Origin and transformation of the in-flight wing-coupling structure in Psocodea (Insecta: Paraneoptera)

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ABSTRACT

Many four-winged insects have mechanisms that unite the fore- and hindwings in a single plane. Such an in-flight wing coupling apparatus may improve flight performance in four-winged insects, but its structure is variable among different insect groups. The wings of bark lice (Insecta: Psocodea: 'Psocoptera') also have an in-flight wing coupling apparatus, but to date, its morphology has not been studied in detail. In this study, we examined the wing-coupling structure in representative species of the three suborders of bark lice (Trogiomorpha, Troctomorpha and Psocomorpha) and inferred its origin and transformation. We conclude that the main

component of the psocodean wing coupling apparatus evolved once in the common ancestor via modification of cuticular structures at the apex of the forewing CuP vein. Morphological differences in components of the coupling structures are phylogenetically informative at the intraorder level and include an autapomorphy that characterizes Troctomorpha and a synapomorphy that supports a sister relationship between Troctomorpha and Psocomorpha.

INTRODUCTION

The evolution of insect wings and powered flight are cited as epochal events in their history (Brodsky, 1994), and insect flight mechanisms have attracted significant interest from functional and comparative biologists (Wootton, 1992; Brodsky, 1994; Grodnitsky, 1995, 1999). Winged insects usually have two pairs of (i.e., four) wings. Some four-winged insects, such as dragonflies (Odonata) and locusts (Orthoptera), flap the fore- and hindwings independently (Chapman, 2013), but this condition is rather exceptional among insects, possibly because this mode is less efficient and less stable (Pope, 1994). Loss of the thrust-generating function in either the fore- or hindwing pair (i.e., dipterous flight) is more frequent; this occurs, for example, in Diptera (true flies) and Strepsiptera (the twisted wing parasites). The forewings of Coleoptera (beetles), the elytra, function to protect the wings from external damage (Linz et al., 2016). The elytra are sclerotized and held away from the body during flight, and they do not

generate thrust. Complete loss of the capacity to generate thrust in either the fore- or hindwing pair occurs in mayflies (Ephemeroptera), earwigs (Dermaptera), crickets (Orthoptera), stick insects (Phasmida), scale insects (Hemiptera), wasps (Hymenoptera), lacewings (Neuroptera), and moths (Lepidoptera) (Grodnitsky, 1995).

The predominant flight mode in four-winged insects is functionally two-winged flight (Grodnitsky, 1999). In such insects, the fore- and hindwings are connected by an in-flight coupling apparatus. Grodnitsky (1999) defined two coupling modes in the functionally two-winged insects: wings that are coupled during the downstroke only (part-time coupling) and wings that are mechanically connected and fully synchronized during flight (full-time coupling). The wing coupling apparatus of "full-time" coupled flyers has been reported in Paraneoptera [bark lice (Psocodea: Weber, 1936), thrips (Thysanoptera: Pesson, 1951a; Moritz, 1997), aphids, cicadas and true bugs (Hemiptera: Pesson, 1951b; Bohne and Schneider, 1979; D'Urso and Ippolito, 1994; Ni et al., 2002)] and Holometabola [wasps (Hymenoptera: Basibuyuk and Quicke, 1997), moths and butterflies (Lepidoptera: Tillyard, 1918; Braun, 1924), and caddisflies (Trichoptera: Tillyard, 1918; Stocks, 2010a)]. Such full-time wing coupling apparatuses are one of two primary types: 1) setae of one wing that interact with setae or other structures on the other wing, such as in Thysanoptera (Pesson, 1951a; Moritz, 1997), Hymenoptera (Basibuyuk and Quicke, 1997), and Trichoptera (Tillyard, 1918; Stocks, 2008, 2010a,b); 2) non-setal cuticular structures,

often in the form of grooves, such as in various Hemiptera (Pesson, 1951b; D'Urso and Ippolito, 1994) and the jugum in Lepidoptera and Trichoptera (Tillyard, 1918; Stocks, 2010ab).

The in-flight wing coupling apparatus of the free-living Psocodea, or "Psocoptera", is located on the distal end of the CuP vein (Fig. 2A, "fli") and clasps the hindwing at all times during wing flapping. The psocopterans also have a repose-coupling apparatus located on the R or Sc vein that engages the costa of the hindwing at rest (New, 1974; Mockford, 1967) (Fig. 2A, "rep"), but this structure is not further examined here. The psocopteran in-flight wing coupling structure is formed from non-setal cuticles and consists of a "hook" that engages the anterior margin of the hindwing (Weber, 1936; Günther, 1974). Although there are some SEM studies on the psocopteran in-flight coupling structures (New, 1974; Lawson and Chu, 1974), the structures have not been studied comprehensively. Therefore, their evolutionary pattern and phylogenetic value are as yet unclear. Furthermore, there is also uncertainty about the homology of the structures with those of other paraneopteran orders (i.e., Thysanoptera and Hemiptera: Lawson and Chu, 1974)

Currently, three suborders of 'Psocoptera' are recognized: Trogiomorpha, Troctomorpha (including the parasitic lice) and Psocomorpha (Yoshizawa et al., 2006). Mockford (1967) and Yoshizawa (2002, 2005) recognized that in-flight wing coupling structures in psocids are phylogenetically informative characters, having a 'hook' composed of

truncated 'spines' fused at their bases as either a synapomorphy supporting the clade Troctomorpha + Psocomorpha (Mockford, 1967) or an autapomorphy of Psocomorpha (Yoshizawa, 2002; 2005). Molecular phylogenetic approaches support Troctomorpha and Psocomorpha as sister taxa (Yoshizawa et al., 2006; Yoshizawa and Johnson, 2014), but few morphological characters that might support this relationship are known. We expanded on the previous wing characters surveys that were mostly based on light microscopy by including additional taxa and using SEM to examine structures at higher magnification and resolution. We evaluated wing coupling characters based on the phylogenetic hypotheses presented by Yoshizawa & Johnson (2010, 2014), Friedemann et al. (2014) and Yoshizawa & Lienhard (2016). We examined the homology and character state transformations of the wing coupling apparatus.

MATERIALS & METHODS

Taxon selection (Table 1)

The taxa examined were as follows: Trogiomorpha, 5 species representing 4 families; Troctomorpha, 7 species representing 9 families; and 16 species representing the 23 families of Psocomorpha. We included a species of Psocomorpha: Calopsocidae, recently synonymized with Pseudocaeciliidae (Yoshizawa and Johnson, 2014), because of the highly modified, elytra-like wings. *Aeolothrips kurosawai* (Thysanoptera: Aeolothripidae) and *Cinara* sp. (Hemiptera: Aphididae) were selected as

outgroups.

Treatment of Specimens

Specimens examined were stored in 80% or 99% ethanol. Forewings were removed and dehydrated in 100% ethanol for 1 hour. Wing cuticle was hardened by soaking with 1,1,1,3,3,3-hexamethyldisilazane for 1 hour and air drying prior to mounting on 10mm aluminum stubs. Wings were held in place with sticky urethane sheets (Kokuyo Hittsuki Sheet, Kokuyo Co. Ltd., Tokyo) and coated with Au-Pd in a Hitachi E101 ion sputter-coater (Hitachi High Technologies Corp., Tokyo) for 120 sec. We used a Jeol JSM-5310LV scanning electron microscope (Jeol Ltd., Tokyo) and photographed screen images with Jeol Digi Capture SUP-7707 Version 1.0.11. Figures were arranged with Adobe Photoshop CC 2014 and Adobe Illustrator CC 2014.

Character Coding

Character state changes were reconstructed on the composite phylogenetic tree (Fig. 1 in Yoshizawa and Johnson 2014), which included almost all psocid families and was used as a backbone tree. Placement of Pachytroctidae and Liposcelididae was based on Yoshizawa & Johnson (2010); those families were not sampled in Yoshizawa & Johnson (2014). The outgroup taxa were based on Friedemann et al. (2014) and Yoshizawa & Lienhard (2016). Unsampled families were trimmed from the tree, and a coded character matrix was reconstructed by the parsimony criterion using

Mesquite version 3.04 (Maddison and Maddison, 2015).

Terminology

Different terms have been used for the wing structures in Psocoptera, but the terms used here are based on Weber (1936) and Günther (1974).

RESULTS

Summary of general morphology (Fig. 2)

Structures forming the forewing in-flight coupling apparatus are near the apical-most region of the CuP vein and are termed the **retinaculum**, **CuP-tip**, and **retainer** (Figs. 2A, B). The term "nodulus" indicates the region where the CuP and A1 veins join near the posterior wing margin (Fig. 2A, B, junction of two green lines). **Rib-like** structures (Fig. 2B, r) are arranged at almost equal intervals along the CuP vein (Günther, 1974) (Fig. 2B) generally with each structure arranged transverse to the vein. The rib-like structures occur on other veins, but their presence is taxonomically variable.

The "**retinaculum**" (Fig. 2B, Rc) is composed of many spine-like cuticles ("**retinacular spines**") that as a unit form a hook-like structure.

The "**CuP-tip**" (Fig. 2B, Ct) refers to the apical-most section of the CuP vein between the Rc and the posterior wing margin that bears modified **rib-like structures**.

The "**retainer**" (Fig. 2B, Rtr) is a highly thickened and bent structure on the posterior wing margin that bears a large number of fine stud-like projections. The retainer is taxonomically variable in the degree of swelling and the morphology of the projections. The retinaculum and retainer together form a 'clip-like' functional unit that engages the costal margin of the hindwing.

The counterpart of the in-flight wing coupling apparatus in hindwings (i.e., the anterior margin) is not specialized among the taxa examined, although the wing coupling apparatus of forewings is diversified. The anterior margin of the hindwing engages in both types of wing coupling (repose and in-flight) and is bent and rolled inwardly (Fig. 2C). At rest, the repose-coupling apparatus (Fig. 2A, "rep") fits into the bend (white arrow, Fig. 2C) and supports the hindwing. During flight, the 'clip-like' unit formed by the retinaculum and retainer catches the hindwing margin.

