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Systematic revision and phylogeny of the plant bug tribe Monaloniini (Insecta: Heteroptera: Miridae: Bryocorinae) of the world

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A systematic revision, redescription and a first generic conspectus on a worldwide basis of the scarcely studied plant bug tribe Monaloniini (Insecta: Heteroptera: Miridae: Bryocorinae) is given. This reclassification is of great significance to agriculture as some monaloniines are major pests of cocoa, cashew, tea and other foodplants. A key to genera is given, as well as generic diagnoses and descriptions, photographs, scanning electron micrographs, illustration of male and female genitalia, host plant information and distributional maps. This reclassification is based on a phylogenetic analysis of external and genitalic characters, with 118 species and 32 genera codified. The phylogenetic analysis resulted in the recognition of a monophyletic Monaloniini, and strongly supported non-monophyly of the previously recognized subtribes Monaloniina and Odoniellina, resulting in the rejection of a formal subtribal classification for the tribe. The following new synonymy is recognized: *Boxia* (= ***Boxiopsis* syn. nov.**), *Chamus* (= ***Chamopsis* syn. nov.**, ***Parachamus* syn. nov.**), *Volkeliopsis* (= ***Mircarvalhoia* syn. nov.**), *Platyngomiris* (= ***Platyngomiriodes* syn. nov.**), *Platyngomiris coreoides* (= ***Platyngomiriodes apliformis* syn. nov.**), *Lycidocoris* (= ***Pantilioforma* syn. nov.**). *Afropeltis* is raised to full generic status. *Onconotellus* and *Pachypeltopsis* are transferred to the Orthotylinae and Deraeocorinae, respectively. ***Volkeliopsis mindanao* sp. nov.** is described as new to science.

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ADDITIONAL KEYWORDS: apomorphy – classification – distribution – identification key – Insecta – morphology – phylogeny – tropical – revision.

INTRODUCTION

The Miridae (Insecta: Hemiptera: Heteroptera) is one of the most diverse family-groups of insects (Cassis, Wall & Schuh, 2007), and is composed of over 11 300 described species worldwide (Schuh, 1995, 2002–2013), which are nested within seven subfamilies and 35+ tribes (Schuh & Slater, 1995; Cassis & Schuh, 2012). As with many hyperdiverse families of organisms, the supraspecific classification of the Miridae has been subject to debate and revision (Carvalho, 1952; Schuh, 1975, 1976, 1995; Cassis & Schuh, 2012). For example, the classification of the mirid subfamily Phylinae has been significantly revised (Menard, Schuh & Wooley, 2013; Schuh & Menard, 2013), with a new tribal and subtribal classification.

More recently, we have revised the tribal-group classification of the lesser known subfamily Bryocorinae, with the recognition of the following infrageneric classification: Dicyphini ((Bryocorini+Eccritotarsini) (Felisaciini+Monaloniini)) (Namyatova, Konstantinov & Cassis, in press). This new tribal classification is of importance to the wider community because of the economic importance of the subfamily, with many species being important biocontrol agents (e.g. Martinez-Cascales *et al*., 2006) or pest species (e.g. Lavabre, 1977a).

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The Monaloniini comprises 41 genera (Schuh, 1995, 2002–2013; Cassis & Schuh, 2012; Namyatova & Cassis, 2013a; Namyatova *et al*., in press). It is a circumtropical group, inhabiting Africa, Australasia, South Asia and South America, with a handful of species known from temperate regions (e.g. Kerzhner, 1988a,b; Namyatova & Cassis, 2013b). The representatives of this tribe feed on flowering plants, and some species are known to be pests of food crops, especially cocoa, cashew and tea. *Sahlbergella singularis* Haglund, 1895, *Distantiella theobroma* (Distant, 1909) and *Helopeltis* spp. are treated as major pests of cocoa (Lavabre, 1977a) in developing countries with high levels of subsistence farming (Room & Smith, 1975).

The genera included in the Monaloniini were previously grouped in two suprageneric groups, as either: the subdivisions Monaloniaria and Odoniellaria (Reuter, 1910), tribes Monaloniini and Odoniellini (Carvalho, 1952, 1955, 1957), as two unnamed infratribes within the subtribe Monaloniina (Schuh, 1976), or subtribes Monaloniina and Odoniellina (Schuh, 1995; 2002–2013; Cassis & Schuh, 2012). Studies of trichobothria (Schuh, 1975), pretarsus (Schuh, 1976), thoracic pleura (Cassis, 1986; Cassis & Schuh, 2012) and male genitalia (Kerzhner & Konstantinov, 1999; Konstantinov, 2000) showed that monaloniines and odoniellines are closely related, having very similar morphology. Namyatova *et al*. (in press) showed that these two groups are both non-monophyletic, and synonymized Odoniellina *sensu* Schuh with Monaloniina *sensu* Schuh, raising the latter to tribal rank.

The most comprehensive generic review of the Monaloniini *sensu stricto* was undertaken by Odhiambo (1962), where he documented the taxonomy of 12 genera. A key to the West African genera was published by China (1944). Carvalho (1955) provided a key to them on a worldwide basis, including 13 monaloniine and 18 odonielline genera. Miller & China (1957) also published a key to odoniellines. Schmitz (1968) discussed the history of Monaloniini and gave a key to Ethiopian monaloniines. Lavabre (1977a) published a redescription for Monaloniini and Odoniellini and included a key to cocoa-feeding odonielline genera. Carvalho (1981) reviewed the bryocorines of Papua New Guinea. Namyatova & Cassis (2013a,b) and Namyatova *et al*. (in press) discussed the generic grouping within monaloniines and odoniellines.

The relationships within the tribe Monaloniini have been examined phylogenetically by Namyatova *et al*. (in press). In that work, we analysed species exemplars of 22 genera of the Monaloniini. The analysis revealed two distinct monophyletic groupings, *Monalonion*-complex and *Odoniella*-complex, with the rest of the genera not nested within multiple-taxon clades. The *Monalonion*-complex was also supported in a phylogenetic analysis of the genus *Rayieria* Odhiambo, 1962 (Namyatova & Cassis, 2013b). Namyatova *et al*. (in press) also found that the genus *Felisacus* Distant, 1904 is not nested within the monaloniines, and the new tribe Felisacini was established to accommodate it.

