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Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera)

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Abstract. Phylogenetic relationships among three paraneopteran clades (Psocodea, Hemiptera and Thysanoptera) were analysed based on the morphology of forewing base structure. Monophyly of Paraneoptera was supported by nine autapomorphies, monophyly of Condylognatha (= Thysanoptera + Hemiptera) by two autapomorphies, monophyly of Thysanoptera by five autapomorphies and monophyly of Hemiptera by one autapomorphy. Thus, (Psocodea + (Thysanoptera + Hemiptera)) were proposed to be the phylogenetic relationships within Paraneoptera. A homoplastic similarity of the third axillary sclerite was observed between Thysanoptera and Heteroptera, and a possible evolutionary factor providing this homoplasy was discussed. The present analysis also suggested a monophyletic Auchenorrhyncha, and reduction of the proximal median plate was considered as an autapomorphy of this clade.

Introduction

Paraneoptera is composed of three (or four) neopteran orders: Psocodea (= Psocoptera + Phthiraptera), Hemiptera and Thysanoptera (Kristensen, 1991). Some authors have included Zoraptera in Paraneoptera (Kristensen, 1975, 1981; Hennig, 1981), but the wing structures (Kukalová-Peck & Peck, 1993) and wing musculature (Boudreaux, 1979) indicate that Zoraptera is related to the blattoid orders. Therefore, in the present sense, it is excluded from Paraneoptera. Monophyly of Paraneoptera is widely accepted (e.g. Boudreaux, 1979; Hennig, 1981; Kristensen, 1981, 1991), but Kristensen (1991) mentioned that 'autapomorphies of this clade may not appear to be ''strong'' ones'.

Within Paraneoptera, Condylognatha, composed of Hemiptera and Thysanoptera, seems generally accepted (Kristensen, 1975, 1981; Boudreaux, 1979; Hamilton, 1981; Hennig, 1981). However, only a few autapomorphies, the stylet mandible and possibly the sclerotized ring between antennal flagellomeres, support the monophyly of Condylognatha (Kristensen, 1975, 1981, 1991; Seeger, 1975; Hennig, 1981; Lyal, 1985). Alternatively, Kristensen (1991) re-evaluated the spermatological studies of Baccetti (1979) and Jamieson (1987) and concluded that the spermatological characters supported Psocodea + Thysanoptera. Based on these studies, Kristensen stated that 'the cautious solution of representing paraneopteran interordinal relationships as an unresolved trichotomy may be preferable at present' (Kristensen, 1991; followed by Maddison, 1995). Fossil studies (Sharov, 1966, 1972) and recent combined molecular and morphology data (Whiting *et al*., 1997) may also suggest a sister-group relationship between Psocodea and Thysanoptera that conflicts with the generally accepted taxonomic system mentioned above.

In addition to the trichotomy problem among paraneopteran orders, phylogeny of Hemiptera also involves some serious problems (Bourgoin, 1996). First, although monophyly of Hemiptera is strongly supported by their highly specialized sucking mouthparts, no other autapomorphic character for this order has been proposed, except Hennig (1981) suggested an uncertain character state, unbranched radial sector. Second, recent morphological (Bourgoin, 1993) and molecular studies (Campbell *et al*., 1994, 1995; von Dohlen & Moran, 1995; Sorensen *et al*., 1995; Bourgoin *et al*., 1997) suggest a paraphyletic Auchenorrhyncha, although monophyly of this group has long been accepted (Kristensen, 1975; Carver *et al*., 1991).

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Lacking a reliable phylogenetic hypothesis within Paraneoptera blinds evolutionary history in this group, although morphology and evolution of head and mouthpart structures in Thysanoptera and Hemiptera have especially attracted the attention of many researchers (DuPorte, 1962; Parsons, 1964; Matsuda, 1965; Heming, 1978; Hamilton, 1981; Bourgoin, 1996). Therefore, a strong phylogenetic framework for Paraneoptera is required for future evolutionary studies of this group. Additionally, for evolutionary studies of the head and mouthpart structures, phylogenetic analysis based on characters assumed to be independent from head and mouthparts are strongly required to avoid a circular argument and to inspect the phylogenetic hypotheses based on head and mouthpart characters.

In this study, phylogenetic relationships were inferred among three winged paraneopteran orders, Psocoptera (non-parasitic Psocodea), Hemiptera and Thysanoptera based on characters of the forewing base structure. Recently, a series of studies by Browne and co-authors (Browne *et al*., 1993; Browne & Scholtz, 1995, 1998) showed that the wing base structure is very informative for phylogenetic studies of Scarabaeoidea (Coleoptera). Wing base structure in Paraneoptera has been studied in Psocoptera (Badonnel, 1934; Cope, 1940; Weidner, 1972; Yoshizawa, 1999), Thysanoptera (Pesson, 1951), Heteroptera (Betts, 1986) and Psocoptera, Cicadomorpha and Heteroptera (Brodsky, 1994). However, these studies did not pursue the phylogenetic significance of this character for order-level phylogeny. Hence, the present study is the first attempt to infer phylogenetic relationships among paraneopteran orders using wing base structure.

Materials and methods

The taxa examined in this study are listed in Appendix 1. Terminology of the wing base structure and associated muscles mainly follows Brodsky (1994) and partly follows Matsuda (1970). Terminology of fold- and flexion-lines follows Wootton (1979). The taxon Acercaria (Börner, 1904) corresponds to Paraneoptera and earlier to Paraneoptera (Martynov, 1925), and the name Hemipterida or Hemipteroid Assemblage is often used for this group (e.g. Maddison, 1995). In this study, names of higher taxa follow Kristensen (1991).

Dried or alcohol specimens were used. The thorax was separated and placed in 5% KOH solution at about 45°C for 1–3 h depending on the size of the specimen. The material was then washed with distilled water and stored in 80% ethanol for subsequent dissection, observation and illustration. To facilitate observation, the sternum, pleuron and ventral layer of forewings were removed. Olympus SZ60 and Leica MZ12 stereoscopic microscopes were used to study and illustrate. Extremely small insects were slide-mounted in euparal and an Olympus BX50 compound light microscope was used for observation and illustration.

Plecoptera, Megaloptera and Mecoptera were used as outgroup taxa. Plecoptera was selected as a plesiomorphic representative of Neoptera, and Megaloptera and Mecoptera were selected as plesiomorphic representatives of Holometabola. Holometabola was treated as a sister group of Paraneoptera and Plecoptera was treated as a distantly related outgroup. Phylogenetic relationships among the outgroup taxa are well supported by morphology (e.g. Kristensen, 1991), paleontology (Kukalová-Peck, 1991) and combined molecular and morphology data (Whiting *et al*., 1997). Based on these outgroup relationships, character states at the outgroup node were estimated preceding the analysis (two-step cladistic analysis: Maddison *et al*., 1984).

Psocodea, Sternorrhyncha, Cicadomorpha, Fulgoromorpha, lower Heteroptera (Enicocephalomorpha), higher Heteroptera (Dipsocoromorpha – Pentatomomorpha) and Thysanoptera were treated as terminal taxa. Psocoptera is treated here as a representative of the clade Psocodea and thus the latter name is used for this clade. The term Homoptera is used for convenience in the text and should not be construed the monophyly of this group. Hemiptera is divided into four monophyletic terminal taxa because of their extremely high diversity.

