Structure and evolution of the stigmapophysis—a unique repose wing-coupling structure in Psocodea

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Short title: Repose wing-coupling structure in Psocodea

Keywords: morphology; evolution; Psocoptera; bark lice; wing fixing

ABSTRACT

The gain of foldable wings is regarded as one of the key innovations enabling the present-day diversity of neopteran insects. Wing folding allows compact housing of the wings and shields the insect body from damage. Wing-fixing systems have evolved in some insects, probably to increase the durability of the shielding function by the wings. Bark lice (Psocodea) are known to possess a unique wing-to-wing repose coupling system, but a detailed morphological and evolutionary study of this system is lacking. In this study, we examined this repose coupling structure by SEM in 32 species including representatives of all three suborders of bark lice (Trogiomorpha, Troctomorpha and Psocomorpha). We concluded that the repose wing-coupling apparatus independently evolved twice within Psocodea. In Trogiomorpha, the apparatus is located on the subcostal vein of the forewing and is composed of elongated rib-like structures. In Troctomorpha and Psocomorpha, in contrast, the repose coupling structure is located on the radius vein of the forewing and is formed by a swollen vein. These morphological and developmental differences in the repose coupling structures also provide phylogenetic information at different systematic levels.

INTRODUCTION

The acquisition of wings is regarded as one of the most crucial events in insect evolution. Wings allow insects to launch into the sky and provide them with more efficient mobility for migration, feeding and escape from predators (Brodsky, 1994). In ancestral pterygote insects (i.e., dragonflies and mayflies), the function of the wings is almost entirely limited to flight. In contrast, neopteran insects can fold their wings over the abdomen: this enables the adaption of new functions for the wings, such as shielding the insect body from damage. Foldable wings also are a prerequisite that neopteran insects can inhabit narrow spaces without losing the ability to fly (Grimaldi & Engel, 2005).

However, simply folded wings are unstable and thus inadequate for defense. To increase the durability of wings, a wide range of mechanisms in the resting position developed in neopteran insects to fix the wings in the resting position (Gorb & Perez Goodwyn, 2003). From a functional point of view, these wing-locking mechanisms can be classified into three coupling types: (1) forewing-forewing, (2) wing-body, and (3) forewing-hindwing (New, 1974; Gorb & Perez Goodwyn, 2003). The first type mechanically fastens forewings to each other and its function is likely to prevent contamination; this type has been reported in Hymenoptera (Gorb, 2001) and Heteroptera (Presswalla & George, 1935). In the second type, the forewings cover the delicate hindwings and the abdomen providing protection against injury; this type has been reported in various insect orders: Hymenoptera (Schrott, 1986), Mecoptera (Hlavac, 1974), Dermaptera (Haas, 1995), Diptera (Rodova, 1968), Coleoptera (Hammond, 1989; Gorb, 1998, 1999), Lepidoptera (Common, 1969) and Hemiptera (Gorb & Perez Goodwyn, 2003; Weirauch & Cassis, 2009). The third type keeps the hindwing fit into the forewing to maintain the wings in the repose position and to conceal the hindwing costal margin. This type of repose coupling system is unique to Psocodea (or generally known as "Psocoptera", which excludes wingless parasitic lice; Badonnel, 1951; New, 1974)

Within “Psocoptera”, two types of wing-coupling systems are known (New, 1974). The first type is an in-flight coupling system, which mechanically unites the fore- and hindwings during flight (Ogawa & Yoshizawa, 2018). The second type is a repose coupling system, which maintains the fore- and hindwings coupled in the resting position. The latter system involves a ventral projection of the forewing, with the hindwing costa as its counterpart (Badonnel, 1951; Ogawa & Yoshizawa, 2018). This projection on the forewing is termed stigmapophysis (used hereafter; Badonnel, 1951), stigmasac (New, 1974), Schloß (Weber, 1936, 1954) or nodus (Yoshizawa, 2005).

The in-flight wing-coupling system of “Psocoptera” has been studied in detail (Lawson & Chu, 1974; New, 1974; Ogawa & Yoshizawa, 2018) and is also used as informative character in phylogenetic analyses (Mockford, 1967; Yoshizawa, 2002; 2005; Ogawa & Yoshizawa, 2018). In contrast, knowledge of the repose coupling system is very restricted. Weber (1936; 1954) briefly described the system along with schematic diagrams. Badonnel (1951) presented detailed drawings of the stigmapophysis of *Stimulopalpus* (Troctomorpha) and *Cerastipsocus* (Psocomorpha), and New (1974) provided the most comprehensive scanning electron microscopy (SEM) study on stigmapophysis to date, including representatives of 20 psocopteran families selected from all three suborders. However, 14 of the 20 families were selected from the suborder Psocomorpha, so the knowledge of this structure in the other two suborders is limited. Furthermore, none of the above authors discussed the evolutionary transformation of the stigmatophysis and its utility as character in phylogenetic analyses..

In this study, we examined the stigmapophysis in a comprehensive taxon sampling of Psocodea using SEM. We evaluated the origin and transformation of stigmapophysis along the phylogenetic hypotheses presented by Yoshizawa & Johnson (2010, 2014), Friedemann et al. (2014) and Yoshizawa & Lienhard (2016).

MATERIALS & METHODS

Taxon selection (Table 1)

We examined the following taxa: Trogiomorpha, five species representing four families; Troctomorpha, seven species representing six families; Psocomorpha, 16 species representing 16 families (Table 1). Vouchers are deposited in the Hokkaido University Insect Collection. We included a species of Calopsocidae (Psocomorpha), recently synonymized with Pseudocaeciliidae (Yoshizawa and Johnson, 2014), because this group is characterized by highly modified, elytra-like wings. *Aeolothrips kurosawai* (Thysanoptera: Aeolothripidae) and *Cinara* sp. (Hemiptera: Aphididae) were selected as outgroup species.