Trogiomorpha

Venation and the rib-like structure (Fig. 3)

The A1 and CuP veins do not join (i.e., the nodulus is absent), although they terminate closely. *Psoquilla* sp. (Psoquillidae) lacks A1. The CuP is thickened as in other veins. The rib-like structure is distributed on all veins, but the ribs on the CuP are more prominent.

Morphology of the retinaculum (Fig. 4)

The retinaculum is present in all examined trogiomorphan taxa, and all are composed of several separated spines (Fig. 4; Character 3:1; 4:0) that are continuous with the row of ribs on the CuP. In *Prionoglaris* (Prionoglaridídae) (Fig. 4A), the retinaculum is composed of approximately nine nearly straight spines. *Echmepteryx* (Lepidopsocidae) also possesses a simple retinaculum composed of approximately 10 straight spines (Fig. 4E). In all other species, the retinaculum is composed of curled spines (Fig. 4C, D). *Psyllipsocus* (Psyllipsocidae) has a simple retinaculum composed of only four bent spines (Fig. 4C). The retinaculum of *Psoquilla* consists of approximately 10 densely arranged and strongly curled and twisted spines (Fig. 4D). The spines of *Psyllipsocus, Echmepteryx* and *Psoquilla* are apically fringed (Fig. 4A, C, D; Character 5:1).

The retinaculum of *Neotrogla* (Prionoglaridídae) (Fig. 4B) shows an extremely different structure from that of the other trogiomorphan species, including a species of the family (*Prionoglaris*). The rib-like structure on the CuP vein becomes gradually recumbent and merges into the vein toward the retinaculum (Character 6:1). The retinaculum is composed of one short and three long, sharp spines projecting posteriorly.

Morphology of the CuP-tip (Fig. 4)

The CuP-tips in *Prionoglaris*, *Psyllipsocus*, *Psoquilla* sp. and *Echmepteryx* are continuous from the basal CuP without remarkable

modification (Fig. 4A, C–E). The ribs on the CuP-tips are transversely arranged without detectable modifications from those on the CuP vein (Character 8:0). The CuP-tip of *Neotrogla* retains only one transversely arranged rib near the base of the retinaculum (Fig. 4B).

Morphology of the retainer (Fig. 4)

The retainer of Trogiomorpha tends to be thickened and bent (Character 11:1), but no further remarkable deformation compared to the unmodified posterior wing margin was detected. The surface is uniformly covered with scaly studs (Characters 14:0; 15:0), but the studs of *Neotrogla* are recumbent and mostly merge into the vein (Fig. 4B). In *Echmepteryx*, the surface studs distal to the retainer are gradually reduced (Fig. 3E; Character 15:2).

Troctomorpha

Venation and rib-like structure (Fig. 5)

The A1 and CuP veins closely approximate at the distal ends. They are clearly joined (= nodulus: Fig. 5C, D, E), separated (Fig. 5B), or are intermediate in condition (Fig. 5A). The rib-like structures are distributed on all veins, but they are more prominent on the CuP.

The species in two families of Nanopsocetae have somewhat simplified forewings. The forewing of *Embidopsocus* (Liposcelididae)

lacks a rib, a coupling structure and most veins (Character 2:1) (Fig. 9A). The forewing of *Tapinella* (Pachytroctidae) lacks the coupling structure and nodulus (Fig. 9C), but all principal veins and the reduced ribs (Character 1:1) are retained (Fig. 9B).

Morphology of the retinaculum (Fig. 5)

The retinaculum is composed of curled, separated spines (Character 3:1: 4:0). The number of spines and their condition are variable: they are numerous and in contact with each other in *Stimulopalpus* (Fig. 5A); they are 5–10 in number and closely approximated in Troctopsocidae Gen. (Troctopsocidae) (Fig. 5B), *Selenopsocus* (Troctopsocidae) (Fig. 6C) and *Manicapsocus* (Electrentomidae) (Fig. 6E); and there are five well-separated spines in *Musapsocus* (Musapsocidae) (Fig. 5D). The spines are apically fringed (Fig. 6A–C, E) except for *Musapsocus* with simple spines (Fig. 6D).

Morphology of the CuP-tips (Fig. 6)

The ribs on the CuP-tip of troctomorphan species are arranged diagonally or vertically against the CuP (Character 8:1) and are thinner than those on the basal CuP vein (Fig. 6A–E). In particular, the ribs on the CuP-tips of *Musapsocus*, *Stimulopalpus, Selenopsocus* and *Manicapsocus* are highly modified; much smaller ribs are arranged densely and vertically in multiple rows (Character 9:1; Fig. 6A, C–E),

although the ribs on the CuP-tips of Troctopsocidae Gen. are not reduced in size and are arranged in a row (Character 9:0) (Fig. 6B).

Morphology of the retainer (Fig. 5)

The retainer is inwardly rolled (Character 10:1) and uniformly ornamented with scale-like studs (Characters 14:0; 15:0). However, the retainers of some troctomophan taxa are more modified. *Musapsocus* has a slightly broadened retainer (Character 12:1), and the studs are more densely arranged on the counterpart of the retinaculum (Fig. 5D). The retainer of *Selenopsocus* is also swollen (Character 12:1; Fig. 5C). *Stimulopalpus* has a wide swelling (Character 12:1) with a narrow dent (Character 13:1) (Fig. 5A). The retainer of *Manicapsocus* is also swollen (Character 12:1), and the retainer is fully expanded and rolled inwardly (Character 10:1) (Fig. 5E). The retainer of Troctopsocidae Gen. is only slightly bent (Character 11:1) (Fig. 5B) and lacks a swelling (Character 12:0).

Psocomorpha

Venation and the rib-like structure (Fig. 7)

The CuP and A1 veins are joined distally, consistently forming the nodulus. The CuP vein has well developed ribs, but ribs are not present on the other veins.

Morphology of the retinaculum (Fig. 8)

The morphology of the retinaculum is quite stable throughout the suborder; it consists of completely fused curled spines (Character 3:1; 4:1). Judging from the numbers and condition of the slits, the retinaculum appears to be composed of many twisted spines in most psocomorphans. In *Archipsocus* (Archipsocidae), the retinaculum is simplified and apically pointed, and it appears to be composed of three spines (Fig. 8A). The retinacular spines are not fringed in the Psocomorpha in general, but the retinacular spines of *Matsumuraiella* (Dasydemellidae) (Fig. 8B), *Amphipsocus* (Amphipsocidae) (Fig. 8D), *Valenzuela* (Caeciliusidae) (Fig. 8E), *Aaroniella* (Philotarsidae) (Fig. 8I), *Goja* (Epipsocidae) (Fig. 8M) and *Psilopsocus* (Psilopsocidae) (Fig. 8O) have apparent to obscure apical fringes.

Morphology of the CuP-tips (Fig. 8)

In *Archipsocus*, the CuP-tip becomes obscure with only a reduced rib (Fig. 8A). In the other infraorders, the morphology of the CuP-tip is stable. The ribs are arranged diagonally (Character 8:1), and the anterior ribs are continuous with the retinaculum (Character 7:1) (cf. Fig. 8B). The CuP-tip of *Calopsocus* (Calopsocidae) (Fig. 8K) lacks the rib (Character 9:2), making the surface of the CuP-tip smooth. The ribs of *Heterocaecilius* (Pseudocaeciliidae) are also reduced and are only

represented by some diagonal slits (Fig. 8L).

Morphology of the retainer (Fig. 7)

The retainer is generally bent and rolled inwardly (Characters 10:1, 11:1). Further deformation of its shape also occurs. In *Archipsocus* (Fig. 7A), the spiny area is restricted to a position in front of the retinaculum, and the other areas lack any ornamentation (Characters 14:2, 15:2). In *Valenzuela* (Caeciliusidae) (Fig. 7E), *Peripsocus* (Peripsocidae) (Fig. 7F), *Aaroniella* (Philotarsidae) (Fig. 7I), *Trichopsocus* (Trichopsocidae) (Fig. 7J) and *Calopsocus* (Calopsocidae) (Fig. 7K), the retainer has a swelling (Character 12:1), which is particularly prominent in *Calopsocus* and *Heterocaecilius* (Character 12:2).

The retainer surface is generally ornamented with fine scale-like studs. However, the retainer decoration of some species (*Valenzuela* (Fig. 7E), *Aaroniella* (Fig. 7I), *Trichopsocus* (Fig. 7J), *Calopsocus* (Fig. 7K) and *Heterocaecilius* (Fig. 7L)) is modified to fine spines (Characters 14:1, 15:1). The shapes of the surface studs of *Amphipsocus* (Amphipsocidae) (Fig. 7D) and *Matsumuraiella* (Dasydemellidae) (Fig. 7B) differ significantly between the proximal and distal regions with the retinaculum as the boundary; the proximal surface is covered with scale-like studs (Character 14:0), but the distal surface is arranged with fine spines (Character 15:0). *Goja* (Epipsocidae) (Fig. 7M) has scale-like

studs only on the proximal surface, and the studs disappear distally (Character 15:2).

Outgroups (Fig. 10)

The wing coupling apparatuses are found consistently in the outgroups (Hemiptera and Thysanoptera), but their conditions are completely different from those of the psocopterans. Aphids (Hemiptera) possess hamuli (= hooked hairs) along the costal margin of the hindwing (Ni et al., 2002). The coupling apparatus of thrips (Thysanoptera) consists of the marginal setae of the fore- and hindwings (Ellington, 1980). Their vein surfaces are decorated occasionally similar to those of Psocoptera (Fig. 10A, C). *Cinara* (Aphididae: Hemiptera) possesses ribs on all of the veins (Character 1:1) (Fig. 10B). The veins of *Aeolothrips* (Aeolothripidae: Thysanoptera) are covered with embossed tiles, each bearing a microtrichium (Fig. 10D) (Character 1:0). In the outgroups, the nodulus is not formed.