The method for using higher taxa as terminal taxa was criticized by Yeates (1995), but in the present case, all character states selected for the phylogenetic analysis are consistent within each terminal taxon. Additionally, monophyly of each terminal taxon is strongly supported by morphology or molecular data or both (Rudolph, 1982, 1983; Mound & Heming, 1991; Wheeler *et al*., 1993; Campbell *et al*., 1995). Hence, the present treatment of terminal taxa does not affect the results of the analysis. Based on the matrix shown in Appendix 3, most parsimonious cladograms were searched using PAUP* 4.0b1 (Swofford, 1998). An exhaustive search was performed. Character states were optimized using MacClade 3.07 (Maddison & Maddison, 1992). The preferred cladogram was translated to a phylogenetic system according to the method of annotated Linnaean system (Wiley, 1981; Wiley *et al*., 1991).

The determination of the homology of the axillae was initiated by identifying the first axillary sclerite, which is easily recognizable by articulations with the anterior and median notal wing processes. Using the first axillary sclerite as a landmark, homology of other sclerites were decided based on their relative positions, articulations, fold- and flexion-lines and relationships with wing veins throughout ingroup and outgroup taxa. The median ridge of basisubcostale, ligament of second axillary sclerite and posterior notal wing process were also used for additional landmarks if necessary. Fold- and flexion-lines were observed by manipulating the forewing of freshly-killed or KOH soaked, non-dissected material.

Twenty characters were selected for the cladistic analysis (Appendix 2), including one multistate character, which was treated as ordered, and nineteen binary characters. Characters have the plesiomorphic state coded ‘0’, and the derived state(s) coded ‘1’ and ‘2’. Character length (number of steps), consistency index and retention index were calculated using MacClade 3.07 (Maddison & Maddison, 1992).

The present phylogenetic analysis was based only on data selected from forewing base structure, and no data were selected from hindwing base structure. As far as known, modifications in the hindwing structure usually show similar trends with those in the forewing base. This suggests that fore- and hindwing base structure are strongly correlated and may be mostly coded by the same gene(s). If so, by using both fore- and hindwing base data in phylogenetic analyses, certain characters would be double-counted. Therefore, to avoid over emphasis of certain characters, hindwing base characters are not included in the present analysis and will be discussed elsewhere (Yoshizawa, 1999).

Morphology

General morphology of forewing base structure (Fig. 1)

Plecoptera, Megaloptera and Mecoptera. The notum has three processes: anterior, median and posterior notal wing processes (ANWP, MNWP and PNWP, respectively). ANWP articulates with the proximal margin of the arm of the first axillary sclerite, MNWP with the proximal margin of the body of the first axillary sclerite and PNWP with the tip of the posterior arm of the third axillary sclerite. Notal processes and axillary sclerites articulate along a concave basal hinge. Two sclerites occur on the anterior margin, or costal margin, of the forewing base. The most proximal sclerite is the tegula (Tg), and the most distal sclerite placed at the base of the costa is the humeral plate (HP). The basisubcostale (BSc) is a basal sclerite of the subcostal vein placed just posterior to HP. BSc always has a median longitudinal ridge. The first axillary sclerite (1Ax) is a roughly triangular sclerite (body) with a characteristically long anterior arm. The apical tip of the arm of 1Ax articulates with the tip of BSc by anterior axillary fold-line, and the distal margin of the body of 1Ax articulates at the anterior and posterior points of the proximal margin of the second axillary sclerite by convex axillary flexion-line. The second axillary sclerite (2Ax) is a large, flat, subtriangular sclerite that articulates anteriorly with the posterior margin of the basiradiale (BR) along anterior axillary fold-line, distally with the proximal median plate along concave axillary fold-line and posteriorly with the anterior arm of the third axillary sclerite (posterior terminal points of convex axillary flexion-line and concave axillary fold-line). The anteroproximal portion of the 2Ax is often fused with BR (e.g. Mecoptera and Megaloptera) and the fused region becomes bending cuticle. Medially, 2Ax always has an invaginated ligament extended toward the ventral 2Ax. The third axillary sclerite (3Ax) has three arms. The anterior arm articulates with the posterior part of 2Ax and the distal arm with the posteroproximal corner of the distal median plate by convex axillary fold-line. The anterior margin of 3Ax is often fused to the proximal median plate. The basanale (BA) is a small sclerite situated between the distal arm of 3Ax and base of the anal veins. It articulates proximally near the tip of the distal arm of 3Ax and distally with the base of the anal veins (jugal fold). This sclerite is often regarded as part of 3Ax (e.g. posterior lobe 'j' of Brodsky, 1994), but apparently is not connected and articulates with 3Ax and should be regarded as an independent sclerite. The terminology of this sclerite follows Matsuda (1970). The proximal median plate (PMP) is a flat triangular sclerite placed just distal to 2Ax, with which it articulates. The distal median plate (DMP) is a flat sclerite placed just distal to PMP, and articulates with it along convex axillary fold-line. PMP and DMP are often fused with each other, with the fused region becoming bending cuticle. The anterior margin of DMP is always associated with the posterior margin of vein R along distal axillary flexion-line and its distal margin is associated with veins M and Cu.

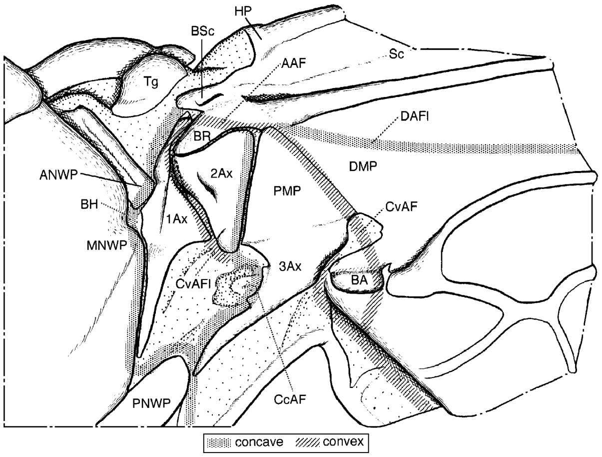

Fig. 1. Forewing base structure of *Alloperla* sp. (Plecoptera). 1Ax = first axillary sclerite, 2Ax = second axillary sclerite, 3Ax = third axillary sclerite, AAF = anterior axillary fold-line, ANWP = anterior notal wing process, BA = basanale, BH = basal hinge, BR = basiradiale, BSc = basisubcostale, CcAF = concave axillary fold-line, CvAF1 = convex axillary flexion-line, CvAF = convex axillary fold-line, DAF1 = distal axillary flexion-line, DMP = distal median plate, HP = humeral plate, MNWP = median notal wing process, PMP = proximal median plate, PNWP = posterior notal wing process, Tg = tegula.

