Systematic Entomology (2005), DOI: 10.1111/j.1365-3113.2005.00323.x

Morphology of male genitalia in lice and their relatives and phylogenetic implications

KAZUNORI YOSHIZAWA[1,2] and KEVIN P. JOHNSON[2]
[1]Systematic Entomology, Hokkaido University, Sapporo, Japan and
[2]Illinois Natural History Survey, Champaign, Illinois, U.S.A.

Abstract. Lice (Insecta: Phthiraptera) have long been considered to compose a monophyletic group of insects on the basis of external morphological characteristics. However, a recent phylogenetic analysis of 18S rDNA sequences suggested that 'Phthiraptera' have arisen twice within the order Psocoptera (booklice and barklice). The external features of lice are highly specialized to a parasitic lifestyle, and convergence may be frequent for such characters. To provide a further test between traditional and recent molecular-based phylogenetic hypotheses, a phylogenetic analysis of lice and relatives based on morphological characters that are independent from the selective pressures of a parasitic lifestyle is needed. Here, we examined the morphology of the male phallic organ in lice and relatives ('Psocoptera': suborders Troctomorpha and Psocomorpha) and detected some novel modifications that were stable within each group and useful for higher level phylogenetic reconstruction. Phylogenetic analysis based on these characters provided a concordant result with the 18S-based phylogeny. In particular, the apomorphic presence of articulations between the basal plate, mesomere and ventral plate (= sclerite on the permanently everted endophallus) is observed consistently throughout the psocid families Pachytroctidae and Liposcelididae and the louse suborder Amblycera, providing support for a clade composed of these three groups, although possible homoplasy was detected in some Ischnocera. This is the first study to provide morphological support for the polyphyly of lice.

Introduction

Lice are permanent ectoparasites of birds and mammals that spend their entire life cycle on the body of the host in a tight association that makes lice a suitable model system to study cospeciation between host and parasite (Johnson & Clayton, 2003). In association with this extreme parasitic lifestyle, numerous modifications of external and internal morphology, physiology and behaviour have evolved in lice. To understand the origins of parasitism and related specialization in lice, a reliable phylogenetic hypothesis of lice and related insects is required.

Correspondence: Kazunori Yoshizawa, Systematic Entomology, Hokkaido University, Sapporo 060-8589, Japan. E-mail: psocid@res.agr.hokudai.ac.jp

Unpublished for the purposes of zoological nomenclature (Art. 8.2. ICZN)

The closest relatives of lice (order Phthiraptera) are thought to be booklice and barklice (order Psocoptera), with these two orders comprising the group Psocodea. The monophyly of Psocodea is supported by the specialized water vapour uptake system (Rudolph, 1982, 1983; Lyal, 1985) and molecular data (Wheeler *et al*., 2001; Yoshizawa & Johnson, 2003; Johnson *et al*., 2004). Psocoptera are free-living insects, but there are many records of various species of Psocoptera in the plumage of birds and pelage of mammals, as well as in their nests (Hicks, 1959; Pearman, 1960; Mockford, 1967). This association is thought to be a short-term commensalism which may have given rise to a permanent association in lice (Hopkins, 1949).

Studies of the higher level systematics of lice have used both morphological (Königsmann, 1960; Clay, 1970; Kim & Ludwig, 1982; Lyal, 1985; Tröster, 1990; Smith, 2001; Marshall, 2003) and molecular (Cruickshank *et al*., 2001; Johnson & Whiting, 2002; Barker *et al*., 2003) approaches. However, the utility of morphological characters for the

phylogenetic reconstruction of lice remains unclear. For example, significant disagreement between morphological and molecular trees for avian feather lice (Ischnocera) has been identified (Smith *et al*., 2004), although morphological and molecular trees of non-parasitic Psocodea (e.g. suborder Psocomorpha and genus *Trichadenotecnum*) show considerable agreement (Yoshizawa, 2002, 2004; Johnson & Mockford, 2003). One possible reason for the incongruence between morphological and molecular phylogenies of parasitic lice is frequent morphological convergence. The external morphological features of lice are tightly associated with their hosts, and a similar ecological niche on the host (e.g. wing lice vs. body lice) could lead to convergence of external structure (Smith *et al*., 2004). If this is the case, phylogenetic analysis could be misled by such homoplastic characters (Wiens *et al*., 2003).

The phylogenetic position of lice has been estimated on the basis of morphological (Königsmann, 1960; Seeger, 1979; Lyal, 1985) and molecular (Yoshizawa & Johnson, 2003; Johnson *et al*., 2004) data sets. All data sets provide support for a close relationship between Liposcelididae (Psocoptera) and lice, but further assessment of the relationships amongst lice and closely related lineages of Psocoptera is difficult because of the extreme modification and simplification of external features of lice linked to parasitism. Furthermore, recent analyses of 18S rDNA data suggest that lice are a polyphyletic group, and that the psocid family Liposcelididae alone is the sister taxon of the louse suborder Amblycera (Johnson *et al*., 2004: Fig. 1). However, no morphological evidence supporting this clade has been provided to date. To test these hypotheses, an evaluation of characters that are less associated with parasitic lifestyle is needed (Wiens *et al*., 2003).

The male phallic organ, or phallosome, is a highly complicated structure. This organ is usually stored in the genitalic chamber and thus is not exposed to the external environment. Although there are a few possible cases of environmental influence (Lyal, 1984), the phallosome is unlikely to be affected strongly by environmental selective pressures linked to parasitic lifestyle, and, as such, may provide useful and more reliable phylogenetic information for lice than provided by the external morphological features.

The morphology of male genitalia in lice has been investigated previously in detail (Schmutz, 1955; Lyal, 1986). However, the homology of the genitalic structure is exceedingly difficult to establish, especially amongst distantly related taxa, which restricts the use of these characters for the higher level phylogenetic study (Smith, 2000, 2001; Marshall, 2003). In the present study, we examine the homologies of sclerites on the phallosome in lice and the psocid suborders Troctomorpha and Psocomorpha and, based on the resulting morphological data, discuss their significance for the higher systematics of psocids and lice.

Materials and methods

The present study was based on the method of comparative morphology, i.e. the homology of each character was decided by its detailed structures, and relationships and relative positions with other structures. The basal plate and endophallus opening were used as the initial landmarks to identify homology of the sclerites.

Alcohol-preserved specimens were used for examination. The abdomen was separated and placed in 10% KOH solution at room temperature overnight. The material was then rinsed with distilled water and dissected and observed in glycerol. Leica MZ12 (Leica Microsystems, Wetzlar, Germany) and Olympus SZX12 (Olympus, Tokyo, Japan) binocular dissection microscopes and an Olympus BX51 light microscope were used for observations and illustrations.