Terminology

The terminology is consistent with that used by Badonnel (1951) and Ogawa and Yoshizawa (2018). First radial vein and subcostal vein are abbreviated to R1 and Sc, respectively. The branched section of the subcostal vein is denoted Sc' (Lienhard, 1998).

Treatment of specimens

Preparation, observation and image processing followed the procedures described in Ogawa and Yoshizawa (2018). Specimens for examination were stored in 80% or 99% ethanol. Forewings and hindwings were removed by forceps and dehydrated in 90%, 95% and 100% ethanol for 1 hour each. Wing cuticle was hardened by soaking with 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. Jeol JSM-5310LV and JSM-6510 scanning electron microscope (Jeol Ltd., Tokyo) were used for SEM examination and the screen images were photographed by Jeol Digi Capture SUP-7707

Version 1.0.11. Olympus SZ61 (Olympus Corp., Tokyo) and Keyence VHX-5000 (Keyence Corp., Osaka) were used for supplementary light microscopy observation and photographing.

Character Coding and Maximum Parsimony Reconstruction

Character coding and phylogenetic analysis was performed as described by Ogawa and Yoshizawa (2018). Character matrix is given in the supplemental information. The data were mapped onto a given phylogenetic tree, which included almost all psocid families. (fig. 2 in Yoshizawa & Johnson, 2014). Pachytroctidae and Liposcelididae were added according to Yoshizawa and Johnson (2010), and the phylogenetic arrangements of the outgroup taxa followed Friedemann et al. (2014) and Yoshizawa and Lienhard (2016). Unsampled families were trimmed from the tree, and a coded character matrix was used for the parsimony analysis using Mesquite version 3.04 (Maddison & Maddison, 2018).

RESULTS

General Morphology

In a reposed bark lice (Fig. 1A), the stigmapophysis supports the anterior margin of hindwing (Fig. 1B). This region of hindwing is slightly bent (Fig. 1D, E) and covered with scary structures, but there is little difference in morphology among the suborders (Fig. 1D, E, 2F, G, 3F, G). A stigmapophysis was observed in almost all species near a pterostigma on the ventral forewing surface (Fig. 1C), either on the R1 or Sc’ vein. The R1 and Sc’ veins are generally decorated by rib-like structures (series of small plate-like structures arranged in equal intervals on the veins), as also observed on the CuP vein (Ogawa & Yoshizawa, 2018) (Fig. 2-4). A stigmapophysis was never observed in the outgroup representatives, although they have rib-like structures on their veins (Ogawa & Yoshizawa, 2018).

Morphological disparity of stigmapophysis

The morphology of the stigmapophysis is significantly different among suborders. In Trogiomorpha, the stigmapophysis is formed by a comb-like cluster of spines (Fig.2). Judging from the structure of the stigmapophysis and the location between the same neighboring vein structures, the comb is very likely homologous to the rib-like structure (Fig. 2E). In *Echmepteryx hageni* (Lepidopsocidae), the stigmapophysis is formed by ca. 16 tightly arranged teeth on Sc' near the Sc'–R1 fork (Fig. 2E). *Psoquilla* sp. (Psoquillidae) lacks Sc', and a vertically arranged stigmapophysis formed by seven tightly arranged teeth is located above the R1 vein, corresponding to the Sc'–R1 fork of other trogiomorphans. A stigmapophysis was not observed in Prionoglarididae and Psyllipsocidae, although the Sc'–R1 fork is present in these families (Fig. 2A-C).

The stigmapophysis of troctomorphans and psocomorphans is formed by a swelling of the R1 vein, exhibiting apparently different conditions from that of Trogiomorpha (Fig. 3). The stigmapophysis in Troctomorpha is decorated with a striped pattern of rows of fine microtrichia. Sc' is retained in Electrentomidae but absent in the others. Species of Amphientomidae and Troctopsocidae (Fig. 3A-C) possess an elongated stigmapophysis. The stigmapophysis of *Musapsocus* sp. (Musapsocidae) is enlarged and arranged in a cluster of spines (Fig. 3D). The stigmapophysis of *Manicapsocus alettae* (Electrentomidae) is located on the R1 vein near the Sc'–R1 fork (Fig. 3E), with a swollen distal end. The rib-like structures on the Sc' vein are set along the vein, although the structures on R vein and the stigmapophysis are arranged vertically. Species of Pachytroctidae and Liposcelididae (both belong to the infraorder Nanopsocetae) lack a stigmapophysis, although the Sc' and R1 veins are retained in *Tapinella* sp. (Pachytroctidae) (Ogawa and Yoshizawa, 2018).

The psocomorphan stigmapophysis (Fig.4) is also placed on the R1 vein near the Sc'–R1 fork (e.g., Fig. 4D) but frequently exhibits extension toward Sc' (e.g., Fig. 4G). The stigmapophysis of *Calopsocus furcatus* (Calopsocidae) is an apically hollowed columnar shape with sparse hairs (Fig. 4K). The stigmapophysis of *Archipsocus* sp. (Archipsocidae) is decorated with tile-shaped rib-like structures (Fig. 4A). The stigmapophysis of the other psocomorphans is a globular or conical projection arranged with fine microtrichia. Species of Archipsocidae, Caeciliucetae, Homilopsocetae, Trichopsocidae (Philotarsetae) and Hemipsocetae (Fig. 4A-H, J, N) retain the residue of Sc' near the proximal end of the stigmapophysis, but Sc' is absent in the other taxa (Fig. 4I, K-M, O, P).

Character coding and phylogenetic reconstruction

Based on the presence/absence of the stigmapophysis, we reconstructed the ancestral condition of the stigmapophysis by using the parsimony method. As a result, the stigmapophysis was discovered to be independently gained twice, once in the infraorder Atropetae (Trogiomorpha) and once in the common ancestor of Troctomorpha and Psocomorpha. Secondary absence of the stigmapophysis was identified in the infraorder Nanopsocetae (Troctomorpha) (Fig. 5). Consistency Index=0.33 Retention Index=0.67.

