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1 Structure and evolution of the stigmatophysis—a unique repose wing-coupling structure in

2 Psocodea

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11 Short title: Repose wing-coupling structure in Psocodea

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

1 **ABSTRACT**

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

16

1 INTRODUCTION

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

10 However, simply folded wings are unstable and thus inadequate for defense. To increase
11 the durability of wings, a wide range of mechanisms in the resting position developed in
12 neopteran insects to fix the wings in the resting position (Gorb & Perez Goodwyn, 2003). From
13 a functional point of view, these wing-locking mechanisms can be classified into three coupling
14 types: (1) forewing-forewing, (2) wing-body, and (3) forewing-hindwing (New, 1974; Gorb &
15 Perez Goodwyn, 2003). The first type mechanically fastens forewings to each other and its
16 function is likely to prevent contamination; this type has been reported in Hymenoptera (Gorb,
17 2001) and Heteroptera (Presswalla & George, 1935). In the second type, the forewings cover the
18 delicate hindwings and the abdomen providing protection against injury; this type has been
19 reported in various insect orders: Hymenoptera (Schrott, 1986), Mecoptera (Hlavac, 1974),
20 Dermaptera (Haas, 1995), Diptera (Rodova, 1968), Coleoptera (Hammond, 1989; Gorb, 1998,
21 1999), Lepidoptera (Common, 1969) and Hemiptera (Gorb & Perez Goodwyn, 2003; Weirauch
22 & Cassis, 2009). The third type keeps the hindwing fit into the forewing to maintain the wings
23 in the repose position and to conceal the hindwing costal margin. This type of repose coupling
24 system is unique to Psocodea (or generally known as “Psocoptera”, which excludes wingless
25 parasitic lice; Badonnel, 1951; New, 1974)

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

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

21 In this study, we examined the stigmatophysis in a comprehensive taxon sampling of
22 Psocodea using SEM. We evaluated the origin and transformation of stigmatophysis along the
23 phylogenetic hypotheses presented by Yoshizawa & Johnson (2010, 2014), Friedemann et al.
24 (2014) and Yoshizawa & Lienhard (2016).

25

1 MATERIALS & METHODS

2 Taxon selection (Table 1)

3 We examined the following taxa: Trogiomorpha, five species representing four families;
4 Troctomorpha, seven species representing six families; Psocomorpha, 16 species representing
5 16 families (Table 1). Vouchers are deposited in the Hokkaido University Insect Collection. We
6 included a species of Calopsocidae (Psocomorpha), recently synonymized with
7 Pseudocaeciliidae (Yoshizawa and Johnson, 2014), because this group is characterized by highly
8 modified, elytra-like wings. *Aeolothrips kurosawai* (Thysanoptera: Aeolothripidae) and *Cinara*
9 sp. (Hemiptera: Aphididae) were selected as outgroup species.

10

11 Terminology

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

15

16 Treatment of specimens

17 Preparation, observation and image processing followed the procedures described in
18 Ogawa and Yoshizawa (2018). Specimens for examination were stored in 80% or 99% ethanol.
19 Forewings and hindwings were removed by forceps and dehydrated in 90%, 95% and 100%
20 ethanol for 1 hour each. Wing cuticle was hardened by soaking with hexamethyldisilazane for 1
21 hour and air drying prior to mounting on 10mm aluminum stubs. Wings were held in place with
22 sticky urethane sheets (Kokuyo Hittsuki Sheet, Kokuyo Co. Ltd., Tokyo) and coated with Au-Pd
23 in a Hitachi E101 ion sputter-coater (Hitachi High Technologies Corp., Tokyo) for 120 sec. Jeol
24 JSM-5310LV and JSM-6510 scanning electron microscope (Jeol Ltd., Tokyo) were used for
25 SEM examination and the screen images were photographed by Jeol Digi Capture SUP-7707

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

3

4 Character Coding and Maximum Parsimony Reconstruction

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

13

14 **RESULTS**

15 General Morphology

16 In a reposed bark lice (Fig. 1A), the stigmapophysis supports the anterior margin of
17 hindwing (Fig. 1B). This region of hindwing is slightly bent (Fig. 1D, E) and covered with scaly
18 structures, but there is little difference in morphology among the suborders (Fig. 1D, E, 2F, G,
19 3F, G). A stigmapophysis was observed in almost all species near a pterostigma on the ventral
20 forewing surface (Fig. 1C), either on the R1 or Sc' vein. The R1 and Sc' veins are generally
21 decorated by rib-like structures (series of small plate-like structures arranged in equal intervals
22 on the veins), as also observed on the CuP vein (Ogawa & Yoshizawa, 2018) (Fig. 2-4). A
23 stigmapophysis was never observed in the outgroup representatives, although they have rib-like
24 structures on their veins (Ogawa & Yoshizawa, 2018).

