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Avian louse phylogeny (Phthiraptera: Ischnocera): a cladistic study based on morphology

VINCENT S. SMITH*

Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow, G12 8QQ

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The louse suborder Ischnocera (Phthiraptera) contains 3060 currently described species from over 150 genera. These lice are permanent obligatory ectoparasites of a diverse selection of birds and mammals with a worldwide distribution. Historically, they have played a major role in the development of our ideas on coevolution, and species hosted by mammals have been used extensively as model organisms for the study of cospeciation. In contrast, avian taxa comprising 90% of ischnoceran species have been neglected due to a lack of data on their wider systematics. A comparative study based on the adult and nymphal instar morphology of avian lice yielded 138 characters from 56 species (51 genera), all of which are illustrated or discussed here for the first time. A further five outgroup taxa were examined from the mammalian ischnoceran family Trichodectidae. Phylogenetic analyses of these data produced three most parsimonious cladograms, the strict consensus of which is highly resolved and broadly consistent with previous classifications. Morphological character variation is extensive, and nymphal character traits are useful in identifying instances of convergent evolution in adult morphology. The role of ontogeny in the development of the major character complexes of the head and abdomen is discussed, and its implications for further work on the phylogeny of avian Ischnocera is considered. Comparison with host taxonomy reveals a series of complex host-parasite associations that do not support a hypothesis of strict one to one cospeciation. However, extrapolation of these associations is compromised by the low sample size. The role of niche specialization to explain the presence of multiple unrelated lineages on the same host taxon is considered.

ADDITIONAL KEY WORDS: lice – Phthiraptera – Ischnocera – ontogeny – bird phylogeny – coevolution – congruence.

INTRODUCTION

The suborder Ischnocera comprises some 3060 species of chewing lice, which are parasitic on over 2300 avian and 240 mammalian hosts (R. Price pers. comm.). As permanent obligate ectoparasites, they are distributed world wide throughout most bird families, and are present on a diverse variety of mammals. Like all lice, Ischnocera are wingless, with a direct life cycle, undergoing three nymphal instars before reaching an adult stage. They are highly specialized for life on their hosts and exhibit a level of host specificity that is unparalleled by most other insect ectoparasites. Much of their biology is poorly known, yet their host specificity has long attracted the attention of systematic biologists interested in their potential to help resolve host relationships (e.g. Hopkins, 1949 and Clay, 1951b). Many of the early studies on coevolution were based on the distribution of chewing lice, particularly those of the suborder Ischnocera, which are putatively more host specific than other louse groups.

More recently, studies on louse cophylogeny and a growing body of data on ischnoceran ecology have fashioned lice as model organisms for the study of cospeciation. They have become a 'textbook' example within this field (e.g. Ridley, 1996) and have been used in the development of analytical models for assessing the patterns and rates of cospeciation. A wider understanding of louse ecology, and the fact that they can be readily quantified on their hosts, lends them to a range of ecological studies. These include research into their demography (Rózsa, Rékási & Reiczigel, 1996;

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* Present address: 17 Barnet Close, Yeovil, Somerset BA21 3NT. E-mail: vincent.s.smith@udcf.gla.ac.uk

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Rózsa, 1997), community structure (Fowler & Williams, 1985; Rékási, Rózsa & Kiss, 1997), the costs of parasitism (Booth, Clayton & Block, 1993; Brown, Brown & Rannala, 1995) and parasite mediated sexual selection (Clayton, 1990, 1991; Clayton, Pruett-Jones & Lande, 1992). Much of this work has been made possible by a few dedicated entomologists who have devoted their careers to unravelling the tangled and often complex alpha taxonomy of these parasites, yet the higher level systematics of ischnoceran lice are comparatively unknown, particularly for avian lice which make up nearly 90% of all ischnoceran species. There is no generally accepted classification for the group, and those that are available make little headway into resolving relationships among genera. In contrast, the mammalian Ischnocera are comparatively well studied, with morphological and molecular phylogenies available for nearly all known species (Lyal, 1985a; Hafner *et al.*, 1994; Page, Price & Hellenthal, 1995; Spradling, 1997).

Here I present the first comparative analysis of morphology for the avian Ischnocera and the first cladogram for the group, based on a diverse selection of ischnoceran lice. This study documents character variation throughout the clade, emphasizing the importance of using data from all instars. The role of ontogeny in the development of the major character complexes of the head and abdomen is considered and its implications for further work on ischnoceran morphology discussed.

CURRENT CLASSIFICATION

The number of families making up the Ischnocera is a matter of some contention. Eichler (1963) recognized 21 families whilst Hopkins & Clay (1952) accepted just three. This discrepancy can partly be explained by the diversity of form exhibited amongst the genera. Ischnocera vary considerably in terms of their size and general morphology, yet these characteristics are apt to grade into each other. Hence, generic groups and even genera are hard to define. This paucity of basic and reliable characters makes comparative morphological studies within the group exceedingly difficult. No comparative account of ischnoceran morphology has ever been published for more than a handful of avian louse taxa, yet similar studies for other major louse suborders are readily available (Ferris, 1951; Clay, 1969; 1970; Kéler, 1938; 1971; Kim & Ludwig, 1978; Kim, Pratt & Stojanovich, 1986). A justification for the classification scheme proposed by Eichler (1963) was never published, and it has subsequently been rejected by most authorities on the assumption that it was unduly biased towards the host classification. However, it provides a useful starting place to assess the diversity of avian ischnoceran lice. A summary of Eichler's scheme is outlined in Table 1 for those genera included in the present study.

The late Theresa Clay, one of the foremost authorities on chewing lice during the twentieth century, attempted to establish a preliminary classification of avian Ischnocera during the 1960s. Clay drafted a 'natural' generic key to the group which she intended publishing as the sequel to her 1951 paper "An introduction to a classification of the avian Ischnocera (Mallophaga): Part I" (Clay, 1951a). The manuscript in which she describes this key contained a preliminary classification, albeit incomplete. However, she refrained from publishing the paper due to her "dissatisfaction with certain aspects of the key" (Ledger, 1980: 87). A complete copy of the original manuscript ("A key to the genera and generic groups of the Ischnocera [Mallophaga]") is present in the collection of Theresa Clay's correspondence maintained at the Natural History Museum, London (BMNH), although figures 1–12 are missing. Despite this work remaining unpublished it provides a useful comparison to Eichler's (1963) scheme. This paper will subsequently be referred to as 'Clay's unpublished key'. A summary of the preliminary classification she proposed is shown in Table 2.

The most recent studies of Ischnocera all recognize at least three monophyletic groups (Lyal, 1985b; Mey, 1994; Smith, 2000a). These are the Trichodectidae restricted to mammalian hosts, the Heptapsogasteridae present on tinamiform birds and the Goniodidae of Galliformes and Columbiformes. Earlier studies usually combined the Goniodidae in a fourth group (the "Philopteridae" *sensu* Hopkins & Clay, 1952). "Philopteridae" comprise some 70% of ischnoceran species and are present on almost all families of birds. However, they are almost certainly para- or polyphyletic with respect to other ischnoceran lice and are generally regarded as a miscellaneous collection of genera defined by their exclusion from other ischnoceran higher taxa. A monotypic taxon (the Trichophilopteridae) represented by a single species present on Madagascan primates (Lemuridae and Indriidae) may be related to the avian "Philopteridae". This species bears a number of significant morphological characters that are apparently intermediate between the "Philopteridae" of birds and the Trichodectidae of mammals. Consequently the affinities of this taxon are unclear, and it has been placed variously amongst both these groups and in an independent family within Ischnocera (Stobbe, 1913; Ferris, 1933; Emerson & Price, 1985).

MATERIAL AND METHODS

SPECIMENS

In the absence of any consensus on the classification of Ischnocera below the rank of suborder, genera were

Table 1. Familial and subfamilial classification of the avian Ischnocera (Philopteridae) *sensu* Eichler (1963). Genera represented in this study are placed according to Eichler's scheme

Family Subfamily	Genera represented in this study	Family Subfamily	Genera represented in this study
Goniodidae		Pseudonirmidae	
Archigonidinae		Pseudoniminae	*Halipeurus, Harrisoniella, Naubates, Pelmatocerandra, Perineus, Philoceanus & Pseudonimus*
Goniodinae	*Goniodes*	Pectinopyginae	*Pectinopygus*
Goniocotinae	*Goniocotes*	Docophoroididae	*Docophoroides*
Homocerinae		Giebeliidae	*Trabeculus*
Chelopistinae	*Chelopistes*	Esthiopteridae	
Physconelloidinae	*Campanulotes & Coloceras*	Esthiopterinae	
Opisthocomiellinae	*Osculotes*	Esthiopteridae	
Heptapsogasteridae		Ibidoecinae	*Anaticola, Ardeicola & Ibidoecus*
Heptapsogasterinae	*Discocorpus*	Anatoecinae	*Craspedonirmus*
Physconellinae		Columbicolinae	*Columbicola*
Megagininae		Aquanirminae	*Aquanirmus*
Strongylocotinae	*Strongylocotes*	Acidoproctidae	
Austrogoniodidae	*Austrogoniodes*	Acidoproctinae	*Acidoproctus*
Nesiotinidae		Bothriometopinae	
Paragoniocotidae		Rallicolidae	
Paragoniocotinae	*Paragoniocotes*	Rallicolinae	*Rallicola*
Psittoecinae		Quadraceptinae	*Quadraceps & Saemundssonia*
Psittaconirminae	*Neopsittaconirmus*	Philopteridae	
Meinertzhageniellidae		Strigiphilinae	*Craspedorrhynchus & Strigiphilus*
Meinertzhageniellinae		Brueeliinae	*Brueelia, Sturnidoecus, Vernoniella & Alcedoecus*
Struthiolipeurinae	*Archolipeurus*	Philopterinae	*Philopterus*
Falcolipeurinae	*Falcolipeurus*		
Dahlemhorniidae			
Lipeuridae			
Lipeurinae	*Cuclotogaster, Lipeurus, Oxylipeurus & Splendoroffula*		
Syrrhaptoecinae	*Syrrhaptoecus*		
Degeeriellidae		Unplaced genera	*Haffneria*
Degeeriellinae	*Degeeriella, Lagopoecus & Upupicola*		*Paraclisis*
			Podargoecus
Paroncophorinae			
Colilipeuridae			

selected using Eichler's (1963) classification in an attempt to sample as much taxonomic diversity as possible. Exemplars were chosen for 51 genera, representing 29 of the 41 subfamilies of avian Ischnocera recognized by Eichler. These include taxa from all 14 families that contain more than a single genus. The sole criterion with which species were selected was the availability of slide mounted nymphal specimens. Earlier studies (Mey, 1994; Page *et al.*, 1995; Price & Hellenthal, 1996) have highlighted the importance of nymphal morphology in helping to elucidate louse relationships. However, nymphal morphology has been overlooked in most studies on the taxonomy of Ischnocera. A total of 56 species were selected for inclusion in the cladistic analysis, of which 36 were represented by complete nymphal series, and partial series (in which one or two nymphal stadia were missing) were available for all but one of the remaining taxa. These species represent lice from 31 bird families and include representatives from 13 of the 23 bird orders recognized by Sibley & Monroe (1990).

Instar status was initially determined from a series of simple morphometric analyses performed on a selection of specimens from each species. The total

Table 2. Preliminary classification of the Philopteridae derived from Clay's unpublished key. Genera in parentheses are considered by Clay to be within or near each complex. Genera in bold are represented in this study

- *Acidoproctus*-complex
    - ***Acidoproctus***
    - *Bothriometopus*
    - *Heteroproctus*
    - *Ornithobius*
- *Brueelia*-complex
    - *Bizarrifrons*
    - ***Brueelia*** (*sensu* Hopkins & Clay, 1952)
    - ***Sturnidoecus***
- *Cummingsiella*-complex
    - *Alcedoffula*
    - *Cirrophthirus*
    - *Cummingsiella*
    - ***Quadraceps***
    - (*Penenirmus*)
- *Degeeriella*-complex (*sensu* Clay, 1958)
    - *Acutifrons*
    - *Austrophilopterus*
    - *Capraiella*
    - *Cuculicola*
    - ***Degeeriella***
    - ***Lagopoecus***
    - *Picicola*
    - *Trogoninirmus*
    - ***Upupicola***
    - (*Buceronirmus*)
    - (*Hopkinsiella*)
    - (*Penenirmus*)
    - (***Syrrhaptoecus***)
    - (*Tinamotaecola*)
- *Eichinophilopterus*-complex
    - *Echinophilopterus*
- *Goniodes*-complex
    - *Auricotes*
    - *Campanulotes*
    - ***Coloceras***
    - ***Goniocotes***
    - ***Goniodes***
    - *Kodocephalon*
    - *Pachyskelotes*
    - *Passonomedea*
    - *Physconelloides*
    - *Austrogoniodes*
    - ***Chelopistes***
    - *Labiocotes*
    - ***Osculotes***
- *Otidoecus*-complex
    - ***Cuclotogaster***
    - *Otidoecus*
    - *Rhynonirmus*
- *Philoceanus*-complex
    - *Bedfordiella*
    - *Episbates*
    - ***Halipeurus***
    - ***Harrisoniella***
    - ***Naubates***
    - ***Pelmatocerandra***
    - ***Perineus***
    - ***Philoceanus***
    - ***Pseudonirmus***
    - ***Trabeculus***
- *Trichophilopterus*-complex
    - *Trichophilopterus*
- Heptapsogasteridae (*sensu* Smith, 2000a)
    - *Austrokelloggia*
    - *Cuclotocephalus*
    - ***Discocorpus***
    - *Heptapsogaster*
    - *Kelloggia*
    - *Lamprocorpus*
    - *Megaginus*
    - *Megapeostus*
    - *Nothocotus*
    - *Ornicholax*
    - *Pectenosoma*
    - *Physconella*
    - *Pterocotes*
    - *Rhopaloceras*
    - ***Strongylocotes***
    - *Trichodopeostus*

length, maximum abdominal width, head length and temporal head width were recorded for a maximum of five specimens of each putative instar. Although there is very little data on the determination of instar status for lice, several studies have shown that a specific stadium size occurs for each instar in most Ischnocera (Wilson, 1939; Arora & Chopra, 1957; Agarwal, 1967; Mey, 1994). These size classes rarely overlap, and instances when they do can usually be accounted for by sexual dimorphism of the adults. Initial hypotheses of instar status were refined in the light of dorsal setal characters on the posterolateral angles of the pterothorax and the clypeal morphology of the head.

Choice of outgroup taxa was made difficult by uncertainty over the monophyly of Ischnocera and its relationship to the other phthirapteran suborders. The subordinal phylogeny established by Lyal (1985b) suggests that members of the suborder Anoplura or Rhyncophthirina (the sister taxa to Ischnocera) would be the most likely candidate outgroup. Lyal's phylogeny is concordant with comments by Clay (1970) and Königsmann (1960), who both considered the Amblycera sister taxa to a monophyletic group comprising the Ischnocera, Rhyncophthirina and Anoplura. However, the divergent morphologies between all the suborders make the establishment of homologous character states extremely difficult. In addition, recent molecular data (Cruickshank *et al.*, in press) casts doubt over the traditional subordinal relationships. The ischnoceran family Trichodectidae present on mammals is more closely allied to the avian Ischnocera and undoubtedly constitutes a monophyletic group. Although its status as a sister group to the avian Ischnocera has never decisively been demonstrated, this relationship has been widely advocated by most authorities studying ischnoceran relationships (Blagoveshtchenskii, 1956; Mey, 1994) and is consistent with the currently available molecular data (Cruickshank *et al.*, in press). In the absence of more suitable taxa, five species representing three subfamilies of Trichodectidae were used as an outgroup for the avian lice.

Including outgroup taxa, a total of 1211 slide mounted specimens from the entomological collections based at the BMNH (Appendix 1) were examined using phase contrast and transmitted light microscopy. These specimens represent 56 genera (61 species). In addition, observations on the external morphology of a large collection of unmounted alcohol preserved material based largely at the BMNH, were made using scanning electron microscopy (SEM).

MORPHOLOGY

The phylogenetic analyses presented in this paper are based on characters from the external morphology of nymphs and adults (characters 1–129), supplemented by characters on the internal genitalia of adult males and females, drawn from observations by Blagoveshtchenskii (1956) and in Clay's 'unpublished key' (130–138). All characters are listed in Appendix 2. Character 46 (♂ scape shape) considers the morphology of the first antennal segment using elliptic Fourier analysis as described and implemented by Rohlf & Archie (1984).

Nomenclature used in morphological and taxonomic descriptions of Phthiraptera is confused and in many cases inadequate. The limited and rather patchy nature of published morphological work means that many structures have not been properly described or named, and when they have, the terms used are often of limited applicability (Lyal, 1983). In addition, a combination of lack of knowledge of previously published work and conflicting morphological interpretations mean that the literature for Phthiraptera is profuse with multiple names for single structures. Consequently, establishing homology between structures is often difficult, particularly as different authorities have variably applied these terms. A broad outline of the terminology used throughout the character descriptions is illustrated in Figure 1. This largely follows terms used by Clay (1951a, 1970) Lyal (1985a) and Smith (2000a), although further clarification of the terminology used here is provided in the results section.

Morphological drawings were made from digital images captured from a single chip JVC video camera, attached to a Nikon YS2 compound microscope. Electron micrographs were recorded electronically from a Philips 500 SEM at 6–12 kV.

CHARACTER AND TAXON SAMPLING

Throughout the initial survey of ischnoceran morphology, homology assessments were made which formed the basis of characters used in the cladistic analysis. In addition to the homology criterion, characters were chosen on the basis of their ease of scoring. Many features of ischnoceran morphology are not discrete and have a tendency to grade into each other upon examination of a large number of specimens. As far as possible, these characters were avoided in the character descriptions as they may be subject to artefacts of specimen preparation, and lack both the reliability and repeatability necessary for character analysis. Consequently, many of the character diagnoses are rather long and complex, while some characters (such as those documenting setal type and position) may be perceived as rather superficial. Nevertheless, within the species sampled here the homologies of the character states have been carefully established.

The large number of ischnoceran taxa prohibits more extensive sampling on practical grounds, whilst a complete lack of data on their phylogeny makes selection of smaller clades, which might be sampled more extensively, an impossibility. A limited test of the congeneric reliability of these characters was achieved by sampling two species from each of five different genera (*Osculotes* Kéler, *Goniodes* Nitzsch, *Saemundssonia* Timmermann, *Pectinopygus* Mjöberg and *Acidoproctus* Piaget). In addition, many of the characters examined

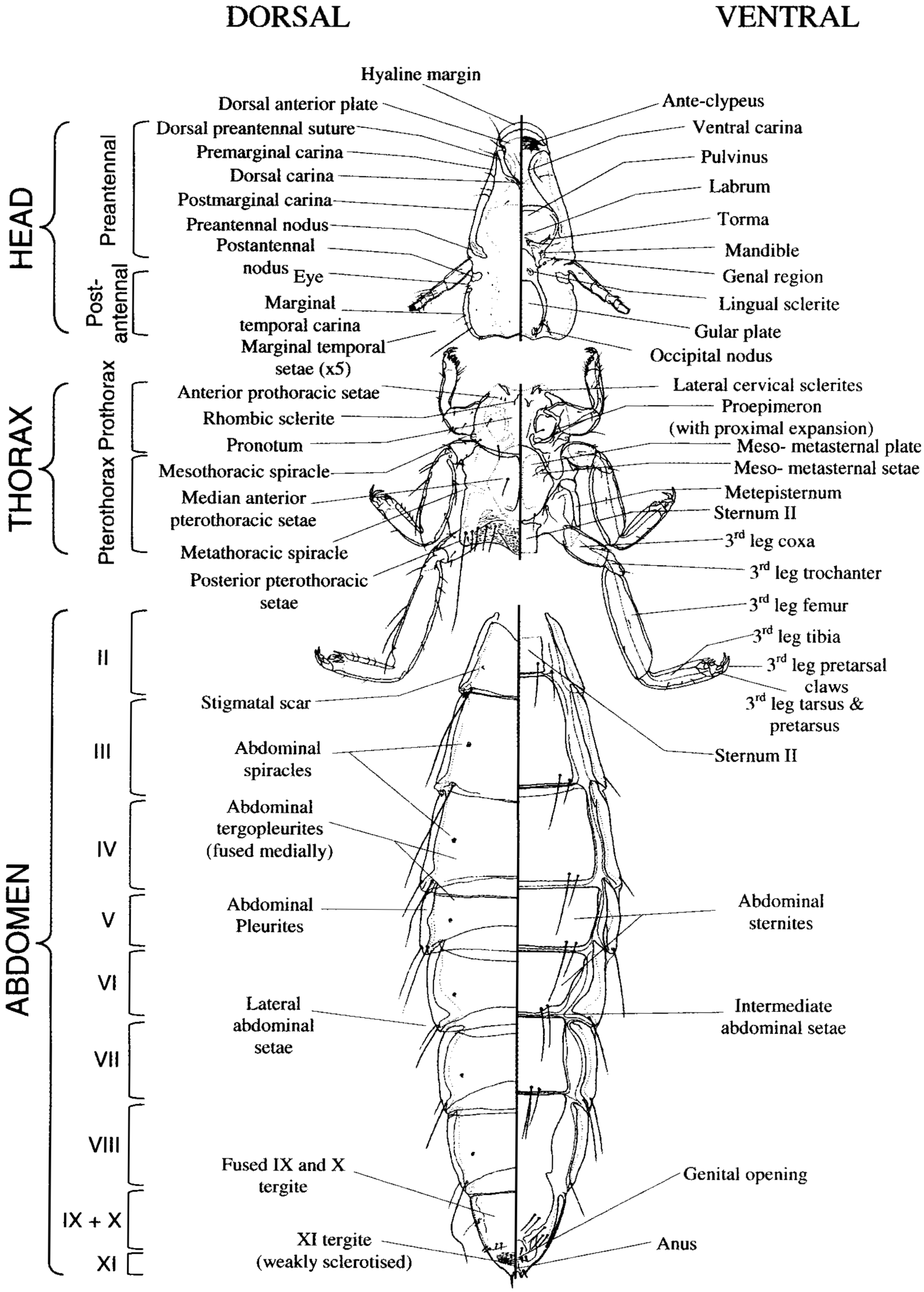

Figure 1. ♂ *Philoceanus garrodiae*, illustrating the major characters and nomenclature used throughout this paper.

tended towards those that describe variation between major character complexes (e.g. preantennal morphology, abdominal segmentation and internal genitalia). These are likely to be considerably more conserved than the more superficial characters typically used in alpha taxonomic descriptions of lice. The exemplars sampling approach has also been sanctioned on theoretical grounds (Yeates, 1995; Bininda-Emonds, Bryant & Russell, 1998), and is extensively used in molecular systematics which is subject to many of the same problems.

In an attempt to present the morphological data as concisely as possible, no special effort was made to code autapomorphies. This decision was taken on purely practical grounds, as the development of novel morphologies is very common within Ischnocera. However, the coding of autapomorphies is essential if the degree of morphological disparity between taxa and rates of morphological change are to be inferred from the tree. Future phylogenetic studies on ischnoceran morphology should consider this when coding characters, particularly if clades are more intensively sampled than was possible in this analysis.

PHYLOGENY RECONSTRUCTION

During the compilation of this data set, considerable use of the program NDE (Nexus Data Editor) (Page, 1999) was made to store character and taxon descriptions, observations and images. Phylogenetic analysis and interpretation was performed using PAUP* release version 4.0b2 (Swofford, 1999) and MacClade version 3.07 (Maddison & Maddison, 1992). The heuristic search option of PAUP* with random starting trees was employed using TBR branch swapping in conjunction with the random stepwise addition feature (10 000 replicates). The latter option was set to examine whether alternative islands of equally parsimonious trees were present in the data. All characters were treated as unordered. Levels of branch support were investigated using the bootstrap and jackknife character resampling techniques, and computation of Bremer support indices (Bremer, 1988, 1994).

The use of resampling methods (particularly the bootstrap) has been questioned as a means of assessing confidence limits on phylogenies (Carpenter, 1992, 1996; Kluge & Wolf, 1993). This is principally because these tests rely on the assumption that the characters are "independently and identically distributed" (Felsenstein, 1985: 785) and that they have been randomly sampled—two assumptions violated by most phylogenetic data. Morphological data sets are particularly susceptible to these problems as they are often replete with examples of redundant (inapplicable) and correlated characters, although molecular data sets are not immune from this (e.g. ribosomal RNA genes which code for a secondary structure). However, as an estimate of the robustness of a data set, these resampling techniques can be useful as a means of discovering ambiguity between characters.

Bootstrap and jackknife analyses of equally weighted data were performed with 1000 replicates using TBR branch swapping. Jackknifing was performed using 33% character deletion per replicate. Bremer support values were calculated with the assistance of the program AutoDecay (Eriksson, 1997) using PAUP* (TBR branch swapping, 100 random addition sequences per calculation).

RESULTS

MORPHOLOGY

Careful reference to the characters described in Appendix 2 and the data matrix in Appendix 3 provides a detailed account of ischnoceran morphology. However, during this study, several new structures came to light that warrant further discussion, whilst some characters of taxonomic interest could not be considered phylogenetically, because their distribution is largely unknown. The following discussion considers these characters in the context of a review of ischnoceran morphology. This is intended to clarify morphological terms used in this study, and draw attention to previous accounts of ischnoceran morphology, many of which are published in journals with a limited circulation and/or various languages.

Head (Characters 1–68; Figs 2–6)

There have been relatively few comparative accounts of the morphology of the ischnoceran head. Early studies were chiefly interested in structures of the mouthparts (Kellogg, 1896; Snodgrass, 1905; Cummings, 1913, 1916). More extensive discussions of head morphology were presented by Cope (1940), Risler (1951) and Haub (1971), although these accounts are confined to single taxa. Kéler presents a comparative description of the external morphology of the head in his monographs of the Trichodectidae and Goniodidae (1938, 1939 respectively), and a similar paper on the "Philopteridae" (*sensu* Eichler, 1963) was presented by Clay (1951a). Clay's paper is especially noteworthy as she attempted to stabilize the nomenclature used by previous authors to describe the ischnoceran head. She was also the first to describe the general patterns of variation observed within avian Ischnocera, which have been used as a basis for the development of the character complexes described here. An attempt to place the major features of the ischnoceran head in their wider context with other phthirapteran suborders was made by Symmons (1952), who took a very different approach from Clay (1951a), focusing on internal structures, notably tentorial form and muscle attachment. Lyal (1985b) also used a number of internal features of the head in his paper on the phylogeny and classification of the Psocodea. Most recently, Mey (1994) has reviewed the external characters of the head, and examined the ontogenetic development of a number of the main head character complexes. Smith

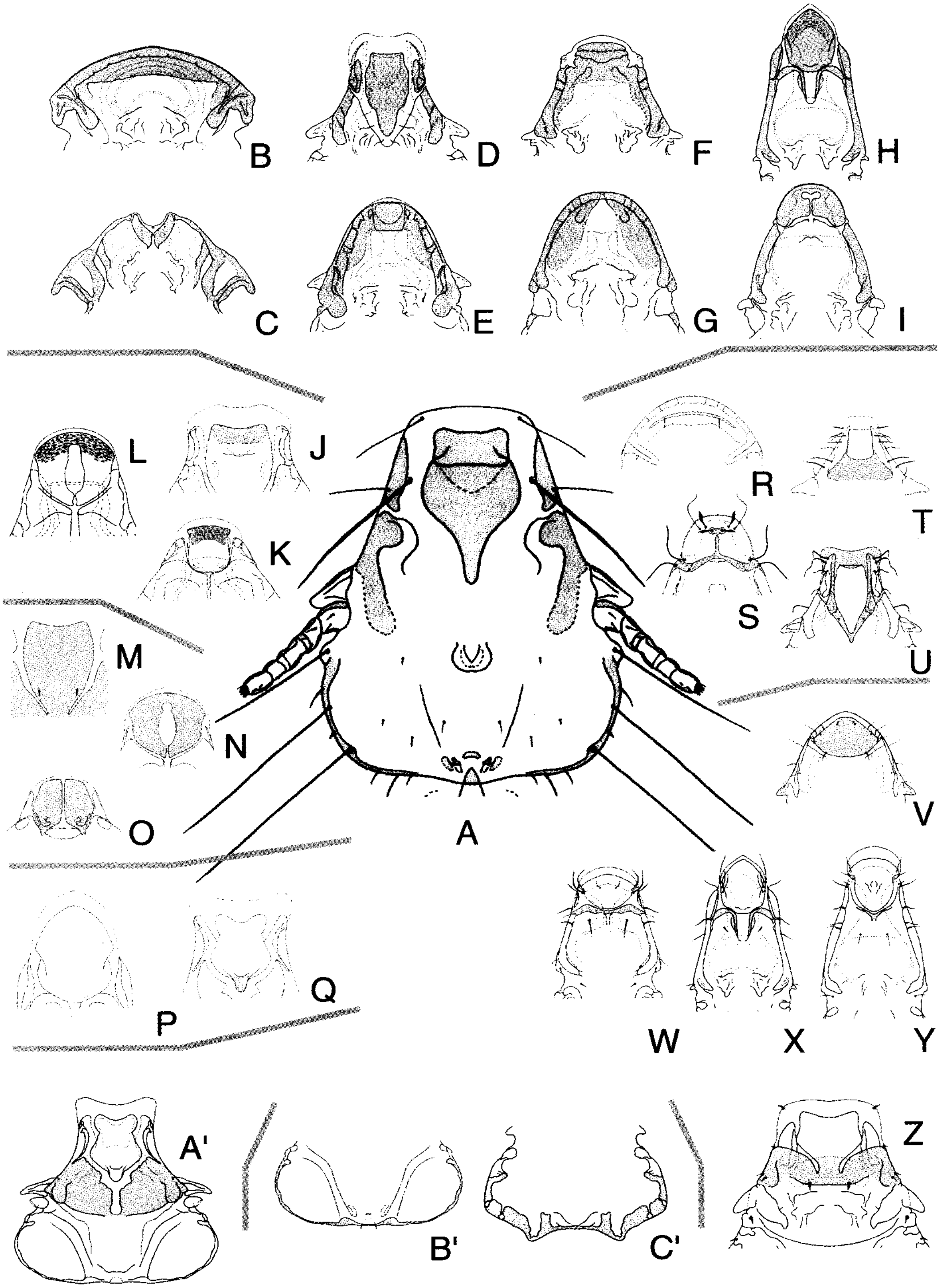

Figure 2. Selected dorsal head character states. Highlighted sections correspond to the principal character states illustrated (see Appendix 2). A, ♂ *Strigiphilus vapidus*. B–I, preantennal region from (B) ♂ *Goniodes pavonis*, (C) ♂ *Geomydoecus* (*Geomydoecus*) *heaneyi*, (D) ♂ *Craspedorrhynchus platystomus*, (E) ♂ *Rallicola lugens*, (F) ♂ *Anaticola crassicornis*, (G) ♀ *Neopsittaconirmus borgiolii*, (H) ♂ *Halipeurus pelagicus* and (I) ♂ *Columbicola columbae*. J–L, ♂ anterior portion of the ante-clypeus from (J) *Philopterus ornatus*, (K) *Pectinopygus bassani* and (L) *Ardeicola smithersi*. M–O, dorsal anterior plate morphology from (M) ♂ *Philopterus ornatus*, (N) ♂ *Ardeicola smithersi* and (O) ♂ *Ibidoecus plataleae*. P, Q, posterior margin of the dorsal anterior plate for (P) ♂ *Halipeurus pelagicus* and (Q) ♂ *Saemundssonia*

(2000b) has also examined the ontogeny and rates of heterochrony for ischnoceran head shape.

The generalized ischnoceran head is dorso-ventrally flattened and more or less prognathous, with reduced mouthparts, short antennae, absent or small compound eyes, no ocelli and a reduced tentorium (Lyal, 1983). It is strongly sclerotized from the first instar, and is characterized by a series of dark thickened bands (carinae), sutures (sulci *sensu* Symmons, 1952) and plates that affect the plasticity of the head capsule. These conspicuous features are functional adaptations to resist or accommodate the various strains on the head, and form the basis for early classifications of the Ischnocera. They comprise the bulk of the pre- and postantennal characters described here.

Preantennal. Symmons (1952) divided the ischnoceran head into three types on the basis of their preantennal morphology. These are characterized by the shape of the clypeus which is complete in the 'goniodid' (circumfasciate) head, forming an uninterrupted semicircle around the anterior margin (Figs 2B, 3B, C); medially reduced in the 'trichodectid' head, so that the ventral portion of the clypeus is more or less divided by the pulvinus (Figs 2C, 3I, K); or completely interrupted in 'philopterid' (non-circumfasciate) forms by a median anterior plate (Figs 2D, E, 3E, F). These descriptions form a useful crude division of the major ischnoceran groups. However, as noted by Lyal (1983), their distribution amongst ischnoceran taxa is not entirely reflected by the names ascribed by Symmons. Nevertheless, the character complexes that form these groups can be subdivided into many homologous traits. Some of these characters were initially described by Clay (1951a), and have been considerably revised and expanded upon in this study.

The anterior rim of the head is usually surrounded by a hyaline margin. This may be greatly reduced (Figs 2B, 3B), in which case it is usually only evident as a thin band medially, or in non-circumfasciate forms is normally expanded (Figs 2D, F, H, 3D, G). The hyaline margin is supported by the marginal carina, which forms the outermost carina running around the margin of the head and terminating each side to form the preantennal nodi. This band may be interrupted laterally (Fig. 2I) and/or medially to varying degrees (Fig. 2D–H). Lateral interruption may be partial or complete, allowing the marginal carina to be divided into its pre- (anterior) and post- (posterior) marginal regions (Fig. 2D, F, H, I), while in cases where a complete medial interruption of the marginal carina occurs, a medial anterior plate (clypeal signature) may be present (Fig. 2D, E, H). This plate is a defining character of many ischnoceran taxa, and may be confined anteriorly between the premarginal carina (Fig. 2L, K), or greatly expanded, filling the medial preantennal region (Fig. 2D). The plate is predominantly a dorsal structure, although a smaller ventral component may be present (Figs 2D, 3E, F, J). In many cases this ventral plate forms a narrow rim beneath the anterior margin of the dorsal anterior plate, having the appearance of an isolated portion of the marginal carina (Clay, 1951a). However, in several taxa the ventral plate is much more substantial, although it usually remains fused anteriorly to the dorsal anterior plate. The dorsal preantennal suture defines the posterior margin of the dorsal plate. This is usually continuous across the head (Fig. 2S), except in those forms where the dorsal anterior plate is fused proximally to the dorsal head sclerotization (Fig. 2M). In many cases this suture arises at the lateral interruption of the marginal carina, and may be continuous with the hyaline margin laterally, around both the inner and outer margin of the premarginal carina (Fig. 2U). In circumfasciate forms the dorsal preantennal suture sits within a weakly sclerotized dorsal carina (*sensu* Mey, 1994) and is isolated from the marginal carina (Fig. 2R). The dorsal carina is more strongly sclerotized in non-circumfasciate forms where it is often only evident postmarginally, posterior to the dorsal preantennal suture. In these cases, the dorsal carina may form a definitive carina (Fig. 2W–Y), or is defined as the margin marking the beginning of the dorsal postmarginal sclerotization of the head (Fig. 2Z).

