

Basal ischnoceran louse phylogeny (Phthiraptera: Ischnocera: Gonioididae and Heptapsogasteridae)

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Abstract. A phylogenetic analysis of generic relationships for avian chewing lice of families Gonioididae and Heptapsogasteridae (Phthiraptera: Ischnocera) is presented. These lice, hosted by galliform, columbiform and tinamiform birds are reputedly basal in the phylogeny of Ischnocera. A cladistic analysis of sixty-two adult morphological characters from thirty-one taxa revealed thirty equally parsimonious cladograms. The phylogeny is well resolved within Heptapsogasteridae and supports the monophyly of subfamily Strongylocotinae (*sensu* Eichler, 1963). Resolution within Gonioididae is lower but suggests that the genera hosted by Columbiformes are largely monophyletic. Mapping host taxonomy on to the phylogeny of the lice reveals a consistent pattern which is largely congruent down to the rank of host family, although at lower taxonomic levels the association appears to be more complex. The inclusion of more louse taxa may help considerably to unravel the coevolutionary history of both the hosts and their parasites.

Introduction

Suborder Ischnocera is recognized by some workers as comprising four families of chewing lice: Gonioididae, Heptapsogasteridae, Philopteridae and Trichodectidae. The former three groups contain over 150 genera, and (with the exception of the monotypic philopterid genus *Trichophilopterus* Stobbe on lemurs) are obligate ectoparasites of birds. Their conservative morphology makes identification and systematic research of the group difficult. Consequently, there have been few, if any, serious attempts to investigate avian ischnoceran relationships. Most publications on chewing lice take the form of species descriptions with keys to selected small genera, or alternatively deal with a heterogeneous collection of lice from closely related groups of hosts. Recent notable exceptions include Lyal (1985a), who revised the taxonomy and phylogeny of Trichodectidae and Mey (1994), who provided a detailed account of character ontogeny for selected avian Ischnocera.

There is no consensus on the classification of Ischnocera below the rank of suborder. Kéler (1957) and Eichler (1963) have developed complex schemes of classification, each favouring the use of subdivisions apparently to emphasize the authors' ideas on the relationships of the

lice. Hopkins & Clay (1952) proposed a far more conservative arrangement, and this scheme is adopted by most authorities, e.g. Palma & Barker (1996), but makes little headway into resolving ischnoceran louse relationships. This paper is concerned with the phylogeny of Gonioididae and Heptapsogasteridae, two of the smaller groups of bird lice that are reputedly basal in the ischnoceran tree, and forms part of a wider investigation into the phylogeny of avian Ischnocera.

Gonioididae, hereafter referred to *sensu* Eichler (1963) (see Table 1), are principally found on galliform (e.g. turkeys, guineafowl and quails) and columbiform (pigeons and doves) birds throughout the world. Their classification is variable depending on the authority consulted and consequently their taxonomic status is somewhat confused. Mjöberg (1910) first proposed Gonioidinae on the basis of their distinctive head shape and host affiliations. He also included those taxa restricted to Tinamiformes that Carriker (1936) later transferred to the new family Heptapsogasteridae. Harrison (1916) adopted Mjöberg's arrangement in his provisional classification of Ischnocera and subsequently Kéler (1939) elevated Gonioidinae to the rank of family in his monograph of Gonioididae. Since then the family has received little attention. Hopkins & Clay (1952) made no distinction between Gonioididae and the remaining philopterids (excluding the Heptapsogasteridae) in their checklist, stating that they preferred to wait until a more natural system of classification became available, a position also adopted by Emerson (1982).

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Table 1. Classifications of Gonioididae and Heptapsogasteridae according to Carriker (1936), Kéler (1939) and Eichler (1963). Taxa subsequently replaced by junior synonymy are not listed.

Gonioididae			
Kéler, 1939		Eichler, 1963	
Subfamily	Genus	Subfamily	Genus
Chelopistinae	<i>Chelopistes</i>	Chelopistinae	<i>Chelopistes</i>
Goniocotinae	<i>Labicotes</i>	Goniocotinae	<i>Labicotes</i>
	<i>Auricotes</i>		<i>Auricotes</i>
	<i>Goniocotes</i>		<i>Goniocotes</i>
Osculotinae	<i>Osculotes</i>	Physconelloidinae	<i>Campanulotes</i>
			<i>Physconelloides</i>
			<i>Coloceras</i>
Goniodinae	<i>Kodocephalon</i>	Goniodinae	<i>Kodocephalon</i>
	<i>Nitzschiella</i>		<i>Nitzschiella</i>
	<i>Pachyskelotes</i>		<i>Pachyskelotes</i>
	<i>Goniodes</i>		<i>Goniodes</i>
			<i>Passonomedea</i>
Heptapsogasteridae			
Carriker, 1936		Eichler, 1963	
Subfamily	Genus	Subfamily	Genus
Strongylocotinae	<i>Strongylocotes</i>	Strongylocotinae	<i>Strongylocotes</i>
Ornicholacinae	<i>Austrokelloggia</i>		<i>Austrokelloggia</i>
	<i>Kelloggia</i>		<i>Kelloggia</i>
	<i>Ornicholax</i>		<i>Ornicholax</i>
Physconellinae	<i>Cuclotocephalus</i>	Megagininae	<i>Cuclotocephalus</i>
	<i>Megaginus</i>		<i>Megaginus</i>
	<i>Nothocotus</i>		<i>Nothocotus</i>
Heptapsogasterinae	<i>Physconella</i>	Physconellinae	<i>Physconella</i>
	<i>Discocorpus</i>	Heptapsogasterinae	<i>Discocorpus</i>
	<i>Heptapsogaster</i>		<i>Heptapsogaster</i>
	<i>Lamprocorpus</i>		<i>Lamprocorpus</i>
	<i>Megapeostus</i>		<i>Megapeostus</i>
	<i>Pectenosoma</i>		<i>Pectenosoma</i>
	<i>Pterocotes</i>		<i>Pterocotes</i>
<i>Rhoplacoceras</i>	<i>Rhoplacoceras</i>		
<i>Trichodeopeostus</i>	<i>Trichodeopeostus</i>		

The precise status of Gonioididae is still disputed, although the group is widely recognized in ischnoceran literature (Ledger, 1980; Lyal, 1985b; Mey, 1997). Eichler (1963) provisionally included thirty genera in the family and many more have subsequently been described. However, the generic status of many of these taxa is questionable (Ledger, 1980). In particular, João Tendeiro, in a series of papers spanning more than 35 years, has described numerous new genera, while Mey (1997) is the most recent to have added to the list of Gonioididae, describing five new genera from brush-turkeys and

scrubfowl (Megapodiidae). Owing to the lack of material for many of these new taxa and controversy surrounding their generic status, the choice of gonioidid genera to be included in this study was largely centred around those taxa accepted as valid by Hopkins & Clay (1952). Only *Austrogoniodes* Harrison (for reasons discussed below) and *Osculotes* Kéler were excluded. *Nitzschiella* Kéler (considered by Hopkins & Clay as inseparable from *Coloceras* Taschenberg), *Nitzschielloides* Tendeiro, *Stephanus* Tendeiro and *Patellinirmus* Tendeiro were present in sufficient numbers at The Natural History Museum,

London (BMNH) to be included, so that a total of fifteen genera was represented in the phylogeny. Further studies on Gonioididae are required to confirm the taxonomic status of the remaining genera.

Austrogoniodes, parasites of penguins (Spheniscidae), generally been included within the group. However, recent work suggests that its morphological similarity with many of Gonioididae may be founded on convergence. Mey (1994) describes differences in the pattern of abdominal tergal plates and chaetotaxy of the prothorax that suggests that *Austrogoniodes* is more closely related to Philopteridae (*sensu* Eichler, 1963). Unpublished molecular data also supports this conclusion (V. Smith & R. Cruickshank). The status of *Chelopistes* Kéler and *Labicotes* Kéler as members of Gonioididae has also been questioned. Clay (1976) suggested that *Chelopistes* and *Labicotes* appear to be related to each other and were possibly derived from the philopterid *Oxylpeurus* Mjöberg. Although Clay never published any morphological evidence to support this notion, there are some karyotype data that suggest *Chelopistes* may not be a gonioid. *Chelopistes meleagridis* (L.) has a chromosome number of 12 (Perrot, 1934), which is typical for most philopterids. However, of the five Heptapsogasteridae and four Gonioididae studied by Kettle (1977), all had a chromosome number of 11. Despite this, both *Chelopistes* and the supposedly related *Labicotes* were included in the analysis due to the lack of morphological data supporting Clay's proposal.

Heptapsogasteridae (tinamou lice) are confined to tinamiform birds of South America, with the exception of two species found on Cariamidae (order Gruiformes) (Ward, 1957). They constitute the smallest family of avian Ischnocera, spread over nine relatively small host genera and are ecologically interesting owing to their limited host distribution. The group was erected by Carriker (1936) on the basis of their supposed unique seven-segmented abdomen and the presence of spiracles on the first visible abdominal segment. Carriker also considered the structure of the thorax to be distinctive, illustrating variable degrees of fusion between the meso- and metathorax. Kéler (1938) and Ward (1957) subsequently showed that Carriker's classification was founded on a misinterpretation of the abdomen and thorax, and Ward proposed that Heptapsogasteridae be considered as part of Philopteridae *sensu* Clay (1957), thus placing all avian Ischnocera in a single family. Eichler (1963) disagreed with this and placed Heptapsogasteridae and Gonioididae in interfamily Gonioidiformia; however, he offered no justification for this arrangement and it has subsequently been ignored by most authorities.

Carriker (1944) included twenty-four genera in Heptapsogasteridae. Hopkins & Clay (1952) placed six of these into synonymy and Ward (1957) synonymized a further two (*Austrokelloggia* Carriker and *Heterogoniodes* Carriker), leaving the sixteen genera included in this study. Ward suggested that *Austrokelloggia* may warrant subgeneric status, and additional characters have been found to support this observation. In particular, a pair of characteristic nodi emanating from the marginal carina between the preantennal

nodi are present in *Austrokelloggia* but absent from all species of *Kelloggia* Carriker. In addition, the morphology of the vulval margin differs between the two genera; in *Kelloggia* the vulval margin is confined to the posterior region of abdominal segment IX, while in *Austrokelloggia* it is positioned more anteriorly and often partially extends over part of abdominal segment VIII. Consequently a generic exemplar of *Austrokelloggia* was also included.

Materials and methods

One hundred and seventy-eight slide-mounted adult specimens representing thirty-one genera of Gonioididae and Heptapsogasteridae (Appendix 1) were examined from entomological collections based at the BMNH. Adult species exemplars for each genus were chosen and used in the analysis. Where possible, type species for each genus (marked with an * in Appendix 1) were selected, however, in a limited number of cases, suitable type material was not available. In these instances, species were selected on the basis of morphological similarity with the type species or, if no such taxon was available, on the basis of there being sufficient specimens present in the BMNH collections.

The limited sampling achieved using the exemplars approach raises questions on the congeneric repeatability of the characters. However, more extensive sampling is prohibitive due to the number of taxa involved (for example there are almost 100 species of *Goniodes*). Future studies could test the congeneric repeatability of the characters among the larger genera by randomly sampling a proportion of these taxa. Nevertheless, the exemplars approach has proven successful at reconstructing phylogenies where more complete sampling is impractical (Yeates, 1995; Bininda-Emonds *et al.*, 1998), and is used extensively in the phylogenetic analysis of molecular sequence data, where many of the same problems apply.

Some features of the external morphology of chewing lice are not visible or are difficult to interpret in cleared slide mounted specimens. Additional insight was sought using scanning electron micrographs. Three taxa (*Campanulotes* Kéler sp., *Goniodes minor* (Piaget) and the tinamou louse *Strongylocotes* Taschenberg) were obtained from spirit collections at the BMNH and examined in a scanning electron microscope (SEM). Specimens selected for SEM preparation were rinsed, dehydrated in an ethanol series, critical point dried and mounted on stubs. The material was then sputter coated with gold-palladium and examined with a Philips 500 scanning electron microscope at 6–12 kV. All images were recorded electronically. Micrographs showing the dorsal and ventral aspects of the head, thorax and abdomen were obtained to substantiate some of the more cryptic external characters. They have been used to illustrate some of the character states presented here.

Choice of outgroup for this analysis was frustrated by the lack of data on the wider phylogeny of Ischnocera. Suitable outgroup taxa might have included members of Trichodectidae or Philopteridae (Philopteroidea, *sensu* Eichler, 1963). However, the relationships of both groups with respect to

Table 2. Character state matrix for Heptapsogasteridae and Gonioididae.