25

1 Morphological disparity of stigmatopophysis

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

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

24 The psocomorphan stigmatopophysis (Fig.4) is also placed on the R1 vein near the Sc'–R1
25 fork (e.g., Fig. 4D) but frequently exhibits extension toward Sc' (e.g., Fig. 4G). The

1 stigmapophysis of *Calopsocus furcatus* (Calopsocidae) is an apically hollowed columnar shape
2 with sparse hairs (Fig. 4K). The stigmapophysis of *Archipsocus* sp. (Archipsocidae) is decorated
3 with tile-shaped rib-like structures (Fig. 4A). The stigmapophysis of the other psocomorphans is
4 a globular or conical projection arranged with fine microtrichia. Species of Archipsocidae,
5 Caeciliucetae, Homilopsocetae, Trichopsocidae (Philotarsetae) and Hemipsocetae (Fig. 4A-H, J,
6 N) retain the residue of Sc' near the proximal end of the stigmapophysis, but Sc' is absent in the
7 other taxa (Fig. 4I, K-M, O, P).

8

9 Character coding and phylogenetic reconstruction

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

16

17

18 **DISCUSSION**

19 Origin and Evolution of stigmapophysis

20 The psocopteran repose coupling system is composed of simple components, including a
21 stigmapophysis on the ventral side of the forewing, which holds the costal margin of the
22 hindwing at rest (Fig.1B). The stigmapophysis is observed in all winged Psocodea but is
23 absent in Prionoglarididae, Psyllipsocidae (basal families of Trogiomorpha), Pachytroctidae
24 and Liposcelididae (specialized families of Troctomorpha). The most parsimonious
25 reconstruction of the presence/absence of the stigmapophysis suggested that the

1 stigmapophysis has experienced two gain (Fig. 5, “G1” and “G2”) and one loss events (Fig. 5,
2 “L”) within Psocodea.

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

12 In contrast, the stigmapophysis of Troctomorpha is always formed by a swelling of
13 the R1 vein. In Musapsocidae, the surface of the stigmapophysis is arranged by an extended
14 rib-like structure (Fig. 3D), which is somewhat similar to that of Trogiomorpha. However, in
15 all other troctomorphans (Fig. 3A–E), the stigmapophysis is also arranged by the rib-like
16 structure. In addition, the stigmapophysis of Musapsocidae is restricted to the R1 vein (Fig.
17 3D). Therefore, the extended rib-like structure in Musapsocidae is likely a derived condition
18 that occurred in Musapsocidae. These structural differences further support the idea that the
19 stigmapophysis structures of Trogiomorpha and Troctomorpha are not homologous. The
20 stigmapophysis of Psocomorpha frequently shows extension toward Sc’ but is always
21 associated with the R1 vein as observed in Troctomorpha. Furthermore, the stigmapophysis of
22 Psocomorpha is apparently a swollen structure. Therefore, in addition to the phylogenetic
23 relatedness between Troctomorpha and Psocomorpha, these structural similarities support the
24 homology of the stigmapophysis between these two suborders. Extension of the
25 stigmapophysis toward Sc’ is likely a derived condition that occurred in Psocomorpha.

1

2 Function of the psocodean repose coupling structure

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

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

20

21 In summary, Psocodea have a unique repose coupling apparatus (stigmapophysis) on
22 the ventral side of their forewings. Although the position and function of this apparatus are
23 common throughout the order, detailed comparative morphology and ancestral condition
24 estimation revealed that this apparatus independently evolved twice within Psocodea (Fig. 5).
25 The functional meaning of the stigmapophysis could be to maintain a stable repose position

1 of the wings and thereby protecting the hindwing margin, including the in-flight coupling
2 structure. However, factors driving the independent origins within the order remain unknown.
3 To reveal these factors, comprehensive analyses of flight behavior and kinematics must be
4 conducted.

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2 hemipteroid insects: new insights from Cretaceous amber. *Zootaxa* 4079, 229-245.