The principal ventral preantennal characters are the ventral carina and the pulvinus (Fig. 3B–G). The latter is homologous with the clypeo-labral suture (Symmons, 1952), and forms a thick unsclerotized pad that serves to support the feather or hair shaft during attachment or feeding (Fig. 3H, I, L). The morphology of the pulvinus is related to the form of the ventral carina. This is a band of sclerotization that extends from the mandibular framework to support the pulvinus laterally. Further support may be provided by a

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desolata. R–U, dorsal preantennal suture morphology from (R) ♀ *Chelopistes guttatus*, (S) ♂ *Columbicola columbae*, (T) ♂ *Vernoniella guimaraesi* and (U) ♂ *Craspedorrhynchus platystomus*. V–Z, dorsal carina morphology from (V) ♂ *Upupicola upupae*, (W) *Pseudonirmus gurlti*, (X) ♂ *Halipeurus pelagicus*, (Y) ♂ *Philoceanus garrodiae* and (Z) ♂ *Craspedonirmus colymbinus*. A′ transverse carina of ♂ *Saemundssonia desolata*. B′, C′, temporal carina of (B′) ♂ *Saemundssonia desolata* and (C′) ♂ *Goniocotes gallinae*.

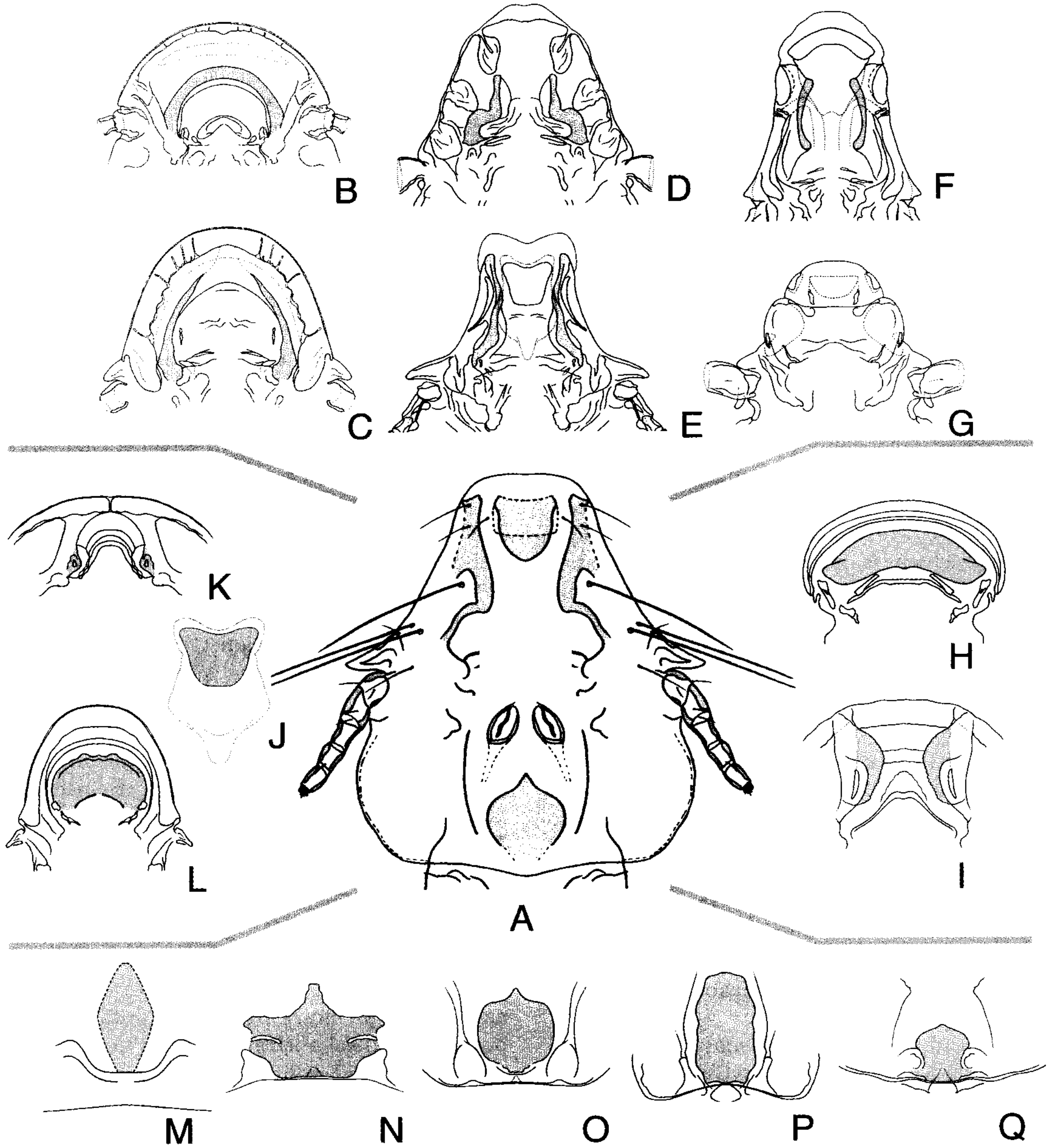

Figure 3. Selected ventral head character states. Highlighted sections correspond to the principal character states illustrated (see Appendix 2). A, ♂ *Strigiphilus vapidus*. B–G, ventral carina morphology from (B) ♂ *Campanulotes bidentatus*, (C) ♂ *Degeeriella rufa*, (D) ♂ *Falcolipeurus affulgeus*, (E) ♂ *Saemundssonia desolata*, (F) ♂ *Naubates fuliginosus* and (G) ♂ *Trabeculus schillingi*. H, I, pulvinus morphology from (H) ♂ *Goniodes pavonis* and (I) *Felicola* (*Felicola*) *viverriculae*. J, ventral anterior plate of ♂ *Saemundssonia desolata*. K, marginal pulvinal bars of ♂ *Bovicola limbatus*. L, pulvinal region of ♂ *Lipeurus caponis*. M–Q, gular plate morphology from (M) ♂ *Cuclotogaster madagascariensis*, (N) ♂ *Splendoroffula ruwenzorornis*, (O) ♂ *Pseudonirmus gurlti*, (P) ♂ *Halipeurus pelagicus* and (Q) ♂ *Saemundssonia desolata*.

pair of marginal pulvinal bars present on the posterolateral angles of the pulvinus (Fig. 3H). In many circumfasciate taxa the pulvinus forms a simple lobe that is held around its margin by a complete ventral carina (Fig. 3H). Alternatively the ventral carina may be interrupted medially and variably extends anteriorly, often forming a flattened extension that may fuse with the marginal carina. In these cases, the

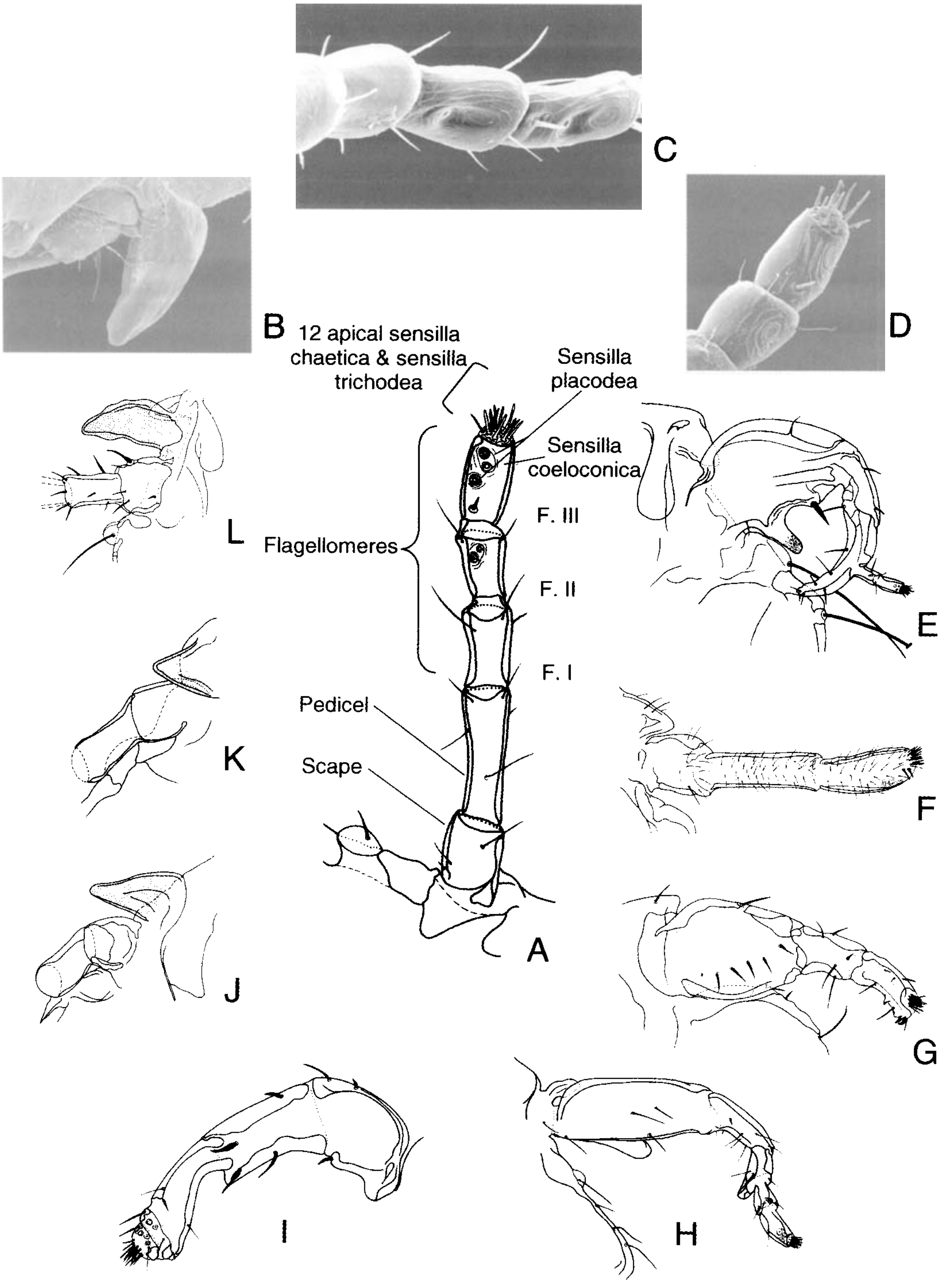

Figure 4. Selected antennal character states. Highlighted sections correspond to the principal character states illustrated (see Appendix 2). A, antennal morphology of ♀ *Ardeicola smithersi*. B–D, scanning electron micrographs illustrating (B) the trabecula of *Philopterus* sp., and antennal sensilla on flagellomeres II and III of (C) *Struthiolipeurus* sp., and (D) *Docophoroides* sp. E–I, antennal morphology of (E) ♂ *Goniodes pavonis*, (F) ♂ *Bovicola limbatus*, (G) ♂ *Trichodectes* (*Trichodectes*) *melis*, (H) ♂ *Lipeurus caponis* and (I) ♂ *Coloceras damicorne*. J, K, ♀ conus morphology for (J) *Strigiphilus vapidus* and (K) *Brueelia semiannulata*. L, trabecula and conus of ♀ *Philopterus ornatus*.

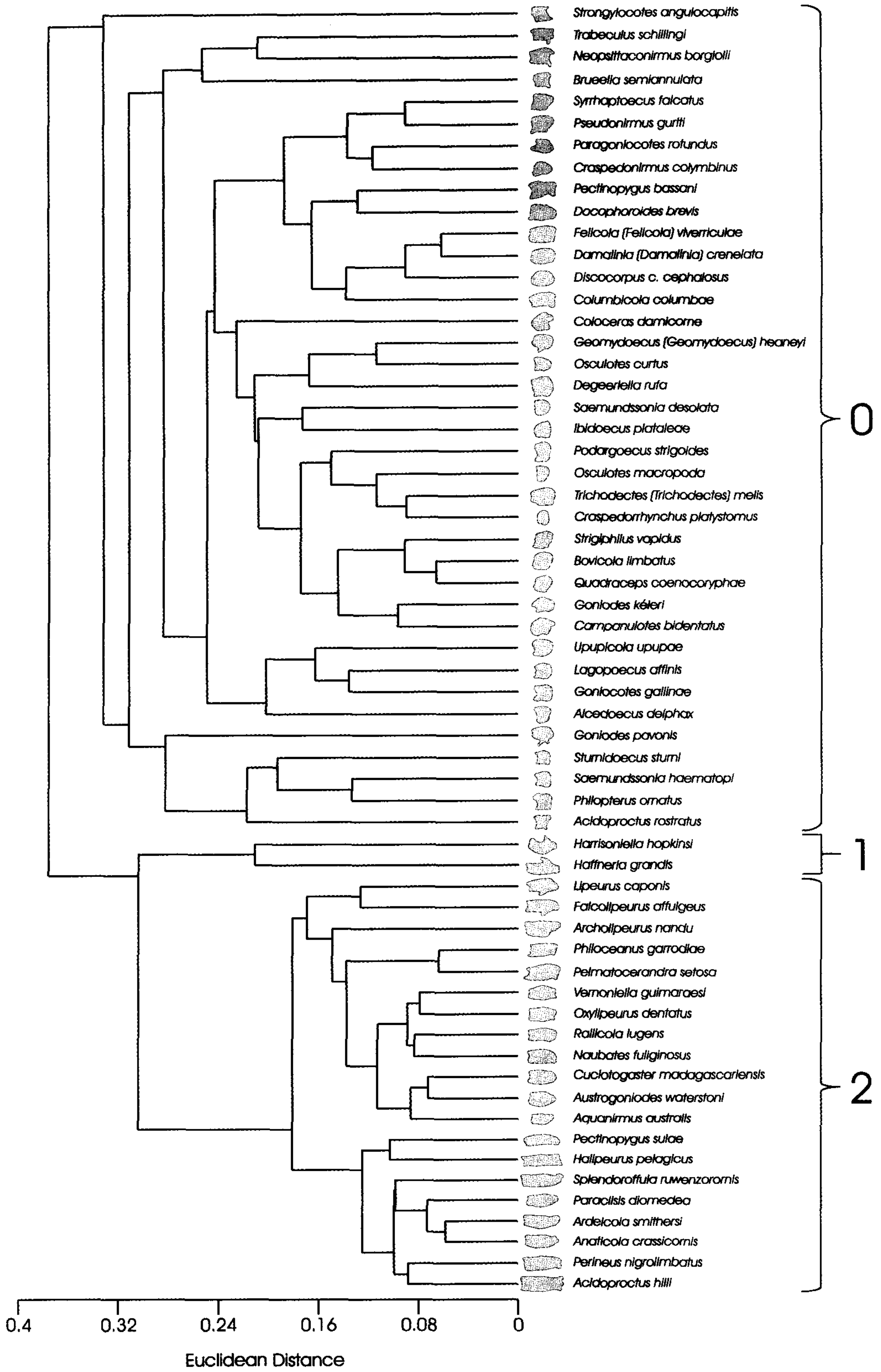

Figure 5. UPGMA dendrogram based on Euclidean distances between the elliptic Fourier coefficients of the male antennal scape oulines (character 46). Three states are recognized and the scape shapes are illustrated.

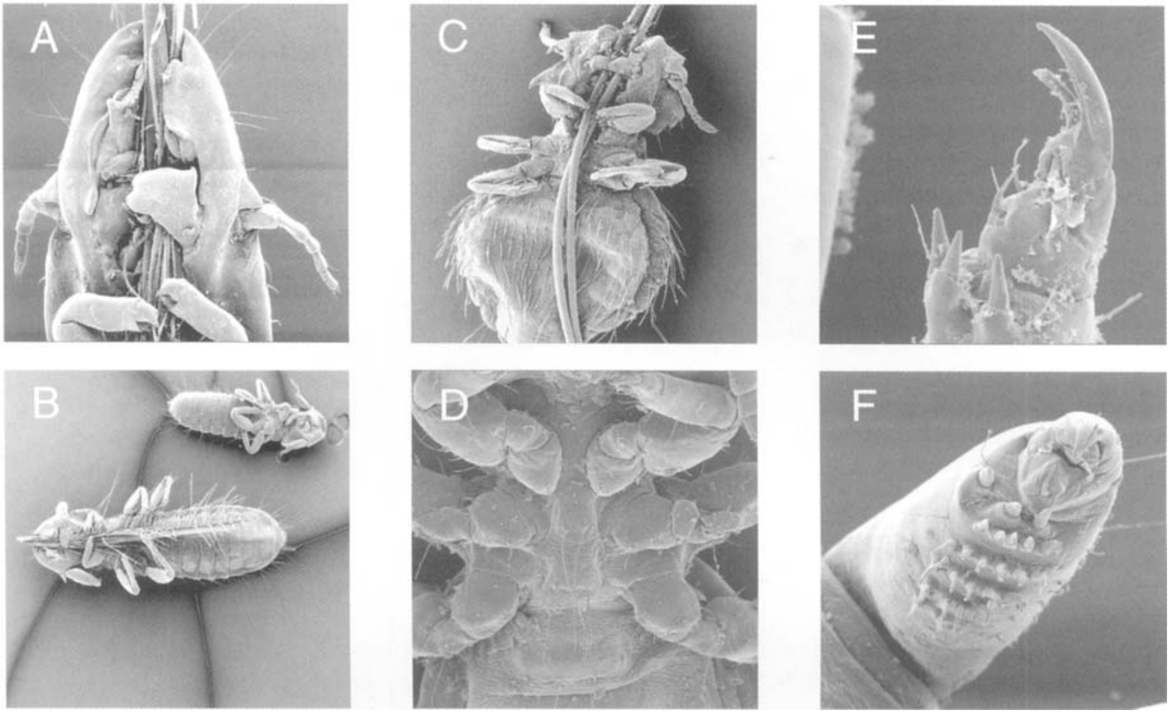

Figure 6. Scanning electron micrographs illustrating various ischnoceran lice. A, close-up on the head of a ♀ *Struthiolipeurus* sp. attached to a feather barb. B, ♂ *Struthiolipeurus* sp. (top) and ♂ *Archolipeurus* sp. (bottom) attached to a feather barb. C, *trichophilopterus babakotophilus* attached to a hair shaft. D, coxal articulations of the first, second and third pairs of legs for *Brueelia* sp. E, the proximal end of the tibia, tarsus, pretarsus and pretarsal claws of *Brueelia* sp. The three thorn-like setae on the broadened apex of the tibia are typical of many avian Ischnocera. F, the tibia, tarsus, pretarsus and pretarsal claws of *Docophoroides* sp. The rows of setae along the inner margin of the tibia are an autapomorphy of this genus.

pulvinus is usually separated into two lateral lobes that are divided by a median groove which helps to channel the feather or hair shaft into the mouth (Kéler, 1938) (Fig. 3I). In many taxa this is also accommodated by a medial break in the anterior margin of the head called an osculum (Fig. 2C). Reed & Hafner (1997) have presented data for gopher lice (*Geomydoecus* Ewing and *Thomomydoecus* Price & Emerson) which suggests that the width of the osculum is correlated with the diameter of the hair shaft on their host. In addition, they suggest that taxon and gender specific differences in the width and depth of the osculum, resulting in differential abilities of the lice to grasp the hair shaft may provide a mechanism for resource partitioning between lice on the same host.

The anterior margin of the labrum is readily identified in most Ischnocera by a small strip of chitin in the preoral cavity (Fig. 3C, L & H). In slide mounted specimens this strip may be partially obscured by the anterior tips of each mandible and is usually divided medially. Symmons (1952) notes that in *Philopterus* Nitzsch, and possibly all Ischnocera, the labrum may be expanded by fluid in its lumen over the pulvinus. A pair of small sclerites (tormae) is usually present in the lateral angles of the labrum (not to be confused with the marginal pulvinal bars) (Fig. 3H). These are normally partially or completely obscured by the mandibles, and are attached to muscles that help retract the labrum from over the pulvinus (Symmons, 1952).

The lateral margin of both sides of the head, immediately anterior to the antennal socket may be developed forming a conus (Fig. 4K, J). This structure was originally defined by Kéler (1938) to distinguish it from a related structure arising predominately from the antennal socket called the trabecula (Fig. 4B, L). Confusion between these structures leading to errors in taxonomic descriptions led Clay (1946) to redefine the terms. However, scanning electron micrographs suggest that Clay's definitions are not entirely correct. Both the conus and trabecula exhibit variable degrees of development and sclerotization. Clay (1946) followed Kéler (1938) in describing the posterior margin of the trabecula as continuous with the anterior margin of the first antennal segment (the scape), in contrast to the conus which forms or is continuous with the anterior margin of the antennal socket. Based on this description the structure shown in Figure 4B from *Philopterus* sp. (ex. *Pitta sordida* (Müller)) would be described as a conus, as it appears to arise from the margin of the head, anterior to the antennal socket. Yet most authorities would regard all *Philopterus sensu lato* to possess a trabecula, and Clay later remarked that members of the genus *Philopterus* from the avian family Pittidae do not possess a conus (Clay, 1951b: 193). Based on this finding the trabecula is best redefined as a lobe shaped structure arising predominantly from the anterior margin of the antennal socket and may be continuous with the anterior margin of the head. In contrast the conus is approximately cone shaped and arises anteriorly at the antero-lateral angles of the head. Unlike the trabecula, it is present in the majority of ischnoceran taxa and is usually smaller, although in some taxa may be elongated, extending beyond the distal margin of the scape.

Antennal. The antennae of most Ischnocera consist of five annuli comprised of a scape, pedicel, and three terminal flagellomeres (Fig. 4A). This condition occurs in all avian Ischnocera and the genus *Trichophilopterus* Stobbe. In contrast the flagellomeres of all male and some female Trichodectidae (subfamilies Neotrichodectinae, Trichodectinae, Bovicolinae and most Eutrichophilinae) are fused into a single flagellum (Lyal, 1983) (Fig. 4F, G). The base of the antennae is set into a small membranous area of the head that may be produced forming a distinct antennal socket. This provides additional support for the antennae. Sexual dimorphism is common, taking the form of an increase in the length and degree of sclerotization of the scape and flagellar segments in males (Fig. 4E, H, I). This permits the male to clasp the female around the abdomen or thorax during copulation. Female antennal annuli are always monomorphic (i.e. approximately the same size and shape) whilst the annuli in approximately one half of all male ischnoceran genera are to some degree heteromorphic (Mey, 1994). This usually takes the form of an enlarged scape that may be greatly elongated or inflated along its width (Fig. 4E, H). Further modification may occur to the first flagellomere, which may be distinctly curved (Fig. 4E) or expanded, and in some cases the terminal two flagellomeres may apically compressed (Fig. 4I).

The prime function of the antennae is sensory. A brief preliminary review of ischnoceran antennal sensilla was made by Clay (1970) who suggested their position and frequency may be phylogenetically informative. Slifer (1976) described in greater detail the antennal sensilla for avian Ischnocera; however, her findings are at odds with those of Clay (1970) and this study. The situation was further confused by Baker & Chandrapatya (1992) who incorrectly summarized the findings of both their own work on the antennal sensilla of Rhyncophthirina, and Slifer's work.

SEM examinations of the antennae from a diverse selection of avian Ischnocera suggest that the morphology and number of sensilla are remarkably uniform. However, the patterns of cuticular ridges surrounding these sensilla and the position of these sensilla relative to each other do exhibit some variation. The scape, pedicel and first flagellomere normally bear several tactile sensilla. These take the form of thin, often whip-like sensilla trichodea that are primarily confined to the distal margin of each segment, and thickened spine-like sensilla chaetica which are less common and are usually positioned away from the segment's margin (Fig. 4C). In many Ischnocera the positions of these simple sensilla are roughly aligned along the length of the antenna on each segment. The second flagellomere always bears a single plate and pit sensilla (sensilla placodea and sensilla coeloconica) distally, which are usually positioned at a slight angle to each other, either ventrally or on the posterolateral surface of the antenna when it is lying in its normal position. These sensilla types are generally regarded as chemosensory (Snodgrass, 1935), and in Ischnocera are usually surrounded by well-developed cuticular ridges that are very pronounced in some taxa (Fig. 4D). Close inspection of the plate sensilla reveals a number of concentric striations emanating from a central plateau to the outer most cuticular ridge of the plate. The number of striations varies considerably between taxa. A small peg is present in the figures of the pit sensilla shown by Clay (1970: figs 15–17). However, these were not observed in any of the pit sensilla of the taxa examined.

The third flagellomere is equipped with the greatest number of sensilla. Two plate and one pit sensilla are present on the ventral to posterolateral surface of the segment. These are usually accompanied by a thick spine-like sensilla that often projects over the more delicate plate and pit sensilla, and may provide some protection. The relative positions of the plate and pit sensilla show some variation. Within most goniodids the sensilla are usually aligned across the width of the flagellum with the pit sensillum situated between the two plate sensilla. In contrast, the pit sensilla of most philopterids (*sensu* Eichler, 1963) are usually clearly associated with one of the plate sensilla and are usually aligned more or less along the length of the flagellum. The greatest concentration of tactile sensilla occurs on the tip of the third flagellomere (Fig. 4D). Their number and type are often difficult to determine. However, there are usually 10 or 11 sensilla trichodea and sensilla chaetica, of variable length and thickness. In addition, a single thin whip-like sensillum is also usually present.

Postantennal. Asymmetrical toothed mandibles are present in all Ischnocera. These usually possess a blunt anterior and larger posterior projection on their outer margins that articulates vertically with the sub and post-genal areas. This restricts the mandibles to movement in a more or less horizontal plane, in contrast to the Amblycera, which possess horizontal articulation of the mandibles, restricting movement to a vertical plane. Variable apical teeth may be present accompanied by ridges on the interior face of the right or both mandibles, so that when the mandibles are folded closed the ridges of one mandible are not covered by the other. When closed the right mandible is always interior to the left and therefore it is always the right mandible that is in contact with the feather or hair shaft (Lyal, 1983) (Fig. 6A). The left mandible sometimes accommodates the right by a small notch on its outer face. Mandibles are involved in mastication of food and, in Ischnocera, play a key role in attaching the louse to the host's feathers or pelage (Fig. 6B & C).

The maxillae and labium are greatly reduced in Ischnocera. Each consists of largely hyaline structures which are usually partially obscured in slide mounted material by the more strongly sclerotized lingual sclerites. In large taxa the lateral walls of the maxillae can be weakly sclerotized and usually terminate in a slightly bulbous enlargement that is membranous, projecting into the cavity posterior to the mandibles. The labium sits slightly posteriorly to the maxillae on the ventral surface of the louse, and is readily identified by two apical labial palps that usually bear minute hyaline setae. Between these sit paired paraglossae and a fused median glossa (Matsuda, 1965).

Structures associated with the water vapour uptake system are present in the hypopharynx. This is the postoral area on the ventral surface of the head, immediately anterior and dorsal to the labium, and is highly modified in all Psocodea (Lyal, 1983, 1985b). A pair of oval, slightly convex lingual sclerites is present on the ventral surface of the hypopharynx in almost all Ischnocera (Fig. 3A). Rudolph (1983) has shown that above a critical humidity threshold, retractor muscles expose the surface of the lingual sclerites and a thin film of iridescent liquid can be observed over them. Water vapour is condensed on their surface and is collected in a gradually flattening median groove, where it is drawn up a sclerotized tubular filament to the dorsal surface of the sitophore sclerite (Fig. 2A). This is an active process brought about by rapid contractions of the clypeo-epipharyngeal muscle that connects the clypeus to the epipharyngeal crest (Rudolph, 1983). At rest the epipharyngeal crest is evident as a small pestle shaped peg that sits within the lumen of the sitophore. However, during water uptake, the crest is drawn in and out of the sitophore lumen. Rudolph (1983) showed that the frequency of contractions of the clypeo-epipharyngeal muscle is correlated with the ambient relative humidity. This system of water uptake is very similar to that for Psocoptera where water is drawn up through the sitophore pump and is passed into the alimentary canal (Rudolph, 1982).

The margin of the postantennal region is enclosed by the marginal temporal carina (Fig. 2B′, C′). This may be variably thickened, particularly around the eye and occipital margin forming ocular and occipital nodi. Two pretemporal and five marginal temporal setae are present in almost all Ischnocera. The homology and various patterns exhibited by these setae are described by Smith (2000a) and Mey (1994) and will not be considered further. Temporal (dorsal) and occipital (ventral) carinae may be evident across the temporal margins of the head. The former, when present, runs from the occipital margin of the head, fusing with either the temple margin or the preantennal nodus. In contrast, the latter runs backward from the mandibular framework and may fuse with the occipital margin. In both cases these carinae may be well developed, but are often only weakly identifiable as a thin margin separating the sclerotized from the unsclerotized region of the frons (dorsal) or post genal area (ventral). Their degree of sclerotization may also be subject to artefacts depending upon the extent of clearing during the slide mounting process. A curved postantennal suture may be present between the preantennal nodi, the anterior margin of which may be marked by a thickened transverse carina (e.g. *Saemundssonia*), separating the pre- and postantennal sclerotization of the head.

Thorax (Characters 69–94; Figs 7–9)

Establishing homology amongst the various sclerites of the phthirapteran thorax is problematic, second only to the external genitalia in terms of difficulty. This is in part due to the considerable variation exhibited by many Phthiraptera, particularly within the Ischnocera. Much of this thoracic variation is linked to changes in the coxal articulations of the second and third pairs of legs, which are completely sternocoxal in many typical 'body-louse' forms, and completely pleurocoxal in most 'wing-lice', although intermediates between these extremes exist. Nevertheless, many of these characters are phylogenetically well conserved, and consequently most thoracic characters are particularly useful at resolving deep branch relationships of the major ischnoceran clades, once the problems of homology have been resolved. This also applies to the setal patterns on the pro- and pterothorax, which show considerably less intergeneric variation than the chaetotaxy of the abdomen, and are well represented amongst the character states described here.

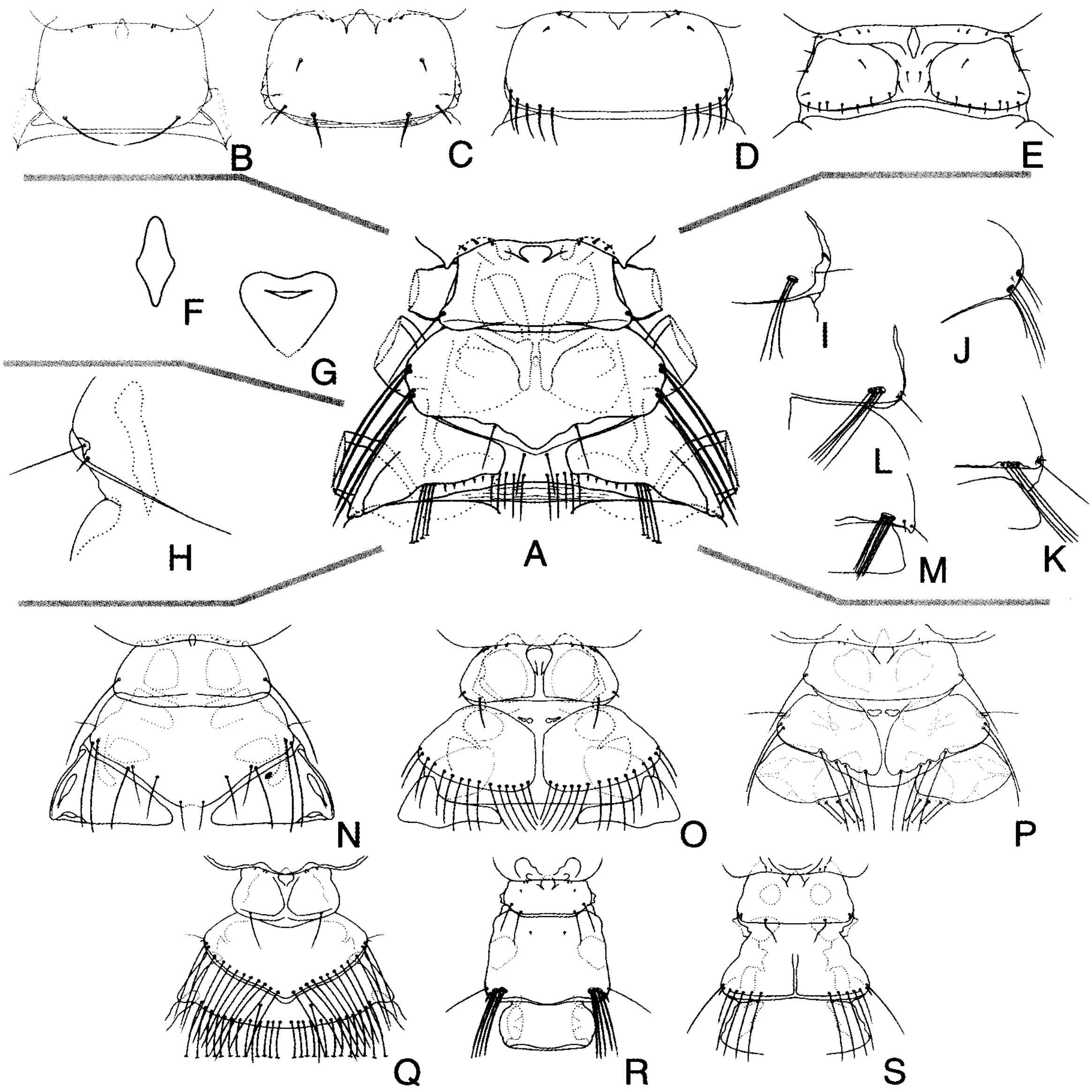

Figure 7. Selected dorsal thoracic character states. A, ♂ *Goniodes pavonis*. B–E, ♀ prothoracic setae from (B) *Anaticola crassicornis*, (C) *Philoceanus garrodiae*, (D) *Docophoroides brevis* and (E) *Bovicola limbatus*. F, G, rhombic sclerite morphology from (F) ♂ *Bovicola limbatus* and (G) ♂ *Goniodes pavonis*. H, Pterothoracic trichoid and thorn-like setae of ♀ *Rallicola lugens*. I–M, ♀ clustered pterothoracic setal arrangements from (I) *Archolipeurus nandu*, (J) *Acidoproctus rostratus*, (K) *Neopsittaconirmus borgiolii*, (L) *Pectinopygus bassani* and (M) *Harrisoniella hopkinsi*. N–S, ♀ pterothoracic setal arrangements from (N) *Campanulotes bidentatus*, (O) *Ibidoecus plataleae*, (P) *Craspedorrhynchus platystomus*, (Q) *Philopterus ornatus*, (R) *Pseudonirmus gurlti* and (S) *Aquanirmus australis*.