Psocodea (Fig. 2)

The forewing base structure in Psocodea consists of the fundamental elements of the neopteran wing base described above. Articulations and fold- and flexion-lines also preserve the plesiomorphic condition except relationships between the distal arm of 3Ax and DMP. Therefore, there is little difficulty in interpretation of homology of the sclerites. Configurations of forewing base structure in Psocodea show some variations among suborders, but the basic structure remains unaltered throughout the order. The following character states are apparently different from those in the outgroup taxa and consistent throughout Psocodea.

HP and BSc of Psocodea are united with each other. In Megaloptera and Mecoptera, HP is clearly separated from BSc by a membranous region. In Plecoptera, HP is unclear but HP and BSc never compose a single sclerite such as in Psocodea.

In outgroup taxa, BSc and 2Ax are broadly separated by BR. In Psocodea, the anteroproximal corner of 2Ax extends

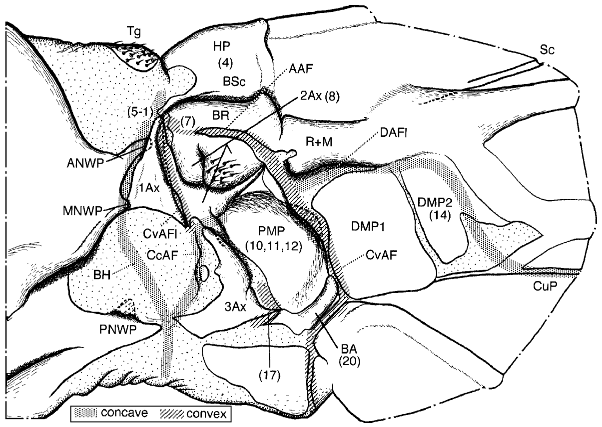

Fig. 2. Forewing base structure of *Psococerastis nubila* (Psocodea). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

anteriorly and is closely proximate with the apex of BSc. Probably associated with this modification, the anterior arm of 1Ax is often shortened, but this character state is not consistent throughout the order.

BR and 2Ax are fused with each other in Psocodea. Fusion of BR and 2Ax is also observed in Megaloptera and Mecoptera whereas they are separated in Plecoptera. Thus, this character state cannot be recognized as an apomorphic feature in Paraneoptera, and is regarded as being derived in the common ancestor of Paraneoptera + Holometabola or an earlier ancestor.

The anterior region of 2Ax is strongly swollen in Psocodea and is quite different from the flattened condition observed in the outgroup taxa. Hence, at first impression its anterior region appears to be an independent structure from the posterior region of 2Ax (Yoshizawa, 1995). Homology of this structure can be easily determined by the ligament toward the ventral 2Ax that occurs at the middle of the swelling (Fig. 9A).

In the outgroup taxa, PMP is flat and evenly sclerotized, whereas PMP of Psocodea is deeply concave and its distal margin is sclerotized much more strongly than its other regions. These modifications reinforce PMP and provide a firm articulation between 2Ax and PMP. Badonnel (1934) referred to the strongly sclerotized distal margin of PMP in Psocodea as arc ‘d’ and Brodsky (1994) called it the ‘rib of PMP’. As mentioned by Brodsky (1994), PMP and 2Ax of some Psocodea are fused and immobilized with each other. This character state is only observed within Psocomorpha (a suborder in Psocoptera), and it can be considered an apomorphic feature that appears within Psocodea (Yoshizawa, 1999). PMP of Psocodea is situated posterodistally to 2Ax, whereas it is distal to 2Ax in the outgroup taxa.

The only modification observed in the psocodean forewing base structure that has a completely different way of articulation from the basic condition is the lack of articulation between 3Ax and DMP. As discussed above, the distal arm of 3Ax always articulates with the posteroproximal corner of DMP in the outgroup taxa. Alternatively, in Psocodea the distal arm of 3Ax does not directly articulate with DMP but articulates with the proximal tip of BA, and the distal tip of BA articulates with the posteroproximal corner of DMP. Judging from the articulation with the anal vein and its position (located between 3Ax and anal vein), the identity of BA is certain. Probably associated with this modification, BA of Psocodea is fused with PMP, whereas it is distantly separated in the outgroup taxa.

In Psocodea, two sclerites are observed between PMP and the bases of veins M and Cu. The proximal sclerite articulates with PMP along the convex axillary fold-line and can be interpreted as DMP. The distal sclerite is associated with the base of Cu, and it can also be interpreted as DMP. Therefore, both sclerites are interpreted as DMP, referring to the proximal fragment as DMP1 and the distal fragment as DMP2. As discussed below, they are not homologous with DMP-1 and DMP-2 of Betts (1986) and Brodsky (1994).

The forewing base structure of Psocodea has been studied by several authors, but reinterpretations of their schemes are provided herein. The 1Ax and 2Ax of Cope (1940) are interpreted here as 1Ax + BSc and 2Ax + distal margin of PMP, respectively, and the anterior part of 2Ax is not illustrated in his Fig. 49. Tg is present throughout the order, especially well developed in Trogiomorpha and Troctomorpha but weaker in Psocomorpha, although Cope (1940) mentioned that it was absent in Psocomorpha. The internal sclerite of 2Ax (=b), arc d′ and arc e in Badonnel (1934) are interpreted here as the ventral 2Ax, distal margin of PMP and external margin of the jugum respectively. H (=Hp) and P1 (=1Ax) of Weidner (1972) probably correspond to Tg and a part of 2Ax, respectively, in the present scheme. The illustrations and interpretations of Brodsky (1994) are in complete agreement with the present scheme.

Sternorrhyncha (Fig. 3)

The forewing base structure in Sternorrhyncha retains a rather plesiomorphic condition, with all apomorphic features present in Psocodea also observed in Sternorrhyncha. Configurations of forewing base structure are quite different between Aphidoidea and Psylloidea (Coccoidea not examined) and some variations are also recognized among taxa within each superfamily. However, most of those modifications are unique for each taxon and are regarded as derived features within Sternorrhyncha. Therefore, they are neglected here because of lack of phylogenetic information at ordinal level, but probably are very useful for family- or genus-level phylogenetic studies. The following apomorphic features that cannot be observed in the outgroup taxa and Psocodea are observed throughout Sternorrhyncha.