MATERIAL AND METHODS

Material

We analysed 2300+ specimens in this project (SI 1, as well as specimens from Namyatova & Cassis, 2013a,b; Namyatova & Cassis, 2014). The study was based on material borrowed and/or housed from the following museums: AM, Australian Museum (Sydney, Australia); AMNH, American Museum of Natural History (New York, USA); ANIC, Australian National Insect Collection (Canberra, Australia); BMN, Berlin Museum für Naturkunde (Berlin, Germany); BMNH, Natural History Museum, London (London, UK); BPBM, Bernice P. Bishop Museum (Honolulu, USA); DEI, Deutsches Entomologisches Institut (Müncheberg, Germany); DPIPWE, Department of Primary Industries, Parks, Water and Environment (Hobart, Australia); HNHM, Hungarian Natural History Museum (Budapest, Hungary); ISNB, Royal Institute of Natural Science of Belgium (Brussels, Belgium); MNHN, Museum National d'Histoire Naturelle a Paris (France, Paris); MRAC, Royal Museum for Central Africa (Belgium, Tervuren); MZH, Finish Museum of Natural History (Helsinki, Finland); NHRS, Naturhistorika riksmuseet (Stockholm, Sweden); NKMU, Nankai University Insect Collection (Tianjin, China); NML, Nationaal Natuurhistorische Museum (Leiden, The Netherlands); NTM, Northern Territory Museum (Darwin, Australia); PPRI, National Collection of Insects (Pretoria, South Africa); QM, Queensland Museum (Brisbane, Australia); SAMA, South Australian Museum (Adelaide, Australia); TAMU, Texas A&M University (USA); UNSW, University of New South Wales (Sydney, Australia); WAMP, Western Australian Museum (Perth, Australia); ZISP, Zoological Institute, Russian Academy of Sciences (St Petersburg, Russia).

A unique specimen identifier (USI) was attached to each specimen, and collected event data were digitized in the Plant Bug Planetary Biodiversity Inventory locality database (https://research.amnh.org/pbi/locality/); these data are also available through the Discover Life website (http://www.discoverlife.org/). The USI codes for specimens used for habitus and scanning electron microscopy (SEM) plates are given in legends to figures.

Dissections and terminology

Specimens were dissected following Kerzhner & Konstantinov (1999). The first author (A.N.N.)

supports the terminology of Kerzhner & Konstantinov (1999) and Konstantinov (2003), including the division of endosoma into conjunctiva and vesica in some mirid taxa. The second author (G.C.) does not support the division of endosoma into conjunctiva and vesica (Cassis, 2008). However, for Monaloniini those opinions do not contradict to each other, as endosoma is undivided in this group. The terminology of female genitalia follows Davis (1955), Schwartz (2011) and Stonedahl (1991).

Imaging

Most dorsal habitus images were made using the Visionary Digital BK Plus Lab photographic system (as developed by Roy Larimer) with a Canon EOS 40D camera. Images of type specimens of *Mircarvalhoia arecae* (Miller & China, 1957), *Villiersicoris sessensis* Odhiambo, 1962, *Platyngomiris apiformis* Ghauri, 1962 and female type of *Boxia khayae* China, 1943 were taken in Sackler's Biodiversity Imaging Lab at the Natural History Museum, London, using a Canon 450D camera attached to a Zeiss Stemi V11 microscope. Images of the specimens of *Boxiopsis madagasacariensis* Lavabre, 1960 were made using a Nikon D700 SLR digtal camera attached to a Nikon SMZ 1500 stereomicroscope in the Department of Entomology, St Petersburg State University. Multiple images of all specimens were merged using Helicon Focus software (http://www.heliconsoft.com).

Scanning electron micrographs of uncoated specimens were taken using a Hitachi TM3000 microscope. All images were processed using Adobe Photoshop CS3 extended and CS5.1 extended software.

Abbreviations

The following abbreviations were used throughout the paper: DLP, dorsal labial plate; ASI, ASII, ASIII and ASIV, antennal segments I to IV; LSI, LSII, LSII and LSIV, labial segments I to IV.

Taxa

We examined around 150 monaloniine species for this study, of which 118 were codified into the phylogenetic data matrix, and included multiple species representatives of each genus. We could not locate specimens of *Eucerocoris* Woodward, 1837 and it was not included in the analysis. We examined *Mircarvalhoia* Kerzhner & Schuh, 1998 and *Boxiopsis* Lavabre, 1960, but the material was not of sufficient quality and we excluded the taxa from our analyses. *Miomonalonion conoidifrons* Sailer & Carvalho, 1957 is a fossil taxon, and was not available for study and was also excluded from the phylogenetic analysis. *Felisacoris* was transferred to Felisacini, and *Onconotellus* Knight, 1935 and *Pachypeltopsis* Poppius, 1912 were transferred to other mirid subfamilies (see below). We also codified data for five other species of other Bryocorinae, which we designated as putative outgroups, including two representatives of the tribe Felisacini, which we previously proposed as the sister-group of the Monaloniini (Namyatova *et al*., in press). The tree was rooted with *Stenotus binotatus* (Fabricius, 1794) of the subfamily Mirinae (see SI 2 for full list of species used for phylogenetic analysis).

Phylogenetic analysis

The character matrix was created in Mesquite software (Maddison & Maddison, 2010), with 117 characters codified, from the head, thorax, hemelytron, appendages, male and female genitalia, as well as the texture and vestiture of the body (see SI 3 for matrix). Characters and character states are listed in Table 1.