Taxa	Characters																
	1			2			3			4			5			6	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12		
<i>Discocorpus c. cephalosus</i>	1311-21211	-----11121	2222121-21	22121112-2	21-1312121	111211-112	1-										
<i>Heptapsogaster mandibularis</i>	1212421212	2112131122	2222221-21	22121112-2	1211322121	111211-112	1-										
<i>Lamprocorpus hirsutus</i>	1212421212	2132131122	2222221-21	22121112-2	11-1312121	111211-112	1-										
<i>Megapeostus asymmetricus</i>	1212221212	2112133122	2222221-21	22122112-2	11-1312121	111????112	1-										
<i>Pectenosoma v. verrucosa</i>	1211-21111	-----11122	2222221-21	2212112-22	2221311111	1111-1-112	1-										
<i>Pterocotes aberrans</i>	1212221212	2122131322	2222221-21	22122112-2	31-1312221	111----112	1-										
<i>Rhoplacoceras carrikeri</i>	1111-22222	2111121122	2122121122	1211213--1	31-1212222	121----212	1-										
<i>Trichodopeostus spinosus</i>	1211-21122	2112131122	2222221-22	22121111-2	21-1212121	222211-241	1-										
<i>Cuclotocephalus secundus</i>	2211-12121	-----11321	2122121-31	22121112-1	3211122121	111211-112	1-										
<i>Megaginus e. emarginatus</i>	2211-21111	-----11121	2122121-31	22121112-2	21-1112121	111??1-112	1-										
<i>Nothocotus parvithorax</i>	2212312112	2132121221	2222121-31	22121111-1	21-1122121	111211-112	1-										
<i>Physconella kelloggi</i>	3211-22122	2112111311	2222121-11	21122111-1	1211121111	113211-132	1-										
<i>Austrokelloggia intermedia</i>	221222121	-----21222	2222111111	2122122-12	2222111111	113221-212	1-										
<i>Kelloggia brevipes</i>	2211-22121	-----21222	2222111111	2122122-12	2222111111	113221-112	1-										
<i>Ornicholax alienus</i>	2211-22121	-----21222	2222111112	2122122-12	2222111111	113221-112	1-										
<i>Strongylocotes complanatus</i>	221212121	-----23112	2222111112	2122112-12	3222121111	1142121212	1-										
<i>Chelopistes meleagridis</i>	1211-22222	2212131222	2122122112	1211113--2	3221112222	211211-1?2	1-										
<i>Auricotes meinertzhageni</i>	1221-21121	-----22111	1-11112112	12111111-1	1221111112	22121??241	1-										
<i>Goniocotes gallinae</i>	1211-21121	-----22111	2122112112	12111111-2	1221121112	221211-241	1-										
<i>Goniodes pavonis</i>	1211-22222	2222122221	2122122212	12111111-2	1221112221	2111-21222	1-										
<i>Passonomea hopkinsi</i>	1111-12222	2122121211	2122122212	12111114--2	3221112222	2112121222	21										
<i>Pachyskelotes orthopleurus</i>	1111-12222	2222121111	2122122212	12111111-1	12211?1112	211221-222	21										
<i>Patellinirmus novaeseelandiae</i>	1211-22221	-----21211	2 121112112	12111111-2	1221111211	1112122231	32										
<i>Stephanus affinis</i>	1221-22121	-----22211	2 122112112	12111111-2	1221112212	221221-2?1	1-										
<i>Kodocephalon suborbiculatus</i>	1221-22222	2111122221	2121112112	12111111-1	1221111112	211221-242	32										
<i>Physconelloides ceratoceps</i>	1221-22121	-----23111	1-11112112	12111111-2	2221111112	2211?22241	1-										
<i>Campanulotes bidentatus</i>	1211-22121	-----21311	2111112112	12111111-2	2221111112	2212122241	1-										
<i>Nitzschiella castroi</i>	1211-22122	1131221111	1-11112112	1211112-3?	22211?2112	2211?22241	22										
<i>Nitzschielloides campanulatus</i>	1211-22121	-----21111	1-11112112	1211112-32	2221112112	2212122241	22										
<i>Coloceras damicornis</i>	1211-22222	1131221211	2111112112	12111111-2	2221112122	2111?22221	32										
<i>Labicotes kourii</i>	1111-21?2?	?????21122	2221122112	12111112-1	12111?111	????211-???	??										

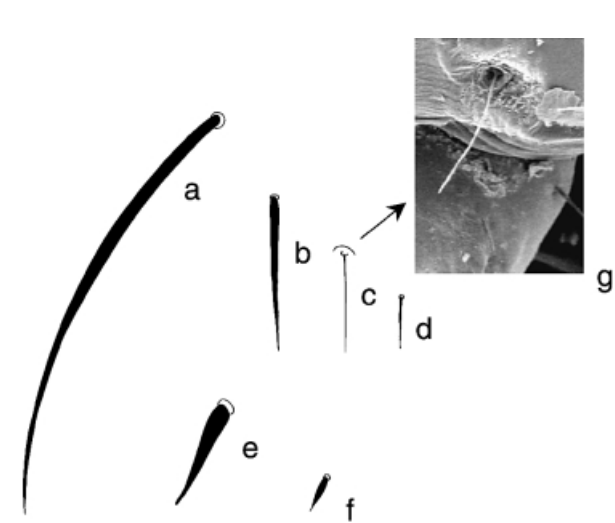


Fig. 1. Ischnoceran setal types. a, Macroseta; b, 'normal' seta; c, trichoid seta; d, microseta; e, thorn-like macroseta; f, thorn-like microseta; g, SEM image of a pterothoracic trichoid seta from *Strongylocotes* sp.

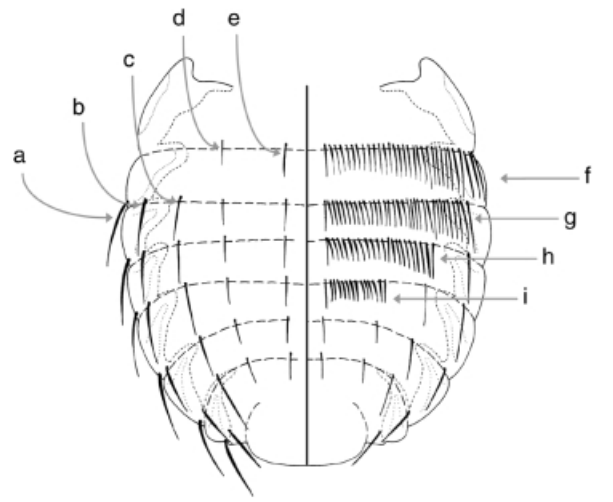


Fig. 2. Abdominal setal arrangements in Ischnocera. Setal columns (a-e) and rows (f-i) may be dorsal (tergal) or ventral (sternal). a, lateral column; b, sublateral column; c, intermediate column; d, submedian column; e, median column; f, lateral row; g, sublateral row; h, intermediate row; i, submedian row.

Goniodidae and Heptapsogasteridae are unknown. A third alternative might have been to use a more distant outgroup such as members of suborder Amblycera, whose phylogenetic affiliations with Ischnocera have been investigated (Lyal, 1985b). However, use of an amblyceran outgroup was abandoned due to difficulties in establishing character homologies. Instead, the tree was rooted between the two louse families, under the assumption that the two groups are monophyletic with respect to each other. This hypothesis is consistent with the study of Mey (1994).

Comparative examination of adult morphology revealed sixty-two characters suitable for phylogenetic analysis. In the case of two taxa, female characters were scored as missing owing to the absence of female specimens in the BMNH collections, and for *Labicotes kourii* (Taschenberg) no male data were available. In addition, some setal characters (e.g. ch. 28) for selected taxa were scored as inapplicable owing to difficulties in establishing character homologies between the two families, and the morphology of the female genitalia in *Rhoplacoceras* Taschenberg and *Pterocotes* Ewing is so derived that characters 54–57 were scored as inapplicable. The complete data matrix is shown in Table 2.

Morphological terminology follows Clay (1951), Lyal (1983) and Mey (1994), except in the case of several setal characters, where new terms were employed to describe setal type and relative setal positioning on the thorax and abdomen. Nomenclature describing setal type (Fig. 1a–g) is largely an anglicised version of the German equivalent proposed by Mey (1994), except for trichoid setae, which are thin setae resembling long trichoid sensilla. These emanate from pits present on the lateral or ventro-lateral margin of the prothorax and the dorsal or dorso-lateral margin of abdominal segment VIII. The terminology used to describe abdominal setal arrangement has largely been adapted from Price & Hellenthal (1996), although extended to describe the distribution of setal rows across the width of each abdominal segment, as shown in Fig. 2. Temple setal terminology in Mey (1994) and Clay (1951) is inconsistent. I have chosen to follow Mey (1994) in identifying two pretemporal setae (the ocular and postocular seta) and five marginal temporal setae owing to the close association of the pretemporal setae in many ischnoceran taxa. Marginal temple setae are labelled consecutively around the temple margin from the lateral to posterior margin of the head. Roman numerals are used to designate 'true' abdominal segment number, as opposed to apparent segment number, which is labelled using Arabic numerals (see Fig. 3).

Phylogenetic analysis and interpretation was performed using PAUP* release version 4.0.0d64 (Swofford, 1998) and MacClade version 3.05 (Maddison & Maddison, 1992). The heuristic search option of PAUP* was employed using TBR branch swapping in conjunction with the random stepwise addition feature using 100 replicates. The latter option was set to examine whether alternative islands of equally parsimonious cladograms were present in the data. All characters were treated as unordered. Bremer support (Bremer, 1988) and character jackknife values (50% character deletion, 100 replicates using NNI branch swapping) (Farris *et al.*, 1996)

were calculated using PAUP* to establish levels of branch support for the clades obtained.

Characters and observations

Head (preantennal)

1. *Frons shape*: (1) broadly convex (Fig. 4c,e–k); (2) narrowly convex (Fig. 4b,d); (3) more or less flat.

Typically broadly convex although in some cases the frons has narrowed, becoming longer and pushing the preantennal nodi back. In the case of *Megaginus* Carriker, the frons is medially indented producing an osculum, while in *Physconella* Paine the frons has become so flattened that the preantennal nodi are level with the middle of the frons.

2. *Marginal carina (m.c.) width*: (1) very thin (Fig. 4f); (2) medium to thick (Fig. 4g); (3) laterally thickened but absent medially.

Clay (1951) discussed the morphology of the marginal carina extensively, however her comments are essentially confined to describing character states within Philopteridae (*sensu* Eichler, 1963). The general morphology of the marginal carina for Goniodidae and Heptapsogasteridae is relatively constant, although modifications to the internal margin are common (Fig. 4b–i). These are described in characters 3–5. The width of the marginal carina is typically thick and more or less constant between the preantennal nodi. In *Discocorpus* Carriker the marginal carina is absent medially but is laterally thickened. Mey (1994) showed that the nymphal stages of *Discocorpus* have a complete marginal carina with a constant width for each instar.

3. *Indentations in the m.c. internal margin*: (1) absent or poorly delimited (Fig. 4b–h); (2) present and deep, well developed (Fig. 4a,i).

Weakly developed suture lines in the marginal carina frequently mark the point of origin for anterior or submarginal head setae. In several of Goniodidae hosted by Columbiformes these suture lines have become strongly developed producing deep irregularly shaped indentations which in some cases extend across the width of the marginal carina.

4. *Nodi emanating from the m.c. between the preantennal nodi*: (1) absent (Fig. 4f–k); (2) present (Fig. 4b–e).

The development of nodi emanating from the marginal carina between the preantennal nodi appears to be a condition unique to Heptapsogasteridae. Their number is variable within the group.

5. *Nodal number (if applicable) between preantennal nodi*: (1) single nodus (Fig. 4b); (2) single pair (Fig. 4c); (3) double pair (Fig. 4d); (4) triple pair, may be weakly developed in some species (Fig. 4e).

6. *Preantennal nodus size*: (1) very small (Fig. 4l); (2) enlarged (Fig. 4m–o).

The preantennal nodi mark the dorsal termination of the marginal carina. Ventrally the marginal carina is fused to a carina that extends to the mandibular framework. The morphology of both the dorsal and ventral aspects of the marginal carina is likely to affect the plasticity of the head

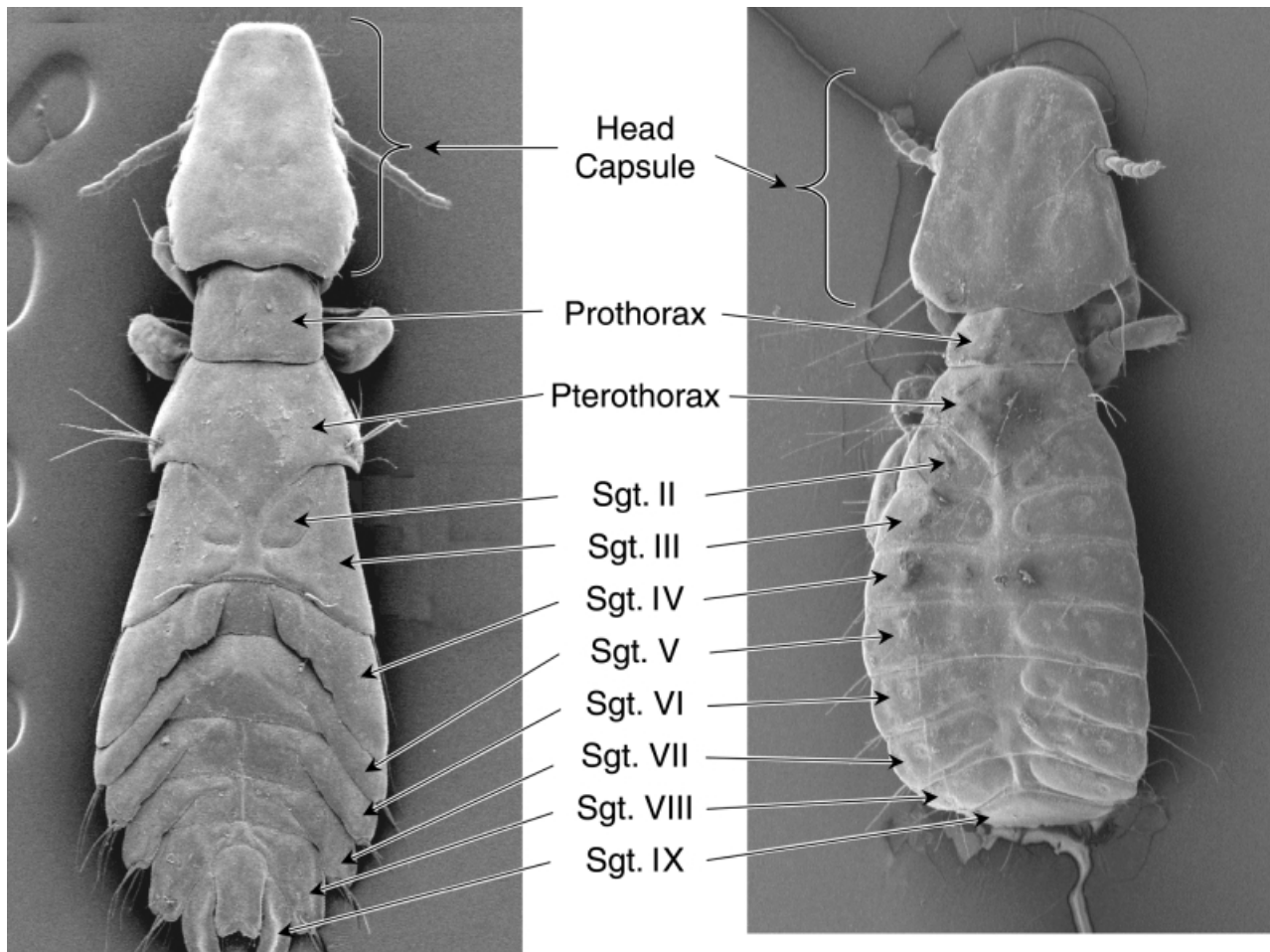


Fig. 3. Dorsal SEM images of *Strongylocotes* sp. $\times 58$ (left) and *Campanulotes* sp. $\times 120$ (right) illustrating typical thoracic and abdominal segmentation in Heptapsogasteridae and Gonioididae.

capsule significantly, particularly due to the absence of other preantennal structures such as the development of a dorsal anterior plate or modifications to the ventral carina, both of which are common in philopterids (*sensu* Eichler, 1963). Typically the preantennal nodi are large and well developed; however, in some taxa the nodi have become significantly reduced. In *Physconella* the preantennal nodi are less well delimited but appear to fuse with a ventral hook which curves beneath the first antennal segment and is characteristic for the genus.