Samples were selected from all four suborders of lice (Amblycera, Ischnocera, Rhynchophthirina, and Anoplura) and suborders Troctomorpha and Psocomorpha of Psocoptera (Appendix 1). Previous phylogenetic analyses of 18S rDNA supported the monophyly of a clade composed of the psocid infraorder Nanopsocetae (Troctomorpha) and lice (Johnson *et al*., 2004). This is also concordant with previous results based on morphology (Lyal, 1985;

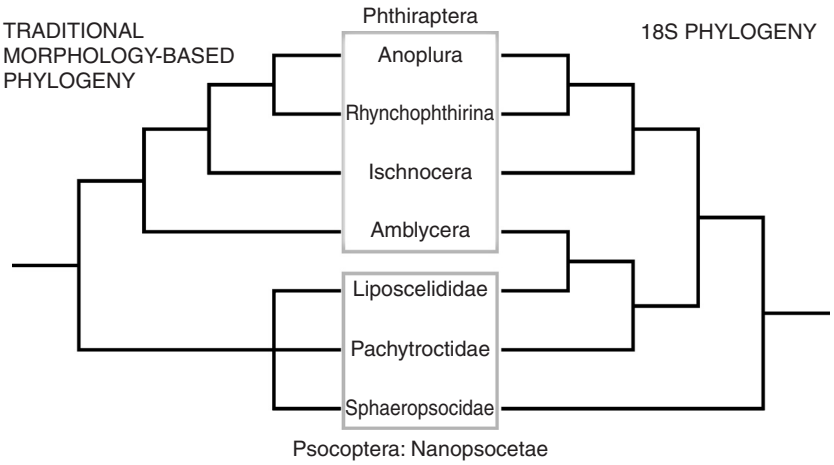

Fig. 1. Two alternative hypotheses on the phylogeny of lice and relatives based on morphology (left) and 18S rDNA (right). Traditionally, lice (Phthiraptera) and the psocopteran infraorder Nanopsocetae are treated as separate monophyletic groups, but both taxa are recovered as non-monophyletic in analyses of 18S data.

Lienhard & Smithers, 2002). Therefore, this clade was treated here as the ingroup. Outgroup taxa were selected from other members of Troctomorpha (i.e. infraorder Amphientometae) and Psocomorpha. Amphientometae are considered to be the closest relatives of Nanopsocetae + lice, and Psocomorpha are the sister of the Troctomorpha + lice clade (Lienhard & Smithers, 2002; Johnson *et al*., 2004).

The following taxa were treated as terminal taxa for the phylogenetic analysis: Psocomorpha, Amphientometae (outgroups); Sphaeropsocidae, Pachytroctidae, Liposcelididae (psocid ingroups); Amblycera, Ischnocera, Rhynchophthirina and Anoplura (louse ingroups). Except for Pachytroctidae, the monophyly of each taxon is well supported by morphological (Königsmann, 1960; Lyal, 1985; Yoshizawa, 2002) and molecular (Johnson & Whiting, 2002; Barker *et al*., 2003; Johnson *et al*., 2004) data. Highly variable characters within genera or families were not used for the analysis. However, when a character was stable but had a few exceptions within a terminal taxon, it was selected for the analysis. If a reliable phylogeny within a terminal taxon was available (Barker *et al*., 2003; Johnson & Mockford, 2003; Johnson *et al*., 2004), the ancestral condition of such a character for the terminal taxon was estimated by most parsimonious reconstruction of the character on the trees (Maddison *et al*., 1984). If not, the character was coded as a polymorphic character (Appendices 2 and 3). Phylogenetic analysis of the data matrix was performed by PAUP* (Swofford, 2002) using parsimony. Parsimony options were set to collapse branches if the maximum length was zero.

Results

General account on phallic morphology and terminology (Figs 2–4)

As mentioned by previous authors (e.g. Badonnel, 1934; Lyal, 1986; Yoshizawa, 1999, 2005), the phallic organ in Psocodea can be divided into the following three principal structures [alternative terminologies are noted in brackets]: basal plate/basal apodeme [phallobase (psocids)], a pair of parameres [external parameres (psocids)] and mesomere [aedeagus, internal paramere (psocids), mesosome (lice)] (Fig. 2). Homologies of these structures between Psocodea and other insect orders are very weakly established. However, homologies of the phallic sclerites within Psocodea can be identified confidently (Lyal, 1986). We also observed further sclerites on the endophallus (genital sclerite and endomeral plate of Scharf & Price (1977)). However, homologies of these sclerites could not be decided without specimens having an everted endophallus, and such specimens were extremely rare. In addition, the presence or absence of such sclerites or numbers of sclerites on the endophallus was quite variable even within a family or genus. Therefore, we did not examine their homologies amongst taxa in the present study, but these characters may be valuable in phylogenetic studies at the specific or generic level.

The basal plate (bp in Fig. 3) supports the anterior and lateral margins of the phallosome. The term phallobase has been adopted for this structure in psocids. Lyal (1986) mentioned that the true phallobase extends dorsally to the genital duct, and the 'phallobase' or 'basal plate' of Psocodea lacks such extension. Therefore, he concluded that the structure should be regarded as the basal plate. The term 'basal apodeme' has also been used synonymously with the basal plate. The basal apodeme (ba in Fig. 3) is adopted here only for an ingrowth of the sclerite extending from the anteromedian margin of the basal plate (Snodgrass, 1935). The basal plate and basal apodeme are bordered by the membrane of the genital chamber (Figs 2, 4).

The parameres (paramere: pr in Fig. 3) are a pair of stick-like sclerites basally articulated with the posteroventral end of the basal plate (Figs 2, 4). The paramere is sometimes fused with the basal plate and the mesomere (see below). The paramere is reduced and even completely absent in a few taxa.

The mesomere (Fig. 3: m) is represented by an arch-like sclerite situated on the posteromedian region of the phallosome between the parameres. It is composed usually of a single sclerite and supports the dorsal and lateral margins of the opening of the endophallus (Figs 2, 4), and articulates usually basally with the posterodorsal end of the basal plate. The mesomere and basal plate may be fused.

In addition to the above-mentioned principal phallic structures, a pair of sclerites is observed almost uniformly

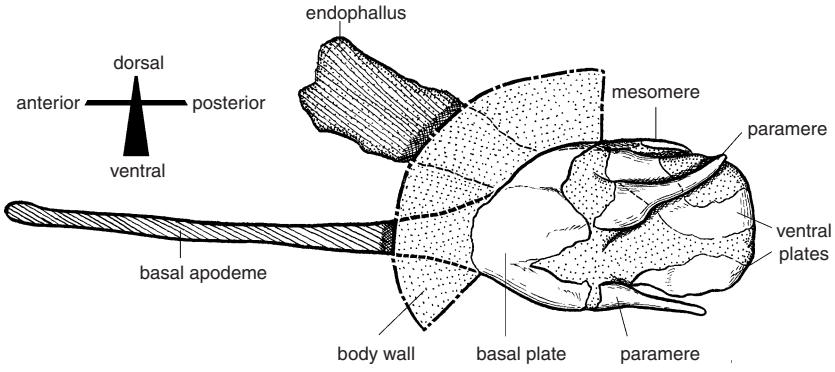

Fig. 2. Phallosome of *Myrsidea shirakii* (Amblycera: Menoponidae), ventrolateral view, showing structures and terminology used in this paper.