All analyses were run using TNT software (Goloboff, Farris & Nixon, 2000, 2008), and NONA (Goloboff, 1999) implemented in Winclada (Nixon, 1999, 2002), with parsimony as the optimality criterion. Traditional searches with the swapping procedure TBR were employed with 10 000 replications and 10 trees saved per replication. All characters were unweighted and unordered. Searches were also undertaken using implied weights with concavity values ranging from $K = 3$ to 10. All unsupported nodes were collapsed after each analysis.

Bremer support values (Bremer, 1994) were calculated in TNT (Goloboff *et al*., 2008) using a Bremer script with standard settings to estimate support of sister-group relationships. Bootstrap resampling (Felsenstein, 1985) based on the unweighted trees was also performed as implemented in Winclada with 10 000 replications and with all other settings left as standard.

RESULTS

Phylogeny

The unweighted analysis produced 3480 most parsimonious trees in NONA and 2380 trees in TNT (Fig. 1). The minimum tree length found was 323 steps, with consistency index (CI) = 0.41 and retention index (RI) = 0.92 (Fig. 1A). The implied weights analyses in TNT resulted in 550–2240 trees. The consensus trees obtained from the analyses with $K = 4$–10 were identical (Fig. 2), whereas the consensus tree from $K = 3$ analysis differed in the position of the basal clades. Bremer support values (=BS) and sootstrap support values (=Bsv) are given in Figure 2 and in the node discussion.

Nodes of major clades are numbered 1–46. The consensus tree obtained from the implied weighting analysis tree with $K = 7$ is used for the discussion. For

Table 1. Character and character states used in the phylogenetic analysis

Head

0 *Head length/width ratio*: 1.2–2.3× as long as wide (Fig. 10A–D, G, J) (0); more than 2.5× as long as wide (Fig. 10E, F, H, I) (1). The state 1 occurs in many species of *Odoniella*-complex, as well as in *Physophoropterella* and *Villiersicoris sessensis*.

1 *Eye position relative to pronotum*: placed close to pronotum (0); removed from pronotum at distance shorter than eye diameter (Fig. 10B, D–J) (1); removed from head at distance as long as or longer than eye diameter (Fig. 10A, C) (2). State 0 occurs only in some outgroup species and in *Pantilioforma thoracica*. State 2 occurs in *Arculanus marshalli*, *Chamus*-complex, *Pararculanus*, *Mansoniella* and *Felisacus*.

2 *Eye position relative to lateral margins of head*: eye not embedded into head (Fig. 10C, E) (0); eye embedded into head (Fig. 10A, B, D, F–J) (1). The state 0 is present in *Chamus*-complex, *Physophoroptera* and *Physophoropterella*.

3 *Tubercules on head dorsally occurrence*: absent (0); present (Fig. 10F) (1). Tubercules on head are present in many species of *Odoniella*-complex.

4 *Bucculae shape*: not merged posteriorly (0); merged posteriorly (1). Buccula are merged posteriorly in *Felisacus* and *Hekista laudator* only.

5 *Frons shape*: not swollen (Fig. 10C, J) (0); at least somewhat swollen (Fig. 10A, B, D–I) (1). Frons is swollen in many taxa of Monaloniini, except for *Monaloniion*, *Ragwelellus*, some *Helopeltis* species and *Chamus*-complex. In outgroup taxa it is also not swollen.

6 *Bifurcated outgrowth or paired tubercules on frons occurrence*: absent (0); present (Fig. 10F) (1). State 1 is present in many species of *Odoniella*-complex.

7 *Three shallow ridges on frons occurrence*: absent (0); present (Fig. 10M) (1). Those tubercules are present in *Dimia*, *Eupachypeltis*, and *Poppiusia*.

8 *Three long outgrowths on frons occurrence*: absent (0); present (Fig. 10K) (1). Three long outgrowths on frons are present in *Chamus*-complex only.

9 *Projection of eyes*: eye not stylate (0); eye stylate, with at least small distance between eye and antennal fossa (Fig. 10E–I) (1). The eyes are stylate in many species of *Odoniella*-complex, *Physophoroptera* and *Physophoropterella*. In *Chamus*-complex species the head is visibly wide, but eyes seem to be placed very close to antennal fossae, not forming 'stalk' (Fig. 10C).

10 *Depression delimiting occipital region occurrence*: indistinct (Fig. 10B, D, F–J) (0); distinct (Fig. 10A, C, E) (1). Occipital region is distinctly delimited in *Arculanus*, *Poppiusia*, *Monalonion*, *Mansoniella*, *Felisacus*, *Villiersicoris sessensis*, *Pararculanus piperis, Ragwelellus vittatus, Pachypeltis cinchonae*, and in some species of *Pachypeltis*.

11 *Wrinkles on lateral side of head occurrence*: absent (0); present (fig. 5B in Namyatova *et al*., in press) (1). Those wrinkles are present in *Chamus*-complex only.

12 *Antennal fossa shape*: rounded (Fig. 10K) (0); oval (fig. 2B in Namyatova & Cassis, 2013a, Fig. 6 in Namyatova & Cassis, 2013b, fig. 2B in Namyatova & Cassis, 2014) (1). Antennal fossae oval in *Odoniella*-complex, *Monalonion*-complex, as well as in *Lycidocoris mimeticus* and *Pantiliforma*.

13 *Margins of antennal fossa shape*: not tuberculate (fig. 2A in Namyatova & Cassis, 2013a, Fig. 7 in Namyatova & Cassis, 2013b, fig. 2C in Namyatova & Cassis, 2014) (0) tuberculate (Fig. 10L) (1). Tuberculate antennal fossa occurs in *Chamus*-complex, *Eupachypeltis*, *Dimia inexpectata* and *Poppiusia leroyi*.

Antenna

14 *Antenna length*: distinctly shorter than body (0); as long as or longer than body (1). Long antennae are present in *Felisacus* and many species of *Monalonion*-complex.

