



The tribe Bryocorini (Insecta: Heteroptera: Miridae: Bryocorinae): phylogeny, description of a new genus, and adaptive radiation on ferns

FEDOR V. KONSTANTINOV* and ALEXANDER A. KNYSHOV

Department of Entomology, Faculty of Biology, St. Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg 199034, Russia

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A cladistic analysis of the tribe Bryocorini based on 68 morphological characters is conducted. Bryocorini are supported as a monophyletic group with Eccritotarsini as their sister taxon. Based on the phylogenetic analysis, we redefine the tribe Bryocorini to contain the following seven genera: *Bryocorella* Carvalho, 1956, *Bryocoris* Fallén, 1829, *Bryophilocapsus* Yasunaga, 2000, *Cobalorrhynchus* Reuter, 1906 gen. dist., ***Diplazicoris* gen. nov.**, *Hekista* Kirkaldy, 1902, and *Monalocoris* Dahlbom, 1851. The genus *Bryocorella* is transferred to Bryocorini from the tribe Eccritotarsini. The subgenus *Cobalorrhynchus* is treated as a separate genus. *Diplazicoris* is described as monotypic to accommodate ***Diplazicoris lombokianus* sp. nov.** An updated diagnosis of the tribe, a key to genera, and a diagnosis of each recognized genus are presented. Selected photomicrographs, scanning micrographs, and illustrations of the pretarsus, metepisternal scent efferent system, metafemoral trichobothria, and morphology of head, pronotum, and male and female genitalia are provided. Mapping of the host data on the revealed tree shows that Bryocorini represent one of the very few currently known examples of the adaptive radiation of a fairly large insect group on ferns.

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INTRODUCTION

The tribe Bryocorini Baerensprung, 1860 belongs to the subfamily Bryocorinae, one of the eight subfamilies of the plant-bug family Miridae. This family represents a large, diverse group of principally host-specific phytophagous insects with more than 11 000 species worldwide, forming one-quarter of all Heteroptera or true bugs (Cassis & Schuh, 2012). The subfamily Bryocorinae includes slightly more than 180 currently recognized genera and has a principally tropical distribution, with relatively few representatives inhabiting temperate regions. Representatives of the group show perhaps the greatest diversity of all Miridae in terms of external morphology and thoracic, pretarsal, and genitalic structures, in particular.

Comparatively little taxonomic attention has been focused on this subfamily within the last 50 years. Most of the recent work on Bryocorinae taxonomy consist of numerous isolated descriptions of species and genera (e.g., Hernández & Stonedahl, 1996; Stonedahl & Hernández, 1996; Ribes & Ribes, 2001; Matocq & Ribes, 2004; Ribes & Baena, 2006) or regional treatments (e.g., Yasunaga, 2000; Hu & Zheng, 2001, 2003; Eyles & Schuh, 2003). The only attempt to establish phylogenetic relationships among bryocorines was that of Schuh (1976), who used a limited number of morphological characters and a groundplan estimation approach for the tribes and subtribes. A classification derived from this analysis received wide acceptance, and three tribes and five subtribes *sensu* Schuh (1976) are still recognized today (Henry & Wheeler, 1988; Schuh & Slater, 1995; Hernández & Henry, 2010; Cassis & Schuh, 2012), although some

*Corresponding author. E-mail: f.konstantinov@spbu.ru

workers (e.g. Kerzhner & Josifov, 1999) treat all these units as distinct tribes.

The tribe Bryocorini is the smallest, and is almost cosmopolitan in its distribution. Four morphologically uniform genera and 31 species were recognized within this group prior to our study. The host associations of Bryocorini appear to be highly unusual given that two genera are known to feed on ferns and one genus was described from moss, although the vast majority of mirid species live on seed plants. The monotypic genus *Bryophilocapsus* (Bryocorini) remains the only moss-feeding plant bug genus, and only three genera of Miridae, all belonging to the subfamily Bryocorinae, viz. *Bryocoris*, *Monalocoris* (Bryocorini), and *Felisacus* (Monaloniini), are known to feed on ferns (Wheeler, 2001). On a broader scale, this feeding strategy appears to be quite rare among other phytophagous insects. Ferns are generally believed to be poorly exploited by insects (Hendrix, 1980). Adaptive radiations on ferns have occurred very rarely, with only a few examples known to date (Weintraub, Lawton & Scoble, 1995; Jensen & Holman, 2000).

Although an association with ferns was sometimes considered a feature of the entire tribe Bryocorini (Wheeler, 2001), this idea has never been tested based on phylogeny. Recent collecting by the senior author in Southeast Asia resulted in the discovery of a new Bryocorini genus and additional host documentation. This article presents the first substantive treatment of the tribe, including phylogenetic analysis, reassessment of the currently accepted generic composition, key to genera, updated generic diagnoses, and the description of a new genus. A broad representation of outgroups for the phylogenetic analysis was chosen to reveal the relationships of the tribe within the subfamily as well. We also test a scenario of the single adaptive radiation of the Bryocorini on ferns.

MATERIAL AND METHODS

SPECIMENS AND COLLECTIONS

The material examined in the present study is mainly retained at the Zoological Institute, Russian Academy of Sciences, St Petersburg (ZISP), with several species borrowed from the American Museum of Natural History, New York (AMNH), National Museum of Natural History, Washington D.C. (NMNH), Natural History Museum, London (NHM), National Museum of Wales, Cardiff (NMC), and Musée royal de l'Afrique centrale, Tervuren (MRAC).

All specimens examined during this study were associated with barcode labels (unique specimen identifiers, USIs), which were printed as a matrix code label that also provides an alphanumeric string, e.g. AMNH_PBI 00337945. USI numbers explicitly

identify particular specimens and are listed for the new species in the 'Material examined' section. Additional specimen information can be obtained from the website of the Planetary Biodiversity Project on Plant Bugs (<http://research.amnh.org/pbi/heteropteraspeciespage/>), and can also be accessed through the <http://www.discoverlife.org> website.

The holotype and most of the paratypes of *Diplazicoris lombokianus* sp. nov. described in this paper are deposited in ZISP, with a representative sample of specimens deposited in AMNH, NMNH, and NHM.

MICROSCOPY AND ILLUSTRATIONS

Observations, measurements, and digital dorsal colour images were made with a Nikon SMZ 1500 stereomicroscope equipped with Nikon D700 digital SLR camera. Drawings and images of the male and female genital structures were taken with a Leica DM2500 microscope equipped with a drawing attachment and a Leica EC3 digital camera. Scanning electron micrographs of selected structures were taken using Quanta 250 and Hitachi TM3000 scanning microscopes. Unless otherwise stated, all measurements are in millimetres.

TERMINOLOGY

The terminology used for male genitalia follows Konstantinov (2003) and for females follows Davis (1955).

PHYLOGENETIC METHODS

Taxa

One of the main purposes of the present analysis was to test the monophyly and limits of the tribe Bryocorini; therefore, we chose species broadly representing the diversity of the main lineages of the entire subfamily Bryocorinae. In addition, five taxa, viz. *Cylapus citus* Bergroth, 1922, *Palaucoris sulawesicus* Konstantinov and Gorczyca, 2001, *Punctifulvius kerzhneri* Schmitz, 1978 (Cylapinae), *Angulonotus grisescens* Knyshov and Konstantinov, 2012 (Orthotylinae), and *Stenotus binotatus* (Fabricius, 1794) (Mirinae) were added as outgroups.

A matrix of characters (Appendix 1) was prepared using MESQUITE 3.01 (Maddison & Maddison, 2001–2014). The data were analyzed in PAUP 4.0 (Swofford, 2000) and TNT (Goloboff, Farris & Nixon, 2000), with all characters treated as unordered and equally weighted. With the limited number of terminal taxa, an implicit enumeration (equivalent to branch-and-bound in PAUP) search strategy was used. Successive approximation weighting (Farris, 1969; Carpenter, 1988) was completed in PAUP 4.0 using rescaled consistency index and implied weighting (Goloboff, 1993)

using a wide range of weighting strengths (concavity constants) from $K = 1$ to 30 was performed in TNT. All characters were treated as unordered. Character-state optimization and editing of the resulting trees was performed by WINCLADA 1.00.08 (Nixon, 2002). The reliability of each branch was assessed using the Bremer support or decay index (Bremer, 1994). Bremer support values were obtained in TNT from suboptimal trees for up to 20 extra steps, and these were shown on the strict consensus tree (Fig. 105).

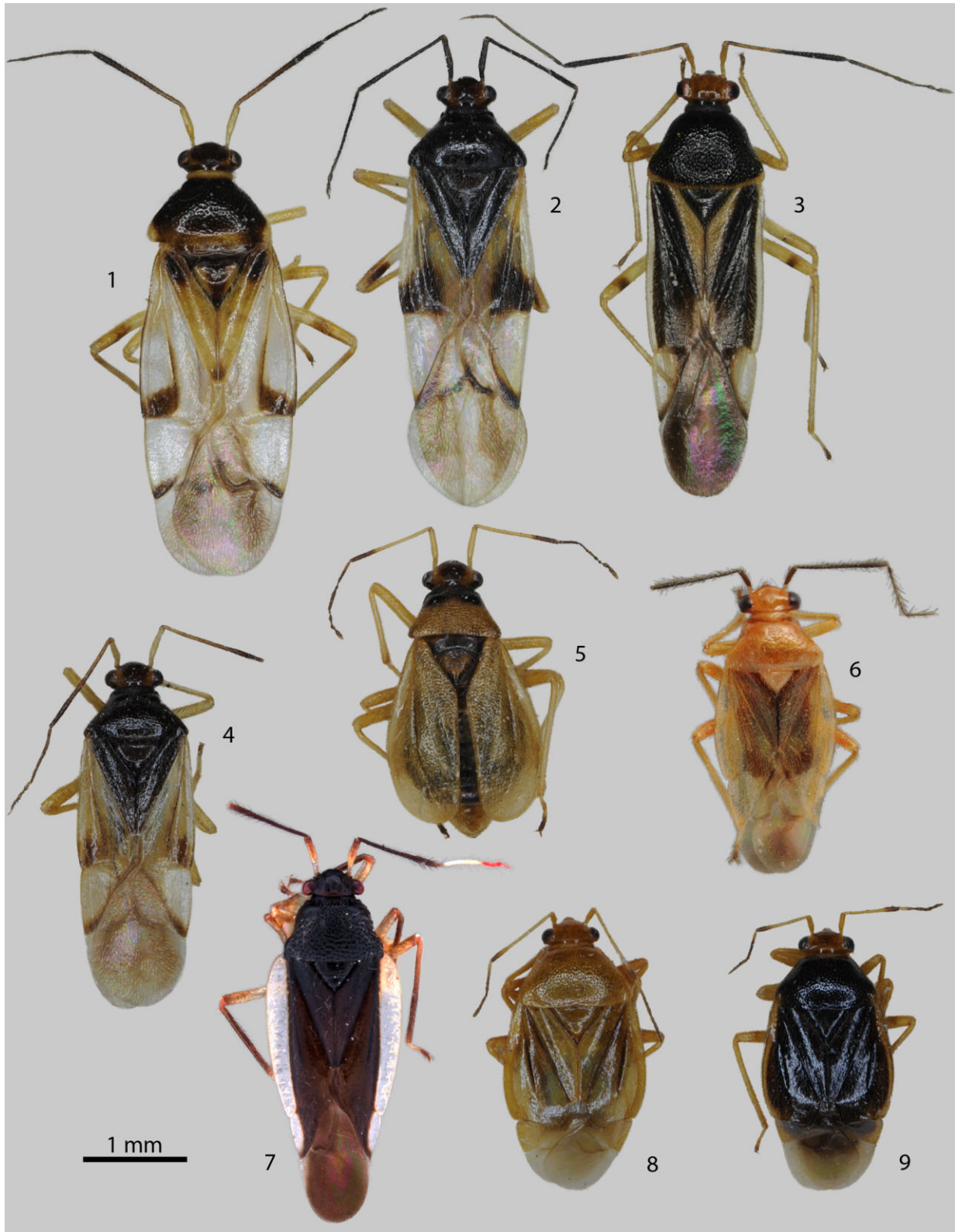
Characters

Head (Figs 10–25)

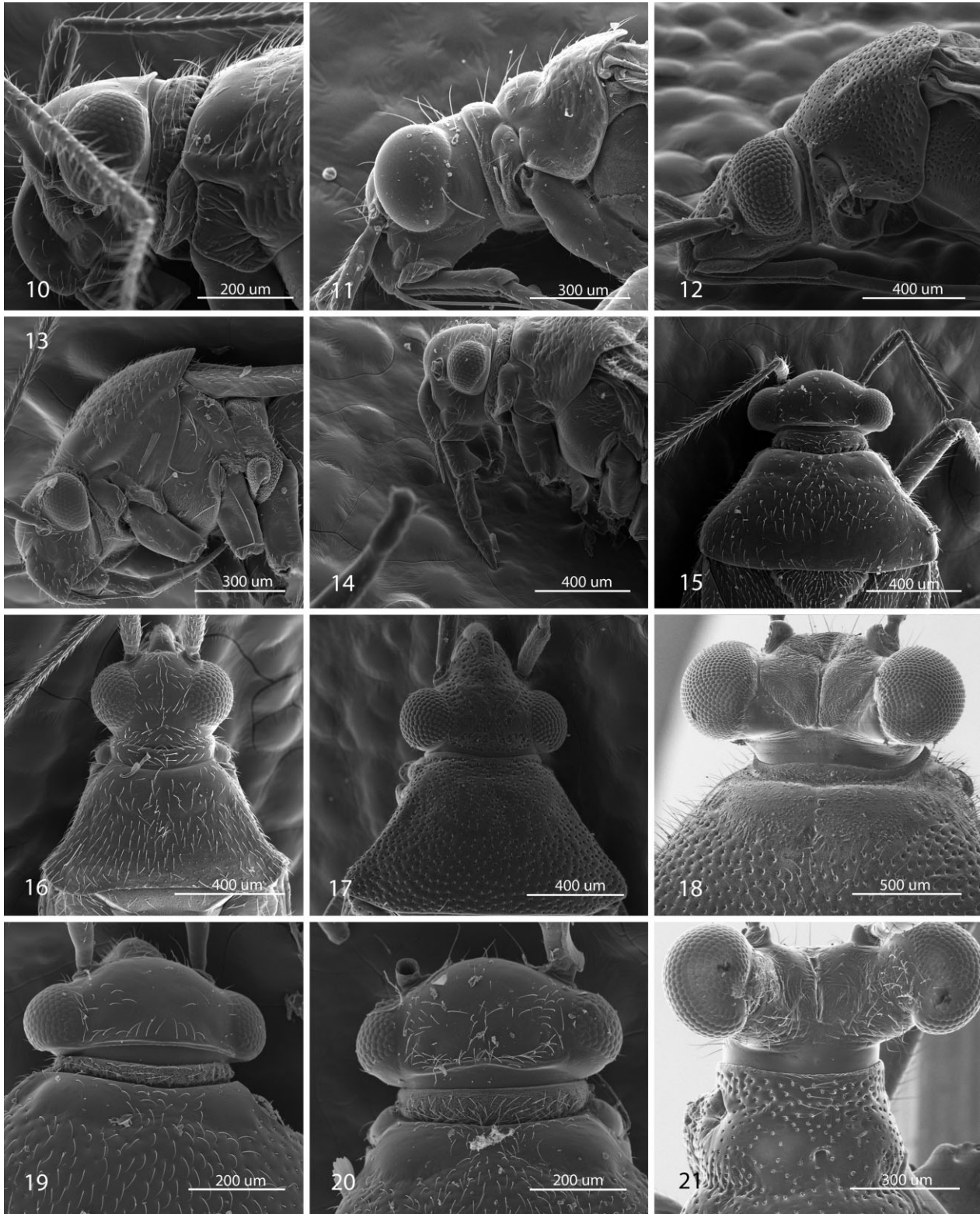
1. *Size of eyes*: (0) small, occupying at most half of head in lateral view (Figs 10, 13, 14); (1) large, occupying more than two-thirds of head capsule in lateral view (Figs 11, 12).
2. *Location of eyes*: (0) in contact with or close to anterior margin of pronotum (Figs 15, 17–21); (1) distinctly removed from anterior margin of pronotum (Fig. 16).
3. *Maxillary plate basally*: (0) not delimited (Fig. 12); (1) delimited by suture or at least depression (Figs 10, 11, 13, 14).
4. *Frontoclypeal suture*: (0) depressed (Figs 16, 19); (1) not depressed (Fig. 17).
5. *Gula*: (0) horizontal; (1) vertical.
6. *Posterior margin of vertex*: (0) not carinate (Figs 16–18, 21); (1) basal edging distinctly carinate (Figs 15, 19, 20).
7. *Antennal fossa*: (0) without tubercle (Figs 15–17, 19, 20); (1) located on a tubercle (Figs 18, 21).
8. *Antennal segment I, length*: (0) equal to or slightly shorter than head width, distinctly longer than width of vertex (Figs 1–5, 7); (1) shorter than width of vertex (Figs 6, 8, 9); (2) distinctly longer than width of head.
9. *Labial segment I*: (0) short and thick, almost as long as wide (Figs 22–24, 26); (1) short, rectangular, 1.5–2.0 times as long as wide; (2) elongated, more than 3.0 times as long as wide (Fig. 25); (3) contrastingly long, distinctly more than 4.0 times as long as wide (Fig. 12).
10. *Labial segment II*: (0) short, less than 2.0 times as long as width (Figs 22–24, 26); (1) somewhat shorter than 3.0 times as long as wide; (2) at least 4.0 times as long as wide (Fig. 25).
11. *Labial segment III*: (0) short, of nearly equal length and width to about twice as long as wide (Figs 22–24, 26); (1) long, more than 4.0 times as long as wide (Fig. 25).
12. *Labial segment IV*: (0) twice as long as wide or even shorter, equal in length to segment III (Figs 22, 23); (1) distinctly longer than wide, as thin as segment III, gradually tapering at apex (Fig. 25); (2) distinctly longer than wide, twice thinner than segment III, strongly tapering from base, claw-shaped (Figs 24, 26).