In Sternorrhyncha, BSc is fused with the anteroproximal part of 2Ax, whereas they are separated from each other in the outgroup taxa and Psocodea. In Psocodea, the apex of BSc and the anteroproximal corner of 2Ax are closely proximate with each other and their fusion can be considered to be derived from it. Therefore, the following transformation series is

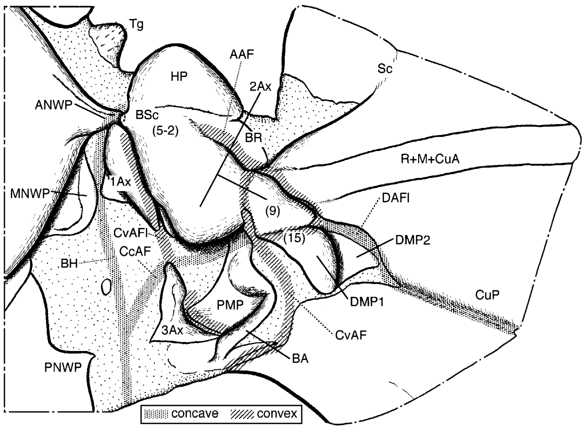

Fig. 3. Forewing base structure of *Petalolyma bicolor* (Sternorrhyncha). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

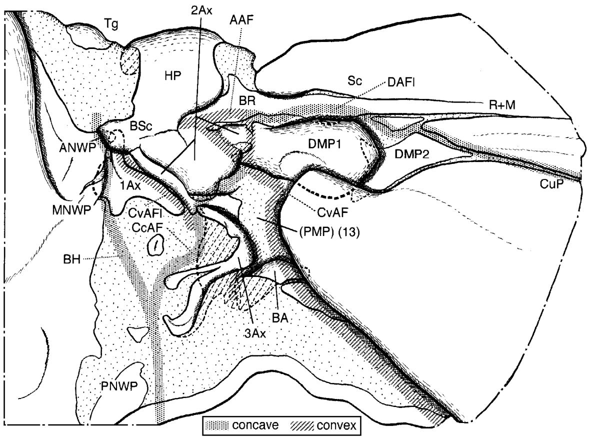

Fig. 4. Forewing base structure of *Drabescus* sp. (Cicadomorpha). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

envisaged: BSc and 2Ax distantly separated from each other → closely proximate → fused.

In the outgroup taxa and Psocodea, DMP and 2Ax are widely separated from each other. In Sternorrhyncha, the anterior margin of DMP is fused with the distal region of 2Ax and articulates along an anterior axillary fold-line with the fused region becoming a bending cuticle. The anterior axillary fold-line also runs between 2Ax and DMP in the outgroup taxa and Psocodea. Thus, although the relative position between 2Ax and DMP is highly modified in Sternorrhyncha, the fold-line preserves its basic condition and thus provides a landmark to aid in the determination of homologous structures.

The interpretation of the homology of 2Ax and DMP in Sternorrhyncha is problematic because these sclerites are fused with each other, and the anterior axillary fold-line, which is a very useful landmark as mentioned above, forks around their fused region. Therefore, the sclerite encircled by the forked anterior axillary fold-line can be interpreted as either 2Ax or DMP. Morphologically, no clear border can be observed around the proximal fork of the fold-line but a clear ridge can be recognized along its posterodistal fork (15). Therefore, the encircled sclerite is interpreted here as a distal fragment of 2Ax (Fig. 9C). This character state is never observed in the outgroup taxa or Psocodea and is apparently an apomorphic modification.

The encircled sclerite may also be considered as PMP because it is positioned just distal to 2Ax and broadly and flexibly attached to 2Ax, the orthodox condition for PMP. However, 2Ax and PMP are always articulated along a concave hinge, whereas the encircled sclerite is articulated with 2Ax along a convex hinge. True PMP of Sternorrhyncha is positioned posterior to 2Ax and articulated with it by a concave hinge anteriorly. Therefore, the idea that the encircled sclerite is PMP is completely excluded.

In Fig. 3, the anterior arm of 3Ax is separated from the posterior ridge of 2Ax. However, this is an artefact created in opening the forewing for illustration. Therefore, in the natural condition, they are articulated with each other, preserving the plesiomorphic state.

Cicadomorpha (Fig. 4)

The forewing base structure in Cicadomorpha is strongly modified but retains the apomorphic features present in Psocodea and Sternorrhyncha. An apomorphic feature, PMP reduced and often completely membranous, is consistently observed throughout Cicadomorpha. Judging from positions of the concave and convex axillary fold-lines, the membranous region just distal to the anterior arm of 3Ax is identified as the region corresponding to PMP. DMP1 may be considered as PMP because it is positioned just distal to 2Ax, an orthodox position for PMP. However, as already mentioned in Sternorrhyncha, 2Ax and PMP are articulated with each other along a concave hinge, whereas 2Ax and DMP1 are articulated along a convex hinge. Reduction of PMP is a unique and prominent character state, especially the desclerotized distal margin of PMP, because it is strongly sclerotized in all paraneopteran taxa except Cicadomorpha and Fulgoromorpha (see below). Although PMP is almost membranous in Cicadomorpha and Fulgoromorpha, this region is deeply concave. Thus, the apomorphic condition, PMP concave, which is observed throughout Psocodea and Sternorrhyncha, is considered to be retained in this group. The shape and size of each sclerite is highly variable among taxa within Cicadomorpha, and most of the modifications are considered as derived features within Cicadomorpha.

Figure 8.11 of Brodsky (1994) is accurate but several sclerites are reinterpreted here. PMP, DMP-1 and DMP-2 are the proximal fragment of 2Ax (swollen region), distal fragment of 2Ax (encircled sclerite mentioned in Sternorrhyncha) and DMP1, respectively.

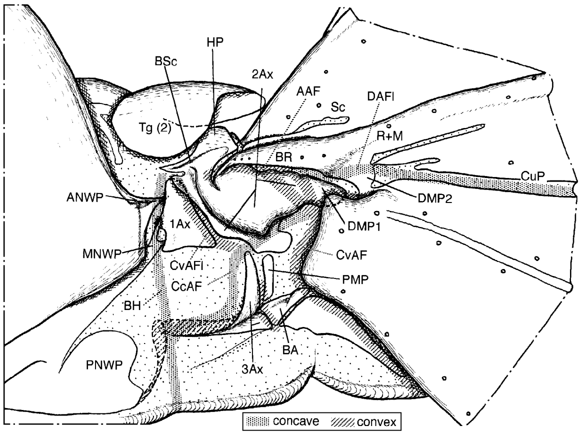

Fig. 5. Forewing base structure of *Oliarus angusticeps* (Fulgoromorpha). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

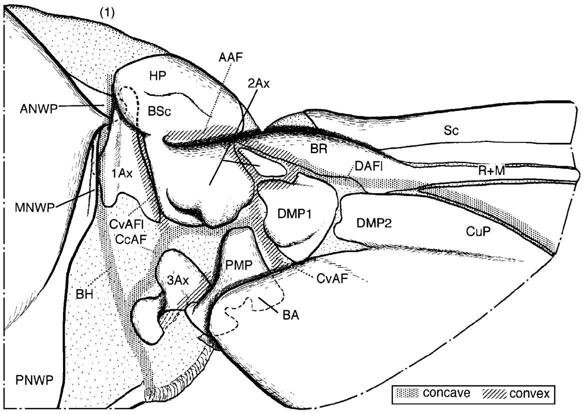

Fig. 6. Forewing base structure of an undetermined genus of Enicocephalinae (lower Heteroptera). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

Fulgoromorpha (Fig. 5)

The forewing base structure in Fulgoromorpha is basically the same as that of Cicadomorpha, and all apomorphic characters present in Psocodea, Sternorrhyncha and Cicadomorpha are also observed. Although a reduced PMP is illustrated in Fig. 5, it is more often completely absent. By contrast, as in Cicadomorpha, the shape and size of each sclerite is highly variable, but are regarded as derived features within Fulgoromorpha. Tg of Fulgoromorpha is consistently enlarged, with a broad extension encircling the entire outer margin (Fig. 10A). This is apparently an apomorphic character state, which has been used as a diagnostic character of Fulgoromorpha (e.g. Carver *et al.*, 1991).