15 *Antennal segment I length*: short, but more than twice as long as wide, sometimes slightly longer than head width (Fig. 10D) (0); very short and stout, ca 1.5–2× as long as width (Fig. 10G, H) (1); slightly longer than head and pronotum combined (fig. 2, 3, 6A–C in Namyatova & Cassis, 2013b, fig. 3E in Namyatova & Cassis, 2014) (2); more than 1.5× as long as head and pronotum combined (3). The state 1 is present in many *Odoniella*-complex, *Villiersicoris sessensis, Lycidocoris mimeticus*, *Pantilioforma*, *Schuhirandella fulva* and some species of *Monalonion*; the state 2 is present in *Rayieria*, *Physophoropterella*, and *Helopeltis cinchonae*; the state 3 occurs in *Ragwelellus*, *Arthriticus* and most of *Helopeltis* species.

16 *Antennal segment I shape*: cylindrical or slightly swollen medially (0); expanded towards apex or swollen apically (fig. 6A–C in Namyatova & Cassis, 2013b) (1). This character was not coded for the species with very short antennal segment I (see state 15-1). The antennal segment I is swollen in many species of *Monalonion*-complex and *Mansoniella*.

17 *Setae on antennal segment I occurrence:* absent (0), present or very scarce (1). Setae on antennal segment I are absent in *Monalonion*, *Physophoroptera mirabilis* and *Physophoropterella*.

Table 1. *Continued*

18 *Setae on antennal segment I, shape*: only simple setae present (0); flattened short setae present (1); flattened elongate setae present (2). This character was not coded for species which do not have setae on antennal segment I (see character 17). State 1 is present in *Distantiella theobroma* and state 2 is present in *Chamus*-complex.

19 *Antennal segment II length*: shorter, as long as or slightly longer than head and pronotum combined (0); more than 1.5× as long as head and pronotum combined (1). Long antennal segment II occurs in many species of *Monalonion*-complex, *Dimia inexpectata*, *Pararculanus piperis* and some species of *Pachypeltis*.

20 *Antennal segment II shape*: cylindrical or filiform, not swollen apically (0); distinctly swollen apically (fig. 3E in Namyatova & Cassis, 2014) (1). Antennal segment II is swollen apically in some species of *Odoniella*-complex, as well as in *Villiersicoris sessensis*, *Lycidocoris mimeticus*, *Pantilioforma*, *Physophoroptera mirabilis*, *Physophoropterella and Schuhirandella*.

21 *Swellings on antennal segment II presence*: absent (0); present (1). Swellings on antennal segment II are present in some species of *Odoniella*-complex.

22 *Swellings on antennal segment III presence*: absent (0); present (1). Swellings on antennal segment III are present in some species of *Odoniella*-complex.

23 *Antennal segment III shape*: filiform (0); widened or clavate (fig. 3E in Namyatova & Cassis, 2014) (1). Antennal segment II widened or clavate in *Odoniella*-complex, *Dimia inexpectata*, *Villiersicoris sessensis, Lycidocoris mimeticus*, *Pantilioforma*, *Physophoroptera mirabilis*, *Physophoropterella and Schuhirandella*.

24 *Antennal segment IV shape*: filiform (0); clavate (fig. 3E in Namyatova & Cassis, 2014) (1). Antennal segment II widened or clavate in *Odoniella*-complex, *Dimia inexpectata*, *Villiersicoris sessensis, Lycidocoris mimeticus*, *Pantilioforma*, *Physophoroptera*, *Physophorpterella and Schuhirandella*.

Labium

25 *Labial segment I length*: very short, as long as or shorter than wide (fig. 7D, E in Namyatova *et al*., in press) (0); at least twice as long as wide (1). The very short antennal segment is present in *Felisacus* only.

26 *Labial segment II length*: very short, as long as or shorter than wide (fig. 7D, E in Namyatova *et al*., in press) (0); at least twice as long as wide (1). The very short antennal segment is present in *Felisacus* only.

27 *Labial segment IV length and width ratio*: more than twice as long as wide (fig. 8A–D in Namyatova & Cassis, 2013b, fig. 2f in Namyatova & Cassis, 2014) (0); twice or less as long as wide III (fig. 8E in Namyatova & Cassis, 2013b) (1). Labial segment IV is distinctly longer than wide in most taxa, except for *Arculanus marshalli* and some *Rayieria* species.

28 *Labial segment III and IV lengths ratio*: segment IV distinctly longer than segment III (fig. 8A–D in Namyatova & Cassis, 2013b, fig. 2f in Namyatova & Cassis, 2014) (0); segment IV almost as long as segment III (e.g. fig. 8E in Namyatova & Cassis, 2013b) (1). Labial segment as long as segment III occurs in Monaloniini, except for *Arculanus marshalli*, *Volkeliopsis mindanao, Distantiella theobroma*, and some *Rayieria* species.

Pronotum

29 *Collar shape*: flat (fig. 7B, E in Namyatova & Cassis, 2013b, fig. 2c in Namyatova & Cassis, 2014) (0); at least slightly swollen (fig. 2A in Namyatova & Cassis, 2013a, fig. 7A, C, D, F in Namyatova & Cassis, 2013b) (1). The swollen collar is present in many genera of *Monalonion*-complex, as well as in *Arculanus marshalli*, *Poppiusia leroyi*, *Mansoniella* and some species of *Pachypeltis*.

30 *Four tubercules on collar occurrence*: absent (0); present (1). Distinct tubercules on collar are present in many species of *Odoniella*-complex.

31 *Depression delimiting calli laterally occurrence*: absent (0); present (Fig. 10A, C) (1). Calli are delimited laterally in all monaloniine taxa, not included into *Monalonion*-complex or *Odoniella*-complex, as well as in *Felisacus*.

32 *Calli position*: separated (0); fused (Fig. 10A) (1). Calli are fused in *Pachypeltis*, *Parapachypeltis punctatus*, *Pararculanus*, *Mansoniella* and *Felisacus*.

33 *Punctures laterally on depression delimiting calli posteriorly occurrence*: absent (0); present (fig. 5E in Namyatova & Cassis, 2014) (1). The state 1 occurs in *Felisacus* only.