The morphology of the ischnoceran thorax has been considered by Cope (1940), Mayer (1954) and Mey (1994) for select taxa, and reviewed by Matsuda (1970) and Lyal (1983). A multiplicity of synonyms has been used to describe the major features of the ischnoceran thorax, and terminological inconsistencies between several authors considerably hamper the establishment of homologies between structures. The terminology used here largely follows Cope (1940) and Lyal (1983), although setal descriptions follow the conventions described by Smith (2000a). Arrangements of clustered setae are explicitly referred

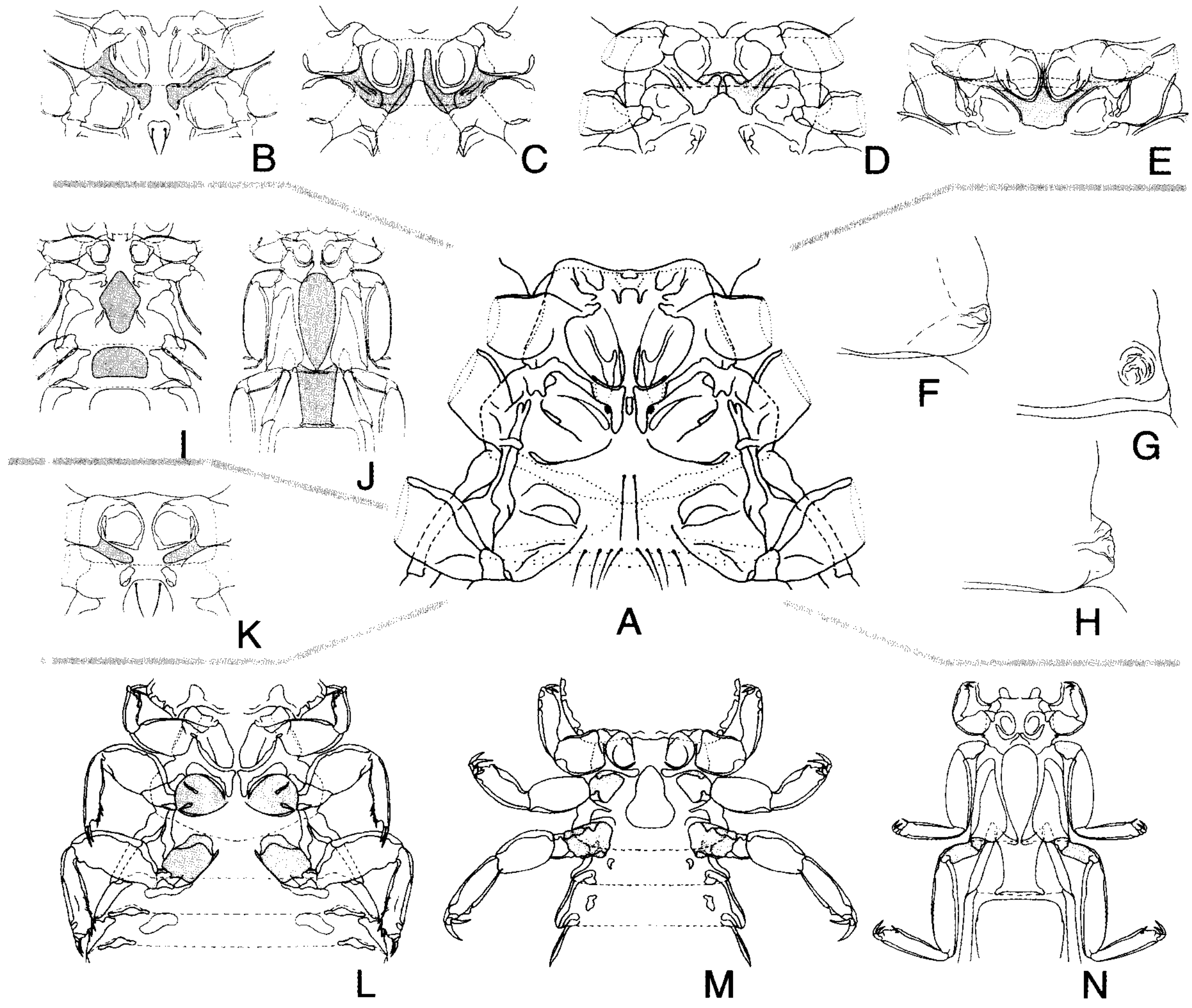

Figure 8. Selected ventral thoracic characters. Highlighted sections correspond to the principal character states illustrated (see Appendix 2). A, ♂ *Goniodes pavonis*. B–E, proepimeron morphology from (B) ♀ *Saemundssonia haematopi*, (C) ♂ *Pseudonirmus gurlti*, (D) ♂ *Trichodectes melis* and (E) ♀ *Discocorpus c. cephalosus*. F–H, prothoracic spiracle morphology from (F) ♂ *Saemundssonia desolata*, (G) ♀ *Damalinia (Damalinia) crenelata* and (H) ♂ *Perineus nigrolimbatus*. I, J, meso-metasternal and second sternal plate from (I) ♂ *Lipeurus caponis* and (J) ♀ *Halipeurus pelagicus*. K, proepimeron proximal development of ♂ *Oxylipeurus dentatus*. L–N, coxal articulation of the legs from (L) ♂ *Goniodes pavonis*, (M) ♂ *Lagopoecus affinis* and (N) ♀ *Halipeurus pelagicus*.

to by the number of setae in each cluster, each side of the midline. For example, the description 3,3 + 3,3 refers to two pairs (clusters) of three setae on both sides of the body.

Prothorax. The morphology of the anterior margin of the prothorax is obscure, largely concealed by the overlapping region of the posterior margin of the head. Within this area a pair of lateral cervical sclerites marks out the cervix (neck) in most Ischnocera. These are often poorly delimited in slide mounted specimens and histological examination of this area is needed in a range of ischnoceran taxa to establish their true morphology. Often the cervical sclerites can be identified by a pair of minute, ventral microsetae on their anterior margin, although these setae are not always present. These setae are not to be confused with the three (or rarely two) pairs of minute microsetae, usually present on the dorsal anterior margin of the prothorax (Fig. 7A–E). These are often partially obscured by the encroaching margin of the head, and may be only readily apparent by the presence of their setal apertures when viewed in phase contrast. In

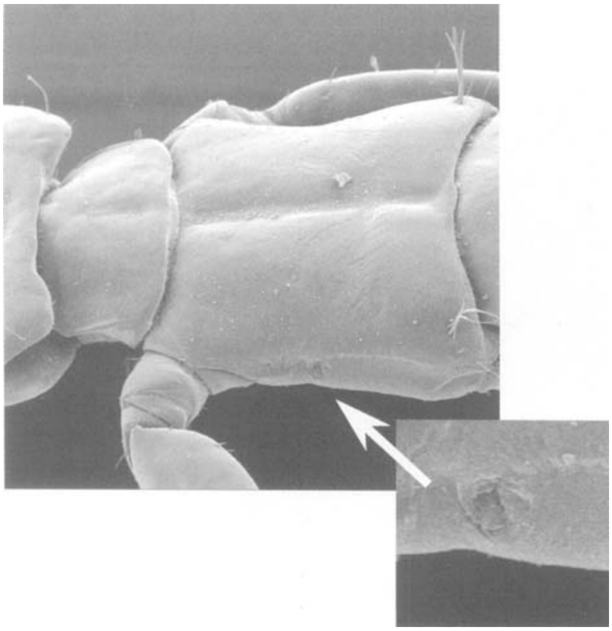

Figure 9. Thorax of *Paraclisis diomedeae* (ex. *Diomedea melanophris*), highlighting the position of the metathoracic spiracle (enlarged).

cases where just two pairs are present (as with most members of the *Philoceanus*-complex), a third pair may occur in an intermediate position on the upper third of the prothorax (Fig. 7C). These are interpreted to be displaced from the anterior margin of the prothorax, although the exact homology of these setae remains unclear.

Between these anterior setae sits a small medial sclerite, termed the 'rhombic sclerite' by Lyal (1985a) because of its characteristic shape in the Trichodectidae (Fig. 7E & F). This is present in almost all Ischnocera although it is often only weakly delimited anteriorly, and is usually fused to the anterior margin of the pronotum. The morphology of this sclerite is somewhat variable, and is usually largest in the *Philopterus*-, *Saemundssonia*- and *Philoceanus*-complexes, although again it may be poorly delimited. Either side or beneath the lateral margins of the rhombic sclerite, a pair of occipital apophyses is sometimes visible, extending from the occipital region of the head into the prothorax (Fig. 8A).

As in many insects, the mesothoracic spiracles have migrated forward (Snodgrass, 1935) and lie either pleurally or ventrally close to the posterior margin of the prothorax on the proximal expansion of the proepimeron (Fig. 8F–H). In several taxa, most notably all members of the *Philoceanus*-complex and their putative close relatives, these spiracles are slightly extended outward on a pleural expansion of the proepimeron (Fig. 8H). The mesothoracic spiracle apertures are usually slit-like and larger than the abdominal spiracle apertures. In the Trichodectidae these spiracles are very well developed, and cuticular ridges inside the aperture of the spiracle are evident (Fig. 8G). These presumably prevent dust and debris from entering the respiratory system of the louse.

The prothoracic legs are short and stout, usually lying with their distal ends carried up under the head. Their articulation with the prothorax is sternocoxal in all Ischnocera (Fig. 8L–N), unlike the articulation of the second and third pairs of legs that show considerable variation among taxa. The coxa, trochanter, femur and tibia of the prothoracic legs exhibit only small variations within Ischnocera and are of little taxonomic value in resolving relationships between genera.

Setal number, type and position on the dorsal posterior margin of the prothorax are amongst the most phylogenetically well-conserved setae in the Ischnocera. Usually a 1+1 (Fig. 7B) or 2+2 (Fig. 7C) arrangement is present. In the latter, the anterior members of each pair are usually closely associated with the mesothoracic spiracle. Mey (1994) has described the ontogenetic variation amongst these setae for several taxa. Generally their number and size is fully developed from the first instar, although some variation does occur. In contrast, the pterothoracic setae show considerably more variation during their development.

Pterothorax. The dorsum of the meso- and metathorax are formed from a fused notal plate in all Ischnocera, although a medial division may be present in some taxa separating the dorsal surface of the pterothorax in half. Fusion between the pterothoracic segments is carried out to such a degree that it is almost impossible to identify a line of segmental division. Some degree of separation may be evident ventrally. Nevertheless, the division of the meso- and metathoracic elements remains ambiguous.

Ventrally the proepimeron of the prothorax is developed proximally and extends under the anterior margin of the pterothorax (Fig. 8A–E). This forms part of the coxal articulation between the first and second pairs of legs and is often greatly expanded medially. This medial expansion may become fused forming a single medial plate as in many Heptapsogasteridae (Fig. 8E). However, these lateral projections usually remain separate, projecting anteriorly under the prothorax such as in the *Philoceanus*-complex (Fig. 8C), or posteriorly under the pterothorax as in the Goniodidae (Fig. 8A). The pro- and mesofurcal pits are closely associated with these projections. These mark the ventral termination of the first and second sternal apophyses and are usually associated with a lightly sclerotized patch of cuticle in the pro- and meso- metasternal region respectively.

The second and third pairs of legs show considerably more variation than the first, but their basic structure remains constant. Typical 'body-lice' usually possess short stout legs similar to the first pair. These articulate with the ventral surface of the pterothorax sternally on the coxa (sternocoxal) (Figs 6D, 8L). In contrast, the legs of lice with more slender body forms, especially the typical 'wing-lice', are usually longer, occasionally approaching the length of the abdomen. These legs are usually thin and articulate with the pterothorax more pleurally on the coxa (pleurocoxal) (Fig. 8N). Nevertheless, clear exceptions to this trend occur. Male *Osculotes macropoda* (Guimarães), a louse of the hoatzin (*Opisthocomus hoazin* (Müller)) possess a massively enlarged third pair of stout legs that have sternocoxal articulation with the pterothorax. These legs exceed the length of the abdomen. This exemplifies the functional importance of the legs. They are used for clasping the feather or hair shaft and their morphology is highly adapted to this task depending upon the structure they are attaching to.

Avian Ischnocera possess two pretarsal claws and lack any of the sophisticated locking mechanisms of the tarsus and pretarsus, which are present in some amblyceran taxa. This perhaps reflects the greater role of the mandibles in the attachment of Ischnocera to the host's feathers. Feather barbs present a more resistant surface on which to grip, in comparison to the relatively smooth shaft of a hair. Nevertheless, in avian Ischnocera, the broadened apex of the tibia usually bears three stout hyaline setae, and numerous thorn-like setae are present along its inner margin (Fig. 6E), increasing friction and helping to maintain attachment. Microsetae present on this inner margin may also have a sensory role (Lyal, 1983). In some avian Ischnocera (e.g. *Struthiolipeurus* Cummings and *Archolipeurus* Mey) the stout hyaline setae are modified into blunt hyaline processes of unknown function—perhaps an adaptation to the unusual feather type present on their hosts, the ostriches and rheas (Chandler, 1916). In other species the number of hyaline setae has greatly increased. *Austrogoniodes* Harrison on penguins possesses six hyaline setae whilst *Docophoroides* Giglioli (Fig. 6F) on albatrosses possesses over twenty. These may be specializations to specific feather types, or reflect an adaptation to the lifestyle of their hosts.

A fused meso- metasternal plate sits between the coxal articulations of the second and third pairs of legs in many Ischnocera (Fig. 8I, J, M), and is particularly well developed in the typical 'wing-louse' clades. Within the *Philoceanus*-complex, this plate is greatly enlarged, filling the pterothoracic sternal area, and is connected to the second abdominal sternite by a small cuticular bridge (Fig. 8J). In all other clades the plate is small and not connected to the second abdominal sternite. In these cases the plate may be poorly delimited, but can usually be readily identified with phase contrast microscopy. Separate rows of mesosternal and metasternal setae may be present in this region, and are often present on the meso- metasternal plate. The arrangement of these setae is phylogenetically well conserved but offers sufficient variation to be taxonomically useful.

The sternal region is bordered pleurally by the mesepisternum and metepisternum. The mesepisternum is greatly reduced and present in front of the articulation of the second pair of legs. This area is usually obscured by the coxa in slide mounted specimens and is only readily apparent in whole unmounted material. In contrast, the metepisternum is much larger, bordering the length of the pterothorax between the second and third pairs of legs. This region is connected on the dorsal surface to the fused meso- metanotum.

A second (anatomically the third) thoracic spiracle is present on the metepisternum of several ischnoceran taxa (Fig. 9). This is the metathoracic spiracle and is principally confined to members of the *Philoceanus*-complex. However, its full distribution within Ischnocera cannot be determined from slide mounted specimens because of its pleural position, close to the coxal articulation of the second pair of legs. Establishing the presence of this spiracle is particularly difficult in taxa where the articulations of the second and third pairs of legs are close together. In these cases the metepisternum is a small area, largely concealed by the leg segments. This spiracle was first described by Cope (1940) for *Harrisoniella densa* (Kellogg). Its presence has been overlooked by several subsequent authors, and it was not discussed by Lyal (1983, 1985a) for the Trichodectidae, or Mey (1994) for a selection of avian Ischnocera including several members of the *Philoceanus*-complex and their close relatives. Further work is needed to establish the true distribution of this character, which may prove to be taxonomically very useful.

The morphology of the dorsal surface of the pterothorax is relatively constant amongst most Ischnocera. The meso- metanotum may be divided medially (Fig. 7O, P) or is complete (Fig. 7N, Q, R). In the latter case, a notal ridge may be present medially fusing each side together (e.g. *Columbicola* Ewing). Occasionally small sclerites may be evident in the unsclerotized region between the prothorax and the anterior margin of the pterothorax (e.g. *Ibidoecus* Cummings) (Fig. 7O). Setae are principally distributed around the posterolateral and posterior margins of the pterothorax. However, a pair of small microsetae may be present medially within the anterior third of the pterothorax (Fig. 7R). These setae are usually fully developed from the first instar and are interpreted by Mey (1994) to be a relic of the mesothorax. In the case of *Falcolipeurus* Bedford and *Archolipeurus*, they are very distinct, forming well developed microsetae. However, more commonly they are greatly reduced (e.g. in members of the *Philoceanus*-complex), forming minute microsetae, which in the first instance are usually only visible by the presence of their setal apertures. A second median submarginal pair of microsetae may be present on the lower third of the pterothorax, although these are less common than the anterior pair.

Characteristic trichoid setae or their setal equivalent (*sensu* Smith, 2000a) occur on the pterothoracic margins of most Ischnocera (Fig. 7H). These are usually present in small pits on the ventral sublateral margin. However, the extent of the pit and the exact position of the setae vary between taxa. Similar trichoid setae in pits are present on the posterolateral margins of abdominal segment VIII. A small thorn-like seta is often closely associated with the pits on the pterothorax.

Setal patterns on the posterior margin of the pterothorax can be broadly divided into those that are in rows or are clustered. Setal rows may be complete (Fig. 7O, Q) or discontinuous (absent medially) (Fig. 7S), and are principally confined to the Trichodectidae and the *Saemundssonia*- and *Philopterus*-complexes. In contrast, clustered setal arrangements are more common. They are characterized by groups of setae which emanate from a common desclerotized patch of cuticle on the posterolateral angles of the pterothorax, although in some cases their setal apertures may simply be contiguous or closely associated (Fig. 7R). The ontogenetic development of these setae has been considered by Mey (1994) who found considerable variation in their arrangement and type. Within most taxa the setae of the nymphs and adults differ throughout their development, and usually exhibit an increase in their length and thickness in each successive instar. There is also a tendency for the number of setae to increase during ontogeny although this trend is less common.

Abdomen (Characters 95–129; Figs 10–14)

Pregenital segments (I–VIII). Segment I is evident as a small separate tergite in mammalian Ischnocera, with the exception of female Trichophilopteridae (Fig. 10). In all avian Ischnocera segment I cannot be delimited and two interpretations have been proposed to explain this. Either this segment is entirely suppressed leaving no trace of a dorsal or ventral sclerite (Cope, 1940), or it has fused with abdominal segment II (Wilson, 1936) and/or the pterothorax (Mey, 1994). Wilson's interpretation is perhaps most likely. He noted that the first apparent segment (abdominal segment II) of the first instar of *Cuclotogaster heterographus* (Nitzsch) is wider than all other segments and bears two transverse rows of setae (instead of just one as on the succeeding segments). In fact, close inspection of adult *Cuclotogaster* reveals two transverse pairs of setae and this is typical of many adult avian Ischnocera, although in these cases the most anterior setae are usually greatly reduced. Nevertheless, this finding is perhaps harder to reconcile with the fact that the species of *Columbicola*, *Falcolipeurus* and *Archolipeurus* examined all possess three transverse pairs or rows of setae on this segment. In contrast to this, Mey (1994) notes parallels between the loss or fusion of abdominal segment I and the reduction of abdominal segment II within the Heptapsogasteridae. With the exception of the genus *Rhopaloceras* Taschenberg, segment II is greatly reduced in all members of this family and in several cases it is partly or completely fused to the pterothorax. This reduction is so striking it led Carriker (1936) to mistakenly interpret abdominal segment II as the metathorax.

The presence of a small cuticular bridge connecting the meso- metasternal plate to sternite II may help in interpreting the homologies of the initial segments and sclerites in this region. This bridge was described by Mey (1994) for the *Philoceanus*-complex (Fig. 8J). He interprets this as the remnants of abdominal segment I; however, this conclusion seems unlikely given that the bridge is also evident in phylogenetically unrelated lice such as *Columbicola*. A functional explanation for this structure may be derived from the fact that all taxa possessing this bridge are long thin 'wing' lice. This bridge may help in providing stability between the thorax and the abdomen that might otherwise be lacking in taxa with this elongate body form. Nevertheless, not all 'wing' lice possess this bridge.

All avian Ischnocera and *Trichophilopterus* bear six pairs of spiracles on segments III–VIII, although a stigmatal scar (*sensu* Harrison, 1915) comprising a small aperture in abdominal segment II apparently marks the former position of a spiracle. These characters are also present in many species of Trichodectidae, however, secondary loss has occurred in some taxa. Consequently trichodectids may have five, four, three, two, one, or no pairs of abdominal spiracles (Lyal, 1985a). Loss of abdominal spiracles is confined to mammal-infesting Phthiraptera, and in all but the case of one anopluran genus (*Neolinognathus* Bedford), this loss has taken place sequentially from abdominal segment VIII (Lyal, 1983).

The atria of the abdominal spiracles in all avian Ischnocera are relatively small and approximately spherical (Fig. 11O). In the Trichodectidae they are typically larger and bulbous with a wider opening. They

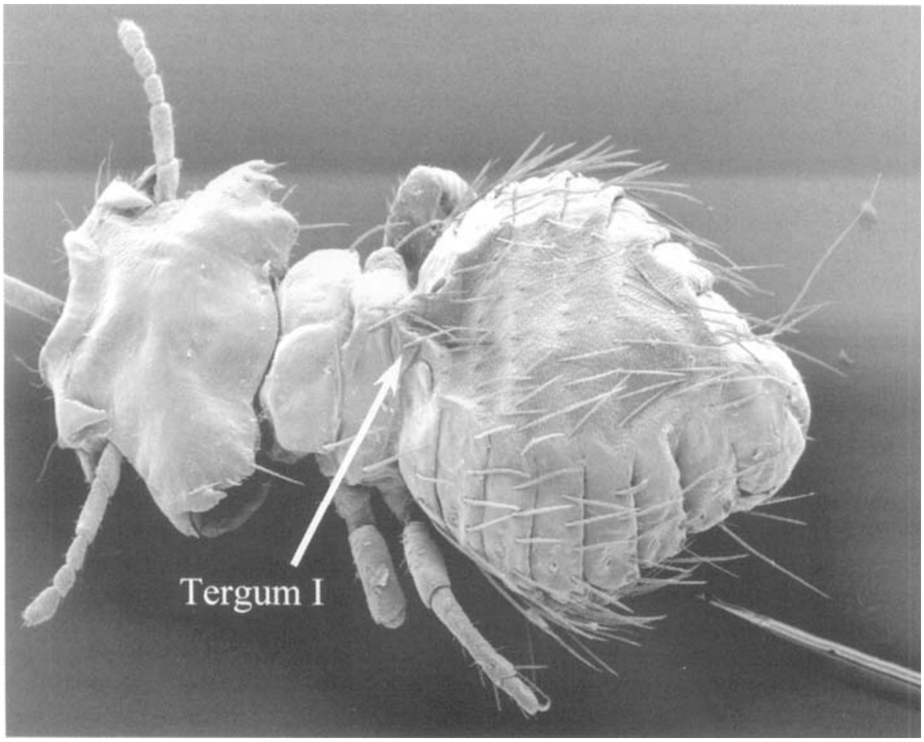

Figure 10. ♂ *Trichophilopterus babakotophilus* attached to a hair shaft. Abdominal segment I is identified.

also possess a distinct cuticular sculpturing around the walls of the atrium (Fig. 11P). These are chitinous ledges, which, according to Webb (1946), help to prevent dust and skin debris from entering the tracheal system. Similar ledges are present within avian Ischnocera, although they are rarely as well developed as in the Trichodectidae.

Abdominal lateral flecks were first noted by Moreby (1978), and are confined to male Trichodectidae. These flecks are small pits either side of the intersegmental line in the sublateral to intermediate region of the abdomen. Lyal (1985a) notes that they are usually positioned on the antero-dorsal angles of pleura III–VII, and occasionally on II to VIII, as well as antero-laterally on terga III–V in many species. They are not recorded from any other species of Phthiraptera.

An apparently undescribed structure is evident on the dorsal and/or ventral abdominal surface of almost all avian Ischnocera and some Trichodectidae. A series of raised cell shaped structures reside in oval pits. These are usually evident both dorsally and ventrally on the spiracle bearing segments, although smaller, less distinctive patches may also be evident on segment IX (Figs 11Q, 13D). Dorsally, the most prominent column of pits occupies a roughly intermediate position on the abdomen, although in some cases these are more closely associated with the spiracle. A second smaller pit is often evident on the margin of the spiracle (Fig. 11Q), although this lacks the distinctive oval shape of the main dorsal pit. Within each pit resides a series of small distinctive cell-shaped structures, typically varying between three and nine in number. In some larger taxa this number may exceed 100. Ventrally these cells are visible each side on the outer margins of the sternites, again usually within an oval shaped depression on the abdominal surface. The relative obscurity of this structure is perhaps explained by the fact that it can only be delimited with phase contrast at high magnification. It is also only visible when viewed against the contrast of a dark sclerotized plate, and consequently is often most readily apparent in third stage nymphs. A SEM examination of many taxa shows the oval shaped pits on each segment, but the cell-like structures are usually not delimited. This may be an artefact caused during the preparation of the specimens for use in the SEM. The presence of these structures on the spiracle bearing segments suggests that they have some sensory function. Further examination of more taxa from different suborders is needed to reveal the true distribution of this character and may help to establish its function on the abdomen.

Mey (1994) extensively discussed the variation within the patterns of abdominal plate sclerotization for Ischnocera. Based principally upon the variation amongst the 15 species he examined in detail, Mey described four schemes of postembryonic development

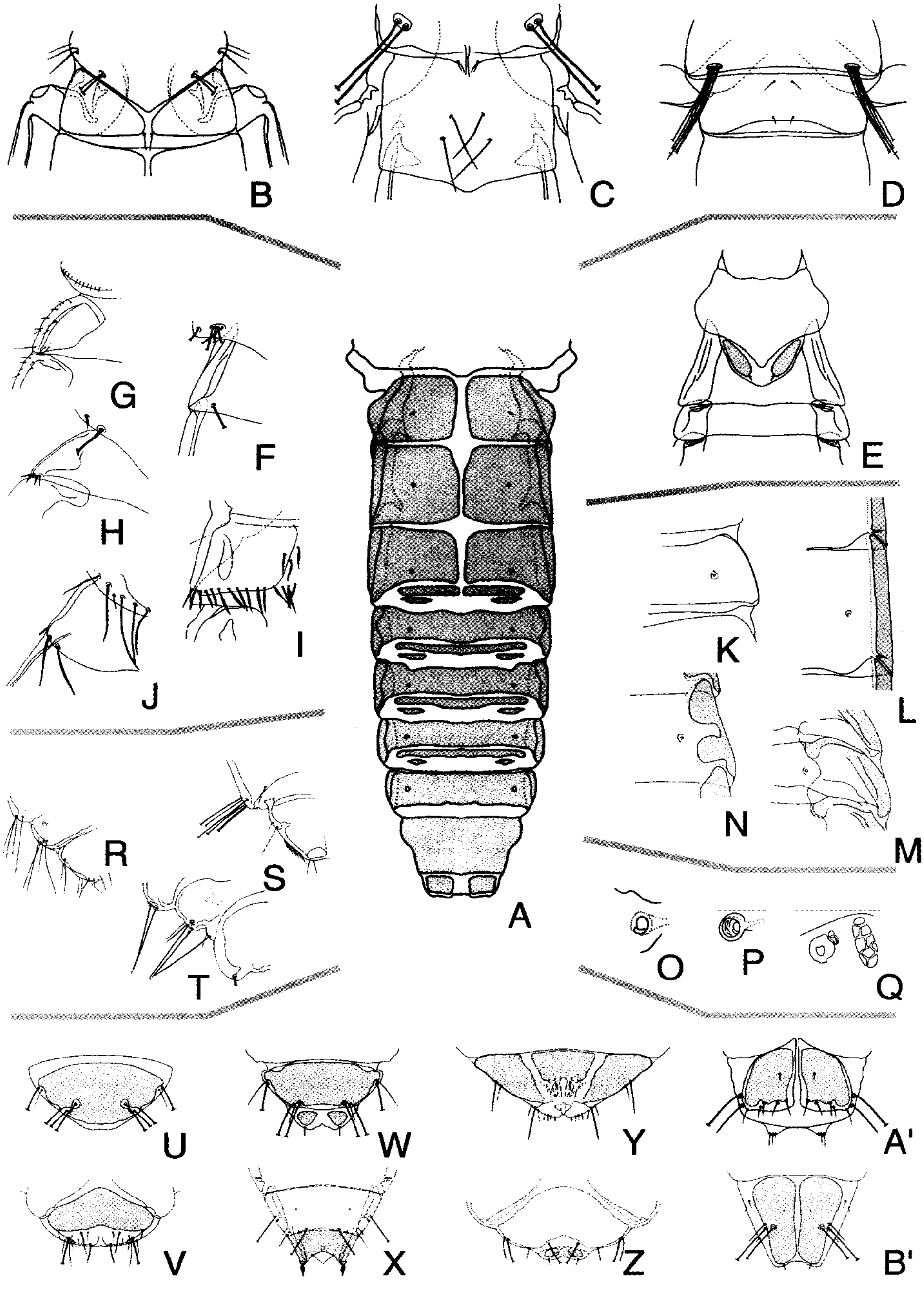

Figure 11. Selected abdominal characters. Highlighted sections correspond to character states (see Appendix 2). A, ♂ *Acidoproctus hilli*. B–D, ♀ submedian to median setae of abdominal segment II from (B) *Rallicola lugens*, (C) *Columbicola columbae* and (D) *Harrisoneilla hopkinsi*. E, abdominal segment II morphology of ♀ *Strongylocotes angulocapitis*. F–J, lateral and/or sublateral setae on abdominal segment II from (F) *Philoceanus garrodiae*, (G) *Bovicola limbatus*, (H) *Austrogoniodes waterstoni*, (I) *Archolipeurus nandu* and (J) *Ibidoecus plataleae*. K–N, ♀ pleural abdominal ribs from (K) *Neopsittaconirmus borgiolii*, (L) *Halipeurus pelagicus*, (M) *Goniodes pavonis* and (N) *Pelmatocerandra setosa*. O, P, abdominal spiracles from (O) *Austrogoniodes waterstoni* and (P) *Bovicola limbatus*. Q, cell shaped cuticular sculpturing on the dorsal abdominal surface of *Pectinopygus bassani*. R–T, ♀ trichoid seta on the posterolateral margin of abdominal segment VIII from (R) *Saemundssonia desolata*, (S) *Pectinopygus bassani* and (T) *Goniodes këleri*. U–B′ ♀ dorsal abdominal plates of the terminal abdominal segments from (U) *Degeeriella rufa*, (V) *Campanulotes bidentatus*, (W) *Quadraceps coenocoryphae*, (X) *Halipeurus pelagicus*, (Y) *Docophoroides brevis*, (Z) *Saemundssonia haematopi*, (A′) *Columbicola columbae* and (B′) *Anaticola crassicornis*.

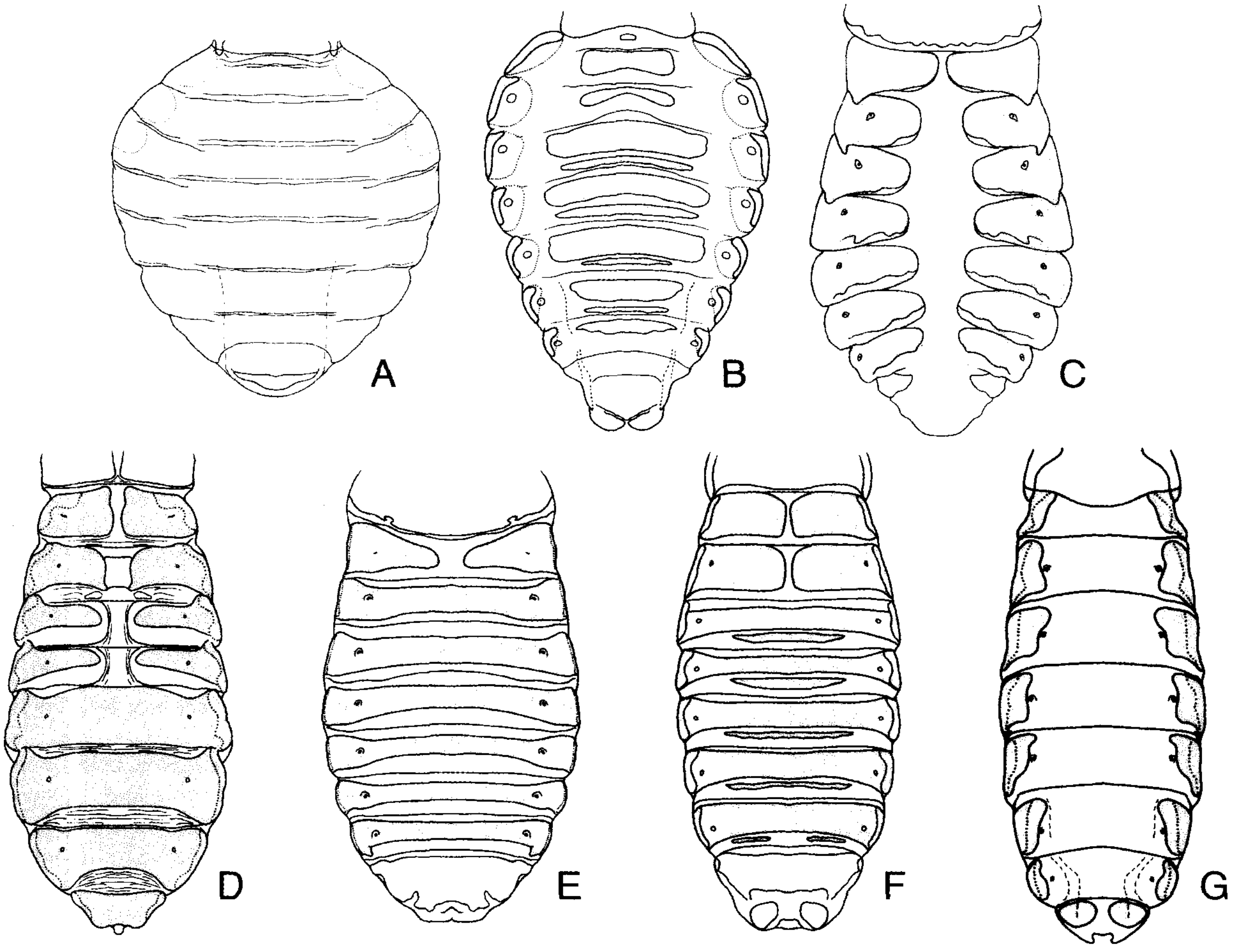

Figure 12. Adult pleural and tergal abdominal plate sclerotization from (A) ♂ *Geomydoecus* (*Geomydoecus*) *heaneyi*, (B) ♂ *Bovicola limbatus*, (C) ♂ *Strigiphilus vapidus*, (D) ♂ *Pectinopygus bassani*, (E) ♂ *Rallicola lugens*, (F) ♂ *Cuclotogaster madagascariensis* and (G) ♀ *Lipeurus caponis*. Highlighted sections correspond to the principal character states illustrated (see Appendix 2).

of abdominal plate sclerotization (see fig. 27 of Mey, 1994). These provide a useful ground plan for investigating the major body forms within Ischnocera, but are difficult to apply universally to the diverse selection of taxa examined in this study. In particular, considerable variation occurs in the patterns of sclerotization within the initial (II & III) and terminal (VIII–XI) body segments. For this reason, character complexes concerning these patterns are confined to describing the variation within segments IV–VII. Patterns of sclerotization amongst nymphal stadia are less variable. Hence, these descriptions are extended to cover segments III–VIII.

Sclerotization in all first stage nymphs is confined to the head and thorax. Further sclerotization on the abdomen is usually completely absent, although in some cases sclerites of the anterior abdominal segments may be weakly delimited. Most Ischnocera exhibit an increasing degree of sclerotization throughout their nymphal development. However, Mjöberg (1910) and Eichler (1948) have reported exceptions to this trend. There is also a tendency to exhibit a decreasing degree of sclerotization from the anterior to the posterior parts of the body, although this does not occur in all taxa and both these trends may be subject to artefacts generated by different degrees of clearing during the slide mounting process.

Some form of abdominal plate sclerotization is present in most taxa from the second stage nymphs onwards. However, the nymphs of several clades either completely lack sclerotized plates or possess weakly delimited, partially sclerotized pleurites in their an-

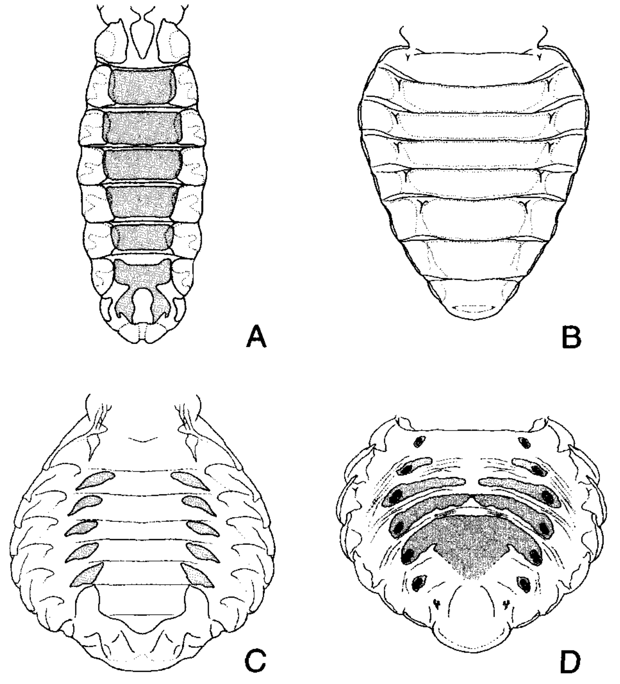

Figure 13. Adult ♂ sternal abdominal plate sclerotization from (A) *Pseudonirmus gurlti,* (B) *Felicola (Felicola) viverriculae,* (C) *Goniodes pavonis* and (D) *Saemundssonia desolata.* Highlighted sections correspond to the principal character states illustrated (see Appendix 2).

terior abdominal segments (Fig. 14A–C). This occurs within most members of the *Philopterus*-complex and to a lesser extent the *Saemundssonia*-complex. In both these groups there is a tendency to show a decreasing degree of sclerotization of the pleurites from the anterior to posterior segments during their ontogeny. The transition in abdominal sclerotization from third instar to adult is dramatic as the adults of both these groups have highly sclerotized abdomens. *Austrogoniodes* exhibits a similar condition in which the abdominal sclerotization of the third instar is restricted to small pleurites in segments II & III, yet the adults possess well developed and highly sclerotized tergopleurites in all the abdominal segments. In contrast, this transition is less significant in the Trichodectidae. With the exception of *Bovicola limbatus* (Gervais), the nymphs examined in this family generally lack sclerotized abdominal plates. When present in the nymphs these are small, weakly delimited pleurites in the anterior abdominal segments. Adult plates are more readily delimited and are accompanied by medial tergites, but are usually only well sclerotized in the Bovicolinae (*sensu* Lyal, 1985a) (Fig. 12B).