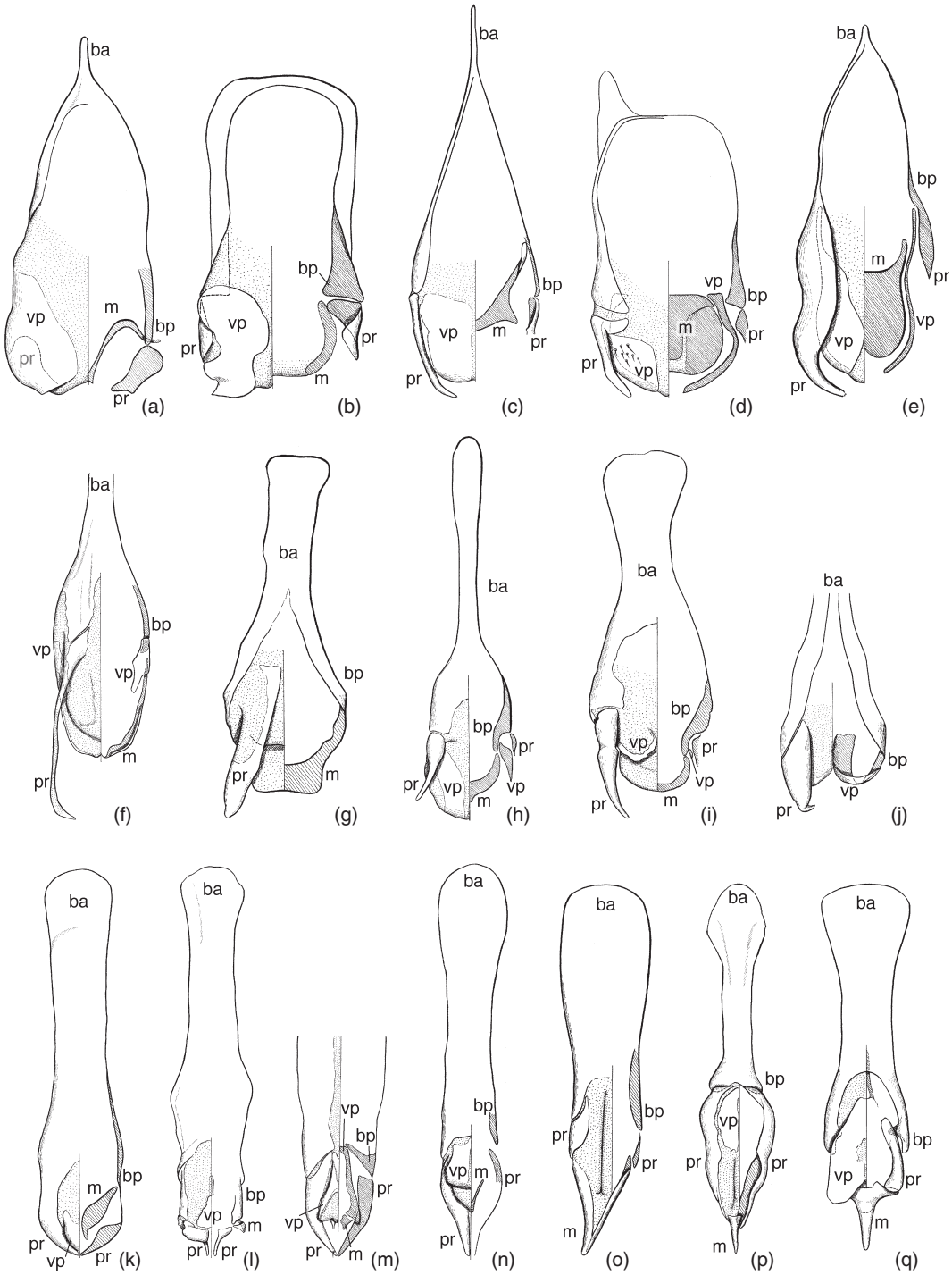

Fig. 3. The phallosome of representative taxa, ventral view. Ventral structures are omitted on right half. Anterior part comes to the top of the illustration. A, *Compsocus elegans* (Amphientometae: Compsocidae); B, *Selenopsocus* sp. (Amphientometae: Troctopsocidae); C, *Badonnelia titei* (Nanopsocetae: Sphaeropsocidae); D, *Pachytroctes neoleonensis* (Nanopsocetae: Pachytroctidae); E, *Liposcelis* sp. (Nanopsocetae: Liposcelididae); F, *Laemobothrion* (*Eulaemobothrion*) *cubense* (Amblycera: Laemobothriidae); G, *Ricinus* sp. (Amblycera: Ricinidae); H, *Myrsidea shirakii* (Amblycera: Menoponidae); I, *Heterodoxus spiniger* (Amblycera: Boopidae); J, *Harrisonia* sp. (Amblycera: Trimenoponidae); K, *Degeeriella* sp. (Ischnocera: Philopteridae); L, *Bovicola bovis* (Ischnocera: Trichodectidae); M, *Lamprocorpus* sp. (Ischnocera: Philopteridae); N, *Haematomyzus elephantis* (Rhynchophthirina: Haematomyzidae); O, *Pediculus humanus* (Anoplura: Pediculidae), ventral plate absent in this species; P, *Linognathus* sp. (Anoplura: Linognathidae); Q, *Polyplax spinulosa* (Anoplura: Polyplacidae). Abbreviations: ba, basal apodeme; bp, basal plate; m, mesomere; pr, paramere; vp, ventral plate.

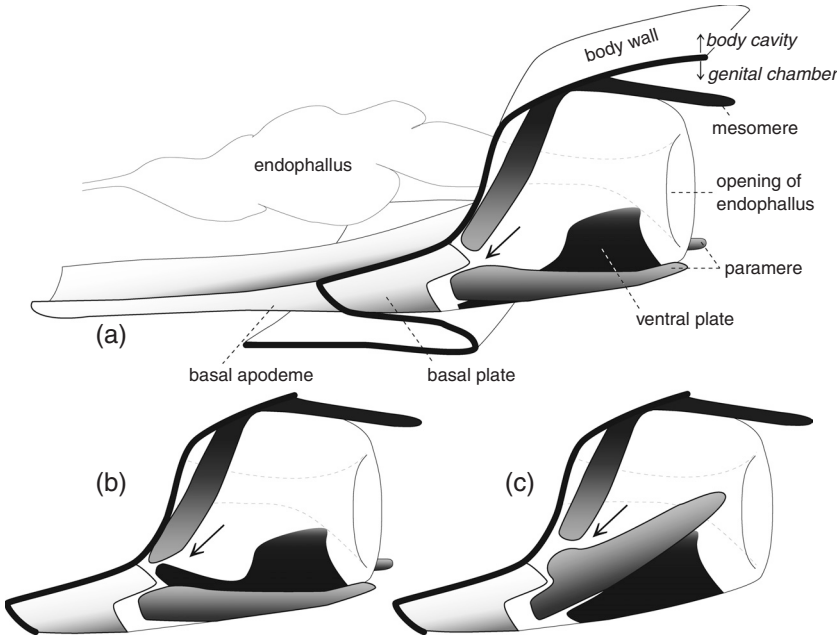

Fig. 4. Schematic representations of male genitalia in Psocodea (modified from Lyal, 1986), showing three different types of articulations between the paramere, mesomere, ventral plate and basal plates (indicated by large arrows). A, most ancestral condition observed in outgroups, Sphaeropsocidae, Rhynchophthirina and most Ischnocera (characters 1(0), 11(0); see Appendix 2 for explanations). B, apomorphic condition observed in Amblycera, Liposcelididae and Pachytroctidae (character 1(1)). C, apomorphic condition observed in Anoplura (character 11(1)).

throughout the Psocodea on the ventral margin of the endophallus opening. These sclerites, termed here the ventral plate (vp in Fig. 3), are situated on the permanently everted part of the endophallus (*sensu* Lyal, 1986; Figs 2, 4) and thus may be a secondary sclerite developed on the membrane of the endophallus. However, the ventral plate is observed widely throughout the Psocodea, and its homology is assured by positional congruence. The relationships between the ventral plate and other sclerites vary and are potentially of phylogenetic significance.

Psocomorpha

Detailed morphology and intrasubordinal transformation series of the phallic structures in Psocomorpha have been described in detail previously (Yoshizawa, 1999, 2002, 2005).

The basal plate is U- or V-shaped and with or without a short basal apodeme. The paramere usually is well developed, but sometimes is reduced or even completely absent. When present, the paramere articulates or fuses basally with the posteroventral end of the basal plate. The mesomere is pointed or rounded apically, and is fused completely with the basal plate basally in many taxa. The ventral plate is only weakly sclerotized and frequently is absent. When present, the paired sclerites are on the ventrolateral margins of the opening of the endophallus and are free from other phallic sclerites.