34 *Pair of punctures on depression delimiting calli medially presence:* absent (0); present (Fig. 10A, fig. 5E in Namyatova & Cassis, 2014) (1). State 1 occurs in *Arculanus marshalli*, *Mansoniella*, and *Felisacus*.

35 *Punctation on pronotum presence*: pronotum impunctate (0); pronotum punctuate, sometimes mixed with wrinkles (Fig. 10D, G, I) (1). Punctures on pronotum are present in many species within *Odoniella*-complex, as well as in *Villiersicoris sessensis*, *Lycidocoris mimeticus*, *Pantilioforma*, *Parapachypeltis punctatus* and *Hekista laudator*.

36 *Wrinkles on pronotum presence*: absent or only some of them mixed with punctures present (0); present, shallow, wide, only longitudinal (Fig. 9H, fig. 2a, d in Namyatova & Cassis, 2014) (1); present, upraised, narrow; longitudinal and transversal (wrinkles similar to those on scutellum on Fig. 10C) (2). State 1 is present in all *Volkelius* species, state 2 is present in *Boxia khayae* only.

Table 1. *Continued*

37 *Tubercle or tumescence behind calli laterally*: absent (0), present (Fig. 10I) (1). State 1 occurs in *Yangambia*, some species of *Sahlbergella* and *Bryocoropsis kasaica*.

38 *Tumescences on pronotum dorsally occurrence*: absent (0), present (Fig. 10I) (1). The character was mentioned in the key of China (1944). The state 1 is present in some genera of *Odoniella*-complex.

39 *Small tubercules on pronotum occurrence*: absent (0), present (1). Small tubercules on pronotum occur in many species of *Chamus*-complex.

40 *Humeral angle of pronotum shape*: rounded, not dilate or acute (0), acute (Fig. 10E) (1), dilate (Fig. 10G, I) (2). Dilate humeral angles are present in many genera of *Odoniella*-complex, acute humeral angles are present in *Physophoropterella*.

41 *Serration of humeral angle of pronotum occurrence*: absent (0), present (Fig. 10I) (1).). State 1 is present in *Yangambia* only.

42 *Posterior margin of pronotum shape*: straight or slightly concave (0), distinctly concave, often angulate at sides of scutellum (Fig. 11D, H, J) (1). State 1 is present in many genera of *Odoniella*-complex.

43 *Setae on pronotum occurrence*: absent or very scarce (0), present, distinct (1). Setae are absent or very scarce on pronotum in many species of *Monalonion*-complex and *Odoniella*-complex, *Arculanus marshalli*, *Pararculanus piperis*, *Mansoniella* and *Felisacus*.

Scutellum

44 *Scutellum shape*: flat, not swollen (0), visibly swollen (Fig. 11B–K) (1). Scutellum is swollen in *Odoniella*-group, *Physophoroptera mirabilis*, *Physophoropterella* and some species of *Pachypeltis*.

45 *Swollen scutellum outline shape dorsally*: round (Fig. 11F) (0), triangular or trapeziform (Fig. 11B–E, G–K) (1), scutellum composed of six parts (2). Swollen and round scutellum is present in some species of *Odoniella*, *Pseudodoniella* and *Rhopaliceschatus quadrimaculatus*; scutellum composed of six parts occurs in *Yangambia*.

46 *Swollen scutellum outline laterally shape:* not divided into parts (Fig. 12A, D) (0), divided into lower and upper parts (Fig. 12B, C) (1). The scutellum is subdivided in *Sahlbergella*, *Distantiella* and *Physophoroptera mirabilis*.

47 *Anterior margin of scutellum position*: not covering pronotum (Fig. 11A, C, D, E, J, K) (0), covering pronotum (Fig. 11F-I) (1). State 1 is present in some genera of *Odoniella*-complex.

48 *Spine on scutellum occurrence*: absent (0), present bifurcate (Fig. 11K, 12D) (1), present, dilate apically, not bifurcate (Fig. 12E, F) (2). Bifurcate spine on scutellum is present in *Physophoropterella* and dilate not bifurcate spine occurs in all species of *Helopeltis*.

49 *Longitudinal depression on scutellum medially occurrence*: absent (0), narrow present (1), wide present (2). The state 1 is present in some species of *Odoniella*-complex, and state 2 is present in *Chamus*-complex and *Dimia* inexpectata.

50 *Punctures on scutellum occurrence*: absent (0), present, on only pair of punctures between scutellum and mesoscutum present (Fig. 11D–H, J) (1). Punctures on scutellum are present in many species of *Odoniella*-complex, as well as in *Lycidocoris mimeticus* and *Pantilioforma*.

51 *Pair of punctures between mesoscutum and scutellum*: absent (0), present (Fig. 10B, 11A) (1). This character was not coded for species where anterior part of pronotum is covering posterior part of scutellum (see character 47), as the suture between mesoscutum and scutellum cannot be observed in those cases. The state 1 is present in monaloniine species not included into *Odoniella*-complex or *Monalonion*-complex. It is also present in *Felisacus*.

52 *Tumescences on scutellum occurrence*: absent (0), present (sometimes very shallow) (Fig. 11D, F–H, J) (1). The state 1 is present in some species of *Odoniella*-complex.

53 *Striations on lateral margin of scutellum*: absent (0), present as a row (sometimes only anteriorly) (Fig. 11A) (1), only furrow anteriorly present (fig. 9H in Namyatova & Cassis, 2013b) (2). In most Monaloniini species, as well as in *Felisacus* and *Hekista laudator* the state 1 is present. The state 0 occurs in the rest of outgroup species. The state 2 is present in many taxa of *Monalonion*-complex.

Thoracic pleura and metasternum

54 *Opening of metathoracic scent gland position*: indistinct, placed almost ventrally (Fig. 13E, fig. 2E in Namyatova & Cassis, 2013a, fig. 3D in Namyatova & Cassis, 2014) (0), distinct (1). Opening of metathoracic scent gland is indistinct in Monaloniini and *Setocoris* sp.