Thorax

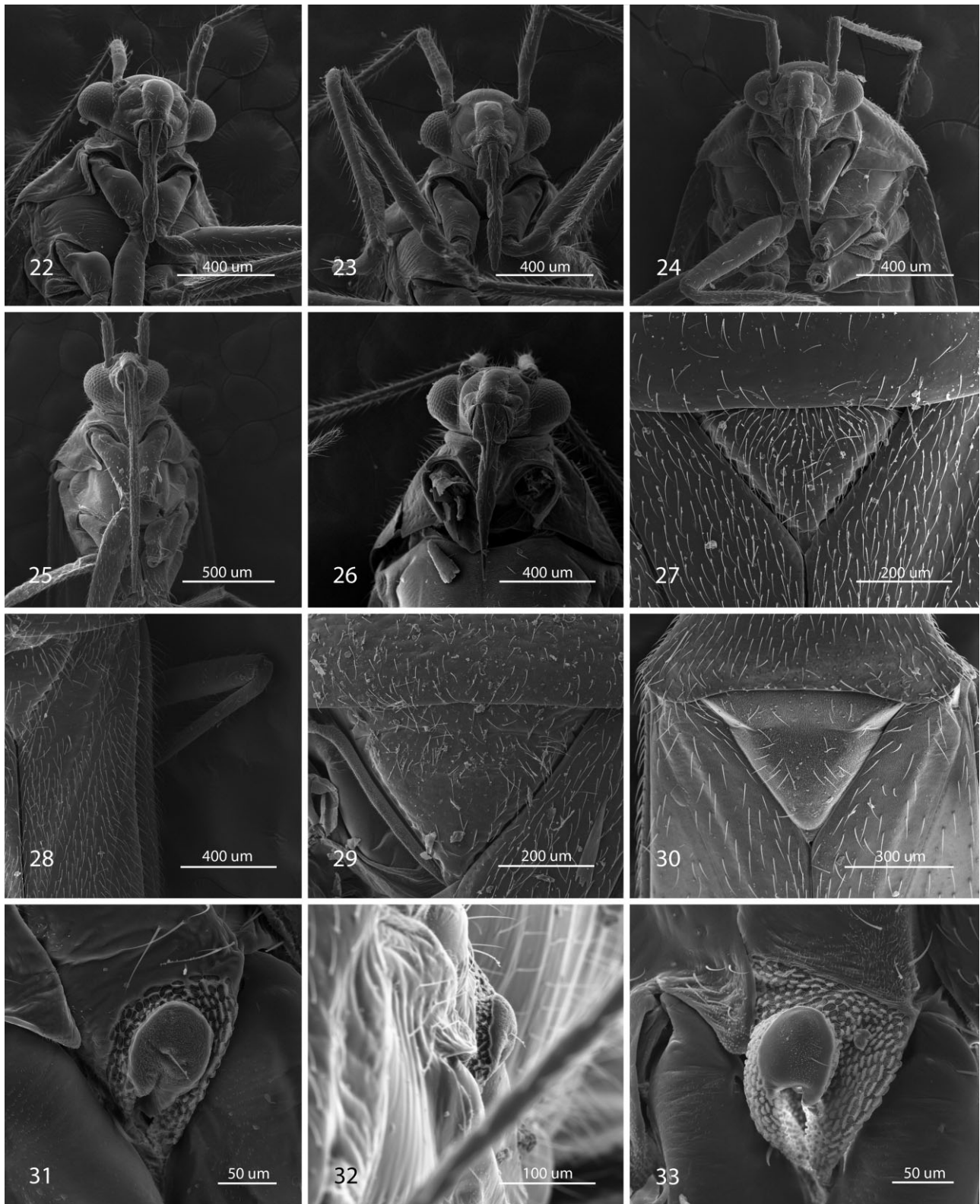
13. *Pronotal collar, presence*: (0) absent (Figs 12, 17); (1) present, convex, dorsally and laterally well delimited by deep suture running anteriorly to propleural suture (Figs 10, 13–15, 18–20; Knyshev & Konstantinov, 2012: fig. 13); (2) present, flat, demarcated by weak depression running anteriorly to propleural suture (Figs 11, 16); (3) present, flat and contrastingly wide, dorsally not delimited, laterally delimited by shallow depression directly continuing into propleural suture (Fig. 21; Konstantinov, 2012: fig. 4E).
14. *Pronotal collar, length*: (0) longer than or at least as long as width of antennal segment I at widest point (Figs 10, 11, 14–16, 18, 20, 21); (1) narrow, distinctly thinner than width of segment I (Figs 13, 18, 19).
15. *Pronotal collar, surface*: (0) shiny (Figs 15–17, 19, 21); (1) matt (Figs 18, 20).
16. *Suture delimiting pronotal collar*: (0) straight (Figs 16, 18); (1) finely scalloped (Figs 13, 14, 19, 20); (2) deeply scalloped (Figs 10, 15).
17. *Location of calli*: (0) located on dorsal surface of pronotum (Figs 10–13, 15–19, 21); (1) laterally extending on sides of pronotum (Figs 14, 20).
18. *Anterior part of pronotum*: (0) not delimited from remainder of pronotum or with weak depression behind calli at sides (Figs 10, 12–20); (1) neck-shaped, posteriorly delimited by constriction behind forecoxae (Figs 11, 21).
19. *Exposed part of mesoscutum*: (0) posterior part of mesonotum not covered by pronotum and partly exposed (Fig. 30); (1) mesonotum not exposed, entirely covered by pronotum (Figs 27, 29).
20. *Sides of scutellum*: (0) smooth, not scalloped (Fig. 30); (1) finely scalloped (Fig. 29); (2) deeply scalloped (Figs 27, 28).
21. *Opening of metathoracic scent gland*: (0) slitlike, small, distinctly shorter than peritreme (Figs 31, 33, 34, 36, 38–40); (1) oval, large, equal to or larger than peritreme (Fig. 37).
22. *Shape of scent gland evaporative area*: (0) broadly triangular (Figs 33, 34, 36, 40); (1) oval, more or less elongated, with smoothly rounded anterior margin (Figs 31, 37, 41); (2) reduced to a narrow area along anterior margin of peritreme (Fig. 38); (3) absent (Fig. 39).
23. *Structure of peritreme*: (0) present, with somewhat jagged margins, not raised above pleural surface (Fig. 40); (1) present, clearly delimited and slightly raised above pleural surface (Figs 38, 41);



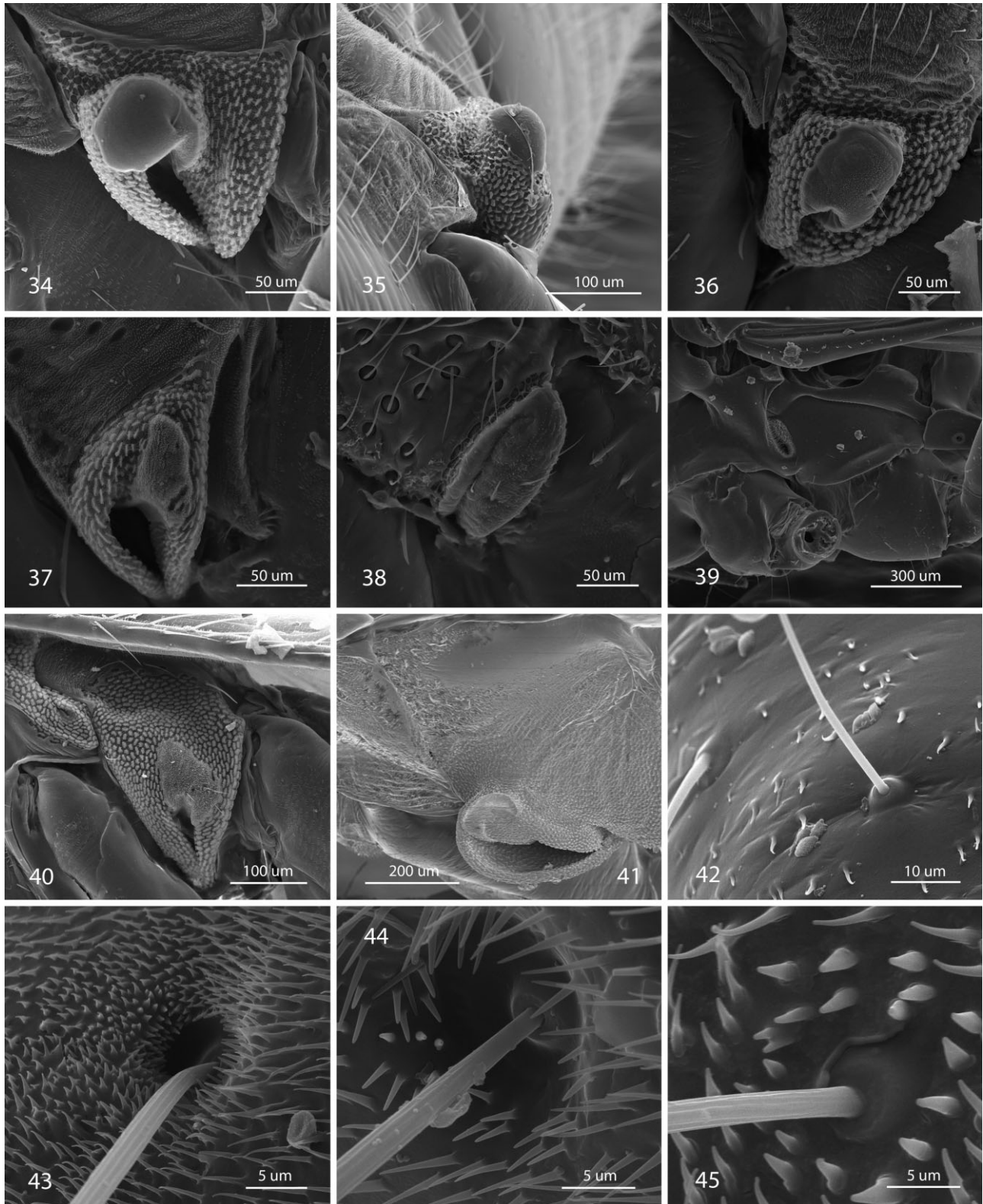
Figures 1–9. Dorsal habitus of Bryocorini: 1, *Coballorhynchus convexicollis*; 2, *Coballorhynchus concavus*; 3, *Hekista laudator*; 4, 5, *Bryocoris pteridis* – 4, macropterous male, 5, brachypterous female; 6, *Diplazicoris lombokianus* sp. nov.; 7, *Bryocorella emboliata* HT; 8, 9, *Monalocoris filicis*, females – 8, pale form, 9, dark form.



Figures 10–21. Scanning electron micrographs of particular characters: 10–14, head and pronotum in lateral view – 10, *Diplazicoris lombokianus* sp. nov., 11, *Dicyphus testaceus*, 12, *Punctifulvius kerzhneri*, 13, *Monalocoris filicis*, 14, *Bryocoris pteridis*; 15–21, head and pronotum in dorsal view – 15, *D. lombokianus* sp. nov., 16, *Nesidiocoris tenuis*, 17, *Punctifulvius kerzhneri*, 18, *Cylapus citus*, 19, *Monalocoris filicis*, 20, *Bryocoris pteridis*, 21, *Sinervus baerensprungi*.



Figures 22–33. Scanning electron micrographs of particular characters: 22–26, head and thorax in ventral view – 22, *Diplazicoris lombokianus* sp. nov., 23, *Bryocoris pteridis*, 24, *Monalocoris filicis*, 25, *Nesidiocoris tenuis*, 26, *Hekista laudator*; 27–30, scutellum and hemelytra – 27, *D. lombokianus* sp. nov., 28, *Hekista laudator*, 29, *Bryocoris pteridis*, 30, *Nesidiocoris tenuis*; 31–33, evaporatory area – 31, 32, *D. lombokianus* sp. nov., 33, *Monalocoris filicis*.



Figures 34–45. Scanning electron micrographs of particular characters: 34–41, evaporatory area – 34, 35, *Hekista laudator*, 36, *Bryocoris pteridis*, 37, *Punctifulvius kerzhneri*, 38, *Pyncoderes* sp., 39, *Helopeltis clavifer*, 40, *Dicyphus testaceus*, 41, *Cylapus citus*; 42–45, femoral trichobotria – 42, *Diplazicoris lombokianus* sp. nov., 43, *Punctifulvius kerzhneri*, 44, *Pyncoderes* sp., 45, *Stenotus binotatus*.

- (2) present, clearly delimited, strongly elevated above pleural surface (Figs 31–36); (3) absent (Fig. 39).
24. *Shape of peritreme*: (0) tongue-shaped, extended dorsoposteriorly (Figs 37, 40; Konstantinov, 2012: fig. 4G); (1) lanceolate, narrow, extended posteriorly along ventral margin of metapleuron (Fig. 38); (2) broadly rounded (Figs 31, 33, 34, 36); (3) auriculate (Fig. 41); (4) broadly triangular (Knyshov & Konstantinov, 2012; fig. 20).
25. *Setae on peritreme*: (0) absent (Figs 37, 41); (1) with single seta (Figs 31, 33, 34, 36); (2) with three or more setae (Figs 38, 40).
26. *Metathoracic spiracle*: (0) without distinctive ornamentation or with quite a few evaporative bodies posteriorly (Fig. 39); (1) surrounded by large area densely covered with evaporative bodies (Fig. 40).
27. *Surface of pronotum*: (0) smooth or finely rugose, rarely with few indistinct punctures (Fig. 16); (1) with shallow punctures (Figs 15, 19–21); (2) with distinct, deep punctures (Figs 17, 18).

Hemelytron

28. *Apex of hemelytra*: (0) straight, not deflected, membrane extending beyond abdomen (Figs 1–3); (1) strongly deflected at base of cuneus (Figs 8, 9).
29. *R + M vein*: (0) clearly reaching or almost reaching apex of corium, straight, exocorium narrow, more or less parallel-sided (Figs 4, 28); (1) reaching half the length of hemelytron or less (Figs 8, 9).
30. *Punctures on R + M*: (0) absent (Konstantinov, 2012: fig. 1A); (1) present at base (Fig. 28).
31. *Exocorium, colour*: (0) unicoloured with corium (Figs 1, 2, 4–6, 9); (1) distinctly paler than corium (Figs 3, 7, 8).
32. *Cuneal fracture*: (0) not incised (Figs 1–5, 7); (1) distinctly incised (Figs 6, 8, 9).
33. *Cuneus, relative length*: (0) elongate, about twice as long as wide at base (Figs 1–5); (1) broadly triangular, slightly longer than basal width (Figs 6–9); (2) narrow, more than 5.0 times as long as basal width.
34. *Membrane*: (0) with two cells; (1) with single cell.
35. *Cell of membrane*: (0) regular, not surpassing apex of cuneus (Figs 1–9); (1) large, surpassing apex of cuneus (Konstantinov, 2012: fig. 1A).
36. *Vestiture of veins on membrane*: (0) absent; (1) veins on membrane clothed with dense, short simple setae.

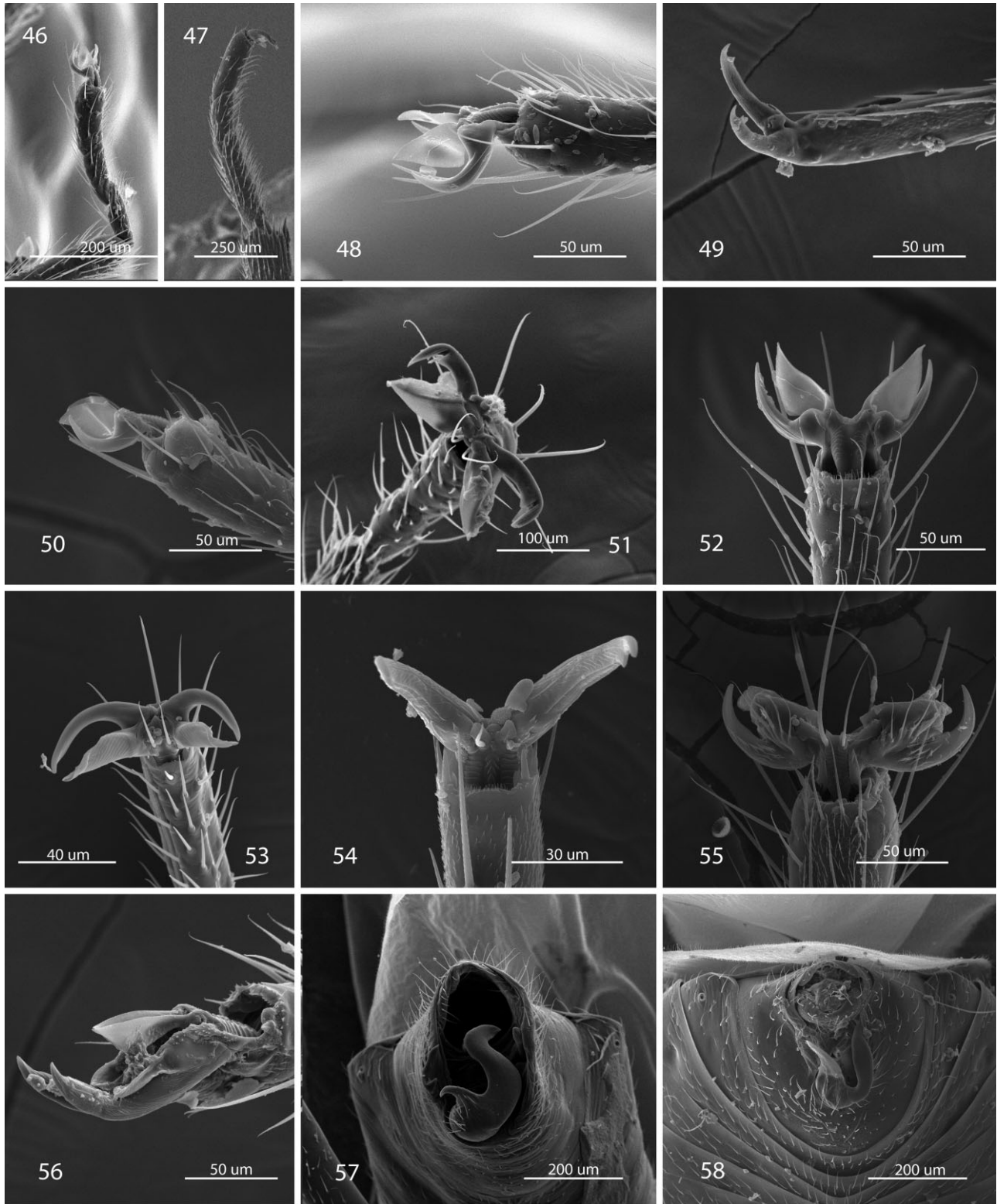
Legs

37. *Metafemoral trichobothria*: (0) simple, not or weakly recessed, and not tuberculate (Fig. 45);