Amphientometae (Fig. 3A, B)

The infraorder Amphientometae consists of two superfamilies, Amphientomoidea and Electrentomoidea, and the phallic structures differ greatly between these two taxa.

The phallosome in Electrentomoidea usually possesses a complete set of the principal sclerites. The basal plate shape varies amongst taxa but, except for a few highly specialized taxa, is V-shaped having a short basal apodeme (Fig. 3A). In *Selenopsocus* of Troctopsocidae (Fig. 3B), the basal plate is U-shaped and has no basal apodeme, but this condition is considered to be an autapomorphic modification derived from the V-shaped phallosome, because its close relatives (Johnson *et al*., 2004) all have a V-shaped phallosome and short basal apodeme. We regard the elongated basal apodeme observed in *Epitroctes* of Electrentomidae also as an autapomorphic modification derived from the short basal apodeme, because *Phallopsocus* of Electrentomidae has the short basal apodeme. The paramere tends to be reduced in size and is well sclerotized in *Selenopsocus* (Fig. 3B), but is very weakly sclerotized in *Epitroctes*, *Compsocus* and *Electrentomopsis* (Fig. 3A). However, in every case, the paramere articulates basally with the posteroventral end of the basal plate. The mesomere is usually rounded posteriorly and articulates basally with the posterodorsal end of the basal plate. However, it is very weakly sclerotized and sometimes is membranous medially (e.g. *Selenopsocus*) or even completely absent (e.g. *Electrentomopsis*). A pair of ventral plates is evident in most taxa and is free from any sclerites or articulated with the posteroventral end of the basal plate.

In contrast, the phallosome in Amphientomoidea is highly specialized and simplified. The basal plate is V-shaped with a short basal apodeme. The homologies of the paramere, mesomere and ventral plate are very difficult to determine with confidence. The paramere is absent or indistinguishably fused with the basal plate. The mesomere is fused basally with the posterodorsal end of the basal plate. The ventral plate probably is represented by a pair of weakly sclerotized plates situated on the ventral margin

of the opening of the endophallus. These specializations are likely to be derived within Amphientometae because such modifications are never observed in close relatives (Electrentomoidea and Nanopsocetae).

Nanopsocetae: Sphaeropsocidae (Fig. 3C)

The basal plate is V-shaped with a short basal apodeme. The paramere is narrow but well developed and articulates basally with the posteroventral end of the basal plate. The mesomere articulates basally with the dorsal margin of the basal plate distant from the posterior end. The ventral plates are paired, very weakly sclerotized and anterolaterally articulated with the base of the paramere and the posteroventral part of the basal plate.

Nanopsocetae: Pachytroctidae (Fig. 3D)

The basal plate is U-shaped and has a broad and rounded apical margin. It lacks the basal apodeme but sometimes has a pair of weakly sclerotized broad ingrowth of sclerites on the anterolateral corners (e.g. *Pachytroctes* and *Peritroctes*). Although the sclerites compose apodemes, they are not homologous with the basal apodeme of other taxa examined here. The paramere is narrow but is well developed and articulates basally with the posteroventral region of the basal plate. The ventral plates are paired, and each plate has an extension which arises from the anterolateral corner of the plate and extends to the posterodorsal end of the basal plate. Therefore, the extension articulates with the posterodorsal end of the basal plate laterally (Fig. 4B). The mesomere articulates basally with the internal margin of the anterodorsal extension of the ventral plate (Fig. 4B).

Nanopsocetae: Liposcelididae (Fig. 3E)

The basal plate is V-shaped with a short basal apodeme. The paramere is wide and long, as long as or even longer than the basal plate. In Liposcelididae, the paramere is fused (Liposcelidinae) or articulates (Embidopsocinae) with the basal plate. In *Embidopsocus*, the paramere is further divided into two articulated sclerites (the basimere and telomere: Snodgrass, 1956). The ventral plates are paired. As in the Pachytroctidae, each ventral plate in Liposcelididae has a long extension arising from the anterolateral corner of the plate. Anteriorly, this extension articulates with the posterodorsal end of the basal plate (Fig. 4B). The mesomere has a pair of anterolateral extensions, which articulate with the posterodorsal end of the basal plate in Embidopsocinae or the anterolateral extension of the ventral plate in Liposcelidinae (Fig. 4B).

Amblycera (Figs 2; 3F–J)

The basal plate in Amblycera usually is Y-shaped with a long and narrow basal apodeme anteriorly. The posterodorsal ends of the basal plate extend posteriorly. The paramere is usually well developed, but sometimes reduced in size (*Trinoton*), weakly sclerotized [*Ricinus*: Fig. 3G; subgenus *Laemobothrion* (*Eulaemobothrion*): Fig. 3F] or completely absent [subgenus *Laemobothrion* (*Laemobothrion*)]. When present, the paramere articulates basally with the posteroventral end of the basal plate. The ventral plates are paired, and each plate articulates basally with the basal end of the mesomere and the extension from the posterodorsal end of the basal plate (Fig. 4B). The ventral plates are sometimes indistinguishable (e.g. *Ricinus*: Fig. 3G). In such cases, it is not certain whether the sclerite is completely membranous or its basal part is indistinguishably fused with the mesomere and the basal plate. The mesomere articulates usually with the posterodorsal end of the basal plate basally. In *Ricinus* (Fig. 3G), the mesomere is completely fused with the basal plate (but the fused region may involve the basal part of the ventral plate).

Ischnocera (Fig. 3K, M)

The phallosome of Ischnocera is highly variable. For example, the structure may be represented only by a pair of weakly sclerotized thin strip of sclerites (e.g. *Auricotes* and *Campanulotes*). In such cases, the mesomere and ventral plate are completely absent, and it is almost impossible to distinguish the paramere from the basal plate. However, in most other taxa, the complete set of phallic sclerites is observed.

Except for the few taxa with a very reduced phallosome, the basal plate has a broad sclerite anteriorly. The anterior part of this sclerite extends into the body wall and thus can be considered to be an expanded basal apodeme. The paramere articulates, or is rarely fused (e.g. *Degeeriella*: Fig. 3K), basally with the posteroventral end of the basal plate. The ventral plates are fused medially in a single plate, situated usually on the membranous region between the paramere and free from other sclerites (Fig. 4A). However, in *Ornithobius*, *Trichophilopterus* and *Lamprocorpus* (Fig. 3M), the ventral plate has a dorsal extension on each side, and articulates with the posterodorsal end of the basal plate, as in Pachytroctidae, Liposcelididae and Amblycera (Figs 3D–J; 4B). The mesomere articulates basally with the posterodorsal end of the basal plate. When the dorsal extension of the ventral plate occurs, the mesomere articulates basally with the posterodorsal margin of the extension of the ventral plate. The shape of the mesomere is highly variable amongst taxa but usually is rounded apically. Absence of the mesomere is also frequent (e.g. *Columbicola* and *Trichophilopterus*).

Rhynchophthirina (Fig. 3N)

The basal plate has a broad basal apodeme (see also Ischnocera) and lacks a posteromedian membranous region. The paramere is basally articulated with the posteroventral corner of the basal plate. The ventral plates are rather weakly sclerotized, partly fused basally and articulate basally with the posteromedian margin of the basal plate. The mesomere is reduced in size and lacks basal articulation with the basal plate. The mesomere is apically pointed.