7. *Preantennal nodus shape*: (1) distinctly bulbous, constricted basally (Fig. 4n); (2) not bulbous (Fig. 4l,m,o).

The bulbous condition is principally confined to Carriker's Heptapsogasterinae, although *Megaginus* and two gonioidids also share this state.

8. *Medial dorsal groove in preantennal and/or mandibular region of the male head*: (1) absent; (2) present (Fig. 5).

The males of many taxa have a thin groove running dorsally down the midline of the preantennal region of the head that terminates above the sitophore. In some cases, this suture line

may be confined above the mandibular framework. Initial examination of slide mounted material suggested that this character was an artefact of specimen preparation, however its identical morphology in multiple specimens on different slides suggested that it warranted further investigation. SEM examination of the dorsal head capsule shows a thin medial depression in the cuticle running down the midline of the preantennal region of the head. This character has perhaps never been figured before because of the tendency in most publications on Phthiraptera to divide drawings of the body down their midline into the respective dorsal and ventral aspects, thus obscuring any medial characters.

9. *Ventral carina*: (1) indistinct, most developed at the anterior margin of the mandibular framework, very weakly sclerotized (Fig. 4j); (2) forms a complete arc which is clearly delineated, moderate to well sclerotized (Fig. 4k).

The morphology of the ventral carina in both Heptapsogasteridae and Gonioididae shows none of the diversity found in their philopterid relatives. The ventral carina passes forward from the mandibular framework each

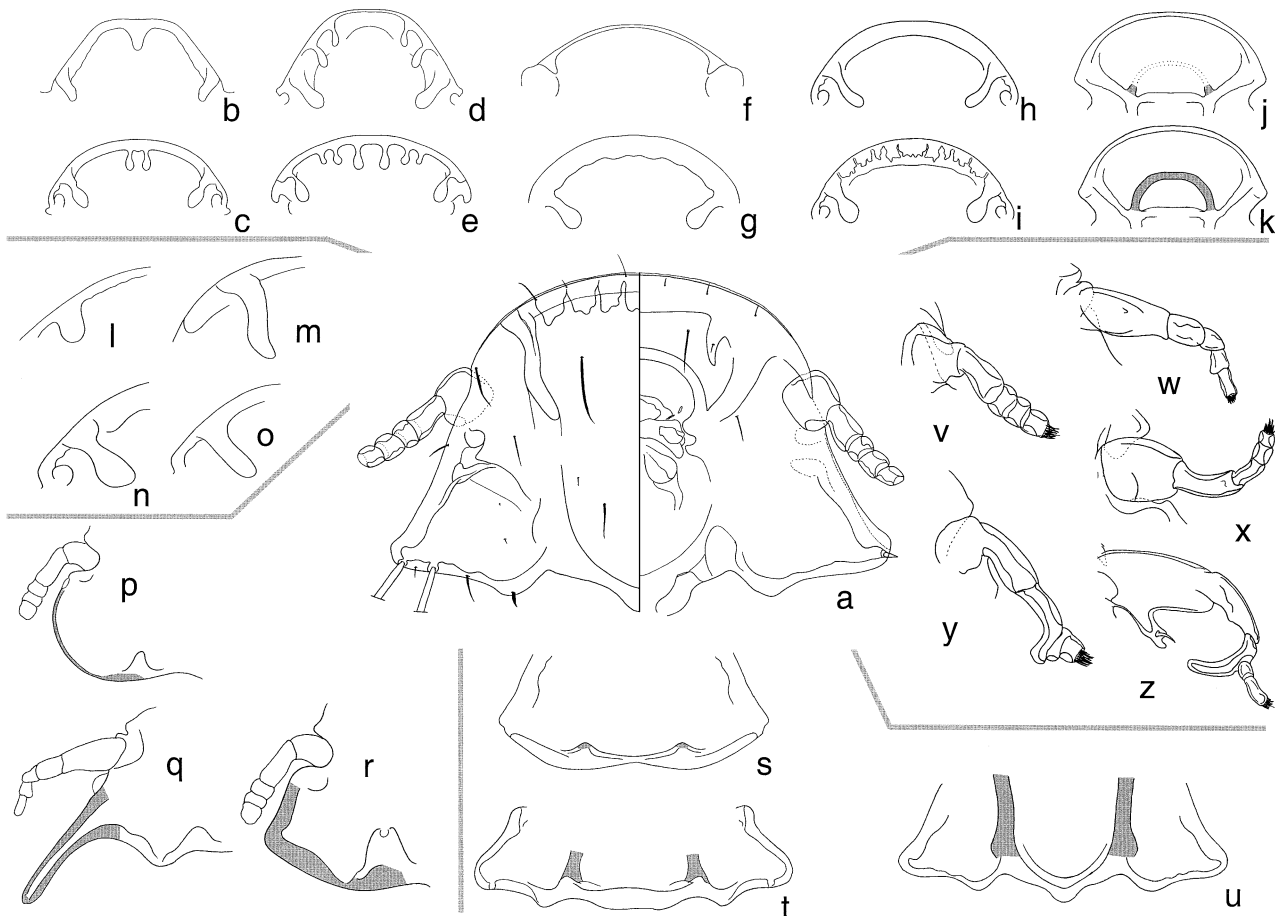


Fig. 4. Diagrammatic representations of head character states. a, Generalized dorsal-ventral view of a goniodid head; b–e, nodal arrangements between preantennal nodi; f–i, marginal carina morphology; j,k, ventral carina morphology; l–o, preantennal nodi morphology; p–r, smooth, pointed and angular temple margins; s–u, temporal carina morphology; v–z, male antennal types.

side forming a complete semicircle which is always most sclerotized close to the mandibular framework, but may be progressively less sclerotized anteriorly. It is always well developed in Goniodidae, but in some Heptapsogasteridae is poorly delimited and less well sclerotized, particularly medially.

Head (antennal)

10. *Male antennal segments*: (1) monomorphic (Fig. 4v); (2) heteromorphic (Fig. 4w–z).

The phylogenetic utility of antennal morphology has frequently been discussed in ischnoceran literature and generally been dismissed due to the variable morphology found within genera (Harrison, 1915; Clay, 1951). However, these discussions are usually limited to the presence or absence of sexual dimorphism, and rarely take into account the diverse morphology of individual antennal segments. Within the two families, approximately half of the male taxa examined had heteromorphic antennal segments; this is close to the proportion for all avian Ischnocera (Mey, 1994).

11. *Male scape (for heteromorphic antennae)*: (1) smaller than pedicel or of a similar size (Fig. 4y); (2) significantly larger than pedicel (Fig. 4w,x,z).

The scape is almost always greatly expanded in those male taxa with heteromorphic antennae, with the exception of *Nitzschiella* and *Coloceras*, both of which have a short rounded scape, comparable to the size of those of the females.

12. *Process on the lateral margin of the male scape (for heteromorphic antennae)*: (1) absent (Fig. 4w–y); (2) present (Fig. 4z).

A large thickened process emanates from the posterolateral margin of the scape in *Goniodes* Nitzsch and *Pachyskelotes* Kéler. In *Pachyskelotes* the tip of this process is slightly forked and bears a distinct thorn-like seta. In *Chelopistes* the process is much reduced but strongly sclerotized.

13. *First flagellomere shape (for heteromorphic antennae)*: (1) unmodified (Fig. 4w,x); (2) gently curved, not club shaped (Fig. 4z); (3) club-shaped, expanded distally (Fig. 4y).
14. *Subterminal attachment of flagellomeres II and III (for heteromorphic antennae)*: (1) absent (Fig. 4w–y); (2) present (Fig. 4z).

Subterminal attachment only occurs in those taxa where flagellomeres II and III are clearly not borne from the tip of flagellomere I. This is usually readily indicated by the lateral

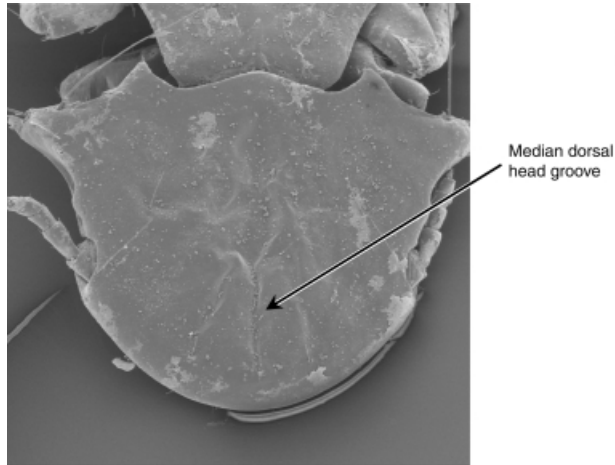


Fig. 5. *Goniodes minor* head capsule showing medial dorsal groove.

sclerotization of the flagellomeres, although in cases where the distal portion of flagellomere I is expanded or is largely hyaline, the position of the tip is difficult to determine.

15. *Apical compression of flagellomeres II and III (for heteromorphic antennae)*: (1) absent (Fig. 4w,x,z); (2) present (Fig. 4y).

This condition is exclusive to two taxa which both have flagellomere I distally expanded. It also occurs in some species of *Goniocotes* Burmeister that have flagellomere I distally expanded, as revealed through SEM examination (personal observation), although in the case of *Goniocotes gallinae* (De Geer) used in the light microscope study, males of this species do not have heteromorphic antennae.

Head (postantennal)

16. *Temple margins*: (1) rounded (Fig. 4p); (2) angular, not projecting significantly behind the posterior margin of the head (Fig. 4r); (3) pointed, projecting significantly behind the posterior margin of the head (Fig. 4q).

The gross head morphology of Gonioididae and Heptapsogasteridae is highly divergent, particularly in the

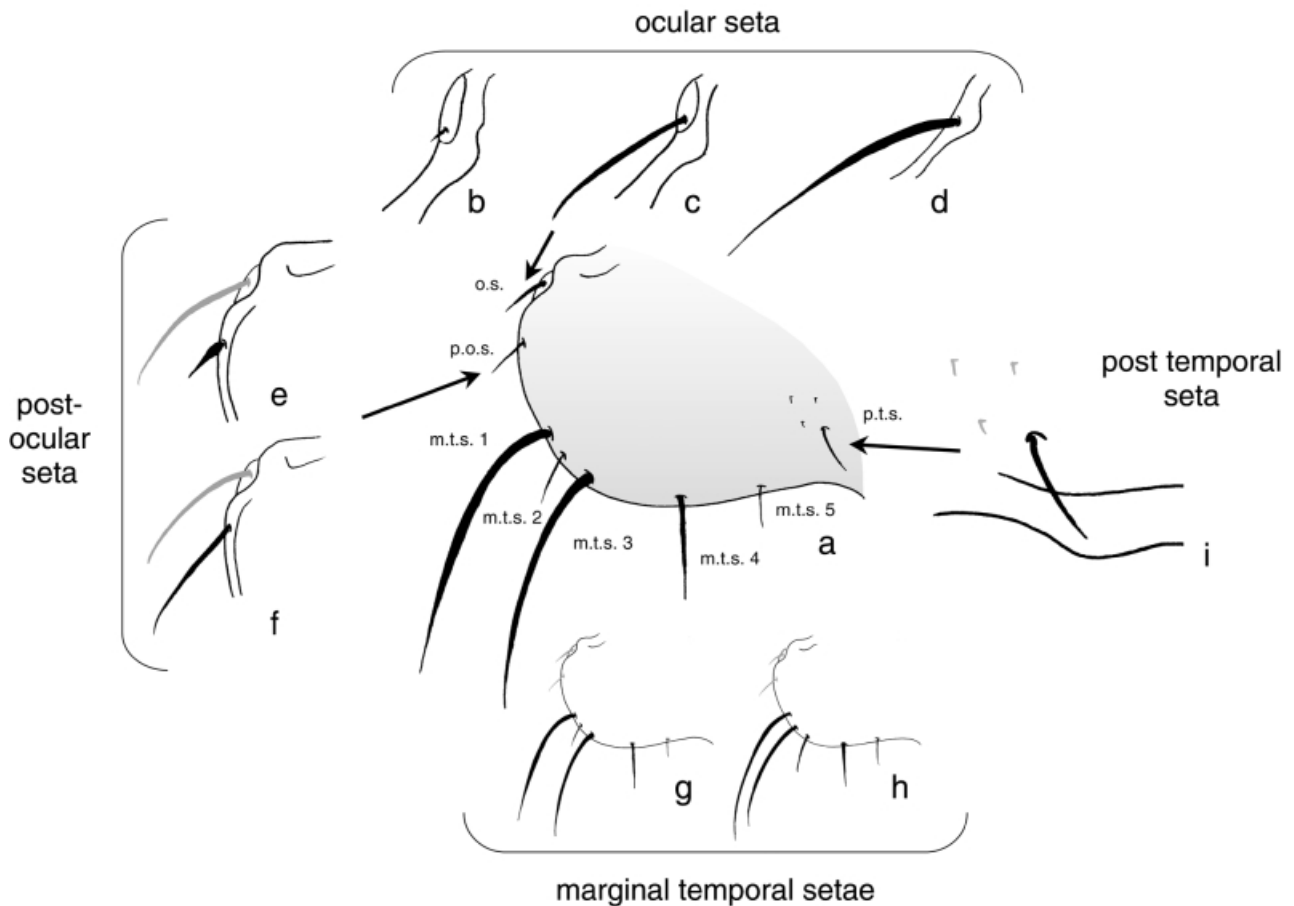


Fig. 6. Postantennal setal types and arrangements in Gonioididae and Heptapsogasteridae.

temporal region. This is typical for many Phthiraptera and has led some authors to develop complex qualitative character descriptions describing the geometry of regions of the head, e.g. Long (1990). In this study, temple outline was divided into three discrete character states. The temple margins in all Gonioididae are angular to a greater or lesser extent. In the case of *Chelopistes* this condition has become exaggerated so that the temples are pointed and produced backwards each side beyond the posterior margin of the head. This state also occurs within Heptapsogasteridae, although in many tinamou lice the angularity of the temple margins is absent so that margins appear smoothly rounded.