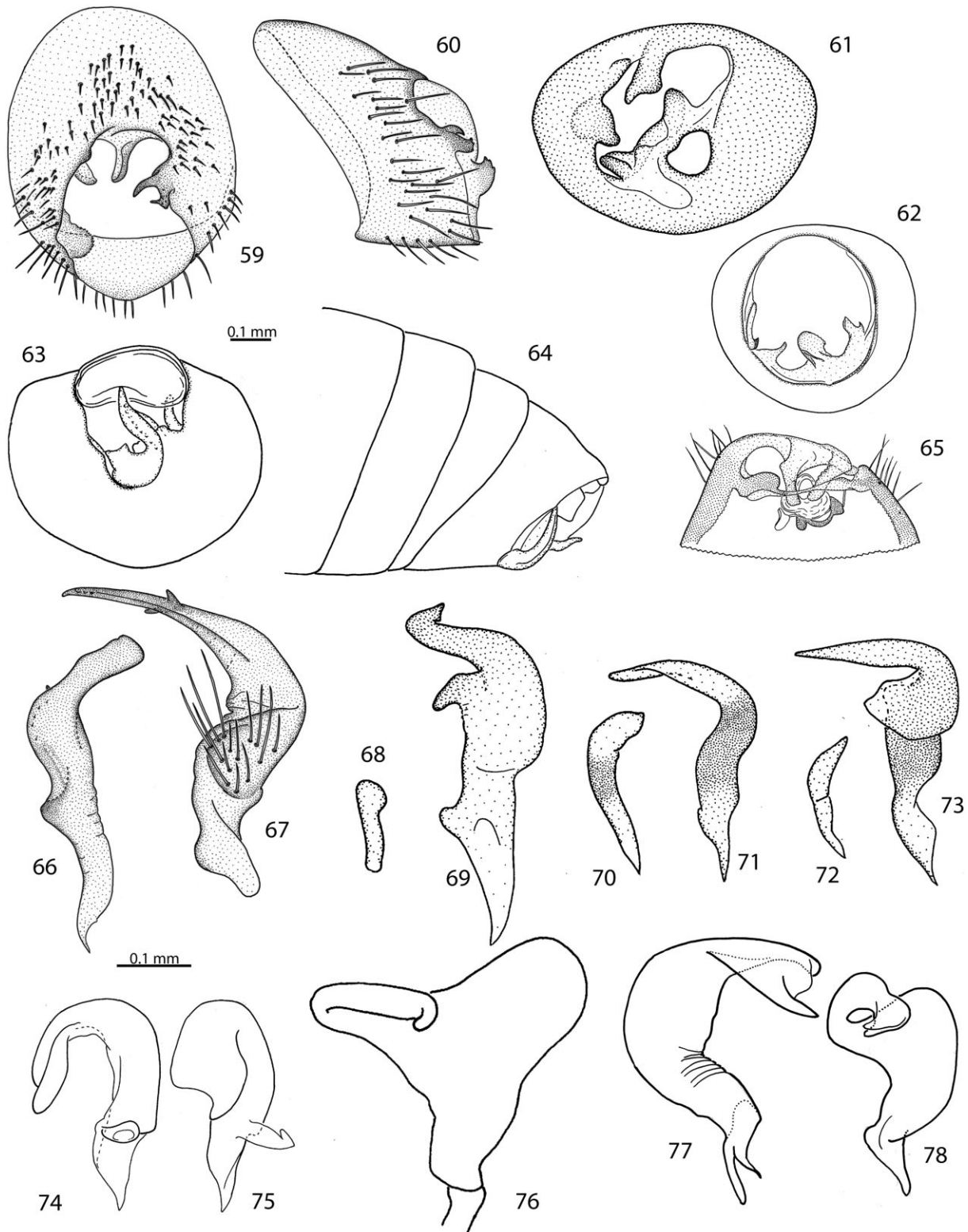
- (1) tuberculate, not recessed (Fig. 42); (2) deeply recessed, but not tuberculate (Fig. 43); (3) deeply recessed and tuberculate (Fig. 44).
38. *Trichoma of metafemoral trichobothria*: (0) absent or weakly developed (Fig. 42); (1) well developed (Figs 43–45).
39. *Number of tarsal segments*: (0) three; (1) two.
40. *Shape of tarsi*: (0) distally not dilated (Fig. 47); (1) distally dilated, last tarsal segment distinctly swollen in apical half (Fig. 46).
41. *Tarsal guard setae*: (0) short (Figs 49, 53, 54, 56); (1) long (Figs 48, 50–52, 55).
42. *Subapical claw tooth*: (0) absent (Figs 48, 50, 52, 53, 55, 56); (1) present, minute (Figs 49, 54); (2) claw apically cleft-like, with large subapical tooth (Fig. 51; Konstantinov, 2012: fig. 4C).
43. *Basal claw tooth*: (0) absent (Figs 48–50, 52–56); (1) present (Fig. 51; Konstantinov, 2012: fig. 4C).
44. *Parempodia, shape*: (0) setiform (Figs 51, 53–55); (1) lamelliform (Fig. 56); (2) spatulate (Konstantinov, 2012; fig. 4C); (3) absent (Fig. 52).
45. *Parempodia, symmetry*: (0) of equal length (Figs 51, 53); (1) outer parempodium slightly shorter than inner parempodium (Fig. 55); (2) outer parempodium reduced, distinctly shorter than inner parempodium (Fig. 54).
46. *Pulvilli, shape*: (0) absent (Figs 52–54); (1) present, narrow, located on ventral margin of claw (Fig. 56); (2) present, wide, semicircular, attached to inner margin of claw (Fig. 55).
47. *Pseudopulvilli*: (0) absent (Figs 54, 55); (1) present (Figs 51–53).

Male genitalia

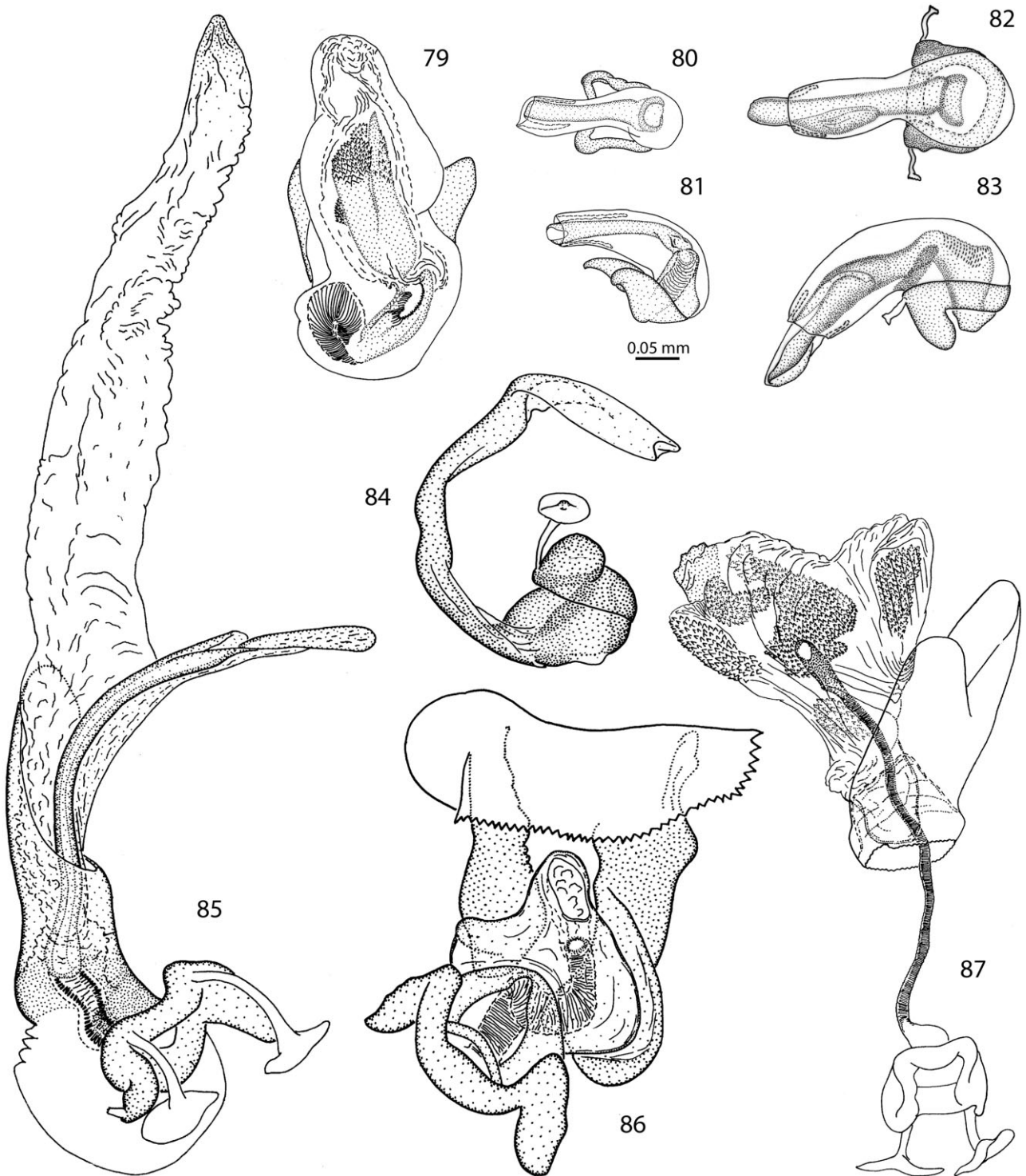
48. *Opening of genital capsule, orientation*: (0) directed dorsally (Figs 61, 65); (1) directed posteriorly (Figs 57–60, 62–64).
49. *Dorsal wall of genital capsule*: (0) well developed (Figs 59, 60, 62, 64); (1) greatly reduced, bridge-shaped (Figs 61, 65).
50. *Left wall of genital capsule*: (0) without processes, of regular shape (Figs 61, 63, 65); (1) with large single-coned process above left paramere (Fig. 48; Hu & Zheng, 2000: fig. 55e); (2) with large twin-coned process above left paramere (Figs 57, 59, 60).
51. *Supragenital bridge*: (0) absent (Figs 57–64); (1) present (Fig. 65).
52. *Capitate processes of dorsal connectives*: (0) well developed (Figs 84, 85, 87); (1) vestigial (Figs 80–83).
53. *Right paramere*: (0) simple, with weakly differentiated apical process, about twice as small as left paramere (Fig. 70); (1) greatly reduced, more than three times as small as left (Figs 68, 72); (2) large,



Figures 46–58. Scanning electron micrographs of particular characters: 46, 47, tarsi in lateral view – 46, *Diplazicoris lombokianus* sp. nov., 47, *Stenotus binotatus*; 48–56, pretarsus – 48, 52, *D. lombokianus* sp. nov., 49, 54, *Punctifulvius kerzhneri*, 50, *Monalocoris filicis*, 51, *Helopeltis clavifer*, 53, *Nesidiocoris tenuis*, 55, *Pycnoderes* sp., 56, *Stenotus binotatus*; 57, 58, genital capsule in caudal view – 57, *Bryocoris pteridis*, 58, *Monalocoris filicis*.



Figures 59–78. Male genital capsule in caudal and lateral view: 59, 60, *Diplazicoris lombokianus* sp. nov., 61, *Sixeonotus* sp., 62, *Bryocoris pteridis*, 63, 64, *Monalocoris filicis*, 65, *Pyncoderes* sp.; 66–78, parameres – 66, 67, *D. lombokianus* sp. nov., 66, right, 67, left; 68, 69, *Bryocoris pteridis*, 68, right, 69, left; 70, 71, *Hekista laudator*, 70, right, 71, left; 72, 73, *Monalocoris filicis*, 72, right, 73, left; 74, 75, left paramere of *Punctifulvius kerzhneri*; 76, left paramere of *Sixeonotus* sp.; 77, 78, *Sinervus baerensprungi*, parameres: 77, left, 78, right.



Figures 79–87. Aedeagi: 79, *Cylapus citus*; 80, 81, *Bryocoris pteridis*, 80, dorsal, 81, lateral; 82, 83, *Diplazicoris lombokianus* sp. nov., 82, dorsal, 83, lateral; 84, *Sinervus baerensprungi*; 85, *Eurycipitia clarus*; 86, *Pynoderes* sp.; 87, *Nesidiocoris tenuis*. Figs 79–81, 85–87 modified from Kerzhner & Konstantinov (1999).

- with developed apical process, equal to or larger than left paramere (Figs 66, 78).
54. *Sensory lobe of left paramere*: (0) absent or in a form of indistinct swelling (Figs 67, 71, 77); (1) well developed, more or less straight, apically blunt outgrowth (Figs 71, 74, 75); (2) present, somewhat flattened and strongly curved (Figs 69, 73).
 55. *Left paramere, shape of apical process*: (0) almost straight, gradually tapering (Figs 71, 73–75); (1) with strongly curved, hook-shaped, flattened apex (Fig. 69); (2) gradually curved, with additional spines and denticles (Fig. 67); (3) curved at base and turned backwards along flattened, roughly triangular body of paramere (Figs 76, 77).
 56. *Phallosome*: (0) entirely membranous (Fig. 86); (1) membranous, dorsal wall with horseshoe sclerite adjacent to phallobase (Figs 80–83); (2) membranous, with distinctly sclerotized dorsal wall (Figs 79, 87); (3) dorsal and ventral walls uniformly sclerotized, only basal sac of ventral wall may be membranous (Figs 84, 85).
 57. *Basal membranous sac of theca*: (0) well developed (Figs 79, 85, 87); (1) absent (Figs 80–84, 86).
 58. *Ductus seminis, length*: (0) short, subequals to phallosome in length (Figs 80–84, 86); (1) long, coiled in repose, distinctly longer than phallosome (Figs 79, 85, 87).
 59. *Distal half of ductus seminis, sclerotization*: (0) entirely membranous (Figs 79, 84, 86, 87); (1) entirely sclerotized (Figs 80–83, 85); (2) membranous, with sclerotized apical part adjacent to secondary gonopore.
 60. *Structure of endosoma*: (0) undifferentiated, sac-like, simple (Figs 80–83, 86); (1) undifferentiated, membranous, voluminous, and multilobed (Fig. 79); (2) undifferentiated, entirely sclerotized, not delimited from phallosome, aedeagus tube-like (Fig. 84); (3) differentiated into conjunctiva and single-lobed membranous vesica (Fig. 87); (4) differentiated into conjunctiva and multilobed membranous vesica; (5) differentiated into conjunctiva and twin-lobed membranous vesica (Fig. 85).

Female genitalia

61. *Bursa copulatrix*: (0) very small, thin-walled, laterally not expanding beyond rami of first and second valvula (Figs 89, 91); (1) thick-walled, rigid, well expanded beyond rami at sides; (2) thick-walled, corrugated, with concentric wrinkles at sides, expanded dorsally (Fig. 93).
62. *Sclerotized rings of dorsal labiate plate*: (0) absent (Fig. 93); (1) round, very small and almost not sclerotized (Fig. 91); (2) well developed,

occupying at least half the length of dorsal labiate plate.

63. *First valvula, shape of apex*: (0) sabre-shaped, gradually tapering (Figs 94, 96, 98, 100, 102); (1) arrow-shaped.
64. *Second valvula, serration*: (0) with dense, very finely serrated dorsal margin (Figs 97, 99, 101); (1) with more or less large, distinctly separated teeth on dorsal margin (Fig. 103); (2) with short series of teeth on inner surface and fine serration laterally (Fig. 95).
65. *Vestibulum*: (0) membranous, with a pair of symmetrical sclerites encircling vulva (Fig. 90); (1) sclerotized, large, and asymmetric, directed laterally (Fig. 92); (2) sclerotized, large and short, almost symmetric, straight and directed dorsally (Fig. 89).

Whole body

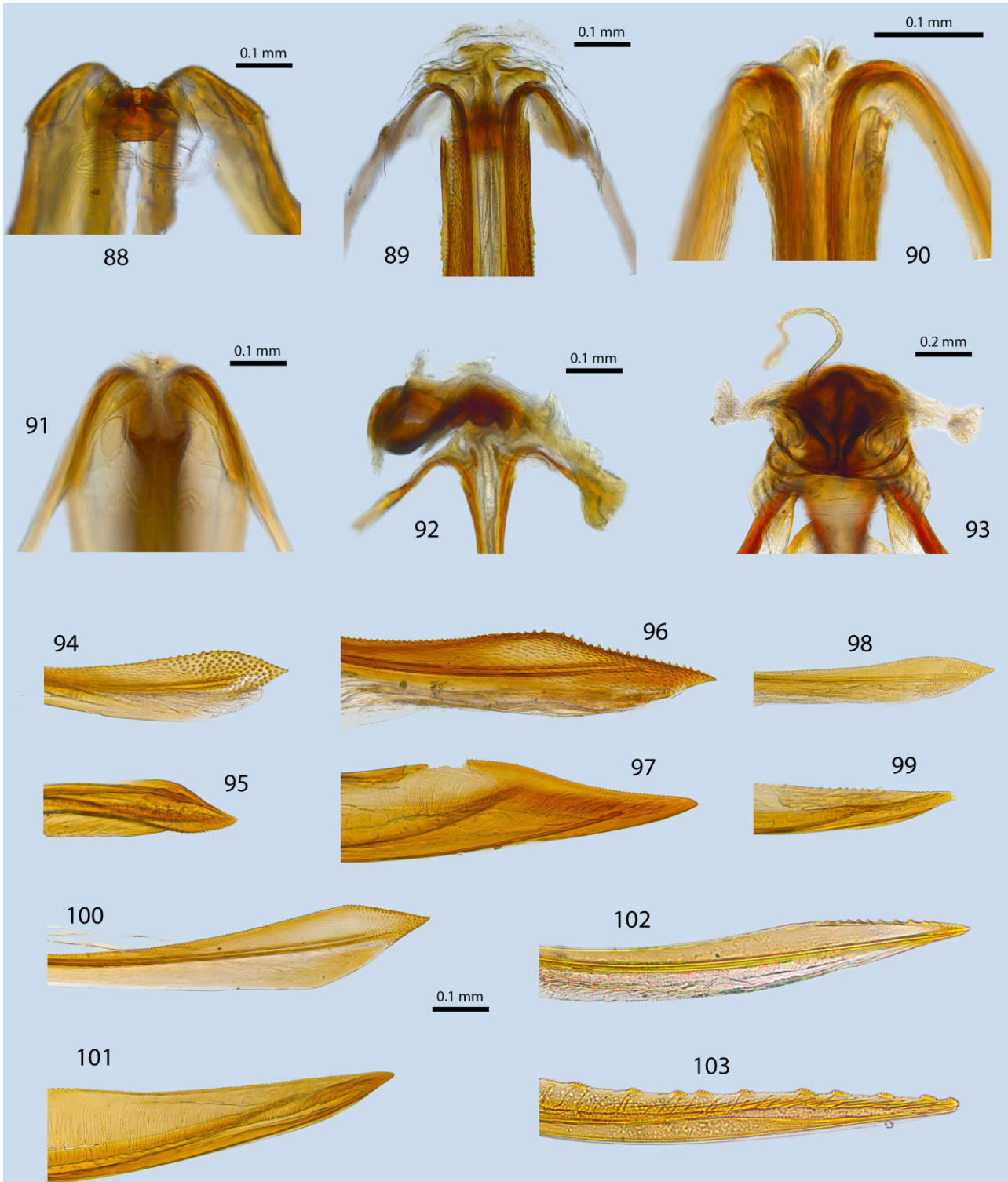
66. *Simple setae on dorsum*: (0) absent; (1) present, short; (2) present, long.
67. *Body shape*: (0) elongate, more than 3.0 times as long as basal width of pronotum, costal margin of hemelytron straight to somewhat convex apically (Figs 1–5, 7); (1) elongate–oval, distinctly less than 3.0 times as long as basal width of pronotum, costal margin of hemelytron convex (Figs 6, 8, 9).
68. *Brachypterous form*: (0) not known; (1) at least females, sometimes both sexes, usually or occasionally brachypterous.