Anoplura (Fig. 3O–Q)

The basal plate usually has a broad basal apodeme as observed in Ischnocera. A narrow and elongate basal apodeme is observed in a few highly specialized taxa (e.g. *Neohaematopinus*). However, this state is likely to be a secondary modification from the broad basal apodeme. As in Rhynchophthirina, the basal plate of Anoplura usually lacks a posteromedian membranous region. The paramere is variable in size: for example, forming a long free process in *Echinophthirius* but reduced to a rather weakly sclerotized plate in *Pediculus* (Fig. 3O). Basally, the paramere articulates with the posteroventral end of the basal plate (Fig. 4C). The ventral plates are partially fused basally or sometimes completely fused and compose a single sclerite (e.g. *Echinophthirius*). The ventral plates usually articulate basally with the posteromedian margin of the basal plate, but are sometimes completely membranous (e.g. *Pediculus*: Fig. 3O). The mesomere is well sclerotized and pointed apically. Basally, the mesomere is separated from the basal plate and lacks articulation with it. Instead, the mesomere articulates basally with the paramere. The paramere and the mesomere are sometimes partially (*Pediculus*) or completely (*Haematopinus*) fused with each other.

Characters and phylogenetic analyses

Although the phallosomal characters are highly variable, even amongst closely related taxa, and higher level homologies were difficult to find, some characters were relatively stable and could be coded for the phylogenetic analysis of higher taxa (for coding of characters and detailed discussions on character states, see Appendices 2 and 3). Based on these characters, a single most parsimonious tree was recovered (Fig. 5).

Autapomorphies were identified for every terminal taxon (Appendices 2 and 3). Only one species was examined for each of Sphaeropsocidae and Rhynchophthirina, and thus no autapomorphy was coded for these taxa. However, the position of the articulation between the basal plate and mesomere is unique to Sphaeropsocideae (Fig. 3C), and the upwardly strongly curved paramere was observed uniquely in Rhynchophthirina. Therefore, these character states probably support the monophyly of each group.

Monophyly of a clade composed of Ischnocera, Rhynchophthirina and Anoplura was supported by two autapomorphies: partial fusion of ventral plates and a broadened basal apodeme. Within this clade, a sister relationship between Rhynchophthirina and Anoplura was supported by two synapomorphies: apically pointed mesomere and lack of posteromedian membranous region of the basal plate.

In Pachytroctidae, Liposcelididae and Amblycera, the posterodorsal corner of the basal plate, mesomere and ventral plate articulate at a point (Fig. 4B), and this

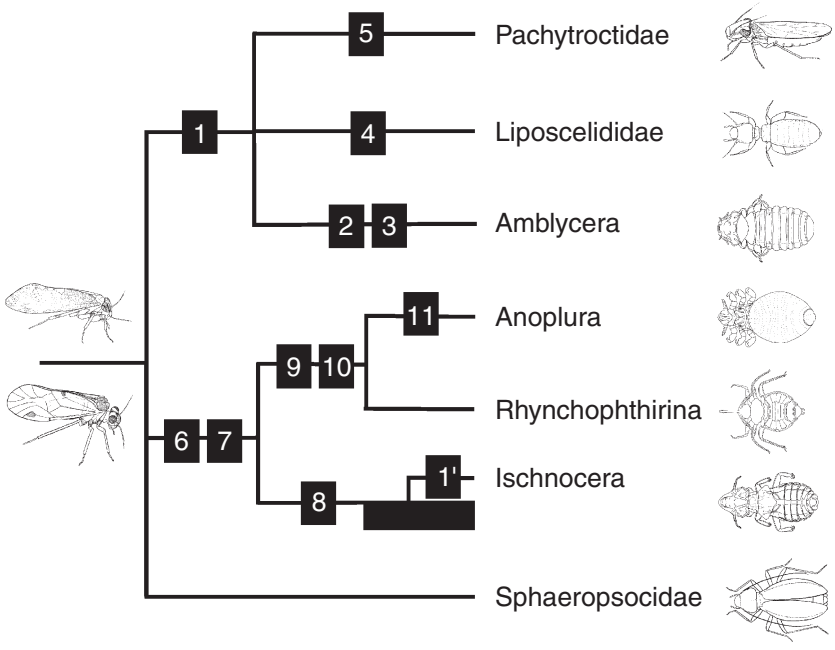

Fig. 5. Phylogeny of lice and relatives derived from characters of the phallosome (Appendices 2 and 3).

condition was observed consistently throughout these groups. Although a similar articulation was observed also in a few taxa of Ischnocera, these articulations were never observed in Amphientometae, Rhynchophthirina and Anoplura. Therefore, the most parsimonious interpretation was that the presence of these articulations is a synapomorphy of Pachytroctidae, Liposcelididae and Amblycera, and the similar state observed in Ischnocera is homoplasious.

Discussion

The monophyly of lice has long and widely been assumed because of their highly specialized modifications for parasitism. No-one has rigorously questioned the monophyly of lice on the basis of morphology, and sometimes it has simply been assumed. For example, based on a detailed spermatological study, Jamieson *et al*. (1999) stated that 'a separate autapomorphy for Phthiraptera is not apparent but there seems no reason to doubt that the Mallophaga and Anoplura comprise a monophyletic group'.

Lyal (1985) described nineteen character states which may support the monophyly of lice. Thirteen are loss character states strongly linked to the parasitic lifestyle in lice (e.g. reductions of labial palpi, the antennal flagellum and compound eye). Therefore, as mentioned by Lyal (1985), such apomorphies may have easily evolved independently as a result of specialization to the parasitic lifestyle. Six gain character states were identified as possibly supporting the monophyly of lice (Lyal, 1985), but one (egg-cement produced from vagina) is also correlated strongly with the parasitic lifestyle and thus is not independent of parasitism. Dorsoventral compression of the head is also considered to be a gain autapomorphy of lice. However, the character state is shared by Liposcelididae and Pachytroctidae and thus cannot unequivocally support the monophyly of lice. Although posteriad movement of the suproesophageal ganglion has not been examined for Liposcelididae and Pachytroctidae, the character state is considered to be strongly linked to the compression of the head. The other spermatological and embryological characters putatively supporting louse monophyly have not been investigated in Liposcelididae and Pachytroctidae.

Only one character state, development of a lacinial gland, may possibly support the monophyly of lice. Although the character state is inconsistent within lice (present in Amblycera, Ischnocera and Anoplura but absent in Rhynchophthirina: Symmons, 1952; Lyal, 1985; Tröster, 1990, 2002), a single gain of the gland in the louse common ancestor and secondary loss in Rhynchophthirina would be the most parsimonious interpretation, if lice are monophyletic. A weakly developed lacinial gland is observed in *Lepinotus* ('Psocoptera': Trogiomorpha), and the condition of the gland in Liposcelididae and Pachytroctidae has not been examined in detail (the gland is difficult to see in slide-mounted specimens, and stained sections are required to observe the structure confidently: Symmons, 1952). The function of the lacinial gland is poorly understood but, in Anoplura, the gland is related to the piercing movement of mouthparts (Tröster, 1990). Therefore, further morphological and functional studies of the gland in psocids and chewing lice are needed to confirm the distribution of the well-developed lacinial gland and whether or not evolution of this structure correlates with parasitism. In summary, although the monophyly of lice has been accepted on the basis of many morphological characters (Königsmann, 1960; Lyal, 1985), all apomorphies observed in lice are either correlated with parasitism or do not unambiguously support louse monophyly, except, possibly, for lacinial gland development.