17. *Temporal carina*: (1) absent (Fig. 4s); (2) evident from posterior margin of the head but not delimited anteriorly (Fig. 4t); (3) forms a complete thickened band (Fig. 4u).

When present, this carina runs from the occipital nodi across the temples. In its most developed form it may become continuous with the preantennal nodi (e.g. *Physconelloides* Ewing) or more commonly becomes rapidly less well delimited, fading into the surrounding cuticle before reaching the posterior margin of the mandibular framework. The prominence of the temporal carina may vary slightly between specimens depending upon the degree of clearing or staining. Careful examination using phase contrast may be required to delimit the lateral margins of this carina from the dorsal sclerotization of the head. This structure is absent in all Heptapsogasteridae with the exception of *Megapeostus* Carriker and *Strongylocotes*. Within Gonioididae the carina is frequently evident posteriorly but is usually indistinguishable from the surrounding cuticle by the mandibular region.

18. *Ocular seta (o.s.)*: (1) a thorn-like micro or very short normal seta (Fig. 6b); (2) short to medium length normal seta (Fig. 6c); (3) thick and long, well developed (Fig. 6d).

This seta arises on the dorsal surface of the lens of the eye, or in those taxa where the eye is absent (e.g. *Discocorpus*) marks the former position of the eye. It forms one of the five pairs of setae noted by Clay (1951) as always present and approximately in the same place throughout Ischnocera. Within Heptapsogasteridae it typically takes the form of a small microseta, although in three instances (*Pterocotes*, *Cuclotocephalus* Carriker and *Physconella*) the seta is significantly more developed, as is the case with the majority of Gonioididae.

19. *Postocular seta (p.o.s.)*: (1) thorn-like micro- or macroseta (Fig. 6e); (2) not thorn-like (Fig. 6f).

This corresponds to marginal temporal seta 1, as defined by Clay (1951), and the preocular seta ('Praeocularborste') of Mey (1994). This is present throughout both families. Generally, most Gonioididae possess a thorn-like postocular seta, whereas most Heptapsogasteridae do not. However, exceptions occur in both groups, such as *Physconella* where the postocular seta has become greatly thickened and enlarged to form a stout thorn-like macroseta.

20. *Marginal temporal seta (M.T.S.) 1 and 3*: (1) both macrosetae (Fig. 6a,g); (2) one or both not macrosetae (Fig. 6h).

With the exception of *Chelopistes* and *Labicotes*, M.T.S. 1 and M.T.S. 3 are thickened and enlarged, almost always

forming the dominant setae on the temple region of the head in Gonioididae. In the case of *Chelopistes*, M.T.S. 1 is reduced to a microseta and pushed up towards the postocular seta, perhaps due to the enlarged temples. For this genus M.T.S. 3 alone is the dominant marginal temporal seta. Within Heptapsogasteridae this condition is confined to *Discocorpus* and *Physconellinae* (*sensu* Carriker, 1936). For the remaining tinamou lice M.T.S. 3 is always dominant, often with M.T.S. 2, while M.T.S. 1 is usually much reduced.

21. *M.T.S. 2*: (1) absent; (2) present (Fig. 6a,g,h).

Mey (1994) has discussed the marginal temple setal number and found that seven or more temple setae (including the postocular seta) was the plesiomorphic condition, whilst five or six was derived. All Heptapsogasteridae possess six temple setae (one postocular seta and five marginal temporal setae), while Gonioididae may possess between four and six. Within Gonioididae M.T.S. 2 is present either as a small microseta (which in some cases is reduced to a short hair-like seta) or entirely absent.

22. *M.T.S. 2 condition (if present)*: (1) microseta (Fig. 6a,g); (2) well developed thorn-like, normal or macroseta (Fig. 6h).

23. *M.T.S. 4 condition*: (1) absent or extremely reduced; (2) present at least as a normal sized microseta or larger (Fig. 6a,g,h).

The possession of four temple setae (one postocular and three marginal temporal setae) disagrees with the general statement of Mey (1994) that avian Ischnocera never possess fewer than five temple setae (including the postocular seta). However, within some Gonioididae, M.T.S. 4 can be greatly reduced to a short, thin hair-like seta or is entirely absent, such as in *Nitzschella*. This seta is frequently so small that it can easily be overlooked. Alternatively, M.T.S. 4 and M.T.S. 5 can be confused with the two or three anterior prothoracic setae present on both sides of the extreme anterior margin of the prothorax. In cleared, slide-mounted material these setae are often visible under the posterior margin of the head, giving the appearance of up to eight marginal temple setae. Careful focusing is sometimes required to discriminate between these setae when attempting to establish temple setal homologies.

24. *Post-temporal setae (P.T.S.)*: (1) absent; (2) present (Fig. 6i).

The post-temporal setae within Heptapsogasteridae are usually well developed and often extend beyond the posterior margin of the head such as in *Pterocotes* and *Lamprocorpus* Carriker. Within Gonioididae this seta is either absent as in many columbiform taxa, or is much smaller and typically pushed back close to the posterior margin of the head. Tiny thorn-like microsetae are common on the dorsal occipital region of the head and should not be confused with small post-temporal setae.

Thorax

25. *Pterothoracic lateral margins*: (1) smooth or slightly bumpy (Fig. 7h); (2) distinctly serrated edge (Fig. 7i).

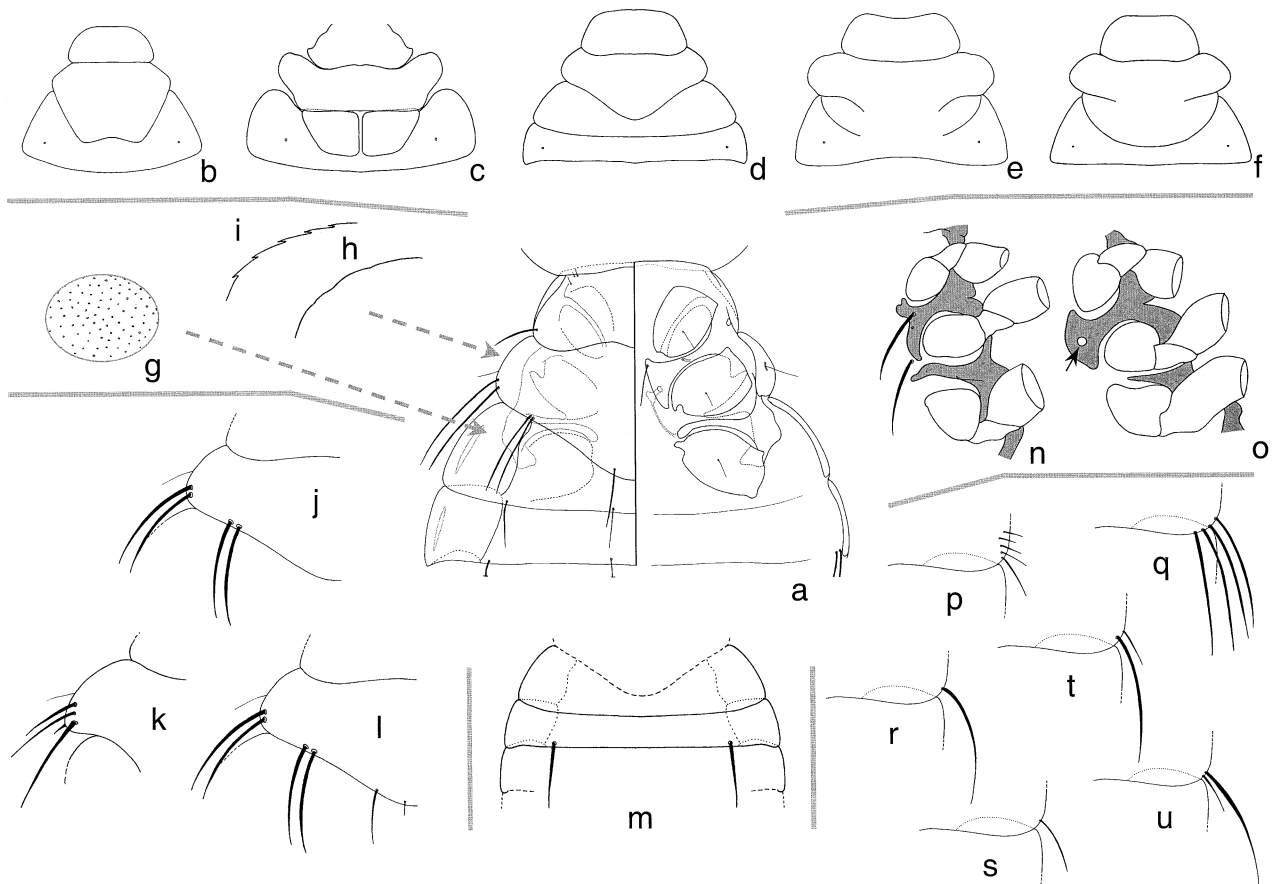


Fig. 7. Diagrammatic representations of thoracic and selected abdominal character states. a, Generalized dorsal-ventral view of a goniodid thorax with abdominal segments II and III; b–f, morphological variation of the pterothorax and initial abdominal segments; g, pitting on the dorsal cuticular surface of abdominal segment II; h, i, pterothoracic lateral margin; j–l, setal variation on the pterothorax; m, intermediate tergal setae on abdominal segment III; n, ventral view of thorax showing meso-metasternal setae; o, ventral view of thorax showing mesofurcal pit (indicated by arrow, cf. Fig. 7n); p–u, setal variation on the posterolateral margin of abdominal segment II.

State two is unique to certain members of Heptapsogasterinae and can also be seen on the anterior lateral margin of abdominal segment III in some of the affected taxa, e.g. *Heptapsogaster*.

26. *Ventral pterothoracic setae in the region of the meso-metasternal plate:* (1) absent; (2) present (Fig. 7n).

Two pairs of setae are usually present on the meso-metasternal region of Heptapsogasteridae. The first pair is usually attached to the medial expansion of the proepimeron (*sensu* Lyal, 1983) in the mesosternal part of the thorax. These expansions may be fused forming a single medial plate or are separate, and correspond to the acetabular bars described by Carriker (1936) in his original description of Heptapsogasteridae. A second pair may be present beneath the posterior margin of the expansion (e.g. *Discocarpus*) or attached to the cuticular bar, which forms part of the coxal articulation for the second pair of legs (e.g. *Megapeostus*). Alternatively a patch of setae may be present in this region, as is the case with *Rhoplacoceras*. These setae are absent within

Strongylocotinae (*sensu* Eichler, 1963) and the majority of Goniodidae.

27. *Two distinct setal pairs both sides on the lateral to posterior margin of the pterothorax:* (1) absent (Fig. 7k); (2) present, clearly paired (Fig. 7a,j,l).

The paired arrangement of the pterothoracic setae is confined to Goniodidae. The outer setal pair is present laterally, usually just behind a thin trichoid seta that emanates from a sublateral pit on the ventral surface of the pterothorax. The second pair has a sublateral to intermediate position on the posterior margin of the pterothorax. Additional setae may be present medially. Within Heptapsogasteridae the dominant setae are usually located on the lateral margin of the pterothorax and show considerable variation in their number, position and size.

28. *Intermediate to median setae on the posterior border of the pterothorax excluding pterothoracic setal pairs:* (1) greatly reduced or absent; (2) well developed normal or macrosetae (Fig. 7l).

Within Heptapsogasteridae this character could only be scored for those taxa where the posterior margin of the pterothorax is clearly visible. Nevertheless, these setae are only present in Gonioidinae (*sensu* Eichler, 1963).

29. *Pterothorax and abdominal segment II*: (1) completely separate (Fig. 7c,d); (2) medially fused (Fig. 7e,f); (3) completely fused (Fig. 7b).

This character was first described by Carriker (1936) in his key to the genera of Ischnocera infesting tinamou, however he incorrectly interpreted the division between the pterothorax and abdominal segment II as a suture line between the meso- and metathorax. This was corrected by Kéler (1938) and later by Ward (1957), who figured the pterothorax and initial abdominal segments for all Heptapsogasteridae.

30. *Mesofurcal pit*: (1) small and poorly developed (Fig. 7n); (2) large and well developed (Fig. 7o, indicated by arrow).

This pit lies on the posterior sublateral expansion of the proepimeron in the mesosternal region of the thorax and corresponds to the sternal apophyseal pit 2 described by Cope (1940). It appears to mark the ventral termination of the second sternal apophysis (*sensu* Cope, 1940) and should not be confused with the profurcal pit, which is present on the proepimeron before it becomes expanded, or setal alveoli, which mark the position of mesosternal setae which have broken off from their site of attachment. This pit is always large and well developed in Gonioididae, but usually smaller with a narrow aperture in Heptapsogasteridae.