HOST PLANT ANALYSIS

We used the mapping of host data to phylogeny in order to examine the sequence of host usage (Futuyma & McCafferty, 1990; Schuh & Brower, 2009). Host plant occurrences were treated as states of a hidden character and optimized on the cladogram. The host data recorded in this publication are from the literature, the label data of studied specimens, and original observations (Appendix 2). Host data were coded at the family level (Fig. 106). The host family classification follows Christenhusz & Chase (2014) for ferns and the Angiosperm Phylogeny Group III system (Angiosperm Phylogeny Group & III, 2009) for Angiosperms.

RESULTS

The analysis resulted in a single most-parsimonious tree of 213 steps with a consistency index (CI) of 0.52 and a retention index (RI) of 0.79 (Fig. 104). The same tree topology was obtained under successive approximation weighting and under implied weighting, with the integers of concavity factor ranging from 3 to 30. Nodes of the major clades are numbered 1–15. Character data



Figures 88–103. Female genitalia: 88, 89, *Diplazicoris lombokianus* sp. nov., 88, posterior wall, 89, vulvar area; 90, 91, *Hekista laudator*, 90, vulvar area, 91, dorsal labiate plate; 92, *Sixeonotus* sp., vulvar area; 93, *Helopeltis clavifer*, dorsal labiate plate; 94–103, valvulae – 94, 95, *D. lombokianus* sp. nov., 94, first, 95, second; 96, 97, *Bryocoris pteridis*, 96, first, 97, second; 98, 99, *Monalocoris filicis*, 98, first, 99, second; 100, 101, *Hekista laudator*, 100, first, 101, second; 102, 103, *Pycnoderes* sp., 102, first, 103, second.



Figure 104. Most parsimonious tree obtained from the analysis using 68 morphological characters (tree length = 213 steps; consistency index, CI = 0.52; retention index, RI = 0.79). Characters are plotted showing fast optimization. Filled circles, non-homoplastic characters mapped by state (discontinuous characters are mapped as homoplasy); open circles, homoplastic characters. Nodes 1–15 are discussed in the text.

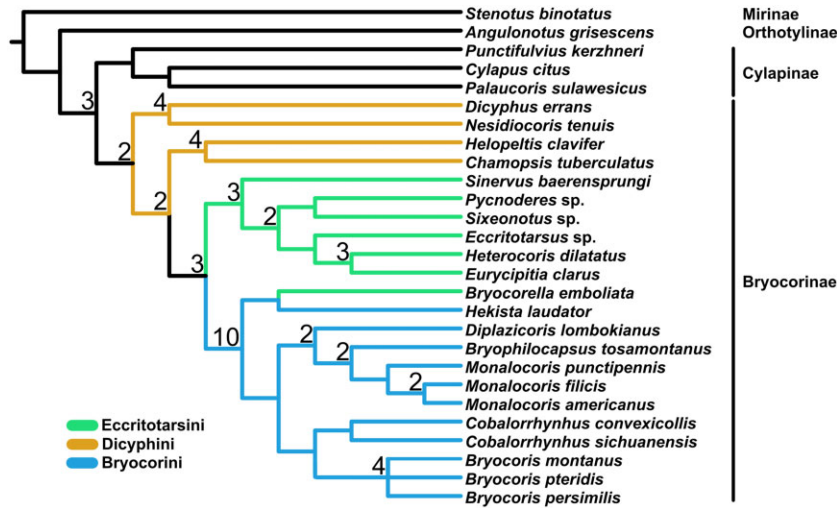


Figure 105. Cladogram based on the topology of Fig. 104 showing tribes and subfamilies. Numbers above nodes indicate Bremer values.

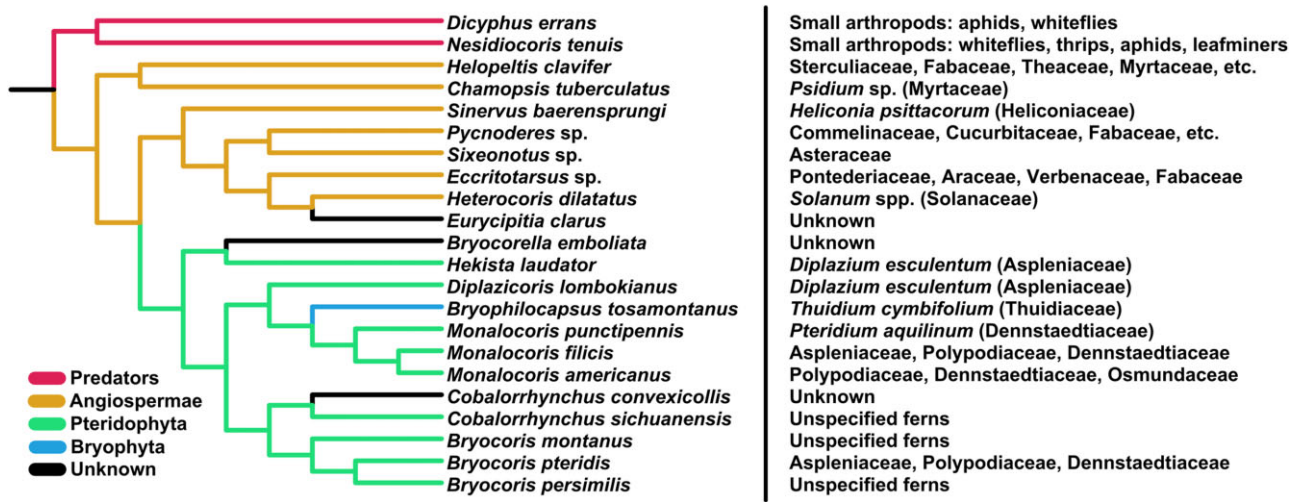


Figure 106. Host associations of Bryocorinae superimposed on phylogeny from Fig. 105.

are plotted on the tree using fast optimization (ACCTRAN). Filled circles represent non-homoplastic characters appearing only once on the tree, homoplastic characters are shown as open circles. Main character states and character numbers (in parentheses) supporting these nodes are indicated below.

The monophyly of the Bryocorinae (node 1) is supported by nine character changes, three of which [basally delimited maxillary plate (character 3, state 1), presence of setae on peritreme (character 25, state 2), and distinctly tuberculate metafemoral trichobotria (character 37, state 1)] appear as unique synapomorphies; however, the suture delimiting the base of maxillary plate is known to occur in some phylines and deraeocorines not included in the present analysis. The

clade is further diagnosed by several reversed characters, R + M vein reaching apex of corium (character 29, state 0; reversed in some Monaloniina and Ecclitotarsini), trichoma of metafemoral trichobotria absent or weakly developed (character 38, state 0; reversed in Ecclitotarsini), and presence of pseudopulvilli (character 47, state 1; reversed in Bryocorini).

Schuh (1976) first recognized the monophyly of Bryocorinae in the currently accepted composition. He followed Carvalho (1952) and diagnosed the subfamily as having a tendency towards the development of distally dilated tarsi, elongate guard setae, and usually a single-celled membrane. He also noted that all of these features are missing in the subfamily Dicyphina, a group that is nonetheless related to Monaloniina by the

presence of pseudopulvilli and eggs with characteristic respiratory horns; however, subsequent combined evidence (Schuh, Weirauch & Wheeler, 2009) and molecular (Jung & Lee, 2012) analyses rendered Bryocorinae as non-monophyletic. Although our data show support for the monophyly of Bryocorinae, the respective clade has relatively low Bremer support. A recent phylogenetic analysis of the entire subfamily based on morphological data and a much broader sampling of taxa (Namyatova, Konstantinov & Cassis, 2015, in press) also favours the monophyly of Bryocorinae.

Dicyphina s.s. (node 2) are supported by nine (four unambiguous) character changes, including three unique synapomorphies: pronotal collar flat, posteriorly demarcated only by weak depression running anteriorly to propleural suture (character 13, state 2); peritreme of metathoracic scent gland flat, not raised above pleural surface, with jagged margins (character 23, state 0); and metathoracic spiracle surrounded with evaporative bodies (character 26, state 1).

Sister relationships of the subtribe Monaloniina and remaining bryocorines (node 3) are supported by seven (four unambiguous) morphological characters, two of which appear as uncontradicted synapomorphies: last tarsal segment distinctly swollen apically (character 40, state 1) and tarsal bearing long guard setae (character 41, state 1). Schuh (1976) used both characters as synapomorphies of Bryocorinae, although mentioning that these features are missing in Dicyphina.

This clade is not consistent with the analysis of Schuh (1976) who treated Dicyphina and Monaloniina as a monophyletic group supported by the presence of respiratory horns on the eggs and similarities in body shape. As we were unable to investigate the egg structure for most of the taxa treated here, we have not included the first character in the analysis. The morphological data examined show no support in favour of a sister relationship for Dicyphina and Monaloniina, although we documented one novel character shared by both groups: i.e. the dorsally expanded bursa copulatrix with characteristic concentric wrinkles at sides (character 61, state 2).

The monophyly of the Monaloniina (node 4) is corroborated by eight (seven unambiguous) character changes, of which one (absence of peritreme; character 23, state 3) appears as a unique synapomorphy. Still, the absence of the evaporative area and peritreme of scent efferent system is documented for several genera of Dicyphina (e.g. Cassis, 1986) not included in the present analysis.

Sister relationships of Ecclitarsini + Bryocorini (node 5) are supported by nine (six unambiguous) reversed character changes, including relatively small eyes (character 1, state 0), mesonotum entirely covered by pronotum (character 19, state 1), punctured pronotum (character 27, state 1), undeveloped basal membra-

nous sac of phallosome (character 57, state 1), short ductus seminis (character 58, state 1), and simple sac-like endosoma (character 60, state 0).

This node corresponds to the tribe Bryocorini *sensu* Carvalho (1952, 1955, 1957) and contradicts the results of Schuh (1976) who treated Bryocorini as a sister group of Dicyphina + Monaloniina based on the presence of pseudopulvilli and trichobothrial pattern. Carvalho (1952) diagnosed the group as having punctured pronotum, labium reaching beyond the apex of forecoxae, and head without distinct neck. All these features were found to be highly variable in the present analysis and could hardly be used to detect the phylogenetic relationships of higher taxa.

Support for the Monophyly of the tribe Ecclitarsini (node 6) comes from 11 character changes, five of which are unique synapomorphies of the clade: scent gland evaporative area reduced, narrow, and falciform (character 22, state 2); peritreme lanceolate, extended posteriorly along ventral margin of metapleuron (character 24, state 1); trichobotria deeply recessed and tuberculate (character 37, state 3); asymmetrical parempodia, with outer parempodium slightly shorter than inner parempodium (character 45, state 1); pulvilli attached to inner surface of a claw, semicircular and equipped with pulvillar combs (character 46, state 2).

Containing 110 recognized genera, Ecclitarsini is the largest tribe within Bryocorini and exhibits fascinating structural diversity, not only in general appearance, but also in characters that are uniform across other tribes of plant bugs, e.g. the pronotal collar and male genitalia; however, Schuh (1976) and Stonedahl (1988) documented a number of common features in the pretarsus, evaporative area and trichobothrial pattern of ecclitarsines, and our results are fully consistent with their findings.

The monophyly of the Bryocorini (node 7) is well corroborated from 18 character changes, including the following uncontradicted synapomorphies: vertex distinctly carinate basally (character 6, state 1); labial segment I short, almost as long as wide (character 9, state 0); suture delimiting pronotal collar scalloped (character 16, state 1); peritreme strongly elevated above pleural surface (character 23, state 2); peritreme broadly rounded (character 24, state 2); peritreme with single seta (character 25, state 1); parempodia absent (character 44, state 3); opening of genital capsule directed posteriorly (character 48, state 1); capitite processes of dorsal connectives greatly reduced (character 52, state 1); phallosome entirely membranous, with horseshoe sclerite at base of dorsal wall (character 56, state 1); sclerotized rings of dorsal labiate plate small, round, almost not sclerotized (character 62, state 1).

The tribe Bryocorini in its currently accepted composition was established by Schuh (1976) based on the

absence of parempodia, which is a unique state within Miridae. Our data show the strongest support for the monophyly of this small tribe because of the large number of highly synapomorphic states. Cobben (1968) emphasized the striking difference in egg structure of Bryocorini genera examined by him (*Bryocoris* and *Monalocoris*), stating that: 'The *Bryocoris* egg type is so distinct from the typical cimicomorphous egg that it is difficult to imagine how the *Bryocoris* type could have evolved from it'.

Results of our analysis clearly show that the monotypic genus *Bryocorella*, currently placed within the tribe Eccritotarsini (Schuh, 1976, 1995, 2002–2013), belongs to the Bryocorini.

Bryocorella + *Hekista* (node 8), the basal clade of Bryocorini, is defined by three homoplasious characters, including deeply scalloped sides of scutellum (character 20, state 2; also occurs in *Diplazicoris lombokianus* sp. nov.), deep punctures on pronotum (character 27, state 2; also present in *Monalocoris punctipennis* Linnavuori, 1975), and pale exocorium (character 31, state 1; occurs in node 11).

The monophyly of the remaining Bryocorini (node 9) appeared to be supported by the presence of a twin-coned process of genital capsule (character 50, state 2; with the reverse in node 11 and *Cobalorrhynchus*) and short simple setae on dorsum (character 66, state 1).

Bryocoris s.l. (node 10) is defined by three character changes, including one synapomorphy: calli extending on sides of pronotum (character 17, state 1). It is further supported by two homoplasious character changes, both also occurring in *Hekista laudator* Kirkaldy, 1902: pronotal collar matt (character 15, state 1); and cuneus elongate, twice as long as wide at base (character 33, state 0).

Cobalorrhynchus (node 11) is corroborated by two character changes, labial segment II comparatively long, slightly shorter than three times as long as wide (character 10, state 1) and left wall of genital capsule with large single-coned process above the left paramere (character 50, state 1). The latter character appears as a synapomorphy on a resulting cladogram.

Bryocoris s.s. (node 12) is supported by five character changes including one synapomorphy, viz. females or both sexes usually or occasionally brachypterous (character 68, state 1).

Node 13, the clade of (*Diplazicoris* (*Bryophilocapsus* + *Monalocoris*)), is supported by three homoplasious characters: antennal segment I shorter than width of vertex (character 8, state 1); cuneal fracture distinctly incised (character 32, state 1); and body oval, less than three times as long as basal width of pronotum (character 67, state 1). All three characters occur in various outgroup taxa, but are absent in other Bryocorini.

Node 14 represents the clade of *Bryophilocapsus* + *Monalocoris* and is defined by three characters, in-

cluding one synapomorphy: strongly deflected apex of hemelytron (character 28, state 1).

Node 15 or *Monalocoris* s.l. (*Monalocoris* + *Sthenarusoides*) is defined by just one homoplasious character: pronotal collar narrow, distinctly thinner than width of antennal segment I (character 14, state 1).

There is no strong statistical confidence in the topology within the Bryocorini, as evidenced by the relatively low Bremer support values of many clades. The only exception is the clade *Bryocoris* s.s. (node 12, Bremer support 4). Other relatively well-supported clades (Bremer support 2) are *Diplazicoris* (*Bryophilocapsus* + *Monalocoris*) (node 13), *Bryophilocapsus* + *Monalocoris* (node 14), and *Monalocoris* s.s.

HOST PLANT ASSOCIATIONS

As pointed out in the introduction, most taxa of plant bugs show a high degree of host specificity and almost exclusively feed on seed plants, especially from rosid and asterid clades (Wheeler, 2001; Cassis & Schuh, 2012); however, the available data suggest that all taxa of the tribe Bryocorini except *Bryophilocapsus tosamontanus* Yasunaga, 2000 are restricted to ferns. The latter species belongs to a monotypic genus and shows a remarkable example of host shift, being the only known moss-feeding plant bug species (Wheeler, 2001) that feeds on the feather moss *Thuidium cymbifolium*. The bryocorines from the genera *Bryocoris*, *Monalocoris* (Kullenberg, 1944; Southwood & Leston, 1959; Srivastava, Lawton & Robinson, 1997; F. V. Konstantinov, pers. observ.), *Hekista*, and *Diplazicoris* (F. V. Konstantinov, orig. observ.) mainly feed on the sporangia, but can also attack fern foliage. Mapping of the host data on the revealed tree shows the fern family Aspleniaceae as an ancestral association for the tribe Bryocorini (Fig. 106).

The classification of ferns has been historically unstable, with significant changes in familial and generic concepts over the last decades (Smith *et al.*, 2006). Christenhusz & Chase (2014) provided an updated consensus fern classification based on recently published molecular phylogenies, and used broad family concepts in comparison with previously published classifications, with particularly expanded families Aspleniaceae, Cyathaceae, Polypodiaceae, and Schizaeaceae. Aspleniaceae, the ancestral host-plant family for Bryocorini, forms a sister group to the fern family Polypodiaceae (Christenhusz & Chase, 2014).

Most bryocorines appear to have small distribution ranges frequently limited to the type locality and known from a single host; however, three species, namely the trans-Nearctic *Monalocoris americanus* Wagner and Slater, 1952, and the trans-Palaearctic *Bryocoris pteridis* (Fallén, 1807) and *Monalocoris filicis* (Linnaeus, 1758), form an exception and were documented from many

fern species (Appendix 2). Mapping of all of these widespread species on the genus-level fern phylogenetic tree published by Christenhusz & Chase (2014) clearly shows their ability to switch between phylogenetically distant fern hosts rather easily. Notably, *M. americanus* is associated with ferns from the basal family Osmundaceae, as well as Dennstaedtiaceae and distantly related family Polypodiaceae. Both *M. filicis* and *B. pteridis* show a similar pattern of distribution across the fern tree; however, in the given area all three species tend to use one or just a few related host species. For instance, in Great Britain *M. filicis* feeds chiefly on *Pteridium aquilinum* (Dennstaedtiaceae), whereas *B. pteridis* feeds on *Athyrium filix-femina* and *Dryopteris filix-mas* (Polypodiaceae) (Southwood & Leston, 1959).

