	1	0
Colimenopon urocolius	1	1	1	1	0	1	1	1	0	0	0	3	2	0	0	1	1	1	0	-	1	0	1	0
Machaerilaemus laticorpus/latifrons	1	1	1	1	0	0	0	0	0	0	0	2	2	0	0	1	0	-	0	-	1	0	1	0
Neomenopon pteroclurus	1	1	1	1	0	0	0	0	0	0	0	2	2	0	0	1	1	1	0	-	1	0	1	0
Dennyus hirundinis	1	1	1	1	0	1	1	0	0	0	0	2	1	0	0	1	1	1	0	-	1	0	1	0
Myrsidea victrix	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0	1	1	1	0	-	1	0	1	0
Ancistrona vagelli	1	1	1	1	0	0	0	1	0	0	0	2	0	0	0	1	0	-	0	-	1	0	1	0
Austromenopon crocatum	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	-	1	0	1	1
Eidmanniella pellucida	1	1	1	1	0	0	1	1	1	0	2	0	0	0	0	1	1	1	0	-	1	0	1	0
Holomenopon brevithoracicum	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	-	1	0	1	0
Plegadiphilus threskiornis	1	1	1	1	0	0	1	0	0	0	1	2	0	0	0	1	1	1	0	-	1	0	1	0
Actornithophilus uniseriatus	1	1	1	1	0	0	1	1	1	0	1	2	0	0	0	1	1	1	0	-	1	0	1	0
Chapinia robusta	1	1	1	1	0	1	0	0	0	0	2	2	1	0	0	1	1	1	0	-	1	0	1	0
Gruimenopon longum	1	1	1	1	0	0	0	1	1	0	0	2	0	0	0	1	1	1	0	-	1	0	1	0
Meromenopon meropis	1	1	1	1	0	0	1	0	0	0	0	2	1	0	0	1	1	1	0	-	1	0	1	0
Eomenopon denticulatum	1	1	1	1	0	1	0	1	0	0	2	0	2	0	0	1	1	1	1	0	1	0	1	0
Hoazineus armiferus	1	1	1	0	0	1	1	0	0	0	2	2	0	0	0	1	1	1	0	-	1	0	1	0
Pseudomenopon pilosum	1	1	1	1	0	0	0	1	0	0	2	2	2	0	0	1	1	1	0	-	1	0	1	0
Trinoton anserinum	1	1	1	1	0	0	0	0	0	0	1	2	0	0	0	1	0	-	0	-	1	0	1	0
Colpocephalum zebra	1	1	1	0	0	1	1	1	0	0	1	1	0	0	0	1	1	1	0	-	1	0	1	0
Comatomenopon elbeli/elongatum	0	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	1	1	0	-	1	0	1	0
Ardeiphilus trochioxus	1	1	1	1	0	1	1	1	0	0	1	2	0	0	0	1	1	1	0	-	1	0	1	0
Ciconiphilus quadripustulatus	1	1	1	1	0	0	1	1	0	0	2	2	0	0	0	1	1	1	0	-	1	0	1	0
Cuculiphilus fasciatus	1	1	1	1	0	0	1	1	1	0	2	2	0	0	0	1	?	1	0	-	1	0	1	1
Odoriphila clayae/phoeniculi	1	1	1	1	0	0	1	1	0	0	2	2	2	0	0	1	1	1	1	1	1	0	1	0
Osborniella crotophagae	1	1	1	1	0	1	1	1	0	0	0	2	0	0	0	1	1	1	0	-	1	0	1	0
Psittacomenopon poicephalus	1	1	1	1	0	0	1	1	0	0	2	2	0	0	0	1	1	1	0	-	1	0	1	0
Piagetiella bursaepelecani	1	1	1	1	0	0	1	1	0	0	2	0	0	0	0	1	1	1	0	-	1	0	1	0

	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Liposcelis bostrychophilus	1	0	0	0	0	-	0	0	-	-	-	-	0	-	0	-	0	0	-	0	0	-	-	0
Laemobothrion maximum	0	1	1	0	1	2	2	0	-	-	-	-	0	-	1	2	1	1	-	0	0	-	-	0
Ricinus fringillae	0	1	1	0	1	3	1	0	-	-	-	-	0	-	0	-	0	1	-	0	0	-	-	0
Trochiloecetes rupununi	0	1	1	0	1	3	1	0	-	-	-	-	0	-	0	-	0	1	-	0	0	-	-	0
Trochiliphagus abdominalis	0	1	1	0	1	3	3	0	-	-	-	-	0	-	0	-	0	1	-	0	0	-	-	0
Therodoxus oweni	0	0	1	0	1	0	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	1