Abdomen (segments II–VIII)

31. *Abdominal segment II*: (1) not deeply embedded dorsally within abdominal segment III (Fig. 7a,d); (2) deeply embedded dorsally within abdominal segment III (Fig. 7b,c,e,f).

Carriker (1936) first described this character, although mistakenly identified abdominal segment II as the metathorax. Within Heptapsogasteridae, all but *Rhoplacoceras* possess a highly modified second abdominal segment that is deeply embedded into abdominal segment III. This gives the impression that abdominal segment III (the first spiracle bearing segment) is the first visible segment in the abdomen. The first visible segment in the abdomen of all Gonioididae and *Rhoplacoceras* is abdominal segment II, which does not bear a pair of spiracles.

32. *Abdominal segment II margin*: (1) completely enclosed by pterothorax and abdominal segment III (Fig. 7c); (2) partially enclosed by pterothorax and abdominal segment III (Fig. 7b,d–f).

The lateral margin of abdominal segment II in all Gonioididae and most Heptapsogasteridae is at least partially free. In Strongylocotinae (*sensu* Eichler, 1963) and *Physconella* this margin is completely encased by the posterior margin of the pterothorax and the anterior margin of abdominal segment III.

33. *Dorsal medial division of abdominal segment II*: (1) absent (Fig. 7a,b,d–f); (2) present (Fig. 7c).

Abdominal segment II is medially divided dorsally and has a bilobed appearance in all Strongylocotinae (*sensu* Eichler, 1963). This is closely linked to the complete enclosure of abdominal segment II by the pterothorax and abdominal segment III.

34. *Abdominal segment II size*: (1) approximately the same size as abdominal segment III (Fig. 7a,d); (2) considerably smaller than abdominal segment III (Fig. 7b,c,e,f).

First described in the key presented by Ward (1957), this character is an additional feature of the initial abdominal segments within Heptapsogasteridae.

35. *Abdominal segment II and III*: (1) completely separate (Fig. 7a–d,f); (2) partially or completely fused dorsally (Fig. 7e).

The dorsal division between abdominal segments II and III is usually well defined, however within some Heptapsogasteridae this division is unclear. In *Physconella* the entire dorsal posterior margin of abdominal segment II is ambiguous and appears to be fused with abdominal segment III. Of the remaining affected taxa, all show partial dorsal fusion with abdominal segment III, such as in *Megapeostus* where the posterior margin is clearly defined up to the middle of the segment.

36. *Abdominal segments II and III dorsal cuticular surface*: (1) smooth; (2) covered in small pits (Fig. 7g).

This pitting is present on the cuticular surface of three of the four genera of Strongylocotinae (*sensu* Eichler, 1963) and in some taxa may extend beyond abdominal segments II and III. This should not be confused with the much larger pits present on *Discocorpus*.

37. *Setae on the posterolateral margin of abdominal segment III, excluding rows of setae on the ventral posterior lateral border*: (1) one pair, one seta either side (Fig. 7r,s); (2) 2 pairs, 2 setae both sides (Fig. 7t,u); (3) more than 2 pairs, more than 2 setae both sides (Fig. 7p,q); (4) absent.

The exact position of many lateral abdominal setae often varies slightly and may appear very slightly dorsal or ventral depending upon the way the specimen was mounted. Nevertheless, these setae can usually be readily distinguished from columns of sublateral setae or rows of setae running across the body on the basis of their setal type.

38. *Single posterolateral setae condition (if present), both sides, on abdominal segment III*: (1) short thin spine not significantly projecting beyond the posterior margin of abdominal segment IV (Fig. 7s); (2) well developed (Fig. 7r).

39. *Two posterolateral setae condition (if present), both sides, on abdominal segment III*: (1) outer setal pair larger than inner setal pair (Fig. 7u); (2) inner setal pair larger than outer setal pair (Fig. 7t); (3) both setae of roughly equal size.

40. *Male intermediate tergal setae on abdominal segment III*: (1) absent; (2) present (Fig. 7m).

Care should be taken when scoring these setae as absent as they are commonly damaged on specimens and may only be evident by the presence of setal apertures.

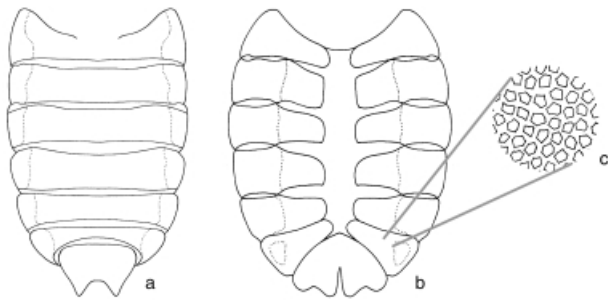


Fig. 8. Selected abdominal character states. a, Abdominal tergopleurites fused medially (dorsal view); b, abdominal tergopleurites broken medially (dorsal view); c, markings over the cuticular surface of the tergopleurites.

41. *Setal number on the posterior lateral margin of abdominal segment IV*: (1) one pair; (2) 2 pairs; (3) more than 2 pairs.

42. *Tergopleurites*: (1) fused medially (Fig. 8a); (2) broken medially (Fig. 8b).

The tergopleurites of most taxa are separated medially, however in most Heptapsogasterinae and two Megagininae (*sensu* Eichler, 1963) they are fused, forming a complete plate which runs around the abdomen terminating sublaterally on the ventral surface.

43. *Tergopleurites (if broken medially)*: (1) separated by a narrow gap; (2) separated by a wide gap.

44. *Small dorsal pits on cuticular surface of abdominal segments IV–VIII*: (1) absent; (2) present.

These pits are identical to those defined in character 36. In this case the cuticular pitting is present in all members of Strongylocotinae (*sensu* Eichler, 1963). They are usually most well developed on segments VII and VIII.

45. *Polygonal marks over the cuticular surface of the abdomen*: (1) absent; (2) very faint, confined to the lateral margins of the pleurites and often restricted to segments VII and VIII; (3) distinct, present over the tergopleurites (Fig. 8c).

These irregularly shaped marks are present on all members of Heptapsogasterinae although in the case of *Trichodopeostus* Carriker and *Rhoplacoceras* they are less well defined. They are particularly distinct when specimens are viewed using phase contrast and often most well developed on males.

46. *Male setal type down the column of intermediate tergal setae*: (1) homogeneous, same setal type excluding small changes in setal size; (2) heterogeneous, different setal types.

With the exception of those taxa whose abdominal chaetotaxy were damaged, intermediate tergal setae were always present on segments IV to VII and often on segment III (see ch. 40). These setae are usually of a single type although typically get slightly shorter towards the terminal segment. In several cases the setal type changes suddenly (often between segment IV and V or V to VI) becoming much shorter, as is the case with *Physconella*.

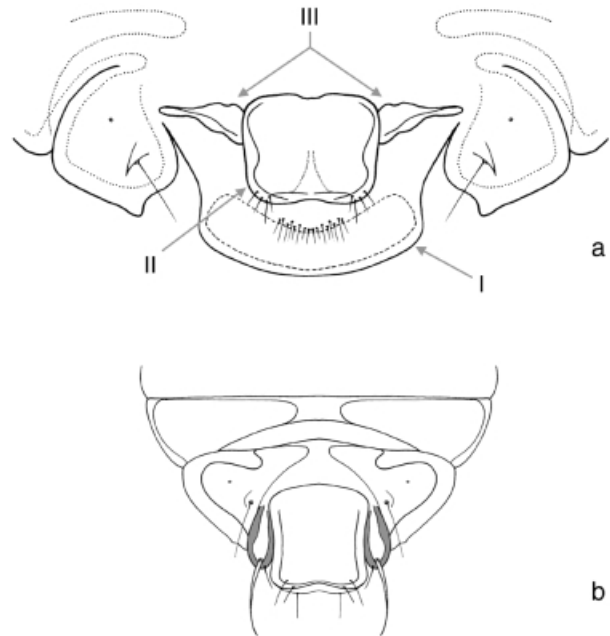


Fig. 9. Diagrammatic male abdominal terminalia (dorsal view). a, Typical goniodid abdominal segment IX showing (I) prominent central lobe (II) weakly bilobed seta-bearing plate with (III) laterally adjacent paired sclerites; b, discrete seta-bearing lobes (shaded) on the lateral margins of abdominal segment IX.

47. *Column of intermediate sternal setae*: (1) absent or incomplete; (2) present at least over segments IV–VII.

These setae are usually evident as thin ‘normal’ or microsetae, however some taxa completely lack them or they may be only evident on the terminal segments of the abdomen. These setae are commonly damaged during preparation of the specimen for slide mounting and consequently should be checked on multiple specimens before they are scored as missing.

48. *Intermediate to submedian tergal setal rows, excluding complete lateral tergal rows*: (1) absent; (2) present at least on abdominal segments III–V.

When present, these setal rows always occur on at least four consecutive abdominal segments. In all but *Passonomedeia* Carriker and *Stephanius* they are matched by equivalent rows on the ventral surface, although the setal distribution may differ slightly from that dorsally.

49. *Sublateral, intermediate and/or submedian setal columns on the ventral abdominal surface of segments III–V*: (1) absent; (2) present.

Abdomen (segment IX) and genitalia

50. *Male abdominal segment IX*: (1) not extending prominently beyond the natural margin of the abdomen; (2) composed of a prominent lobe extending beyond the natural margin of the abdomen (I, Fig. 9a).

The morphology of abdominal segment IX within male Gonioididae has been considered by Ledger (1980), Kéler (1939) and on various occasions by Tendeiro, who has used it to help diagnose species for several genera (e.g. Tendeiro, 1980). Kéler (1939) attempted to interpret the homologies of the sclerites within and adjacent to the male segment IX; however, a more comprehensive study that considers the ontogeny of these sclerites is needed before Kéler's interpretation can be accepted. This character complex is largely restricted to Gonioididae and has been divided into three distinct characters (50–52). With the exception of *Goniodes pavonis* (L.), abdominal segment IX in all male Gonioididae prominently extends out from the abdomen. This condition is present in most species of *Goniodes*, although in *G. pavonis* segment IX is expanded laterally and distinctly less prominent.

51. *Weakly bilobed seta-bearing plate embedded or partially enclosed within male abdominal segment IX*: (1) absent; (2) present (II, Fig. 9a).

This plate sits within abdominal segment IX and is usually thickened laterally. To a greater or lesser extent this plate may appear to be medially divided, giving it a bilobed appearance. Microsetae are present on each lobe of the plates posterior margin. In *Chelopistes* the homologies within segment IX are difficult to interpret, although this plate appears to be pushed back, forming part of the posterior margin of abdominal segment IX.

52. *Single pair of sclerites laterally adjacent to the seta-bearing plate of segment IX*: (1) absent; (2) present (III, Fig. 9a).

These sclerites sit either side of the plate described in character 51. Their morphology is variable and may take the form of a thin sclerite whose inner lateral margin projects just under the plate, e.g. *Physconelloides*, or may form a distinct plate which sits close to but does not project under the setose plate, e.g. *Campanulotes*.

53. *Discrete seta-bearing lobes on the male lateral margins of segment IX*: (1) absent; (2) weakly developed; (3) prominent (Fig. 9b); (4) greatly modified.

These lobes are present on the lateral margin of the abdomen and are confined to Heptapsogasteridae. They are weakly evident in *Trichodopeostus* but otherwise are most well developed in *Physconella* and *Strongylocotinae* (*sensu* Eichler, 1963). Within *Strongylocotes* the lobes are highly modified and form the dominant part of abdominal segment IX.

54. *Vulval margin*: (1) setal fringe absent; (2) fringed by one or more rows of setae (Fig. 10a,b).

55. *Vulval margin setal fringe number (if present) regardless of setal type*: (1) single (Fig. 10a); (2) double (Fig. 10b).

In those cases where a double setal margin is evident the outer row are predominantly thin microsetae, whereas the inner are usually more widely spaced and composed of thicker microsetae or thorn-like microsetae as in *Austrokelloggia*. Often both setal rows are interrupted or more widely spaced medially.

56. *Setae both sides on the lateral edge of the vulval margin*: (1) absent; (2) present (Fig. 10c,d).

57. *Lateral edge vulval margin setal number (if present)*: (1) patch or row of normal to microsetae (Fig. 10c); (2) 2 or 3 distinct setae (Fig. 10d).

Most Gonioididae have two, or more commonly three, distinct setae either side on the lateral edge of the vulval margin. In *Goniodes* a distinctive patch of setae is present in this region, while in *Passonomedeia* and *Strongylocotes* a single microsetal row is present.

58. *Male external genitalia length assuming apical tip of the parameres is level with the posterior margin of abdominal segment IX*: (1) does not protrude into abdominal segment IV; (2) extends into the abdomen at least as far as abdominal segment IV.

External genitalia (*sensu* Lyal, 1986) comprise the parameres, mesomeres and accompanying sclerites in addition to the basal apodeme. This character crudely considers the size of the external genitalia in relation to the size of the abdomen. Because the external genitalia show variable degrees of protrusion from the genital opening, the measurement is made assuming that the most posterior tip of the parameres is level with the posterior margin of abdominal segment IX.

59. *Basal apodeme lateral strut sclerotization*: (1) thickly sclerotized leaving a wide gap between struts (Fig. 11a); (2) thickly sclerotized leaving a narrow gap between struts (Fig. 11c); (3) thinly sclerotized leaving a wide gap between struts; (4) thinly sclerotized leaving a narrow gap between struts (Fig. 11b).

In all Gonioididae and Heptapsogasteridae the basal apodeme is faintly sclerotized medially and strongly sclerotized laterally, giving the appearance of two disconnected rods ('lateral struts'). The width of the weakly sclerotized region between these rods is variable but falls into the four discrete categories described above.

60. *Male external genitalia*: (1) simple, principally composed of a basal apodeme with other structures greatly reduced or absent (Fig. 11b); (2) complex, composed of a basal apodeme with other genital apparatus significantly developed (Fig. 11a,c).