During their nymphal stages many taxa, including most of the *Lipeurus*-complex, Goniodidae and Heptapsogasteridae possess pleurites and separate paired tergites (Fig. 14E, G). These are present in segments IV–VII and often have a wider distribution throughout other abdominal segments. However, the tergites in the posterior segments of some taxa may be weakly delimited or absent. The *Degeeriella*-complex exhibits a similar condition. Here the paired tergites are absent from the second stage nymphs but present in the third stage, although again they may be weakly delimited or absent from the posterior segments. Almost all taxa in those groups whose nymphs possess separate, paired tergites and pleurites, have tergopleurites in the adult instar. These are probably derived from the fusion of the pleurites and tergites during the transition from third instar to adult. Evidence for this comes from the intermediate condition exhibited by second and third instar nymphs of the genus *Pectinopygus*. These possess well developed tergites and pleurites which are largely separate except for a thin cuticular band along the posterior margin of each sclerite, above which is positioned the spiracle in an unsclerotized part of the insect cuticle (Fig. 14H). Only in segment VIII of both the second and third instars are the tergites and pleurites completely separate.

Members of the *Philoceanus*-complex exhibit well developed tergopleurites from the second instar to adult (Fig. 14I). These are not fused medially in the nymphal instars, but are generally fused in the adults. This medial fusion is strongly developed in all males but females often exhibit traces of a medial division between the tergopleurites, and in the case of female *Haffneria* Timmermann and *Harrisoniella* Bedford, the tergopleurites remain distinctly separated.

The trichoid seta (*sensu* Smith, 2000a) is a distinctive setal type that probably functions as modified trichoid sensilla. When present this occurs on the posterolateral margin of abdominal segment VIII (Fig. 11T) and its morphology is similar to the pair of trichoid setae on the pterothorax of most Ischnocera. It is identifiable from other posterolateral setae in this region as a relatively short seta that is typically thinner than other seta of the same size and rapidly tapers to a distinct point, unlike other setal types that gradually taper from their base to the tip. Carriker (1936) was the first to describe this seta, noting its similarity to a blade of grass. The seta usually emanates from a distinctive pit and consequently the setal aperture is commonly obscured. However, this pit does not occur in all cases and a distinction is made between these types in the character states describing this character.

Genital Segments (IX, X & XI). Clay's 'unpublished key', considered the terminal segments of male avian Ischnocera in detail. She divided them into four 'types' based primarily on the position of the genital and anal

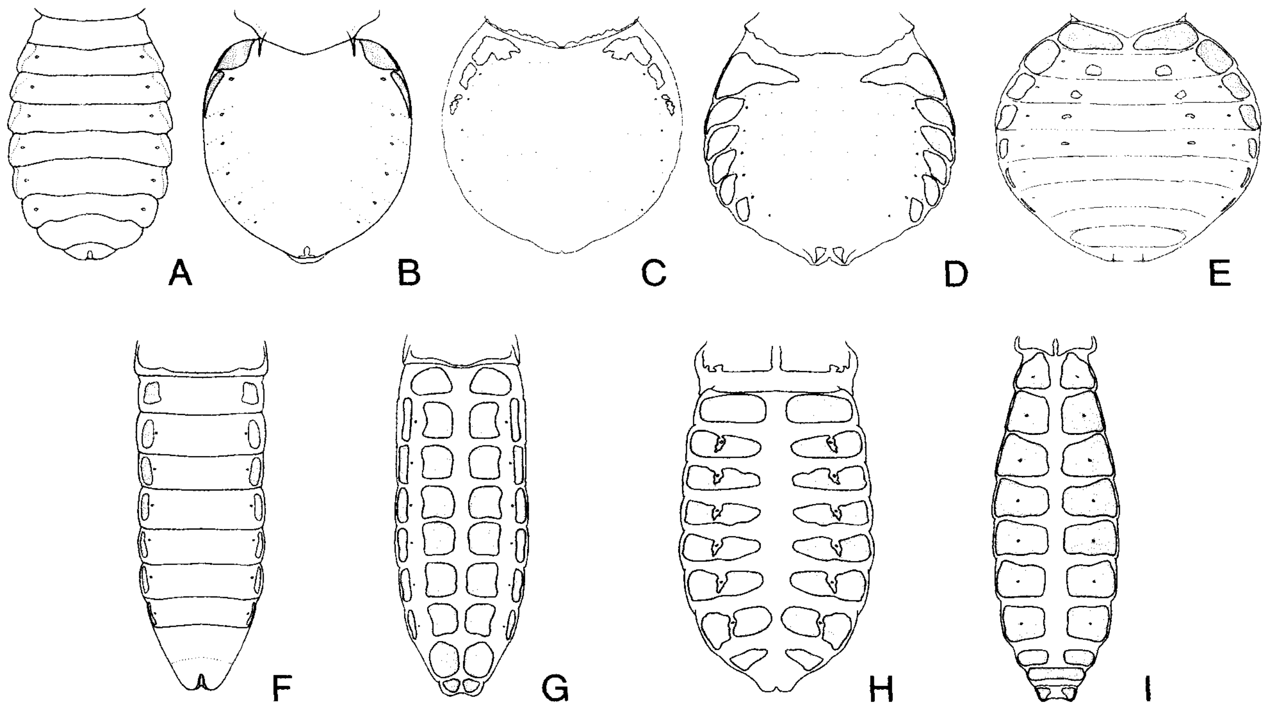

Figure 14. N III pleural and tergal abdominal plate sclerotization from (A) *Quadraceps coenocoryphae*, (B) *Austrogoniodes waterstoni*, (C) *Philopterus ornatus*, (D) *Goniocotes gallinae*, (E) *Lagopoecus affinis*, (F) *Falcolipeurus affulgeus*, (G) *Lipeurus caponis*, (H) *Pectinopygus bassani* and (I) *Philoceanus garrodiae*. Highlighted sections correspond to the principal character states illustrated (see Appendix 2).

openings and three pairs of anal setae. Although these groupings were useful for generating a key, the divergent morphology of these terminal segments precluded direct use of Clay's character complexes. Whilst each 'type' is often characteristic for particular groups of taxa, related forms may either be sufficiently different that they could not be placed within Clay's scheme, or tend towards an intermediate 'type'. Instead, attention was focused on the development of the tergal and sternal plates within the terminal segments.

This region has been the subject of conflicting interpretations by various authors. In particular, the number of terminal segments and the homology amongst their various sclerites has received some attention. Because of their intimate association and the lack of clear intersegmental sutures in many taxa, this region, comprising segments IX, X and XI, is typically treated together. Most authorities rarely make a distinction between these terminal segments, usually incorrectly referring to them all as segment IX. However, these segments can usually be distinguished on the basis of alternative criteria such as the position of lateral setae and folds or sculpturing in the hyaline cuticle present in this region. Matsuda (1976) proposed that segment XII is retained, whilst segment XI is lost or retained as cerci (see Lyal, 1983: 151). In contrast, Snodgrass (1935) and Richards & Davies (1977) consider segment XI (the paraprocts and epiproct) to be the final segment in most insects, with segment XII (the periproct or telson) normally lost. Nevertheless, Richards & Davies (1977) note that the morphology of the abdomen requires further investigation. The latter interpretation of the terminal segments was accepted by Lyal (1983), and is supported in this study, based on their ontogeny. In those taxa that possess sclerotized terminal abdominal plates, the tergites act as landmarks that can be tracked during their ontogeny. This was first attempted by Wilson (1936) for *Cuclotogaster heterographus*, and most recently by Mey (1994). Sclerites in the terminal segments of ischnoceran lice may either be absent, present and separate (IX, X, XI), present and partially fused (IX+X, XI) (Fig. 11W), or present and completely fused (IX+X+XI) (Fig. 11U). These conditions may be further subdivided according to whether each side is fused or separated medially. In the latter case, an isolated medial tergite may be present between the lateral pleurites or tergopleurites (Fig. 11Y). In the adult instar the tergites of segments IX and X are often fused transversely along their anterior and posterior margin, whilst the tergite belonging to segment XI is either separate or lost. This assertion is supported by the position of the plates relative to the hyaline segmental sutures delimiting each segment and the position of the lateral setae. Sexual dimorphism amongst the sclerites of this terminal region is common, and in such cases the homology amongst the sclerites of males is often difficult to establish. For this reason only characteristics of the adult female terminalia were scored in the character analysis.

Internal genitalia (Characters 130–138; Figs 15 & 16)

A large number of dissections of internal male genitalia were described and figured by Blagoveshtchenskii (1956) in a study that included over 200 species of chewing louse, belonging to 69 genera. This broad cross section of taxa (including 140 species from 41 ischnoceran genera) in conjunction with a preliminary outline of character complexes described within Clay's 'unpublished key', led to the development of nine characters describing internal genital morphology. Male internal genital characters are particularly useful in taxonomic studies of lice, as they present the systematist with a large number of discrete characters that are relatively conserved at the suprageneric level. Conversely, external genitalia of male lice (parameres, mesomeres, basal apodeme and associated sclerites *sensu* Lyal (1986)) are notoriously variable. This is particularly apparent within avian Ischnocera where structural homologies even at the generic level are often hard to delimit beyond the general ground plan (Smith, 2000a). Unfortunately, only external genitalia are preserved in cleared slide-mounted specimens and consequently, observations on these characters are based entirely on figures and descriptions in Blagoveshtchenskii (1956) and/or comments in Clay's 'unpublished key'. Therefore, many taxa could not be scored, either because these authors did not consider congeneric species, or because they did not describe particular states for some taxa. Nevertheless, data for approximately half the genera included in this study were figured by Blagoveshtchenskii (1956) and further specific comments in Clay's 'unpublished key' were used to supplement this information. Specific data on the sources used to assign character states to taxa are available in the attribute comments section of the full data file. This is available on-line (see data availability).

The internal genitalia of male Ischnocera (Fig. 15) consist of two closely connected testes on each side. These comprise two follicles which are either joined or in close proximity, giving a bilobed appearance. Vasa diferentia pass from the testes and connect to the seminal vesicle. These are usually of the same diameter throughout their length, although they may be widened at the point of connection. According to Clay's 'unpublished key', the seminal vesicle may consist of two completely separate structures, or a single more or less divided structure, although Blagoveshtchenskii (1956) makes no mention of the former condition. Nevertheless, this is approached by members of the Goniodidae, where the seminal vesicle is elongated and divided for over half its length (Fig. 15G). In those taxa where the seminal vesicle is completely undivided, the original dual structure is shown externally by a median furrow (Clay, 'unpublished key'). Each vesicle may be further subdivided into 2, 3, or 4 lobes (e.g. Fig. 15E & F), and may bear additional 'lateral lobes' towards the base (Fig. 15H) or along its length (Fig. 15A). The ejaculatory duct connects to the base of the seminal vesicle. In its simplest form this is a short muscular tube that connects to the penis (Fig. 15I), although it may be greatly swollen (Fig. 15J) or long and coiled (Fig. 15K). An appendix-like structure at the junction of the seminal vesicle and ejaculatory duct is present in members of the *Otidoecus*-complex (*sensu* Clay, 'unpublished key') (Fig. 15L).

The internal genitalia of female Ischnocera (Fig. 16) is more conserved and of less suprageneric value. The ovaries connect via paired oviducts to a common oviduct. This is folded dorsally above the genital chamber and opens into its anterior end. A spermatheca may be present connecting to the dorsal wall of the genital chamber near the opening of the common oviduct. This consists of a thin-walled sac from which runs a fine weakly sclerotized tube opening in the dorsal wall of the genital chamber. At the base of this sac a valve-like structure may be present. This is associated with a modified region (calyx) that is often strongly sclerotized and striated (Clay, 1956) (Fig. 16B). The presence of the spermatheca in cleared slide-mounted specimens is usually only indicated by the calyx which frequently survives the clearing process. Nevertheless, the spermatheca appears to be absent in several avian Ischnocera (Blagoveshtchenskii, 1956). Blagoveshtchenskii also failed to find the spermatheca in the Trichodectidae although Lyal (1983) reports that a similar structure of uncertain homology developed from the wall of the common oviduct was present in a species of *Dasyonyx* Bedford. The occurrence of the spermatheca within Ischnocera appears to parallel that in Anoplura. Ferris (1951) reports that while this structure can be regarded as part of the basic reproductive structures in Anoplura, it appears to be missing in several genera.

ONTOGENY

The significance of ontogeny in the development of the major preantennal characters of the head was first recognized by Oudemans (1912) and later discussed by Clay (1951a: 178). However, the brief mention that she gave to this issue belies its significance as an aid

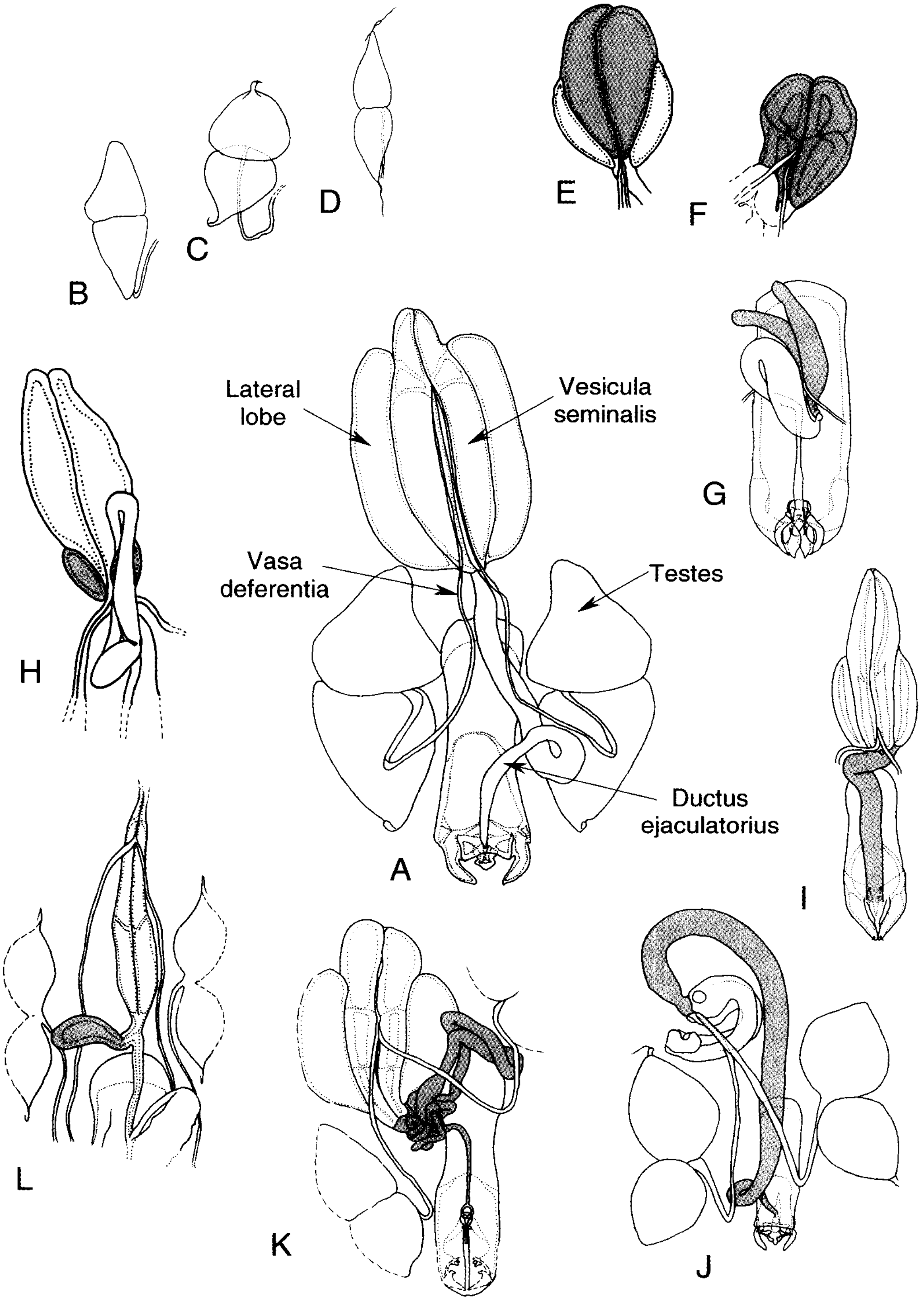

Figure 15. Ischnoceran internal male genitalia. Highlighted sections correspond to the principal character states illustrated (see Appendix 2). All figures redrawn and modified from Blagoveshtchenskii (1956). Original figure numbers in superscript. A, *Craspedorrhynchus spathulatus*$^{(20:2)}$. B–D, testes morphology from (B) *Degeeriella d. discocephalus*$^{(20:4)}$, (C) *Sturnidoecus sturni*$^{(18:4)}$ and (D) *Falcolipeurus frater*$^{(23:4)}$. E, F, internal subdivisions of the vesicula seminalis from (E) *Quadraceps ochropi*$^{(21:6)}$ and (F) *Brueelia argula*$^{(21:1)}$. G, vesicula seminalis morphology from *Goniodes bituberculatus*$^{(24:6)}$. H, lateral lobe morphology from *Syrrhaptoecus alchatae*$^{(22:4)}$. I–K, ductus ejaculatorius morphology from (I) *Columbicola columbae*$^{(24:3)}$, (J) *Philopterus thryptocephalus*$^{(18:3)}$ and (K) *Lagopoecus pallidovittatus*$^{(22:2)}$. L, unpaired diverticulum from *Cuclotogaster heterographus*$^{(23:2)}$.

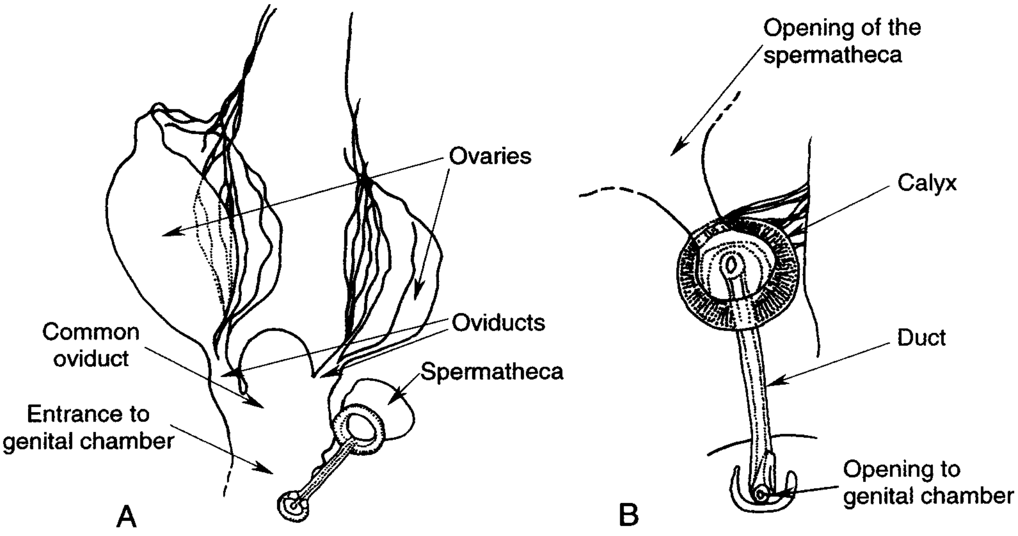

Figure 16. Ischnoceran internal female genitalia. Redrawn and modified from Blagoveshtchenskii (1956). Original figure numbers in superscript. A, typical genital morphology in avian Ischnocera modified from *Philopterus ocellatus*$^{(2:2)}$. B, enlarged view of the calyx and duct connecting the spermatheca to the genital chamber in *Philopterus guttatus*$^{(7:1)}$.

to understanding the development of the preantennal region in Ischnocera. Mey (1994) was the first to make direct use of these characters as an aid to understanding ischnoceran phylogeny, and subsequently Page *et al.* (1995) and Price & Hellenthal (1996) have used first instar nymphs to help establish the phylogeny and taxonomy of trichodectid gopher lice. Most of the adult character states for the major preantennal characters can be directly observed in some or all of their nymphs. In the light of the phylogeny, this information on the transformation series of these characters can be used to highlight instances of convergent evolution that would go largely unrecognized if only adult characteristics were considered.

The principal characters that exhibit ontogenetic variation concern the preantennal region and the tergal and sternal plate morphology over the abdomen. These developmental trends were initially summarized by Mey (1994) and are expanded upon here, with further examples of each group. Although taxa can usually be readily assigned within the ontogenetic trends described below, these character complexes were not directly coded in the phylogenetic analysis. Instead, each complex was broken up into several component characters and coded separately for each instar. This allows the variation described by particular characters to be coded in greater detail. Also, incorporating descriptions of ontogenetic variation into these characters would require knowledge of the character states in all instars of the taxa scored. Since only partial instar series were available for about one third of the taxa examined, a large proportion of the data set would have to be scored as missing if this coding strategy was adopted.

Preantennal morphology

Three distinct ontogenetic lines are evident in avian Ischnocera that are described in terms of their clypeal morphology. Specifically the development of a medial interruption in the marginal carina and the development of a dorsal anterior plate:

(A) All instars possess a circumfasciate head, with a complete marginal carina present in the first instar. This is essentially unchanged in subsequent stages. Examples of this group are represented throughout the Goniodidae, most Heptapsogasteridae, *Lipeurus*- and *Degeeriella*-complexes.

(B) The first instars possess a circumfasciate head with a complete marginal carina, but before the adult instar the marginal carina is medially interrupted. Mey (1994) divides this category into three groups, based on when the transition occurs between the circumfasciate and non-circumfasciate head. However, a more natural division should take into account the cause of the transition to a non-circumfasciate form:

(1) The head is circumfasciate from first to third stage nymphs, but is non-circumfasciate in the adults as the marginal carina thins on each side, fusing with the dorsal sclerotization of the head, and does not meet medially e.g. *Discocorpus* Carriker (based partly the nymphal description of *Discocorpus* by

Mey, 1994). A dorsal anterior plate is not present in the adult instar.

(2) The head is circumfasciate from first to third stage nymphs, but is non-circumfasciate in the adults, caused by the medial interruption of the marginal carina by the development of a dorsal anterior plate. This condition occurs in most members of the *Philoceanus*-complex, although in these taxa the medial interruption is considered primarily dorsal in the nymphal stadia. It is also particularly well exhibited by *Alcedoecus* Clay & Meinertzhagen, which shows a dramatic change in preantennal morphology from third instar to adult.

(3) The head is circumfasciate from first to second stage nymphs, but is non-circumfasciate in the third and adult instars, caused by the medial interruption of the marginal carina by the development of a dorsal anterior plate. This occurs in some members of the *Philoceanus*-complex.

(4) Only the first instar is completely circumfasciate, all others are non-circumfasciate. This condition is only represented by *Haffneria,* where the marginal carina remains complete ventrally until the adult instar, however a weakly developed dorsal anterior plate is present in the second, third and adult instar.

(C) All instars are non-circumfasciate, with a medially interrupted marginal carina and a dorsal anterior plate. Examples represented in this data set are restricted to members of the *Philopterus*- and *Saemundssonia*-complexes in addition to *Aquanirmus* Clay & Meinertzhagen and *Ibidoecus*.

These ontogenetic transitions suggest a trend from the circumfasciate to non-circumfasciate head. Mey (1994) considers the circumfasciate head to represent the "original" (symplesiomorphic?) head type, and the non-circumfasciate head to be derived, present in phylogenetically younger taxa. This is supported by the fact that no cases of reversal (either ontogenetic or phylogenetic) from non-circumfasciate to circumfasciate head were found in any of the taxa examined.

Abdominal morphology

Transformation series in the development of the ischnoceran abdomen are much harder to delimit than those of the preantennal region. This is due in part to the difficulty of delimiting the terminal abdominal segments in slide mounted specimens, particularly as these often do not bear sclerotized abdominal plates until the adult stage. Sexual dimorphism further complicates any interpretation of the patterns of abdominal sclerotization. Mey (1994) describes four schemes of postembryonic development for the abdomen. However, the diverse selection of taxa examined in this study rarely conforms exactly to any of his groups. Until a clearer understanding of the postembryonic development of the abdomen is available for a wider selection of avian Ischnocera, the number of abdominal segments will be considered separately from the pattern of abdominal sclerotization. Character state descriptions for these traits describe their ontogenetic variation for the taxa considered here. However, several broad trends are evident with respect to both these features, which are listed below:

Tergal, pleural and sternal sclerotization

(1) Abdominal plates of first stage nymphs are rarely delimited and never sclerotized, except for members of the *Philoceanus*-complex, which often exhibit weakly sclerotized tergopleurites.

(2) Sclerotization of the tergal and pleural abdominal plates increases in almost all cases with the transition to each successive instar.

(3) The tergal, pleural and sternal abdominal plates of all but the initial abdominal segments may be completely absent or weakly delimited and unsclerotized in the nymphal instars of many genera. This particularly concerns *Austrogoniodes* and the *Philopterus*- and *Saemundssonia*-complexes.

(4) When present, sternal abdominal plates are poorly delimited and weakly sclerotized in most taxa.

(5) Sternal plate morphology is apparently constant from second instar to adult, although these plates are often difficult if not impossible to delimit in many taxa. Particularly those that possess a single complete sternal plate in each segment in the adult stage.

(6) Tergal and pleural abdominal plate morphology is usually similar or unchanged between the second and third stage instars. However, the transition in morphology from third instar to adult is usually dramatic.

Abdominal segmentation

(1) All adult avian Ischnocera have eight distinct abdominal segments, except in most members of the Heptapsogasteridae in which segment II may be greatly reduced and is sometimes inseparable from the pterothorax. This gives the impression that just seven distinct abdominal segments are present in this family.

(2) The terminal abdominal segment in adult stadia (generally referred to as segment IX) is a fusion product of the IXth, Xth, and XIth segment. The reduction of this segment can be followed in some taxa during nymphal development, based on the pleural and tergal abdominal plate morphology and abdominal chaetotaxy.

(3) The degree of fusion between the terminal segments in the adult stadium varies between taxa. Dorsally the fusion may be complete, leaving little trace of the separate segments except in the pattern of pleural chaetotaxy. Alternatively, the segments may be partially fused, evident dorsally by the retention of segment XI (often unsclerotized) and the fusion of segments IX and X. These segments are usually sexually dimorphic.

(4) In the nymphs of taxa where the terminal abdominal segments are readily delimited, fusion usually occurs between the third and adult instar.

Note that this interpretation of the reduction of abdominal segments is broadly consistent with the findings of Mey (1994). However, Mey regards taxa with nymphs that have 10 visible abdominal segments as primitive, whilst he considers taxa with nine, eight or seven segments as derived. Based on the distribution of these character states for the taxa examined here, and our current understanding of ischnoceran relationships, this general trend cannot be supported for all species.

CLADISTIC ANALYSIS

A total of 138 characters (59 binary and 79 multistate), was identified in this study, including 108 from adults and 30 from nymphs. Of these, 131 were parsimony informative. The 10 000 random addition sequence replicates found three most parsimonious trees in a single tree island. A strict consensus of these trees is shown in Figure 17 and the major clades identified in the analysis are indicated. Jackknife (bold) and bootstrap (italics) values are shown above each node whilst Bremer support values (decay indices) are presented beneath the nodes. The most parsimonious trees had a length (L) of 912, a consistency index (CI) of 0.292, and retention index (RI) of 0.650 ($L=902$; $CI=0.284$ excluding uninformative characters).

The following discussion considers the character states that diagnose the major clades presented in Figure 17. The results of the Bremer support, jackknife and bootstrap analyses are also discussed, although the values for the major nodes are generally low. This reflects the difficulty of finding unambiguous character state synapomorphies to support these clades.

The basal split between the mammalian outgroup family Trichodectidae and the ingroup avian taxa has a bootstrap value of 100 and a Bremer support value of 9. This is where the tree was rooted. The relationships within the trichodectid outgroup taxa are broadly concordant with Lyal (1985a), highlighting the split between the Bovicolinae found principally on bovid mammals and the Trichodectinae–Neotrichodectinae clade. Within the latter group, *Felicola* Ewing is a sister taxon to *Geomydoecus* (a gopher louse), contrary to Lyal (1985a), who places *Felicola* with *Trichodectes* Nitzsch. This unexpected relationship is possibly an artefact that may have been generated by the limited number of trichodectid taxa sampled.

Basal avian Ischnocera comprise *Archolipeurus* and *Falcolipeurus* hosted by ratite and falconiform birds respectively, in addition to *Brueelia* Kéler, a large widespread genus principally confined to Passeriformes. All other avian taxa are divided into two clades that are broadly characterized by the morphology of their preantennal region. These characters play a key role in resolving the basal nodes in the ischnoceran tree.

Circumfasciate taxa

The *Lipeurus*- and *Degeeriella*-complex (with the exception of the genus *Columbicola*), in addition to the Goniodidae, Heptapsogasteridae and the *Neopsittaconirmus* Conci–*Paragoniocotes* Cummings clade, form a group that possesses a circumfasciate head from first instar to adult. In contrast, all other taxa (with the probable exception of *Osculotes* and *Acidoproctus*) possess a non-circumfasciate head in at least the adult and possibly the earlier instars. In circumfasciate taxa the hyaline margin is usually absent or weakly developed, running anteriorly around a complete marginal carina that is not interrupted laterally or medially. In adult *Discocorpus* the marginal carina is absent medially whilst in *Neopsittaconirmus* the marginal carina is interrupted by a thin dorsal suture. However, the nymphal instars of both these taxa possess a complete uninterrupted marginal carina. All circumfasciate taxa lack a dorsal and ventral anterior plate, and the dorsal preantennal suture is usually confined to a thin isolated strip in the dorsal carina. The ventral carina forms a complete semicircular band around the pulvinus except in the case of the *Degeeriella*-complex where it is medially interrupted forming a broken arch.

Within this clade the Goniodidae and the apparently paraphyletic 'Heptapsogasteridae' are monophyletic, and form a sister group to a clade comprising the *Lipeurus*- and *Degeeriella*-complex. The parrot lice (*Neopsittaconirmus* and *Paragoniocotes*) are monophyletic and form a sister group to these taxa at the base of the circumfasciate clade.

Goniodidae and Heptapsogasteridae. Smith (2000a) recently examined the generic relationships within these families. The subset of taxa considered here is broadly concordant with this phylogeny, and is in complete agreement with recent molecular data (R. Cruickshank *et al.*, in review) to the exclusion of the genus *Chelopistes* Kéler. In particular, the columbiform lice (*Coloceras* Taschenberg & *Campanulotes* Kéler)

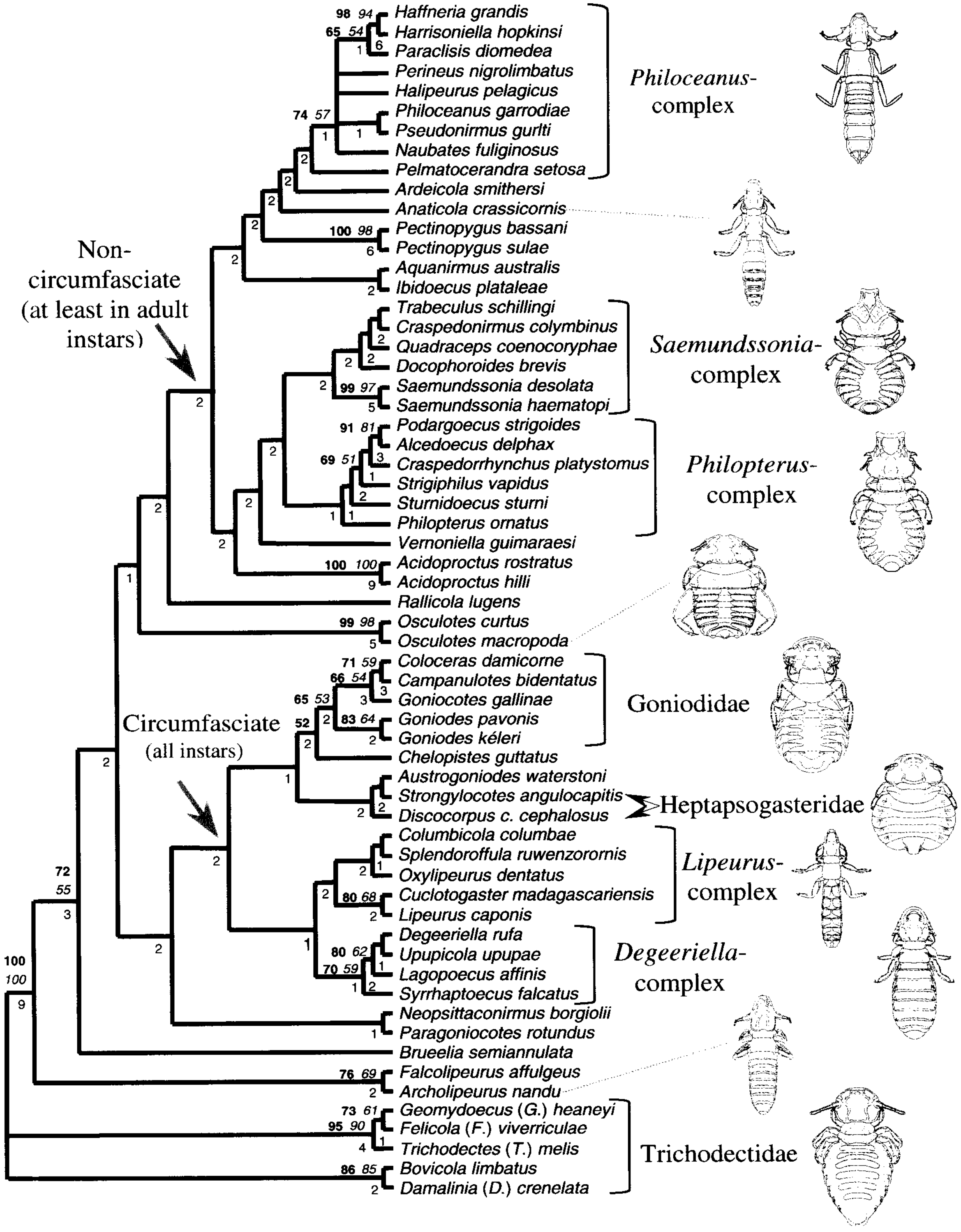

Figure 17. Strict consensus of the three most parsimonious trees obtained from the parsimony analysis (L = 912, CI = 0.284, RI = 0.650). The major clades resolved in the phylogeny are highlighted. Bootstrap (italics) and jackknife (bold) values are shown above each node, whilst Bremer support values (decay indices) are presented beneath.

are monophyletic and form a sister group to the lice of Galliform birds (*Goniocotes* Burmeister and *Goniodes*).