Character coding and phylogenetic reconstruction

Based on the observations, 16 characters that may be relevant to psocid phylogeny were selected and coded from the wing coupling structure (Table 2). Only qualitative or discontinuous quantitative characters were coded, although some continuous characters were also mentioned in the above morphological descriptions. The result of the

parsimonious reconstruction of these characters is shown in Fig. 11. The character indices are as follows: Consistency Index = 0.41; Retention Index = 0.65.

Character 1. Decoration of CuP: tile pattern with microtrichia (0); rib-like structure (1). State 0 was only observed in *Aeolothrips* (Thysanoptera) (Fig. 10C, D). State 1 was observed in *Cinara* sp. (Hemiptera) (Fig. 10A, B) and all Psocoptera (Figs. 3A–E; 5A–E; 7A–P) except for the veinless *Embidopsocus* (Liposcelididae) (Fig. 9A).

Character 2. Venation. Present (0); reduced (1). Almost all examined taxa possessed venation (State 0), but the venation is reduced in *Embidopsocus* (Liposcelididae: Troctomorpha) (Fig. 9A), which almost entirely lacks veins (state 1).

Character 3. Retinaculum on CuP. Absent (0); present (1). This is identified as an autapomorphy of Psocodea (state 1), but its secondary absence was detected in *Embidopsocus* and *Tapinella* (state 0).

Character 4. Arrangement of retinacular spines. Clearly, separated from each other (0); fused with each other (1). State 1 was identified as an autapomorphy of Psocomorpha (Fig. 7A–P) (State 1).

Character 5. Tip of the retinacular spines. Not divided (0); fringed (1). State 1 was observed in some taxa of all three suborders (Fig. 6B–E) and was identified as a highly homoplasious condition.

Character 6. Retinacular spines. Standing (0); laying (1). State 1 was only observed in *Neotrogla* (Prionoglarididae) (Fig. 4B).

Character 7. Retinaculum and ribs on CuP-tip. Separated (0); anterior rib merged into the retinaculum (1). State 1 was identified as an autapomorphy of Psocomorpha (Fig. 8A–P).

Character 8. Angle of the ribs against the CuP-tip. Transversal (0); diagonal to vertical (1). State 1 was identified as a synapomorphy of Troctomorpha and Psocomorpha.

Character 9. Number of rows of ribs on CuP-tip. 1 (0); 2 or more (1); absent (2). State 1 was observed in almost all troctomorpha except for Troctopsocidae Gen. (Fig. 6A, B, D, E). The CuP-tip of *Calopsocus* completely lacks ribs, and this was coded as state 2.

Character 10. Retainer. No inward rolling (0); rolling inwardly (1). State 1 was detected in all Psocoptera (Fig. 3A–E; 5A–E; 7A–P) except for the species lacking the wing coupling structure (*Tapinella* and *Embidopsocus*). Although the outgroups lack the retainer, state 0 was adopted due to it having a non-rolling forewing hind margin (Figs. 9A, B; 10A, C)

Character 11. Posterior margin of the retainer. Not bent (0); bent (1). Almost all examined taxa have a bent retainer (State 1), but the retainer of *Stimulopalpus* (Amphientomidae), *Tapinella* (Pachytroctidae), *Embidopsocus* (Liposcelididae), *Heterocaecilius* (Pseudocaeciliidae), *Hemipsocus* (Hemipsocidae), and *Psilopsocus* (Psilopsocidae) is not bent (Figs. 5B; 7L, N, O; 9A, B) (State 0).

Character 12. Retainer. No swelling (0); with swelling (1); strongly swelling and forming a protrusion (2). State 1 was observed in several scattered taxa (Figs. 5A, B, D; 7E–G, I, J, M, O), and *Heterocaecilius* (Pseudocaeciliidae) and *Calopsocus* (Calopsocidae) have a huge protrusion on the retainer (State 2) (Fig. 7K, L).

Character 13. Surface of the retainer swelling. No dent (0); with dent (1). State 1 was only observed in *Stimulopalpus* (Amphientomidae) (Fig. 5B).

Character 14. Surface of the proximal region of the retainer. Covered with scale-like studs (0); with trichomes (1); bare (2). The proximal region of the retainer surface of *Cinara* sp. and almost all psocopterans is covered with tiny scale-like studs (State 0). The surface of several psocopteran and thysanopteran taxa is covered by fine trichomes (Figs. 7E, I–L). The proximal retainer surface of *Archipsocus* sp. is bare (Fig. 7A) (State 2).

Character 15. The surface of the distal region of the retainer. Covered with scale-like studs (0); with trichomes (1); bare (2). The distal retainer surface of *Cinara* sp. and almost all psocopterans is also covered with tiny scale-like studs (State 0). The distal surface ornamentations of Thysanoptera and psocopteran taxa are trichomes (Fig. 7 B, D, E, I–L) (State 1). This region is bare in *Echmepteryx* (Lepidopsocidae), *Archipsocus* (Archipsocidae) and *Goja* (Epipsocidae) (Figs. 3E; 7A, M) (State 2).

DISCUSSION

Origin and homology

The psocopteran wing coupling system is composed of three functional units: two on the forewing— the retinaculum and retainer (Fig. 2B)— and the costal margin of the hindwing, in which the retinaculum and retainer engage the anterior margin of the hindwing during flight.

SEM observations clearly suggest that the retinaculum is composed of highly modified rib-like structures. Their homology is most clearly indicated in *Prionoglaris* (Trogiomorpha: Prionoglarididae; Fig. 3A), in which the retinacular spines and normal ribs differ only by the degree to which their apexes are extended.

Wing veins in other insects are often arrayed with rows of microtrichia (Fig. 10), and the microtrichia are probably homologous with the ribs. The rib-like structures are thin and semi-circular projections that give the CuP vein a rasp-like appearance. Similar rib-like structures occur in *Cinara* (Hemiptera: Aphididae) (Fig. 10B) but are not part of a wing-coupling system. Therefore, the presence of the retinaculum is apparently an autapomorphic condition for Psocodea.

The retainer is formed by various but relatively simple modifications of the cuticle on the surface of the posterior wing margin. The retainers in all specimens examined curved inward to some degree (Fig. 2) with additional bends and/or protrusions in some species of Troctomorpha and Psocomorpha.

We conclude that the psocopteran wing coupling system is unique. The morphology of the components is distinct from those of outgroup taxa, although Lawson and Chu (1974) suggested the homology of the structure between Psocoptera and Hemiptera. The wing coupling system in Thysanoptera is formed by setae located on the fore- and hindwing margins (Ellington, 1980). In Hemiptera: Sternorrhyncha it is composed of 'hamuli-like' projections on the hindwing margin (Ni et al., 2002), and in Hemiptera: Auchenorrhyncha the coupling system is composed of grooves on the fore- and hindwing margins (D'Urso and Ippolito, 1994). The wing-coupling system of some Heteroptera is morphologically and functionally similar to that of Psocoptera (Bohne and Schneider, 1979; Stocks, 2008), although the forewing components are on the A vein.

Phylogenetic significance

The retinacular spines are clearly separated in Trogiomorpha and Troctomorpha, although they are more closely set in the latter (cf. Fig. 5E) and are fused in Psocomorpha (cf. Fig. 7P). Since outgroup taxa lack this structure, there is no basis on which to assess the polarity of the transformation series. However, homology of the retinacular spines and the ribs on the CuP vein permit estimation of character polarity; we might for example consider distinctly separated retinacular spines as a plesiomorphy. The surface structure of the CuP-tip is identical to the that of the ribs on the

basal CuP vein in the Trogiomorpha (cf. Fig. 3A) and is also considered a plesiomorphy with gradual modification throughout Troctomorpha and Psocomorpha taxa. The troctomorphan CuP-tip has multiple rows of diagonally to vertically arranged ribs (cf. Fig. 6A), but the ribs are clearly separated from the retinaculum, whereas the psocomorphan CuP-tip is arranged diagonally (cf. Fig. 7P) with anterior ribs integrated into the retinaculum (cf. Fig. 2B).

The wing coupling apparatus in Trogiomorpha and Troctomorpha is less modified. However, the multiple rows of ribs on the CuP-tip (Character 9:1), which have not been reported previously, is an autapomorphy supporting the monophyly of Troctomorpha. Troctopsocidae Gen. (Fig. 5B) has a single row of diagonal ribs, as observed in Trogiomorpha and Psocomorpha (Character 9:0), but this trait is a reversal in the most parsimonious reconstruction (Fig. 11). However, this condition may be plesiomorphic, since the higher-level relationships among troctomorphan families are poorly understood (Yoshizawa and Johnson, 2014).

A close relationship between Troctomorpha and Psocomorpha is supported by molecular data (Yoshizawa and Johnson, 2014), but there is little support based on morphology. The ribs arranged diagonally to vertically (Character 8:1) was identified here as a synapomorphy supporting a close relationship. Based on light microscopy, Mockford (1967) suggested that a retinaculum composed of truncated spines fused at their bases is a potential synapomorphy of Troctomorpha and Psocomorpha. However, the

SEM images reveal more detail, and we could not discern such fusion in Troctomorpha. The following character states were recovered as autapomorphies of Psocomorpha: retinacular spines fused (Character 4:1) (Yoshizawa, 2002, 2005) and anterior ribs on the CuP-tip merged into the retinaculum (Character 7:1) (Fig. 11).