Recent molecular phylogenetic analyses based on mitochondrial (Yoshizawa & Johnson, 2003) and nuclear (Johnson *et al*., 2004) gene sequences do not support the monophyly of lice. Furthermore, 18S rDNA data (Johnson *et al*., 2004) strongly suggest the polyphyly of lice, and the booklice family Liposcelididae is identified as a sister group of the louse suborder Amblycera. This result does not agree with the morphological evidence presented by Lyal (1985). Incongruence between morphological and molecular data sets is also evident within groups of lice (Smith *et al*., 2004), and this is, at least in part, derived from frequent convergence in the external morphology of these parasites (Smith *et al*., 2004).

Although convergence of external morphological characters can be frequent for lice as a result of an adaptation to the parasitic lifestyle, genital structure is less likely to be constrained by such environmental selective pressures. Therefore, genital characters might have greater utility than external morphological characters for inferring the phylogenetic relationships of lice and relatives (Wiens *et al*., 2003). However, genital characters are highly variable, even in closely related taxa. For example, differences in the shape of the mesomere and ventral plate are considered to be one of the most important taxonomic characters to identify species of lice (Ledger, 1980; Price *et al*., 2003). This variation makes it difficult to find informative genital characters to infer the higher level phylogeny of lice and relatives.

In the present study, we have identified eleven characters in the phallosome which have potential information for inferring the higher level phylogeny of lice and relatives. Based on parsimony analysis of these characters, a tree that is broadly concordant with a molecular phylogeny based on 18S rDNA sequences (Johnson *et al*., 2004) was obtained. Most importantly, the louse suborder Amblycera forms a clade together with psocid families Pachytroctidae and Liposcelididae, and is separated from the other louse suborders Ischnocera, Rhynchophthirina and Anoplura.

The monophyly of a clade composed of Ischnocera, Rhynchophthirina and Anoplura is well supported by two autapomorphies. Within this clade, Rhynchophtirina and Anoplura are sister taxa. These results (i.e. non-monophyly of chewing lice, 'Mallophaga') completely agree with phylogenetic analyses based on external morphology (Königsmann, 1960; Lyal, 1985; Tröster, 1990) and DNA sequences (Johnson & Whiting, 2002; Barker *et al*., 2003; Johnson *et al*., 2004).

Monophyly of the clade composed of Pachytroctidae, Liposcelididae and Amblycera is supported by a single autapomorphy. In addition, a similar character state is also observed in a limited number of Ischnocera. Therefore, it remains a possibility that the character evolved in the common ancestors of lice, Pachytroctidae and Liposcelididae, and has been secondarily lost in Rhynchophthirina, Anoplura and most Ischnocera. However, this interpretation is less parsimonious (requires at least three steps for character 1, instead of two). In contrast, we cannot find any apomorphic feature in the phallic organ which potentially supports the monophyly of lice. Therefore, the present result provides the first possible morphological support for the polyphyly of lice. Furthermore, the present data set provides no support for the monophyly of Nanopsocetae. In particular, Sphaeropsocidae is separated from Pachytroctidae and Liposcelididae, a concordant result with the 18S-based analysis.

The only major disagreement between 18S-based trees and our morphological tree concerns the monophyly of Pachytroctidae. In the 18S tree, Pachytroctidae formed a grade basal to Liposceldidae + Amblycera. In contrast, an unambiguous autapomorphy (lack of the basal apodeme) supporting the monophyly of Pachytroctidae is identified here. Support for the paraphyly of Pachytroctidae in the analysis of the 18S data was very weak (< 50% bootstrap) and thus Pachytroctidae may indeed be monophyletic, but the 18S data may have contained insufficient signal to resolve the relevant nodes.

To date, the polyphyly of lice has been suggested only by one nuclear gene (18S rDNA) and one morphological character. In contrast, many external morphological features still support the monophyly of lice, even though convergence may be frequent in such morphological characters. The phallosome is a most divergent morphological structure in insects (Hosken & Stockley, 2004), and thus other useful apomorphies may be eroded by such high diversity of this structure. Therefore, further analyses of other gene regions and other morphological characters (particularly those not linked to parasitism, e.g. internal reproductive organs) are required to test the multiple origins of parasitism in lice.

Although the present study focuses only on the relationships amongst lice and relatives, the phallosomal characters probably also contain useful information for estimating relationships within Amblycera, Ischnocera and Anoplura. For example, the paramere and the ventral plate are weakly sclerotized or completely absent in Ricinidae and Laemobothriidae, and these modifications probably have common origins. Therefore, reduction of the paramere and ventral plate possibly supports a sister group relationship between these two families, and this is concordant with the traditional taxonomic view (e.g. Clay, 1970) and a recent molecular tree (Barker *et al*., 2003), but contradicts a recent cladistic analysis of external morphological data (Marshall, 2003). In a morphological cladistic analysis of avian Ischnocera (Smith, 2000, 2001), characters of the phallosome were not included. Thus, phylogenetic analyses based on the phallosomal characters might also provide further insight into louse phylogeny. Decisive identification of homologies of the phallic structures in lice should also be valuable for descriptive studies of these insects.

Taxonomic note

Recent molecular (Yoshizawa & Johnson, 2003; Johnson *et al*., 2004) and morphological (Lyal, 1985; present work) analyses have pointed out the possibility that both Psocoptera and Phthiraptera are non-monophyletic. Support for the paraphyly of Psocoptera is particularly robust across all data sets (but Seeger (1979) provided a putative embryological autapomorphy of Psocoptera). Therefore, a classification that reflects only monophyletic groupings (Hennig, 1966) would have both Psocoptera and Phthiraptera as invalid taxa. Furthermore, if Phthiraptera is polyphyletic, as these recent molecular and morphological data suggest, then, even under the taxonomic system which accepts a paraphyletic group (Mayr, 1969), the order Phthiraptera would be rejected. Therefore, the classification of Psocoptera and Phthiraptera should be revised.

Based on the recent 18S tree and the present result, there are two possibilities to reclassify the Psocoptera and Phthiraptera to reflect monophyletic groups: (1) divide Psocoptera and Phthiraptera into several independent orders; (2) recognize the monophyletic Psocodea (= Psocoptera + Phthiraptera) as a single order. The first proposal would provide an unacceptable proliferation of insect orders. In contrast, the second possibility has been proposed already by some previous researchers focused on higher insect classification (Hennig, 1981; Lyal, 1985; Kristensen, 1991). In addition, recognition of Psocodea is the most conservative with respect to any lingering uncertainties regarding the polyphyly of Phthiraptera, and the order Psocodea would be maintained regardless of the final status of Phthiraptera. Therefore, we suggest recognition of Psocodea as a valid order of insects which includes booklice, barklice and parasitic lice. To establish stable subordinal divisions within Psocodea, more molecular and morphological analyses are required.

Acknowledgements

We thank the following people for providing specimens for this study: Charles Lienhard, Edward L. Mockford, Vincent S. Smith and Naoki Takahashi. We also thank Vincent S. Smith for critical comments on the manuscript. This study was supported by JSPS (Japan Society for Promotion of Science) grant (13740486 and 15770052) to KY and NSF (National Science Foundation) grant (DEB-0107891) to KPJ. Some of KY's field trips were supported by a JSPS grant to Osamu Yata (14255016).

References

Badonnel, A. (1934) Recherches sur l'anatomie des Psoques. *Bulletin Biologique de France et de Belgique Suppl.*, **18**, 1–241.

Badonnel, A. (1967) *Psocoptères édaphiques du Chili (2e note). Biologie de l'Amérique Australe*, **3**, 541–585.

Barker, S.C., Whiting, M.F., Johnson, K.P. & Murrell, A. (2003) Phylogeny of the lice (Insecta, Phthiraptera) inferred from small subunit rRNA. *Zoologica Scripta*, **32**, 407–414.