The available data suggest that ferns are generally underused by insects (Ehrlich & Raven, 1964; Cooper-Driver, 1978; Hendrix, 1980; Ottosson & Anderson, 1983), although this rule contains certain exceptions (Lawton, 1976; Balick, Furth & Cooper-Driver, 1978; Auerbach & Hendrix, 1980). According to the calculations of Hendrix (1980) the ratio of fern-feeding insects to fern species is 1 : 19, whereas the ratio of angiosperm-feeding insects to angiosperm species is less than 1 : 1. Moreover, fern species are generally more widespread than angiosperms and therefore might be more easily accessible. Hendrix further argued that adaptive radiations appear to be extremely rare among fern-feeding insects at the generic or suprageneric levels, and slightly more than 70% of fern-feeding insect genera have only one oligophagous species on pteridophytes.

Although the data on hosts suggest that several insect lineages appear to radiate on ferns, this idea had not been tested in the phylogenetic context at the time of Hendrix's (1980) review, and only a handful of phylogeny-based studies have been published to date. Weintraub *et al.* (1995) gave a detailed account of the insect–pteridophagy association, providing a pioneering phylogenetic study of insect–fern interactions and documenting adaptive radiation on ferns for *Ischalis* and several sister genera of the looper moth from the tribe Lithiniini (Lepidoptera, Geometridae). Jensen & Holman (2000) published a phylogenetic analysis of the aphid genus *Macrosiphum* (Hemiptera: Aphidiidae), and demonstrated the monophyly of a fern-feeding clade containing 16 species. Isaka & Sato (2014a, b) recently examined the evolution of host associations within sawflies and provided evidence for adaptive radiation on ferns in two lineages: the small family Blasticotomidae containing 13 species and the subfamily Selandriinae (Hymenoptera: Tenthredinidae) containing slightly fewer than 1000 species.

Weintraub *et al.* (1995) stressed that the looper moth radiating on ferns uses a broad range of hosts both in terms of taxonomy and growth forms, which may

suggest a successful, but late initial colonization with subsequent host shifts unconstrained by fern phylogeny. The same conclusion may be derived from two other cases of adaptive radiation on ferns known from the literature. Five out of 16 species of the fern-feeding *Macrosiphum* clade use more than one host, including *Macrosiphum dryopteridis* (Holman, 1959) and *Macrosiphum walkeri* (Robinson, 1980) that feed on a wide range of phylogenetically distant hosts from two and five fern families, respectively (Jensen & Holman, 2000). Published information on hosts of blasticotomid and selandriine sawflies is scarce, and is mainly limited to the European species, but virtually all species with known biology were reported from several fern families (Taeger *et al.*, 1998; Vikberg & Liston, 2009).

Thus, Bryocorini represent one of the very few currently known examples of the adaptive radiation of a fairly large insect group on ferns; however, more such cases might be revealed in the future, apparently including one more group within the subfamily Bryocorinae, namely the recently erected tribe Felisacini, which contains the fern-feeding genus *Felisacus* (Namyatova *et al.*, 2015, in press).

It is noteworthy that all taxa radiating on ferns show an ability to switch between phylogenetically distant hosts, and no group is currently known that feeds on a single fern clade. Overall, the phytophagous insect fauna of ferns is largely derived, switching from seed plants in all cases, with the exception of the basal sawfly family Blasticotomidae (Ward, Hackshaw & Clarke, 2003). Weintraub *et al.* (1995) suggested that the host shifts could be facilitated by immunity to a common defensive chemistry found in many families of ferns, which are generally believed to have a relatively simple and far less diverse secondary chemistry in comparison with angiosperms (Balick *et al.*, 1978; Cooper-Driver, 1985; Tahvanainen & Niemelä, 1987). Lafont *et al.* (2010) suggested that ecdysteroids may play a major role in phytophagous insect control in the case of ferns. This seems probable, as phytoecdysteroids are comparatively rare in angiosperms and mainly occur in ferns and gymnosperms (Harborne, 1993); however, this idea has never been tested in detail, and more studies are needed to get a better understanding of fern–insect interactions.

TAXONOMY

BRYOCORINI BAERENSPRUNG, 1860

Bryocorini Baerensprung, 1860: 13 (Bryocorides).

Diagnosis

Readily recognized by the following characters: eyes small, contiguous to anterior margin of pronotum (Figs 10, 13–15, 19, 20); posterior margin of vertex cari-

KEY TO GENERA

1. Entire exocorium and outer part of cuneus contrastingly white, pronotum, corium, and inner part of cuneus uniformly dark brown (Figs 3, 7). Pronotum with dense deep punctures, hemelytron smooth or shallowly punctate. Simple setae on dorsum distinctly longer than width of tibiae.....2
 - Colour pattern variable, if exocorium pale yellow or transparent, corium with large areas of similar colour, or at least posterior margins of pronotum pale. Pronotum smooth or with shallow punctures similar to those on hemelytron. Simple setae on dorsum short, recumbent, not longer than width of tibiae.....3
2. Costal margin convex, exocorium wide, gradually narrowing apically (Fig. 7). Pronotal collar comparatively wide, shining, distinctly scalloped posteriorly. Antennal segment I shorter than width of vertex.....*Bryocorella*
 - Costal margin straight, hemelytra parallel-sided, exocorium narrow along entire length (Fig. 3). Pronotal collar narrow, matt, posteriorly delimited by straight suture. Antennal segment I equal to width of head.....*Hekista*
3. Body elongate, hemelytra in macropterous form parallel-sided, slightly widened in apical half. Costal fracture without incision (Figs 1, 2, 4).....4
 - Body oval, hemelytra with more or less convex costal margin, costal fracture with obvious incision (Figs 6, 8, 9). Always macropterous.....5
4. Labial segment IV apically blunt, short, almost equal in length to segment III (Fig. 22). Macropterous or brachypterous. Costal margin of hemelytron in lateral view without dark line, usually darkened in apical one-quarter. Left paramere with well-developed, curved sensory lobe and modified, strongly curved or bifid apical process (Fig. 69).....
 -*Bryocoris*
 - Labial segment IV long and distinctly tapering, distinctly longer than segment III (as in Fig. 26). Hemelytron in lateral view with narrow dark-brown line along costal margin, sometimes indistinct at base. Brachypterous forms unknown. Left paramere L-shaped, not modified.....*Cobalorrhynchus*
5. Pronotal collar narrow, distinctly thinner than width of antennal segment I (Fig. 19).....*Monalocoris*
 - Pronotal collar distinctly wider than width of antennal segment I (Figs 10, 15).....6
6. Pronotal collar distinctly scalloped posteriorly (Figs 10, 15). Hemelytron more or less straight, membrane not deflected. Right paramere large, almost equal in length to left paramere. Left paramere with long characteristic spine (Fig. 67).....*Diplazicoris*
 - Posterior margin of pronotal collar and sides of scutellum straight, not scalloped. Membrane deflected. Right paramere shorter than left paramere. Apical process of left paramere finely serrate, without spine.....*Bryophilocapsus*

nate (Figs 10, 14, 15, 19, 20); labial segment I short and thick, almost as long as wide (Figs 22–24, 26); pronotal collar narrow, posteriorly delimited by deep, more or less scalloped suture (Figs 10, 14, 15, 19, 20); peritreme of scent efferent system broadly oval, strongly raised and convex, with single seta (Figs 31–36), R + M vein in macropterous specimens with row of punctures at base (Fig. 28), ungitractor with large lamellate pseudopulvilli and without parempodia (Figs 48, 50, 52), genital capsule with wide, posteriorly directed opening (Figs 57–60, 62–64); aedeagus small, with reduced capitate processes, phallosome membranous, with horseshoe sclerite at base of dorsal wall, ductus seminis almost entirely sclerotized, its distal two-thirds located at almost right angles with proximal third, and almost reaching aperture of phallosome in repose, endosoma small and simple, without sclerotizations (Figs 80–83); dorsal labiate plate membranous, thin-walled, with small, round, weakly sclerotized, and barely visible rings (Fig. 91).

Remarks

Based on the phylogenetic analysis, we redefine the tribe Bryocorini to contain the following seven genera, including one genus described as new: *Bryocorella*

Carvalho, 1956, *Bryocoris* Fallén, 1829, *Bryophilocapsus* Yasunaga, 2000, *Cobalorrhynchus* Reuter, 1906 gen. dist., *Diplazicoris* gen. nov., *Hekista* Kirkaldy, 1902, and *Monalocoris* Dahlbom, 1851. The genus *Bryocorella* agrees in all essential characters with the diagnosis of the tribe given above, and is therefore transferred to Bryocorini from the tribe Ecritotarsini. *Cobalorrhynchus*, synonymized with *Bryocoris* by Yasunaga & Kerzhner (1998), and then reinstated as a subgenus of *Bryocoris* by Hu & Zheng (2000), is treated here as a separate genus. Although both taxa are superficially similar and form a distinct clade in our analysis, they differ in many important features, including the structure of labium, male genitalia, and the occurrence of brachyptery.

BRYOCORELLA CARVALHO, 1956
FIG. 7

Bryocorella Carvalho, 1956: 22. Type species: *Bryocorella emboliata* Carvalho, 1956 (by monotypy).

Diagnosis

Recognized by the following combination of characters: dorsum dark brown, with contrastingly whitish

exocorium and outer margin of cuneus (Fig. 7); antennal segment I slightly shorter than vertex width; pronotal collar flat, shining, distinctly longer than width of antennal segment I; labium reaching to slightly surpassing fore coxa; suture delimiting pronotal collar and sides of scutellum deeply scalloped; pronotum with deep, coarse punctures; exocorium wide, widest at basal quarter, with slightly and evenly convex costal margin; cuneus somewhat longer than width at base; membrane not deflected; right paramere simple, distinctly smaller than left paramere, broadly rounded apically; left paramere falciform, without distinct sensory lobe (Carvalho, 1956: fig. 14).

Somewhat similar to *Hekista* Kirkaldy, 1902 in body proportions, whitish exocorium and outer margin of cuneus, deep punctures on pronotum, distinctly scalloped sides of scutellum, and long simple setae on dorsum; however, clearly differs from *Hekista* in having narrow, matt, and posteriorly straight pronotal collar, narrow exocorium with straight costal margin, cuneus narrowly triangular, twice as long as width at base, and shape of both parameres.

Remarks

The genus was described to accommodate a single species, *Bryocorella emboliata* Carvalho, 1956, described from four specimens sampled in Kosrae Island, Micronesia. No new data on the genus have been published since the original description, and nothing is known about the host plant. Examination of the holotype retained at the National Museum of Natural History (Washington D.C.) allowed us to include the genus in the analysis and revealed its affinity to *Hekista* and other bryocorine genera.

BRYOCORIS FALLÉN, 1829

FIGS 4, 5, 14, 20, 23, 29, 36, 57, 62, 68, 69, 80, 81, 96, 97

Bryocoris Fallén, 1829: 151. Type species: *Capsus pteridis* Fallén, 1807 (by monotypy).

Diagnosis

Recognized by the following combination of characters: antennal segment I slightly shorter than head width and distinctly longer than vertex width; labium slightly surpassing fore coxa, labial segment IV short, about twice as long as wide, slightly tapering at apex (Fig. 23); pronotal collar matt, narrow, equal to width of antennal segment I, finely scalloped posteriorly (Fig. 20); pronotum with shallow punctures; sides of scutellum finely scalloped or almost smooth (Fig. 29); costal margin of hemelytron pale yellow, sometimes darkened in apical one-quarter; genital capsule with large twin-coned process above left paramere (Figs 57, 62); left paramere more than three times as large as

right paramere, with distinct sensory lobe and strongly bent apex (Fig. 69); both sexes, sometimes only females, occasionally or usually brachypterous (Fig. 5).

The genus is most similar in body proportions and coloration to *Cobalorrhynchus* Reuter, 1906; however, species of *Cobalorrhynchus* clearly differ from species of *Bryocoris* in having claw-shaped, long, thin, and strongly tapering labial segment IV, brown line on the costal margin of hemelytron, and by the structure of genital capsule and left paramere.

Diversity and distribution

Bryocoris includes ten species: *Bryocoris bui* Hu and Zheng, 2000; *Bryocoris concavus* Hu and Zheng, 2000; *Bryocoris formosensis* Lin, 2003; *Bryocoris gracilis* Linnavuori, 1962; *Bryocoris insuetus* Hu and Zheng, 2000; *Bryocoris montanus* Kerzhner, 1972; *Bryocoris nitidus* Hu and Zheng, 2004; *Bryocoris persimilis* Kerzhner, 1988; *Bryocoris pteridis* (Fallén, 1807), and *Bryocoris xiongi* Hu and Zheng, 2000. Most of these species are restricted to southern China (Sichuan and Yunnan provinces, Taiwan). *Bryocoris persimilis* and *B. montanus* are known from the Russian Far East, with *B. montanus* also recorded from Japan (Yasunaga, 2000). The distributional range of *B. gracilis* extends from Sichuan and Hunan provinces of China, Taiwan, and Japan to New Guinea. Only *B. pteridis* has a wide trans-Palaeartic range, which is almost entirely confined to forest regions.

Remarks

Relatively little attention had been given to this genus until Hu & Zheng's (2000) work on the *Bryocoris* of China. These authors described four new species, restored *Cobalorrhynchus* as a subgenus of *Bryocoris*, and provided an illustrated key to species and detailed diagnoses for both subgenera.

BRYOPHILOCAPSUS YASUNAGA, 2000

Bryophilocapsus Yasunaga, 2000: 95. Type species: *Bryophilocapsus tosamontanus* Yasunaga, 2000 (by monotypy).

Diagnosis

Recognized by the following combination of characters: antennal segment I about one-half the width of head and somewhat shorter than width of vertex; labium long, reaching apex of middle coxa; pronotal collar wider than width of antennal segment I; pronotum with shallow punctures; margin of exocorium convex; cuneal fracture incised; cuneus broadly triangular, slightly longer than basal width; membrane strongly deflected; right paramere about twice as small as left paramere; left paramere falciform, with indistinct sensory lobe, apically dentate (see figs in Yasunaga,

2000). It is similar to *Monalocoris* in the short antennal segment I, incised cuneal fracture, and membrane deflected at base of cuneus, but has many distinctive features, e.g. larger size (3.0–3.6), pronotal collar distinctly wider than width of antennal segment I, and shape of left paramere.

Diversity and distribution

The genus was originally described and remains monotypic with *Bryophilocapsus tosamontanus* Yasunaga, 2000 known from Shikoku Island, southern Japan.

Remarks

In contrast to all other species of the tribe, *B. tosamontanus* was found on a thuidiaceus moss, *Thuidium cymbifolium* (Dozy & Molk.) Dozy & Molk. (Bryophyta: Thuidiaceae). No material of this genus was available for examination; the above account is based on the original description and figures presented in Yasunaga (2000).

COBALORRHYNCHUS REUTER, 1906

FIGS 1, 2

Cobalorrhynchus Reuter, 1906: 1. Type species: *Cobalorrhynchus biquadrangulifer* Reuter, 1906 (by monotypy). Synonymized with *Bryocoris* Fallén by Yasunaga & Kerzhner, 1998: 88. Restored to subgeneric status by Hu & Zheng, 2000.

Diagnosis

Recognized by the following combination of characters: labium reaching middle of mesosternum, labial segment IV claw-shaped, distinctly longer than wide, twice thinner than segment III, and strongly tapering from base; antennal segment I distinctly shorter than head width, but somewhat longer than vertex width; pronotal collar matt, slightly longer than width of antennal segment I, finely scalloped posteriorly; pronotum with shallow punctures; hemelytron in lateral view with narrow dark-brown line along entire costal margin, sometimes indistinct at base; genital capsule with large single-coned process above left paramere or without any processes; right paramere about twice as small as left paramere; left paramere falciform, with indistinct sensory lobe and almost straight, gradually tapering apical process; both sexes always macropterous.

The genus is most similar to *Bryocoris* in size range, overall body proportions, and colour pattern of hemelytron; however *Bryocoris* clearly differs from *Cobalorrhynchus* in the short and thick labial segment IV, absence of the brown line along costal margin, the genital capsule with characteristic twin-coned process above the left paramere, the reduced right

paramere, the complex shape of left paramere with well-defined sensory lobe and twisted apical process, and the occurrence of brachyptery.

Diversity and distribution

Cobalorrhynchus has 11 species: *Cobalorrhynchus biquadrangulifer* Reuter, 1906 comb. nov.; *Cobalorrhynchus convexicollis* (Hsiao, 1941) comb. nov.; *Cobalorrhynchus flaviceps* (Zheng and Liu, 1992) comb. nov.; *Cobalorrhynchus hsiaoi* (Zheng and Liu, 1992) comb. nov.; *Cobalorrhynchus latiusculus* (Hu and Zheng, 2007) comb. nov.; *Cobalorrhynchus latus* (Lin, 2003) comb. nov.; *Cobalorrhynchus lii* (Hu & Zheng, 2000) comb. nov.; *Cobalorrhynchus lobatus* (Hu & Zheng, 2000) comb. nov.; *Cobalorrhynchus paravittatus* (Lin, 2003) comb. nov.; *Cobalorrhynchus sichuanensis* (Hu & Zheng, 2000) comb. nov.; and *Cobalorrhynchus vittatus* (Hu & Zheng, 2000) comb. nov. The distributional range of this genus is restricted to southern and central China (Xizang, Sichuan, Gansu, Yunnan, Shaanxi, and Guangxi provinces, Taiwan) with just one species, *C. hsiaoi*, also known from Japan.

Remarks

Hu & Zheng (2000) defined *Cobalorrhynchus* in the currently accepted sense and treated it as a subgenus of *Bryocoris* without discussing the diagnostic features of the latter. Our results are fully congruent with the treatment of Hu and Zheng, but show little support for the monophyly of *Bryocoris* s.l. Therefore, we propose regarding *Bryocoris* Fallén, 1829 and *Cobalorrhynchus* Reuter, 1906 as two separate genera.

DIPLAZICORIS GEN. NOV.

FIGS 6, 10, 15, 22, 27, 31, 32, 42, 46, 48, 52, 59, 60, 66, 67, 82, 83, 88, 89, 94, 95

Type species: *Diplazicoris lombokianus* sp. nov.

Diagnosis

Recognized by the following combination of characters: antennal segment I short, almost one-half the head width and distinctly shorter than vertex width; labial segment IV apically blunt, thick, and short (Fig. 22); pronotal collar flat and wide, deeply scalloped along posterior margin (Figs 10, 15); corium with distinctly convex lateral margin; cuneal fracture incised; genital capsule (Figs 59, 60) with characteristic twin-coned process above left paramere and broadly rounded, apically serrated lamella in front of right paramere; right paramere (Fig. 66) large, almost equal in length to left paramere; left paramere with long spine at base of apical process and small teeth close to midpoint; vestibulum well sclerotized, straight, symmetrical, running in caudal direction; second valvula as in Fig. 95, apically twisted, with peculiar row of large teeth on inner surface.