The retainer is less variable throughout Psocoptera. The posterior forewing margin covered by scale-like studs and curved inward (Character 10:1) is considered an autapomorphy of Psocoptera, and its absence in Nanopsocetae (Pachytroctidae and Liposcelididae: Fig. 9A, B) is a secondary loss. A bent retainer (Character 11:1) may be an autapomorphy of the order, but several taxa of Troctomorpha and Psocomorpha (Figs. 3A, 7N, O, 9A, B) indicate secondary reversal. The shapes of the surface studs on the posterior wing margin (Characters 14:0; 15:0) are highly variable. Trichome-like studs were observed only in Caeciliusetae and Philotarsetae (Characters 14:1; 15:1) (Fig. 7B, D, E, I–L), but the distant phylogenetic relationship of the families suggests independent origins (Fig. 11). Trichome-like studs occur in *Matsumuraiella* and *Amphipsocus* (Caeciliusetae) but are restricted to the distal region with scale-like studs proximally (Character 14:0). The retainer of *Archipsocus* is almost completely devoid of surface decorations (Fig. 7A), and those of *Echmepteryx* (Lepidopsocidae) and *Goja* (Epipsocidae) diminish gradually distally from the junction of the CuP (Character 14:2; 15:2) (Fig. 11). Modifications of the bent retainer, retinaculum and CuP-tip occurred independently in different taxa and overall appear to be highly

homoplasious. If variation in these character systems contains a phylogenetic signal, a much denser taxon sampling is needed.

The modifications observed in the retainer displayed by some taxa may be phylogenetically informative at a lower level of phylogeny. For example, the strongly developed, thumb-like protrusion in *Calopsocus* (Calopsocidae) (Figs. 7K, 8K, L) and *Heterocaecilius* (Pseudocaeciliidae) (Figs. 7L, 8L) (Character 12:2) may be a synapomorphy that supports a close relationship; this is supported by other morphological (Yoshizawa, 2002) and molecular (Yoshizawa and Johnson, 2014) data.

Among Psocoptera, there are two different cases of reduction of the wing coupling apparatus. *Neotrogla* (Prionoglarididae) has a simplified wing coupling structure in which the retinaculum consists of a few recumbent spines (cf. Fig. 4B), and the hindwings are largely diminished. In most analyses, taxa of Prionoglarididae are considered to be the most plesiotypic overall, and the simplified retinaculum may also represent a plesiomorphy. However, the most parsimonious reconstruction (MPR) of the retinacular character (Character 6) implies that the simplified retinaculum of *Neotrogla* is an autapomorphy (Fig. 11). *Neotrogla* species inhabit caves and exhibit many specialized behaviors (Yoshizawa et al., 2014), and the simplified retinaculum is probably associated with diminution of the hindwing (Lienhard and Ferreira, 2013).

Liposcelididae and Pachytroctidae also have simplified wings, and they completely lack a wing coupling apparatus. However, their hindwings

keep their size, unlike *Neotrogla*. Based on phylogenetic analysis and MPR, loss of wing coupling structures and the nodulus in Liposcelididae (Fig. 9A) and Pachytroctidae (Fig. 9B) (Troctomorpha: Nanopsocetae) is considered as a secondary loss (Characters 10:0: 11:0) (Fig. 11). The insects can flap the fore- and hindwings independently during flight, and the reduction of their wing coupling apparatus may be involved with the different ecology of *Neotrogla* in its functional aspect.

In summary, the common ancestor of Psocodea gained a unique wing coupling apparatus composed of the retainer, CuP-tip and a retinaculum at the end of the CuP vein. These structures are consistently retained throughout the Psocodea, and some modifications reflect their deep phylogenetic relationships, including the first potential autapomorphy of Troctomorpha (Character 9:1) and synapomorphy of Troctomorpha and Psocomorpha (Character 8:1). Independent origins of the wing coupling apparatus among the paraneopteran orders were suggested by the morphological analysis. The factors driving the independent evolution of the wing coupling apparatus are still unknown. To answer this question, comprehensive observations of the morphology and flight behavior must be conducted throughout the paraneopteran orders.

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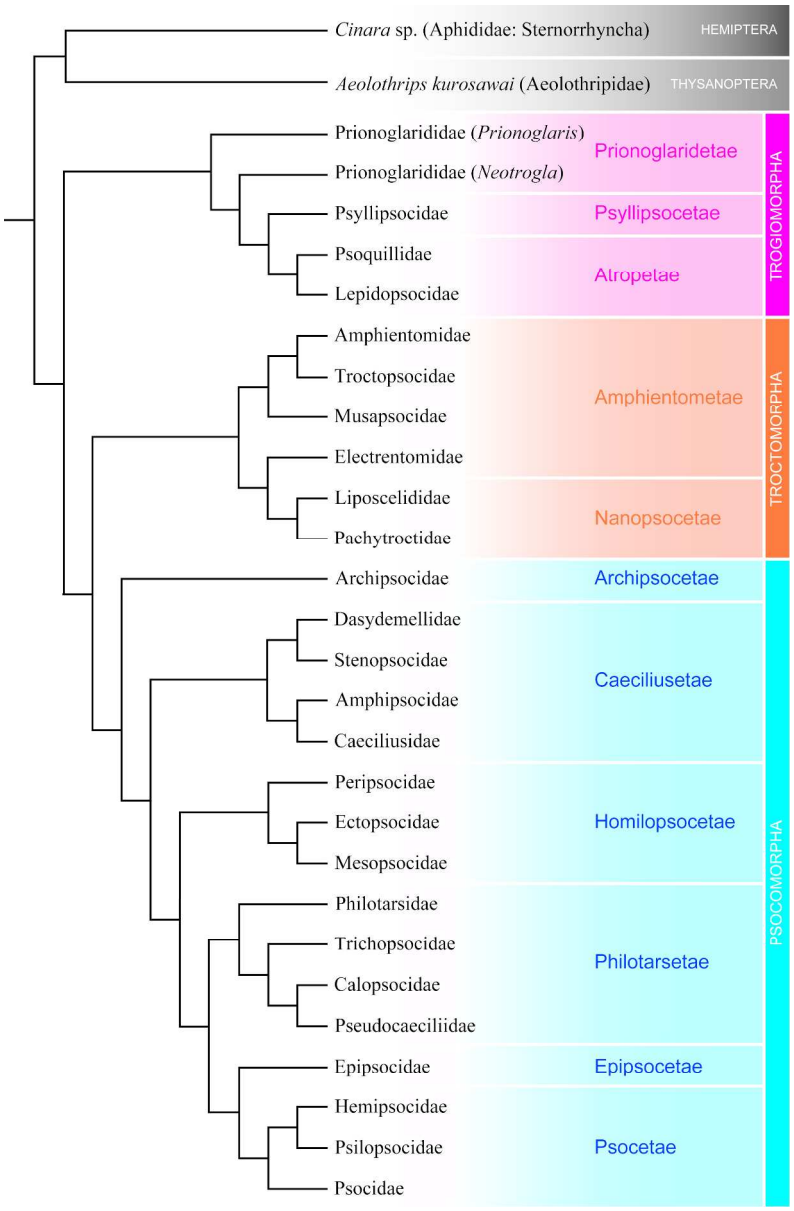

Fig. 1. Phylogeny of 'Psocoptera' and relatives adopted in this study. This tree was constructed based on Yoshizawa & Johnson (2010, 2014) (for 'Psocoptera') and Friedmann et al. (2014) and Yoshizawa & Lienhard (2016) (for the relationship with the outgroups).

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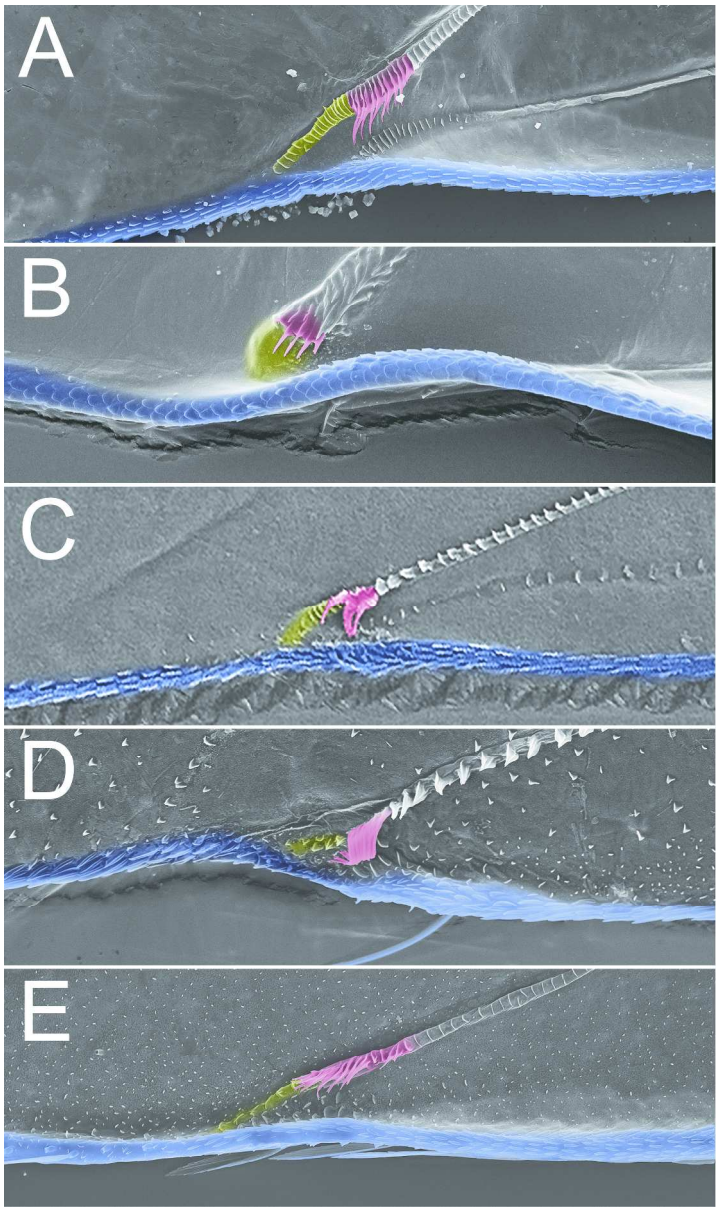

Fig. 3. In-flight wing coupling structures in Trogiomorpha, ventral view. A. Prionoglaris stygia (Prionoglarididae). B. Neotrogla curvata (Prionoglarididae). C. Psyllipsocus yucatan (Psyllipsocidae). D. Psoquilla sp. (Psoquillidae). E. Echmepteryx hageni (Lepidopsocidae).