Clay, T. (1970) The Amblycera (Phthiraptera: Insecta). *Bulletin of the British Museum (Natural History), Entomology*, **25**, 75–98.

Cruickshank, R.H., Johnson, K.P., Smith, V.S., Adams, R.J., Clayton, D.H. & Page, R.D.M. (2001) Phylogenetic analysis of partial sequences of elongation factor 1a identifies major groups of lice (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution*, **19**, 202–215.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Illinois.

Hennig, W. (1981) *Insect Phylogeny*. Wiley, Chichester.

Hicks, E.A. (1959) *Check-List and Bibliography of the Occurrence of Insects in Birds' Nests*. Iowa State College Press, Iowa.

Hopkins, G.H.E. (1949) The host associations of the lice of mammals. *Proceedings of the Zoological Society of London*, **119**, 387–604.

Hosken, D.J. & Stockley, P. (2004) Sexual selection and genital evolution. *Trends in Ecology and Evolution*, **19**, 87–93.

Jamieson, B.G.M., Dallai, R. & Afzelius, B.A. (1999) *Insects: Their Spermatozoa and Phylogeny*. Sciences Publishers Inc, New Hampshire.

Johnson, K.P. & Clayton, D.H. (2003) The biology, ecology, and evolution of chewing lice. *The Chewing Lice: World Checklist and Biology Overview* (ed. by R. D. Price, R.A. Hellenthal, R.L. Palma, K.P. Johnson & D.H. Clayton), pp. 449–475. *Illinois Natural History Survey Special Publication 24*. Illinois Natural History Survey, Illinois.

Johnson, K.P. & Mockford, E.L. (2003) Molecular systematics of Psocomorpha (Psocoptera). *Systematic Entomology*, **28**, 409–416.

Johnson, K.P. & Whiting, M.F. (2002) Multiple genes and the monophyly of Ischnocera (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution*, **22**, 101–110.

Johnson, K.P., Yoshizawa, K. & Smith, V.S. (2004) Multiple origins of parasitism in lice. *Proceedings of the Royal Society of London, Series B*, **271**, 1771–1776.

Kim, K.C. & Ludwig, H.W. (1982) Parallel evolution, cladistics, and the classification of parasitic Psocodea. *Annals of the Entomological Society of America*, **75**, 537–548.

Königsmann, E. (1960) Zur Phylogenie der Parametabola unter besonderer Berücksichtigung der Phthiraptera. *Beiträge zur Entomologie*, **67**, 235–239.

Kristensen, N.P. (1991) *Phylogeny of Extant Hexapods. The Insects of Australia*, Vol. 1, 2nd edn., pp. 125–140. Melbourne University Press, Victoria.

Ledger, J.A. (1980) *The Arthropod Parasites of Vertebrates in Africa South of the Sahara*, Vol. IV, *Phthiraptera (Insecta). Publication of the South African Institute for Medical Research No. 56*. South African Institute for Medical Research, Johannesburg.

Lienhard, C. & Smithers, C.N. (2002) *Psocoptera (Insecta) – World Catalogue and Bibliography. Instrumenta Biodiversitatis, 5*. Muséum d'Histoire Naturelle, Genève.

Lyal, C.H.C. (1984) A cladistic analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera). *Bulletin of the British Museum (Natural History), Entomology*, **51**, 187–346.

Lyal, C.H.C. (1985) Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocodea: Phthiraptera). *Systematic Entomology*, **10**, 145–165.

Lyal, C.H.C. (1986) External genitalia of Psocodea, with particular reference to lice (Phthiraptera). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, **114**, 277–292.

Maddison, W.P., Donoghue, M.J. & Maddison, D.R. (1984) Outgroup analysis and parsimony. *Systematic Zoology*, **33**, 83–103.

Marshall, I.K. (2003) A morphological phylogeny for four families of amblyceran lice (Phthiraptera: Amblycera: Menoponidae, Boopiidae, Laemobothriidae, Ricinidae). *Zoological Journal of the Linnean Society*, **138**, 39–82.

Mayr, E. (1969) *Principles of Systematic Zoology*. McGraw-Hill, New York.

Mockford, E.L. (1967) Some Psocoptera from the plumage of birds. *Proceedings of the Entomological Society of Washington*, **69**, 307–309.

Pearman, J.V. (1960) Some African Psocoptera found on rats. *Entomologists*, **93**, 246–250.

Price, R.D., Hellenthal, R.A., Palma, R.L., Johnson, K.P. & Clayton, D.H. (2003) *The Chewing Lice: World Checklist and Biology Overview. Illinois Natural History Survey Special Publication 24*. Illinois Natural History Survey, Illinois.

Rudolph, D. (1982) Occurrence, properties and biological implications of the active uptake of water vapour from the atmosphere in the Psocoptera. *Journal of Insect Physiology*, **28**, 111–121.

Rudolph, D. (1983) The water-vapour uptake system of the Phthiraptera. *Journal of Insect Physiology*, **29**, 15–25.

Scharf, W.C. & Price, R.D. (1977) A new subgenus and two new species of *Amyrsidea* (Mallophaga: Menoponidae). *Annals of the Entomological Society of America*, **70**, 815–822.

Schmutz, W. (1955) Zur Konstruktionsmorphologie des männlichen Geschlechtsapparates der Mallophagen. *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere*, **74**, 189–338.

Seeger, W. (1979) Spezialmerkmale an Eihüllen und Embryonen von Psocoptera im Vergleich zur anderen Paraneoptera (Insecta); Psocoptera als monophyletische Gruppe. *Stuttgarter Beiträge zur Naturkunde (A)*, **55**, 1–57.

Smith, V.S. (2000) Basal ischnoceran louse phylogeny (Phthiraptera: Ischnocera: Goniodidae and Heptapsogasteridae). *Systematic Entomology*, **25**, 73–94.

Smith, V.S. (2001) Avian louse phylogeny (Phthiraptera: Ischnocera): a cladistic study based on morphology. *Zoological Journal of the Linnean Society*, **132**, 81–144.

Smith, V.S., Page, R.D.M. & Johnson, K.P. (2004) Data incongruence and the problem of avian louse phylogeny. *Zoologica Scripta*, **33**, 239–259.

Snodgrass, R.E. (1935) *Principles of Insect Morphology*. McGraw-Hill, New York.

Snodgrass, R.E. (1956) A revised interpretation of the external reproductive organs of male insects. *Smithsonian Miscellaneous Collections*, **135** (6), 1–60.

Swofford, D.L. (2002) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*, Version 4. Sinauer, Massachusetts.

Symmons, S. (1952) Comparative anatomy of the mallophagan head. *Transactions of the Zoological Society of London*, **27**, 349–436.

Tröster, G. (1990) Der Kopf von *Hybophthirus notophallus* (Neumann) (Phthiraptera: Anoplura). Eine funktionsmorphologische und konsequent-phylogenetische Analyse. *Stuttgarter Beiträge zur Naturkunde (A)*, **442**, 1–89.

Tröster, G. (2002) Morphological evidence for the systematic position of *Hybophthirus notophallus* (Neumann) as the sister species of the rest of the Anoplura (Insecta: Psocodea: Phthiraptera). *Zoology*, **105** (Suppl. V), 95.

Wheeler, W.C., Whiting, M., Wheeler, Q.D. & Carpenter, J.M. (2002) The phylogeny of the extant hexapad orders. *Cladistics*, **17**, 113–169.

Wiens, J.J., Chippindale, P.T. & Hillis, D.M. (2003) When are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. *Systematic Biology*, **52**, 501–514.