DISCUSSION

Origin and Evolution of stigmapophysis

The psocopteran repose coupling system is composed of simple components, including a stigmapophysis on the ventral side of the forewing, which holds the costal margin of the hindwing at rest (Fig.1B). The stigmapophysis is observed in all winged Psocodea but is absent in Prionoglarididae, Psyllipsocidae (basal families of Trogiomorpha), Pachytroctidae and Liposcelididae (specialized families of Troctomorpha). The most parsimonious reconstruction of the presence/absence of the stigmapophysis suggested that the stigmapophysis has experienced two gain (Fig. 5, “G1” and “G2”) and one loss events (Fig. 5, “L”) within Psocodea.

The independent origins of the stigmapophysis are further suggested by homology assessment of this structure. The stigmapophysis of trogiomorphans is never associated with the R1 vein. In Lepidopsocidae (Fig. 2E; New, 1974), the stigmapophysis is placed on Sc’ near the Sc’–R1 fork. Sc’ is absent in Psoquillidae, but its stigmapophysis apparently separates from the R1 vein (Fig. 2D). This positional relationship suggests that the stigmapophysis of Psoquillidae is homologous with the stigmapophysis of Lepidopsocidae. In addition, the stigmapophysis of Trogiomorpha is formed by extension of the rib-like structure (see also New, 1974), as observed in the in-flight wing-coupling structure in Psocodea (Ogawa & Yoshizawa, 2018).

In contrast, the stigmapophysis of Troctomorpha is always formed by a swelling of the R1 vein. In Musapsocidae, the surface of the stigmapophysis is arranged by an extended rib-like structure (Fig. 3D), which is somewhat similar to that of Trogiomorpha. However, in all other troctomorphans (Fig. 3A–E), the stigmapophysis is also arranged by the rib-like structure. In addition, the stigmapophysis of Musapsocidae is restricted to the R1 vein (Fig. 3D). Therefore, the extended rib-like structure in Musapsocidae is likely a derived condition that occurred in Musapsocidae. These structural differences further support the idea that the stigmapophysis structures of Trogiomorpha and Troctomorpha are not homologous. The stigmapophysis of Psocomorpha frequently shows extension toward Sc’ but is always associated with the R1 vein as observed in Troctomorpha. Furthermore, the stigmapophysis of Psocomorpha is apparently a swollen structure. Therefore, in addition to the phylogenetic relatedness between Troctomorpha and Psocomorpha, these structural similarities support the homology of the stigmapophysis between these two suborders. Extension of the stigmapophysis toward Sc’ is likely a derived condition that occurred in Psocomorpha.

Function of the psocodean repose coupling structure

The function of the stigmapophysis is unknown. However, the morphology of the stigmapophysis seems to be closely associated with wing folding, so the stigmapophysis likely functions to maintain the wings in the repose position and to conceal the hindwing costal margin. Psocomorpha fold their wings steeply (New, 1974), and the well-swollen stigmapophysis of Psocomorpha (Fig. 4A-P) may help to fold the wings and maintain the fixed position of the wings during repose. Atropetae (Trogiomorpha) and Amphientometae (Troctomorpha) possess a smaller stigmapophysis and hold their wings at a shallower angle (New, 1974). Liposcelididae and Pachytroctidae lack a stigmapophysis and, during repose, these insects maintain their wings in a horizontal position (New, 1974) so that they can hold their wings without a stigmapophysis.

The stigmapophysis can also be assumed to protect the in-flight coupling mechanism. The counterpart to the stigmapophysis is the costal margin of the hindwing, which is grasped by the in-flight wing-coupling apparatus during flight (Ogawa & Yoshizawa, 2018). If the costal hindwing margin remains uncovered, it can be damaged easily, destroying the in-flight wing-coupling mechanism. Maintenance of the hindwing under the forewing by using the stigmapophysis is considered to play an important role in preserving the in-flight wing-coupling function.

In summary, Psocodea have a unique repose coupling apparatus (stigmapophysis) on the ventral side of their forewings. Although the position and function of this apparatus are common throughout the order, detailed comparative morphology and ancestral condition estimation revealed that this apparatus independently evolved twice within Psocodea (Fig. 5). The functional meaning of the stigmapophysis could be to maintain a stable repose position of the wings and thereby protecting the hindwing margin, including the in-flight coupling structure. However, factors driving the independent origins within the order remain unknown. To reveal these factors, comprehensive analyses of flight behavior and kinematics must be conducted.

ACKNOWLEDGEMENTS

We are grateful to Charles Lienhard, Rodrigo Ferreira, Tadaaki Tsutsumi, and Toshifumi Nonaka for providing identified samples, Shin-ichi Akimoto for assistance with specimen identification, and Masahiro Ôhara, Masanori Yasui and the Electron Microscope Laboratory, Research Faculty of Agriculture, Hokkaido University for support with electron microscopy. This study was supported by JSPS KAKENHI [Grant No. 15J03697 (Grant-in-Aid for JSPS Research Fellow)] to NO, and JSPS KAKENHI [Grant No. 15H04409 (Grant-in-Aid for Scientific Research)] to KY.

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LEDGENDS OF FIGURES AND SUPPLEMENT FILE

Fig. 1. *Matsumuraiella radiopicta* (Dasydemellidae). A. Habitus, left view. B. Exact engagement position of right fore- (yellow) and hindwing (blue), dorsal view. C. Forewing, dorsal view. D. Hindwing, dorsal view. E. Ditto, enlarged view of the anterior margin of hindwing. White arrow indicates the engagement point with stigmapophysis. Abbreviations: FW, forewing; HW, hindwing; Sp, stigmapophysis (violet). Scale (B-D) 500**µ**m, (E) 50**µ**m.