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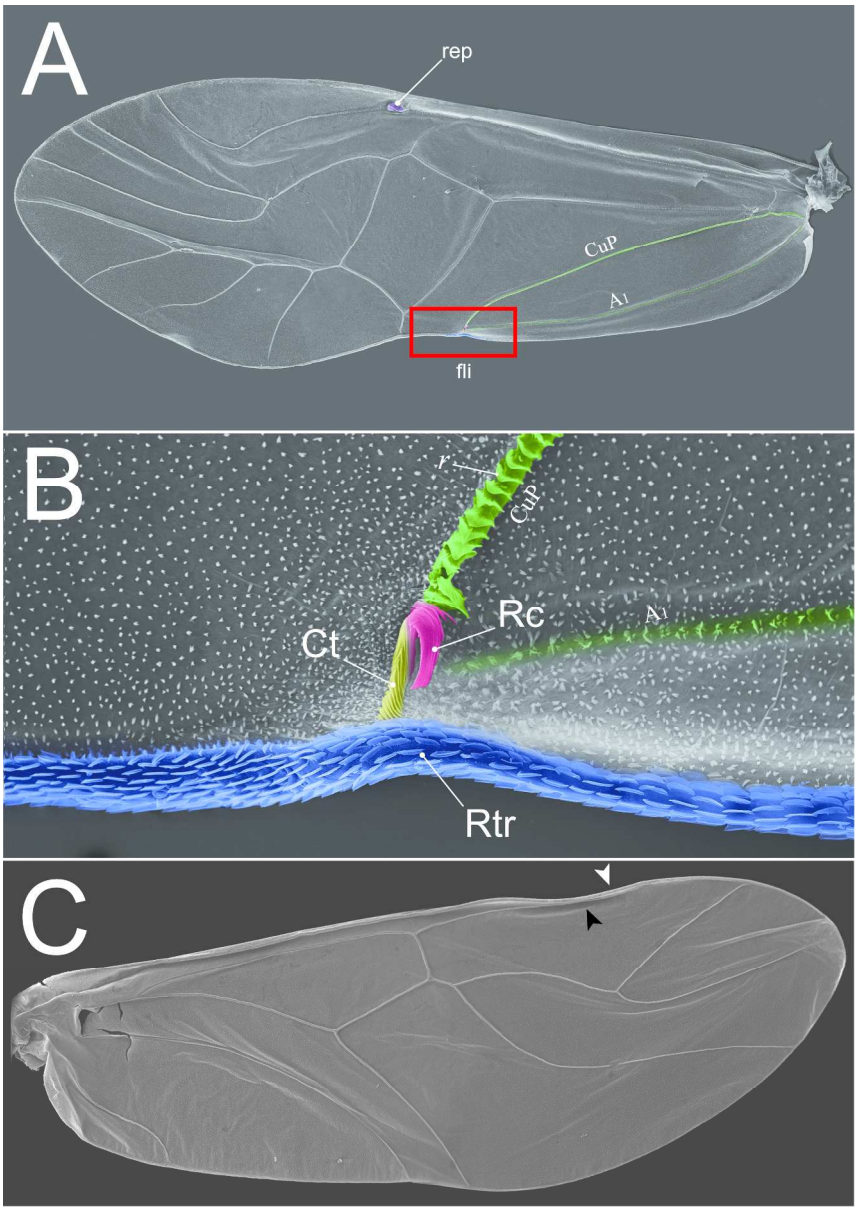

Fig. 2. Right fore- and hindwing of Metylophorus sp. (Psocidae). A. Ventral view of the forewing, with names of relevant veins. Red rectangle indicates the in-flight wing coupling region (fli). Abbreviations: rep, repose-coupling apparatus; fli, in-flight coupling apparatus. B. Enlarged in-flight wing coupling structure. Abbreviations: Rc, retinaculum; Ct, CuP tip; Rtr, retainer; r, rib-like structure; A1, First Anal vein; CuP, Posterior Cubital vein. C. Dorsal view of the hindwing. White and black arrows indicate engagement point with repose-coupling appatarus and in-flight coupling apparatus, respectively.

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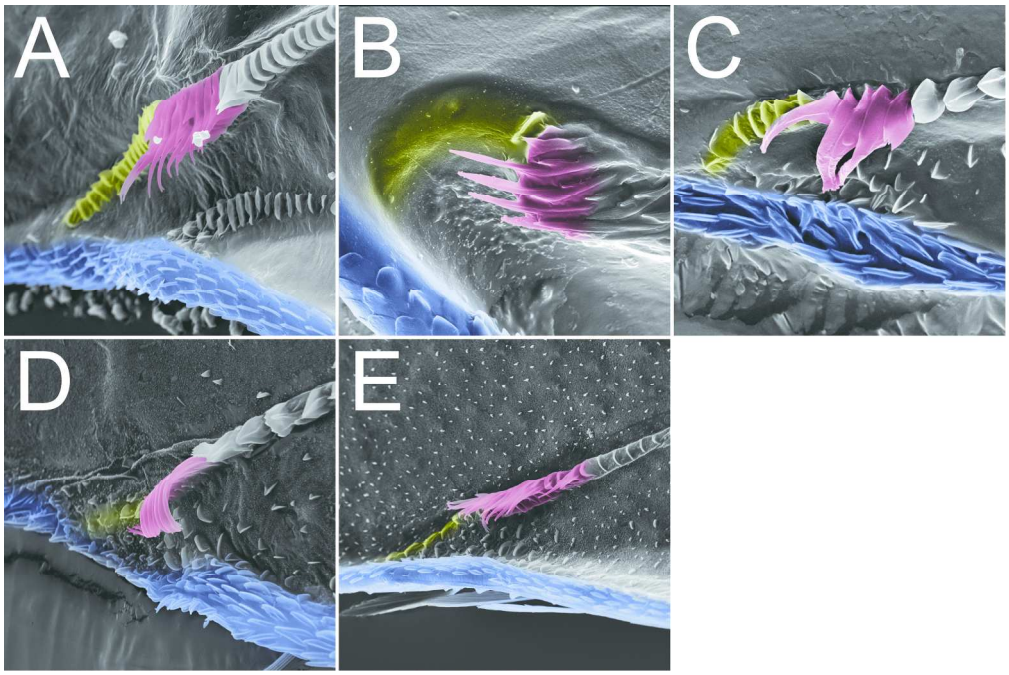

Fig. 4. In-flight wing coupling structures in Trogiomorpha, ventrolateral view. A. Prionoglaris stygia (Prionoglarididae). B. Neotrogla curvata (Prionoglarididae). C. Psyllipsocus yucatan (Psyllipsocidae). D. Psoquilla sp. (Psoquillidae). E. Echmepteryx hageni (Lepidopsocidae).

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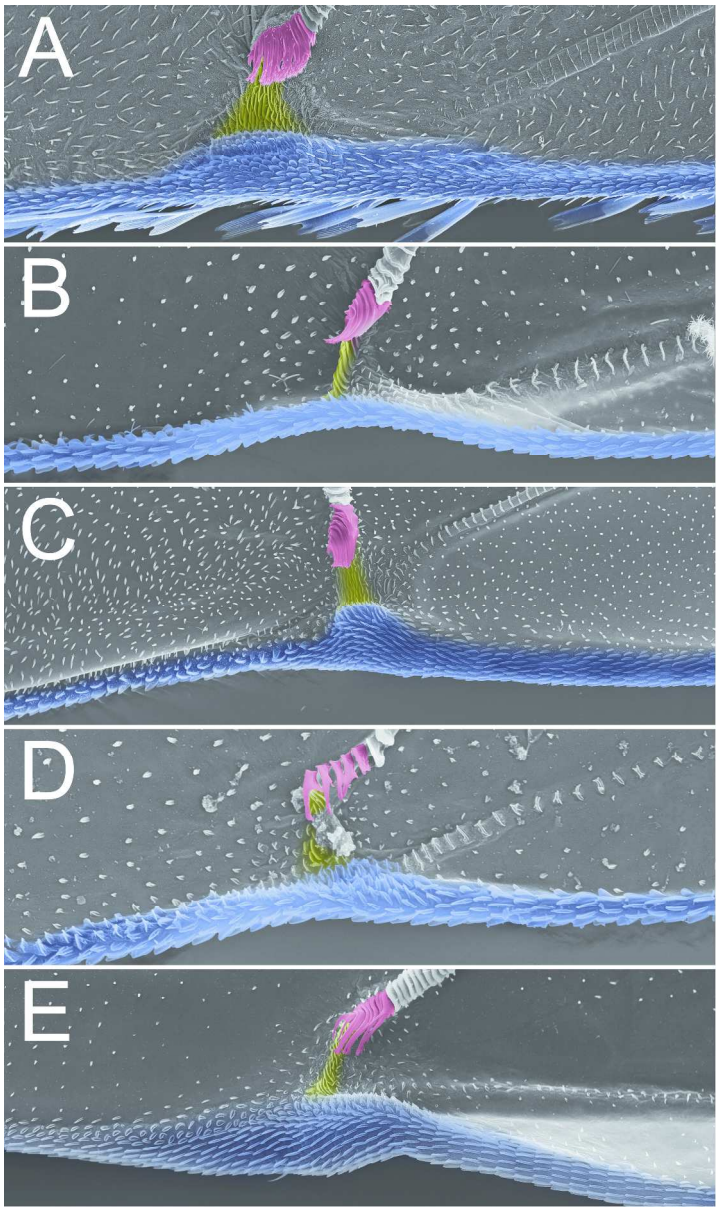

Fig. 5. In-flight wing coupling structures in Troctomorpha, ventral view. A. Stimulopalpus japonicus (Amphientomidae). B. Gen. sp. (Troctopsocidae). C. Selenopsocus sp. (Troctopsocidae). D. Musapsocus sp. (Musapsocidae). E. Manicapsocus alettae (Electrentomidae).