The new genus clearly differs from all other representatives of the tribe in the oval scent gland evaporative area with smoothly rounded anterior margin (Fig. 31), the large right paramere that is almost equal in length to the left paramere (Fig. 66), the shape and serration of the left paramere, the strongly sclerotized vestibulum, and the shape of the second valvula. *Diplazicoris* is somewhat similar to *Bryophilocapsus* Yasunaga, 2000 in body proportions and coloration, but clearly differs from *Bryophilocapsus* by the following features: scalloped margins of pronotal collar and scutellum; straight, not deflexed membrane; and by the other diagnostic characters mentioned above.

Description

Male

Coloration: Dorsum and venter almost uniformly pale yellowish brown to dirty pale brown; clypeus and labrum dark brown; antennal segment I with diffuse brown ring apically and usually with somewhat darkened base; segment II dark brown entirely or in apical half; remaining antennal segments pale to dark brown, somewhat paler than apex of segment II; hemelytron usually with narrowly darkened claval commissure and indistinct pale brown macula medio-apically; membrane with diffuse pale brown stripe along midline or at least with darkened area around apex of vein; pregenital segments of abdomen at least partly darkened, usually dark brown with dirty yellow areas.

Structure: Body elongate-oval, macropterous.

Head: Vertical, rather wide, nearly as wide as high, almost triangular below eyes in frontal view; vertex broad and almost flat, distinctly carinate at base; frons convex, epistomal suture distinctly depressed; clypeus prominent, oriented ventroposteriorly; mandibular plate broadly triangular; maxillary plate rectangular, twice as long as high; bucculae short, merging behind base of labium; gula reduced, one-half length of buccula; eyes relatively small, less than half height of head in lateral view, not stylate, slightly projecting beyond anterolateral margins of pronotum; antennal fossa located slightly above ventral margin of eye; first antennal segment relatively short, swollen in apical three-quarters; second segment thin; segments III and IV filiform; labium thick, reaching to middle of mesosternum, segment IV short, twice as long as broad at base, apically blunt.

Thorax: Pronotum trapeziform, with somewhat carinate anterior angles, weakly concave lateral margins, broadly rounded posterior angles, and almost straight posterior margin; pronotal collar demarcated by deep suture, flat and wide, 1.3–1.4 times as wide as antennal segment I at middle, deeply scalloped along posterior

margin; calli weakly delimited, disc only slightly raised at base; metathoracic scent-gland evaporative area comparatively small, elongate-oval, with widely rounded anterior margin; peritreme large, distinctly raised, oval; entire mesonotum and usually base of scutellum covered by posterior margin of pronotum, lateral margins of scutellum deeply scalloped.

Hemelytron: Semitransparent, corium with distinctly convex lateral margin, R + M vein distinctly depressed, slightly S-curved, almost reaching apex of corium, with a row of punctures at basal one-quarter, medial fracture distinctly elevated, straight, almost reaching apex of corium, and terminating at same level with claval suture; costal fracture distinct, deeply incised at base; cuneus relatively wide, only slightly longer than wide; membrane with single cell not surpassing apex of cuneus.

Legs: All femora comparatively short, cylindrical, hind femur not swollen; tibia straight and rather short; tarsus three-segmented, segments I and II almost equal in length, segment III 1.3 times as long as segment II, distinctly swollen apically, with long guard setae; unguitractor with large and very wide, broadly triangular, pseudopulvilli surpassing apex of claw, parempodia absent; claw falcate, strongly and gradually curved.

Surface and vestiture: Head, pronotal collar, calli, and scutellum smooth and shiny; remainder of pronotum and hemelytron shiny, with dense but indistinct, shallow punctures (as in Fig. 27); thoracic pleura and abdomen shiny, smooth to weakly rugose. Dorsum and appendages with dense, relatively short, semi-adpressed pale simple setae; thoracic pleura with a few similar setae; abdomen with dense simple setae almost twice as long as those on hemelytra; tibial spines absent, tibiae with dense pale simple setae only.

Genitalia: Genital capsule: comparatively large, about half of abdomen, short and very wide, about twice as wide as long (Fig. 60), with base partly retracted into abdominal segment VIII; dorsal wall straight, ventral wall strongly sloping and extending caudally; supragenital bridge absent; opening of genital capsule wide, with large twin-coned process in front of left paramere and broadly rounded, apically serrated lamella in front of right paramere (Fig. 59); plane of phallic structures turned slightly more than 20°. Parameres: left paramere (Fig. 67) L-shaped, with swollen base; apical process large, flattened, twisted at base, with long spine and small teeth close to midpoint, apically curved and finely serrate; right paramere (Fig. 66) large, almost equal in length to left paramere, L-shaped, with blunt apical process. Aedeagus: small and simple (Figs 82, 83); phallobase with strongly reduced capitate

processes; phallotheca entirely membranous, with slightly sclerotized area at base of dorsal wall adjacent to phallobase; ductus seminis almost entirely sclerotized, its proximal third with rings, strongly swollen, and sclerotized at base; distal two-thirds of ductus seminis placed at an angle to proximal third, sclerotized, deeply incised apically and reaching apex of phallotheca in repose; opening of secondary gonopore without sculpture, large and slit-like; endosoma small and simple, without sclerotizations.

Female

Coloration, surface, vestiture, and structure: As in male.

Genitalia: Dorsal labiate plate small, entirely membranous, sclerotized rings round, very small and weakly sclerotized; posterior wall with heavily sclerotized, large, and dorsally expanded sclerite bearing proximal incision along midline; sclerites encircling vulva symmetrical, large, expanding at sides (Fig. 89); vestibulum well sclerotized, straight, symmetrical, running in caudal direction; apex of first valvula (Fig. 94) gradually tapering, with outer surface clothed with dense minute teeth; second valvula as in Fig. 95, apically twisted, with peculiar row of large teeth on inner surface and finely dentate outer surface.

Etymology

The new genus is named for host association with ferns belonging to the genus *Diplazium* (Aspleniaceae). The gender is masculine.

DIPLAZICORIS LOMBOKIANUS SP. NOV.

Holotype

Indonesia. West Nusa Tenggara: Lombok Island, Senaru, track to Rinjani, 8.31956°S, 116.405°E, 31 August 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), ♂ (AMNH_PBI 00337343) (ZISP).

Paratypes

Indonesia. West Nusa Tenggara: Lombok Island, Senaru, track to Rinjani, 8.31956°S, 116.405°E, 29 August 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 3♂ (AMNH_PBI 00337315-AMNH_PBI 00337317), 13♀ (AMNH_PBI 00337318, AMNH_PBI 00337319, AMNH_PBI 00337321-AMNH_PBI 00337331), 1 larva (AMNH_PBI 00337332) (ZISP); 31 August 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 24♂ (AMNH_PBI 00337380-AMNH_PBI 00337388, AMNH_PBI 00337333-AMNH_PBI 00337342, AMNH_PBI 00337344, AMNH_PBI 00337345, AMNH_PBI 00337371, AMNH_PBI 00337373, AMNH_PBI 00337374), 31♀ (AMNH_PBI 00337389-AMNH_PBI 00337396, AMNH_PBI 00337347-AMNH_PBI 00337364, AMNH_PBI 00337375-

AMNH_PBI 00337379), 6 larvae (AMNH_PBI 00337365-AMNH_PBI 00337370) (ZISP); 01 Sep 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 1♂ (AMNH_PBI 00337291), 9♀ (AMNH_PBI 00337292-AMNH_PBI 00337300) (ZISP). Lombok Island, Senaru, track to waterfalls, 8.30111°S, 116.40833°E, 28 August 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 4♂ (AMNH_PBI 00337306-AMNH_PBI 00337308, AMNH_PBI 00337320), 6♀ (AMNH_PBI 00337309-AMNH_PBI 00337314) (ZISP); 31 Aug 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 1♂ (AMNH_PBI 00337301), 4♀ (AMNH_PBI 00337302-AMNH_PBI 00337305) (ZISP). Lombok Island, nr Senaru, 8.31956°S 116.405°E, 31 August 2012, F. Konstantinov, *Diplazium esculentum* Swartz (Aspleniaceae), 1♂ (AMNH_PBI 00337397), 6♀ (AMNH_PBI 00337398-AMNH_PBI 00337402, AMNH_PBI 00337404) (ZISP).

Diagnosis

Same as generic diagnosis.

Description

Coloration, surface, vestiture, structure, and genitalia: As in generic description.

Measurements (see Appendix 3): Male: total body length 2.2–2.8, body 2.4–2.9 times as long as basal width of pronotum. Vertex 2.3–2.8 times as broad as eye. Antennal segment I 0.3–0.4 times as long as head width, segment II 1.4–1.5 times as long as head width and 0.8–1.0 times as long as basal width of pronotum. Pronotum 1.7–1.9 times as wide as long and 1.5–1.7 times as wide as head.

Female: total body length 2.7–2.9, body 2.6–2.8 times as long as basal width of pronotum. Vertex 2.6–3.2 times as broad as eye. Antennal segment I 0.3–0.4 times as long as head width, segment II 1.2–1.3 times as long as head width and 0.7–0.8 times as long as basal width of pronotum. Pronotum 1.8–2.0 times as broad as long and 1.7–1.9 times as broad as head.

Etymology

Named after the type locality, Lombok Island, Indonesia.

Host

Adults and larvae of *D. lombokianus* sp. nov. were clearly associated with *Diplazium esculentum* Swartz (Aspleniaceae), and were never sampled from individuals of other fern species growing nearby.

HEKISTA KIRKALDY, 1902

FIGS 3, 26, 28, 34, 35, 70, 71, 90, 91, 100, 101

Hekista Kirkaldy, 1902: 248. Type species: *Hekista laudator* Kirkaldy, 1902 (by monotypy).*Diagnosis*

Recognized by the following combination of characters: body elongate, parallel-sided (Fig. 3); antennal segment I equal to or slightly shorter than head width; labium reaching middle of mesosternum, labial segment IV claw-shaped, distinctly longer than wide, twice thinner than segment III and strongly tapering from base (Fig. 26); pronotal collar matt, equal to width of antennal segment I; pronotum with deep punctures (Fig. 3); exocorium narrow, whitish; cuneal fracture not incised; cuneus narrowly triangular, at least twice as long as wide at base; genital capsule without additional processes; right paramere large, less than twice as small as left paramere; left paramere falciform, with indistinct sensory lobe and almost straight, gradually tapering apical process (Fig. 71).

Hekista is somewhat similar to *Bryocorella* (see relevant section) and *Cobalorrhynchus*. Differs from the latter in the narrow, parallel-sided body, colour pattern of hemelytron, deep punctures on pronotum, and deeply scalloped sides of scutellum.

Diversity and distribution

The genus includes four species, *Hekista papuensis* Carvalho, 1981 and *Hekista similis* Carvalho, 1981 known from Papua New Guinea, *Hekista laudator* Kirkaldy, 1902 known from Indonesian islands, and *Hekista novitiis* (Distant, 1904) described from north-eastern India.

MONALOCORIS DAHLBOM, 1851

FIGS 8, 9, 13, 19, 24, 33, 50, 63, 64, 72, 73, 98, 99

Monalocoris Dahlbom, 1851: 209. Type species: *Cimex filicis* Linnaeus, 1758 (by monotypy).

Sthenarusoides Distant, 1913: 183 (as genus). Synonymized by Carvalho, 1952: 56. Restored to subgeneric status by Linnavuori, 1975: 4. Type species by monotypy: *Sthenarusoides montanus* Distant, 1913.

Diagnosis

Recognized by the following combination of characters: body elongate-oval, about three times as long as basal width of pronotum, with convex margin of exocorium; antennal segment I about one-half width of head; pronotal collar very narrow, distinctly thinner than width of antennal segment I; labium reaching at least middle of mesosternum, sometimes reaching base of hind coxa, labial segment IV claw-shaped, distinct-

ly longer than wide, twice as thin as segment III, and strongly tapering from base (Fig. 24); cuneal fracture deeply incised, cuneus broadly triangular to falciform, somewhat longer than width at base; membrane strongly deflected at base of cuneus; genital capsule without additional processes (Figs 58, 63, 64); right paramere simple, twice to more than three times as small as left paramere; left paramere falciform, with gradually curved and tapering apical process (Figs 72, 73).

The genus clearly differs from other Bryocorini in the small sizes, broadly oval body, narrow pronotal collar, and deflected membrane. Refer to the diagnosis of *Bryophilocapsus* for comparative comments with that genus.

Diversity and distribution

The genus has an almost worldwide distribution and contains 19 species, including *Monalocoris amamianus* Yasunaga, 2000 (southern Japan, and Guangxi and Yunnan Provinces of China), *Monalocoris americanus* Wagner and Slater, 1952 (North America), *Monalocoris bipunctipennis* Walker, 1873 (Sri Lanka), *Monalocoris carioca* Carvalho and Gomes, 1971 (south-eastern Brazil), *Monalocoris eminulus* (Distant, 1893) (southern Mexico, Peru), *Monalocoris filicis* (Linnaeus, 1758) (trans-Palaeartic), *Monalocoris flaviceps* (Poppius, 1915) (north-western Indonesia), *Monalocoris fulviscutellatus* Hu and Zheng, 2003 (Yunnan Province of China), *Monalocoris minutus* (Reuter, 1907) (Jamaica), *Monalocoris montanus* (Distant, 1913) (Seychelles, South Africa), *Monalocoris neotropicalis* Carvalho and Gomes, 1969 (Ecuador), *Monalocoris nigrocollaris* Carvalho, 1989 (Guadeloupe), *Monalocoris nigroflavis* Hu and Zheng, 2003 (Yunnan Province of China), *Monalocoris nigrus* Carvalho, 1981 (New Guinea), *Monalocoris ochraceus* Hu and Zheng, 2003 (Yunnan and Sichuan provinces of China), *Monalocoris pallidiceps* (Reuter, 1907) (southern Brazil), *Monalocoris pallipes* (Carvalho, 1981) (New Guinea), *Monalocoris parvulus* (Reuter, 1881) (Madeira), and *Monalocoris punctipennis* Linnavuori, 1975 (Nigeria, South Sudan).

Remarks

The genus *Sthenarusoides* Distant, 1913 was synonymized with *Monalocoris* by Carvalho (1952), and subsequently restored by Linnavuori (1975) as a subgenus of *Monalocoris* containing all three African species: *M. montanus*, *M. parvulus*, and *M. punctipennis*. Linnavuori correctly pointed out that *Sthenarusoides* differs from the nominal subgenus by the convex and distinctly punctate hemelytron and the shape of the left paramere with strongly produced sensory lobe; however, we are not able to draw firm conclusions on the status of *Sthenarusoides* because of the limited material at hand.

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REFERENCES

- Alayo DP. 1974.** Los Hemipteros de Cuba. Parte XIII. Familia Miridae. *Torreia* **32**: 1–41.
- Angiosperm Phylogeny Group III. 2009.** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161**: 105–121.
- Auerbach MJ, Hendrix SD. 1980.** Insect–fern interactions: macrolepidopteran utilization and species–area association. *Ecological Entomology* **5**: 99–104.
- Baerensprung F. 1860.** *Catalogus Hemipterorum Europae. Hemiptera Heteroptera Europea systematice disposita.* Berlin.
- Balick MJ, Furth DG, Cooper-Driver G. 1978.** Biochemical and evolutionary aspects of arthropod predation on ferns. *Oecologia* **35**: 55–89.
- Bremer K. 1994.** Branch support and tree stability. *Cladistics* **10**: 295–304.
- Bruner SC, Scaramuzza LC, Otero AR. 1975.** *Catálogo de insectos que atacan a las plantas económicas de Cuba.* Havana: Academia de Ciencias de Cuba, Instituto de Zoología.
- Carpenter J. 1988.** Choosing among multiple equally parsimonious cladograms. *Cladistics* **4**: 291–296.
- Carvalho JCM. 1948.** Mirideos neotropicais, XXXI: Genero *Pseudobryocoris* Distant e uma espécie nova de *Neella* Reuter (Hemiptera). *Anais da Academia Brasileira de Ciências* **20**: 96–104.
- Carvalho JCM. 1952.** On the major classification of the Miridae (Hemiptera) (With keys to subfamilies and tribes and a catalogue of the world genera). *Anais da Academia Brasileira de Ciências* **24**: 31–110.
- Carvalho JCM. 1955.** Keys to the genera of Miridae of the world (Hemiptera). *Boletim do Museu Paraense Emilio Goeldi, Zoologia* **11**: 1–151.
- Carvalho JCM. 1956.** Insects of Micronesia: Miridae. *Bishop Museum, Honolulu* **7**: 1–100.
- Carvalho JCM. 1957.** A catalogue of the Miridae of the world. Part I. *Arquivos do Museu Nacional, Rio de Janeiro* **44**: 1–158.
- Carvalho JCM. 1966.** Neotropical Miridae, XCVII: new species of *Ecritotarsus* Stål of the collection of the U. S. National Museum and remarks on *Odontocerochoris* Carvalho and China (Hemiptera). *Revista Brasileira de Biologia* **26**: 231–237.
- Cassis G. 1986.** A systematic study of the subfamily Dicyphinae (Heteroptera: Miridae). PhD Dissertation. Oregon State University, Corvallis.
- Cassis G, Schuh RT. 2012.** Systematics, biodiversity, biogeography, and host associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha). *Annual Review of Entomology* **57**: 377–404.
- Christenhusz MJ, Chase MW. 2014.** Trends and concepts in fern classification. *Annals of Botany* **113**: 571–594.
- Cobben RH. 1968.** *Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embryology and eclosion.* Wageningen: Centre for Agricultural Publishing and Documentation.
- Cooper-Driver GA. 1978.** Insect-fern associations. *Entomologia Experimentalis et Applicata* **24**: 310–316.
- Cooper-Driver GA. 1985.** Anti-predation strategies in pteridophytes—a biochemical approach. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences* **86**: 397–402.
- Dahlbom AG. 1851.** Anteckningar öfver Insekter, som blifvit observerade på Gottland och i en del af Calmare Län, under sommaren 1850. *Kongliga Svenska Vetenskaps akademiens handlingar* **1850**: 155–229.
- Davis NT. 1955.** Morphology of the female organs of reproduction in the Miridae (Hemiptera). *Annals of the Entomological Society of America* **48**: 132–150.
- Distant WL. 1913.** Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905. No. IX Rhynchota. Part I: Suborder Heteroptera. *Transactions of the Linnean Society of London* **16**: 139–190, pls., 11–13.
- Ehrlich PR, Raven PH. 1964.** Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.
- Eyles AC, Schuh RT. 2003.** Revision of New Zealand Bryocorinae and Phylinae (Insecta: Hemiptera: Miridae). *New Zealand Journal of Zoology* **30**: 263–325.
- Fallén CF. 1829.** *Hemiptera Sueciae. Sectio prior. Hemelytrata.* Londini: Gothorum.
- Farris JS. 1969.** A successive approximations approach to character weighting. *Systematic Zoology* **18**: 374–385.
- Ferreira PSF, Silva ER, Coelho LB. 2001.** Miridae (Heteroptera) fitófagos e predadores de Minas Gerais, Brasil, com ênfase em espécies com potencial econômico. *Iheringia, Série Zoologia* **91**: 159–169.
- Futuyma DJ, McCafferty SS. 1990.** Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera, Chrysomelidae). *Evolution* **44**: 1885–1913.
- Goloboff PA. 1993.** Estimating character weights during tree search. *Cladistics* **9**: 83–91.
- Goloboff PA, Farris S, Nixon K. 2000.** *TNT (Tree analysis using New Technology) ver. 1.1.* Tucumán: Published by the authors.