The external genitalia of male Gonioididae and Heptapsogasteridae are extremely variable and structural homologies beyond the general ground plan are often difficult to assess. In this case I have divided the taxa between those where the basal apodeme forms the predominant part of the male genitalia and the parameres and additional endomeral structures are either greatly reduced or absent, and those where both the parameres and mesomeres are well developed, such as in *Goniodes pavonis*. The former 'simple' character state is largely restricted to Gonioididae from Columbiformes, while the latter 'complex' state is more common and present in all Heptapsogasteridae except *Trichodopeostus*.

61. *Genital sac sclerotization*: (1) not visible; (2) lightly sclerotized; (3) heavily sclerotized.

The genital sac is articulated to the basal apodeme and is usually visible as a faint hyaline structure between the

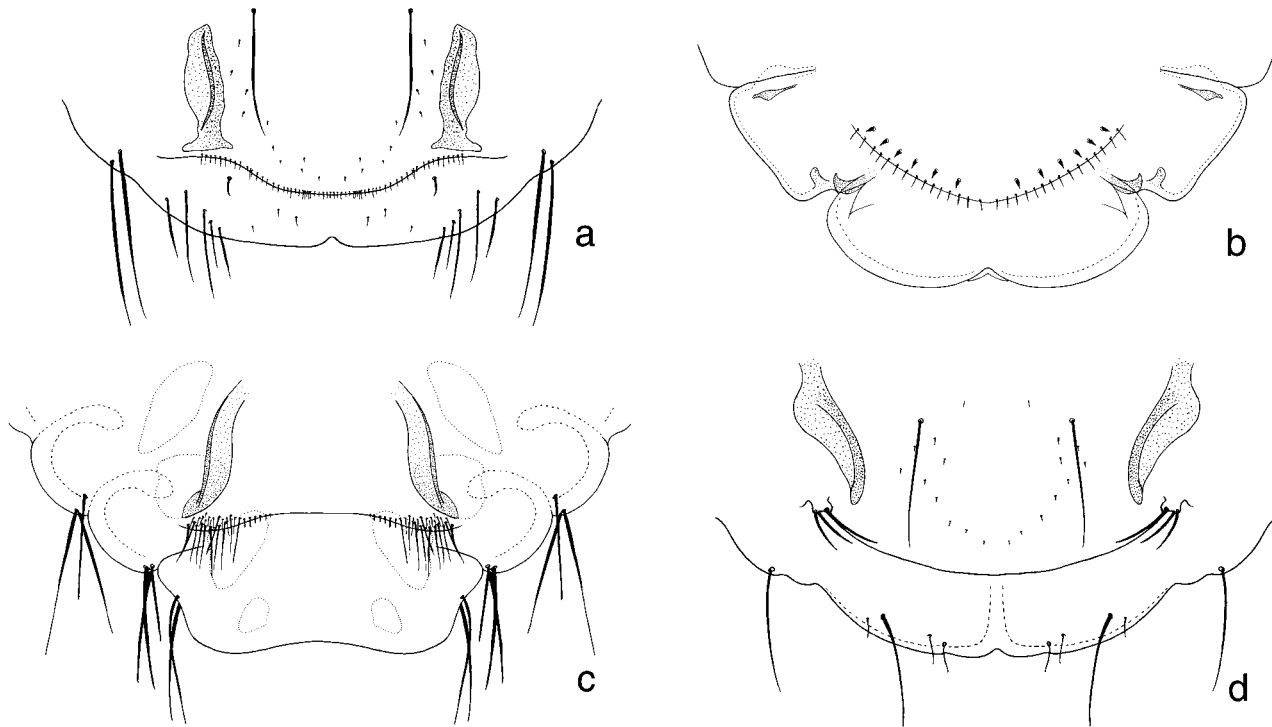


Fig. 10. Diagrammatic female abdominal terminalia (ventral view). a,b, Vulval margin setal fringe; c,d, setae on the lateral edge of the vulval margin.

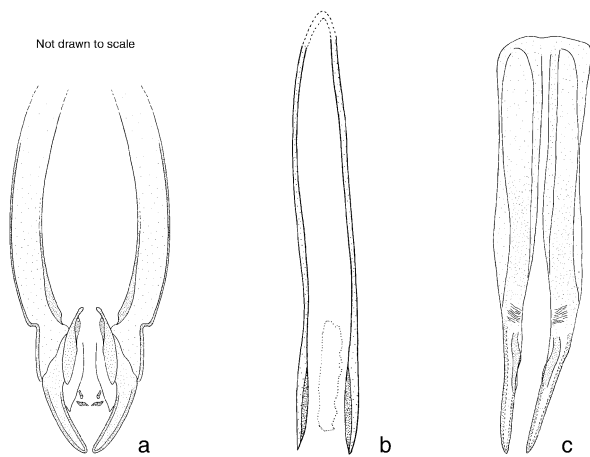


Fig. 11. Male external genital types. a, *Heptapsogaster* sp.; b, *Nitzschiella* sp.; c, *Coloceras damicornis* (Nitzsch).

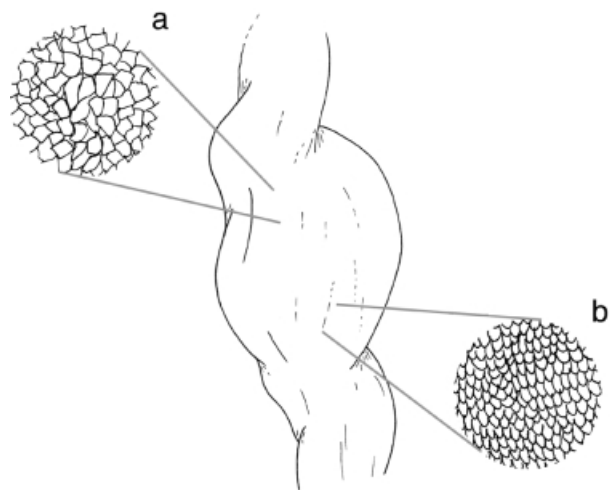


Fig. 12. Genital sac sclerites.

basal apodeme lateral struts. In those taxa where the sac is lightly to well sclerotized, small sclerites may be visible over the surface as described in character 62.

62. *Genital sac sclerites (if present)*: (1) small roughly circular sclerites dotted over the genital sac (Fig. 12b); (2) medium to large irregularly shaped sclerites over the genital sac (Fig. 12a).

Results

The 100 addition sequence replicates found two islands of cladograms each containing fifteen equally parsimonious cladograms (215 steps, CI=0.377, RI=0.695). A strict and Adams consensus for the combined cladograms from both islands is presented in Fig. 13. Bremer support values are

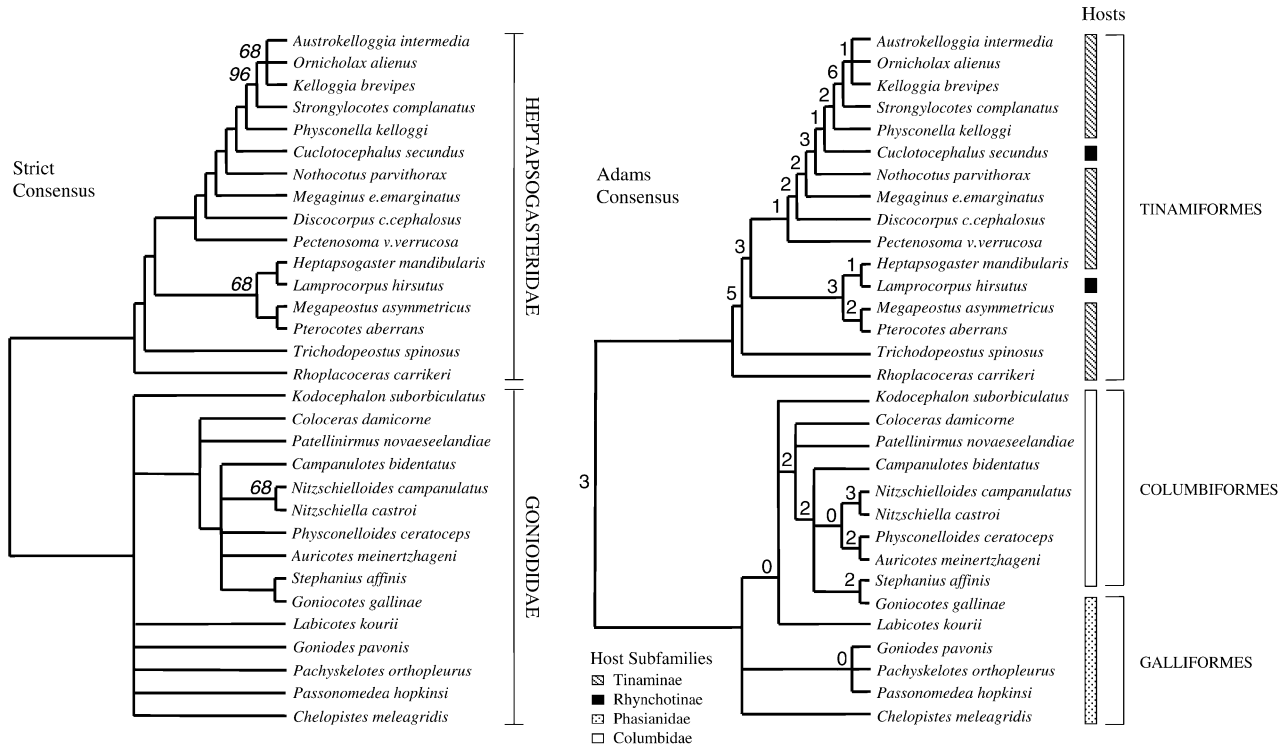


Fig. 13. Strict and Adams consensus of the thirty most parsimonious cladograms. Jackknife values above 50% based on 100 replicates are shown on the strict consensus and Bremer support values (decay indices) are given above each node on the Adams consensus. The latter indicate the number of additional steps required to collapse the clade. Host distribution is also indicated.

shown above each node and jackknife values for those nodes that were present in the 50% majority-rule consensus cladogram are given. Despite the presence of two distinct islands, the strict consensus incorporating cladograms from both islands is relatively resolved. Inspection of the strict consensus cladograms obtained separately from each island (Fig. 14) shows that the incongruence between the islands is restricted within the columbiform Gonioididae and that the branching pattern of Heptapsogasteridae and Gonioididae from Galliformes is identical. Within the discordant taxa from Columbiformes the principle cause of disagreement between the islands concerns the position of the *Goniocotes*–*Stephanius* clade. In the first island this clade is placed basally to the majority of the columbiform taxa, whilst in the second island the clade is nested at the apex of the columbiform gonioidids.

Cladistic analysis

The following discussion considers the character states that diagnose the clades presented in Fig. 13 and their relative support obtained from the Bremer support and jackknife analyses. Unambiguous character state changes are shown plotted on to one of the thirty most parsimonious cladograms in Fig. 15. For each supporting character (indicated by numbers in parentheses), superscripts correspond to the character states common to all or most members of the clade.

Character state synapomorphies are identified preceding the character number with an asterisk (*).

The basal split between the two families has a Bremer support value of 3. This is where the cladogram was rooted. All Heptapsogasteridae lack the distinctive abdominal segment IX present in most Gonioididae (50¹, 51¹). However, some gonioidid characteristics are evident in both *Rhoplacoceras* and *Trichopeostus*, the two most basal Heptapsogasteridae. The head chaetotaxy of Gonioididae is also characteristic, emphasizing the split between the two groups. With the exception of *Chelopistes meleagridis* and *Labicotes kourii*, M.T.S. 1 and M.T.S. 3 form well developed macrosetae (20¹) in all Gonioididae. Also where M.T.S. 2 is present in Gonioididae its condition normally takes the form of a small microseta (22¹). In the majority of Heptapsogasteridae M.T.S. 2 is well developed, either as a thorn-like, normal or macroseta (22²). Only *Cuclotocephalus*, *Megaginus* and the basal *Rhoplacoceras* lack this state. The most distinctive features characterizing the two families concern the morphology of the thorax. All Gonioididae have two distinct pairs of setae both sides of the lateral to posterior margin of the pterothorax (*27²). Within Heptapsogasteridae, the homologues of these setae are difficult to establish, although the unique paired arrangement of Gonioididae is absent from all the tinamou lice. With the exception of *Rhoplacoceras carrikeri* Eichler, abdominal segment II of Heptapsogasteridae is deeply embedded within abdominal segment III and is always much