Paraheterodoxus insignis	0	0	1	0	1	0	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	1
Boopia tarsata	0	0	1	0	1	0	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	1
Latumcephalum lesouefi/macropus	0	1	1	0	1	2	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	1
Paraboopia flava	0	1	1	0	1	0	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	1
Amyrsidea ventralis	0	0	1	1	1	0	0	1	1	0	1	1	0	-	1	3	1	2	1	1	1	1	0	0
Rediella mirabilis	0	0	1	1	0	-	0	1	1	0	0	0	0	-	0	-	0	2	0	0	1	1	1	0
Somaphantus lusius	0	0	1	1	0	-	0	1	1	0	1	0	0	-	0	-	1	2	1	1	1	1	0	0
Bonomiella columbae	0	1	1	0	1	2	0	1	0	0	1	1	0	-	0	-	1	2	0	1	1	0	0	0
Menopon gallinae	0	0	1	1	1	0	0	1	1	0	1	1	0	-	1	1	1	2	1	1	1	1	0	0
Numidicola antennatus	0	0	1	1	1	0	0	1	1	0	1	1	0	-	1	1	1	2	1	0	0	-	-	0
Hohorstiella lata	0	1	1	0	1	3	0	1	1	0	1	1	1	1	1	0	1	2	0	1	1	1	0	0
Menacanthus stramineus	0	1	1	0	1	3	0	1	0	0	1	1	0	-	1	0	1	2	1	1	1	1	0	0
Colimenopon urocolius	0	1	1	0	1	1	0	1	0	0	1	0	0	-	1	3	1	2	1	1	1	1	0	0
Machaerilaemus laticorpus/latifrons	0	1	1	0	1	1	0	0	-	-	-	-	0	-	1	4	1	2	1	1	1	0	0	0
Neomenopon pteroclurus	0	1	1	0	1	3	0	1	1	0	1	0	0	-	1	4	1	2	0	1	1	1	0	0
Dennyus hirundinis	0	1	1	0	1	2	0	1	1	0	0	0	0	-	0	-	1	2	1	1	1	0	0	0
Myrsidea victrix	0	1	1	0	1	2	0	1	1	0	0	0	0	-	0	-	1	2	1	1	1	0	0	0
Ancistrona vagelli	0	1	1	0	1	3	0	0	-	-	-	-	0	-	0	-	1	2	1	1	1	1	0	0
Austromenopon crocatum	0	1	1	0	1	3	0	1	1	1	1	0	0	-	0	-	1	2	1	1	1	1	0	0
Eidmanniella pellucida	0	1	1	0	1	1	0	1	1	1	1	1	0	-	0	-	1	2	0	1	1	1	0	0
Holomenopon brevithoracicum	0	1	1	0	1	1	0	1	1	0	1	0	0	-	0	-	1	2	0	1	1	1	0	0
Plegadiphilus threskiornis	0	1	1	0	1	3	0	1	1	1	1	0	1	1	0	-	1	2	0	1	1	1	0	0
Actornithophilus uniseriatus	0	1	1	0	1	2	0	1	1	0	0	0	0	-	0	-	1	2	0	1	1	1	1	0
Chapinia robusta	0	1	1	0	1	3	4	1	0	0	1	0	0	-	0	-	1	2	1	1	1	1	0	0
Gruimenopon longum	0	0	1	0	1	3	0	1	1	0	0	1	1	2	0	-	1	2	1	1	1	1	0	0
Meromenopon meropis	0	1	1	0	1	2	0	1	1	1	1	1	1	0	0	-	1	2	1	1	1	1	0	0
Eomenopon denticulatum	0	1	1	0	1	3	0	1	0	0	1	1	1	1	0	-	1	2	1	1	1	1	0	0
Hoazineus armiferus	0	0	1	0	1	0	0	1	1	0	0	1	1	2	0	-	1	2	1	1	1	1	0	0
Pseudomenopon pilosum	0	1	1	0	1	3	0	1	1	0	1	0	0	-	0	-	1	2	1	1	1	1	0	0
Trinoton anserinum	0	1	1	0	1	1	0	1	0	0	1	1	0	-	0	-	1	2	1	1	1	1	1	0
Colpocephalum zebra	0	1	1	1	1	2	0	1	1	0	0	1	1	0	1	4	1	2	0	1	1	1	0	0
Comatomenopon elbeli/elongatum	0	0	1	0	1	2	0	1	1	0	0	1	1	0	1	4	1	2	0	1	1	1	0	0
Ardeiphilus trochioxus	0	1	1	0	1	3	0	1	1	0	1	1	1	0	1	4	1	2	0	1	1	1	0	0
Ciconiphilus quadripustulatus	0	1	1	0	1	3	0	1	0	0	1	1	1	0	0	-	1	2	0	1	1	1	0	0