Fig. 2. Stigmapophysis in Trogiomorpha, ventral view of forewing anterior margin. (SEM) A. *Prionoglaris stygia* (Prionoglarididae). B. *Neotrogla curvata* (Prionoglarididae). C. *Psyllipsocus yucatan* (Psyllipsocidae). D. *Psoquilla* sp. (Psoquillidae). E. *Echmepteryx hageni* (Lepidopsocidae). F. Hindwing of *Echmepteryx hageni* (Lepidopsocidae), dorsal view. G. Ditto, enlarged view of the region indicated by white rectangle in Fig. 2F. White arrow indicates the engagement point with stigmapophysis. Abbreviations: R1, first radius vein (orange); ri, rib-like structure; Sc, subcostal vein (green); Sc', branched section of subcostal vein (green); Sp, stigmapophysis (violet). Scale (A-E, G) 50 **µ**m, (F) 500 **µ**m.

Fig. 3. Stigmapophysis in Troctomorpha, ventral view of forewing anterior margin. (SEM) A. *Stimulopalpus japonicus* (Amphientomidae). B. Gen. sp. (Troctopsocidae). C. *Selenopsocus* sp. (Troctopsocidae). D. *Musapsocus* sp. (Musapsocidae). E. *Manicapsocus alettae* (Electrentomidae). F. Hindwing of *Stimulopalpus japonicus* (*Amphientomidae*), dorsal view. G. Ditto, enlarged view of the region indicated by white rectangle in Fig. 3F. White arrow indicates the engagement point with stigmapophysis. Abbreviations: R1, first

radius vein (orange); ri, rib-like structure; Sc’, branched section of subcostal vein (green); Sp, stigmapophysis (violet). Scale (A-E, G) 50 **µ**m, (F) 500 **µ**m..

Fig. 4. Stigmapophysis in Psocomorpha, ventral view of forewing anterior margin. (SEM) 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). Abbreviations: R1, first radial vein (orange); ri, rib-like structure; Sc’, branched section of subcostal vein (green); Sp, stigmapophysis (violet). Scale 100 **µ**m.

Fig. 5. The most parsimonious reconstruction of the presence/absence condition of the stigmapophysis characters mapped onto a cladgram of ‘Psocoptera’. Tree mapping analyses are conducted with Mesquite 3.40 (Maddison & Maddison, 2018). Two gain and one loss events of stigmapophysis are indicated by G1, G2 and L, respectively.

Supplemenal information. Data matrix used for the parsimonious reconstruction of stigmapophysis.

Table 1. Taxa examined for this study. The specimens examined are stored at Systematic Entomology, Hokkaido University (SEHU).

ORDER HEMIPTERA

Cinara sp. (Aphididae)

1ex. VI. 2015. Hokkaido, Japan. Naoki Ogawa leg. [Collection No: NOJM-STN01]

ORDER THYSANOPTERA

Aeolothrips kurosawai Bhatti, 1971 (Aeolothripidae)

1ex. VI. 2015. Fukushima, Japan. Tadaaki Tsutsumi col. [Collection No: NOJM-THY01]

ORDER PSOCODEA

SUBORDER TROGIOMORPHA

Prionoglaris stygia Enderlein, 1909 (Prionoglarididae)

1ex. 25. XI. 1986. Camou, France. B. Houses leg. [Collection No: NOJM-PS17B]

Neotrogla curvata Lienhard & Ferreira, 2013 (Prionoglarididae)

1 ex. 19. X. 2012.Bahia, Brasil. Ferreira R.L. leg. [Collection No: NOJM-PS13]

Psyllipsocus yucatan Gurney, 1943 (Psyllipsocidae)

1 ex. 2011. Bahia, Brasil [Collection No: NOJM-PS18]

Psoquilla sp. (Psoquillidae)

1 ♂. 2011. Ghana [Collection No: NOJM-PS22]

Echmepteryx hageni (Packard, 1870) (Lepidopsocidae)

1 ex. 12. VII. 2010. Illinois, USA. Kazunori Yoshizawa leg. [Collection No: NOJM-PS07, NOJM-PS07B]

SUBORDER TROCTOMORPHA

Stimulopalpus japonicus Enderlein, 1906 (Amphientomidae)

1ex. 07. X. 2005. Nepal. Kazunori Yoshizawa leg. [Collection No: NOJM-PS12, NOJM-PS12B]

Gen. sp. (Troctopsocidae, genus and species undetermined)

3-10. II. 2008. Mae Hong Son, Thailand. A. Kamkoon leg. T3497 [Collection No: NOJM-PS24]

Selenopsocus sp. (Troctopsocidae)

1ex. 9-16. IV. 2009. Kanchanaburi, Thailand. Boonnam & Phumarin leg. T4793 [Collection No: NOJM-PS25]

Musapsocus sp. (Musapsocidae)

1ex. 20-31. VII. 1987. Monagas, Venezuela. S. & J. Peck. [Collection No: NOJM-PS23]

Manicapsocus alettae Smithers, 1966 (Electrentomidae)

1♂. 30. I.–13. II. 2001. Kenya. Minakawa et al. leg. [Collection No: NOJM-PS27]

Embidopsocus sp. (Liposcelididae)

1ex. 06-18. X. 2015. Roura, French Guiana. Naoki Ogawa leg.