3

4

5 **LEGENDS OF FIGURES AND SUPPLEMENT FILE**

6 Fig. 1. *Matsumuraiella radiopicta* (Dasydemellidae). A. Habitus, left view. B. Exact
7 engagement position of right fore- (yellow) and hindwing (blue), dorsal view. C.
8 Forewing, dorsal view. D. Hindwing, dorsal view. E. Ditto, enlarged view of the anterior
9 margin of hindwing. White arrow indicates the engagement point with stigmapophysis.
10 Abbreviations: FW, forewing; HW, hindwing; Sp, stigmapophysis (violet). Scale (B-D)
11 500µm, (E) 50µm.

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

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

1 radius vein (orange); ri, rib-like structure; Sc', branched section of subcostal vein (green);
2 Sp, stigmapophysis (violet). Scale (A-E, G) 50 μm , (F) 500 μm .

3 Fig. 4. Stigmapophysis in Psocomorpha, ventral view of forewing anterior margin. (SEM) A.
4 *Archipsocus* sp. (Archipsocidae). B. *Matsumuraiella radiopicta* (Dasydemellidae). C.
5 *Stenopsocus nigricellus* (Stenopsocidae). D. *Amphipsocus japonicus* (Amphipsocidae). E.
6 *Valenzuela flavidus* (Caeciliusidae). F. *Peripsocus quercicola* (Peripsocidae). G.
7 *Ectopsocus briggsi* (Ectopsocidae). H. *Idatenopsocus orientalis* (Mesopsocidae). I.
8 *Aaroniella badonneli* (Philotarsidae). J. *Trichopsocus clarus* (Trichopsocidae). K.
9 *Calopsocus furcatus* (Calopsocidae syn: Pseudocaeciliidae). L. *Heterocaecilius*
10 *solocipennis* (Pseudocaeciliidae). M. *Goja* sp. (Epipsocidae). N. *Hemipsocus chloroticus*
11 (Hemipsocidae). O. *Psilopsocus malayensis* (Psilopsocidae). P. *Metylophorus* sp.
12 (Psocidae). Abbreviations: R1, first radial vein (orange); ri, rib-like structure; Sc',
13 branched section of subcostal vein (green); Sp, stigmapophysis (violet). Scale 100 μm .

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

18 Supplemental information. Data matrix used for the parsimonious reconstruction of
19 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]

Neotroglia 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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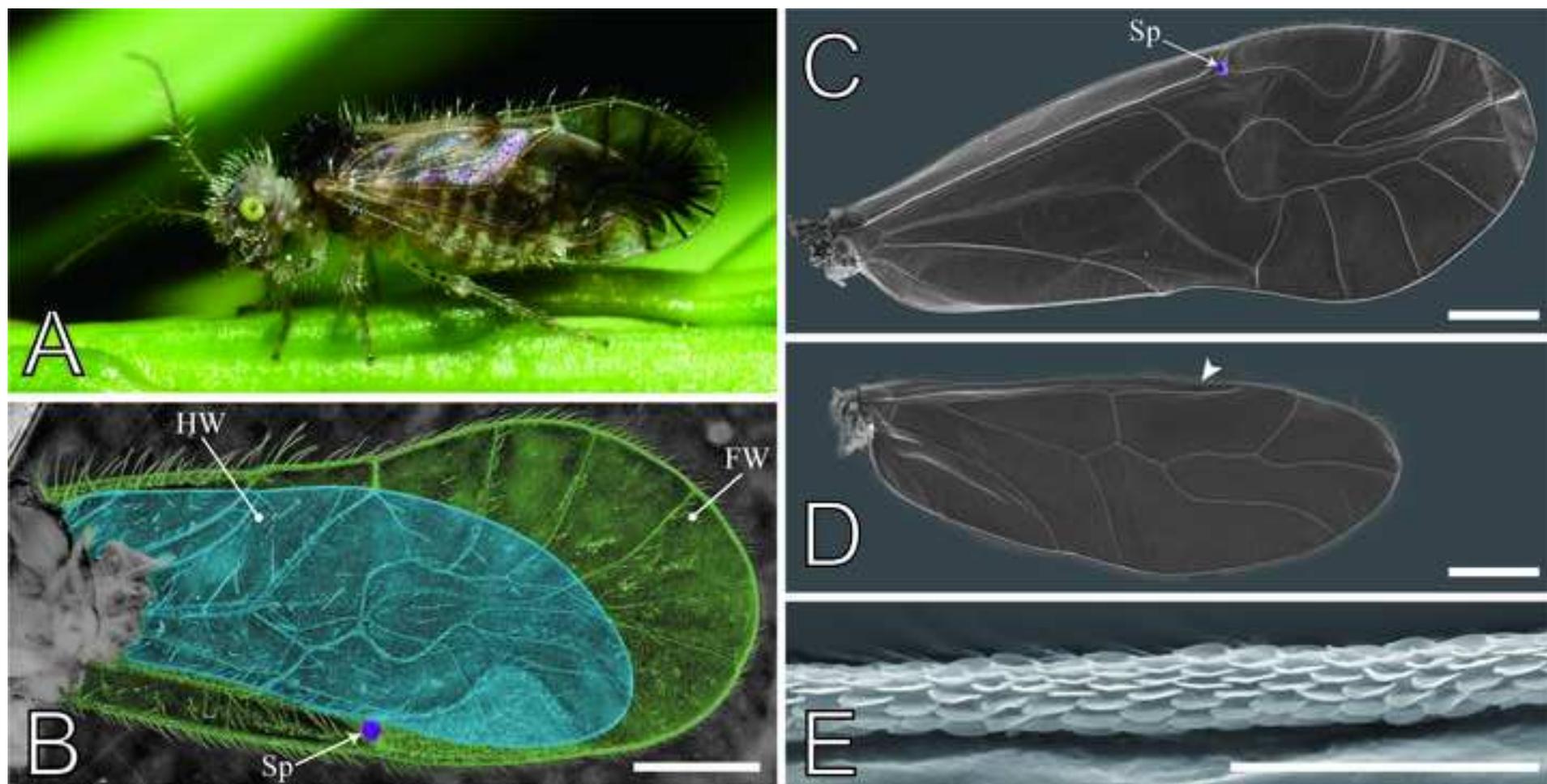