55 *Microsculpture of evaporative area of metathoracic scent gland occurrence*: absent (Fig. 13E, fig. 2E in Namyatova & Cassis, 2013a, fig. 3D in Namyatova & Cassis, 2014) (1) (0), present (1). Microsculpture of evaporative area of methathoracic scent gland is absent in Monaloniini and *Setocoris* sp.

56 *Posterior part of metepimeron size:* narrow and broadly rounded (fig. 9C in Namyatova & Cassis, 2013b) (0), distinctly enlarged, with outgrowth (1). In many species of Monaloniini posterior part on metepimeron enlarged, except for *Arculanus marshalli* and *Rayieria*. In outgroup taxa state 0 is present.

Table 1. *Continued*

57 *Metepimeron outgrowth shape*: wider than long, with single apex, sometimes apex rounded (Fig. 13C, E) (0), wider than long, with two distinct apices (Fig. 13D) (1), as wide as long, rectangular or rounded (fig. 12A, 2E in Namyatova & Cassis, 2013a) (2), longer than wide, with round apex (Fig. 13B) (3). This character was not coded for the taxa with narrow posterior part of metepimeron (see Character 56). State 0 is most common among included taxa. State 1 is present in many *Pachypeltis* species, *Parapachypeltis punctatus*, *Lycidocoris mimeticus* and *Pantilioforma*. State 2 is characteristic for the species of *Helopeltis* subgen. *Afropeltis*. State 2 is present in many genera of *Monalonion*-complex.

58 *Posterior margin of metasternum shape*: rounded (0), protruding to abdominal segment II in shaped of triangular outgrowth (fig. 18A in Namyatova *et al*., in press) (1). State 1 is present in many taxa of Monaloniini, except for *Arculanus marshalli* and *Monalonion*-complex. In outgroup taxa state 0 is present.

Hemelytron

59 *Setae on hemelytron occurrence*: absent or scarce (0), present, distinct (1). Setae on hemelytron are absent in most species of *Monalonion*-complex and in *Felisacus*.

60 *Flattened setae on hemelytron occurrence*: absent (0), present (1). This character was not coded for species without setae on hemelytron (see characters 59). Flattened setae are present in many species of *Odoniella*-complex and in *Chamus*-complex.

61 *Flattened setae on hemelytron colour*: mostly pale (0), mostly dark (1). This character was not coded for taxa without flattened setae (see characters 59 and 60). Pale flattened setae are present in *Chamus*-complex, *Boxia khayae* and *Volkelius*. Dark flattened setae are present in many genera of *Odoniella*-complex.

62 *Row of punctures on clavus occurrence*: absent (0), present (fig. 12A, C in Namyatova *et al*., in press) (1). Punctures on clavus are present in species of Monaloniini, except for *Monalonion*-complex and *Odoniella*-complex. Within outgroup taxa they are present in *Felisacus*.

63 *Claval commissure length*: distinctly shorter than scutellum (fig. 13E in Namyatova *et al*., in press) (0), as long as or longer than scutellum (1). Very short claval commissure is present in many species of *Odoniella*-complex.

64 *Margins of claval commissure*: straight (0), curved (fig. 9A in Namyatova & Cassis 2013b) (1). Curved margins of claval commissure are present in all species of *Monalonion*-complex.

65 *Margins of corial fracture*: straight (fig. 9D in Namyatova & Cassis 2013b) (0), curved (Fig. 9E in Namyatova & Cassis 2013b) (1). Curved margins of corial fracture are present in *Arthriticus*, *Helopeltis*, *Monalonion*, and *Ragwelellus*.

66 *Swelling on corium posteriorly*: absent (0), present (fig. 13F in Namyatova *et al*., in press) (1). Swellings on corium posteriorly are present on *Physophoroptera mirabilis* and *Physophoropterella*.

67 *Row of punctures on R + M occurrence*: absent (0), present (1). Punctures on R + M are present in Monaloniini, except for *Monalonion*-complex and *Odoniella*-complex. Within outgroup taxa they are present in *Hekista laudator*.

68 *R + M length*: far not reaching posterior margin of corium (0), reaching posterior margin of corium (1). R + M is short in *Chamus*-complex and in *Odoniella*-complex.

69 *Medial fracture length*: short, almost indistinct (fig. 12A in Namyatova *et al*., in press) (0), long, reaching middle of corium (1). Short medial fracture is present in *Felisacus*, *Nesidiocoris tenuis* and *Setocoris* sp.

70 *Medial fracture direction*: directed towards midline (0), subparallel to R + M (1). This character was not coded for taxa with short medial fracture (see characters 69). The medial fracture subparallel to R + M occurs in *Monalonion*-complex.

71 *Costal margin of hemelytron in male shape*: almost straight or slightly concave or convex (0), distinctly convex near posterior margin of corium (1). The state 1 is present in *Arculanus marshalli*, *Mansoniella*, and *Chamus*-complex.

72 *Costal margin of hemelytron in female shape*: almost straight or slightly concave or convex (0), distinctly convex near posterior margin of corium (1). State 1 is present in following taxa: *Arculanus marshalli*, *Mansoniella*, *Chamus*-complex, and *Poppiusia leroyi*.

73 *Inner margin of cuneus shape*: straight or slightly concave (0), slightly convex (fig. 14E, G in Namyatova *et al*., in press) (1), distinctly concave (fig. 14C in Namyatova *et al*., in press) (2). State 2 occurs in many species of *Monalonion*-complex, and in some species of *Pachypeltis*. State 1 is present in *Felisacus*, *Nesidiocoris tenuis*, and *Setocoris* sp.

74 *Length of cuneus/ length of scutellum ratio*: cuneus longer than scutellum (0), cuneus as long as or shorter than scutellum (1). State 1 is present in *Odoniella*-complex, *Physophoroptera mirabilis* and *Physophoropterella*.

75 *Membranal cell/ pronotum length ratio*: membranal cell less than 1.5× as long as pronotum (0), membranal cell more than 1.5× as long as pronotum. State 1 is present in many genera of *Monalonion*-complex, *Dimia inexpectata*, *Parapachypeltis punctatus*, and some species of *Pachypeltis*.