The genus *Chelopistes*, a louse of turkeys and related genera (Phasianidae & Cracidae) is generally considered a goniodid or a close relative. However, chromosomal data (Perrot, 1934) do not support this, and recent molecular data (K. Johnson, pers. comm.) places *Chelopistes* with the genus *Oxylipeurus*, another circumfasciate taxon present in the *Lipeurus*-complex. This is further supported by Clay (1976) who cites affinities between these genera based on the geographic isolation of their hosts. The taxa sampled in my previous morphological phylogeny (Smith, 2000a) combined with the method employed to root the tree could not unequivocally support either hypothesis. However, the data presented here suggest a strong association between *Chelopistes* and the family Goniodidae. Characters supporting this relationship include the absence of a gular plate, thickened and enlarged temporal carina, 2,2+2,2 (or 2,2,1+1,2,2) pterothoracic setal arrangements and the development of the pleural ribs (*sensu* Mey, 1994) within each abdominal segment. In addition, male internal genitalia are similar in both *Chelopistes* and the Goniodidae (Clay, unpublished key) leading Blagoveshtchenskii (1956) to place these taxa in the same group and separate from *Oxylipeurus*.

The Heptapsogasteridae are a morphologically distinctive family represented by the genera *Strongylocotes* Taschenberg and *Discocorpus* in this data set. They are confined to the tinamiform birds of South America and are almost certainly monophyletic, based on the morphology of abdominal segment II. However, all three most parsimonious trees placed this family as paraphyletic with respect to the louse genus *Austrogoniodes*, a parasite of penguins. This unorthodox relationship can perhaps be explained by the poor sampling of the tinamou louse family within this data set (principally because of a lack of available nymphal material) and the unusual morphology of *Austrogoniodes*. Some authorities have tentatively considered this louse a member of the Goniodidae based on the morphology of the head. However, morphological data based on the ontogeny of the abdominal plate sclerotization in the nymphs (Mey, 1994), combined with molecular data from the 12S rRNA gene (Paterson *et al.*, 2000) and a phylogeny based on the EF1-α gene (R. Cruickshank *et al.*, in review) suggests this is not the case. These data serve to highlight the uniqueness of this louse, perhaps a reflection of the unique biology of its host.

Lipeurus-complex. This group, along with members of the *Degeeriella*-complex, superficially resembles the *Philoceanus*-complex and occupies a similar niche on the wings of their hosts. They are primarily found on galliform birds and, like the *Degeeriella*-complex, are difficult to define based on their adult morphology. This is partly reflected by the low support values for these clades. Unlike the *Degeeriella*-complex, all male members of the *Lipeurus*-complex have heteromorphic antennal segments with an elongated scape that lacks a lateral process. The most distinctive feature of this group is the morphology of the abdominal plates in second and third stage nymphs. Each abdominal segment possesses a pair of well developed pleurites and tergites that are separate and sclerotized. This serves to distinguish them from members of the *Philoceanus*-complex; another 'wing' louse clade that possesses well developed tergopleurites from the second to adult instars. The tergites of segments IX, X and XI are particularly distinctive, in that they are well developed and readily differentiate these segments. On the posterior margin of the pterothorax, the setal morphology is similar, with all but *Cuclotogaster* possessing a 4+4 or 4,1+1,4 clustered setal arrangement.

The presence of *Columbicola* within this clade is unexpected. This taxon and the closely related genus *Turturicola* Clay & Meinertzhagen possess a distinctive preantennal morphology that is unlike other members of this group. In *Columbicola* the second, third and adult instars possess a non-circumfasciate head, due to a lateral interruption separating the pre- and postmarginal carina. However, the premarginal carina is not interrupted medially and despite being less well developed than in circumfasciate taxa is clearly present. Several other features of this genus serve to identify its uniqueness from other ischnoceran taxa. These include the distinctive form of the dorsal preantennal suture that arises from the ends of the premarginal carina across the head. However, it also extents anteriorly, dividing the dorsal sclerotization of the head medially. This condition is unique to *Columbicola*, as are the distinctive blade-like anterior setal pairs that emanate from the medial extension of the dorsal suture. The position of *Columbicola* in the *Lipeurus*-complex is very weakly supported (Bremer support of just 1) and its unstable position in this part of the trees is exemplified by the changes in overall tree length if this genus is moved. Placing *Columbicola* close to the base of the *Philoceanus*-complex adds just two steps to the overall tree length, despite the fact that this movement almost spans the base of the ischnoceran tree. Clearly more effort needs to be directed towards placing this genus in a wider phylogenetic context, especially as it is increasingly used in studies of cophylogeny (Johnson & Clayton, in press) and as the taxon of choice in studies of host-louse ecology (Clayton, 1990; Clayton & Tompkins, 1994; Clayton *et al.*, 1999).

Degeeriella-complex. The affinities of these taxa to members of the *Lipeurus*-complex are supported by the distinctive thoracic morphology of these two groups. This is likely to be associated with the coxal articulation of the second and third pairs of legs, which are intermediate between the sternocoxal articulation of the goniodids and heptapsogasterids, and the pleurocoxal condition of the *Philoceanus*-complex and their close relatives. The morphology of the proepimeron proximally is also unusual in the *Lipeurus*- and *Degeeriella*-complex, in that it is blunt ended and not expanded. Unlike many members of the adult circumfasciate clade, most adult members of the *Lipeurus*- and *Degeeriella*-complexes have a greatly expanded pulvinus and possess a well developed gular plate.

Characters separating the *Degeeriella*-complex from other avian Ischnocera are somewhat harder to list. In a revision of the group from Falconiformes, Clay concluded "[t]he stability of certain characters and the divergence of the ancestral degeerielline stocks on the various host groups together with parallel evolution makes it impossible to define a subfamily for the *Degeeriella*-complex, and further causes great difficulty in generic separation". (Clay, 1958: 125). One of the most distinctive characters of this group concerns the morphology of the ventral carina, which is medially interrupted in all instars, having the appearance of a broken arch. Unlike the *Lipeurus*-complex, members of the *Degeeriella*-complex possess monomorphic antennal segments (except male *Degeeriella mookerjeei*) (Clay, 1958).

Non-circumfasciate taxa

With the probable exclusion of the genus *Acidoproctus*, all members of this group possess a non-circumfasciate head in at least the adult instar and often in one or more of their nymphs. They comprise the *Saemundssonia*-complex which are largely restricted to seabird hosts, and form a sister group to the *Philopterus*-complex. Basal to this clade is *Vernoniella* and *Acidoproctus*, which together with the *Saemundssonia*- and *Philopterus*-complex is sister to a large clade that includes the *Philoceanus*-complex of procellariiform seabirds.

Characters supporting the monophyly of the non-circumfasciate taxa are, not surprisingly, primarily restricted to the head, and in particular the preantennal region. These include the expansion of the hyaline margin, which is usually enlarged and continuous with the preantennal suture, and the interruption of the marginal carina, which is always divided medially in the adult instar and usually is interrupted laterally. All taxa with the exclusion of *Acidoproctus* have a dorsal anterior plate in the adult stage, although this has been secondarily lost in *Perineus* Harrison and only a faint trace of the plate remains fused to the dorsal sclerotization of the head. The ventral carina is always interrupted medially, occasionally forming a broken arch but more commonly with a flattened anterior extension which fuses with the premarginal carina. Although non-head characters are important in defining subclades within this group, only the size of the rhombic sclerite, which is typically large in non-circumfasciate taxa, helps define this clade.

The sister group relationship between the *Philopterus*- and *Saemundssonia*-complexes is relatively strongly supported by a number of characters and does not rely solely on preantennal characters of the head. These characters include the complete lateral division of the pre- and postmarginal carina, except in *Sturnidoecus* Eichler where the premarginal carina remains partially attached. In contrast the marginal carina of most third stage nymphs is only interrupted medially and the pre- and postmarginal carinae are often separable by the presence of a setal aperture. The most characteristic feature of the group is the presence of a well developed dorsal anterior plate, which is extended posteriorly and, when fully delimited, usually bears a distinct posterior extension. This plate is present in most third and some second stage nymphs of these taxa. However, only *Saemundssonia* has a dorsal anterior plate in all four instars. A well developed ventral anterior plate is also present in most members of these clades, although this has apparently been independently lost in *Trabeculus* Rudow and *Craspedonirmus* Thompson of the *Saemundssonia*-complex and the nymphs of *Podargoecus* Emerson & Price and *Alcedoecus* in the *Philopterus*-complex. The female abdominal segments of these taxa usually possess dorsal setal rows at least on segments III to VI, and mature adult females also possess a distinct calyx close to the genital chamber in all but *Docophoroides*, *Quadraceps* Clay & Meinertzhagen and *Trabeculus*.

Philopterus-complex. Of the six genera of lice represented in this clade, five are found on different host orders and include lice present on the passerines (song birds). The nymphs of these taxa usually possess a ventral carina with a flattened extension that approaches, but does not fuse with, the marginal carina until the adult instar. The ontogeny of this character when mapped on to the phylogeny suggests the delay in fusing to the marginal carina is a derived condition, as fusion is complete by the third stage nymphs of *Sturnidoecus* and is fully developed in the second and third stage nymphs of *Philopterus*. The loss of fusion between these structures in the nymphs may be adaptive, perhaps increasing the plasticity of the head capsule. As in the *Saemundssonia*-complex, there is a general reduction in the number of abdominal plates, particularly in the nymphs, which completely lack differentiation of their terminal abdominal segments, while the initial abdominal segments are only weakly differentiated by the presence of small pleurites. This reduction of nymphal abdominal sclerotization is not evident in the adults, which possess well sclerotized tergopleurites. However, ventrally, both males and females usually lack abdominal sternites.

Saemundssonia-complex. This clade is principally found on procellariiform and some charadriiform seabirds, although the genus *Saemundssonia* has a relatively wide host distribution and is also found on Pelecaniformes and Gruiformes. Its morphology clearly links the group to the *Philopterus*-complex, particularly in the development of a large and distinctive dorsal anterior plate. However, a number of characters distinguish these taxa from all other avian lice. In particular, unlike the *Philopterus*-complex, the nymphal ventral carina possesses a flattened anterior extension that always fuses with the premarginal carina. A distinctive transverse carina is also evident in the postantennal region, although the extent to which this is developed or sclerotized often varies. The lens of the eye in all but *Trabeculus* and *Craspedonirmus* bears two distinct setae. These are the ocular seta that is almost always found on the lens, and the postocular seta, which normally resides on the temporal margin posterior to the eye. Certain features of the morphology of the pterothorax and abdomen are also distinctive. Along with several basal members of the *Philopterus*-complex, all members of this group possess a row of setae along their pterothoracic margin. Laterally the pterothorax lacks the distinctive trichoid seta which is present on most ischnoceran taxa, although the thorn-like seta that is normally associated with the trichoid seta is always present. Trichoid setae are also absent from the lateral margins of abdominal segment VIII and their loss may be a trait associated with host ecology, since these setae are also absent in most members of the *Philoceanus*-complex, another group confined to seabirds.

Philoceanus-complex and its close relatives. This clade can be divided into the *Philoceanus*-complex (a distinctive and closely related group confined to procellariiform seabirds) and their immediate sister taxa. The latter are present on a more diverse selection of aquatic birds including ducks, storks, herons, and divers in addition to Procellariiformes. With the exception of *Ibidoecus*, and possibly its sister taxon *Aquanirmus* at the base of this clade, all members of the group are typical 'wing-lice', with an elongate body form putatively adapted to the wing niche on their hosts. *Ibidoecus* and *Aquanirmus* lack many of the characteristics typical of this group and unless otherwise mentioned are excluded from the following discussion, which considers the characters that diagnose the 'wing-louse' clade above *Ibidoecus* and *Aquanirmus*.

The nymphal stages of all these taxa possess a marginal carina that is only interrupted dorsally; although in the adults the medial interruption becomes fully developed and a lateral division forms between the pre- and postmarginal carina. Distinct striations are present ventrally on the ante-clypeus of the adults of all taxa except *Pseudonirmus* Mjöberg and *Anaticola* Clay. These are perhaps an adaptation to their seabird hosts as they are also found in the genus *Docophoroides* of the *Saemundssonia*-complex. In the case of *Ardeicola* Clay, these markings are particularly well developed, forming distinctive crescent shapes. Members of the *Philoceanus*-complex and *Pectinopygus* possess a characteristic dorsal carina. This is usually broken medially and variably projects inward posteriorly forming two parallel bars, although in the case of *Pseudonirmus* and the unrelated genus *Vernoniella* Guimarães the dorsal carina is continuous across the head. For most members of the *Philoceanus*-complex and their immediate sister taxa, the dominant marginal temporal seta of the head is MTS 3, and in cases where it is not, MTS 3 is among the dominant temporal setae.

Setal characters are also useful on the prothorax. The distribution of anterior prothoracic setae is disjunct in all members of the *Philopterus*-complex and its sister taxon *Ardeicola* except in *Halipeurus* Thompson. Other prothoracic characters include the development of the mesothoracic spiracle, which protrudes out on a small expansion of the prothorax. The presence of a metathoracic spiracle on the metepisternum is also likely to be characteristic of the *Philoceanus*-complex, although as has been mentioned elsewhere, the full distribution of this character is not known. All taxa in this clade in addition to *Ibidoecus*, although not *Aquanirmus*, possess an expanded proepimeron that projects anteriorly into the prothorax. In contrast, this expansion, when present, projects posteriorly towards the abdomen in most other Ischnocera. This may be an adaptation due to the pleurocoxal articulation of the second and third pairs of legs present in these taxa.

The ventral surface of this group is characterized by the presence of an elongated meso- metasternal plate and large medially fused sternal plates on the underside of the abdomen. These are present in both males and females, and the second sternal plate is connected to the meso- metasternal plate via a thin sclerotized cuticular bridge. The dorsal abdominal surface is covered by tergopleurites in the adults of the *Philoceanus*-complex. These are fused medially in adults except for female *Haffneria* and *Harrisoniella*. In contrast, the second and third stage nymphs of this complex have well developed tergopleurites that are not fused medially.

Acidoproctus & Osculotes. Acidoproctus, present on ducks and geese (Anseriformes), in addition to the aberrant louse genus *Osculotes* present on the hoatzin (Cuculiformes), both possess a deep indentation (osculum) in the anterior margin of the head. This interrupts the marginal carina medially in the second to adult instars of these taxa, forcing the preantennal morphology to take on characteristics common to non-circumfasciate taxa. This may help to explain their position in the phylogeny close to the base of the non-circumfasciate clade.

Osculotes was considered a member of the Goniodidae by Kéler (1939), who placed the genus in its own subfamily *Osculotinae*. Clay (unpublished key) followed this arrangement, as did Eichler (1963) who renamed the group *Opisthocomiella*. This taxon is robust and squat, typical of many lice found on the body and head of their hosts. Its highly derived morphology bears superficial resemblance to the Goniodidae that occupy the same ecological niche. However, the compression of the preantennal region makes interpretation the morphology of this region difficult, and consequently it is hard to place this genus confidently in any of the groups outlined in this paper.

Similarly, the unusual morphology of *Acidoproctus* makes the classification of this louse difficult. Timmermann (1962) highlighted the close association of this genus with the louse *Ornithobius* Denny; another parasite of Anseriformes (present on swans) and the classification presented in Clay's unpublished key supports this. Clay placed these genera with *Heteroproctus* Harrison, which is probably a subgenus of *Acidoproctus* (Hopkins & Clay, 1952), and *Bothriometopus* Taschenberg, a louse of screamers (Anhimidae: Anseriformes). Although these taxa, with the exception of *Acidoproctus*, were not represented in this study, a preliminary examination of the morphology of the vulval margin and preantennal region of specimens based at the BMNH suggests that these genera are closely related. However, their position within the ischnoceran phylogeny remains uncertain and its association with *Saemundssonia*- and *Philopterus*-complex is unexpected, particularly as *Acidoproctus* lacks many of the gross morphological characteristics common to most members of this clade.

DISCUSSION

Comparative anatomy of the Ischnocera reveals a remarkable level of character diversity that has largely gone unrecognized in previous studies of the avian members of this group. This is, in part, due to conflicting interpretations of homology amongst the major character complexes, and because nymphal material, a considerable source of character variation, has until recently been largely ignored. The research described here lays the groundwork for a generic level revision of the major complexes outlined in this paper, and suggests that morphological character variation is sufficient to facilitate such studies.

The classification scheme tentatively adopted here largely follows that used throughout the various publications of Clay (e.g. 1938, 1940, 1953, 1958) employing genera that typify the morphology of each complex to represent the major groups. These names will be well recognized by the various authorities who work on lice and may form the starting place for a classification once more genera can be studied. Eichler's (1963) scheme is not adopted at this stage because many of the higher taxonomic names he employs are unavailable under the rules of nomenclature. In addition, the vast majority of genera included by Eichler (1963) were not included in this study, making a detailed assessment on the validity of his groups difficult. Nevertheless, for those taxa that are included, Eichler's familial classification is remarkably concordant with the phylogeny presented here. This is despite the criticism that Eichler's scheme was excessively based on the host's classification to be of much practicable use. The tentative classification in Clay's 'unpublished key' and to a slightly lesser extent, that of Blagoveshtchenskii (1956) is also broadly consistent with this phylogeny.

Only Eichler's classification contains any hierarchical structure above the rank of family and it is at this level that the major discrepancy between this scheme and my phylogeny occurs. Eichler (1963) recognized a single major division within the avian Ischnocera, separating the Goniodidae, Heptapsogasteridae and a family of parrot lice (Paragoniocotidae) from all other members of this group. However, this division is not recognized in the phylogeny presented here and only with the inclusion of the *Lipeurus*- and *Degeeriella*-complex does this group become monophyletic. All members of this clade, with the possible exception of *Neopsittaconirmus*, possess a circumfasciate head from first instar to adult, although the superficial morphology of their abdomen differs considerably. The data presented here suggest that this forms the principal division within the avian Ischnocera, although the circumfasciate clade is not basal in the phylogeny, as might be suggested by Eichler's (1963) assertion that taxa with this head morphology are 'primitive'. Nevertheless, support for most deep nodes in the phylogeny is relatively weak (Bremer support values of 1, 2, and 3) and rests almost entirely on characters of the head, particularly the preantennal characteristics that separate circumfasciate from non-circumfasciate taxa. If these characters were shown to be homoplasious, much of the deep branch resolution would collapse, although the resolution delimiting the generic complexes and families would be retained.

The monophyly of avian Ischnocera is strongly supported in this study (bootstrap and jackknife values of 100, Bremer support 9), however, several key taxa, including the lemur louse genus *Trichophilopterus* and a more distant outgroup (perhaps an amblyceran), are needed before this can be confirmed. At this stage it seems likely that only molecular data will be able to resolve this issue with any certainty, given the difficulty in establishing character homologies at this level with our current understanding of louse morphology.

At least two issues central to the evolution of ischnoceran lice warrant further discussion. The first considers the degree to which they have coevolved with their hosts. As obligate host specific ectoparasites, host phylogeny and ecology underpin louse phylogeny and play a crucial role in interpreting their present distribution. The second issue concerns the role of niche specialization as an aid to understanding the diversification of the major ischnoceran louse clades. Within the circumfasciate and non-circumfasciate lice, subclades can be identified which are putatively adapted to different ecological niches on their hosts. These subclades are characterized by their general body form, which is flattened and elongate in taxa found on the wings, back and occasionally the vane of tail feathers, in contrast to lice from the head, neck and rump feathers which are short, robust and squat. The cladogram presented here (Fig. 17) suggests that at least one of these forms has evolved a minimum of two times within Ischnocera. Convergence in this and other characters may be adaptations to their ecological niche on their hosts or reflect their host's biology. These are considered in the light of the louse phylogeny, helping to provide insight into the morphological adaptation and disparity exhibited by this group.

HOST–PARASITE RELATIONS

Reciprocal natural selection (coevolution) has been demonstrated in host-louse systems at both micro- and macroevolutionary levels. These range from phenotype selection between individual hosts and lice (e.g. Clayton *et al.*, 1992; Clayton *et al.*, 1999) to parallel cladogenesis (cospeciation) of host and louse lineages (e.g. Hafner & Nadler, 1988; Paterson *et al.*, 2000). Broad scale patterns of coevolution and, in particular, instances of cospeciation, are attractive to comparative biologists as they allow events of the same age in host-parasite phylogenies to be identified. These can be used to test hypotheses of coadaptation (Page & Hafner, 1996). However, attempts to assess these patterns in host-louse systems have been confined to the terminal branches of the wider louse tree, due to a paucity of data on the systematics of Phthiraptera. This study provides the first opportunity to assess the broad scale patterns of coevolution across a diverse selection of avian Ischnocera in a manner similar to that of Lyal (1987) for the Trichodectidae of mammals. However, with just over one fiftieth of all avian ischnoceran species sampled in this data set, and less than a third of all avian ischnoceran genera represented, any rigorous study of host-louse cospeciation is clearly ruled out. Therefore, the following discussion is confined to assessing the degree of topological congruence between the major louse and host clades.

The distribution of host orders mapped on to the louse phylogeny is illustrated in Figure 18 and full host details for each louse species included in this study can be found in Appendix 1. A cursory glance at Figure 18 suggests that cospeciation alone cannot explain the current distribution of louse assemblages. Several host orders are represented more than once and there is no immediate correspondence between the louse and host phylogeny. This is not surprising given the wide assortment of hosts represented and the poor sampling of louse taxa. Nevertheless, some immediate trends are apparent from the louse phylogeny, in conjunction with data on the wider distribution of these taxa.

Firstly, every higher bird taxon (orders and isolated families) appears to be infested by a distinctive louse fauna of unmistakable composition. This was also the conclusion of Mauersberger & Mey (1993) based on an extensive survey of the distribution of chewing lice. In many cases these host assemblages of lice are clearly monophyletic, as is the case with the Tinamiform birds of South America that are almost exclusively host to the louse family Heptapsogasteridae. Almost 200 species of this distinctive clade are found on just 39 host species, making this one of the most dramatic radiations of lice on any single bird order. The sympatric occurrence of six to eight species from separate genera on a single tinamou individual is common, while figures of up to 15 louse species belonging to 12 genera have been reported from one tinamou species (*Tinamus major* (Gmelin)) (Clay, 1949). This suggests a long association between host and parasite, providing ample opportunity for resource partitioning necessary to support so many members of this louse clade.

Lice of the Psittaciformes (parrots, cockatoos and relatives) provide a similar example although their radiation is far less dramatic than that of the Heptapsogasteridae. They are host to eight ischnoceran genera, which are almost exclusively confined to this distinctive bird group (Guimarães, 1974). The data

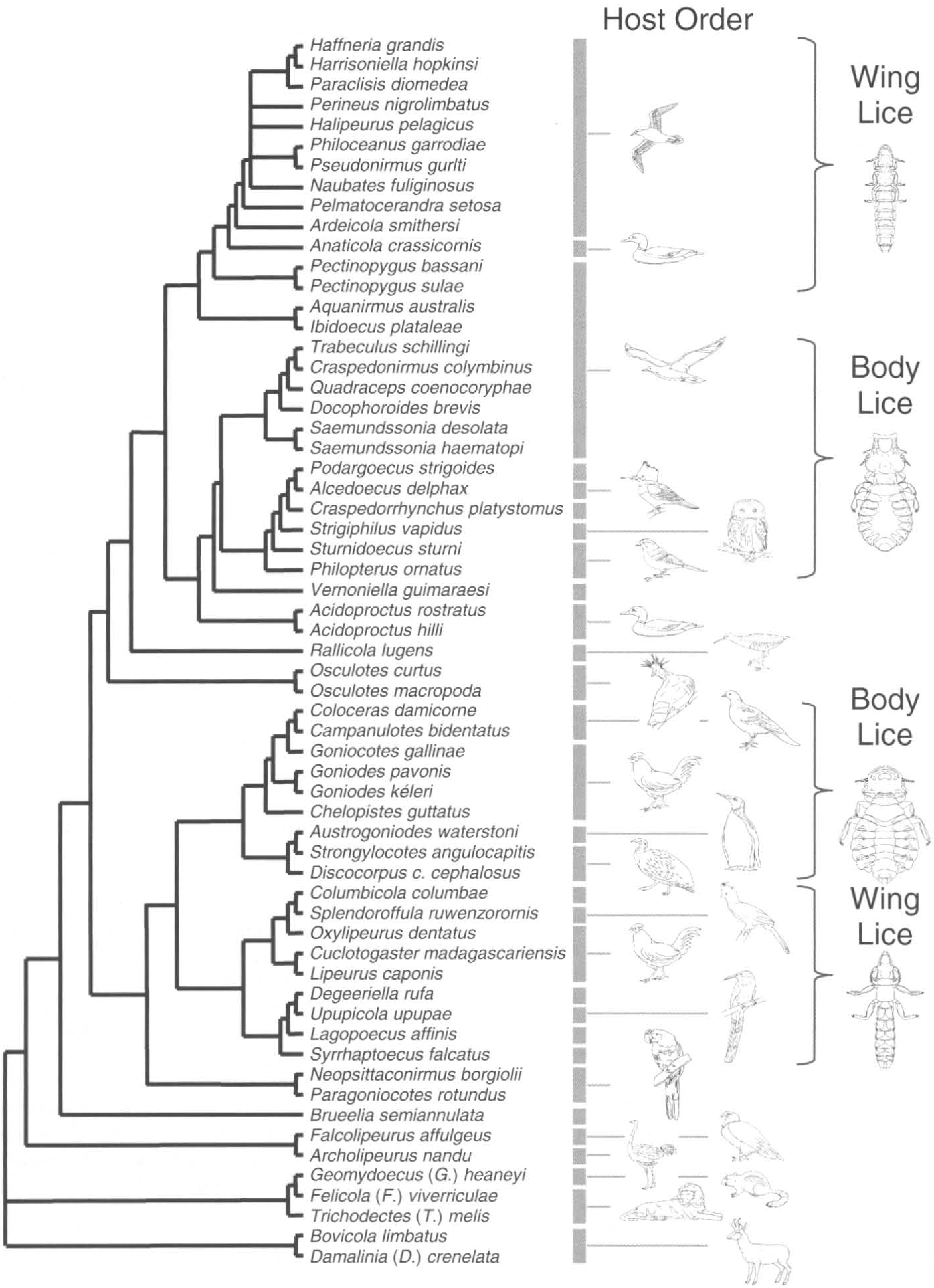

Figure 18. Host associations mapped on to a strict consensus of the three most parsimonious trees. The grey vertical bar delimits host order. The principal ecological niche of the major avian louse clades is also indicated.

presented here suggest that two of the more disparate genera (*Paragoniocotes* and *Neopsittaconirmus*) form a monophyletic group. However, only with improved sampling will the question of monophyly for all these genera be resolved.

The lice of the hoatzin are a good example of a case where overzealous use of the host classification may have unduly influenced the classification of their lice. Two ischnoceran genera have been reported from this unusual host, of which *Osculotes* has long been considered a member of the Goniodidae, a group principally confined to galliform birds. This would agree with the traditional classification of the hoatzin that placed this bird near the Cracidae (Galliformes), but is in conflict with recent molecular data which suggests an association with the Cuculiformes (Sibley & Ahlquist, 1990) or the turacos (Musophagiformes) (Hughes & Baker, 1999). The phylogeny presented here does not support the goniodid relationship, and instead places *Osculotes* as the sister taxon to a large clade of lice, none of which are present on Galliformes, Cuculiformes or Musophagiformes.

In many cases the louse fauna of some host groups are clearly not monophyletic. Often bird clades may be host to several distinct clades of ischnoceran lice. For example, galliform lice include most members of the Goniodidae and *Lipeurus*-complex, not to mention several menoponid lice of the Amblycera. Interestingly, columbiform birds (pigeons and doves) are host to lice from all three of these groups, suggesting a phylogenetic or ecological affinity between these hosts that predates the radiation of these lice. These ischnoceran columbiform lice include *Columbicola* and the closely related *Turturicola* from the *Lipeurus*-complex and a distinct clade of goniodid lice, represented in this phylogeny by *Coloceras* and *Campanulotes*.

A large radiation of ischnoceran lice occurs on procellariiform seabirds. These are host to the *Philoceanus*-complex, in addition to several members of the *Saemundssonia*-complex that are also found on charadriiform seabirds. Despite the high densities and colonial nesting habits of their hosts, these lice are highly host specific and reported instances of 'straggling' (cases where ectoparasites are found on 'unusual' hosts) are remarkably low (Furness & Palma, 1991). Early studies by comparative parasitologists such as Timmermann (1965) asserted that the distribution of procellariiform lice strongly supported the phylogeny of their hosts, and this has been confirmed by recent molecular and morphological data (Paterson, Gray & Wallis, 1993; Paterson, Gray & Wallis, 1995; Paterson *et al.*, 2000). The phylogeny presented here is relatively unresolved within the *Philoceanus*-complex, however several interesting points can be gleaned from those nodes that are resolved. In particular, the sister group relationship between *Haffneria* of skuas (Stercorariidae) and *Harrisoniella* on albatrosses (Diomedeidae) is strongly supported in the cladogram. This is despite the distant relationship between their hosts (in separate orders) and highlights a likely host switch within this clade, perhaps a result of the similar environment provided by their hosts. Interestingly, *Paraclisis*, the sister taxon to this clade, is present on both albatrosses and giant petrels (*Macronectes* sp.) (both Procellariiformes) possibly suggesting that these lice are adapted to large hosts.

Members of the *Philopterus*-complex are found on a diverse assemblage of host groups. These include the songbirds (Passeriformes) whose lice are particularly poorly represented in the phylogeny, largely because they are host to a small number of genera that contain numerous morphologically diverse species. These taxa have been neglected taxonomically and several genera (e.g. *Philopterus* and *Brueelia*) may prove para- or polyphyletic when subjected to increased sampling.

These data suggest that association by colonization (host switching) as opposed to association by descent (cospeciation) plays a key role in the historical ecology of host-louse assemblages. However, the extent to which either of these processes can explain the distribution of ischnoceran lice remains unclear. Other processes including lineage sorting due to louse extinction or a patchy distribution of lice amongst host taxa are also likely to be major factors shaping host-louse assemblages (Hopkins, 1942; Clay, 1949; Paterson, Palma & Gray, 1999). Only with phylogenies that incorporate more extensive sampling than was possible here will the relative importance of these processes be established. To this end, molecular data offers the best prospect for unravelling these complex associations. Not because these are inherently better than morphological data, but because they permit comparisons of host and parasite divergence using comparable units (i.e. base pairs from homologous host and parasite genes) (Hafner & Page, 1995). They also allow us to distinguish between the two primary explanations of incongruent host-parasite phylogenies—host switching and multiple lineages (Page, Clayton & Paterson, 1996). These data, in conjunction with a sound knowledge of the ecology and comparative morphology of lice, are crucial to understanding the factors that influence the diversification of this group.

NICHE SPECIALIZATION

Most lice spend their entire life history on a single host individual and are highly adapted to their host environment. These adaptations have been proposed as barriers that help to maintain host specificity and are likely to play a key role in understanding patterns of louse diversification. The phylogeny presented here strongly suggests that louse assemblages on many host species are not monophyletic and instead comprise groups that are not closely related. Consequently, niche specialization within a host species is also likely to influence parasite diversity, providing an opportunity to investigate the host characteristics that may be correlated with louse diversification, and the evolution of specialization within this parasite group.

The habitat of bird lice (i.e. the host's plumage) is diverse, composed of several types of feathers that are adapted for specific tasks on their host, including insulation, provision of a flight surface and protection of the skin. These present lice with a range of habitats to occupy, providing the raw material for niche specialization. Our knowledge of the territory for most lice is lamentably small; however, two apparent niches have been noted which are occupied by distinct types of lice. These are characterized by differences in their general body form. Those occupying the head, neck and in some cases the rump feathers, usually possess a short round abdomen that is not particularly flattened, with short robust legs and a large head. In contrast, lice occupying the wings, back and occasionally the vane of birds tail feathers are usually flattened and elongate, with long thin legs and a smaller elongate head (Rothschild & Clay, 1952). Clay (1949) proposed that these extremes in body form were a response to the preening habits of their host. The 'fat-bodied' forms of the head and neck are out of reach from the host's beak and have no need for rapid movement; instead they are adapted to a relatively sedentary lifestyle. Conversely, those on the wing and back feathers are always in danger of being preened off by their host, and consequently must be able to move rapidly, slipping sideways between the feathers or aligning themselves between the feather barbs to escape the host's beak.

The phylogeny presented here suggests that these major body forms are not monophyletic, and have independently evolved in both the circumfasciate and non-circumfasciate clades of lice. Their combined presence on the same host suggests that these multi-species assemblages have either been associated with their hosts for a long period of time, or have independently colonized their present host. However, testing these hypotheses will require data on the phylogeny of lice that incorporates more extensive sampling than was possible here. This will help to establish whether the 'wing' and 'head/body' clades within the circumfasciate and non-circumfasciate groups are monophyletic, and has implications for studies on the frequency of cospeciation vs host switching (colonization) events.

This crude example of habitat preference is likely to underlie far greater niche specialization in many louse taxa. The diverse morphologies of species assemblages on many hosts in conjunction with their limited host distribution suggest that niche specialization is highly correlated with the diversification of lice. This provides an opportunity to investigate the evolution of specialization within host-louse systems and is also linked to recent studies on louse cophylogeny. For example, it seems likely that cospeciation predominates amongst highly host specific clades. If so, is specialization an evolutionary 'dead end', or can highly host specific clades re-evolve the ability to colonize new hosts? Linked to this are questions on the modes of speciation in lice. If lice speciate sympatrically on the same host, multi-species assemblages confined to single host taxa should be monophyletic. In contrast, niche specialization might predict a high degree of allopatric speciation. In this case, lice adapted to a particular ecological niche on different hosts are likely to be more closely related than those adapted to other niches on the same host.

FURTHER WORK

Robust phylogenies are crucial to answering many of the questions outlined in the previous section. These need to incorporate more extensive sampling than was possible here, however, practical limitations are likely to prohibit the sampling necessary to achieve this. With nearly 2700 described species of avian Ischnocera and undoubtedly many more undescribed taxa, judicious sampling is needed to address questions of cospeciation and coadaptation. The familial and subfamilial groupings outlined in this paper provide the first opportunity to target likely clades of lice, as opposed to host groups which until now have been the only way of identifying possible avian louse clades.

DATA AVAILABILITY

A website containing the data presented in this paper in addition to extensive additional information can be viewed at:
http://taxonomy.zoology.gla.ac.uk/~vsmith/papers/ischnocera/

The full data matrix includes detailed notes and observations on the character states and taxon attributes. These are supplementary to the descriptions in this paper and can be downloaded in NEXUS format from this site. Character and taxon illustrations accompany these descriptions and can also be downloaded. A summary of the morphometric data used to help establish the instar status for the taxa examined can be viewed in PDF format and links to accompanying data, including an image library containing 600 scanning electron micrographs of 23 ischnoceran genera, are available. The data matrix and cladograms described in this paper are also available from TreeBASE:

http://www.herbaria.harvard.edu/treebase/, study accession # S535.

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Appendix 1. Taxa included in the cladistic analysis. Hosts for the material examined are also listed. Abbreviations: Brit. Mus. refers to the British Museum of Natural History accession number. Mein. # refers to the Meinertzhagen number attached to the slide. Hop. Coll. refers to slides from the Hopkins collection. Recent evidence (Knox, 1993) has shown that on more than one occasion Meinertzhagen fabricated data on the collection of birds. Whilst there is no evidence to suggest that this problem extends to his collection of chewing lice, this fact should be remembered when considering the host affiliations of this material.