Cuculiphilus fasciatus	0	1	1	0	1	3	0	1	0	0	1	1	1	0	0	-	1	2	0	1	1	1	0	0
Odoriphila clayae/phoeniculi	0	1	1	0	1	3	0	1	1	0	0	1	1	1	1	4	1	2	0	1	1	1	0	0
Osborniella crotophagae	0	1	1	0	1	3	0	1	1	0	1	1	1	0	0	-	1	2	0	1	1	1	0	0
Psittacomenopon poicephalus	0	1	1	0	1	2	0	1	1	0	1	1	1	0	0	-	1	2	0	1	1	1	0	0
Piagetiella bursaepelecani	0	1	1	0	1	3	0	1	0	0	1	1	1	0	0	-	1	2	1	1	1	1	0	0

	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
Liposcelis bostrychophilus	1	0	0	-	1	1	0	-	1	1	4	0	-	1	1	0	0	0	0	-	0	0	0
Laemobothrion maximum	1	0	1	1	1	2	0	-	0	1	3	0	-	1	1	1	0	1	4	-	0	1	1
Ricinus fringillae	1	1	0	-	1	2	0	-	0	0	0	1	0	1	1	1	2	1	6	-	0	1	1
Trochiloecetes rupununi	1	1	0	-	1	2	0	-	0	0	5	1	0	1	1	1	2	1	6	-	0	1	1
Trochiliphagus abdominalis	1	1	0	-	1	2	0	-	0	0	0	1	0	1	1	1	2	1	6	-	0	1	1
Therodoxus oweni	0	1	0	-	1	1	1	1	1	0	1	0	-	2	1	1	2	1	5	-	0	1	1
Paraheterodoxus insignis	0	1	0	-	1	2	0	-	1	1	0	0	-	1	1	1	2	1	5	-	0	1	1
Boopia tarsata	0	1	0	-	1	2	0	-	1	0	0	0	-	1	1	1	2	1	5	-	0	1	1
Latumcephalum lesouefi/macropus	0	1	0	-	1	1	1	1	1	1	1	0	-	2	1	1	2	1	5	-	0	1	0
Paraboopia flava	0	1	0	-	1	2	1	1	1	1	1	0	-	2	1	1	0	1	5	-	0	1	0
Amyrsidea ventralis	0	0	1	1	1	1	0	-	0	0	1	0	-	1	1	1	0	1	2	-	0	1	1
Rediella mirabilis	0	0	1	1	1	2	0	-	0	0	6	0	-	1	1	1	0	1	5	-	0	1	1
Somaphantus lusius	0	0	1	1	1	1	0	-	0	0	4	0	-	1	1	1	0	1	2	-	0	1	1
Bonomiella columbae	0	0	1	0	0	1	1	1	0	0	-	-	-	1	1	1	0	1	5	-	0	1	1
Menopon gallinae	0	0	1	0	0	1	1	1	0	0	-	-	-	0	0	1	0	1	2	-	0	1	1
Numidicola antennatus	0	0	1	1	1	1	0	-	0	0	1	0	-	1	1	1	0	1	2	-	0	1	1
Hohorstiella lata	0	0	1	0	1	1	1	0	0	0	2	1	1	1	1	1	0	1	2	-	0	1	1
Menacanthus stramineus	0	0	1	0	1	1	0	-	0	0	2	1	1	1	1	1	1	1	2	-	0	1	1
Colimenopon urocolius	0	0	1	0	1	2	0	-	0	1	2	1	1	1	1	1	1	1	2	-	0	1	1
Machaerilaemus laticorpus/latifrons	0	0	1	0	1	1	0	-	0	1	2	1	1	1	1	1	1	1	1	-	0	1	1
Neomenopon pteroclurus	0	0	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	1	2	-	0	1	1
Dennyus hirundinis	0	0	1	1	1	1	0	-	1	1	3	1	2	1	1	1	0	1	2	-	0	1	1
Myrsidea victrix	0	0	1	1	1	0	-	-	1	0	3	1	2	2	1	1	0	1	2	-	0	1	1
Ancistrona vagelli	0	0	1	0	1	1	1	0	0	0	0	1	2	1	1	1	1	1	5	-	0	1	1
Austromenopon crocatum	0	0	1	0	1	1	1	0	0	0	1	0	-	0	1	1	1	1	2	-	0	1	1
Eidmanniella pellucida	0	0	1	0	1	1	1	0	0	0	2	1	1	1	1	1	1	1	2	-	0	1	1
Holomenopon brevithoracicum	0	0	1	0	1	1	1	0	0	0	2	1	1	1	1	1	0	1	2	-	0	1	1
Plegadiphilus threskiornis	0	0	1	0	1	1	1	0	0	0	0	0	-	1	1	1	0	1	2	-	0	1	1
Actornithophilus uniseriatus	0	0	1	1	1	2	0	-	0	1	3	0	-	1	1	1	0	1	2	-	0	1	1
Chapinia robusta	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0	1	2	-	1	1	1