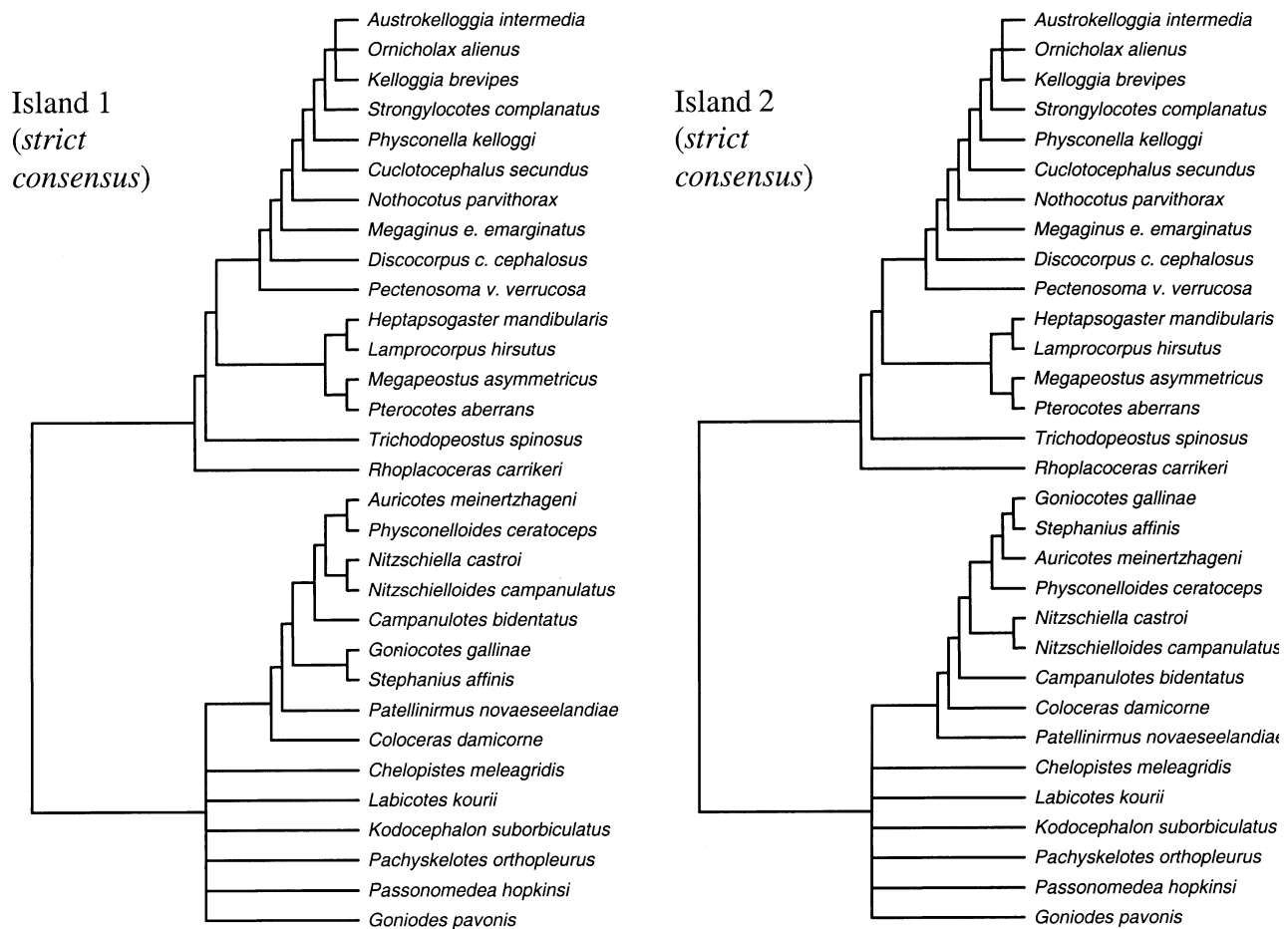


Fig. 14. Strict consensus of the two islands (each of fifteen cladograms) identified using the random stepwise addition feature of PAUP* (100 replicates).

smaller than segment III (*31² and *34², respectively). These two characters support the basal position of *Rhoplacoceras* in Heptapsogasteridae. The node containing all the tinamou lice with the exception of *Rhoplacoceras* has a Bremer support value of 5 and these taxa lack the prominent central lobe of male segment IX found in Gonioididae (50¹).

Within the tinamou lice subfamily 'Heptapsogasterinae' (*sensu* Carriker, 1936) forms a paraphyletic group which is basal to the other tinamou lice. Four of these taxa (*Heptapsogaster* Carriker, *Lamprocorpus*, *Megapeostus* and *Pterocotes*) form a monophyletic group and have a Bremer support value of 3. These taxa all possess nodi emanating from the inner margin of the marginal carina between the preantennal nodi (4²) and have distinctly pointed temple margins which project significantly beyond the posterior margin of the head (16³). Within this group, *Heptapsogaster* and *Lamprocorpus* are sister taxa and share three pairs of nodi on the marginal carina (*5⁴). These form a sister group to *Megapeostus* and *Pterocotes*. The 'Physconellinae' (*sensu* Carriker, 1936) are also paraphyletic and are basal to the monophyletic Strongylocotinae (*sensu* Eichler, 1963).

Strongylocotinae form the most strongly supported clade in the tree with a Bremer support value of 6 and a jackknife value of 96%. This group corresponds to Strongylocotinae and Ornicholacinae *sensu* Carriker (1936). The condition of abdominal segment II is particularly distinctive in this group. It is completely enclosed by the surrounding pterothorax and abdominal segment III, leaving no free lateral margin. This state is also found in *Physconella kelloggi* (Paine), which is immediately basal to this clade (*32¹). Segment II is also medially divided, giving it a bilobed appearance (*33²). This bilobed condition in *Austrokelloggia intermedia* Carriker is less well developed but close inspection reveals that each lobe is clearly separated by a less well sclerotized area. The dorsal surface of this group is characterized by a distinctive fine pitting in the cuticular surface of abdomen (*44²). This pitting occurs beyond the area outlined in character 44 to cover abdominal segments II and III in the *Austrokelloggia-Kelloggia-Ornicholax* Carriker clade (*36²); and in the case of *Ornicholax alienus* (Giebel) the cuticular dorsal surface of the entire body with the exception of abdominal segment IX is pitted.

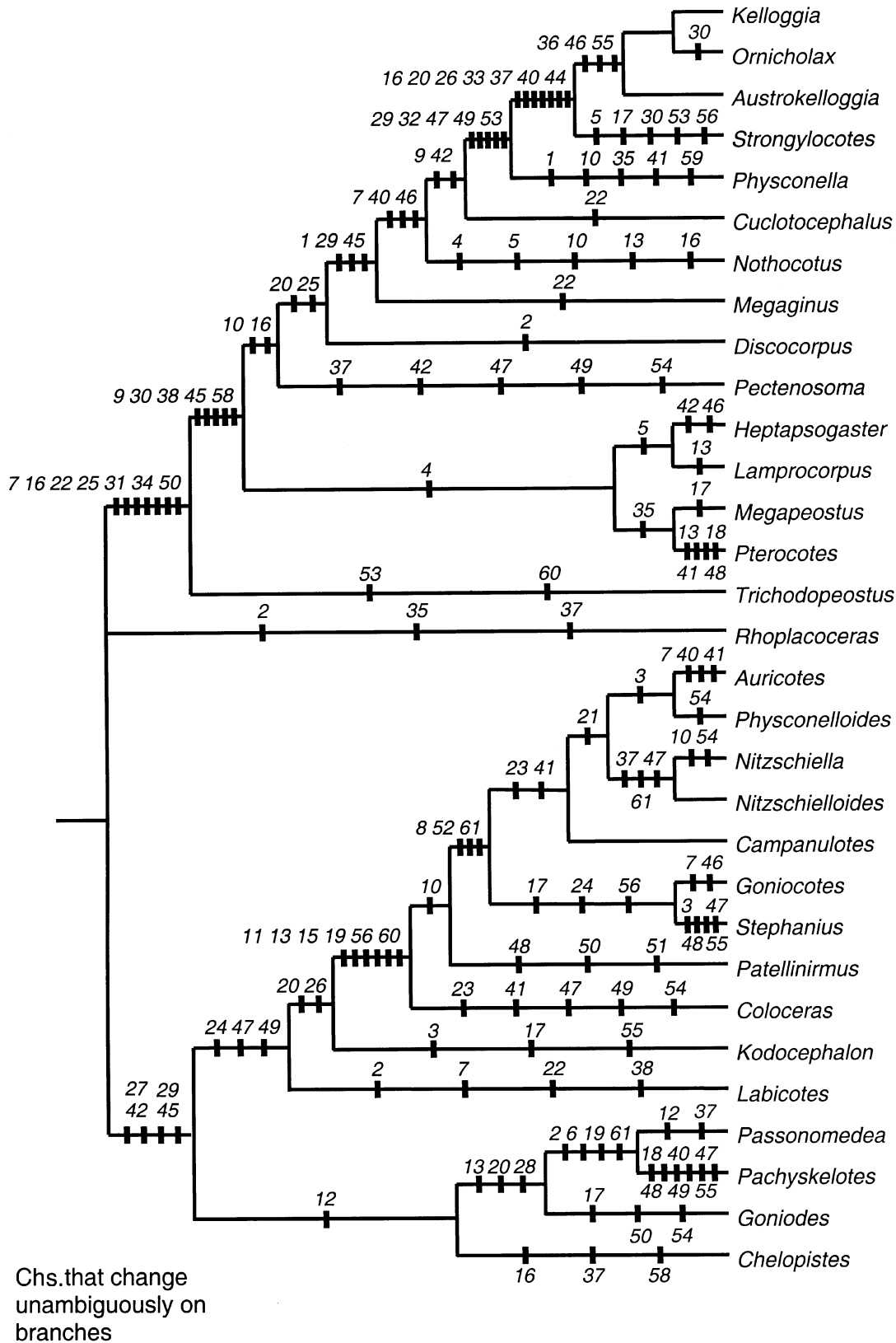


Fig. 15. Characters mapped on to one of the thirty most parsimonious cladograms.

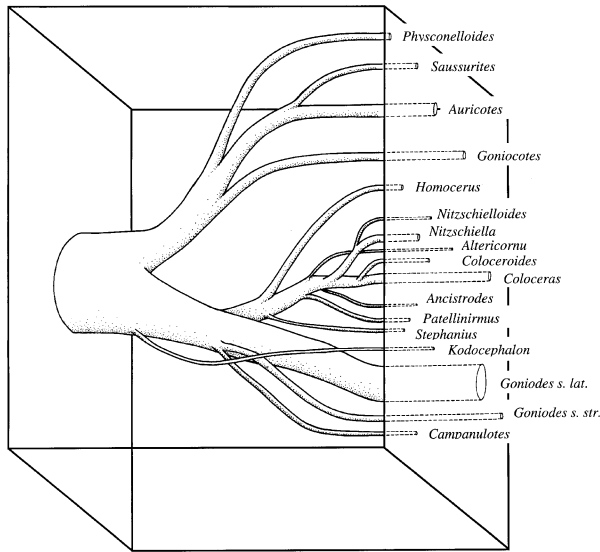


Fig. 16. Tendeiro's evolutionary tree of Gonioididae from Columbiformes. Redrawn from Tendeiro (1980).

Gonioididae were markedly less resolved, although several distinct clades are present. The strict consensus shows a split between those taxa hosted by Galliformes and those from Columbiformes. The galliform gonioidids are either basal, or form a sister group to the largely monophyletic columbiform gonioidids, although *Goniocotes gallinae* is a clear exception. The strict consensus was completely unresolved for these taxa (excluding *Goniocotes*), however the Adams consensus grouped *Goniodes*, *Pachyskelotes* and *Passonomea*, which corresponds to Eichler's subfamily Gonioidinae (Eichler, 1963). This arrangement was not supported by the Bremer support analysis. The Adams consensus shows that there are equally parsimonious cladograms in which both *Chelopistes* and *Labicotes* are embedded within Gonioididae. This suggests that Clay's (1976) assertion that both these taxa are philopterids (*sensu* Eichler, 1963) is likely to be incorrect. *Patellinirmus* and *Coloceras* occupy a basal position within the columbiform gonioidids, excluding *Kodocephalon suborbiculatus* (Piaget), at the base of the clade. This position has a Bremer support value of 2. The clade differs in a number of respects to the other taxa included in this analysis. Their head chaetotaxy typically lacks M.T.S. 4 (23¹) and with the exception of the *Goniocotes*–*Stephanius* clade, these taxa also lack a distinct post-temporal setae (24¹). Their genital morphology is also distinct from both the tinamou lice and the remaining Gonioididae. Their male external genitalia are typically simple, comprising a thinly sclerotized basal apodeme with greatly reduced or absent parameres and mesomeres (60¹). This contrasts to the well developed parameres and mesomeres of all other Gonioididae and all but one of the tinamou lice. The female vulval margin also shows some modification, typically possessing two (or more commonly three) distinct setae either side of the entrance to the genital chamber (57²). Resolution within this clade is relatively

low. *Auricotes* Kéler and *Physconelloides* are sister taxa that form a sister group to the *Nitzschella*–*Nitzschelloides* clade although this arrangement was not maintained in the strict consensus. These taxa all lack the second marginal temporal seta (*21¹). The relationship between *Nitzschella* and *Nitzschelloides* has a Bremer support value of 3. Both taxa have two pairs of setae on the posterior lateral corners of abdominal segment III (37²), a condition absent in all other Gonioididae which are of a similar length (*39³). This placement is at odds with the findings of Hopkins & Clay (1952), who considered *Nitzschella* inseparable from *Coloceras*. The *Physconelloides*–*Auricotes* group has a Bremer support value of 2. Both taxa possess deep indentations on the inner margin of their marginal carina. Most, although not all, of these indentations mark the attachment site for the submarginal and marginal microsetae in this region (3²).

Discussion

The phylogeny is partially consistent with the limited early classifications presented by Carriker (1936), Kéler (1939) and Eichler (1963) (Table 1). Within Heptapsogasteridae, Strongylocotinae (*sensu* Eichler, 1963) is monophyletic and forms a sister group to the monogenic Physconellinae. The other two subfamilies are paraphyletic, however both can be described as convex (*sensu* Meacham & Duncan, 1987), with members of 'Heptapsogasterinae' occupying the most basal position in the cladogram. Classifications for Gonioididae are less complete than for the tinamou lice, particularly with respect to the columbiform gonioidids, making comparison between various schemes difficult. The Adams consensus supports the Gonioidinae subgroup (*sensu* Eichler, 1963), however 'Physconelloidinae' from Columbiformes are more problematic. A clade incorporating all members of this group except *Kodocephalon* Kéler with Goniocotinae (*Goniocotes* and *Auricotes*) was formed, although Goniocotinae are paraphyletic in the strict consensus. Tendeiro (1980) produced an evolutionary tree for selected gonioidid taxa which is redrawn in Fig. 16. This tree, although not constructed empirically, does provide some insight into Tendeiro's views on the evolutionary relationships of Gonioididae, and in particular the columbiform gonioidids. The tree contains many subgenera that have not been included in the present study, nevertheless some of the groupings identified are consistent with those present in the Adams consensus. Despite this, his tree is, in general, largely incongruent with both this phylogeny, and previous classifications. Tendeiro's tree is difficult to interpret but appears to show a three-way basal split between the *Goniodes* complex (listed as *Goniodes sensu lato*), which presumably includes related taxa like *Passonomea* and *Pachyskelotes* not included by Tendeiro, a related but much larger group restricted entirely to Columbiformes and a third more distantly related clade containing taxa from both major host groups.