Genus and species/subsp.	Authority	Host and Authority	Host common name	Material examined	Slide code #	No. of slides
Bovicola (Bovicola) limbatus	(Gervais, 1844)	Goat [presumably *Capra hircus* (L., 1758)]	Goat, Wild and Angora variety	2 adult ♂ and 2 adult ♀; 6 N III, 9 N II [2 ?] and 3 N I	Brit. Mus. 1966-266, 1967-65 and 1967-678	4
Damalinia (Damalinia) crenelata	(Piaget, 1880)	*Damaliscus dorcas* (Pallas, 1767) [= *D. pygargus*]	Bontebok	2 adult ♂ and 2 adult ♀; 6 N III, 9 N II and 8 N I	Brit. Mus. 1972-19, 1973-184 and 1975-51	4
Trichodectes (Trichodectes) melis	(Fabricius, 1805)	*Meles meles* (L., 1758)	Eurasian Badger	2 adult ♂ and 2 adult ♀; 4 N III and 2 N II	2 unlabelled slides	2
Felicola (Felicola) viverriculae	(Stobbe, 1913)	*Viverricula indica* (Desmarest, 1804)	Unknown	3 adult ♂ and 3 adult ♀; 5 N III, 5 N II and 1 N I	Brit. Mus. 1974-286	4
Geomydoecus (Geomydoecus) heaneyi	Timm and Price, 1980	*Geomys bursarius* (Shaw, 1800)	Plains Pocket Gopher	3 adult ♂ and 3 adult ♀; 4 N III, 3 N II and 9 N I	Brit. Mus. 1981-529	1
Discocorpus c. cephalosus	Carriker, 1936	*Crypturellus noctivagus* ssp. (Weid, 1820)	Yellow-legged Tinamou	2 adult ♂ and 1 adult ♀	Brit. Mus. 1968-730	1
Strongylocotes angulocapitis	Carriker, 1936	*Tinamus major* (Gmelin, 1789)	Great Tinamou	1 adult ♂ and 1 adult ♀; 1 immature adult, 1 N II and 1 N I	Brit. Mus. 1968-644	3
Chelopistes guttatus	(Carriker, 1945)	*Odontophorus c. capueira* (Spix, 1825)	Spot-winged Wood-Quail	1 adult ♀	Mein. # 17705	1
Chelopistes sp.	Kéler, 1939	*Odontophorus c. capueira* (Spix, 1825)	Spot-winged Wood-Quail	1 N III, 3 N II and 1 N I	Brit. Mus. 1971-540	1
Goniodes pavonis	(L., 1758)	*Pavo cristatus* L., 1758	Indian Peafowl	2 adult ♂ and 3 adult ♀; 5 N III, 3 N II and 4 N I	Brit. Mus. 1967-599 (×2), Brit. Mus. 1970-370 and 1 unlabelled slide	4
Goniodes keleri	Clay, 1940	*Margaroperdix madagarensis* (Scopoli, 1786)	Madagascar Partridge	1 adult ♂ and 1 adult ♀; 3 N III, 1 N II? and 1 N I	Brit. Mus. 1966-641, Brit. Mus. 1971-10	2
Coloceras damicorne	(Nitzsch, 1866)	*Columba livia* Gmelin, 1789 and *Columba palumbus* L., 1758	Rock Pigeon/Common Pigeon	6 adult ♂ and 15 adult ♀; 2 N III and 2 N II	Mein. # 11489, 15038, 15052, 16754 and 16778-9; Brit. Mus. 1930-232 and 1967-154	5
Campanulotes bidentatus	(Scopoli, 1763)	*Columba palumbus* L., 1758 plus two slides listed domestic pigeon	Common Wood-Pigeon	4 adult ♂ and 3 adult ♀; 2 N III?	Brit. Mus. 1965-592, Brit. Mus. 1967-154	2
Goniocotes gallinae	(De Geer, 1778)	Chicken [presumably *Gallus gallus* (L., 1758)]	Red Junglefowl	1 adult ♂ and 5 adult ♀; 2 N III, 1 N II and 2 N I	Brit. Mus. 1975-564, 1980-40 and 1968-383	3
Osculotes curtus	(Burmeister, 1838)	*Opisthocomus hoazin* (Müller, 1776)	Hoatzin	3 adult ♂ and 3 adult ♀; 1 immature adult and 1 N II	Brit. Mus. 1961-188, 1921-433; Mein. # 12617	4
Osculotes macropoda	(Guimarães, 1940)	*Opisthocomus hoazin* (Müller, 1776)	Hoatzin	2 adult ♂ and 1 adult ♀; 1 N III and 1 N II	Brit. Mus. 1955-661, 1961-188	2
Austrogoniodes waterstoni	(Cummings, 1914)	*Eudyptula minor* (Forster, 1781)	Little Penguin	4 adult ♂ and 3 adult ♀; 12 N III, 3 N II and 4 N I	Brit. Mus. 1959-667, 1968-431, 1973-49	6
Neopsittaconirmus borgiolii	Conci, 1942	*Calyptorhynchus banksii* (Latham, 1790), *Calyptorhynchus [funerus] funerus* (Shaw, 1794) and *Calyptorhynchus [funerus] baudinii* Lear, 1832	Red-Tailed Black-Cockatoo, Yellow-Tailed Black-Cockatoo and Long-Billed Black-Cockatoo	3 adult ♂ and 3 adult ♀ [+1 dissected ♂]; 6 N III, 5 N II and 1 N I	Brit. Mus. 1962-18, 1968-292, 1968-293 and 1975-81	7
Paragonicotes rotundus	Guimarães, 1947	*Amazona amazonica* (L., 1766)	Orange-Winged Parrot	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 1 N III and 1 N II	Brit. Mus. 1961-188 and 1 unlabelled slide	3
Falcolipeurus affulgeus ? (probably *F. suturalis*)	(Rudow, 1869)	*Aquila audax* (Latham, 1801)	Wedge-Tailed Eagle	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 7 N III [1 ?] and 3 N II	Mein. # 11134 and 4 unlabelled slides	5
Archolipeurus nandu	(Eichler, 1950)	*Rhea americana* (L., 1758)	Greater Rhea	2 adult ♂ and 2 adult ♀ [+1 dissected ♂]; 4 N III, 8 N II and 7 N I	Brit. Mus. 1967-142	3
Cuclotogaster madagascariensis	(Mjöberg, 1910)	*Margaroperdix madagarensis* (Scopoli, 1786)	Madagascar Partridge	5 adult ♂ and 12 adult ♀; 5 N III and 2 N II	Brit. Mus. 1966-641; Mein. # 12518	2

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Appendix 1—*continued*

Genus and species/subsp.	Authority	Host and Authority	Host common name	Material examined	Slide code #	No. of slides
Lipeurus caponis	(L., 1758)	Domestic chicken, *Gallus gallus* (L., 1758) and *Gallus gallus jabouillei* ?	Red Junglefowl	8 adult ♂ and 7 adult ♀ [+2 dissected ♂]; 3 N III, 5 N II [2 ?] and 3 N I	Brit. Mus. 1968-383, 1968-482 and 1974-2; Mein. # 3847	7
Oxylipeurus dentatus	(Sugimoto, 1934)	*Gallus gallus* (L., 1758)	Red Junglefowl	2 adult ♂ and 5 adult ♀; 6 N III, 3 N II and 2 N I	Brit. Mus. 1968-292, 1969-396 and 1971-292	4
Splendoroffula ruwenzorornis	Kéler, 1955	*Tauraco* [*hartlaubi*] *hartlaubi* (Fischer and Reichenow, 1884)	Hartlaub's Turaco	1 adult ♂ and 1 adult; 1 immature adult, 6 N II and 1 N I	Brit. Mus. 1970-618	3
Syrrhaptoecus falcatus	Waterston, 1928	*Pterocles exustus* Temminck, 1825	Chestnut-Bellied Sandgrouse	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 2 N III and 1 N II	Brit. Mus. 1969-96	3
Degeeriella rufa	(Burmeister, 1838)	*Falco berigora* Vigors and Horsfield, 1827	Brown Falcon	2 adult ♂ and 2 adult ♀; 11 N III, 8 N II and 4 N I	Brit. Mus. 1968-431, 1971-449	5
Lagopoecus affinis	(Children, 1836)	*Lagopus lagopus scoticus* (Latham, 1789)	Red Grouse	3 adult ♂ and 5 adult ♀; 5 N III, 2 N II and 1 N I	Brit. Mus. 1963-501, 1964-102, 1967-154	5
Upupicola upupae	(Schranh, 1803)	*Upupa epops* L., 1758 and *Upupa epops africana* Bechstein, 1811	Eurasian Hoopoe and African Hoopoe	4 adult ♂ and 4 adult ♀; 2 N III, 4 N II and 3 N I	Brit. Mus. 1960-233; Mein. # 4719-4721 and 1 unlabelled slide	3
Pectinopygus bassani	(O. Fabricius, 1780)	*Morus* [*bassanus*] *serrator* (Gray, 1843)] and *Morus* [*bassanus*] *bassanus* (L., 1758)	Australian Gannet and Northern Gannet	12 adult ♂ and 20 adult ♀ [+1 dissected ♂]; 13 N III [1 ?], 15 N II [3 ?] and 3 N I	Brit. Mus. 1958-194, 1960-268, 1961-674, 1968-751, 1968-752 and 1971-137; Mein. # 10700 and 11291	8
Pectinopygus sulae	(Rudow, 1869)	*Sula sula* (L., 1766)	Red-Footed Booby	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 5 N II and 2 N I	Brit. Mus. 1968-333 and 1969-625	3
Harrisoniella hopkinsi	Eichler, 1962	*Diomedea exulans* L., 1758	Wandering Albatross	2 adult ♂ and 2 adult ♀ [+1 dissected ♂]; 1 immature adult, 5 N III and 2 N II	Brit. Mus. 1958-150; Mein. # 11236 and 1 unlabelled slide (Hop. Coll.)	3
Haffneria grandis	(Piaget, 1880)	*Catharacta* [*skua*] *skua* Brünnich, 1764, *Catharacta* [*skua*] *lonnbergi* Mathews, 1912, *Catharacta* [*skua*] *maccormicki* (Saunders, 1893)	Great Skua, Brown Skua and South Polar Skua	3 adult ♂ and 3 adult ♀ [+3 dissected ♂]; 4 N III, 4 N II and 2 N I	Brit. Mus. 1959-299, 1962-724, 1963-331, 1965-203, 1970-208; Mein. # 13733	6
Halipeurus pelagicus	(Denny, 1842)	*Oceanodroma castro* (Harcourt, 1851), *Oceanodroma leucorhoa* (Vieillot, 1818) and *Pelagodroma marina* (Latham, 1780)	Band-Rumped Storm-Petrel, Leach's Storm-Petrel and White-Faced Storm-Petrel	2 adult ♂ and 3 adult ♀; 3 N III, 8 N II [1 ?] and 2 N I	Brit. Mus. 1961-188, 1968-53, 1968-752, 1974-307; Mein. # 10980	6
Paraclisis diomedea	(J. C. Fabricius, 1775)	*Diomedea cauta cauta* Gould, 1841, *Diomedea cauta salvini* (Rothschild, 1893), *Diomedea melanophris* Temminck, 1828, *Diomedea chrysostoma* Forster, 1785 and *Phoebetria fusca* (Hilsenberg, 1822)	Shy Albatross, Salvin's Albatross, Black-Browed Albatross, Grey-Headed Albatross and Sooty Albatross	9 adult ♂ and 10 adult ♀; 5 N III [1 ?], 10 N II [2 ?] and 3 N I	Brit. Mus. 1958-660, 1969-48, 1969-166, 1971-450, 1974-307 and 1 unlabelled slide (Hop. Coll.)	6
Naubates fuliginosus	(Taschenberg, 1882)	*Procellaria* [*aequinoctialis*] *aequinoctialis* L., 1758, *Procellaria* [*aequinoctialis*] *steadi* (?) and *Procellaria cinerea* Gmelin, 1758	White-Chinned Petrel and Grey Petrel	7 adult ♂ and 8 adult ♀ [+1 dissected ♂]; 12 N III, 7 N II and 1 N I	Brit. Mus. 1951-171, 1960-199, 1962-725 and 1970-208; Mein. # 19198 and 19201 and 1 unlabelled slide	8
Pelmatocerandra setosa	(Giebel, 1876)	*Pelecanoides urinatrix* (Gmelin, 1789)	Common Diving-Petrel	4 adult ♂ and 13 adult ♀; 1 N III, 6 N II and 2 N I	Brit. Mus. 1951-252, 1966-28, 1967-339, 1973-409 and 1 unlabelled slide	6
Perineus nigrolimbatus	(Giebel, 1874)	*Fulmarus* [*glacialis*] *glacialis* (L., 1761)	Northern Fulmar	14 adult ♂ and 21 adult ♀; 1 immature adult, 5 N III, 3 N II and 1 N I	Mein. # 2478, 11522, 11541-3, 20345 and 1 unlabelled slide	5
Philoceanus garrodiae	(Clay, 1940)	*Garrodia nereis* (Gould, 1841)	Grey-Backed Storm-Petrel	1 adult ♂ and 3 adult ♀ [+1 dissected ♂]; 8 N III and 7 N II	Brit. Mus. 1963-738, 1967-89, 1970-187 and 1970-208	6
Pseudonirmus gurlti	(Taschenberg, 1882)	*Daption capense* (L., 1758)	Cape Petrel	1 adult ♂ and 1 adult ♀; 1 immature adult, 4 N III, 4 N II and 6 N I	Brit. Mus. 1969-48, 1973-204 and 1973-409	4
Trabeculus schillingi	Rudow, 1866	*Pterodroma* [*mollis*] *mollis* (Gould, 1844)	Soft-Plumaged Petrel	1 adult ♂ and 2 adult ♀ [+1 dissected ♂]; 3 N III, 12 N II and 5 N I [1 ?]	Brit. Mus. 1953-360, 1970-187 and 1970-208	6

continued

Appendix 1—*continued*

Genus and species/subsp.	Authority	Host and Authority	Host common name	Material examined	Slide code #	No. of slides
Craspedonirmus colymbinus	(Denny, 1842)	*Gavia stellata* (Pontoppidan, 1763) and *Gavia* [*arctica*] *arctica* (L., 1758)	Red-Throated Loon and Black-Throated Loon	2 adult ♂ and 15 adult ♀ [+3 dissected ♂]; 4 N III, 3 N II and 4 N I	Mein. # 10716 and 20298	7
Quadraceps coenocoryphae	Timmemann, 1955	*Coenocorypha aucklandica* (Gray, 1845), *Coenocorypha* [*aucklandica*] *pusilla* (Butler, 1869) and *Coenocorypha aucklandica huegeli* ?	Subantarctic Snipe and Chatham Island Snipe	3 adult ♂ and 2 adult ♀ [+1 dissected ♂]; 6 N III [1 ?], 4 N II and 5 N I	Brit. Mus. 1963-738, 1967-339 and 1970-208	6
Saemundssonia desolata	Timmemann, 1959	*Pachyptila belcheri* (Mathews, 1912), *Pachyptila* [*vittata*] *desolata* (Gmelin, 1789), *Pachyptila* [*vittata*] *vittata* (Forster, 1777) and *Pachyptila* [*vittata*] *salvini* (Mathews, 1912)	Slender-Billed Prion, Antarctic Prion, Broad-Billed Prion and Medium-Billed Prion	2 adult ♂ and 1 adult ♀; 3 N III, 5 N II [1 ?] and 2 N I ?	Brit. Mus. 1969-48, 1970-619, 1971-450 and 1974-278	6
Saemundssonia haematopi	(L., 1758)	*Haematopus ostralegus occidentalis* ?	Unknown	7 adult ♂ and 8 adult ♀; 1 immature adult and 3 N III	Mein. # 194.277, 15035	2
Docophoroides brevis	(Dufour, 1835)	*Diomedea exulans* (L., 1758) and *Diomedea epomophora* Lesson, 1825	Wandering Albatross and Royal Albatross	4 adult ♂ and 3 adult ♀; 4 N III, 11 N II and 8 N I [+1 set of adult mouth parts]	Brit. Mus. 1963-331, 1969-166; Mein. # 3703, 16263, 2 unlabelled slides and 1 unlabelled slide (Hop. Coll.)	8
Rallicola lugens	(Giebel, 1874)	*Porphyrio porphyrio melanotus* Temminck, 1820 and *Porphyrio porphyrio* (L., 1758)	Eastern Swamphen and Purple Swamphen	15 adult ♂ and 26 adult ♀ [+3 dissected ♂]; 1 immature adult, 5 N III, 6 N II and 1 N I	Brit. Mus. 1964-1, 1964-10, 1964-162, 1968-401; Mein. # 8609 and 12535	8
Aquanirmus australis	Kettle, 1974	*Podiceps* [*poliocephalus*] *poliocephalus* (Jardine & Selby, 1827)	Hoary-Headed Grebe	2 adult ♂ and 2 adult ♀; 1 immature adult, 1 N III and 1 N I	Brit. Mus. 1972-320	3
Columbicola columbae	(L., 1758)	*Columba livia* Gmelin, 1789	Feral Pigeon	9 adult ♂ and 8 adult ♀ [+2 dissected ♂]; 2 N II and 16 N I	Brit. Mus. 1964-685, 1964-687, 1967-678 and 2 unlabelled slides	6
Anaticola crassicornis	(Scopoli, 1763)	*Anas* [*superciliosa*] *superciliosa* Gmelin, 1789, *Anas undulata* Dubois, 1837 and *Anas* [*platyrhynchos*] *platyrhynchos* L., 1758	Pacific Black Duck, Yellow-Billed Duck and Mallard	4 adult ♂ and 4 adult ♀ [+2 dissected ♂]; 3 N III, 4 N II and 4 N I	Brit. Mus. 1954-694, 1961-670, 1962-187 and 1968-431	7
Ardeicola smithersi	Büttiker, 1967	*Platalea alba* Scopoli, 1786	African Spoonbill	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 3 N II	Brit. Mus. 1951-171; Mein. # 7604 and 1 unlabelled slide	4
Ibidoecus plataleae	(Denny, 1842)	*Platalea alba* Scopoli, 1786, *Platalea* [*leucorodia*] *regia* Gould, 1838 and *Platalea* [*leucorodia*] *leucorodia* L., 1758	African Spoonbill, Royal Spoonbill and Eurasian Spoonbill	10 adult ♂ and 3 adult ♀ [+2 dissected ♂]; 5 N III, 3 N II and 3 N I	Brit. Mus. 1952-143, 1954-619, 1965-304, 1969-535; Mein. # 4989, 7605, 18609 and 1 unnumbered Mein. slide	8
Acidoproctus rostratus	(Rudow, 1866)	*Dendrocygna viduata* (L., 1766)	White-Faced Whistling-Duck	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 2 N III, 7 N II and 1 N I	Brit. Mus. 1960-295, 1961-188 and 1 unlabelled slide	5
Acidoproctus hilli	(Harrison, 1915)	*Anseranas semipalmata* (Latham, 1798)	Magpie Goose	6 adult ♂ and 5 adult ♀ [+1 dissected ♂]; 2 N III	Brit. Mus. 1968-752; Mein. # 8002	3
Craspedorrhynchus platystomus	(Burmeister, 1838)	*Buteo* [*buteo*] *oreophilus* Hartlaub & Neumann, 1914 and *Buteo* [*buteo*] *buteo* (L., 1758)	Mountain Buzzard and Common Buzzard	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 4 N III, 6 N II and 3 N I	Brit. Mus. 1963-8 and 1970-618	5
Strigiphilus vapidus	Clay, 1977	*Ninox novaeseelandiae* (Gmelin, 1788)	Morepork	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 4 N III, 6 N II and 8 N I	Brit. Mus. 1968-431, 1968-752 and 1974-278	5
Podargoecus strigoides	Emerson & Price, 1966	*Podargus strigoides* (Latham, 1801)	Tawny Frogmouth	2 adult ♂ and 2 adult ♀; 5 N III, 9 N II and 4 N I	Brit. Mus. 1968-293, 1969-565 and 1970-619	5
Alcedoecus delphax	(Nitzsch, 1866)	*Dacelo gigas* (Boddaert, 1783) [=*Dacelo novaeguineae* (Hermann, 1783)]	Laughing Kookaburra	1 adult ♂ and 1 adult ♀ [+1 dissected ♂]; 4 N III, 7 N II and 4 N I	Brit. Mus. 1968-23, 1969-48 and 1976-469	5
Brueelia semiannulata	(Piaget, 1883)	*Gymnorhina tibicen dorsalis* Cambell, 1895	Western Magpie	2 adult ♂ and 2 adult ♀; 1 immature adult, 8 N III, 18 N II and 7 N I	Brit. Mus. 1968-293, 1968-298, 1969-595, 1971-450	7
Sturnidoecus sturni	(Shrank, 1776)	*Sturnus vulgaris* (L., 1758) and *Turdus musians* ?	Common Starling	1 adult ♂ and 1 adult ♀; 2 N III, 6 N II and 5 N I	Brit. Mus. 1962-18, 1966-330, 1968-401	3
Vernoniella guimaraesi	Thompson, 1948	*Crotophaga ani* L., 1758	Smooth-Billed Ani	2 adult ♂ and 5 adult ♀; 9 N III, 7 N II and 2 N I	Brit. Mus. 1961-188 and 1 unlabelled slide; Mein. # 10830	5
Philopterus ornatus	(Nitzsch, 1866)	*Oriolus oriolus* (L., 1758)	Eurasian Golden-Oriole	2 adult ♂ and 3 adult ♀; 2 N III and 9 N II	Brit. Mus. 1962-325	5

APPENDIX 2

CHARACTER LIST AND OBSERVATIONS

Figure references list the principal illustration/s that described each character state. However, inspection of the data matrix will show that in many cases these states are also illustrated in supplementary figures that document the morphology of other characters. These serve to show the variable morphology of the states. All multistate character states are unordered. Character states that are phylogenetically uninformative for the taxa examined are marked with an asterisk. Characters 130–138 were based on comments in Clay's unpublished key and data drawn from Blagoveshtchenskii (1956).

HEAD

Preantennal

1. *Adult hyaline margin*: **(0)** absent or greatly reduced, forming a thin margin running anteriorly around the marginal carina (Fig. 2B); **(1)** confined to a medial indent in the marginal carina, not evident laterally; **(2)** confined medially between or around the premarginal carina and usually continuous with the dorsal preantennal suture (Fig. 2H); **(3)** expanded and enlarged, enclosing the premarginal carina and filling the premarginal region anteriorly (Fig. 2D).

The full extent of the hyaline margin is often only visible in phase contrast, particularly in those taxa where the hyaline margin is greatly expanded. Its morphology is highly dependent upon the shape of the preantennal region. Circumfasciate heads usually possess a thin margin which is most evident medially, cf. non-circumfasciate forms where its morphology is highly variable.

2. *Adult marginal carina*: **(0)** forms a complete thickened band running anteriorly around the preantennal region of the head (Fig. 2B); **(1)** forms a band which is interrupted laterally (partially or completely), medially (dorsally and/or ventrally) or both (Fig. 2I).

In some cases the marginal carina may be considered complete despite the absence of a definite anterior band if the anterior sclerotization of the head is unbroken (e.g. *Episbates* Harrison, see Clay, 1951a). A medial indent in the anterior margin also does not necessarily mean that the marginal carina is broken e.g. *Brueelia* spp. The form of the marginal carina is inseparably linked to almost all other preantennal characters. Mey (1994) considers circumfasciate taxa (with a complete marginal carina) to represent the 'original' head morphology, whilst taxa with a non-circumfasciate head (with an interrupted marginal carina) as derived.

3. *Adult marginal carina (if interrupted)*: **(0)** ventrally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region ventrally but complete dorsally (Fig. 2C); **(1)** dorsally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region dorsally but complete ventrally* (Fig. 2G); **(2)** completely interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region (Fig. 2E); **(3)** interrupted laterally (either partially or completely) but not interrupted medially* (Fig. 2I); **(4)** interrupted laterally (either partially or completely) and completely interrupted medially (Fig. 2A).

This may be interrupted laterally and/or medially to varying degrees. Lateral interruption may be partial or complete, allowing the marginal carina to be divided into its pre- (anterior) and post- (posterior) marginal regions.

4. *Adult premarginal carina*: **(0)** seamlessly continuous with the postmarginal carina (Fig. 2B); **(1)** greatly reduced or absent* (Fig. 2F); **(2)** present and partially attached (not seamlessly continuous) to the postmarginal carina (Fig. 2H); **(3)** present and completely separate from the postmarginal carina (Fig. 2D).

In the case of the lateral interruption, the ventral anterior end of the postmarginal carina may extend forward under the dorsal posterior portion of the premarginal carina before terminating. This gives the appearance that the marginal carina is only partially interrupted laterally. However, only in cases where the postmarginal carina is clearly still attached to the premarginal carina should this thickening be scored thus.

5. *N III marginal carina*: **(0)** forms a complete thickened band running anteriorly around the preantennal region of the head; **(1)** forms a band which is interrupted laterally (partially or completely), medially (dorsally and/or ventrally) or both.

6. *N III marginal carina (if interrupted)*: **(0)** ventrally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region ventrally but complete dorsally; **(1)** dorsally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region dorsally but complete ventrally; **(2)** completely interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region; **(3)** interrupted laterally (either partially or completely) but not interrupted medially*; **(4)** interrupted laterally (either partially or completely) and completely interrupted medially.

7. *N III premarginal carina*: **(0)** seamlessly continuous with the postmarginal carina; **(1)** greatly reduced or absent*; **(2)** present both dorsally and ventrally, although not seamlessly continuous with the postmarginal carina; **(3)** present and completely separate from the postmarginal carina.

8. *N II marginal carina*: **(0)** forms a complete thickened band running anteriorly around the preantennal region of the head; **(1)** forms a band which is interrupted laterally (partially or completely), medially (dorsally and/or ventrally) or both.

9. *N II marginal carina (if interrupted)*: **(0)** ventrally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region ventrally but complete dorsally; **(1)** dorsally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region dorsally but complete ventrally; **(2)** completely interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region; **(3)** interrupted laterally (either partially or completely) but not interrupted medially; **(4)**

interrupted laterally (either partially or completely) and completely interrupted medially.

10. *N II premarginal carina*: **(0)** seamlessly continuous with the postmarginal carina; **(1)** greatly reduced or absent*; **(2)** present both dorsally and ventrally, although not seamlessly continuous with the postmarginal carina; **(3)** present and completely separate from the postmarginal carina.

11. *N I marginal carina*: **(0)** forms a complete thickened band running anteriorly around the preantennal region of the head; **(1)** forms a band which is interrupted laterally (partially or completely), medially (dorsally and/or ventrally) or both.

12. *N I marginal carina (if interrupted)*: **(0)** ventrally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region ventrally but complete dorsally; **(1)** dorsally interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region dorsally but complete ventrally; **(2)** completely interrupted medially, so that the marginal carina is restricted to both sides of the preantennal region; **(3)** interrupted laterally (either partially or completely) but not interrupted medially; **(4)** interrupted laterally (either partially or completely) and completely interrupted medially.

13. *N I premarginal carina*: **(0)** seamlessly continuous with the postmarginal carina; **(1)** greatly reduced or absent*; **(2)** present both dorsally and ventrally, although not seamlessly continuous with the postmarginal carina; **(3)** present and completely separate from the postmarginal carina*.

14. *Adult male anterior portion of the ante-clypeus*: **(0)** unsculptured, smooth (Fig. 2J); **(1)** covered by numerous horizontal striations (Fig. 2K); **(2)** covered by numerous cresentric markings* (Fig. 2L).

The possession of horizontal striations on the ante-clypeus appears to be a character largely restricted to lice of procellariiform seabirds. These markings are often principally evident ventrally on the ante-clypeus. In *Ardeicola smithersi*, small cresentric markings are present ventrally in this region.

15. *Adult dorsal anterior plate*: **(0)** absent (Fig. 2B); **(1)** present, always delineated anteriorly and laterally but not necessarily posteriorly (Fig. 2M–O).

This plate is only evident in non-circumfasciate taxa where the marginal carina is broken medially and is probably derived from an isolated median portion of the premarginal carina. Its presence serves to stabilize the preantennal region, giving greater plasticity to the head. However, its exact morphology varies considerably, and there may be considerable scope for expanding this character in future studies to consider the shape of the plate in adult stadia and the extent to which it is delimited from the dorsal sclerotization of the head. Note that in some members of the *Philoceanus*-complex, e.g. *Perineus*, the dorsal anterior plate is evident as suggested by the pattern of sclerotization but not delineated from the surrounding cuticle.

16. *Adult dorsal anterior plate (if present)*: **(0)** undivided (Fig. 2M); **(1)** partially divided medially* (Fig. 2N); **(2)** completely separated medially* (Fig. 2O).

This character is not phylogenetically informative for the taxa sampled in this data set.

17. *Adult posterior margin of the dorsal anterior plate (if dorsal anterior plate is present)*: **(0)** not delimited, merges into dorsal sclerotization of the head capsule (Fig. 2M); **(1)** clearly delimited, separated from surrounding cuticle by the dorsal preantennal suture (Fig. 2N–Q).

In some taxa with a dorsal anterior plate the posterior margin may merge with the anterior margin of the dorsal carina. This may be difficult to delimit without phase contrast and is particularly common in taxa where the posterior margin of the plate extends significantly into the postmarginal region of the head.

18. *Adult male posterior prolongation of the dorsal anterior plate (if both the dorsal anterior plate is present and its posterior margin is delimited)*: **(0)** absent, with the posterior margin rounded or slightly pointed but not significantly developed posteriorly (Fig. 2P); **(1)** strongly developed forming a distinct posterior prolongation (Fig. 2Q).

Note that *Ibidoecus* possesses a double posterior prolongation each side, on account of the medial division of the dorsal anterior plate.

19. *N III dorsal anterior plate*: **(0)** absent; **(1)** present but poorly developed, having the appearance of an isolated (either partially or completely) portion of the marginal carina; **(2)** present and well developed (extended posteriorly), always delineated anteriorly and laterally but not necessarily posteriorly.

20. *N II dorsal anterior plate*: **(0)** absent; **(1)** present but poorly developed, having the appearance of an isolated (either partially or completely) portion of the marginal carina; **(2)** present and well developed (extended posteriorly), always delineated anteriorly and laterally but not necessarily posteriorly.

21. *N I dorsal anterior plate*: **(0)** absent; **(1)** present but poorly developed, having the appearance of an isolated (either partially or completely) portion of the marginal carina; **(2)** present and well developed (extended posteriorly), always delineated anteriorly and laterally but not necessarily posteriorly.

22. *N I posterior prolongation of the dorsal anterior plate (if the dorsal anterior plate is present and well developed)*: **(0)** absent. Posterior margin rounded but not developed posteriorly; **(1)** posterior margin strongly pointed but not significantly developed posteriorly*; **(2)** strongly developed forming a distinct posterior prolongation*.

This character is not phylogenetically informative for the taxa sampled in this data set.

23. *Adult male ventral anterior plate*: **(0)** absent; **(1)** present but well developed, forming a distinct plate which is extended posteriorly (Fig. 3J).

In both the adults and the nymphs the plate must be extended posteriorly to be regarded as being present i.e. more than just a faint rim under the dorsal anterior plate.

24. *N III ventral anterior plate*: **(0)** absent; **(1)** present and well developed, forming a distinct plate which is extended posteriorly.

25. *N II ventral anterior plate*: **(0)** absent; **(1)** present and well developed, forming a distinct plate which is extended posteriorly.

26. *N I ventral anterior plate*: **(0)** absent; **(1)** present and well developed, forming a distinct plate which is extended posteriorly.

27. *Adult dorsal preantennal suture*: **(0)** absent, or forms a discrete suture isolated from the marginal carina (Fig. 2R); **(1)** present, arising from the ends of the premarginal carina and divides the dorsal preantennal carina medially* (Fig. 2S); **(2)** developed and enlarged behind the posterior margin of the dorsal anterior plate or marginal carina, but not evident laterally and not arising from the postmarginal carina (Fig. 2T); **(3)** usually arises from the ends of the postmarginal carina and surrounds the dorsal anterior plate at least laterally. Anteriorly it is continuous with the hyaline margin (Fig. 2U).

This suture in circumfasciate and trichodectid taxa usually sits within the dorsal sclerotization of the head and is often hard to delimit. Its position can usually be identified by a pair of distinct anterior dorsal setae which sit within it or close to the sutures margin. In the Trichodectidae the suture may be continuous with a second thin suture which divides the marginal carina medially.

28. *Adult dorsal carina*: **(0)** absent or forms a continuous or medially broken anterior band, dorsally supporting the pre- and postmarginal carina (Fig. 2B); **(1)** expanded premarginally filling the anterior region of the head. Either not evident postmarginally or forms a thin carina above but laterally continuous with the postmarginal carina (Fig. 2V); **(2)** predominantly developed postmarginally, either absent or weakly developed premarginally (Fig. 2Z).

Clay (1951a) makes no reference to the dorsal carina in taxa with a circumfasciate head, instead applying the term to non-circumfasciate taxa where it forms the thickening on the posterior margin of the dorsal preantennal suture. This definition is also adopted by Mey (1994). However, he also considers the thickening that is continuous around the dorsal anterior margin of the head, on the inner margin of the marginal carina as homologous to this structure in circumfasciate taxa. Mey's interpretation is adopted here.

29. *Adult dorsal carina form (if predominantly restricted to the postmarginal region of the head)*: **(0)** restricted to the lateral margins of the head in the region of the postmarginal carina, not expanded across the head*; **(1)** continuous across the head (Fig. 2W); **(2)** broken medially and variably project inward posteriorly forming two parallel bars, although the posterior projection may be weakly sclerotized (Fig. 2X); **(3)** developed medially but not forming a continuous band across the head, present although less well developed premarginally* (Fig. 2Y); **(4)** developed each side from the postmarginal carina, often weakly sclerotized and not forming a definitive carina. May be continuous with the posterior margin of the dorsal anterior plate (Fig. 2Z).

This character refers principally to the thickened dorsal carina. However, when the carina is expanded postmarginally a definitive thickening may not be present. In these cases the dorsal carina is considered homologous with the area of increased sclerotization, marking the posterior boundary of the dorsal preantennal suture.

30. *Adult ventral carina*: **(0)** entire, usually well marked semicircular band around the oral cavity (Fig. 3B); **(1)** interrupted medially forming a broken arch. Usually extends close to but never fuses with the marginal carina and lacks a flattened distal extension (Fig. 3C); **(2)** interrupted medially, each side possess a flattened anterior extension which approaches but does not fuse with the marginal carina (Fig. 3D); **(3)** interrupted medially, each side possess a flattened anterior extension which fuses with a marginal carina that is always interrupted, either completely or only ventrally (Fig. 3A, E); **(4)** joined to the ends of the premarginal carina but appear as bands only anteriorly (Fig. 3F); **(5)** poorly developed, apparently fused with the postmarginal carina* (Fig. 3G).

The ventral carina refers only to the thickened well sclerotized carina which extends both sides from the ventral mandibular framework anteriorly. It is often continuous with the marginal carina via a thin less well sclerotized thickening which merges with the ventral sclerotization of the head. However, this thickening is not considered by the character states listed here. Only if the well sclerotized part of the ventral carina extends to the marginal carina should this character be scored such. This also applies to the equivalent characters describing the condition for nymphal taxa.

31. *N III ventral carina*: **(0)** entire, usually well marked semicircular band around the oral cavity; **(1)** interrupted medially forming a broken arch. Usually extends close to but never fuses with the marginal carina; **(2)** interrupted medially, each side possess a flattened anterior extension which approaches but does not fuse with the marginal carina; **(3)** interrupted medially, each side possess a flattened anterior extension which fuses with a marginal carina that is always interrupted, either completely or only ventrally; **(4)** joined to the ends of the premarginal carina but appear as bands only anteriorly.