[Collection No: NOJM-PS21]

Tapinella sp. (Pachytroctidae)

1ex. 22. XI. 1997. Kaohsiung, Taiwan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS19]

SUBORDER PSOCOMORPHA

Archipsocus sp. (Archipsocidae)

1ex. 18. XI. 1997. Taichung, Taiwan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS14]

Matsumuraiella radiopicta Enderlein, 1906 (Dasydemellidae)

1ex. 8-17. 07. 1998 Aichi, Japan. Kenzo Yamagishi leg. [Collection No: NOJM-PS09B, NOJM-PS09C]

Stenopsocus nigricellus Okamoto, 1907 (Stenopsocidae)

1ex. 20. VII. 2014. Hokkaido, Japan. Naoki Ogawa leg. [Collection No: NOJM-PS05]

Amphipsocus japonicus (Enderlein, 1906) (Amphipsocidae)

1ex. 19-26. VII. 2007. Hokkaido, Japan. K. Konishi leg. [Collection No: NOJM-PS01B]

Valenzuela flavidus (Stephens, 1836) (Caeciliusidae)

1ex. 20-27. VIII. 2003. Hokkaido, Japan. K. Konishi leg. [Collection No: NOJM-PS11B]

Peripsocus quercicola Enderlein, 1906 (Peripsocidae)

1 ex. 21. VI. 1993. Fukuoka, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS04]

Ectopsocus briggsi McLachlan, 1899 (Ectopsocidae)

1 ex. 21. VI. 1993. Fukuoka, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS06]

Idatenopsocus orientalis (Vishnyakova, 1986) (Mesopsocidae)

1 ex. 22. VI. 1994. Fukuoka Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS08]

Aaroniella badonneli (Danks, 1950) (Philotarsidae)

1 ex. 29. VII. 1999. Ōita, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS02]

Trichopsocus clarus (Banks, 1908) (Trichopsocidae)

1 ex. 20. VIII. 2004. California, USA. Kazunori Yoshizawa leg. [Collection No: NOJM-PS26]

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

1ex. 14. III. 2003. Malaysia. Kazunori Yoshizawa leg. [Collection No: NOJM-PS20B]

Heterocaecilius solocipennis (Enderlein, 1907) (Pseudocaeciliidae)

1ex. 17. VII. 1993. Hokkaido, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS03B]

Goja sp. (Epipsocidae)

1ex. 23. VI. 2014. Mexico DF, Mexico. Kazunori Yoshizawa leg. [Collection No: NOJM-PS16]

Hemipsocus chloroticus (Hagen, 1958) (Hemipsocidae)

1ex. 01. XII. 1991. Fukuoka, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS10]

Psilopsocus malayensis New & Lee, 1991 (Psilopsocidae)

1ex. 07. III. 2003. Malaysia. Kazunori Yoshizawa leg. [Collection No: NOJM-PS28]

Metylophorus sp. (Psocidae)

1ex. 02. X. 2002. Hokkaido, Japan. Kazunori Yoshizawa leg. [Collection No: NOJM-PS15B]

Figure 1

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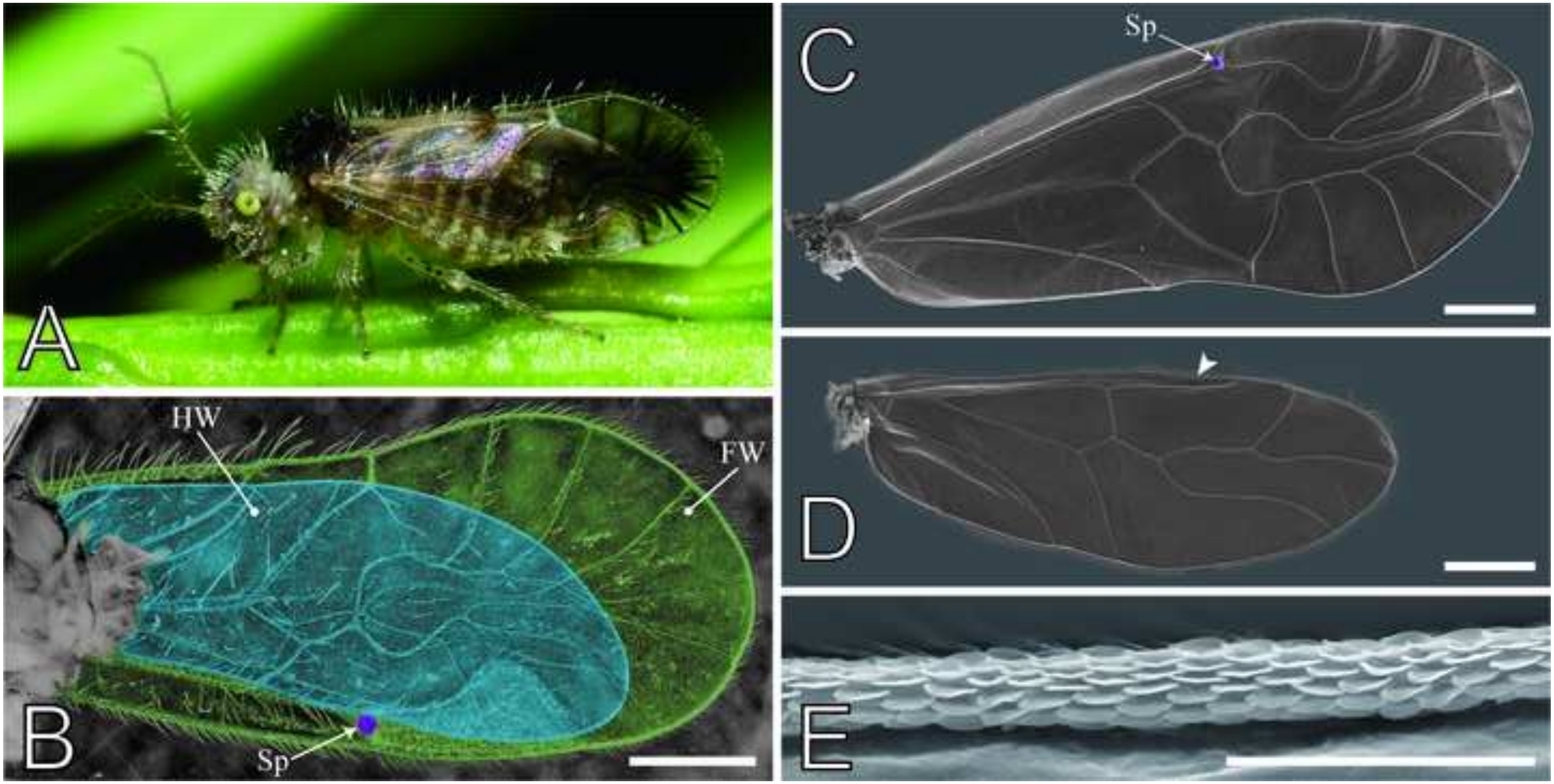