Figure 2
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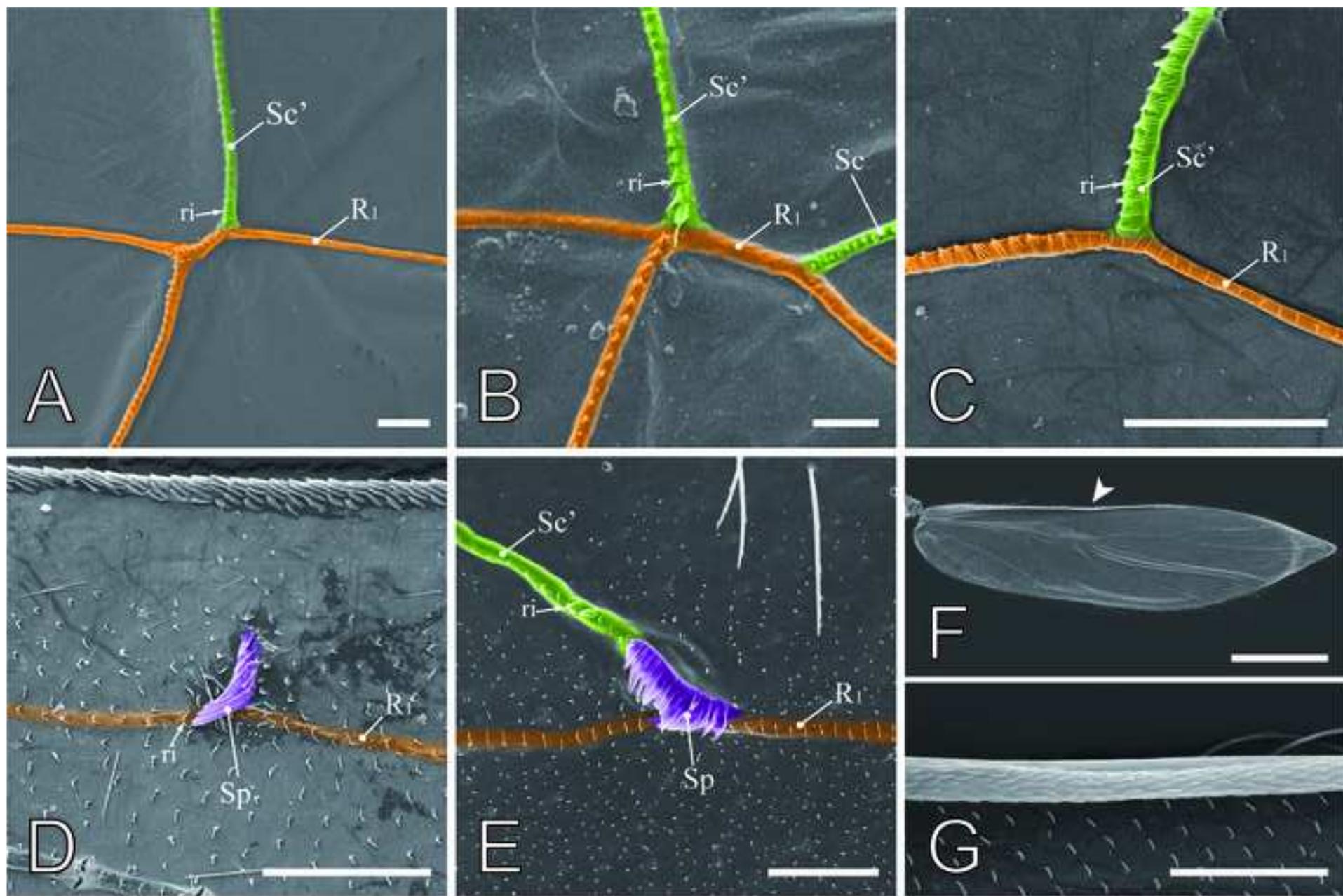