32. *N II ventral carina*: **(0)** entire, usually well marked semicircular band around the oral cavity; **(1)** interrupted medially forming a broken arch. Usually extends close to but never fuses with the marginal carina; **(2)** interrupted medially, each side possess a flattened anterior extension which approaches but does not fuse with the marginal carina; **(3)** interrupted medially, each side possess a flattened anterior extension which fuses with a marginal carina that is always interrupted, either completely or only ventrally; **(4)** joined to the ends of the premarginal carina but appear as bands only anteriorly*.

33. *N I ventral carina*: **(0)** entire, usually well marked semicircular band around the oral cavity; **(1)** interrupted medially forming a broken arch. Usually extends close to but never fuses with the marginal carina; **(2)** interrupted medially, each side possess a flattened anterior extension which approaches but does not fuse with the marginal carina; **(3)** interrupted medially, each side possess a flattened anterior extension which fuses with a marginal carina that is always interrupted, either completely or only ventrally; **(4)** joined to the ends

of the premarginal carina but appear as bands only anteriorly*.

34. *Adult pulvinus*: **(0)** single lobe attached to the ventral carina (Fig. 3H); **(1)** divided into two lateral lobes (Fig. 3I).

The morphology of the pulvinus is closely connected to the form of the ventral carina. However, the pulvinus is usually completely hyaline, and its shape can only be delimited in phase contrast by the direction of the thin folds present within this structure.

35. *Adult male coni*: **(0)** undeveloped, marked only by a slight bump before the anterior margin of the antennal socket; **(1)** developed, forming a significant blunt or pointed process extending laterally from the margin of the head. May be hyaline, sclerotized or both.

See comments in the morphology section of this paper for a full discussion of this structure. In some taxa the conus may be greatly expanded, taking on the superficial appearance of a trabecula. This elongation of the conus is only considered for females where the conus may extend beyond the first antennal segment.

36. *Adult female conus*: **(0)** undeveloped, marked only by a slight bump before the anterior margin of the antennal socket (Fig. 4A); **(1)** developed, forming a significant blunt or pointed process extending laterally from the margin of the head. May be hyaline, sclerotized or both (Fig. 4J–L).

37. *Adult female coni morphology (if coni are developed)*: **(0)** shorter or as long as the scape (Fig. 4K, L); **(1)** longer than the scape (Fig. 4J).

38. *Adult trabecula*: **(0)** absent; **(1)** present* (Fig. 4B, L).

See comments in the morphology section of this paper for a full discussion of this structure. This character is not phylogenetically informative for the taxa described in this data set.

39. *Adult transverse carina*: **(0)** absent; **(1)** present, either complete or broken medially (Fig. 2A').

See comments in the morphology section of this paper for a full discussion of this structure. This thickening forms the anterior margin of the postantennal suture and is usually continuous with the postmarginal sclerotization of the head. In some taxa this may form a distinctive thickened carina e.g. *Saemundssonia*. However, in many cases this thickening is not present, and this structure is only delimited on its posterior margin by the postantennal suture, separating it from the sclerotized area over the temporal region. This is usually only evident in phase contrast as a weak line of sclerotization starting each side above the preantennal nodi, often crossing above the base of each mandible. If this line is evident the transverse carina is considered to be present.

40. *Adult marginal pulvinal band*: **(0)** absent; **(1)** present as a distinct band separate from the torma (Fig. 3H, L [not shaded]); **(2)** fused at either end to the ventral carina (Fig. 3K).

If present, this band usually lies in the posterolateral angles of the pulvinus. Note that in the Trichodectidae the band is apparently fused at either end to the ventral carina, whilst in most avian Ischnocera, the band is either detached or absent. This band is not to be confused with the tormae, which when present lie on the posterior margin of the pulvinus.

41. *Adult torma*: **(0)** absent; **(1)** present and distinctly separate from the marginal pulvinal band (Fig. 3H, L [not shaded]).

When present these sclerites are often partially obscured by the mandibles.

42. *Adult pulvinus size*: **(0)** small, unmodified; **(1)** greatly expanded filling the ventral preantennal region (Fig. 3L).

In some taxa the pulvinus may be greatly expanded, filling the bulk of the preantennal region.

43. *N III marginal pulvinal band*: **(0)** absent; **(1)** present as a distinct band separate from the torma; **(2)** fused at either end to the ventral carina.

44. *N III torma*: **(0)** absent; **(1)** present and distinctly separate from the marginal pulvinal band.

Antennal

45. *Male antennal segments*: **(0)** not significantly heteromorphic; **(1)** significantly heteromorphic (Fig. 4E, G–I [not shaded]).

Note comments regarding antennal form in the morphology section of this paper.

46. *Male scape shape based on elliptic Fourier analysis*: **(0)** partition 0, short and rounded; **(1)** partition 1, elongated with lateral process; **(2)** partition 2, elongated without lateral process.

The dendrogram showing the three character state partitions along with illustrations of scape morphology for all the taxa considered in this data set is shown in Figure 5.

47. *Process on anterior lateral margin of the male scape (if antennal segments are significantly heteromorphic)*: **(0)** absent (Fig. 4F, G, I); **(1)** present (Fig. 4E, H).

48. *5–6 microsetae in a row across the length of the male scape*: **(0)** absent (Fig. 4E, F, H, I); **(1)** present (Fig. 4G).

These setae are positioned dorsally towards the posterior margin of the scape.

49. *Male and female pedicel and flagellum/flagellomeres*: **(0)** not covered in numerous fine microsetae (Fig. 4E, G–I); **(1)** covered in numerous fine microseta (Fig. 4F).

50. *Male flagellomeres*: **(0)** unfused (Fig. 4E, H, I); **(1)** fused (Fig. 4F, G).

51. *First flagellomere shape (if antennal segments are significantly heteromorphic and unfused)*: **(0)** unmodified; **(1)** derived, not forming a simple flagellomere (Fig. 4E, H, I).

52. *Subterminal attachment of flagellomeres II and III (if antennal segments are significantly heteromorphic and unfused)*: **(0)** absent (Fig. 4F–I); **(1)** present (Fig. 4E).

53. *Apical compression of flagellomeres II and III (if antennal segments are significantly heteromorphic and unfused)*: **(0)** absent (Fig. 4E–H); **(1)** present (Fig. 4I).

Postantennal

54. *Gular plate*: **(0)** absent; **(1)** present forming a distinct sclerotized region on the ventral surface of the head, although not necessarily clearly delimited.

In some cases the gular plate may only be identified as an area of increased sclerotization in the gular region. This particularly concerns the posterior margin of the plate, which usually merges into the sclerotized area that forms part of the occipital ring on the heads posterior margin.

55. *Gular plate form (if present)*: **(0)** not delimited, only evident as a distinct sclerotized region on the ventral surface of the head (Fig. 3M); **(1)** clearly distinct anteriorly but laterally and posteriorly more or less continuous with the ventral sclerotization of the head (Fig. 3N); **(2)** clearly delimited anteriorly and laterally but not necessarily posteriorly (Fig. 3O).

56. *Anterior margin of the gular plate (if present and delimited)*: **(0)** smoothly rounded (Fig. 3P); **(1)** pointed (Fig. 3A, N, O, Q).

57. *Pointed anterior margin of the gular plate (if present, delimited and has a pointed anterior margin)*: **(0)** completely tapered to a distinct point; **(1)** pointed medially on an otherwise flat anterior margin (Fig. 3N, O); **(2)** pointed medially on an otherwise rounded anterior margin (Fig. 3A, Q).

58. *Marginal temporal carina*: **(0)** thin, forming a more or less evenly thick band around the temples (Fig. 2B′); **(1)** thickened and enlarged, forming a band of uneven thickness around the temporal margin (Fig. 2C′).

There is scope for an intermediate state for this character, differentiating the medium thick margins of the lipeurids from the very thick margins of the goniodid-like taxa and the very thin margins of the *Quadraceps*-like taxa.

59. *Postocular nodus*: **(0)** absent or weakly developed, identifiable as a slight expansion of the marginal temporal carina; **(1)** well developed and enlarged (Fig. 2B′, C′).

60. *Female ocular setal condition*: **(0)** thorn-like or normal microseta; **(1)** normal or macroseta (not thorn-like); **(2)** thorn-like macroseta*.

61. *Female postocular setal condition*: **(0)** thorn-like or normal microseta; **(1)** normal or macroseta (not thorn-like)*; **(2)** thorn-like macroseta.

62. *Female postocular setal position*: **(0)** on the lens of the eye; **(1)** not on the lens of the eye.

Occasionally the postocular seta may be present on the margin of the lens. These instances have been noted in the attribute comments of the full data matrix, along with a justification of the character state scored for that taxon.

63. *Female marginal temporal setal number*: **(0)** three*; **(1)** four; **(2)** five; **(3)** six or more*.

64. *Female dominant marginal temporal setae (for taxa with 5 MTS)*: **(0)** all subordinate microsetae; **(1)** MTS 1 and 3 dominant; **(2)** MTS 2 and 3 dominant; **(3)** MTS 1, 2 and 3 dominant; **(4)** MTS 1, 2, 3 and 5 dominant*; **(5)** MTS 3 dominant; **(6)** MTS 2 and 5 dominant*; **(7)** MTS 3 and 4 dominant*; **(8)** MTS 1–4 dominant; **(9)** MTS 1–5 dominant.

Note that for this and the following characters describing setal pattern, the term dominant refers to those setae which are large and well developed, relative to the other setae on the marginal temporal carina. These may be any of the following setal types: macro ‘normal’ setae, ‘normal’ thorn-like macrosetae and very well developed microsetae. Various patterns of marginal temporal setae are present in Ischnocera, and these are described in the preceding four characters.

65. *Female MTS patterns (where MTS 1 and 3 are dominant)*: **(0)** MTS 1 and 3 dominant microsetae, MTS 2, 4 and 5 microsetae; **(1)** MTS 1 and 3 dominant normal or macrosetae, MTS 2, 4 and 5 microsetae.

66. *Female MTS patterns (where MTS 1, 2 and 3 are dominant)*: **(0)** MTS 1, 2 and 3 dominant normal or microsetae, MTS 4 and 5 microsetae; **(1)** MTS 1 thorn-like macrosetae, MTS 2 and 3 dominant normal or microseta, MTS 4 and 5 microsetae*; **(2)** MTS 1 developed microseta, MTS 2 thorn-like macroseta, MTS 3 dominant macroseta, MTS 4 and 5 thorn-like microseta*.

67. *Female MTS patterns (where MTS 3 is dominant)*: **(0)** MTS 3 dominant microseta, MTS 1, 2, 4 and 5 subordinate microsetae; **(1)** MTS 3 dominant normal or macroseta, MTS 1, 2, 4 and 5 subordinate microsetae.

68. *Female MTS patterns (where MTS 1–5 are dominant)*: **(0)** MTS 1 dominant microseta, MTS 3 normal or microsetae, MTS 2, 4 and 5 thorn-like macrosetae; **(1)** MTS 3 normal or macrosetae, MTS 1, 2, 4 and 5 thorn-like macrosetae*; **(2)** MTS 1–4 normal or macroseta, MTS 5 thorn-like microseta*.

THORACIC

69. *Anterior prothoracic setal distribution*: **(0)** absent or confined to the anterior margin of the prothorax without a disjunct distribution (Fig. 7A); **(1)** not confined to the extreme anterior margin, distribution disjunct (Fig. 7C).

These setae are not to be confused with the two microsetae present on each cervical sclerite.

70. *Rhombic sclerite shape*: **(0)** small discrete oblong, rhombic or rounded sclerite, may be weakly developed or only delimited anteriorly (Fig. 7F); **(1)** medium to large sclerite, may not be strongly delimited (Fig. 7G).

Within most avian Ischnocera the rhombic sclerites are weakly delimited and usually partially fused on their posterior margin to the pronotom.

71. *Mesothoracic spiracle position*: **(0)** ventral sublateral without an enlarged atrium; **(1)** more or less pleural, not sublateral, without extension on a slight lateral protuberance or with an enlarged atrium (Fig. 8F); **(2)** more or less pleural with an enlarged atrium and thickening of the atrial walls (Fig. 8G); **(3)** extended out on a slight lateral protuberance of the prothorax without an enlarged atrium (Fig. 8H).

The mesothoracic spiracle has migrated forward in Phthiraptera and is present on the posterolateral angle of the prothorax. There may be scope for coding the shape of the atrium of this spiracle within generic groups of Ischnocera, as coded by Lyal (1985a) for the Trichodectidae. Note that in most trichodectids the thickening of the atrial walls is often accompanied by some cuticular sclupturing giving a distinctive pattern. A metathoracic thoracic spiracle is present in some Ischnocera (see the morphology section of this paper for a full discussion). This character cannot be clearly observed in slide mounted material and until the full distribution of this character is known, this character is not scored.

72. *Female lateral and/or posterior prothoracic setal arrangement*: **(0)** 0+0*; **(1)** 1+1, may be lateral or sublateral (Fig. 7B); **(2)** 2+2 (Fig. 7C); **(3)** 4+4 or 5+5* (Fig. 7D); **(4)** numerous setae along the lateral and posterolateral margin becoming sub-posterior medially (Fig. 7E).

The post spiracular seta, if present, may be very small and only readily evident from its setal aperture.

73. *Female lateral and/or posterior prothoracic setal position (if a 1+1 arrangement is present)*: **(0)** single setal pair on the lateral or posterior margin, not sublateral; **(1)** single sublateral setal pair slightly anterior to the posterior margin of the prothorax (Fig. 7B).

74. *Proepimeron proximal development*: **(0)** more or less blunt ended (usually rounded) (Fig. 8K); **(1)** expanded (occasionally may be fused across the middle to form a single medial plate) (Fig. 8A–E).

75. *Direction of proximal development of the proepimeron (if expanded)*: **(0)** more or less equally expanded anteriorly and posteriorly (Fig. 8B); **(1)** predominantly anteriorly (towards/into the prothorax) (Fig. 8C); **(2)** predominantly posteriorly (towards the abdomen) (Fig. 7A); **(3)** predominantly posteriorly (towards the abdomen) but partially fused anteriorly (Fig. 8D); **(4)** completely fused medially* (Fig. 8E).

Note that the proximal development may be less well sclerotized than the horizontal portion of the proepimeron.

76. *Small medial sclerite between or beneath the proximal ends of the proepimeron*: **(0)** absent; **(1)** present (Fig. 8A).

77. *Meso-metasternal plate*: **(0)** absent; **(1)** present (Fig. 8I, J).

There may be scope for expanding this character to consider the size, shape and development of this plate. Note that during the slide mounting process this plate is occasionally damaged and may appear slightly displaced.

78. *Second sternal plate*: **(0)** absent; **(1)** present (Fig. 8I, J).

This is the first visible sternal plate and may partially extend under the posterior margin of the pterothorax. This plate is often damaged during the slide mounting process and may be very weakly sclerotized.

79. *Cuticular bridge between the meso-metasternal plate and the 2nd sternal plate (if both the meso-metasternal plate and 2nd sternal plate are present)*: **(0)** absent (Fig. 8I); **(1)** present (Fig. 8J).

80. *Ventral pterothoracic setae in the region of the meso- to metasternal plate*: **(0)** absent; **(1)** present (Fig. 8K).

Note that setae are often missing or absent from this region due to damage during collection and specimen preparation. Therefore multiple specimens should be examined before absence is scored.

81. *Female ventral pterothoracic setal arrangement in the region of the meso- to metasternal plate (if present)*: **(0)** single setal pair (may be meso- or metasternal); **(1)** mesosternal setae absent, row of four or five metasternal setae present*; **(2)** pair of mesosternal and a pair of metasternal setae present; **(3)** single pair (rarely 3) mesosternal setae and at least 3 (usually 4 although sometimes 5, 6 or 8) metasternal setae.

Setae present on the ventral anterior third of the pterothorax (close to the prothorax and usually on or just below the proximal development of the proepimeron) are referred to as mesosternal. Setae in the ventral posterior two-thirds of the pterothorax (just above or between the third pair of coxa and roughly level with the development of the metepisternum) are referred to as metasternal. Additional variation in the setal patterns beyond that described here occurs for some taxa not included in this data set.

82. *Attachment of the 2nd and 3rd pairs of legs*: **(0)** sternocoxal, approximately 95% of the coxal surface present beneath the thorax and abdomen (Fig. 8L); **(1)** sterno-pleurocoxal, approximately 30–70% of the coxal surface present beneath the thorax and abdomen (Fig. 8M); **(2)** pleurocoxal, approximately 5–15% of the coxal surface present beneath the thorax and abdomen (coxa attached at the corners of the pterothorax) (Fig. 8N).

The position of the coxa are constrained by their type of attachment to the surface of the pterothorax. Therefore, although the exact position of the legs vary considerably between specimens depending upon how they were mounted, the extent to which the coxa are covered by the pterothorax is a reliable factor of how they are attached. Typically the 2nd pair of coxa are slightly more sternal than the 3rd pair which tend to be more pleural.

83. *Pteronotum*: **(0)** undivided (Fig. 7A, N, Q, R); **(1)** divided medially (Fig. 7O, P, S).

Take care not to confuse damage caused during specimen preparation with a medial suture. Often the pterothorax is more or less broken in half giving the impression a suture is present when in fact this is just an artefact of specimen preparation. Medial sutures are most convincingly demonstrated in stained specimens. They are characterized by the presence of a clear suture line dividing the pteronotum into two halves.

84. *Pterothoracic lateral margins*: **(0)** more or less parallel (Fig. 7R); **(1)** divergent (Fig. 7O).

85. *Pterothoracic lateral margins (if parallel)*: **(0)** without setae (Fig. 7R); **(1)** with setae on the lateral margins.

This character does not include the ventral trichoid seta and its accompanying thorn-like seta.

86. *Pterothoracic posterior margin*: **(0)** more or less flat (Fig. 7R); **(1)** curved or distinctly 'v' shaped (Fig. 7O–Q).

87. *Female medial pair of microseta on the first third of the pterothorax*: **(0)** absent (Fig. 7Q); **(1)** present (Fig. 7R).

These setae may be extremely small and difficult to see without phase contrast.

88. *Female medial pair of setae on the last third of the pterothorax*: **(0)** absent (Fig. 7R); **(1)** present.

These setae may be extremely small (they are usually microsetae) and difficult to see without phase contrast, although in the case of *Campanulotes bidentatus* they are well developed small 'normal' setae. Occasionally, they may also approach the posterior margin of the pterothorax although in all cases remain distinct from the setae on the posterior margin.

89. *Female pterothoracic trichoid seta*: **(0)** absent; **(1)** present, must be a typical trichoid seta emanating from a distinct ventral or lateral pit (Fig. 7H).

These pterothoracic trichoid setae, like those present on abdominal segment VIII, are usually very thin and of a constant width but rapidly taper towards the end. Unlike 'normal' setae which are usually longer, thicker and taper more or less from their base to tip. In cases where a typical trichoid seta is absent, a 'normal' seta is usually present in its place.

90. *Female pterothoracic thorn-like seta, associated with, although not dependent upon the presence of a trichoid seta*: **(0)** absent; **(1)** present (Fig. 7H).

Take care not to confuse these setae with a thorn-like setae on the trochanter. The relative position of the thorn-like setae (whether they are anterior or posterior to the trichoid setae) may also be phylogenetically informative.

91. *Female setal pattern on the lateral and posterior margin of the pterothorax, excluding the trichoid setae or its setal equivalent and its associated thorn-like setae*: **(0)** rarely three, four or more commonly at least five well spaced setae forming a complete or broken row along the margin both sides (Fig. 7O, Q, S); **(1)** mainly clustered, not forming a complete or broken row along the margin (Fig. 7N, R); **(2)** clustered single outer pair and three or four inner setae in a row both sides (Fig. 7P).

92. *Female setal pattern on the posterior margin of the pterothorax, excluding the trichoid setae or its setal equivalent and its associated thorn-like seta (if present as a complete or broken row along the margin)*: **(0)** complete, setae in some cases may be well spaced (Fig. 7O, Q); **(1)** discontinuous, setae absent within the submedian and median region of the pterothorax (Fig. 7S).

93. *Female setal patterns on the lateral and posterior margin of the pterothorax, excluding the trichoid setae or its setal equivalent and its associated thorn-like seta (if clustered along the margin)*: **(0)** loosely grouped on the posterolateral margin in various arrangements, not closely associated; **(1)** 2,2+2,2 arrangement (rarely 2, 2,1+1,2,2) (Fig. 7N); **(2)** 3+3 arrangement (Fig. 7I); **(3)** 2,3+3,2, 3,2+2,3 or 3,3+3,3 (Fig. 7J); **(4)** 4+4 arrangement (rarely 4,1+1,4) (Fig. 7K); **(5)** 5+5 arrangement* (Fig. 7L); **(6)** 7+7 arrangement* (Fig. 7M).

Setae usually of a similar or related type, although the inner setal pair are sometimes less well developed.

94. *Female setal patterns on the lateral and posterior margin of the pterothorax, excluding the trichoid setae or its setal equivalent and its associated thorn-like seta (if clustered and present as a 2,2+2,2 or 2,2,1+1,2,2 arrangement)*: **(0)** 2,2+2,2; **(1)** 2,2,1+1,2,2 (Fig. 7N).

Delimits the columbiform goniodids from the remaining Goniodidae. This character documents the presence of a single or pair of intermediate to mediate setae on the posterior margin of the pterothorax (character 28 of Smith, 2000a). The inner setal pair are not to be confused with the medial pair of setae (usually microsetae) on the last third of the pterothorax.

ABDOMINAL

95. *Adult male tergum I*: **(0)** absent or fused to tergum II; **(1)** present, identified by a small isolated and weakly sclerotized tergite (Fig. 10).

This is the true tergum I which originally belonged to segment I. In Ischnocera tergum I is present only in the Trichodectidae and male *Trichophilopterus* (see Fig. 10), though in both families it is reduced in size (Lyal, 1983). Within the avian Ischnocera tergum I is apparently fused to tergum II as described by Wilson (1939) for *Lipeurus caponis*, and Clay (1958) for *Degeeriella* Neumann.

96. *Adult female submedian to median dorsal setae on abdominal segment II*: **(0)** absent; **(1)** single pair or row (Fig. 11B); **(2)** two pairs or rows, one behind the other (Fig. 11D); **(3)** three or more pairs or rows, each more or less behind each other (Fig. 11C).

This character stems from Wilson's (1936) observation that the first apparent tergum of *Cuclotogaster heterographus* bares two transverse rows of setae while other abdominal segments have just one. This again suggests that the first apparent tergum is the product of a fusion between terga I and II. These setae are often extremely small and in some cases may only be evident by their setal apertures.

97. *Adult female abdominal segment II*: **(0)** not deeply embedded within abdominal segment III; **(1)** deeply embedded within abdominal segment III (Fig. 11E).

The presence of abdominal segment II deeply embedded within abdominal segment III is a synapomorphy of the Heptapsogasteridae, to the exclusion of *Rhopaloceras*. In its most extreme form, segment II is completely embedded between the pterothorax and abdominal segment III. This occurs in the Strongylocotinae (*sensu* Eichler, 1963) and *Physconella* Paine.

98. *Adult female lateral and/or sublateral setae on abdominal segment II*: **(0)** absent; **(1)** present, may be lateral, dorsal and/or ventral.

The presence of setae on the lateral and/or sublateral margin of abdominal segment II is predominantly confined to the *Philoceanus*-complex and the Trichodectidae.

99. *Adult female lateral and/or sublateral setal type and arrangement on abdominal segment II (if present)*: **(0)** micro, normal or macroseta or setal pair, present each side on the posterolateral or sublateral margin (Fig. 11F); **(1)** numerous microsetae covering the lateral margins of the pleurites or tergopleurites (Fig. 11G); **(2)** three or four clustered thorn-like setae* (Fig. 11H); **(3)** two or more short blade-like setae, may be present as part of a continuous setal row (Fig. 11I); **(4)** three or four short normal or microsetae present both sides on the lateral and dorsal sublateral margin of the pleurites* (Fig. 11J).

100. *Abdominal spiracle number*: **(0)** six pairs; **(1)** less than six pairs.

101. *Atria of abdominal spiracles*: **(0)** small (Fig. 11O); **(1)** greatly enlarged (Fig. 11P).

102. *Abdominal male lateral flecks (sensu Moreby, 1978)*: **(0)** absent; **(1)** present (see figs 7–10 in Moreby, 1978).

103. *Cell shaped cuticular sculpturing on the dorsal and/or ventral abdominal surface*: **(0)** absent in all stadia examined; **(1)** present, either dorsally and/or ventrally in any stadium (Figs 11Q, 13D).

These are apparently present in all avian Ischnocera although because of the difficulty of delimiting these structures I have scored them as present if they can be delimited in any instar. Nevertheless, I have been unable to establish the presence of these structures in the two Heptapsogasteridae examined, *Austrogoniodes*, and a trichodectid clade comprising members of the Trichodectinae and Neotrichodectinae (*sensu* Lyal, 1985a).

104. *Adult female pleural and tergal abdominal plate sclerotization. Segment IV to VII ONLY*: **(0)** absent (completely unsclerotized) or greatly reduced, limited to dorsal tergites; **(1)** restricted to pleurites that extend no more than sublaterally over the dorsal surface* (Fig. 12G); **(2)** restricted to separate pleurites and tergites; **(3)** restricted to tergopleurites that are unfused medially; **(4)** restricted to tergopleurites that are fused medially.

105. *Adult female pleural abdominal ribs. Segment IV to VII ONLY*: **(0)** absent or restricted to thin folds over the lateral side of the abdomen (Fig. 11K); **(1)** enlarged although not greatly expanded (Fig. 11L); **(2)** greatly expanded with an enlarged pleural knot (Fig. 11M); **(3)** greatly expanded with an anterior and posterior process (Fig. 11N).

Note that the condition when expanded with an anterior and posterior process is unique to some members of the *Philoceanus*-complex. This condition was referred to as a buttress *sensu* Edwards (1961).

106. *Adult female sternal abdominal plates. Segment IV to VII ONLY*: **(0)** absent; **(1)** present, may be medially fused forming a single sternite or broken forming paired sternites on each segment.

Abdominal sternal plates are often very weakly sclerotized. Absence of this state can only be scored once specimens have been carefully examined at high magnification with phase contrast.

107. *Adult female sternal plate morphology (if present). Segment IV to VII ONLY*: **(0)** sclerotized and complete, fused medially across the abdomen; **(1)** unsclerotized and complete, fused medially across the abdomen; **(2)** separate, present both sides of the abdomen; **(3)** separate in the anterior segments but complete in the posterior segments.

108. *Adult male pleural and tergal abdominal plate sclerotization. Segment IV to VII ONLY*: **(0)** absent (completely unsclerotized) or greatly reduced, limited to dorsal tergites (Fig. 12A); **(1)** restricted to separate pleurites and tergites (Fig. 12B); **(2)** restricted to tergopleurites that are unfused medially (Fig. 12C); **(3)** restricted to tergopleurites that are unfused medially in segments IV and possibly V but medially fused in the remaining segments* (Fig. 12D); **(4)** restricted to tergopleurites that are fused medially (Fig. 12E); **(5)** restricted to tergopleurites that are unfused medially and accompanied by a separate isolated medial tergite on the posterior region of each segment (Fig. 11A); **(6)** restricted to tergopleurites that are fused medially and accompanied by a separate isolated medial tergite on the posterior margin of the fused tergopleurite* (Fig. 12F).

109. *Adult male sternal abdominal plates. Segment IV to VII ONLY*: **(0)** absent; **(1)** present, may be medially fused forming a single sternite or broken forming paired sternites on each segment.

110. *Adult male sternal plate morphology (if present). Segment IV to VII ONLY*: **(0)** complete, fused medially across the abdomen (Fig. 13A); **(1)** unsclerotized and complete, fused medially across the abdomen (Fig. 13B); **(2)** separate, present both sides of the abdomen (Fig. 13C); **(3)** separate in the anterior segments but complete in the posterior segments (Fig. 13D).

Note that in cases where the sternal plates are separate in the anterior segments but complete in the posterior segments, the segment in which the sternites change from being separate to fused is variable depending on the taxon.

111. *Adult female dorsal abdominal setal rows. Segment III to VI ONLY*: **(0)** absent; **(1)** present, may be discontinuous and with at least four or more setal pairs present per segment.

112. *Adult female dorsal abdominal setal row arrangement (if present). Segment III to VI ONLY*: **(0)** present laterally to intermedially, usually microsetae or short small normal setae. May also be present more medially and possibly continuous across the abdomen; **(1)** continuous sublateral to intermediate microsetal or short normal setal rows; **(2)** continuous sublateral to intermediate normal or macrosetal rows; **(3)** discontinuous, single sublateral or intermediate normal or macroseta and a submedian normal or macrosetal row; **(4)** discontinuous, two or three sublateral or intermediate normal or macroseta and a submedian normal or macrosetal row; **(5)** continuous submedian normal setal row*.

113. *Adult female dorsal abdominal setal type (if present in rows, laterally to intermedially). Segment III to VI ONLY*: **(0)** short small microsetae; **(1)** normal setae*.

Character not phylogenetically informative.

114. *Adult female dorsal abdominal setae (if not in rows). Segment III to VI ONLY*: **(0)** median normal or macrosetal pairs only; **(1)** median microsetal pairs only; **(2)** median and submedian or intermediate microsetal pairs; **(3)** intermediate setal pairs regardless of type on the posterior margin of each segment, no median setae; **(4)** median and intermediate setal pairs, may be normal or macrosetae; **(5)** submedian and median pairs only*; **(6)** median blade-like and intermediate normal setal pairs with submedian pairs on segments VII and VIII*; **(7)** sublateral pairs only*.

115. *Adult female ventral abdominal setal rows. Segment III to VI ONLY*: **(0)** absent; **(1)** present, not necessarily complete but with at least four setal pairs per segment.

116. *Adult female ventral abdominal setal type (if present in rows). Segment III to VI ONLY*: **(0)** microsetae, may be discontinuous sublateral or intermedially; **(1)** not microsetae, either normal setae or macrosetae. May be discontinuous sublateral or intermedially.

117. *Adult female trichoid seta on the posterolateral margin of abdominal segment VIII*: **(0)** absent, not identifiable from the other setae on the posterolateral margin of this segment (Fig. 11R); **(1)** present and identifiable although not emanating from a distinctive pit (Fig. 11S); **(2)** present with a distinct trichoid seta emanating from a distinct well developed pit (Fig. 11T).

118. *Adult female dorsal abdominal plates of the terminal abdominal segments*: **(0)** fused, giving the appearance that the segment forms a single unit (Fig. 11U); **(1)** terminal division absent, no evidence of a terminal XI tergite although divisions are present between the lateral portions of the fused IX and X tergite (Fig. 11A′, B′); **(2)** terminal division present separating the segment into its anterior (tergite IX and X) and posterior (tergite XI) regions, additional divisions within these regions may also be present (Fig. 11W).

119. *Adult female fused IX and X tergites, not necessarily delimited from tergite XI*: **(0)** divided into separate pleurites and a single medial tergite* (Fig. 11Y); **(1)** fused medially forming a single tergopleural plate (Fig. 11V); **(2)** divided into tergopleurites, no medial tergite.

Abdominal segments IX and X have interpreted to of fused in adults forming a single unit which may be divided medially into separate tergopleurites or separate pleurites with a medial tergite. See the morphology section of this paper for a full discussion of this character.

120. *Adult female XI tergite (if present and delimited from tergite IX and X)*: **(0)** medially fused forming a single terminal tergal plate (Fig. 11X); **(1)** medially divided into two terminal tergites (Fig. 11Z).

121. *N III dorsal abdominal plates of abdominal segment II*: **(0)** absent, unsclerotized; **(1)** pleurites only; **(2)** pleurites and isolated tergites; **(3)** tergopleurites.

122. *N III dorsal abdominal plate sclerotization. Segments III to VIII ONLY*: **(0)** absent (completely unsclerotized) although a few pleurites may be weakly delimited (Fig. 14A); **(1)** restricted to pleurites in abdominal segment III, all other segments not bearing sclerotized plates* (Fig. 14B); **(2)** restricted to pleurites in abdominal segments III and IV only, all other segments not bearing sclerotized plates (Fig. 14C); **(3)** restricted to pleurites in abdominal segments III to VII only, segment VIII not bearing sclerotized plates* (Fig. 14D); **(4)** restricted to pleurites in abdominal segments III to VIII only, no evidence of any separate tergites (Fig. 14F); **(5)** pleurites and tergites separate and sclerotized plates (Fig. 14G); **(7)** tergopleural plates that are only connected to each other along their posterior margins except in segment VIII which possesses separate tergites and pleurites (Fig. 14H); **(8)** tergopleurites unfused medially (Fig. 14I).

Note that in N III (and N II) *Pectinopygus*, tergopleural plates are only connected to each other along their posterior margins except in segment VIII which possesses separate tergites and pleurites. This condition highlights an intermediate condition between separate tergites and pleurites and fused tergopleural plates. In this taxon the spiracle sits in the gap between the plates on their anterior margin.

123. *N III abdominal pleurite shape (if abdominal sclerotization is restricted to pleurites in segments III to VIII)*: **(0)** thin similar sized elongated plates bordering the edges of each segment (Fig. 14F); **(1)** rounded plates on the lateral margin within each segment which get significantly smaller in each proceeding segment.

124. *N III terminal abdominal segments*: **(0)** undifferentiated by sclerotized abdominal plates (Fig. 14A–F); **(1)** differentiated either partially or completely by sclerotized abdominal plates (Fig. 14G–I).

This character refers to the differentiation of segments IX, X and XI only.

125. *N III terminal abdominal segments (if undifferentiated by sclerotized abdominal plates)*: **(0)** completely undivided, no evidence of intersegmental division in the integument of the terminal segment (Fig. 14B–D); **(1)** divided, with evidence of an intersegmental division via folds in the integument of the terminal segments (Fig. 14A, E, F).

For taxa in which the terminal abdominal segments are completely undivided the only evidence of intersegmental division is based on the position of lateral setae. In most cases these usually suggest the presence of two segments. One possible interpretation of this is that segments IX and X have already fused. This means that the terminal segments are composed of a fused product of segment IX and X and a separate segment XI.

126. *N III terminal abdominal segments (if differentiated by sclerotized abdominal plates)*: **(0)** delimited by an isolated pair of tergal and/or sternal plates only (Fig. 14H); **(1)** delimited by a single tergopleural plate (a pair of sternites may also be evident)*; **(2)** differentiated into two or three rows of plates (Fig. 14G, I).

Note that the term isolated with reference to the first character state refers to the plates being surrounded by unsclerotized cuticle. These plates are not on the lateral margin of the segment and therefore are not considered tergopleural.

127. *N III terminal abdominal segments (if differentiated into two or three rows of sclerotized abdominal plates)*: **(0)** two rows present (Fig. 14G); **(1)** three rows present (Fig. 14I).

In cases where two rows are present, the first row forms the fused product of segments IX and X. The second row corresponds to segment XI. In contrast when three rows are present, each row corresponds to segments IX, X and XI respectively.

128. *N III segment X (if terminal segments IX, X and XI are differentiated into three rows of sclerotized abdominal plates)*: **(0)** medially separated into two isolated tergites or tergopleurites; **(1)** medially fused forming a single tergite or tergopleurite across the segment (Fig. 14I).

129. *N II abdominal plates sclerotization. Segments III to VIII ONLY*: **(0)** absent (completely unsclerotized) although a few pleurites may be weakly delimited; **(1)** restricted to pleurites in abdominal segment III, all

other segments not bearing sclerotized plates*; **(2)** restricted to pleurites in segments III and IV only, all other segments not bearing sclerotized plates*; **(3)** restricted to pleurites in segments III–V, absent in segments VI–VIII; **(4)** restricted to pleurites in segments III–VI, absent in segments VII–VIII*; **(5)** restricted to pleurites in segments III–VIII, no evidence of any separate tergites; **(6)** pleurites and tergites separate and sclerotized; **(7)** tergopleural plates that are only connected to each other along their posterior margin except in segment VIII which possesses separate tergites and pleurites; **(8)** tergopleurites unfused medially.