211x357mm (300 x 300 DPI)

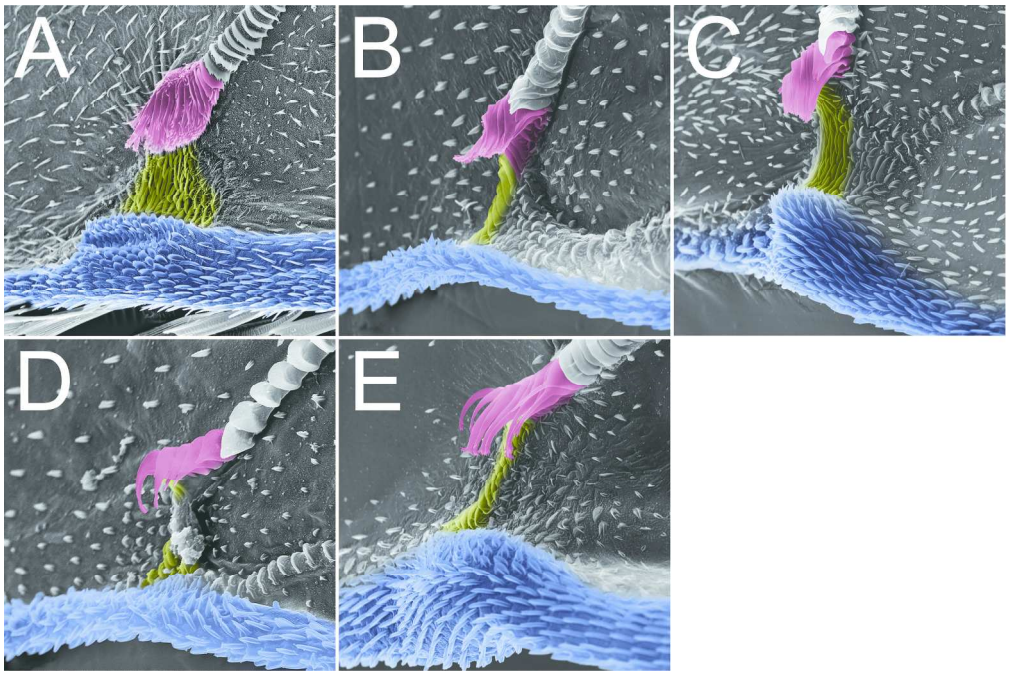

Fig. 6. In-flight wing coupling structures in Troctomorpha, ventrolateral view. A. Stimulopalpus japonicus (Amphientomidae). B. Gen. sp. (Troctopsocidae). C. Selenopsocus sp. (Troctopsocidae). D. Musapsocus sp. (Musapsocidae). E. Manicapsocus alettae (Electrentomidae).

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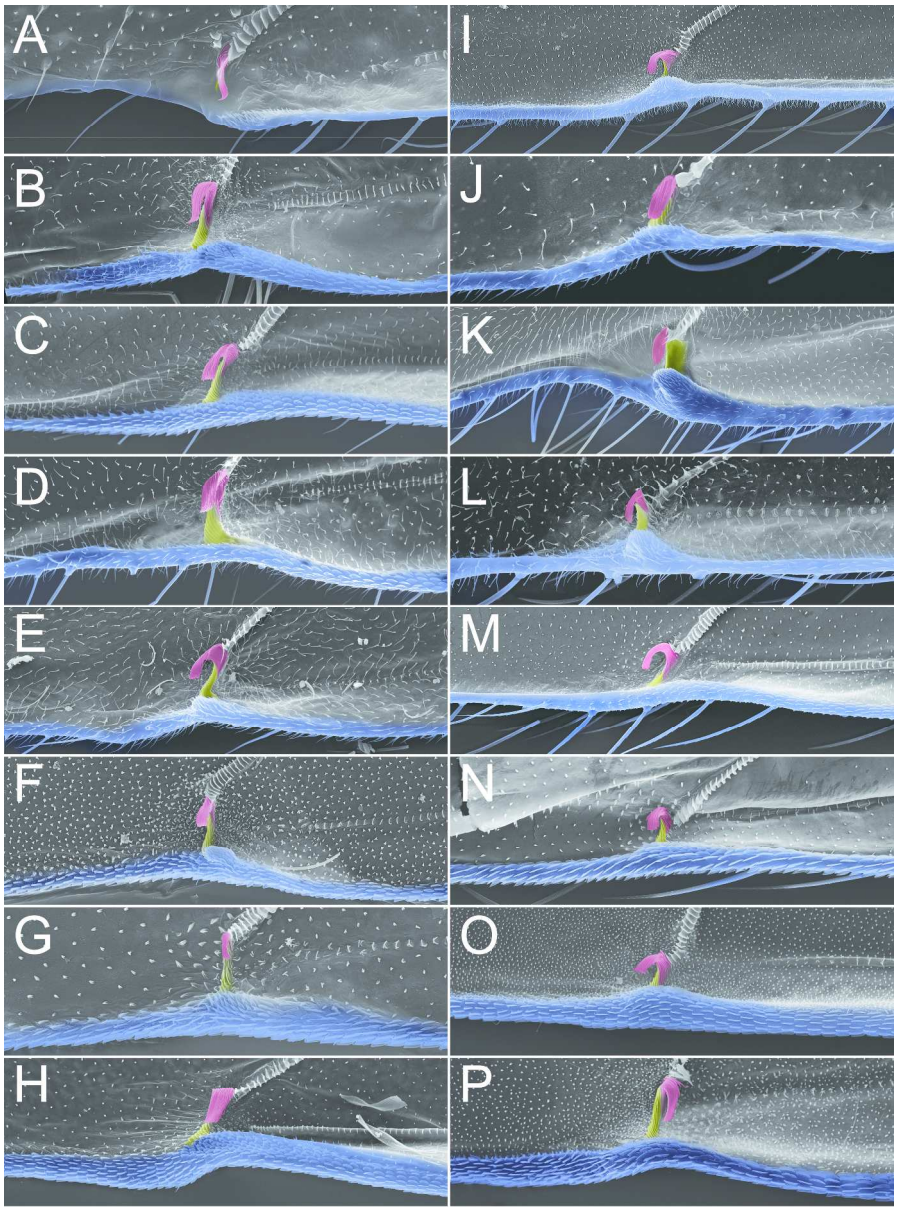

Fig. 7. In-flight wing coupling structures in Psocomorpha, ventral view. A. Archipsocus sp. (Archipsocidae). B. Matsumuraiella radiopicta (Dasydemellidae). C. Stenopsocus nigricellus (Stenopsocidae). D. Amphipsocus japonicus (Amphipsocidae). E. Valenzuela flavidus (Caeciliusidae). F. Peripsocus quercicola (Peripsocidae). G. Ectopsocus briggsi (Ectopsocidae). H. Idatenopsocus orientalis (Mesopsocidae). I. Aaroniella badonneli (Philotarsidae). J.Trichopsocus clarus (Trichopsocidae). K. Calopsocus furcatus (Calopsocidae syn: Pseudocaeciliidae). L. Heterocaecilius solocipennis (Pseudocaeciliidae). M. Goja sp. (Epipsocidae). N. Hemipsocus chloroticus (Hemipsocidae). O. Psilopsocus malayensis (Psilopsocidae). P. Metylophorus sp. (Psocidae).

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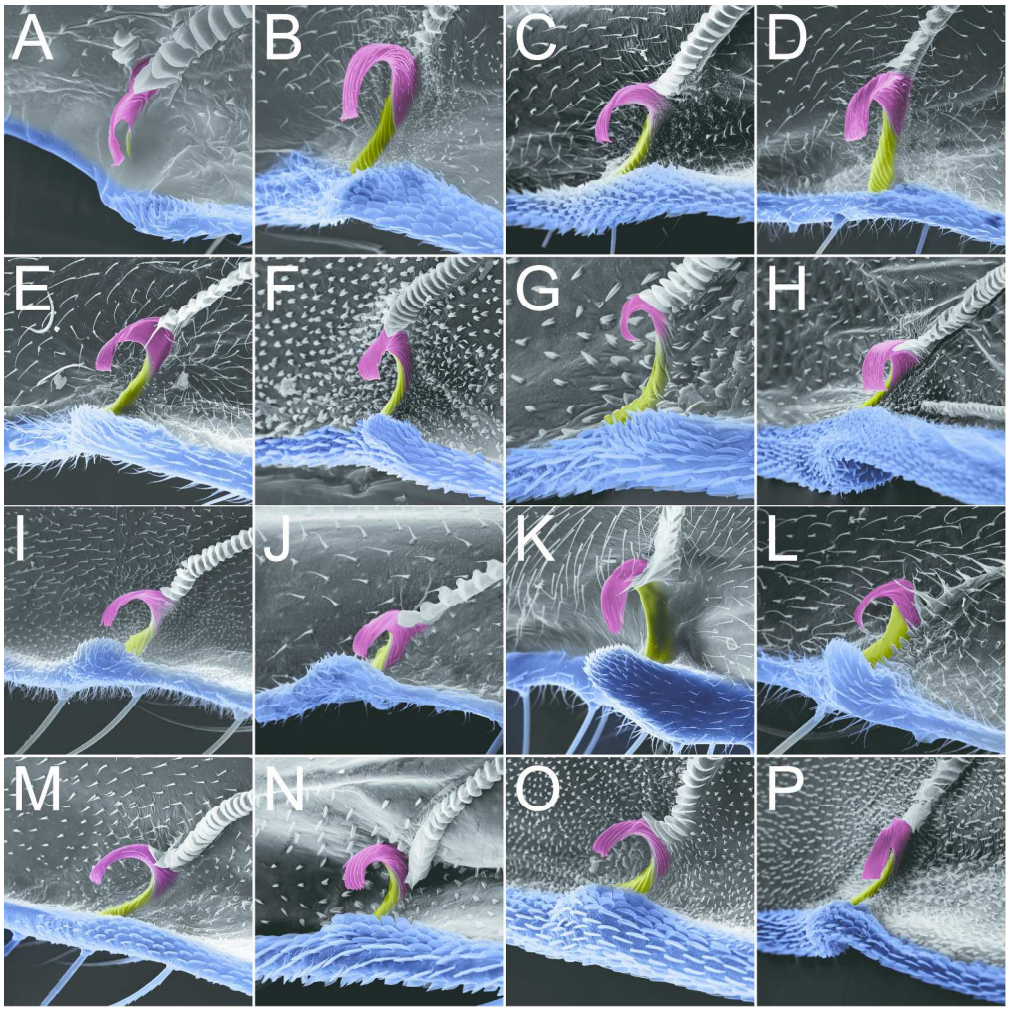