Much of the confusion surrounding the columbiform Gonioididae concerns their generic status, as many previously well defined genera appear to grade into each other in the light

of new species descriptions. This is a recurring theme in the literature on Goniididae and in Ischnocera more widely, forcing many authorities (most notably Hopkins & Clay, 1952) to accept only the broadest possible generic definitions. Ledger (1980) provides a more specific account of some of these problems faced by taxonomists working on Goniididae and it seems likely that further work on their phylogeny will require an extensive review of the taxonomic status of most, if not all, goniidid taxa.

Host–parasite relations

The extent to which the lice have cospeciated with their hosts is difficult to assess owing to the lack of cladistic data available for their host taxa. There are no cladistic hypotheses for generic relationships of Tinamiformes and data are similarly lacking for many of the columbiform hosts of Goniididae. At the level of host order there is significant correspondence between the louse and host phylogeny, however at lower taxonomic levels the association appears to be more complex.

Within Tinamiformes, Boettischer (1934) separates the order into three subfamilies on the basis of colour pattern, bill, nostril, tarsi, toe and tail morphology in addition to their ecological distribution. Generic exemplars from two of the three subfamilies were included in the phylogeny, however at a subfamilial and generic level the host taxonomy does not appear to be congruent with the louse phylogeny. Nevertheless, this conclusion is somewhat premature given the limited number of taxa included in the tinamou louse phylogeny. On the basis of his study on the distribution of tinamou lice, Ward (1957) concluded that louse species groups can be used to define host genera, and that with one exception Boettischer's (1934) classification conforms perfectly to the divisions present within the tinamou lice. Ward's study suggests that a more complete tinamou louse phylogeny incorporating exemplars within genera may reveal greater correspondence between the host and parasite phylogenies than is indicated by this generic phylogeny. This situation parallels that found by workers investigating Trichodectid phylogeny (Lyal, 1987), and in particular the coevolutionary relationships of pocket gopher lice. Deep branches within the gopher louse cladogram revealed only partial congruence with host phylogeny (Page *et al.*, 1995), however close inspection of the terminal taxa can reveal a near 1 : 1 match (Hafner *et al.*, 1994; Hafner & Page, 1995; Page, 1996).

The host–parasite relationships within Goniididae are comparable. Louse species confined to Galliformes are predominantly found in a single clade, as are those confined to Columbiformes, however within these groups correspondence between the host and parasite phylogenies is lacking, perhaps due to the limited number of louse taxa included.

Prospects for understanding more about the complex coevolutionary history of these louse families will require robust phylogenies for both host and parasite which incorporate more extensive sampling than is presented here. However, such studies are usually limited by the practicalities of dealing

with large numbers of distantly related taxa. It is hoped that this preliminary study of the generic relationships for these two families will permit more meaningful coevolutionary studies, employing more exhaustive sampling of louse taxa than was possible during this investigation. In this regard, the use of morphological data from instars may help to establish clearer character homologies within these groups. Prospects for future coevolutionary studies are greatly improved by comparable studies currently underway to establish generic relationships of their hosts (D. Clayton, S. Bertelli & A. L. Porzecanski, personal communication).

A complete data matrix including cladograms presented in this paper is available from TreeBASE (<http://herbaria.harvard.edu/treebase>). Study accession #S358. All SEM images taken during this investigation, in addition to images of a further twenty philopterid genera, can be viewed at <http://taxonomy.zoology.gla.ac.uk/~vsmith/SEM/LOUSE.htm>.

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Appendix 1. Taxa included in the cladistic analysis. Hosts for the material examined and type hosts for each taxon are also provided. Species marked * represent the type species for the genus, Brit. Mus. refers to the British Museum of Natural History accession number, Mein. # refers to the Meinertzhagen number attached to the slide and 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. While 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 his material.

Taxon	Host and type host	Material examined
<i>Discocorpus c. cephalosus</i> * Carriker, 1936	<i>Crypturellus noctivagus</i> ssp. Weid, 1820 Type host: <i>Crypturellus garleppi affinis</i> ?	2 adult ♂ and 1 adult ♀ (Brit. Mus. 1968–730)
<i>Heptapsogaster mandibularis</i> * Carriker, 1936	<i>Crypturellus soui cauae</i> (Chapman, 1912) Type host: <i>Crypturellus tataupa</i> Temminck, 1815	4 adult ♂ and 2 adult ♀ (Brit. Mus. 1968–720 & one unnumbered slide – Hopkins Coll.)
<i>Lamprocorpus hirsutus</i> * Carriker, 1936	<i>Nothoprocta ornata branickii</i> Taczanowski, 1875 and <i>N. o. ornata</i> (Gray, 1867) Type host: <i>Nothoprocta branickii</i> (= <i>Nothoprocta ornata branickii</i> Taczanowski, 1875)	2 adult ♂ and 2 adult ♀ (Brit. Mus. 1956–90 1975–308 & one unnumbered slide – Hopkins Coll.)
<i>Megapeostus asymmetricus</i> * Carriker, 1936	<i>Crypturellus undulatus adspersus</i> (Temminck, 1815) Type host: <i>Crypturellus u. undulatus</i> (Temminck, 1815)	1 adult ♂ (Brit. Mus. 1956–90)
<i>Pectenosoma v. verrucosa</i> * (Taschenberg, 1882)	<i>Crypturellus soui inconspicuus</i> Carriker, 1935; <i>C. noctivagus</i> Weid 1820 and <i>C. v. variegatus</i> Gmelin, 1789 Type host: <i>Crypturellus vs. variegatus</i> Gmelin, 1789	4 adult ♂ and 5 adult ♀ (Brit. Mus. 1961–188, Mein. # 14693 & 3178)
<i>Pterocotes aberrans</i> * (Carriker, 1903)	<i>Tinamus major robustus</i> Sclater & Slavin, 1868 Type host: <i>Tinamus major castaneiceps</i> Salvadori, 1895	1 adult ♂ and 1 adult ♀ (Hopkins coll. # 560)
<i>Rhoplacoceras carrikeri</i> Eichler, 1947	<i>Tinamus bolitanus</i> ? Type host: <i>Tinamus tao septentrionalis</i> Braborne & Chubb, 1913	2 adult ♂ and 2 adult ♀ (Hopkins coll., unnumbered)
<i>Trichodopeostus spinosus</i> * Carriker, 1936	<i>Nothocercus nigricapillus</i> Gray, 1867 Type host: <i>Nothocercus n. nigricapillus</i> (Gray, 1867)	1 adult ♂ and 2 adult ♀ (Mein. # 14673)
<i>Cuclotocephalus secundus</i> Carriker, 1936	<i>Nothoprocta p. pentlandi</i> (Gray, 1867) Type host: <i>Nothoprocta pentlandi ambigua</i> Cory, 1915	2 adult ♂ and 3 adult ♀ (Brit. Mus. 1953–305 & Mein. # 13506)
<i>Megaginus e. emarginatus</i> * Carriker, 1936	<i>Crypturellus obsoletus crucis</i> ? and <i>Crypturellus obsoletus punensis</i> (Chubb, 1917) Type host: <i>Crypturellus obsoletus punensis</i> (Chubb, 1917)	2 adult ♂ and 1 adult ♀ (unnumbered slide)
<i>Nothocotus parvithorax</i> * Carriker, 1936	<i>Nothocercus nigricapillus</i> Gray, 1867 Type host: <i>Nothocercus nigricapillus cadwaladeri</i> Carriker, 1933	3 adult ♂ and 2 adult ♀ (Mein. # 17670)
<i>Physconella kelloggi</i> * (Paine, 1913)	<i>Crypturellus nigriceps</i> ? Type host: <i>Crypturellus soui panamensis</i> (Carriker, 1910)	2 adult ♂ and 2 adult ♀ (Brit. Mus. 1956–90)
<i>Austrokelloggia intermedia</i> * Carriker, 1936	<i>Nothocercus nigricapillus</i> Gray, 1867 and <i>N. bonapartei intercedens</i> Salvadori, 1895 Type host: <i>Nothocercus n. nigricapillus</i> (Gray, 1867)	3 adult ♂ and 1 adult ♀ (Mein. # 17670–1 and 3170)
<i>Kelloggia brevipes</i> * Carriker, 1903	<i>Crypturellus t. tataupa</i> (Temminck, 1815) and <i>Tinamus guttatus</i> (Natterer) Type host: <i>Tinamus major castaneiceps</i> Salvadori, 1895	2 adult ♂ and 4 adult ♀ (Mein. # 3184 & 3164)
<i>Ornicholax alienus</i> (Giebel, 1874)	<i>Tinamus m. major</i> (Gmelin, 1789) Type host: <i>Tinamus solitarius</i> (Vieillot, 1819)	1 adult ♂ and 5 adult ♀ (Mein. # 3168–2 slides)
<i>Strongylocotes complanatus</i> * (Piaget, 1880)	<i>Crypturellus v. variegatus</i> Gmelin, 1789	

Appendix 1 continued.

Taxon	Host and type host	Material examined
	Type host: <i>Crypturelus o. obsoletus</i> (Temminck, 1815)	3 adult ♂ and 3 adult ♀ (Brit. Mus. 1935–260–2 slides & Mein. # 2878)
<i>Chelopistes meleagridis</i> * (L., 1758)	Turkey, presumably <i>Meleagris gallopava</i> L., 1758 Type host: <i>Meleagris gallopava</i> L., 1758	7 adult ♂ and 5 adult ♀ (Brit. Mus. 1968–482 & Hopkins coll., unnumbered)
<i>Auricotes meinertzhageni</i> Tendeiro, 1976	<i>Ptilonopus huttoni</i> Finsch, 1874 Type host: <i>Ptilinopus huttoni</i> Finsch, 1874	2 adult ♂ (Mein. # 100758)
<i>Gonicocotes gallinae</i> * (De Geer, 1778)	Chicken, presumably <i>Gallus gallus</i> (L., 1758) Type host: <i>Gallus domesticus</i> [= <i>Gallus gallus</i> (L., 1758)]	1 adult ♂ and 10 adult ♀ (Brit. Mus. 1975–564 1980–40; Mein. # 15126, 3199; & Hopkins coll., unnumbered)
<i>Goniodes pavonis</i> * (L., 1758)	<i>Pavo cristatus</i> L., 1758 Type host: <i>Pavo cristatus</i> L., 1758	1 adult ♂ and 1 adult ♀ (Brit. Mus. 1967–599)
<i>Passonomedea hopkinsi</i> * Carriker, 1944	<i>Odontophorus capueira capueira</i> (Spix, 1825) Type host: <i>Odontophorus capueira capueira</i> (Spix, 1825)	3 adult ♂, 2 adult ♀ and 2 nymphs (Hopkins coll., unnumbered)
<i>Pachyskelotes orthopleurus</i> * (Nitzsch, 1874)	<i>Argusianus argus argus</i> (L., 1766) Type host: <i>Argusianus argus argus</i> (L., 1766)	2 adult ♂ and 6 adult ♀ (Mein. # 4455 & 10889)
<i>Patellinirmus novaeseelandiae</i> Tendeiro, 1972	<i>Hemiphaga novaeseelandiae</i> (Gmelin, 1789) Type host: <i>Hemiphaga novaeseelandiae</i> (Gmelin, 1789)	1 adult ♂, 1 adult ♀ and 3 nymphs (Brit. Mus. 1974–201 & 1974–285)
<i>Stephanius affinis</i> Taschenberg, 1882	<i>Ducla rufigaster</i> (Quoy & Gaimard, 1830) Type host: <i>Ducla rufigaster</i> (Quoy & Gaimard, 1830) and <i>Ducla bicolor</i> (Scopoli, 1786)	6 adult ♂ and 3 adult ♀ (Mein. # 10783–2 slides & 10774)
<i>Kodocephalon suborbiculatus</i> (Piaget, 1890)	<i>Goura victoria</i> (Fraser, 1844) Type host: <i>Goura victoria</i> (Fraser, 1844)	6 adult ♂ and 8 adult ♀ (Mein. # 10821 & 10824)
<i>Physconelloides ceratoceps</i> * Ewing, 1927	<i>Leptotila verreauxi brasiliensis</i> (Bonaparte, 1956) Type host: <i>Leptotila verreauxi chalcauchenia</i> Sclater & Slavin? (Possibly <i>L. v. megalura</i> Sclater & Slavin, 1879)	3 adult ♂ and 3 adult ♀ (Brit. Mus. 1961–188)
<i>Campanulotes bidentatus</i> (Scopoli, 1763)	Domestic pigeon, presumably <i>Columba livia</i> Gmelin, 1789 Type host: <i>Columba palumbus</i> L., 1758	4 adult ♂ and 3 adult ♀ (Brit. Mus. 1965–592 & 1969–64)
<i>Nitzschiella castroi</i> Tendeiro, 1969	<i>Turtur tympanistria</i> (Temminck, 1810) Type host: <i>Turtur tympanistria fraseri</i> Bonaparte, 1969	1 adult ♂ and 1 adult ♀ (Brit. Mus. 1981–173)
<i>Nitzschielloides campanulatus</i> Tendeiro, 1969	<i>Streptopelia pictutata</i> Temminck Type host: <i>Streptopelia pictutata</i> Temminck	1 adult ♂ and 5 adult ♀ (Brit. Mus. 1981–173)
<i>Coloceras damicorne</i> * (Nitzsch, 1866)	<i>Columba livia</i> Gmelin, 1789 Type host: <i>Columba palumbus</i> L., 1758	6 adult ♂ and 15 adult ♀ (Mein. # 11489, 16754 & 16778–9) (Latter two numbers on one slide)
<i>Labicotes kourii</i> Tendeiro, 1975	<i>Crax globulosa</i> Spix, 1825 Type host: <i>Crax globulosa</i> Spix, 1825	2 adult ♀ (Mein. # 12663) (Holotype)