Yoshizawa, K. (1999) Morphology, phylogeny and higher classification of the suborder Psocomorpha (Insecta: Psocoptera). PhD Thesis. Kyushu University, Fukuoka.

Yoshizawa, K. (2002) Phylogeny and higher classification of suborder Psocomorpha (Insecta: Psocodea: 'Psocoptera'). *Zoological Journal of the Linnean Society*, **136**, 371–400.

Yoshizawa, K. (2004) Molecular phylogeny of major lineages of *Trichadenotecnum* and a review of diagnostic morphological characters (Psocoptera: Psocidae). *Systematic Entomology*, **29**, 383–394.

Yoshizawa, K. (2005) Morphology of Psocomorpha (Psocodea: 'Psocoptera'). *Insecta Matsumurana, New Series*, **62**, 1–44.

Yoshizawa, K. & Johnson, K.P. (2003) Phylogenetic position of Phthiraptera (Insecta: Paraneoptera) and elevated rate of evolution in mitochondrial 12S and 16S rDNA. *Molecular Phylogenetics and Evolution*, **29**, 102–114.

Accepted 16 June 2005

Appendix 1. Taxa examined

PSOCOMORPHA – see Yoshizawa (2002). AMPHIENTOMETAE – Amphientomidae: *Cymatopsocus*; Electrentomidae: *Epitroctes*, *Phallopsocus* (not examined, but information on the basal apodeme was obtained from Badonnel (1967)); Compsocidae: *Compsocus*, *Electrentomopsis*; Musapsocidae: *Musapsocus*; Troctopsocidae: *Selenopsocus*. NANOPSOCETAE – Sphaeropsocidae: *Badonnelia*; Pachytroctidae: *Pachytroctes*, *Peritroctes*, *Tapinella*; Liposcelididae: *Belapha*, *Embidopsocus*, *Liposcelis*. AMBLYCERA – Boopidae: *Heterodoxus*; Gyropidae: *Gliricola*; Laemobothriidae: *Laemobothrion* (subgenera *Eulaemobothrion* and *Laemobothrion*); Menoponidae: *Heleonomus*, *Heteromenopon*, *Menacanthus*, *Myrsidea*, *Trinoton*; Ricinidae: *Ricinus*; Trimenoponidae: *Harrisonia*. ISCHNOCERA – Philotarsidae: *Anaticola*, *Ardeicola*, *Auricotes*, *Brueelia*, *Cuclotogaster*, *Campanulotes*, *Columbicola*, *Degeeriella*, *Fulicoffula*, *Lamprocorpus*, *Ornithobius*, *Pectinopygus*, *Physconelloides*, *Quadraceps*, *Saemundssonia*, *Strigiphilus*; Trichodectidae: *Bovicola*, *Trichodectes*. RHYNCHOPHTHIRINA – Haematomyzidae: *Haematomyzus*. ANOPLURA – Echinophthiriidae: *Echinophthirius*; Haematopinidae: *Haematopinus*; Linognathidae: *Linognathus*; Pediculidae: *Pediculus*; Polyplacidae: *Polyplax*.

Appendix 2. Characters used for the analysis

1. Articulations between the mesomere, anterodorsal extension of ventral plate and posterior end of basal plate: (0) absent; (1) present.

Note. State 1 is observed consistently in Amblycera, Liposcelididae and Pachytroctidae and is considered to be their synapomorphy. State 1 is also observed in some taxa of Ischnocera, but the resulting tree suggested that the condition observed in Ischnocera is not homologous with that in the other groups.

2. Length of basal apodeme: (0) short; (1) long, longer than basal plate.

Note. State 1 is considered to be an autapomorphy of Amblycera. The basal plate + basal apodeme of many species of Ischnocera, Rhynchophthirina and Anoplura is elongated, and thus looks somewhat similar to the elongated basal apodeme of Amblycera. However, in most cases, the elongation in Ischnocera, etc. is of the basal plate, not the basal apodeme. For example, in *Degeeriella*, the true basal apodeme is represented only by the anterior one-fifth of the basal plate + basal apodeme (the border is indicated by fine slashes in Fig. 3K). A short basal plate + basal apodeme is also frequent in Ischnocera (e.g. *Columbicola*, *Cuclotogaster*).

3. Posterodorsal corner of basal plate: (0) not extended; (1) extended posteriorly.

Note. State 1 is observed throughout Amblycera, except for *Ricinus*, in which the basal plate and the mesomere are fused completely with each other and the extension of the basal plate cannot be distinguished. The character state observed in *Ricinus* is considered to be an autapomorphic modification for the genus (or possibly the family Ricinidae) and, thus, state 1 is regarded as an autapomorphy of Amblycera.

4. Parameres: (0) not elongated and broadened; (1) elongated and broadened, as long as or even longer than basal plate.

Note. Paramere shape is highly variable amongst different taxa and, in most cases, such differences are not used in the present analysis. However, the parameres in Liposcelididae are exceptionally elongated and broadened, and the state is consistent throughout the family.

5. Basal apodeme: (0) present; (1) absent.

Note. State 1 is considered to be an autapomorphy of Pachytroctidae. The basal plate in *Peritroctes* has a pair of apodemes arising from the anterolateral corners. However, the apodemes observed in *Peritroctes* are not homologous with the basal apodeme, which extends from the anteromedian portion of the basal plate.

6. Width of basal apodeme: (0) narrow; (1) broad, as broad as or broader than basal plate.

Note. State 1 is considered to be a synapomorphy of Ischnocera, Rhynchophthirina and Anoplura.

7. Ventral plates 1: (0) bilaterally separated; (1) partly fused anteriorly.

Note. Complete fusion of the ventral plates is also observed (see character 8). Such a condition is also coded as state 1 for this character. State 1 is considered to be a synapomorphy of Ischnocera, Rhynchophthirina and Anoplura.

8. Ventral plates 2: (0) separated or partly fused; (1) completely fused.

Note. Character 7(1) probably represents the intermediate condition of character 8(1). State 1 of character 8 is considered to be an autapomorphy of Ischnocera and is also observed in a very limited member of Anoplura. However, these states apparently have different origins.

9. Mesomere: (0) rounded posteriorly; (1) pointed posteriorly.

Note. State 1 is observed throughout Rhynchophthirina and Anoplura and is considered here to be their synapomorphy. A somewhat similar condition is also observed in some species of Amphientometae but should be regarded as homoplasy.

10. Posteromedian part of basal plate: (0) membranous; (1) sclerotized.

Note. State 1 is considered to be a synapomorphy of Rhynchophthirina and Anoplura. Related to this modification, the ventral plate of many species of Rhynchophthirina and Anoplura articulates anteriorly with the posteromedian margin of the basal plate.

11. Anterior end of mesomere: (0) articulated with basal plate; (1) articulated with paramere.

Note. State 1 is observed throughout Anoplura and is considered to be an autapomorphy of the suborder.

Appendix 3. Data matrix of morphological characters

Character	1	2	3	4	5	6	7	8	9	10	11
Psocomorpha	0	0	0	0	01	0	0	0	01	0	0
Amphientometae	0	0	0	0	0	0	0	0	0	0	0
Sphaeropsocidae	0	0	0	0	0	0	0	0	0	0	0
Pachytroctidae	1	0	0	0	1	0	0	0	0	0	0
Liposcelididae	1	0	0	1	0	0	0	0	0	0	0
Amblycera	1	1	1	0	0	0	0	0	0	0	0
Anoplura	0	0	0	0	0	1	1	0	1	1	1
Rhynchophthirina	0	0	0	0	0	1	1	0	1	1	0
Ischnocera	01	0	0	0	0	1	1	1	0	0	0