Figure 2

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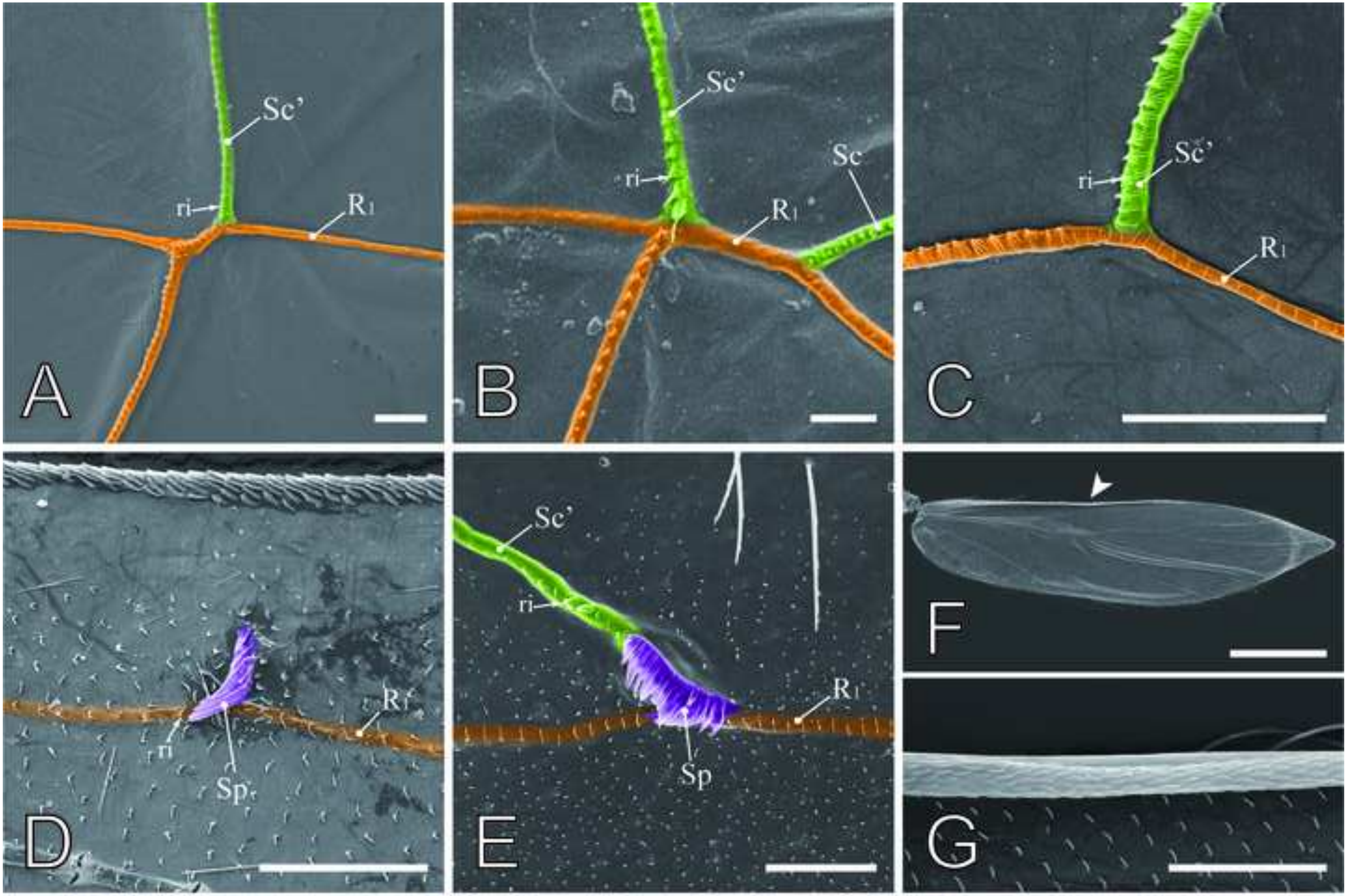