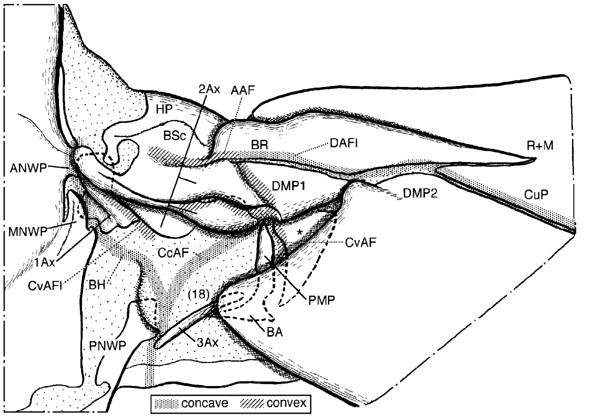

Fig. 7. Forewing base structure of *Paradasynus spinosus* (higher Heteroptera). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

Lower Heteroptera: Enicocephalomorpha (Fig. 6)

The forewing base structure in Enicocephalomorpha retains apomorphic features present in Psocodea and Sternorrhyncha and bears the rather primitive condition of the shape of sclerites, articulations and fold- and flexion-lines. Therefore, homology of each structure can rather easily be determined, except for the triangular sclerite between BR, 2Ax and DMP. The sclerite is encircled by the fork of the anterior axillary fold-line and, compared with Sternorrhyncha, it can be interpreted as the distal fragment of 2Ax (Fig. 9D). Forewing base structure is consistent throughout Enicocephalidae, but the other enicocephalomorphan family, Aenictopecheidae, was not examined. Absence of Tg is apparently an apomorphic feature that is never observed in the outgroup taxa or other orders in Paraneoptera.

In Fig. 6, the anterior arm of 3Ax is separated from the posterior ridge of 2Ax. However, as for Sternorrhyncha, it is an artefact resulting from opening the forewing for illustration.

Higher Heteroptera: Dipsocoromorpha-Pentatomomorpha (Fig. 7)

As mentioned in the Materials and methods, Heteroptera is here divided into lower and higher Heteroptera at the node between Enicocephalomorpha and Dipsocoromorpha, and they were treated as independent terminal taxa for the cladistic analysis because the following morphological gap in forewing base structure was observed between them. In Enicocephalomorpha, the anterior arm of 3Ax is well developed and articulates with 2Ax, whereas anterior arm of 3Ax is completely absent and 3Ax is reduced to a simple band-like sclerite in Dipsocoromorpha. Heteropteroid infraorders, except Enicocephalomorpha, consistently share this prominent and apparently apomorphic character state of 3Ax. Monophyly

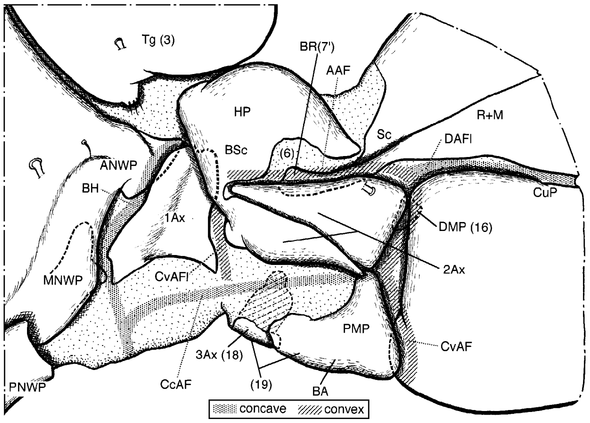

Fig. 8. Forewing base structure of *Bactrothrips brevitubus* (Thysanoptera). Numbers indicate characters used for phylogenetic analysis. Abbreviations as indicated for Fig. 1.

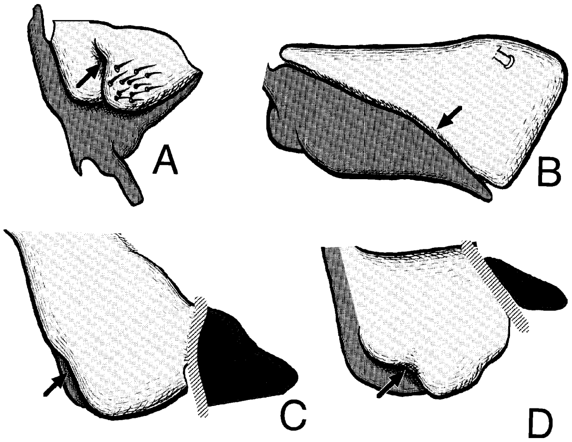

Fig. 9. Second axillary sclerite, dorsal aspect. Arrows indicate the ligament toward to ventral 2Ax. Shaded lines indicate the proximal fork of the anterior axillary fold-line. Homologous region is shown with same darkness. A, *Psococerastis nubila*; B, *Bactrothrips brevitubus*; C, *Petalolyma bicolor*; D, an undetermined genus of Enicocephalinae.

of both terminal taxa are well supported by morphological and molecular data (Wheeler *et al*., 1993).

The forewing base structure in the higher Heteroptera retains the apomorphic features present in Psocodea, Sternorrhyncha and Enicocephalomorpha. Apart from these features, forewing base structure in the higher Heteroptera is highly modified and the shape and size of each sclerite is highly variable. In most heteropteran taxa, except Dipsocoromorpha and Cimicomorpha, a sclerite occurs distal to PMP (asterisk in Fig. 7). Betts (1986) regarded this sclerite as a fragment of DMP and called it DMP-2. However, the area where this sclerite is situated is completely membranous in Dipsocoromorpha, the most basal clade of higher Heteroptera. Additionally, this sclerite is not associated with veins M or Cu. For this reason, the sclerite is not DMP but possibly a *de novo* structure not homologous with any fundamental sclerite in the wing base. DMP2, as defined herein, is fused with the base of the clavus (= anal region) and often indistinguishable.

Betts (1986) provided the most comprehensive morphological study of heteropteran wing base structure. His interpretations are almost in agreement with the present scheme, except that his humeral complex, composed of HP and 2Ax, actually also includes BSc. PMP, DMP-1, DMP-2 and 3Ax, *sensu* Brodsky (1994), are interpreted here as the swollen region of 2Ax, distal fragment of 2Ax, DMP1 and PMP, respectively.

Thysanoptera (Fig. 8)

The forewing base structure of Thysanoptera is highly specialized, but all apomorphic features observed in Psocodea and Sternorrhyncha are also present, except fusion of BR and 2Ax and fork of the anterior axillary fold-line. As mentioned under Psocodea, the fused condition of BR and 2Ax is considered plesiomorphic for Paraneoptera and the separated condition in Thysanoptera should be regarded as a secondary derivation.