INTERNAL GENITALIA

130. *Testes*: **(0)** weakly bilobed; **(1)** strongly bilobed (Fig. 15A, C).

From the figures in Blagoveschtchenskii (1956), the bilobed condition appears to be least well developed in *Degeeriella d. discocephalus* (Burmeister) and most well developed in the species of *Philopterus* examined.

131. *Distal termination of the testes*: **(0)** blunt without a short process or flagellate extension* (Fig. 15B); **(1)** blunt with a short process which may or may not carry a short flagellate extension (Fig. 15A, C); **(2)** flagellate but not carried by a short process (Fig. 15D).

Note that in *Syrrhaptoecus* Waterston the testes appear to be blunt ended without bearing a short process or flagellate extension. However, the exact condition is unclear (based on *Syrrhaptoecus alchatae* (Rodow) in Blagoveschtchenskii, 1956, fig 22:4).

132. *Vesicula seminalis*: **(0)** forms a more or less single structure which appears internally divided medially (Fig. 15A); **(1)** separated distally but apparently fused proximally with the vas deferens entering the separated organ before it becomes fused (Fig. 15G); **(2)** forms two distinct separate strucures*.

Note that the condition of the seminal vesicle in *Pectinopygus* appears somewhat derived from the typical morphology and is unclear from the figures of *Pectinopygus gyricornis* (Denny), (referred to as *P. longicornis* in Blagoveschtchenskii, 1956, fig. 23:8). Note that the lateral lobes and ejaculatory duct of this taxon are also somewhat derived and consequently these data are scored as missing.

133. *Subdivisions within each vesicula*: **(0)** absent (Fig. 15E); **(1)** present, each vesicula must be clearly lobed internally (Fig. 15F).

Clay's unpublished key often refers to some taxa as either having subdivisions of each vesicula and/or lateral lobes. These character states are treated under separate characters here and consequently taxa have only been scored where the exact condition can be corroborated in Blagoveschtchenskii (1956). Data for the remaining taxa have been scored as missing, although specific data concerning the combined presence of character states for characters treated separately in this study has been documented within the attribute comments of the full data set.

134. *Lateral lobe on each vesicula*: **(0)** absent; **(1)** present (Fig. 15A, E, H, I, K).

In *Saemundssonia lobaticeps* (Giebel) (fig 19:7 of Blagoveschtchenskii, 1956) the lateral lobes are greatly reduced, present close to the base of the seminal vesicle at the opening of the ejaculatory duct.

135. *Lateral lobe size on each vesicula (if present)*: **(0)** small (Fig. 15E, H, I); **(1)** large, lying along more than half the length of each vesicula (Fig. 15A, K).

136. *Ductus ejaculatorius, joining each vesicula at the base*: **(0)** forms a short simple tube only slightly longer than the length of the basal apodeme (Fig. 15I); **(1)** greatly swollen, at least $1\frac{1}{2}$ × length of the basal apodeme (Fig. 15J); **(2)** long and coiled (Fig. 15K).

137. *Unpaired diverticulum at the junction of the vesicula seminalis and ductus ejaculatorius*: **(0)** absent (Fig. 15A, H–K); **(1)** present* (Fig. 15L).

Within this data set this character state is an autapomorphy for *Cuclotogaster* Carriker. Clay (unpublished key) considers this state a synapomorphy of the *Otidoecus*-complex i.e. *Otidoecus* Bedford, *Cuclotogaster* and *Rhynonirmus* Thompson. This appendix-like process is not figured in any taxon other than *Cuclotogaster heterographus* (fig. 23:2 in Blagoveschtchenskii, 1956).

138. *Genital chamber calyx*: **(0)** unsclerotized, extremely hyaline or not visible; **(1)** sclerotized and striated, clearly visible in cleared slide mounted specimens (Fig. 16A, B).

Scored primarily from slide mounted material and supplemented by data from Blagoveschtchenskii (1956). This character essentially considers the degree of sclerotization of the calyx structure at the base of the spermatheca. This may be partly affected by the degree of clearing that the specimens have gone through during the slide-mounting process. Nevertheless, a distinct group of taxa that possess a well developed calyx are present. The calyx may be striated and/or strongly sclerotized.

Appendix 3. Character matrix for the avian Ischnocera and trichodectid outgroup taxa. Polymorphic character states are indicated by the '&' (and) or '/' (or) symbols. Inapplicable data is scored by '–' and missing entries are indicated by '?'

Characters	1 *Bovicola limbatus*	2 *Damalinia (D.) crenelata*	3 *Trichodectes (T.) melis*	4 *Felicola (F.) viverriculae*	5 *Geomydoecus (G.) heaneyi*	6 *Discocorpus c. cephalosus*	7 *Strongylocotes angulocapitis*	8 *Chelopistes guttatus*	9 *Goniodes pavonis*	10 *Goniodes këleri*	11 *Coloceras damicorne*	12 *Campanulotes bidentatus*	13 *Goniocotes gallinae*	14 *Osculotes curtus*	15 *Osculotes macropoda*	16 *Austrogoniodes waterstoni*	17 *Neopsittaconirmus borgiolii*	18 *Paragoniocotes rotundus*	19 *Falcolipeurus affulgeus*	20 *Archolipeurus nandu*	21 *Cuclotogaster madagascariensis*	22 *Lipeurus caponis*	23 *Oxylipeurus dentatus*	24 *Splendoroffula ruwenzorornis*	25 *Syrrhaptoecus falcatus*	26 *Degeeriella rufa*	27 *Lagopoecus affinis*	28 *Upupicola upupae*	29 *Pectinopygus bassani*	30 *Pectinopygus sulae*
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
2	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1
3	0	0	0	0	0	2	–	–	–	–	–	–	–	2	2	–	1	–	–	0	–	–	–	–	–	–	–	–	4	4
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2
5	?	1	1	1	1	?	?	0	0	0	0	0	0	?	1	0	0	0	0	1	0	0	0	?	0	0	0	0	1	?
6	?	0	0	0	0	?	?	–	–	–	–	–	–	?	0	–	–	–	–	0	–	–	–	?	–	–	–	–	1	?
7	0	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	2	0	?
8	1	1	1	1	1	?	0	0	0	0	0	?	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
9	0	0	0	0	0	?	–	–	–	–	–	?	–	0	0	–	–	–	–	0	–	–	–	–	–	–	–	–	1	1
10	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
11	1	1	?	1	1	?	0	0	0	0	?	?	0	?	?	0	0	?	?	0	?	0	0	0	?	0	0	0	1	1
12	0	0	?	0	0	?	–	–	–	–	?	?	–	?	?	–	–	?	?	–	?	–	–	–	?	–	–	–	1	1
13	0	0	?	0	0	?	0	0	0	0	?	?	0	?	?	0	0	?	?	0	?	0	0	0	?	0	0	0	0	0
14	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0
19	0	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	?
20	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
21	0	0	?	0	0	?	0	0	0	0	?	?	0	?	?	0	0	?	?	0	?	0	0	0	?	0	0	0	1	1
22	–	–	?	–	–	?	–	–	–	–	?	?	–	?	?	–	–	?	?	–	?	–	–	–	?	–	–	–	–	–
23	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
24	0	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?
25	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	?	0	0	?	0	0	0	0	?	?	0	?	?	0	0	?	?	0	?	0	0	0	?	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3
28	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	2	2
29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2
30	3	3	3	3	3	0	0	0	0	0	0	0	0	3	3	0	2	1	2	3	0	0	0	0	0	1	1	1	3	3
31	3	3	3	3	3	?	?	0	0	0	0	0	0	?	3	0	2	1	2	3	0	0	0	?	1	1	1	1	3	?
32	3	3	3	3	3	?	0	0	0	0	0	?	0	2	3	0	2	1	2	3	0	0	0	0	1	1	1	1	3	3
33	2	3	?	3	3	?	0	0	0	0	?	?	0	?	?	0	2	?	?	1	?	0	0	0	?	1	1	1	3	3
34	0	0	1	1	1	0	0	0	0	0	0	0	0	?	?	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1
35	1	1	0	1	1	1	1	?	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1
36	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1
37	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	–	0	–	0	0	0	0	–	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

continued

Appendix 3—*continued.*

Characters	1 *Bovicola limbatus*	2 *Damalinia (D.) crenelata*	3 *Trichodectes (T.) melis*	4 *Felicola (F.) viverriculae*	5 *Geomydoecus (G.) heaneyi*	6 *Discocorpus c. cephalosus*	7 *Strongylocotes angulocapitis*	8 *Chelopistes guttatus*	9 *Goniodes pavonis*	10 *Goniodes keleri*	11 *Coloceras damicorne*	12 *Campanulotes bidentatus*	13 *Goniocotes gallinae*	14 *Osculotes curtus*	15 *Osculotes macropoda*	16 *Austrogoniodes waterstoni*	17 *Neopsittaconirmus borgiolii*	18 *Paragoniocotes rotundus*	19 *Falcolipeurus affulgeus*	20 *Archolipeurus nandu*	21 *Cuclotogaster madagascariensis*	22 *Lipeurus caponis*	23 *Oxylipeurus dentatus*	24 *Splendoroffula ruwenzorornis*	25 *Syrrhaptoecus falcatus*	26 *Degeeriella rufa*	27 *Lagopoecus affinis*	28 *Upupicola upupae*	29 *Pectinopygus bassani*	30 *Pectinopygus sulae*
40	2	2	2	2	2	1	1	1	1	1	1	1	1	?	?	0	1	1	0	0	1	1	1	1	1	1	1	1	0	0
41	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
42	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0
43	2	2	2	2	2	?	?	1	1	1	1	1	1	?	?	0	1	1	0	0	1	1	1	?	1	1	1	1	0	?
44	1	0	1	1	1	?	?	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	?
45	0	1	1	1	1	0	1	?	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1
46	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	2	0	0	2	2	2	2	2	2	0	0	0	0	0	2
47	–	0	0	0	0	–	0	?	1	0	0	–	–	–	–	0	0	–	1	0	0	1	0	0	–	–	–	–	0	0
48	0	0	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	–	–	–	–	–	–	0	?	1	1	1	–	–	–	–	0	0	–	1	1	1	1	1	1	–	–	–	–	1	1
52	–	–	–	–	–	–	0	?	1	0	0	–	–	–	–	0	0	–	1	1	1	0	0	0	–	–	–	–	0	0
53	–	–	–	–	–	–	0	?	0	0	1	–	–	–	–	1	0	–	0	0	0	0	0	0	–	–	–	–	0	0
54	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
55	0	2	2	2	2	2	1	–	–	–	–	–	–	1	1	1	2	1	2	2	0	2	2	1	2	2	2	2	2	2
56	–	1	0	0	0	0	0	–	–	–	–	–	–	1	1	0	1	1	1	1	–	0	0	1	1	1	1	1	1	1
57	–	0	–	–	–	–	–	–	–	–	–	–	–	0	0	–	0	0	0	0	–	–	–	1	0	0	0	0	0	0
58	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1
60	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1	0	0
61	0	0	2	0	0	0	2	2	2	2	2	2	0	2	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
62	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1
63	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	1	2	1	2	2	2	2	2	2
64	0	0	5	0	0	4	8	3	1	1	1	1	1	9	9	6	5	9	–	3	1	–	5	–	1	1	1	1	1	1
65	–	–	–	–	–	–	–	–	1	1	1	1	1	–	–	–	–	–	–	–	1	–	–	–	1	1	1	1	1	1
66	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
67	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	1	–	–	–	–	–	–	–
68	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
69	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1
71	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	1	1	1	3	3	1	1	0	0	0	0	1	0	1	3
72	4	4	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	1	1	1	1	2	1
73	–	–	–	–	–	0	0	0	0	0	0	0	0	0	0	0	1	1	–	1	1	1	–	–	1	0	1	0	–	1
74	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	1	0	0	0	0	0	0	0	0	1	1
75	2	2	3	3	3	4	2	2	2	2	2	2	2	2	2	2	–	?	–	2	–	–	–	–	–	–	–	–	1	1
76	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
77	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	1	0	1	1
78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	1
79	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	0	0	–	0	0
80	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1

continued

Appendix 3—*continued.*

Characters	1 *Bovicola limbatus*	2 *Damalinia (D.) crenelata*	3 *Trichodectes (T.) melis*	4 *Felicola (F.) viverriculae*	5 *Geomydoecus (G.) heaneyi*	6 *Discocorpus c. cephalosus*	7 *Strongylocotes angulocapitis*	8 *Chelopistes guttatus*	9 *Goniodes pavonis*	10 *Goniodes kéleri*	11 *Coloceras damicorne*	12 *Campanulotes bidentatus*	13 *Goniocotes gallinae*	14 *Osculotes curtus*	15 *Osculotes macropoda*	16 *Austrogoniodes waterstoni*	17 *Neopsittaconirmus borgiolii*	18 *Paragoniocotes rotundus*	19 *Falcolipeurus affulgeus*	20 *Archolipeurus nandu*	21 *Cuclotogaster madagascariensis*	22 *Lipeurus caponis*	23 *Oxylipeurus dentatus*	24 *Splendoroffula ruwenzorornis*	25 *Syrrhaptoecus falcatus*	26 *Degeeriella rufa*	27 *Lagopoecus affinis*	28 *Upupicola upupae*	29 *Pectinopygus bassani*	30 *Pectinopygus sulae*
81	0	0	–	–	–	2	–	3	2	–	0	–	0	0	0	–	2	2	0	2	2	2	3	2	2	3	2	2	3	3
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	2	2
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0
84	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0
85	1	1	1	–	1	1	–	–	1	1	1	–	–	–	–	–	–	–	0	–	0	0	0	0	0	0	0	–	0	0
86	0	0	0	0	0	?	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0
88	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0
89	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
90	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	0
91	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1
92	0	0	0	1	0	–	–	–	–	–	–	–	–	–	–	0	–	1	–	–	–	–	–	–	1	–	–	0	–	–
93	–	–	–	–	–	0	0	1	1	1	1	1	1	1	1	–	4	–	2	2	1	4	4	4	–	1	1	–	5	5
94	–	–	–	–	–	–	–	0	0	?	1	1	0	0	0	–	–	–	–	–	0	–	–	–	–	0	0	–	–	–
95	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	1	1	1	1	1	1	2	2	2	?	0	0	2	1	1	2	2	2	3	3	2	2	2	2	2	2	2	2	2	2
97	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
99	1	1	1	1	1	–	–	–	–	–	–	–	–	–	–	2	–	–	3	3	–	–	–	–	–	–	–	–	–	–
100	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	1	1	1	1	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
104	2	2	0	0	0	4	3	3	3	3	3	3	3	3	3	3	4	3	3&4	3	3	1	3	3	3	4	3	4	3	3
105	1	1	0	0	0	1	1	2	2	2	2	2	2	2	2	2	0	0	0	1	1	1	1	1	1	1	1	1	1	1
106	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	?	1	1	0	1	1
107	0	1	1	1	2	2	2	2	2	2	2	2	2	2	–	2	2	0&2	2	–	0	0	0	?	2	2	–	2	2	
108	1	1	0	0	0	4	2	?	2	2	2	2	2	2	2	2	4	2	2&4	4	6	2	2	2	2	4	2	4	3	3
109	1	1	1	1	1	1	1	?	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1
110	0	0	1	1	1	2	2	?	2	2	2	–	2	0	0	–	2	2	0&2	2	0	0	0	0	2	0	2	–	0	0
111	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0
112	0	0	0	–	2	–	–	–	4	4	–	–	–	–	–	3	–	–	1	1	–	–	–	–	3	3	3	3	–	–
113	0	0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
114	–	–	–	1	–	3	3	4	–	–	3	3	4	0	0	–	3	4	–	–	5	4	4	4	–	–	–	–	5	5
115	1	1	1	1	1	0	0	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0
116	0	0	0	0	1	–	–	–	1	0&1	0&1	–	–	1	1	1	–	1	1	1	1	–	–	–	–	1	–	–	–	–
117	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	2	1	2	1	1	1	1
118	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	2	2	2	2	0	0	2	2	2	0	0	0	2	0
119	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1/2	1	2	2	1	1	1	1	1	1	1	2
120	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	1	1	1	–	–	1	1	0	–	–	–	1	–
121	1	1	0	0	0	?	?	3	3	3	2	2	2	?	3	1	3	3	1	0	3	3	3	?	3	2	3	3	3	?

continued

Appendix 3—*continued.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Characters	*Bovicola limbatus*	*Damalinia (D.) crenelata*	*Trichodectes (T.) melis*	*Felicola (F.) viverriculae*	*Geomydoecus (G.) heaneyi*	*Discocorpus c. cephalosus*	*Strongylocotes angulocapitis*	*Chelopistes guttatus*	*Goniodes pavonis*	*Goniodes keleri*	*Coloceras damicorne*	*Campanulotes bidentatus*	*Goniocotes gallinae*	*Osculotes curtus*	*Osculotes macropoda*	*Austrogoniodes waterstoni*	*Neopsittaconirmus borgiolii*	*Paragoniocotes rotundus*	*Falcolipeurus affulgeus*	*Archolipeurus nandu*	*Cuclotogaster madagascariensis*	*Lipeurus caponis*	*Oxylipeurus dentatus*	*Splendoroffula ruwenzorornis*	*Syrrhaptoecus falcatus*	*Degeeriella rufa*	*Lagopoecus affinis*	*Upupicola upupae*	*Pectinopygus bassani*	*Pectinopygus sulae*
122	4	0	0	0	0	?	?	6	6	6	6	6	3	?	6	1	6	6	4	0	6	6	6	?	6	5	5	5	7	?
123	0	–	–	–	–	?	?	–	–	–	–	–	–	?	–	–	–	–	0	–	–	–	–	?	–	–	–	–	–	?
124	0	0	0	0	0	?	?	1	1	1	0	0	0	?	1	0	1	?	0	0	1	1	1	?	1	0	0	0	1	?
125	1	1	1	0	0	?	?	–	–	–	0	0	0	?	–	0	–	?	1	1	–	–	–	?	–	0	1	1	–	?
126	–	–	–	–	–	?	?	0	0	0	–	–	–	?	0	–	0	?	–	–	2	2	2	?	0	–	–	–	0	?
127	–	–	–	–	–	?	?	–	–	–	–	–	–	?	–	–	–	?	–	–	1	0	1	?	–	–	–	–	–	?
128	–	–	–	–	–	?	?	–	–	–	–	–	–	?	–	–	–	?	–	–	0	–	0	?	–	–	–	–	–	?
129	3	0	0	0	0	?	6	6	6	6	6	?	4	?	6	1	6	0	5	0	6	6	6	6	?	5	5	5	7	6
130	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	0	?	0	0	0	?	?	?
131	2	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	2	2	1	?	?	0	1	?	?	?
132	0	?	?	?	?	0	0	0	1	1	1	1	1	0	0	0	?	?	0	?	0	0	0	?	0	0	0	?	?	?
133	1	?	?	?	?	?	?	1	0	0	0	0	0	?	?	?	?	?	1	?	1	1	1	?	0	1	1	?	?	?
134	0	?	?	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	0	?	0	0	1	?	1	1	1	?	?	?
135	–	?	?	?	?	?	?	–	–	–	–	–	–	?	?	?	?	?	–	?	–	–	1	?	0	0	1	?	?	?
136	0	?	1	?	?	?	?	1	2	2	1/2	1/2	1/2	?	?	?	?	?	1	?	0	1	1	?	1	2	2	?	1	1
137	0	?	0	?	?	?	?	0	0	0	?	?	?	?	?	?	?	?	0	?	1	0	0	?	0	0	0	?	0	0
138	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

continued

Appendix 3—*continued.*

Characters	31 *Harrisoniella hopkinsi*	32 *Haffneria grandis*	33 *Halipeurus pelagicus*	34 *Paraclisis diomedea*	35 *Naubates fuliginosus*	36 *Pelmatocerandra setosa*	37 *Perineus nigrolimbatus*	38 *Philoceanus garrodiae*	39 *Pseudonirmus gurlti*	40 *Trabeculus schillingi*	41 *Craspedonirmus colymbinus*	42 *Quadraceps coenocoryphae*	43 *Saemundssonia desolata*	44 *Saemundssonia haematopi*	45 *Docophoroides brevis*	46 *Rallicola lugens*	47 *Aquanirmus australis*	48 *Columbicola columbae*	49 *Anaticola crassicornis*	50 *Ardeicola smithersi*	51 *Ibidoecus plataleae*	52 *Acidoproctus rostratus*	53 *Acidoproctus hilli*	54 *Craspedorrhynchus platystomus*	55 *Strigiphilus vapidus*	56 *Podargoecus strigoides*	57 *Alcedoecus delphax*	58 *Brueelia semiannulata*	59 *Sturnidoecus sturni*	60 *Vernoniella guimaraesi*	61 *Philopterus ornatus*
1	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	0	2	2	2	0	0	3	2	3	3	1	2	3	2
2	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	4	2	4	4	4	4	–	2	4	4	4	4	4	4	4	2	4	3	4	2	4	2	2	4	4	4	4	0	4	2	4
4	2	0	2	2	3	2	2	0	2	3	3	3	3	3	3	0	3	3	1	0	2	0	0	3	3	3	3	0	2	0	3
5	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	?	0	?	1	1	1	1	1	1	0	1	1	1	1
6	1	1	1	1	1	1	–	1	1	4	4	2	2	2	2	1	4	?	–	?	4	2	2	2	2	2	–	0	4	2	4
7	0	0	0	0	0	0	0	0	0	3	3	0	2	0	2	0	2	?	0	?	2	0	0	0	0	0	0	0	2	0	3
8	1	1	1	1	1	1	0	1	1	1	1	1	1	?	1	1	?	1	0	1	1	1	?	1	1	0	0	1	1	1	1
9	1	1	1	1	1	1	–	1	1	4	0	2	2	?	2	1	?	3	–	2	4	2	?	2	2	–	–	0	4	2	4
10	0	0	0	0	0	0	0	0	0	3	0	0	2	?	2	0	?	3	0	0	2	0	?	0	0	0	0	0	2	0	3
11	?	0	1	0	1	1	0	?	0	1	1	0	1	?	0	0	1	0	0	?	1	1	?	1	0	0	0	0	1	1	?
12	?	–	1	–	1	3	–	?	–	4	0	–	2	?	–	–	2	–	–	?	4	2	?	2	–	–	–	–	2	1	?
13	?	0	0	0	0	3	0	?	0	2	0	0	0	?	0	0	0	2	0	?	2	0	?	0	0	0	0	0	0	0	?
14	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
15	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	1	1
16	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	–	0	1	2	–	–	0	0	0	0	–	0	0	0
17	1	1	1	1	1	1	–	1	1	1	0	1	1	1	1	1	1	–	0	1	1	–	–	1	1	1	1	–	0	1	0
18	0	0	0	0	0	0	–	0	0	0	–	1	1	1	1	0	0	–	–	0	1	–	–	1	1	0	1	–	–	0	–
19	1	1	0	1	1	0	0	?	0	2	0	2	2	2	2	2	2	?	0	?	2	0	0	2	2	1	0	0	2	2	2
20	1	1	0	0	0	0	0	?	0	2	0	2	2	?	2	2	?	0	0	1	2	0	?	2	2	0	0	0	2	2	2
21	1	0	0	0	0	0	0	?	0	2	0	0	2	?	0	0	2	0	0	?	2	0	?	2	0	0	0	0	1	2	?
22	–	–	–	–	–	–	–	?	–	0	–	–	2	?	–	–	0	–	–	?	0	–	?	0	–	–	–	–	–	0	?
23	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	1	1	0	1	0	1
24	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	?	0	?	0	0	0	1	1	0	0	0	1	0	1
25	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	0	?	0	0	0	0	0	?	1	1	0	0	0	1	0	1
26	?	0	0	0	0	0	0	?	0	0	0	0	1	?	0	0	1	0	0	?	0	0	?	1	0	0	0	0	0	0	?
27	3	2	3	3	3	3	2	3	3	3	3	3	3	3	3	0	3	1	3	3	3	0	0	3	3	3	3	0	3	2	3
28	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	1	2	2	2	0	0	2	2	2	2	0	2	2	2
29	2	2	2	2	2	2	2	3	1	4	4	4	4	4	4	–	4	–	4	4	2	–	–	4	4	4	4	–	4	1	4
30	1	1	1	1	4	3	1	3	3	5	3	3	3	3	3	3	3	0	1	3	3	4	4	3	3	3	3	2	3	3	3
31	1	1	1	1	3	2	1	3	3	3	3	3	3	3	3	3	3	?	1	?	3	4	4	2	2	2	2	2	3	3	3
32	1	1	1	1	3	2	1	3	3	3	3	3	3	?	3	2	?	0	1	3	3	4	?	2	2	2	2	2	2	2	3
33	?	1	1	1	1	2	1	?	3	3	3	3	3	?	3	2	3	0	1	?	3	4	?	2	2	2	2	2	2	2	?
34	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1
35	0	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1
36	0	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1
37	–	0	0	–	0	0	–	0	–	1	1	1	1	1	1	0	0	0	0	–	0	–	–	1	1	1	1	0	1	1	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
39	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	?	0	0	0	1	0	0	0	1
41	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1

continued

Appendix 3—*continued.*

Characters	31 *Harrisoniella hopkinsi*	32 *Haffneria grandis*	33 *Halipeurus pelagicus*	34 *Paraclisis diomedea*	35 *Naubates fuliginosus*	36 *Pelmatocerandra setosa*	37 *Perineus nigrolimbatus*	38 *Philoceanus garrodiae*	39 *Pseudonirmus gurlti*	40 *Trabeculus schillingi*	41 *Craspedonirmus colymbinus*	42 *Quadraceps coenocoryphae*	43 *Saemundssonia desolata*	44 *Saemundssonia haematopi*	45 *Docophoroides brevis*	46 *Rallicola lugens*	47 *Aquanirmus australis*	48 *Columbicola columbae*	49 *Anaticola crassicornis*	50 *Ardeicola smithersi*	51 *Ibidoecus plataleae*	52 *Acidoproctus rostratus*	53 *Acidoproctus hilli*	54 *Craspedorrhynchus platystomus*	55 *Strigiphilus vapidus*	56 *Podargoecus strigoides*	57 *Alcedoecus delphax*	58 *Brueelia semiannulata*	59 *Sturnidoecus sturni*	60 *Vernoniella guimaraesi*	61 *Philopterus ornatus*
42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
43	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	?	0	0	1	1	0	0	1	1
44	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	0	1	1	1	1	1	1	1	1	1	1
45	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0
46	1	1	2	2	2	2	2	2	0	0	0	0	0	0	0	2	2	0	2	2	0	0	2	0	0	0	0	0	0	2	0
47	1	1	0	0	0	0	0	0	0	1	–	–	–	–	0	1	–	0	0	0	–	–	0	–	–	–	–	–	–	0	–
48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	1	1	1	1	1	1	1	1	1	1	–	–	–	–	1	1	–	1	1	1	–	–	1	–	–	–	–	–	–	1	–
52	1	1	1	1	1	1	1	0	0	0	–	–	–	–	1	0	–	0	0	0	–	–	0	–	–	–	–	–	–	0	–
53	0	0	0	0	0	0	0	0	0	0	–	–	–	–	0	0	–	0	0	0	–	–	0	–	–	–	–	–	–	0	–
54	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
55	–	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2
56	–	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	–	1	1	0	1	1	1	1	1	1	1	1	1	1
57	–	1	–	1	0	2	1	1	1	–	–	2	2	2	2	2	0	–	0	0	–	0	0	2	2	0	2	2	1	2	2
58	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
59	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0
60	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	1
61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1
62	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
63	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2
64	5	5	5	5	3	7	5	5	5	8	3	1	2	2	–	5	5	–	5	5	9	1	1	3	1	1	1	5	5	1	3
65	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	0	0	–	1	1	1	–	–	1	–
66	–	–	–	–	1	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	0
67	1	1	1	1	–	–	1	1	1	–	–	–	–	–	–	1	0	–	0	0	–	–	–	–	–	–	–	1	1	–	–
68	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
69	1	1	0	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
70	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	1	1
71	3	3	3	3	3	3	3	3	3	1	3	3	1	1	1	0	0	0	3	3	1	1	1	0	0	0	1	0	0	1	0
72	2	2	1	2	2	2	2	2	2	0	1	1	1	1	3	1	2	2	1	2	2	1	1	1	1	1	1	1	1	1	1
73	–	–	1	–	–	–	–	–	–	–	0	0	0	0	–	0	–	–	1	–	–	0	0	0	0	0	0	0	0	0	0
74	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1
75	1	1	1	1	1	1	1	1	1	–	2	2	0	0	–	2	–	–	1	1	1	2	2	2	2	–	0	2	2	2	2
76	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
77	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	?	1	0	0	0	0	0	0	1	0	0	0
78	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	1	?	0	0	0	0	0	0	0	1	0	0	0
79	1	1	1	1	1	1	1	1	1	–	0	–	–	–	–	–	–	1	1	?	–	–	–	–	–	–	–	0	–	–	–
80	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
81	2	2	2	2	2	2	2	2	2	2	0	2	0	0	3	2	3	2	2	1	3	3	3	2	3	2	2	2	3	2	2
82	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	1	2	2	2	0	0	0	0	0	0	0	0	0	0	0

continued

Appendix 3—*continued.*

Characters	31 *Harrisoniella hopkinsi*	32 *Haffneria grandis*	33 *Halipeurus pelagicus*	34 *Paraclisis diomedea*	35 *Naubates fuliginosus*	36 *Pelmatocerandra setosa*	37 *Perineus nigrolimbatus*	38 *Philoceanus garrodiae*	39 *Pseudonirmus gurlti*	40 *Trabeculus schillingi*	41 *Craspedonirmus colymbinus*	42 *Quadraceps coenocoryphae*	43 *Saemundssonia desolata*	44 *Saemundssonia haematopi*	45 *Docophoroides brevis*	46 *Rallicola lugens*	47 *Aquanirmus australis*	48 *Columbicola columbae*	49 *Anaticola crassicornis*	50 *Ardeicola smithersi*	51 *Ibidoecus plataleae*	52 *Acidoproctus rostratus*	53 *Acidoproctus hilli*	54 *Craspedorrhynchus platystomus*	55 *Strigiphilus vapidus*	56 *Podargoecus strigoides*	57 *Alcedoecus delphax*	58 *Brueelia semiannulata*	59 *Sturnidoecus sturni*	60 *Vernoniella guimaraesi*	61 *Philopterus ornatus*
83	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0
84	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
85	0	0	0	0	0	0	0	0	0	–	–	–	–	–	–	–	–	0	0	0	–	–	–	–	–	–	–	–	–	–	–
86	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
87	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1
90	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
91	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	0	1	1	2	2	0	2	0	0	0	0
92	–	–	–	–	–	–	–	–	–	1	1	0	0	0	1	–	1	–	–	–	0	–	–	–	–	0	–	1	0	1	0
93	6	4	2	4	4	3	4	4	4	–	–	–	–	–	–	1	–	4	3	4	–	3	3	–	–	–	–	–	–	–	–
94	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
96	2	2	1	2	1	2	2	0	1	2	2	2	1	1	2	1	1	3	2	2	2	2	2	1	2	2	2	1	1	1	2
97	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	–	–	–	2	0	–	–	–	0	4	0	0	–	–	–	–	–	–	–	–
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
103	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
104	3	3	4	4	4	4	4	4	4	4	4	4	3	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
105	3	3	1	3	3	3	3	1	3	3	1	1	1	1	1	0	1	1	1	0	1	1	1	2	2	1	1	0	1	1	1
106	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	1
107	0	0	0	0	0	0	0	0	0	0	0	0	3	–	3	2	2	0	2	2	2	2	2	–	–	–	–	0	–	2	2
108	4	4	4	4	4	4	4	4	4	4	4	4	2	2	4	4	2	2	2	4	2	5	5	2	2	2	2	2	2	2	2
109	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	1
110	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	0	0	2	2	2	2	2	2	2	–	–	–	0	–	2	2
111	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	1
112	–	–	–	–	–	–	–	–	–	–	–	3	3	3	5	–	–	–	–	–	2	–	–	3	2	2	2	–	2	–	2
113	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
114	2	2	1	1	1	1	1	7	1	4	0	–	–	–	–	0	0	5	1	6	–	1	1	–	–	–	–	4	–	4	–
115	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1
116	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	1	1	1	1	–	–	–	1
117	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	0	0	2	2	2	1	2	2	2	2
118	2	2	2	2	2	0	2	2	2	0	2	2	2	2	0	0	0	1	1	0	0	2	2	0	0	0	0	0	2	2	2
119	2	2	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	2	2	1	1	1	1	1	1	1	1	1	1	2	1
120	1	1	0	0	0	–	1	1	1	–	1	1	1	1	–	–	–	–	–	–	–	0	1	–	–	–	–	–	1	1	1
121	3	3	3	3	3	3	3	3	3	3	0	0	1	1	3	3	3	1	3	?	2	3	3	1	1	0	0	1	1	3	1
122	8	8	8	8	8	8	8	8	8	8	0	0	4	4	6	6	6	6	6	?	6	6	8	0	2	0	0	4	2	6	2
123	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	?	–	–	–	–	–	–	–	1	–	–	–

continued

Appendix 3—*continued.*

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
Characters	*Harrisoniella hopkinsi*	*Haffneria grandis*	*Halipeurus pelagicus*	*Paraclisis diomedea*	*Naubates fuliginosus*	*Pelmatocerandra setosa*	*Perineus nigrolimbatus*	*Philoceanus garrodiae*	*Pseudonirmus gurlti*	*Trabeculus schillingi*	*Craspedonirmus colymbinus*	*Quadraceps coenocoryphae*	*Saemundssonia desolata*	*Saemundssonia haematopi*	*Docophoroides brevis*	*Rallicola lugens*	*Aquanirmus australis*	*Columbicola columbae*	*Anaticola crassicornis*	*Ardeicola smithersi*	*Ibidoecus plataleae*	*Acidoproctus rostratus*	*Acidoproctus hilli*	*Craspedorrhynchus platystomus*	*Strigiphilus vapidus*	*Podargoecus strigoides*	*Alcedoecus delphax*	*Brueelia semiannulata*	*Sturnidoecus sturni*	*Vernoniella guimaraesi*	*Philopterus ornatus*
124	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	1	1	?	1	1	1	0	0	0	0	0	0	1	0
125	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	?	–	–	–	0	0	0	0	0	0	–	0
126	2	2	2	2	2	2	2	2	2	1	–	–	–	–	2	0	2	2	2	?	2	2	2	–	–	–	–	–	–	2	–
127	1	1	1	0	1	1	1	1	1	–	–	–	–	–	1	–	0	1	0	?	1	1	1	–	–	–	–	–	–	1	–
128	0	0	1	–	0	1	0	1	–	–	–	–	–	–	0	–	–	0	–	?	0	1	1	–	–	–	–	–	–	0	–
129	8	8	8	8	8	8	8	8	8	8	0	0	3	?	0	6	?	?	6	6	6	6	?	0	2	0	0	0	0	6	0
130	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	0	?	?	0	1	?	?	?	1	?	?	?	0	1	?	1
131	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	2	?	?	1	2	?	?	?	1	?	?	?	1	1	?	1
132	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	?	1	0	?	0
133	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	0	1	0	0	0	1	0	0	1	1	?	?	1	1	?	0
134	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	0	1	1	1	1	0	1	1	1	1	?	?	0	0	?	1
135	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	–	0	0	0	0	–	0	0	1	1	?	?	–	–	?	0
136	?	?	?	?	?	?	?	?	?	?	?	1	0	0	?	1	1	0	0	0	1	0	0	1	1	?	?	1	1	?	1
137	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?	?	0	0	?	0
138	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1