Figure 3

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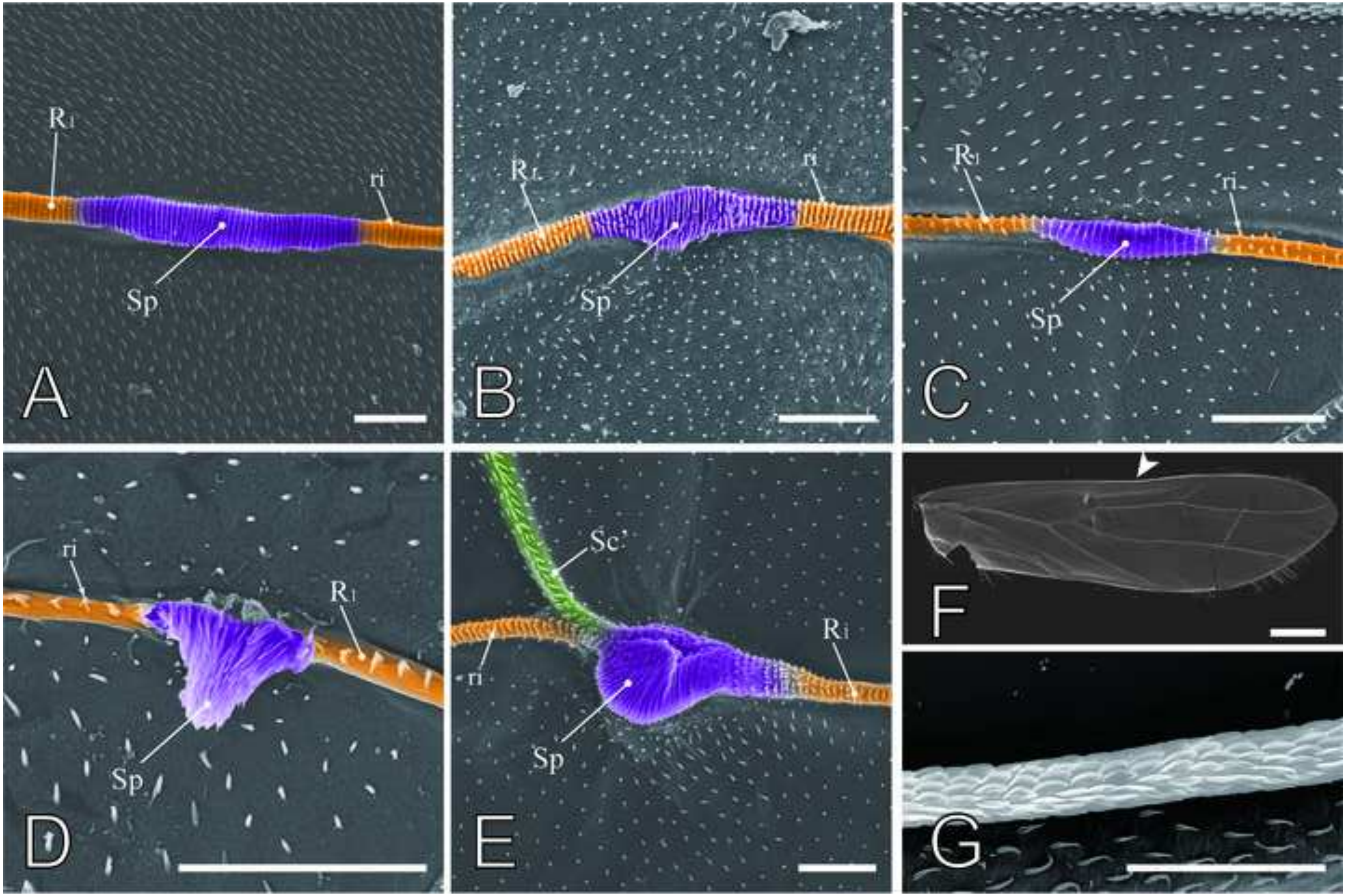