The 2Ax of Thysanoptera is clearly divided into posteroproximal and anterodistal sclerites. This character state is similar to that of Heteroptera (Figs 7, 9D) and its anterodistal sclerite may be considered to be homologous with the distal fragment of 2Ax in Hemiptera (Yoshizawa & Saigusa, 1997a,b). However, the following two character states in Thysanoptera show that divided sclerites of Thysanoptera and Hemiptera are not homologous: the anterior axillary fold-line (Fig. 9, faded lines) does not run between them; the invaginated ligament extending towards the ventral 2Ax (Fig. 9A–D, arrows) occurs between them.

The forewing base structure of Thysanoptera is similar in apomorphic condition to that of the higher Heteroptera in the absence of the anterior arm of 3Ax. Tg of Thysanoptera is enlarged as in Fulgoromorpha, but they are morphologically distinct (Fig. 10). Tg of Fulgoromorpha has a small attachment to the body wall and a very broad extension encircling the entire outer margin (Fig. 10A). By contrast, Tg of Thysanoptera is very broadly attached to the body wall and has a relatively narrow extension along the posterodistal margin only (Fig. 10B). Therefore, they are considered different in origin.

The forewing articulation in Thysanoptera is strongly modified but rather more consistent throughout the order than in Psocodea and Hemiptera. The following three apomorphic character states are unique to Thysanoptera: BR separated from HP and BSc by membrane; 3Ax and BA situated on posterior margin of forewing base; DMP reduced in size.

DMP of Thysanoptera is extremely small and situated on the distal margin of 2Ax. The articulation and relative position of DMP and 2Ax are the same as in Hemiptera. DMP2 is not distinguishable. In some thysanopteran taxa, a weakly

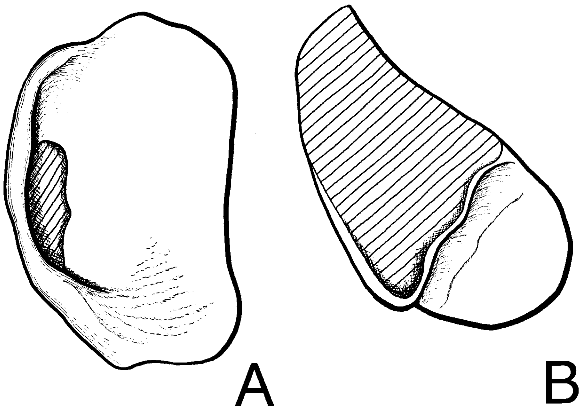

Fig. 10. Tegula, posteroventral aspect. A, *Oliarus angusticeps*; B, *Bactrothrips brevitubus*.

sclerotized structure is observed just distal to PMP and proximal to the anal region. Judging from its relative position to PMP, this sclerite looks somewhat like DMP but its distal region is not associated with Cu or M. Additionally, this structure is not observed in Merothripidae and Phlaeothripidae. From the most parsimonious reconstruction (Swofford & Maddison, 1987) of these structures on available cladograms of Thysanoptera (Crespi *et al*., 1996), it is likely that this sclerite was not present in their common ancestors. Therefore, this structure is interpreted as being derived in Thysanoptera and does not correspond to any fundamental wing base element. As mentioned above, a similar structure is also observed in some taxa of higher Heteroptera, but is apparently a homoplastic character.

The forewing base structure of Thysanoptera was studied by Pesson (1951). His pt1 (= 1Ax) and distal part of pt3 (= 3Ax) are interpreted here as HP + BSc and PMP + BA, respectively.

Phylogenetic analysis and higher classification

Analysis of the dataset (Appendix 3) resulted in only one most parsimonious cladogram (Fig. 11: L = 23; CI = 0.91; RI = 0.94). Therefore, this cladogram is accepted as the best hypothesis of phylogenetic relationships among paraneopteran orders, and serves as the basis for the following classification of Paraneoptera.

- Paraneoptera
  - Psocodea
    - ‘Psocoptera’
    - Phthiraptera
  - Condylognatha
    - Thysanoptera
    - Hemiptera

No autapomorphy of Psocodea was found in the forewing base structure, but its monophyly is well supported by the specialized hypopharynx (Rudolph, 1982, 1983). By contrast, monophyly of Psocoptera remains controversal (Smithers, 1972, 1991; Kim & Ludwig, 1978; Seeger, 1979; Lyal, 1985). As all phthirapteran insects are apterous, this argument cannot be resolved by analysis of the present data. Therefore, in the classification proposed here, the name Psocoptera is put in quotation marks to indicate that its status is presently unknown (Wiley, 1981; Wiley *et al*., 1991).

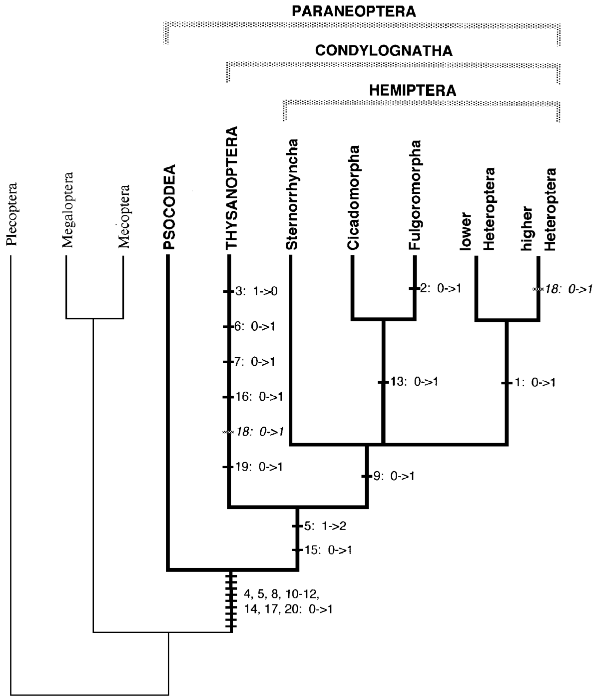

Fig. 11. The most parsimonious cladogram for Paraneoptera derived from the forewing base structure, with the most parsimonious reconstruction of character states.

Monophyly of Heteroptera and Auchenorrhyncha were supported but relationships among Sternorrhyncha, Auchenorrhyncha and Heteroptera were not resolved solely on the basis of forewing base data. Phylogenetic relationships within Hemiptera have been studied by many authors (e.g. Wheeler *et al*., 1993; Campbell *et al*., 1994, 1995; von Dohlen & Moran, 1995; Sorensen *et al*., 1995; Bourgoin *et al*., 1997; see also the last paragraph of the Discussion).

Discussion

In the present analysis, monophyly of Paraneoptera was supported by nine autapomorphies: HP united with BSc, apex of BSc in close proximity to the anteroproximal corner of 2Ax, anterior region of 2Ax swollen, PMP located posterodistally to 2Ax, PMP concave, distal margin of PMP strongly sclerotized, distal arm of 3Ax not articulated with DMP, BA fused with PMP and DMP divided into two sclerites. As mentioned above, some of these modifications are possibly associated with each other and may not be independent characters. However, in total, these autapomorphies provide strong evidence for the monophyly of Paraneoptera. Monophyly of Paraneoptera has been accepted widely for some time, based on several autapomorphies: slender lacinia, enlarged postclypeus, at most three-segmented tarsus and at most six Malpighian tubules (Hennig, 1981; Kristensen, 1991). In contrast, Kristensen (1991) mentioned that these characters may not appear to be 'strong' ones. Therefore, the result of the present analysis provides important additional evidence supporting the monophyly of Paraneoptera. The characters treated here are complex and constant throughout this group, and as mentioned by Browne & Scholtz (1995), they can be considered as taxonomic characters with 'high weight' (Mayr & Ashlock, 1991).