Fig. 8. In-flight wing coupling structures in Psocomorpha, ventrolateral view. A. Archipsocus sp. (Archipsocidae). B. Matsumuraiella radiopicta (Dasydemellidae). C. Stenopsocus nigricellus (Stenopsocidae). D. Amphipsocus japonicus (Amphipsocidae). E. Valenzuela flavidus (Caeciliusidae). F. Peripsocus quercicola (Peripsocidae). G. Ectopsocus briggsi (Ectopsocidae). H. Idatenopsocus orientalis (Mesopsocidae). I. Aaroniella badonneli (Philotarsidae). J.Trichopsocus clarus (Trichopsocidae). K. Calopsocus furcatus (Calopsocidae syn: Pseudocaeciliidae). L. Heterocaecilius solocipennis (Pseudocaeciliidae). M. Goja sp. (Epipsocidae). N. Hemipsocus chloroticus (Hemipsocidae). O. Psilopsocus malayensis (Psilopsocidae). P. Metylophorus sp. (Psocidae).

282x282mm (300 x 300 DPI)

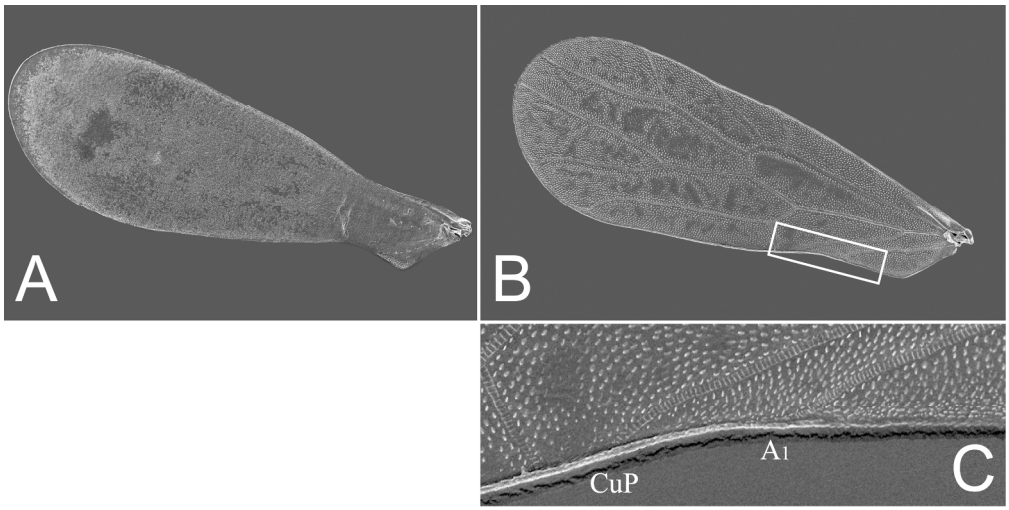


Fig. 9. Forewings of Nanopsocetae species (Troctomorpha) lacking the in-flight wing coupling structure, ventral view. A. Embidopsocus sp. (Liposcelididae). B. Tapinella sp. (Pachytroctidae). C. ditto, enlarged view of the end of the CuP and A1 in B.

223x111mm (300 x 300 DPI)

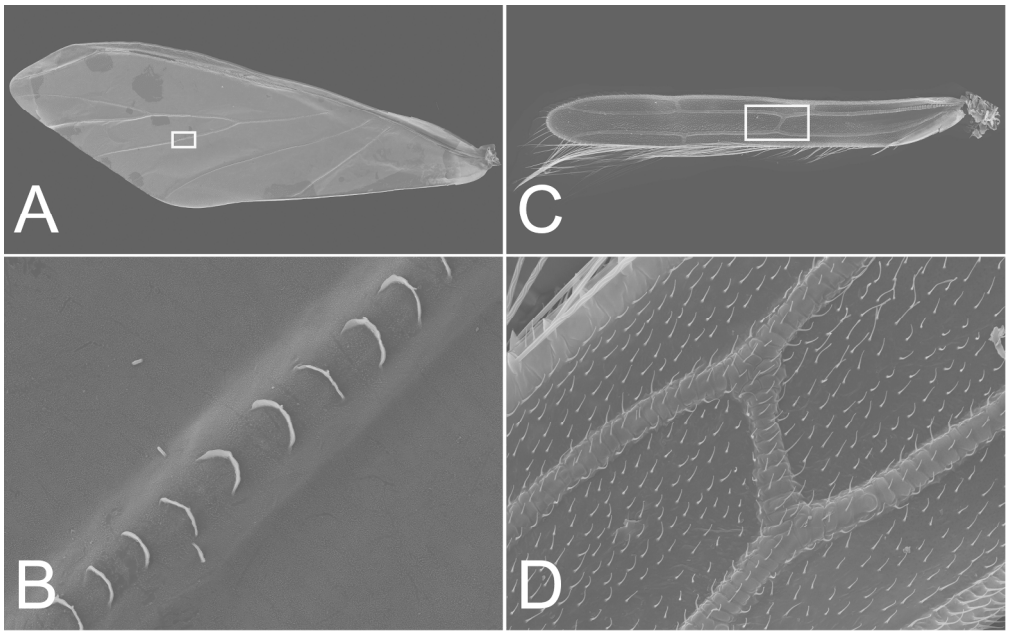


Fig. 10. Right forewing and vein decorations of the outgroups. A. Cinara sp. (Hemiptera: Sternorrhyncha: Aphididae), ventral view. B. ditto, enlarged view of the vein indicated by red rectangle in A. C. Aeolothrips kurosawai (Thysanoptera: Aeolothripidae), ventral view. D. ditto, enlarged view of the vein indicated by red rectangle in C.

211x132mm (300 x 300 DPI)

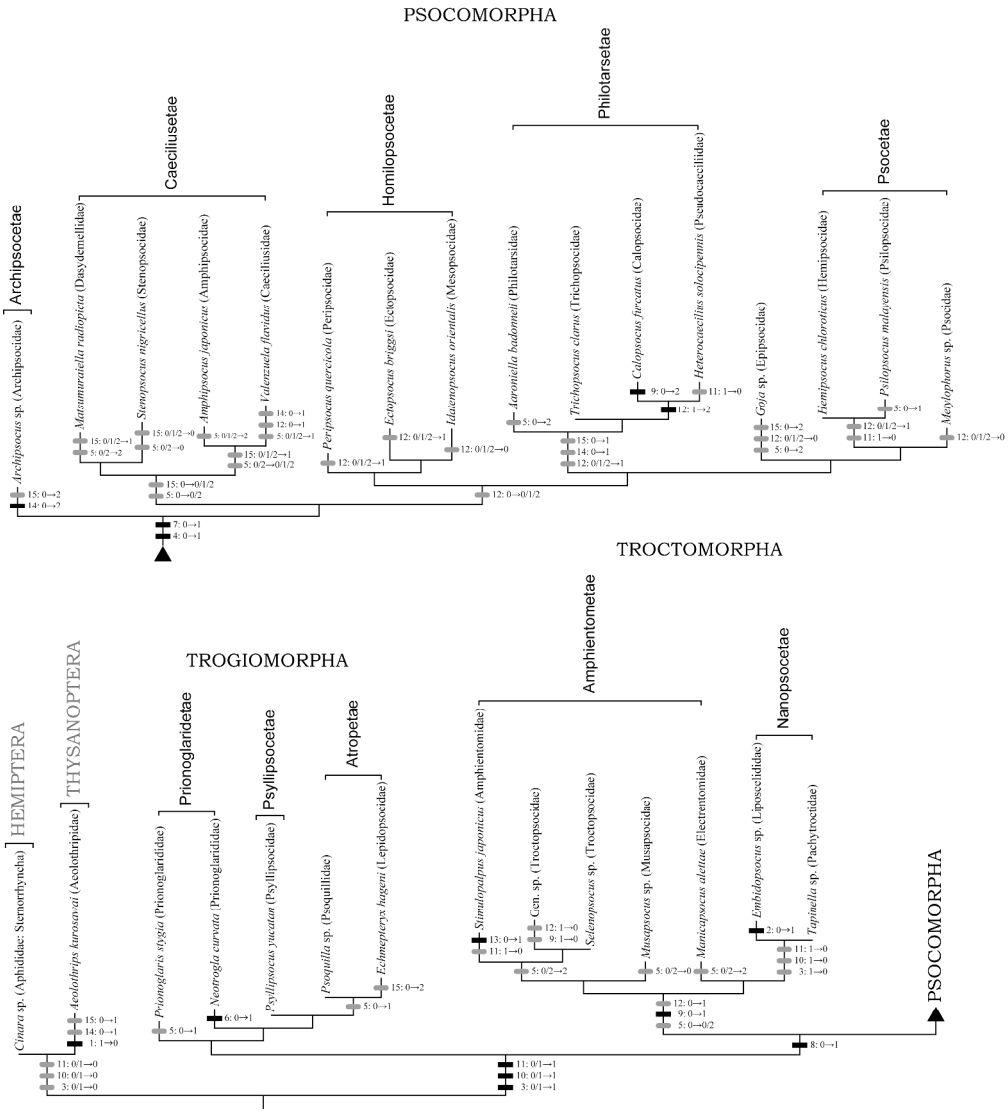


Fig. 11. The parsimonious reconstruction of selected 16 characters. Character and character state changes reconstructed on the branches are indicated by black (non-homoplasious) and gray bars (homoplasious).