- Harborne JB. 1993.** *Introduction to ecological biochemistry*. New York: Gulf Professional Publishing.
- Hendrix SD. 1980.** An evolutionary and ecological perspective of the insect fauna of ferns. *American Naturalist* **115**: 171–196.
- Henry TJ, Wheeler AG Jr. 1988.** Family Miridae Hahn, 1833 (= Capsidae Burmeister, 1835). The plant bugs. In: Henry TJ, Froeschner RC, eds. *Catalog of the Heteroptera, or true bugs, of Canada and the continental United States*. Leiden: E.J. Brill, 251–507.
- Hernández LM, Henry TJ. 2010.** The plant bugs, or Miridae, (Hemiptera: Heteroptera), of Cuba. *Pensoft Series Faunistica* **92**: 1–212.
- Hernández LM, Stonedahl GM. 1996.** *Cubanomis pilosus*, a new genus and species of Eccritotarsini (Heteroptera: Miridae: Bryocorinae) from Cuba. *Caribbean Journal of Science* **32**: 151–157.
- Hill MP, Cilliers CJ. 1996.** Biology and hot range of *Eccritotarsus catarinensis* [Heteroptera: Miridae], a new potential biological control agent for water hyacinth (*Eichhornia crassipes*) (Pontederiaceae) in South Africa. In: Moran VC, Hoffmann JH, eds. *Proceedings of the XI International Symposium on Biological Control of Weeds, 19–26 January 1996*. South Africa: University of Cape Town, 229.
- Hu Q, Zheng L-Y. 2000.** A revision of Chinese species of *Bryocoris* Fallen (Hemiptera: Miridae). *Acta Zootaxonomica Sinica* **25**: 241–267.
- Hu Q, Zheng L-Y. 2001.** The Monaloniina from mainland China (Hemiptera: Miridae: Bryocorinae). *Acta Zootaxonomica Sinica* **26**: 414–430.
- Hu Q, Zheng L-Y. 2003.** A study on the Chinese species of *Monalocoris* Dahlbom and tribe Eccritotarsini Berg (Hemiptera, Miridae, Bryocorinae). *Acta Zootaxonomica Sinica* **28**: 116–125.
- Isaka Y, Sato T. 2014a.** Molecular phylogenetic and divergence time estimation analyses of the sawfly subfamily Selandriinae (Hymenoptera: Tenthredinidae). *Entomological Science* **17**: 435–439.
- Isaka Y, Sato T. 2014b.** Was species diversification in Tenthredinoidea (Hymenoptera: Symphyta) related to the origin and diversification of angiosperms? *The Canadian Entomologist*, 1–16. <http://dx.doi.org/10.4039/tce.2014.60>.
- Jensen AS, Holman J. 2000.** *Macrosiphum* on ferns: taxonomy, biology and evolution, including the description of three new species (Hemiptera: Aphididae). *Systematic Entomology* **25**: 339–372.
- Jung S, Lee S. 2012.** Molecular phylogeny of the plants bugs (Heteroptera: Miridae) and the evolution of feeding habits. *Cladistics* **28**: 50–79.
- Kelton LA. 1980.** *The insects and arachnids of Canada part 8. The plant bugs of the prairie provinces of Canada. Heteroptera: Miridae*. Agriculture Canada Research Branch Publication 1703, Quebec: Canadian Government Publishing Centre.
- Kerzhner IM. 1978.** Heteroptera of Saghalien and Kurile Islands. *Trudy Biologo-Pochvennogo Instituta Dalnevostochnogo Nauchnogo Tsentra Akademii Nauk AN SSSR, novaya seriya* **50**: 31–57 (in Russian).
- Kerzhner IM. 1988.** *New and little known heteropteran insects (Heteroptera) from the Far East of the USSR*. Vladivostok: Academy of Sciences, USSR (in Russian).
- Kerzhner IM, Josifov M. 1999.** Miridae Hahn, 1833. In: Aukema B, Rieger C, eds. *Catalogue of the Heteroptera of the Palaearctic Region, Vol. 3*. Amsterdam: The Netherlands Entomological Society, 1–576.
- Kerzhner IM, Konstantinov FV. 1999.** Structure of the aedeagus in Miridae and its bearing to suprageneric classification. *Acta Societatis Zoologicae Bohemicae* **63**: 117–137.
- Kirkaldy GW. 1902.** Memoir upon the Rhyncotal family Capsidae Auct. *Transactions of the Entomological Society of London* **1902**: 243–272, pls. V & VI.
- Knyshov AA, Konstantinov FV. 2012.** A new genus and species of the tribe Orthotylini (Heteroptera: Miridae: Orthotylinae) from Central Asia. *European Journal of Entomology* **109**: 117–128.
- Konstantinov FV. 2003.** Male genitalia in Miridae (Heteroptera) and their significance for suprageneric classification of the family. Part I: general review, Isometopinae and Psallopinae. *Belgian Journal of Entomology* **5**: 3–36.
- Konstantinov FV. 2012.** A new species of *Palaucoris* (Heteroptera: Miridae) from Sulawesi. *Entomologica Americana* **118**: 121–129.
- Kullenberg B. 1944.** Studien über die Biologie der Capsiden. *Zool. Bidrag Fran Uppsala (Suppl.)* **23**: 1–522.
- Lafont R, Ho R, Raharivelomanana P, Dinan L. 2010.** Ecdysteroids in ferns: distribution, diversity, biosynthesis, and functions. In: Fernández H, Kumar A, Revilla A, eds. *Working with ferns. Issues and applications*. New York: Springer, 305–319.
- Lawton JH. 1976.** The structure of the arthropod community on bracken. *Botanical Journal of the Linnean Society* **73**: 187–216.
- Lindberg H. 1959.** Hemiptera Heteroptera from Newfoundland, collected by the Swedish-Finnish Expedition of 1949 and 1951. *Acta Zoologica Fennica* **96**: 1–25.
- Linnavuori RE. 1975.** Hemiptera of the Sudan, with remarks on some species of the adjacent countries. 4. Miridae and Isometopidae. *Annales Zoologici Fennici* **12**: 1–118.
- Maddison WP, Maddison DR. 2001–2014.** Mesquite: a modular system for evolutionary analysis. Version 3.01. Available at: <http://mesquiteproject.org>
- Matocq A, Ribes J. 2004.** Un nouveau Dicyphus de l'île de Madère (Heteroptera, Miridae, Bryocorinae, Dicyphini). *Revue française d'Entomologie* **26**: 43–46.
- Miles PW. 1987.** Plant sucking bugs can remove the content of cells without mechanical damage. *Experientia* **43**: 937–939.
- Namyatova AA, Konstantinov FV, Cassis G. 2015.** Phylogeny and systematics of the subfamily Bryocorinae with the emphasis on the tribe Dicyphini sensu Schuh, 1976 derived from morphological characters. *Systematic Entomology* in press.
- Nixon KC. 2002.** *WinClada ver. 1.00.08*. Ithaca, NY: Published by the author.

- Ottosson JG, Anderson JM. 1983.** Number, seasonality and feeding habits of insects attacking ferns in Britain: an ecological consideration. *The Journal of Animal Ecology* **52**: 385–406.
- Pazyuk IM, Musolin DL, Reznik SY. 2013.** Geographic variation in thermal and photoperiodic effects on development of zoophytophagous plant bug *Nesidiocoris tenuis*. *Journal of Applied Entomology* **138**: 36–44.
- Reuter OM. 1906.** Capsidae in prov. Sz'tschwan Chinae a DD. G. Potanin et M. Beresowski collectae. *Annuaire du Musee Zoologique, St. Petersburg* **10**: 1–81.
- Ribes J, Baena M. 2006.** Two new species of *Dicyphus* Fieber 1858 from the Iberian Peninsula and Canary Islands with additional data about the *D. globulifer*-group of the subgenus *Brachyceroea* Fieber 1858 (Hemiptera, Heteroptera, Miridae, Bryocorinae). *Denisia* **19**: 589–598.
- Ribes J, Ribes E. 2001.** *Campyloneuropsis filva* n. sp., une spece nouvelle de iles Canaries (Heteroptera, Miridae). *Bulletin de la Societe Entomologique de France* **106**: 61–64.
- Rigby C, Lawton JH. 1981.** Species-area relationships of arthropods on host plants: herbivores on bracken. *Journal of Biogeography* **8**: 125–133.
- Schmutterer H. 1969.** *Pests of crops in northeast and central Africa*. Stuttgart: Gustav Fisher Verlag.
- Schuh RT. 1976.** Pretarsal structure in the Miridae (Hemiptera) with a cladistic analysis of relationships within the family. *American Museum Novitates* **2601**: 1–39.
- Schuh RT. 1995.** *Plant bugs of the World (Heteroptera: Miridae): systematic catalog, distributions, host list, and bibliography*. New York: Entomological Society.
- Schuh RT. 2002–2013.** On-line systematic catalog of plant bugs (Insecta: Heteroptera: Miridae). Available at: <http://research.amnh.org/pbi/catalog/>
- Schuh RT, Brower AVZ. 2009.** *Biological systematics: principles and applications, Second edn*. Ithaca, NY: Cornell University Press.
- Schuh RT, Slater JA. 1995.** *True bugs of the world (Hemiptera: Heteroptera): classification and natural history*. Ithaca, NY: Cornell University Press.
- Schuh RT, Weirauch C, Wheeler WC. 2009.** Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total-evidence analysis. *Systematic Entomology* **34**: 15–48.
- Smith AR, Pryer KM, Schuettpelz E, Korall P, Schneider H, Wolf PG. 2006.** A classification for extant ferns. *Taxon* **55**: 705–731.
- Southwood R, Leston D. 1959.** *Land and water bugs of the British Isles*. London: Frederick Warne and Co.
- Srivastava D, Lawton J, Robinson G. 1997.** Spore-feeding: a new, regionally vacant niche for bracken herbivores. *Ecological Entomology* **22**: 475–478.
- Stonedahl GM. 1988.** Revisions of *Dioclerus*, *Harpedona*, *Mertila*, *Myiocapsus*, *Prodromus* and *Thaumastomiris* (Heteroptera: Miridae, Bryocorinae: Eccritotarsini). *Bulletin of the American Museum of Natural History* **187**: 1–99.
- Stonedahl GM. 1991.** The Oriental species of *Helopeltis* (Heteroptera: Miridae): a review of economic literature and guide to identification. *Bulletin of Entomological Research* **81**: 465–490.
- Stonedahl GM, Hernández L. 1996.** Two new genera of Eccritotarsini (Heteroptera: Miridae: Bryocorinae) from Southeast Asia. *Tijdschrift voor Entomologie* **139**: 257–266.
- Swofford DL. 2000.** *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4*. Sunderland, MA: Sinauer Associates.
- Taeger A, Altenhofer E, Blank SM, Jansen E, Kraus M, Pschorn-Walcher H, Ritzau C. 1998.** Kommentare zur Biologie, Verbreitung und Gefährdung der Pflanzenwespen Deutschlands (Hymenoptera, Symphyta). In: Taeger A, Blank SM, eds. *Pflanzenwespen Deutschlands (Hymenoptera: Symphyta)*. Kelttern: Goecke and Evers, 49–135.
- Tahvanainen J, Niemelä P. 1987.** Biogeographical and evolutionary aspects of insect herbivory. *Annales Zoologici Fennici* **24**: 239–247.
- Tamanini L. 1982.** Gli eterotteri dell'Alto Adige (Insecta: Heteroptera). *Studi Trentini di Scienze Naturali, Acta Biologica* **59**: 65–194.
- Vikberg V, Liston AD. 2009.** Taxonomy and biology of European Heptamelini (Hymenoptera, Tenthredinidae, Selandriinae). *Zootaxa* **2112**: 1–24.
- Wagner E. 1974.** Die Miridae Hahn, 1831, des Mitteleerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). Teil. 1. *Entomologische Abhandlungen* **37** (Suppl.): 1–484.
- Ward LK, Hackshaw A, Clarke RT. 2003.** Do food-plant preferences of modern families of phytophagous insects and mites reflect past evolution with plants? *Biological Journal of the Linnean Society* **78**: 51–83.
- Weintraub JD, Lawton JH, Scoble MJ. 1995.** Lithinine moths on ferns: a phylogenetic study of insect-plant interactions. *Biological Journal of the Linnean Society* **55**: 239–250.
- Wheeler AG. 2001.** *Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists*. xv+507 pp. Ithaca, NY: Cornell University Press.
- Wheeler AG Jr, Henry TJ, Mason TL. 1983.** An annotated list of the Miridae of West Virginia (Hemiptera-Heteroptera). *Transactions of the American Entomological Society* **109**: 127–159.
- Yasunaga T. 2000.** An annotated list and descriptions of new taxa of the plant bug subfamily Bryocorinae in Japan (Heteroptera: Miridae). *Biogeography* **2**: 93–102.
- Yasunaga T, Kerzhner IM. 1998.** New synonymies in the East Palearctic Miridae (Heteroptera). *Zoosystematica Rossica* **7**: 1–88.

APPENDIX 1. BRYOCORINI MORPHOLOGICAL DATA MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Stenotus binotatus</i>	1	0	0	1	0	0	0	1	2	2	1	1	1	1	0	0	
<i>Punctifulvius kerzhneri</i>	1	0	0	1	0	0	0	1	3	2	1	1	0	–	–	–	0
<i>Cylapus citus</i>	0	0	0	1	1	0	1	2	3	2	1	1	1	1	1	0	0
<i>Palaucoris sulawesicus</i>	0	1	0	1	1	0	1	2	2	1	0	1	3	0	0	–	0
<i>Angulonotus grisescens</i>	1	0	0	1	0	0	0	1	1	2	1	1	1	1	1	0	0
<i>Helopeltis clavifer</i>	1	1	1	1	0	0	1	2	1	2	1	1	3	0	0	–	0
<i>Chamopsis tuberculatus</i>	1	1	1	1	0	0	1	0	1	1	0	1	3	0	0	–	0
<i>Dicyphus errans</i>	1	1	1	0	0	0	0	1	2	2	1	1	2	0	0	–	0
<i>Nesidiocoris tenuis</i>	1	1	1	0	0	0	0	1	2	2	1	1	2	0	0	0	0
<i>Pycnoderes</i> sp.	0	0	1	0	0	0	0	1	1	1	0	0	3	0	0	–	0
<i>Eccritotarsus</i> sp.	0	0	1	0	0	0	0	1	1	1	0	0	3	0	0	–	0
<i>Sixeonotus</i> sp.	0	0	1	0	0	0	0	1	1	1	0	0	3	0	0	–	0
<i>Heterocoris dilatatus</i>	0	0	1	1	0	0	0	1	1	2	1	1	0	–	–	–	0
<i>Eurycipitia clarus</i>	0	0	1	1	0	0	0	1	1	0	0	0	0	–	–	–	0
<i>Sinervus baerensprungi</i>	0	0	1	0	0	0	1	0	1	1	0	0	3	0	0	–	0
<i>Bryocorella emboliata</i>	0	0	1	0	0	1	0	0	0	0	0	?	1	0	0	2	0
<i>Hekista laudator</i>	0	0	1	0	0	1	0	0	0	0	0	2	1	0	1	1	0
<i>Bryocoris pteridis</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1
<i>Bryocoris persimilis</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1
<i>Bryocoris montanus</i>	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1
<i>Bryocoris convexicollis</i>	0	0	1	0	0	1	0	0	0	1	0	2	1	0	1	1	1
<i>Bryocoris sichuanensis</i>	0	0	1	0	0	1	0	0	0	1	0	2	1	0	1	1	1
<i>Monalocoris filicis</i>	0	0	1	0	0	1	0	1	0	0	0	2	1	1	0	1	0
<i>Monalocoris americanus</i>	0	0	1	0	0	1	0	1	0	0	0	2	1	1	0	1	0
<i>Monalocoris punctipennis</i>	0	0	1	0	0	1	0	1	0	0	0	2	1	1	0	1	0
<i>Diplazicoris lombokianus</i> sp. nov.	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	2	0
<i>Bryophilocapsus tosamontanus</i>	0	0	1	0	0	1	0	1	0	0	0	?	1	0	?	1	?