The forewing base structure in Psocodea consists of the fundamental elements of the neopteran wing base, and preserves the plesiomorphic condition. Additionally, apomorphic character states present in Psocodea are also consistently observed throughout paraneopteran orders, and no autapomorphy of Psocodea is found in the forewing base. Therefore, wing base structure of Psocodea apparently retains the most plesiomorphic condition among paraneopteran orders, and well represents the ground plan of Paraneoptera. One must consider, however, that forewing base structure of Psocodea is already more specialized than that in the most ancestral taxon of Paraneoptera.

Two apomorphic character states, fusion of BSc and 2Ax and DMP placed next to 2Ax, support the monophyly of Condylognatha. Monophyly of Condylognatha is also suggested by morphological studies of head and mouthpart structures (Kristensen, 1975; Hamilton, 1981; Lyal, 1985). Characters used in the present analysis can be considered as independent from those structures, thus the results here strongly support the hypothesis about transformation series of head and mouthpart structures suggested by the above authors. The sclerotized ring between the antennal flagellomeres (Seeger, 1975) is also probably an autapomorphy of Condylognatha. By contrast, spermatological similarity between Thysanoptera and Phthiraptera (Baccetti, 1979; Jamieson, 1987) conflicts with the results of the present analysis, and should be regarded as homoplastic rather than underlying synapomorphy (Kristensen, 1991).

In Thysanoptera, the following five autapomorphies are observed: Tg enlarged, BR separated from HP, BR separated from 2Ax, 3Ax and BA situated on the posterior margin of the wing base and DMP reduced in size. Forewing base structure of Thysanoptera is highly modified but rather constant throughout the order. It is possibly associated with the highly specialized wing structure, including its functional aspect (Pringle, 1957), that is rather consistent throughout the order.

Only one autapomorphy, fork of the anterior axillary foldline, supports the monophyly of Hemiptera. Other possible autapomorphies of Hemiptera may be hidden by extreme high diversity in the forewing base structure, including its functional diversity. Monophyly of Hemiptera is strongly supported by the highly derived sucking mouthparts (e.g. Hamilton, 1981), but no other autapomorphy of this order has been proposed, except Hennig (1981) suggested an uncertain unbranched radial sector. Therefore, the present analysis provides an important additional character supporting the monophyly of Hemiptera that can be considered as independent from head and mouthpart characters.

The forewing base structure in Thysanoptera is similar to that of the higher Heteroptera in the absence of the anterior arm of 3Ax. However, as mentioned above, monophyly of Hemiptera is strongly supported, and monophyly of Heteroptera is supported by an autapomorphic absence of Tg. Thus, the similarity of 3Ax in these taxa is considered as homoplasy, possibly caused by functional similarity of the wing folding mechanism. Both Heteroptera and Thysanoptera fold their wings flat, and the tips often overlap with each other. This character state is considered to be independently evolved from roof-like wing folding such as in Psocodea and Homoptera. When wings of Psocodea and Homoptera are folded backward, 3Ax rotates and its anterior arm moves upward by contraction of the t-p13 muscle. Then, with the tip of the anterior arm of 3Ax used as a fulcrum, 2Ax rotates and its anterior margin moves downward, resulting in roof-like wing folding. In Heteroptera and Thysanoptera, in contrast, 3Ax rotates only a limited degree when the wings are folded backward, and, because the anterior arm is absent, 2Ax shifts posterointernally without rotating. When the forewing is completely closed, deep wrinkles appear on the membranous region between 2Ax and 3Ax, and the posterior margin of 2Ax often touches the anterior margin of 3Ax, resulting in flat folding of the forewing. Of course, the functional similarity mentioned here is only one possibility among many evolutionary factors that provide homoplasy in wing base structure, and further functional studies of flight and wing folding mechanisms are required to understand the evolution of the wing base structure.

The present analysis provides an additional interesting insight into the phylogenetic relationship between Cicadomorpha and Fulgoromorpha. Auchenorrhyncha, composed of Cicadomorpha and Fulgoromorpha, has long been regarded as a monophyletic group, with a complex tymbal acoustic system, aristoid antennal flagellum and configuration of the pregenital abdomen considered as autapomorphies (Kristensen, 1975; Carver *et al*., 1991; Sweet, 1996). By contrast, some authors have suggested the possibility of a sister-group relationship between Fulgoromorpha and Heteroptera (Goodchild, 1966; Hamilton, 1981; Hennig, 1981; Bourgoin, 1986, 1993; Wootton & Betts, 1986; D'Urso & Ippolito, 1994; Sweet, 1996). Possible synapomorphies were summarized by Campbell *et al*. (1995) and the presence of a field of abdominal trichobothria was noted by Sweet (1996). Recent phylogenetic analyses based on 18S rDNA sequence data also suggested that Fulgoromorpha is a sister group of Heteroptera (von Dohlen & Moran, 1995; Sorensen *et al*., 1995; Campbell *et al*., 1994, 1995; Bourgoin *et al*., 1997). However, the results of molecular studies do not seem to provide strong evidence of non-monophyly of Auchenorrhyncha: the semi-parsimonious cladograms, only one step longer than the most parsimonious cladogram obtained by von Dohlen & Moran (1995), support the monophyly of Auchenorrhyncha; the result of the analysis by Campbell *et al.* (1995) was unstable when Coleorrhyncha was included in the analysis; monophyly of Auchenorrhyncha and Fulgoromorpha + Heteroptera were equally parsimonious when Psyllidae was excluded from the analysis (Bourgoin *et al.*, 1997).

In the present analysis, Auchenorrhyncha was considered as a monophyletic group and autapomorphic reduction of PMP supported the clade. This character state is prominent and never observed in other insect groups, and apparently independent from the tymbal acoustic system, antennal flagellum and pregenital abdominal characters. Additionally, sclerites in wing base are closely related with each other and compose a highly complex structure morphologically and functionally. Consequently, reduction of PMP seems to be a reliable autapomorphy of Auchenorrhyncha, although reduction characters usually have lesser weight than gain characters in phylogeny. Further investigations are required to understand the relationships between Cicadomorpha, Fulgoromorpha and Heteroptera, but it should be noted that wing base structure suggests a sister-group relationship between Cicadomorpha and Fulgoromorpha.

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Appendix 1. Taxa included in the study.