Figure 3
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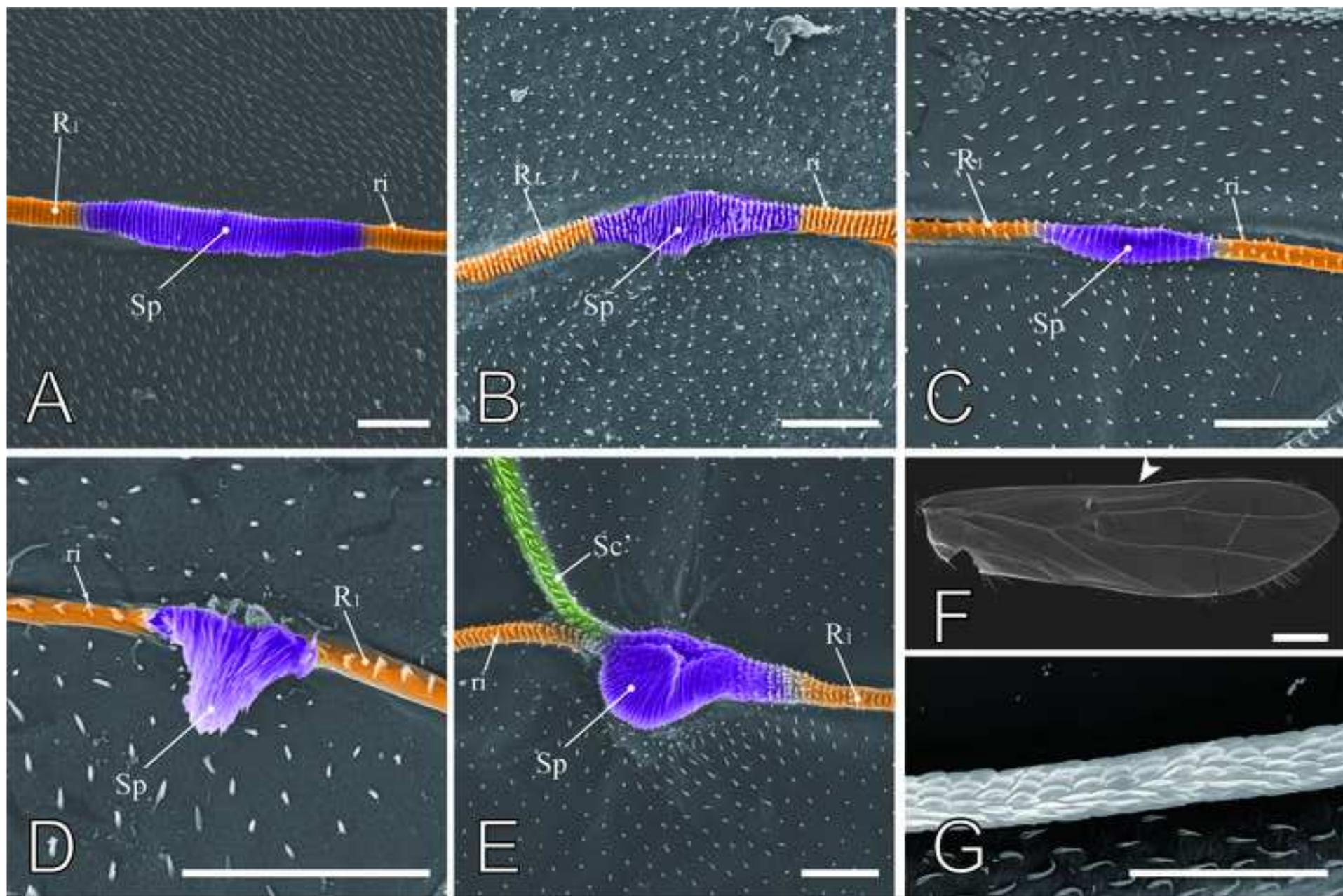