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Stenotus binotatus</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
<i>Punctifulvius kerzhneri</i>	0	0	0	1	1	1	0	0	0	2	0	1	0	0	0	1	0
<i>Cylapus citus</i>	0	0	0	1	1	1	3	0	0	2	0	0	0	0	0	0	1
<i>Palaucoris sulawesicus</i>	0	1	1	1	1	1	0	0	0	2	0	1	0	0	0	1	1
<i>Angulonotus grisescens</i>	0	0	0	0	3	1	4	0	0	0	0	1	0	0	0	0	0
<i>Helopeltis clavifer</i>	1	0	0	0	3	3	–	–	0	0	0	0	0	0	0	2	1
<i>Chamopsis tuberculatus</i>	1	0	1	0	3	3	–	–	0	0	0	1	1	0	0	1	1
<i>Dicyphus errans</i>	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
<i>Nesidiocoris tenuis</i>	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
<i>Pycnoderes</i> sp.	0	1	0	0	2	1	1	2	0	2	0	0	0	0	0	1	1
<i>Eccritotarsus</i> sp.	0	1	0	0	2	1	1	2	0	2	0	0	0	0	0	1	1
<i>Sixeonotus</i> sp.	0	1	0	0	2	1	1	2	0	2	0	0	0	0	0	1	1
<i>Heterocoris dilatatus</i>	0	0	0	0	2	1	1	2	0	2	0	1	0	0	1	1	1
<i>Eurycipitia clarus</i>	0	1	0	0	2	1	1	2	0	0	0	0	0	0	1	1	1
<i>Sinervus baerensprungi</i>	1	1	1	0	2	1	1	2	0	1	0	0	0		0	2	1
<i>Bryocorella emboliata</i>	0	1	2	0	?	2	2	1	0	2	0	0	1	1	0	1	1
<i>Hekista laudator</i>	0	1	2	0	0	2	2	1	0	2	0	0	1	1	0	0	1
<i>Bryocoris pteridis</i>	0	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	1
<i>Bryocoris persimilis</i>	0	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	1
<i>Bryocoris montanus</i>	0	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	1
<i>Bryocoris convexicollis</i>	0	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	1
<i>Bryocoris sichuanensis</i>	0	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	1
<i>Monalocoris filicis</i>	0	1	1	0	0	2	2	1	0	1	1	1	1	0+1	1	1	1
<i>Monalocoris americanus</i>	0	1	1	0	0	2	2	1	0	1	1	1	1	0+1	1	1	1

APPENDIX 1. CONTINUED

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Monalocoris punctipennis</i>	0	1	1	0	0	2	2	1	0	2	1	1	1	0	1	0	1
<i>Diplazicoris lombokianus</i> sp. nov.	0	1	2	0	1	2	2	1	0	1	0	0	1	0	1	1	1
<i>Bryophilocapsus tosamontanus</i>	0	1	?	0	?	2	2	1	0	1	1	1	1	1	1	1	1
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
<i>Stenotus binotatus</i>	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>Punctifulvius kerzhneri</i>	1	0	2	1	0	0	0	1	0	0	2	0	0	0	0	0	1
<i>Cylapus citus</i>	1	0	2	1	1	0	0	1	0	0	2	0	0	0	0	0	0
<i>Palaucoris sulawesicus</i>	1	0	2	1	0	0	0	2	1	2	0	0	0	0	0	0	0
<i>Angulonotus grisescens</i>	0	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Helopeltis clavifer</i>	1	0	1	0	0	1	1	2	1	0	0	0	1	0	0	0	1
<i>Chamopsis tuberculatus</i>	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	1
<i>Dicyphus errans</i>	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0
<i>Nesidiocoris tenuis</i>	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Pycnoderes</i> sp.	1	1	3	1	0	1	1	0	0	0	1	2	0	0	1	0	1
<i>Ecritotarsus</i> sp.	1	1	3	1	0	1	1	0	0	0	1	2	0	0	1	0	0
<i>Sixeonotus</i> sp.	1	1	3	1	0	1	1	0	0	0	1	2	0	0	1	0	0
<i>Heterocoris dilatatus</i>	1	0	3	1	0	1	1	0	0	0	1	2	0	0	1	0	1
<i>Eurycipitia clarus</i>	1	1	3	1	0	1	1	0	0	0	1	2	0	0	1	0	1
<i>Sinervus baerensprungi</i>	1	1	3	1	1	1	1	0	0	0	1	2	0	0	0	0	0
<i>Bryocorella emboliata</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	?	0
<i>Hekista laudator</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	0	0
<i>Bryocoris pteridis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	2	0
<i>Bryocoris persimilis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	2	0
<i>Bryocoris montanus</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	2	0
<i>Bryocoris convexicollis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	1	0
<i>Bryocoris sichuanensis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	1	0
<i>Monalocoris filicis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	0	0
<i>Monalocoris americanus</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	0	0
<i>Monalocoris punctipennis</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	0	0
<i>Diplazicoris lombokianus</i> sp. nov.	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	2	0
<i>Bryophilocapsus tosamontanus</i>	0	0	1	0	0	1	1	0	0	3	–	0	1	1	0	?	0
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
<i>Stenotus binotatus</i>	0	0	0	0	2	0	0	2	4	1	2	0	0	0	1	0	0
<i>Punctifulvius kerzhneri</i>	0	0	1	0	2	0	1	0	3	0	0	1	1	0	1	0	0
<i>Cylapus citus</i>	0	0	0	0	2	0	1	0	1	0	0	1	1	0	2	0	0
<i>Palaucoris sulawesicus</i>	0	0	0	0	2	0	1	0	1	0	0	0	1	0	2	0	0
<i>Angulonotus grisescens</i>	0	2	1	0	2	0	1	2	1	1	2	0	0	0	2	0	0
<i>Helopeltis clavifer</i>	0	0	0	0	2	0	1	0	1	2	0	1	1	0	0	0	0
<i>Chamopsis tuberculatus</i>	0	0	0	0	2	0	1	0	1	2	0	1	1	0	2	1	0
<i>Dicyphus errans</i>	0	1	0	0	2	0	1	0	3	2	2	0	1	0	2	0	0
<i>Nesidiocoris tenuis</i>	0	1	0	0	2	0	1	0	3	2	2	0	1	0	2	0	0
<i>Pycnoderes</i> sp.	0	2	1	3	0	1	0	0	0	0	0	0	1	1	1	1	0
<i>Ecritotarsus</i> sp.	0	2	1	3	2	1	0	1	5	0	0	0	1	0	2	0	0
<i>Sixeonotus</i> sp.	0	2	1	3	0	1	0	0	0	0	0	0	1	1	2	1	0
<i>Heterocoris dilatatus</i>	0	2	0	1	3	0	1	1	5	0	0	0	1	2	2	1	0
<i>Eurycipitia clarus</i>	0	2	0	1	3	0	1	1	5	0	0	0	1	0	2	1	0
<i>Sinervus baerensprungi</i>	0	2	0	3	3	1	0	0	2	0	0	0	1	0	1	0	0
<i>Bryocorella emboliata</i>	1	0	0	0	1	1	0	1	0	?	?	?	?	?	2	0	0
<i>Hekista laudator</i>	1	0	0	0	1	1	0	1	0	0	1	0	0	0	2	0	0
<i>Bryocoris pteridis</i>	1	1	2	1	1	1	0	1	0	0	1	0	0	0	1	0	1

APPENDIX 1. CONTINUED

	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
<i>Bryocoris persimilis</i>	1	1	2	1	1	1	0	1	0	0	1	0	0	0	1	0	1
<i>Bryocoris montanus</i>	1	1	2	1	1	1	0	1	0	0	1	0	0	0	1	0	1
<i>Bryocoris convexicollis</i>	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0
<i>Bryocoris sichuanensis</i>	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	0
<i>Monalocoris filicis</i>	1	1	2	0	1	1	0	1	0	0	1	0	0	0	1	1	0
<i>Monalocoris americanus</i>	1	1	2	0	1	1	0	1	0	0	1	0	0	0	1	1	0
<i>Monalocoris punctipennis</i>	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1	0
<i>Diplazicoris lombokianus</i> sp. nov.	1	2	0	2	1	1	0	1	0	0	1	0	2	2	1	1	0
<i>Bryophilocapsus tosamontanus</i>	1	0	0	0	1	1	0	1	0	?	?	?	?	?	1	1	0

APPENDIX 2. LIST OF HOSTS FOR SPECIES USED IN PHYLOGENETIC ANALYSIS

Bryocorine species	Host	Reference
<i>Helopeltis clavifer</i> (Walker, 1871)	<i>Theobroma cacao</i> (Sterculiaceae)	Miles, 1987; Wheeler, 2001
	<i>Leucaena leucocephala</i> (Fabaceae)	Konstantinov and Knyshev (orig. observ.) Stonedahl, 1991
<i>Chamopsis tuberculatus</i> (Distant, 1918)	<i>Camellia sinensis</i> (Theaceae), <i>Anacardium occidentale</i> (Anacardiaceae), <i>Acalypha caturus</i> (Euphorbiaceae), <i>Annona</i> spp. (Annonaceae), <i>Bixa orellana</i> (Bixaceae), <i>Cassia fistula</i> , <i>Centrosema pubescens</i> , <i>Flemingia strobilifera</i> , <i>Gliricidia sepium</i> , <i>Mimosa diplotricha</i> , and <i>Pueraria phaseoloides</i> (Fabaceae), <i>Eucalyptus deglupta</i> (Myrtaceae), <i>Ixora</i> spp. (Rubiaceae), <i>Mangifera indica</i> (Anacardiaceae), <i>Passiflora edulis</i> (Passifloraceae), <i>Persea americana</i> (Lauraceae), <i>Polyscias</i> sp. (Araliaceae), <i>Psidium guajava</i> (Myrtaceae)	Schmutterer, 1969; Wheeler 2001
	<i>Psidium</i> sp. (Myrtaceae)	Wheeler, 2001
<i>Dicyphus errans</i> (Wolff, 1804)	Mainly attacks aphids and whiteflies, but also requires plant food for development	Wheeler, 2001
<i>Nesidiocoris tenuis</i> (Reuter, 1895)	Small arthropods, e.g. whiteflies, thrips, aphids, leafminers, etc.	Pazyuk, Musolin & Reznik, 2013
<i>Pycnoderes</i> spp.	<i>Tradescantia subaspera</i> (<i>P. dilatatus</i>); <i>Commelina</i> sp. (Commelinaceae) (<i>P. medius</i>); <i>Cucumis</i> spp. (Cucurbitaceae) (<i>P. quadrimaculatus</i> , <i>P. monticulifer</i>)	Wheeler, 2001
	<i>Cucurbita pepo</i> , <i>Sechium edule</i> (Cucurbitaceae) (<i>P. incurvus</i>); <i>Amaranthus</i> spp., (Amaranthaceae), <i>Cucurbita maxima</i> (Cucurbitaceae), <i>Phaseolus vulgaris</i> (Fabaceae) (<i>P. quadrimaculatus</i>)	Ferreira <i>et al.</i> , 2001
<i>Eccritotarsus</i> spp.	<i>Hypitidis</i> sp. (Lamiaceae), <i>Ipomoea</i> spp. (Convolvulaceae) (<i>P. angustatus</i>); <i>Commelina</i> sp. (Commelinaceae); <i>Ipomoea batatas</i> (Convolvulaceae) (<i>P. vanduzeei</i>)	Hernández & Henry, 2010
	<i>Laportea canadensis</i> (Urticaceae) (<i>P. drakei</i>) <i>Eichornia crassipes</i> (Pontederiaceae) (<i>E. catarinensis</i>)	PBI database Hill & Cilliers, 1996; Wheeler, 2001
<i>Sixeonotus</i> spp.	<i>Colocasia esculenta</i> (Araceae) (<i>E. colocasicus</i>) <i>Cornutia pyramidata</i> (Verbenaceae), <i>Erythrina rubrinervia</i> (Fabaceae) (<i>E. insignis</i>)	Carvalho, 1948 Carvalho, 1966
	<i>Lactuca canadensis</i> (<i>S. albicornis</i>), <i>Gaillardia</i> sp. (<i>S. areolatus</i>), <i>Coreopsis</i> sp., <i>Bidens</i> sp. (<i>S. unicolor</i>) (Asteraceae) <i>Coreopsis</i> spp. (Asteraceae) (<i>S. albohirtus</i>)	Wheeler, 2001 PBI database

APPENDIX 2. CONTINUED

Bryocorine species	Host	Reference
<i>Heterocoris dilatatus</i> Guerin-Meneville, 1857	<i>Solanum donianun</i> , <i>S. melongena</i> , <i>S. torvun</i> (Solanaceae)	Hernández & Henry, 2010
<i>Eurycipitia clarus</i> (Distant, 1883)	Host unknown	
<i>Sinervus baerensprungi</i> Stål, 1860	<i>Heliconia psittacorum</i> (Heliconiaceae)	Ferreira <i>et al.</i> , 2001
<i>Bryocorella emboliata</i> Carvalho, 1956	Host unknown	
<i>Hekista laudator</i> Kirkaldy, 1902	<i>Diplazium esculentum</i> Swartz (Aspleniaceae)	Konstantinov and Knyshov (orig. observ.)
<i>Bryocoris pteridis</i> (Fallén, 1807)	<i>Asplenium</i> sp., <i>Athyrium filix-femina</i> , <i>A. distentifolium</i> , <i>Oreopteris limbosperma</i> (Aspleniaceae), <i>Dryopteris filix-mas</i> , <i>D. dilatata</i> , <i>D. carthusiana</i> , <i>Polystichum</i> sp. (Polypodiaceae), <i>Pteridium aquilinum</i> (Dennstaedtiaceae)	Balick <i>et al.</i> , 1978; Wagner, 1974; Rigby & Lawton, 1981; Tamanini, 1982
<i>Bryocoris persimilis</i> Kerzhner, 1988	Unspecified ferns	Kerzhner, 1988
<i>Bryocoris montanus</i> Kerzhner, 1972	Unspecified ferns	Kerzhner, 1978
<i>Bryocoris convexicollis</i> Hsiao, 1941	Unknown	
<i>Bryocoris sichuanensis</i> Hu and Zheng, 2000	Unspecified ferns	Hu and Zheng, 2000
<i>Monalocoris filicis</i> (Linnaeus, 1758)	<i>Asplenium</i> sp., <i>Athyrium filix-femina</i> , <i>A. distentifolium</i> , <i>Oreopteris limbosperma</i> (Aspleniaceae), <i>Dryopteris filix-mas</i> , <i>D. dilatata</i> , <i>D. carthusiana</i> , <i>Polystichum</i> sp. (Polypodiaceae), <i>Pteridium aquilinum</i> (Dennstaedtiaceae)	Wagner, 1974; Balick <i>et al.</i> , 1978; Rigby & Lawton, 1981; Tamanini, 1982
<i>Monalocoris americanus</i> Wagner and Slater, 1952	<i>Dryopteris oligophylla</i> , <i>Dryopteris</i> sp. (Polypodiaceae), <i>Dennstaedtia punctilobula</i> (Dennstaedtiaceae), <i>Osmundastrum cinnamomeum</i> , <i>Osmunda</i> sp. (Osmundaceae)	Wheeler <i>et al.</i> , 1983; Kelton, 1980; Alayo, 1974; Bruner <i>et al.</i> , 1975; Lindberg, 1959
<i>Monalocoris punctipennis</i> Linnavuori, 1975	<i>Pteridium aquilinum</i> (Dennstaedtiaceae)	Linnavuori, 1975
<i>Diplazicoris lombokianus</i> sp. nov. gen et sp n.	<i>Diplazium esculentum</i> Swartz (Aspleniaceae)	Konstantinov and Knyshov (orig. observ.)
<i>Bryophilocapsus tosamontanus</i> Yasunaga, 2000	<i>Thuidium cymbifolium</i> (Bryophyta: Thuidiaceae)	Yasunaga, 2000

APPENDIX 3. MEASUREMENTS (MM)

		Total length	Clyp–Cun	Pronotal length	Head width	Pronotal width	AS I length	AS II length	AS III length	AS IV length	InterOcDi
<i>Diplazicoris lombokianus</i> sp. nov.											
Males <i>N</i> = 10	Mean	2.64	2.16	0.55	0.60	0.96	0.23	0.90	0.49	0.30	0.34
	SD	0.18	0.14	0.03	0.03	0.02	0.01	0.05	0.04	0.02	0.01
	Range	0.60	0.50	0.09	0.10	0.06	0.01	0.18	0.13	0.05	0.03
	Minimum	2.20	1.80	0.49	0.54	0.93	0.23	0.76	0.43	0.28	0.33
	Maximum	2.80	2.30	0.58	0.64	0.99	0.24	0.94	0.55	0.33	0.35
Females <i>N</i> = 10	Mean	2.79	2.30	0.55	0.60	1.05	0.20	0.77	0.42	0.30	0.35
	Standard Deviation	0.08	0.08	0.02	0.03	0.03	0.01	0.05	0.05	0.02	0.01
	Range	0.25	0.25	0.06	0.09	0.14	0.03	0.14	0.14	0.08	0.03
	Minimum	2.65	2.20	0.53	0.55	0.98	0.19	0.69	0.35	0.28	0.34
	Maximum	2.90	2.45	0.59	0.64	1.11	0.21	0.83	0.49	0.35	0.36
<i>Monalocoris filicis</i>											
Males <i>N</i> = 3	Mean	2.70	2.23	0.56	0.53	1.07	0.19	0.78	0.35	0.30	0.33
	SD	0.05	0.06	0.01	0.02	0.02	0.01	0.04	0.03	0.01	0.01
	Range	0.10	0.10	0.02	0.04	0.04	0.01	0.09	0.05	0.01	0.03
	Minimum	2.65	2.20	0.55	0.51	1.05	0.19	0.74	0.33	0.29	0.33
	Maximum	2.75	2.30	0.58	0.55	1.09	0.20	0.83	0.38	0.30	0.35
Females <i>N</i> = 3	Mean	2.73	2.28	0.63	0.54	1.15	0.18	0.61	0.33	0.28	0.35
	SD	0.08	0.10	0.03	0.01	0.02	0.01	0.01	0.00	0.01	0.00
	Range	0.15	0.20	0.05	0.01	0.04	0.01	0.03	0.00	0.01	0.00
	Minimum	2.65	2.20	0.60	0.54	1.13	0.18	0.60	0.33	0.28	0.35
	Maximum	2.80	2.40	0.65	0.55	1.16	0.19	0.63	0.33	0.29	0.35
<i>Hekista laudator</i>											
Males <i>N</i> = 3	Mean	3.85	3.15	0.76	0.62	1.13	0.30	1.15	0.76	0.38	0.33
	SD	0.10	0.10	0.04	0.04	0.04	0.02	0.09	0.03	0.02	0.01
	Range	0.20	0.20	0.08	0.08	0.08	0.04	0.16	0.06	0.04	0.03
	Minimum	3.75	3.05	0.73	0.59	1.09	0.29	1.05	0.73	0.36	0.33
	Maximum	3.95	3.25	0.80	0.66	1.16	0.33	1.21	0.79	0.40	0.35
Females <i>N</i> = 3	Mean	4.35	3.57	0.85	0.67	1.37	0.35	1.18	0.71	0.39	0.35
	SD	0.05	0.06	0.03	0.02	0.09	0.09	0.04	0.05	0.02	0.02
	Range	0.10	0.10	0.05	0.04	0.18	0.16	0.08	0.09	0.04	0.04
	Minimum	4.30	3.50	0.83	0.65	1.30	0.29	1.13	0.68	0.38	0.34
	Maximum	4.40	3.60	0.88	0.69	1.48	0.45	1.20	0.76	0.41	0.38
<i>Bryocoris pteridis</i>											
Males <i>N</i> = 3	Mean	3.38	2.60	0.49	0.55	1.01	0.32	1.11	–	–	0.34
	SD	0.03	0.05	0.02	0.01	0.01	0.01	0.02	–	–	0.02
	Range	0.05	0.10	0.04	0.01	0.01	0.01	0.02	–	–	0.04
	Minimum	3.35	2.55	0.46	0.55	1.00	0.31	1.10	–	–	0.33
	Maximum	3.40	2.65	0.50	0.56	1.01	0.33	1.13	–	–	0.36
Females <i>N</i> = 3	Mean	3.63	2.83	0.60	0.60	1.14	0.28	0.83	0.50	0.38	0.37
	SD	0.08	0.03	0.01	0.01	0.01	0.01	0.03	–	–	0.01
	Range	0.15	0.05	0.03	0.01	0.01	0.01	0.05	–	–	0.01
	Minimum	3.55	2.80	0.59	0.59	1.14	0.28	0.80	–	–	0.36
	Maximum	3.70	2.85	0.61	0.60	1.15	0.29	0.85	–	–	0.38

Clyp–Cun, distance between apex of clypeus and apex of corium in dorsal view; AS I–AS IV, length of antennal segments I–IV; InterOcDi, width of vertex between inner margins of eyes in dorsal view.