Figure 4

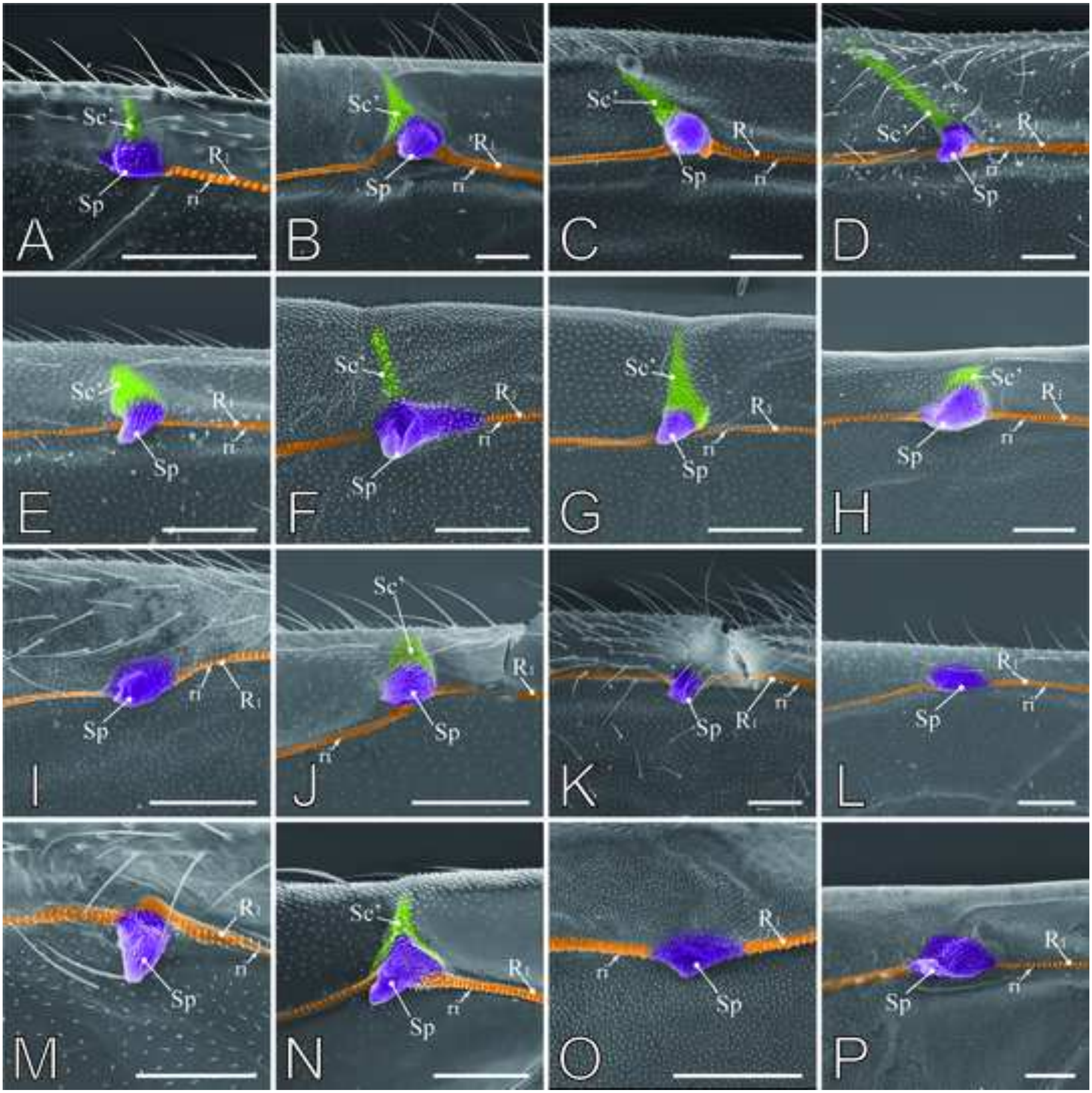
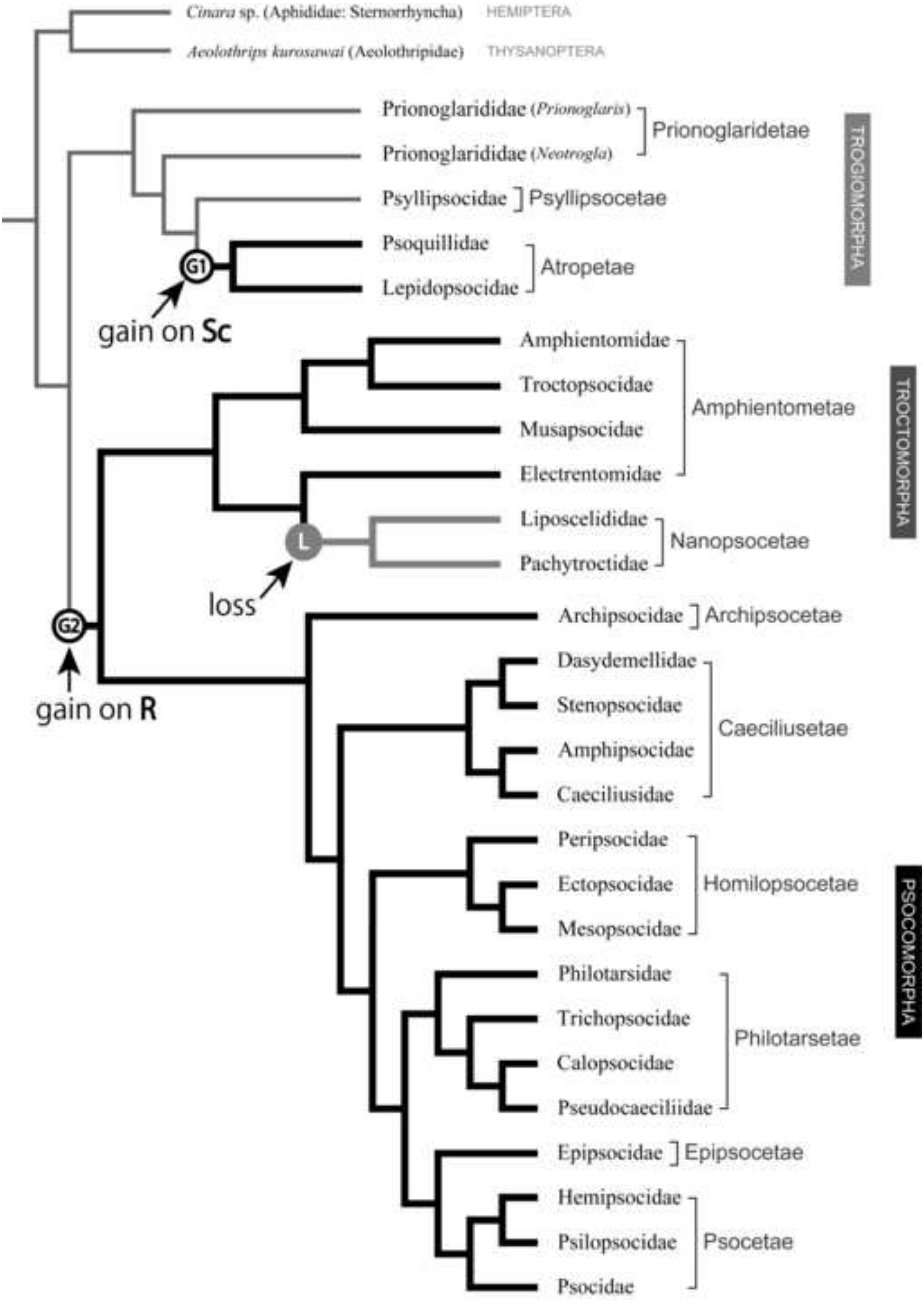


Figure 5



Cinara sp. (Aphididae: Sternorrhyncha)
HEMIPTERA
Aeolothrips kurosawai (Aeolothripidae)
THYSANOPTERA
Prionoglarididae (*Prionoglaris*)
Prionoglarididae (*Neotrogla*)
Prionoglaridetae
Psyllipsocidae
Psyllipsocetae
Psoquillidae
Lepidopsocidae
Atropetae
TROGIOMORPHA
G1
gain on Sc
Amphientomidae
Troctopsocidae
Musapsocidae
Electrentomidae
Amphientometae
Liposcelididae
Pachytroctidae
Nanopsocetae
TROCTOMORPHA
L
loss
G2
gain on R
Archipsocidae
Archipsocetae
Dasydemellidae
Stenopsocidae
Amphipsocidae
Caeciliusidae
Caeciliusetae
Peripsocidae
Ectopsocidae
Mesopsocidae
Homilopsocetae
Philotarsidae
Trichopsocidae
Calopsocidae
Pseudocaeciliidae
Philotarsetae
Epipsocidae
Epipsocetae
Hemipsocidae
Psilopsocidae
Psocidae
Psocetae
PSOCOMORPHA