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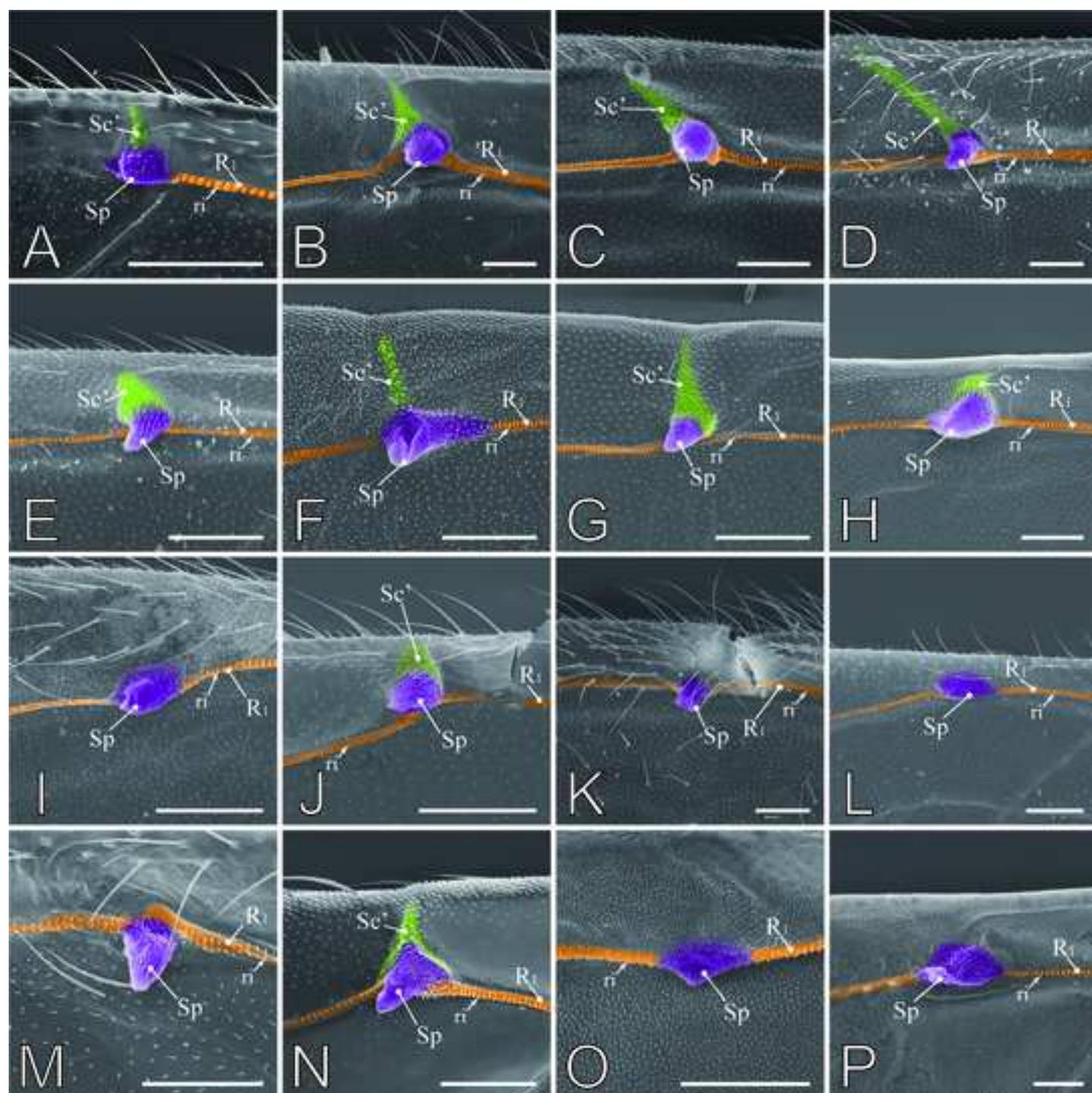


Figure 5
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