Gruimenopon longum	0	0	1	1	0	1	1	1	0	0	-	-	-	1	1	1	0	1	2	-	1	1	1
Meromenopon meropis	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	1	0	1	2	-	1	1	1
Eomenopon denticulatum	0	0	1	0	1	2	1	1	0	0	1	0	-	1	1	1	1	1	2	-	0	1	1
Hoazineus armiferus	0	0	1	1	0	1	1	0	0	0	-	-	-	1	1	1	0	1	2	-	1	1	1
Pseudomenopon pilosum	0	0	1	0	1	2	1	1	0	0	1	0	-	1	1	1	0	1	2	-	0	1	1
Trinoton anserinum	0	0	1	0	1	2	1	1	0	1	1	1	1	1	1	1	0	1	2	-	0	1	1
Colpocephalum zebra	0	0	1	1	0	1	1	1	0	0	-	-	-	1	1	1	0	1	2&3	1	1	1	1
Comatomenopon elbeli/elongatum	0	0	1	1	0	1	1	1	0	0	-	-	-	1	1	1	0	1	3	1	1	1	1
Ardeiphilus trochioxus	0	0	1	0	0	1	1	1	0	0	-	-	-	1	1	1	0	1	2&3	2	1	1	1
Ciconiphilus quadripustulatus	0	0	1	0	0	1	1	1	0	0	-	-	-	1	1	1	0	1	2&3	1	1	1	1
Cuculiphilus fasciatus	0	0	1	0	1	1	1	1	0	0	1	0	-	2	1	1	0	1	2&3	2	1	1	1
Odoriphila clayae/phoeniculi	0	0	1	2	1	1	0	-	0	1	0	0	-	1	1	1	0	1	3	0	1	1	1
Osborniella crotophagae	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	1	2&3	1	1	1	1
Psittacomenopon poicephalus	0	0	1	0	1	1	1	1	0	0	0	1	1	1	1	1	0	1	3	1	1	1	1
Piagetiella bursaepelecani	0	0	1	1	1	1	0	-	0	1	0	1	1	1	1	1	0	1	2&3	2	1	1	1

	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114
Liposcelis bostrychophilus	-	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	-	-	0
Laemobothrion maximum	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0
Ricinus fringillae	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	1
Trochiloecetes rupununi	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	1	1	1
Trochiliphagus abdominalis	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	1	0	1
Therodoxus oweni	2	0	0	0	1	0	0	0	0	0	0	0	-	1	0	2	0	1	1
Paraheterodoxus insignis	2	0	0	0	2	0	1	1	1	1	1	1	-	1	2	2	0	1	1
Boopia tarsata	2	0	0	0	1	0	0	0	0	0	0	0	-	1	1	2	0	0	1
Latumcephalum lesouefi/macropus	-	0	0	0	1	0	1	1	1	1	1	1	-	1	1	1	0	1	1
Paraboopia flava	-	0	0	0	1	0	1	1	1	1	1	1	-	1	1	1	0	1	1
Amyrsidea ventralis	0	0	0	0	2	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Rediella mirabilis	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Somaphantus lusius	0	0	0	0	2	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Bonomiella columbae	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Menopon gallinae	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Numidicola antennatus	0	0	0	0	2	0	0	0	0	0	0	1	1	1	0	1	0	1	1
Hohorstiella lata	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Menacanthus stramineus	0	0	0	0	2	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Colimenopon urocolius	1	0	0	0	2	1	1	1	1	1	1	1	1	1	0	1	0	0	1