446x491mm (300 x 300 DPI)

Table 1. Taxa examined for this study.

ORDER HEMIPTERA

Cinara sp. (Aphididae)

ORDER THYSANOPTERA

Aeolothrips kurosawai Bhatti, 1971 (Aeolothripidae)

ORDER PSOCODEA

SUBORDER TROGIOMORPHA

Prionoglaris stygia Enderlein, 1909 (Prionoglarididae)

Neotrogla curvata Lienhard & Ferreira, 2013 (Prionoglarididae)

Psyllipsocus yucatan Gurney, 1943 (Psyllipsocidae)

Psoquilla sp. (Psoquillidae)

Echmepteryx hageni (Packard, 1870) (Lepidopsocidae)

SUBORDER TROCTOMORPHA

Stimulopalpus japonicus Enderlein, 1906 (Amphientomidae)

Gen. sp. (Troctopsocidae)

Selenopsocus sp. (Troctopsocidae)

Musapsocus sp. (Musapsocidae)

Manicapsocus alettae Smithers, 1966 (Electrentomidae)

Embidopsocus sp. (Liposcelididae)

Tapinella sp. (Pachytroctidae)

SUBORDER PSOCOMORPHA

Archipsocus sp. (Archipsocidae)

Matsumuraiella radiopicta Enderlein, 1906 (Dasydemellidae)

Stenopsocus nigricellus Okamoto, 1907 (Stenopsocidae)

Amphipsocus japonicus (Enderlein, 1906) (Amphipsocidae)

Valenzuela flavidus (Stephens, 1836) (Caeciliusidae)

Peripsocus quercicola Enderlein, 1906 (Peripsocidae)

Ectopsocus briggsi McLachlan, 1899 (Ectopsocidae)

Idatenopsocus orientalis (Vishnyakova, 1986) (Mesopsocidae)

Aaroniella badonneli (Danks, 1950) (Philotarsidae)

Trichopsocus clarus (Banks, 1908) (Trichopsocidae)

Calopsocus furcatus (New, 1978) (Calopsocidae syn: Pseudocaeciliidae)

Heterocaecilius solocipennis (Enderlein, 1907) (Pseudocaeciliidae)

Goja sp. (Epipsocidae)

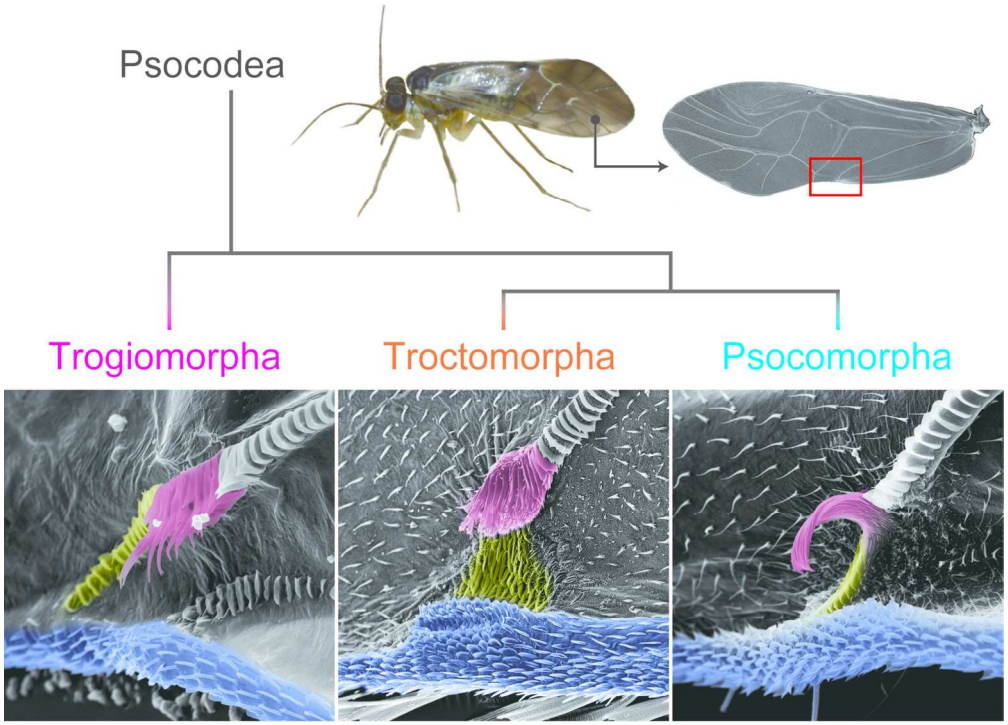
Hemipsocus chloroticus (Hagen, 1958) (Hemipsocidae)

Psilopsocus malayensis New & Lee, 1991 (Psilopsocidae)

Metylophorus sp. (Psocidae)

Table 2. Data matrix used for the parsimonious reconstruction. See text for characters and their states.

					5					10					15
Cinara sp. (Aphididae)	1	0	0	?	?	?	?	0	?	0	0	0	?	0	0
Aeolothrips kurosawai (Aeolothripidae)	0	0	0	?	0	0	0	0	0	0	0	0	?	1	1
Prionoglaris stygia (Prionoglarididae)	1	0	1	0	1	0	0	0	0	1	1	0	?	0	0
Neotrogla curvata (Prionoglarididae)	1	0	1	0	0	1	?	0	0	1	1	0	?	0	0
Psyllipsocus yucatan (Psyllipsocidae)	1	0	1	0	0	0	0	0	0	1	1	0	?	0	0
Psoquilla sp. (Psoquillidae)	1	0	1	0	1	0	?	0	0	1	1	0	?	0	0
Echmepteryx hageni (Lepidopsocidae)	1	0	1	0	1	0	0	0	0	1	1	0	?	0	2
Stimulopalpus japonicus (Amphientomidae)	1	0	1	0	2	0	0	1	1	1	0	1	1	0	0
Gen. sp. (Troctopsocidae)	1	0	1	0	2	0	0	1	0	1	1	0	?	0	0
Selenopsocus sp. (Troctopsocidae)	1	0	1	0	2	0	0	1	1	1	1	1	0	0	0
Musapsocus sp. (Musapsocidae)	1	0	1	0	0	0	0	1	1	1	1	1	?	0	0
Manicapsocus alettae (Electrentomidae)	1	0	1	0	2	0	0	1	1	1	1	1	?	0	0
Embidopsocus sp. (Liposcelididae)	1	1	0	?	?	0	?	?	?	0	0	?	?	?	?
Tapinella sp. (Pachytroctidae)	1	0	0	?	?	0	?	?	?	0	0	?	?	?	?
Archipsocus sp. (Archipsocidae)	1	0	1	1	0	0	1	1	0	1	1	0	0	2	2
Matsumuraiella radiopicta (Dasydemellidae)	1	0	1	1	2	0	1	1	0	1	1	0	?	0	1
Stenopsocus nigricellus (Stenopsocidae)	1	0	1	1	0	0	1	1	0	1	1	0	?	0	0
Amphipsocus japonicus (Amphipsocidae)	1	0	1	1	2	0	1	1	0	1	1	0	?	0	1
Valenzuela flavidus (Caeciliusidae)	1	0	1	1	1	0	1	1	0	1	1	1	0	1	1
Peripsocus quercicola (Peripsocidae)	1	0	1	1	0	0	1	1	0	1	1	1	0	0	0
Ectopsocus briggsi (Ectopsocidae)	1	0	1	1	0	0	1	1	0	1	1	1	?	0	0
Idatenopsocus orientalis (Mesopsocidae)	1	0	1	1	0	0	1	1	0	1	1	0	?	0	0
Aaroniella badonneli (Philotarsidae)	1	0	1	1	2	0	1	1	0	1	1	1	0	1	1
Trichopsocus clarus (Trichopsocidae)	1	0	1	1	0	0	1	1	0	1	1	1	0	1	1
Calopsocus furcatus (Calopsocidae)	1	0	1	1	0	0	1	1	2	1	1	2	0	1	1
Heterocaecilius solocipennis (Pseudocaeciliidae)	1	0	1	1	0	0	1	1	0	1	0	2	0	1	1
Goja sp. (Epipsocidae)	1	0	1	1	2	0	1	1	0	1	1	0	?	0	2
Hemipsocus chloroticus (Hemipsocidae)	1	0	1	1	0	0	1	1	0	1	0	1	0	0	0
Psilopsocus malayensis(Psilopsocidae)	1	0	1	1	1	?	1	1	0	1	0	1	?	0	0
Metylophorus sp. (Psocidae)	1	0	1	1	0	0	1	1	0	1	1	0	?	0	0



Graphical Abstract Image

141x103mm (300 x 300 DPI)

Wing-coupling structures of insects mechanically unite the fore- and hindwings. The structure in different "Psocoptera" (barklice) groups consists of three functional units, termed retinaculum, CuP tip and retainer, which originated in the common ancestor, and are phylogenetically informative at different levels in the order.