Psocodea
  Trogiomorpha
    Lepidopsocidae: *Echmepteryx*
  Troctomorpha
    Amphientomidae: *Paramphientomum*; Pachytroctidae: *Tapinella*; Troctopsocidae: an undetermined genus
  Psocomorpha
    Amphipsocidae: *Matsumuraiella*; Caeciliusidae: *Caecilus*, *Dypsocus*; Calopsocidae: *Calopsocus*; Ectopsocidae: *Ectopsocopsis*; Elipsocidae: *Elipsocus*; Epipsocidae: *Epipsocopsis*; Hemipsocidae: *Hemipsocus*; Lachesillidae: *Lachesilla*; Mesopsocidae: *Idatenopsocus*, *Mesopsocus*; Myopsocidae: *Lichenomima*; Peripsocidae: *Peripsocus*; Philotarsidae: *Haplophallus*; Pseudocaeciliidae: *Heterocaecilius*, *Phallocaecilius*; Psocidae: *Psococerastis*; *Sigmatoneura*; Stenopsocidae: *Stenopsocus*
Thysanoptera
  Terebantia
    Aeolothripidae: *Aeolothrips*, *Franklinothrips*, *Heolothrips*; Merothripidae: *Merothrips*, *Erotidothrips*; Thripidae: *Heliothrips*, *Megaleurothrips*, *Thrips*
  Tubulifera
    Phlaeothripidae: *Bactrothrips*, *Liothripis*
Hemiptera
  Sternorrhyncha
    Psyllidae: *Petalolyma*, several undetermined genera; Aphididae: *Cinara*, several undetermined genera
  Cicadomorpha
    Aphrophoridae: *Aphrophora*; Cercopidae: *Eoscartopis*; Cicadidae: *Mogannia*, *Tanna*; Ledridae: *Ledra*; Membracidae: *Machaerotypus*; Cicadellidae: *Bothrogonia*, *Drabescus*, *Ledra*, *Penthimia*
  Fulgolomorpha
    Achilidae: *Catanidia*, *Rhotala*; Cixiidae: *Oliarus*; Flatidae: *Geisha*; Issidae: *Gergithus*; Ricaniidae: *Orosanga*
  Enicocephalomorpha
    Enicocephalidae: *Hoplitocoris*, an undetermined genus of subfamily Enichocephalinae
  Dipsocoromorpha
    Schizopteridae: an undetermined genus of subfamily Schizopterinae
  Gerromorpha
    Gerridae: *Gerris*, *Hydrometra*
  Neopmorpha
    Belostomatidae: *Diplonychus*; Notonectidae: *Notonecta*; Ochteridae: *Ochterus*
  Cimicomorpha
    Anthocoridae: *Amphiareus*; Miridae: *Deraeocoris*, *Lygocoris*; Nabidae: *Nabis*; Reduviidae: *Agriosphodrus*, *Onchocephalus*; Tingidae: *Stephanitis*
  Pentatomomorpha
    Acanthosomatidae: *Sastragala*; Aradidae: *Neuroctenus*; Coreidae: *Paradasynus*; Cydnidae: *Macroscytus*; Largidae: *Physopelta*; Lygaeidae: *Nysius*; Pentatomidae: *Erthesina*, *Nezara*; Scutelleridae: *Calliphara*
Plecoptera
    Nemouridae: *Nemoura*; Chloroperlidae: *Alloperla*; Perlidae: *Oyamia*
Megaloptera
    Corydalidae: *Protohermes*, *Parachauliodes*; Sialidae: *Sialis*
Mecoptera
    Bittacidae: *Bittacus*; Panorpidae: *Panorpa*

Appendix 2. Characters used in the cladistic analysis.

1. *Tg*: (0) present; (1) absent (Fig. 6). Length = 1; CI = 1; RI = 1.
2. *Tg*: (0) small; (1) enlarged, with broad extention encircling the entire margin (Figs 5, 10A). Length = 1; CI = 1; RI = 0/0.
3. *Tg*: (0) with small attachment to body wall; (1) with broad attachment to body wall (Figs 8, 10B). Length = 1; CI = 1; RI = 0/0.
4. *HP and BSc*: (0) separate from each other; (1) united with each other (Fig. 2). Length = 1; CI = 1; RI = 1.
5. *BSc*: (0) distant from 2Ax; (1) close proximity to anteroproximal corner of 2Ax; (2) fused with anteroproximal part of 2Ax (Fig. 2). Length = 2; CI = 1; RI = 1.
6. *BR and HP + BSc*: (0) fused with each other; (1) separated from each other (Fig. 8). Length = 1; CI = 1; RI = 0/0.

7. *BR and 2Ax*: (0) separate from each other; (1) fused (Fig. 2). Length = 2; CI = 0.5; RI = 0.5.
8. *2Ax*: (0) nearly flat; (1) anterior region swollen (Fig. 2). Length = 1; CI = 1; RI = 1.
9. *Anterior axillary fold-line*: (0) not forked; (1) forked around distal end of 2Ax, and its proximal branch running through the distal portion of 2Ax (Fig. 3). Length = 1; CI = 1; RI = 1.
10. *PMP*: (0) located distal to 2Ax; (1) located posterodistally to 2Ax (Fig. 2). Length = 1; CI = 1; RI = 1.
11. *PMP*: (0) nearly flat; (1) deeply concave (Fig. 2). Length = 1; CI = 1; RI = 1.
12. *PMP*: (0) almost evenly sclerotized; (1) distal margin sclerotized more strongly than its other regions (Fig. 2). Length = 1; CI = 1; RI = 1.

State of this character in Cicadomorpha and Fulgoromorpha cannot be decided because their PMP is reduced, and coded as '?'.

13. *PMP*: (0) well sclerotized; (1) reduced, often completely membranous (Fig. 4). Length = 1; CI = 1; RI = 1.
14. *DMP*: (0) not divided; (1) divided into 2 sclerites (Fig. 2). Length = 1; CI = 1; RI = 1.

This character is coded as '?' for Thysanoptera because of its reduction of DMP.

15. *DMP*: (0) distant from 2Ax; (1) placed next to 2Ax, articulating along a convex hinge (Fig. 3). Length = 1; CI = 1; RI = 1.
16. *DMP*: (0) large; (1) reduced in size (Fig. 8). Length = 1; CI = 1; RI = 0/0.
17. *Distal arm of 3Ax and DMP*: (0) articulate with each other; (1) not articulate with each other (Fig. 2). Length = 1; CI = 1; RI = 1.
18. *Anterior arm of 3Ax*: (0) present; (1) absent (Figs 7, 8). Length = 2; CI = 0.5; RI = 0.
19. *3Ax and BA*: (0) separate from posterior margin of forewing base; (1) situated on posterior margin of forewing base (Fig. 8). Length = 1; CI = 1; RI = 0/0.
20. *BA and PMP*: (0) separate from each other; (1) fused with each other (Fig. 2). Length = 1; CI = 1; RI = 1.

Appendix 3. Data matrix for the cladistic analysis of Paraneoptera. 0–2 = character states; ? = inapplicable data.

Plecoptera	00000	00000	00000	00000
Mecoptera	00000	01000	00000	00000
Megaloptera	00000	01000	00000	00000
Psocoptera	00011	01101	11010	01001
Thysanoptera	00112	10101	110?1	11111
Sternorrhyncha	00012	01111	11011	01001
Cicadomorpha	00012	01111	1?111	0100?
Fulgoromorpha	01012	01111	1?111	0100?
Lower Heteroptera	10012	01111	11011	01001
Higher Heteroptera	10012	01111	11011	01101