Machaerilaemus laticorpus/latifrons	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Neomenopon pteroclurus	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Dennyus hirundinis	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Myrsidea victrix	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Ancistrona vagelli	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Austromenopon crocatum	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Eidmanniella pellucida	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Holomenopon brevithoracicum	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Plegadiphilus threskiornis	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Actornithophilus uniseriatus	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Chapinia robusta	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Gruimenopon longum	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Meromenopon meropis	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1
Eomenopon denticulatum	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Hoazineus armiferus	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Pseudomenopon pilosum	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Trinoton anserinum	1	0	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1
Colpocephalum zebra	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Comatomenopon elbeli/elongatum	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Ardeiphilus trochioxus	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Ciconiphilus quadripustulatus	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Cuculiphilus fasciatus	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1
Odoriphila clayae/phoeniculi	1	0	0	0	2	1	1	1	1	1	1	0	1	1	0	1	0	1	1
Osborniella crotophagae	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
Psittacomenopon poicephalus	1	0	0	1	2	1	1	1	1	1	1	1	1	1	0	1	0	1	1
Piagetiella bursaepelecani	1	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1

	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132
Liposcelis bostrychophilus	-	-	-	-	-	-	0	1	1	1	1	1	1	0	-	-	0	-
Laemobothrion maximum	-	-	-	-	-	-	0	1	1	1	1	1	1	0	-	-	0	-
Ricinus fringillae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	-
Trochiloecetes rupununi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	-
Trochiliphagus abdominalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	-
Therodoxus oweni	1	1	1	2	2	2	0	0	0	1	1	1	1	0	-	-	0	-