Table 1. *Continued*

76 *Apex of membranal cell position*: not surpassing apex of cuneus (0), surpassing apex of cuneus (1). State 1 is present in most species of Monaloniini, except for *Arculanus marshalli* and *Yangambia*. In outgroup state 0 is present.

77 *Membranal cell shape*: forming right angle (fig. 14B, E–G in Namyatova *et al*., in press) (0), forming acute angle (fig. 14A, C in Namyatova *et al*., in press) (1). The state 1 is present in many species of *Monalonion*-complex, *Dimia inexpectata*, *Parapachypeltis punctatus*, and some species of *Pachypeltis*.

78 *Number of cells on membrane*: one (fig. 14A–C, E in Namyatova *et al*., in press) (0), two (fig. 14F, G in Namyatova *et al*., in press) (1). Two cells on membrane are present in some outgroup taxa, i.e. *Stenotus binotatus*, *Felisacus magnificus* and *Nesidiocoris tenuis*.

Legs

79 *Forecoxae position*: separated (fig. 9I in Namyatova & Cassis, 2013b) (0), contiguous (1). Forecoxae are separated in *Monalonion*-complex, except for the genus *Monalonion*.

80 *Hind coxae position*: separated (fig. 9J in Namyatova & Cassis, 2013b) (0), contiguous (1). Hind coxae are separated in all Monaloniini species, *Felisacus* and *Hekista laudator*.

81 *Apices of femora shape*: now swollen or only slightly swollen (0), distinctly swollen (Fig. 13G, H) (1). Apices of femora are swollen in most species of Monalonion-complex, except for some species of *Rayieria*.

82 *Fore- and middle femora shape*: straight (0), curved (1). Fore- and middle femora are curved in *Arthriticus*, *Ragwelellus* and *Helopeltis*.

83 *Hind femur shape*: straight (0), curved (Fig. 13H, fig. 19A in Namyatova *et al*., in press) (1). Hind femur is curved in many species of *Monalonion*-complex, except of *Physophoroptera mirabilis*, some species of *Pachypeltis*, and *Poppiusia leroyi*.

84 *Trichoma around trichobothria occurrence*: absent or very rare (as in fig. 19G, I in Namyatova *et al*., in press) (0), present, distinct (as in fig. 19H, J in Namyatova *et al*., in press) (1). Trichoma around trichobothria are present in *Felisacus* and *Stenotus binotatus*.

85 *Foretibia length*: shorted or as long as head and pronotum combined (0), distinctly longer than head and pronotum combined (1). State 1 is present in *Arthriticus*, *Ragwelellus* and *Helopeltis*.

86 *Setation on hind tibia, density*: regular (0), very dense (1)

87 *Small black spinules on tibia occurrence*: absent or only apically present (0), present (1). The state 0 occurs in Monalonion-complex, except for *Physophoroptera mirabilis*.

88 *Small black spinules on tibia position*: placed in rows (0), irregularly distributed (1). This character was not coded for taxa, where spinules are absent or placed apically only (see character 86). Black spinules are placed irregularly in *Odoniella*-complex, *Physophoroptera mirabilis, Physophoropterella, Hekista laudator* and *Stenotus binotatus*.

89 *Swellings on hind tibia occurrence*: absent (0), present (1). Swellings on hind tibia are present only in some species of *Odoniella*-complex.

90 *Tarsal segments relative length*: subequal in length to each other or segment III slightly shorter than segments I and II each (fig. 3h in Namyatova & Cassis, 2014) (0), tarsal segment I longer than segments II and III each (fig. 13I, Fig. 2C in Namyatova & Cassis, 2013a, fig. 8F in Namyatova & Cassis, 2013b) (1). Tarsal segment I longer than II and III occurs in *Monalonion*-complex.

91 *Basal tooth on claw occurrence*: absent (0), present (Fig. 13J–I, fig. 10 in Namyatova & Cassis, 2013b, fig. 3f, h, i in Namyatova & Cassis, 2014) (1). Basal tooth is present in Monaloniini and *Felisacus magnificus*.

92 *Basal tooth on claw shape*: short, subtriangular, as long as wide (fig. 10B in Namyatova & Cassis, 2013b) (0), elongate, longer than wide (fig. 13J-I, fig. 10H in Namyatova & Cassis, 2013b, fig. 3f, h, i in Namyatova & Cassis, 2014) (1). This character was not coded for the taxa where basal tooth on claw is absent (see character 90). Elongate basal tooth is present in most of the taxa. The short basal tooth is present in many species of *Monalonion*-complex, some species of *Odoniella*-complex and in *Felisacus magnificus*.

93 *Parempodia asymmetry*: parempodia symmetrical (0), parempodia asymmetrical (fig. 21A, C in Namyatova *et al*., in press) (1). This character was not coded for *Hekista laudator*, as it does not have parempodia. Asymmetrical parempodia are present in *Felisacus* only.

94 *Guard setae length*: short (0), long (1). Short guard setae are present in *Stenotus binotatus*, *Nesidiocoris tenuis* and *Setocoris* sp.

Male genitalia

95 *Relative length of parameres*: right parameres shorter than left one (0), right parameres longer than left one (1). Right paramere longer than left one is present in *Felisacus* only.

96 *Supragenital bridge occurrence*: absent (0), present (Figs 14–17) (1). Supragenital bridge is present in *Monaloniini* and absent in outgroup taxa.

Table 1. *Continued*

97 *Apex of genital capsule direction*: directed posteriorly, not curved (0), directed dorsally, curved (Fig. 14D) (1). State 1 is present in species of *Helopeltis* subgen. *Afropeltis*.

98 *Ventral wall of genital capsule length*: not shortened anteriorly (0), shortened anteriorly (Fig. 15Q) (1). The state 1 is present in *Monalonion*-complex.