Paraheterodoxus insignis	3	3	3	2	2	2	0	0	1	1	1	1	1	0	-	-	0	-
Boopia tarsata	3	3	3	2	2	2	0	0	1	1	1	1	1	0	-	-	0	-
Latumcephalum lesouefi/macropus	1	1	1	2	2	2	0	0	1	1	1	1	1	0	-	-	0	-
Paraboopia flava	1	1	1	2	2	2	0	0	1	1	1	1	1	0	-	-	0	-
Amyrsidea ventralis	2	2	2	2	2	2	0	1	1	1	1	1	1	1	0	-	1	0
Rediella mirabilis	1	1	1	1	2	2	0	1	1	1	1	1	1	0	-	-	0	-
Somaphantus lusius	1	1	1	1	1	1	0	1	1	1	1	1	1	0	-	-	1	1
Bonomiella columbae	2	2	2	2	2	2	0	0	0	0	0	0	0	0	-	-	0	-
Menopon gallinae	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	0
Numidicola antennatus	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	1
Hohorstiella lata	2	2	2	2	2	2	0	1	1	1	1	1	1	1	1	-	1	0
Menacanthus stramineus	2	2	2	2	2	2	0	1	1	1	1	1	1	1	0	-	1	0
Colimenopon urocolius	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	1
Machaerilaemus laticorpus/latifrons	2	2	2	2	2	2	0	1	1	1	1	1	1	1	1	-	1	1
Neomenopon pteroclurus	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	1
Dennyus hirundinis	2	2	2	2	2	2	0	0	0	0	0	0	0	0	-	-	0	-
Myrsidea victrix	2	2	2	2	2	2	0	0	0	0	0	0	0	1	1	-	1	0
Ancistrona vagelli	2	2	2	2	2	2	0	0	0	0	0	0	0	0	-	-	1	1
Austromenopon crocatum	2	2	2	2	2	2	0	1	1	1	1	1	1	1	1	-	1	1
Eidmanniella pellucida	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	0
Holomenopon brevithoracicum	2	2	2	2	2	2	0	0	1	1	1	1	1	0	-	-	1	0
Plegadiphilus threskiornis	2	2	2	2	2	2	1	0	1	1	1	1	1	0	-	-	1	1
Actornithophilus uniseriatus	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	0
Chapinia robusta	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	0
Gruimenopon longum	2	2	2	2	2	2	0	1	1	1	1	1	1	0	-	-	1	0
Meromenopon meropis	2	2	2	2	2	2	1	1	1	1	1	1	1	0	-	-	1	0
Eomenopon denticulatum	2	2	2	2	2	2	0	1	1	1	1	1	1	2	-	0	2	-
Hoazineus armiferus	1	1	1	1	1	1	0	1	1	1	1	1	1	0	-	-	1	0
Pseudomenopon pilosum	2	2	2	2	2	2	1	0	0	0	0	0	0	0	-	-	1	1
Trinoton anserinum	2	2	2	2	2	2	0	0	1	1	1	1	1	0	-	-	1	0
Colpocephalum zebra	3	3	3	3	3	3	0	1	1	1	1	1	1	2	-	1	0	-
Comatomenopon elbeli/elongatum	2	2	2	2	2	2	0	1	1	1	1	1	1	2	-	1	0	-
Ardeiphilus trochioxus	3	3	3	3	3	3	0	1	1	1	1	1	1	2	-	1	2	-
Ciconiphilus quadripustulatus	3	3	3	2	2	2	0	1	1	1	1	1	1	2	-	1	0	-
Cuculiphilus fasciatus	3	3	3	2	2	2	0	1	1	1	1	1	1	2	-	1	2	-
Odoriphila clayae/phoeniculi	3	3	3	3	3	3	0	1	1	1	1	1	1	2	-	0	2	-
Osborniella crotophagae	2	2	2	2	2	2	0	1	1	1	1	1	1	2	-	1	0	-
Psittacomenopon poicephalus	3	3	3	3	3	3	0	1	1	1	1	1	1	2	-	1	0	-
Piagetiella bursaepelecani	2	2	2	2	2	2	0	0	0	1	1	1	1	2	-	1	2	-

	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147
Liposcelis bostrychophilus	-	0	-	0	-	0	-	0	-	0	-	-	-	-	-
Laemobothrion maximum	-	2	0	2	0	0	-	0	-	0	1	1	0	2	0
Ricinus fringillae	-	0	-	0	-	0	-	0	-	0	1	1	0	2	1
Trochiloecetes rupununi	-	0	-	0	-	0	-	0	-	0	1	0	0	2	1
Trochiliphagus abdominalis	-	0	-	0	-	0	-	0	-	0	1	1	0	2	1
Therodoxus oweni	-	0	-	0	-	0	-	0	-	1	1	1	0	3	0
Paraheterodoxus insignis	-	0	-	0	-	0	-	0	-	1	1	1	1	3	0
Boopia tarsata	-	0	-	0	-	0	-	0	-	1	1	1	1	3	0
Latumcephalum lesouefi/macropus	-	0	-	0	-	0	-	0	-	1	1	1	1	3	0
Paraboopia flava	-	0	-	0	-	0	-	0	-	1	1	1	1	3	0
Amyrsidea ventralis	-	1	1	0	-	0	-	1	3	0	0	0	0	0	-
Rediella mirabilis	-	0	-	0	-	0	-	0	-	0	0	0	0	1	2
Somaphantus lusius	-	0	-	0	-	0	-	0	-	0	1	0	0	0	-
Bonomiella columbae	-	0	-	0	-	0	-	1	0	0	-	-	-	-	-
Menopon gallinae	-	0	-	0	-	0	-	1	2	0	0	0	0	0	-
Numidicola antennatus	-	1	1	1	1	0	-	1	2	0	0	0	0	2	1
Hohorstiella lata	-	1	0	1	1	0	-	1	0	0	0	0	0	2	1
Menacanthus stramineus	-	1	0	1	1	0	-	1	0	0	1	1	0	2	1
Colimenopon urocolius	-	1	1	1	1	0	-	1	0	0	1	0	0	2	1
Machaerilaemus laticorpus/latifrons	-	1	1	1	1	1	1	1	0	0	0	0	0	2	0
Neomenopon pteroclurus	-	1	0	1	0	1	0	?	?	0	-	-	-	-	-
Dennyus hirundinis	-	1	0	1	0	0	-	1	0	0	1	0	0	2	1
Myrsidea victrix	-	1	0	1	0	1	0	1	0	0	0	0	0	2	1
Ancistrona vagelli	-	1	1	1	1	0	-	1	1	0	1	0	0	2	4
Austromenopon crocatum	-	1	1	1	1	1	1	1	0	0	1	0	0	2	1
Eidmanniella pellucida	-	1	0	1	0	0	-	1	0	0	0	0	0	2	0
Holomenopon brevithoracicum	-	1	0	0	-	0	-	1	1	0	1	0	0	2	1
Plegadiphilus threskiornis	-	1	0	1	0	0	-	1	0	0	1	0	0	1	2
Actornithophilus uniseriatus	-	0	-	0	-	0	-	1	1	0	1	0	0	1	2
Chapinia robusta	-	1	0	1	0	0	-	1	0	0	0	0	0	2	4
Gruimenopon longum	-	0	-	0	-	0	-	1	1	0	1	0	0	2	2
Meromenopon meropis	-	1	0	1	1	0	-	1	0	0	1	0	0	2	1
Eomenopon denticulatum	0	0	-	0	-	0	-	1	0	0	1	0	0	2	1
Hoazineus armiferus	-	1	0	0	-	0	-	1	0	0	1	0	0	2	1
Pseudomenopon pilosum	-	1	1	0	-	0	-	1	0	0	1	0	0	2	1
Trinoton anserinum	-	1	0	1	1	0	-	1	0	0	1	0	0	1	3
Colpocephalum zebra	-	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Comatomenopon elbeli/elongatum	-	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Ardeiphilus trochioxus	1	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Ciconiphilus quadripustulatus	-	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Cuculiphilus fasciatus	2	0	-	0	-	0	-	1	0	0	0	0	0	2	1
Odoriphila clayae/phoeniculi	0	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Osborniella crotophagae	-	0	-	0	-	0	-	1	0	0	1	0	0	1	3
Psittacomenopon poicephalus	-	0	-	0	-	0	-	1	0	0	1	0	0	2	1
Piagetiella bursaepelecani	0	0	-	0	-	0	-	1	0	0	1	0	0	1	3