99 *Outgrowths on genital capsule at sides:* absent (0), outgrowth only from left-hand side present (Fig. 17T) (1), outgrowth from both sides present (Fig. 17K) (2). The state 1 is present in some species of *Ragwelellus*, and state 2 is present in *Yangambia* only.

100 *Outgrowths on phallobase from lateral side of ductus seminis occurrence*: absent (0), present, sometimes short (e.g. Figs 14E, P, T, X, AB, 15I, 16T, X, AB, AF, 17A) (1). The state one is present in many genera of Monaloniini, but very rarely in *Monalonion*-complex and *Odoniella*-complex.

101 *Outgrowth on phallobase in front of ductus seminis base occurrence*: absent (0), present (Fig. 15M) (1). The state 1 is present in many species of *Helopeltis* subgen. *Helopeltis*.

102 *Coils on ductus seminis occurrence*: absent or faint and indistinct (Figs 14T, X, AB, 15I, 16T, X, AB, AF, 17A, I) (0), present, distinct (1). Coils on ductus seminis are absent in *Pararculanus*, *Pachypeltis*, *Parapachypeltis punctatus*, *Eupachypeltis*, *Poppiusia leroyi*, *Chamus*-complex, and *Physophoroptera mirabilis*.

103 *Coils on ductus seminis occurrence*: forming narrow tube (Figs 14E, 16A, E) (0), forming wide tube (1). Coils in shape of narrow tube are present in *Arculanus marshalli* and *Mansoniella*.

104 *Sclerotisation of basal part of ductus seminis occurrence*: absent (0), present (Fig. 16I) (1). Sclerotization of basal part of ductus seminis is present in *Monalonion* only.

105 *Sclerotisation around secondary gonopore occurrence*: absent (0), present (Figs 14B, 16I) (1). The state 1 is present in *Monalonion*, some species of *Odoniella*-complex and some outgroup taxa.

106 *Sclerotized part of theca shape*: theca more or less uniformly sclerotized, dorsal part not distinctly delimited (0), dorsal side sclerotised stronger than other parts, sclerotisation broad, rounded apically, not tapering (e.g. 14A, E, M, P, T, X, AB) (1), dorsal side sclerotised stronger than other parts, sclerotization distinctly tapering apically (Figs 14I, 15V, Z, 17A, AD) (2). State 1 is present in most of the Monaloniini species. State 0 is present in all outgroup taxa. State 2 is present in *Lycidocoris mimeticus*, *Pantilioforma*, *Arthriticus eugeniae*, *Physophoroptera mirabilis* and *Physophoropterella*.

107 *Dentate outgrowth on theca medially occurrence*: absent (0), present (Fig. 17U) (1). State 1 is present in some species of *Ragwelellus*.

108 *Outgrowth on theca from left-hand side presence*: absent (0), present (Fig. 15V, Z) (1). The state 1 occurs in *Lycidocoris mimeticus* and *Pantilioforma*.

Female genitalia

109 *Sclerotized circle on dorsal labiate plate occurrence*: absent (0), present (e.g. 18G, I, R, 19N, P, R) (1). The state 1 is present in many species of *Pachypeltis*, *Monalonion*, *Ragwelellus*, as well as in *Odoniella*-complex.

110 *Shape of sclerotized circle on dorsal labiate plate*: present, longer than wide, placed dorsally and often laterally (e.g. Figs 18G, I, R, 19N, P, 20A, S, 21A, P, R, S) (0), present, small, as long as wide, placed dorsally only (Figs 19R, 21E) (1). This character was not coded for taxa without sclerotized circle (see character 108). The small sclerotized circle is present only in *Pseudodoniella chinensis*, *Platyngomiris coreoides* and *Platyngomiriodes apiformis*, and *Rhopaliceschatus quadrimaculatus*.

111 *Sclerotized rings occurrence*: absent (0), present (Figs 18A, 20M, E) (1). The sclerotized rings are present in *Arculanus madagascariensis*, some species of *Pachypeltis*, *Helopeltis* subgen. *Afropeltis* and in outgroup species.

112 *Spermathecal gland position*: placed medially (0), placed from right-hand side (Figs 18G, 19P, R, 21A, S) (1), placed from left-hand side (Fig. 21R) (2). State 1 is present in many species of *Odoniella*-complex, and state 2 is present in *Sahlbergella maynei* and *S. tai*.

113 *Paired sclerotized areas on posterior wall of bursa copulatrix posteriorly*: absent (0), present (Fig. 21B, F) (1). This state 1 is present in *Pseudodoniella* and *Platyngomiris coreoides*.

114 *Small tubercles on posterior wall*: absent (0), present (1). Tubercules on posterior wall are present in almost all species of Monaloniini, except for *Pararculanus piperis, Arculanus madagascariensis*, and *Felisacus*.

115 *Paired apical membrane outgrowths clothed with small spicules on posterior wall of bursa copulatrix occurrence*: absent (0), present (Fig. 19D) (1). The state 1 is present in most species of *Helopeltis* subgen. *Helopeltis*.

116 *Base of second valvula shape*: straight, concave or convex (0), with bifurcate outgrowth (Fig. 19D, O) (1). The state 1 is present in *Schuhirandella fulva*, *Monalonion*, and many species of *Helopeltis* subgen. *Helopeltis*.

Figure 1. Strict consensus tree for the tribe Monaloniini, unweighted analysis. Number of nodes is given in circles, Bremer support values above nodes and bootstrap support values below nodes.

character optimization one of the trees obtained from this analysis was chosen (Figs 3–5). The distribution of character states by node found in this tree was as follows:

Node 1. Felisacus+Monaloniini (BS = 3, Bsv = 99).

This clade is supported by four non-contradicted apomorphies: depression delimiting calli laterally present (31-1) (Fig. 10A–C); pair of punctures between mesoscutum and scutellum present (Fig. 11A, fig. 11A–D in Namyatova *et al*., in press) (51-1); row of punctures on clavus present (fig. 12A, C in Namyatova *et al*., in press) (62-1); small tubercles on posterior wall present (Figs 18–21) (114-1). It is also

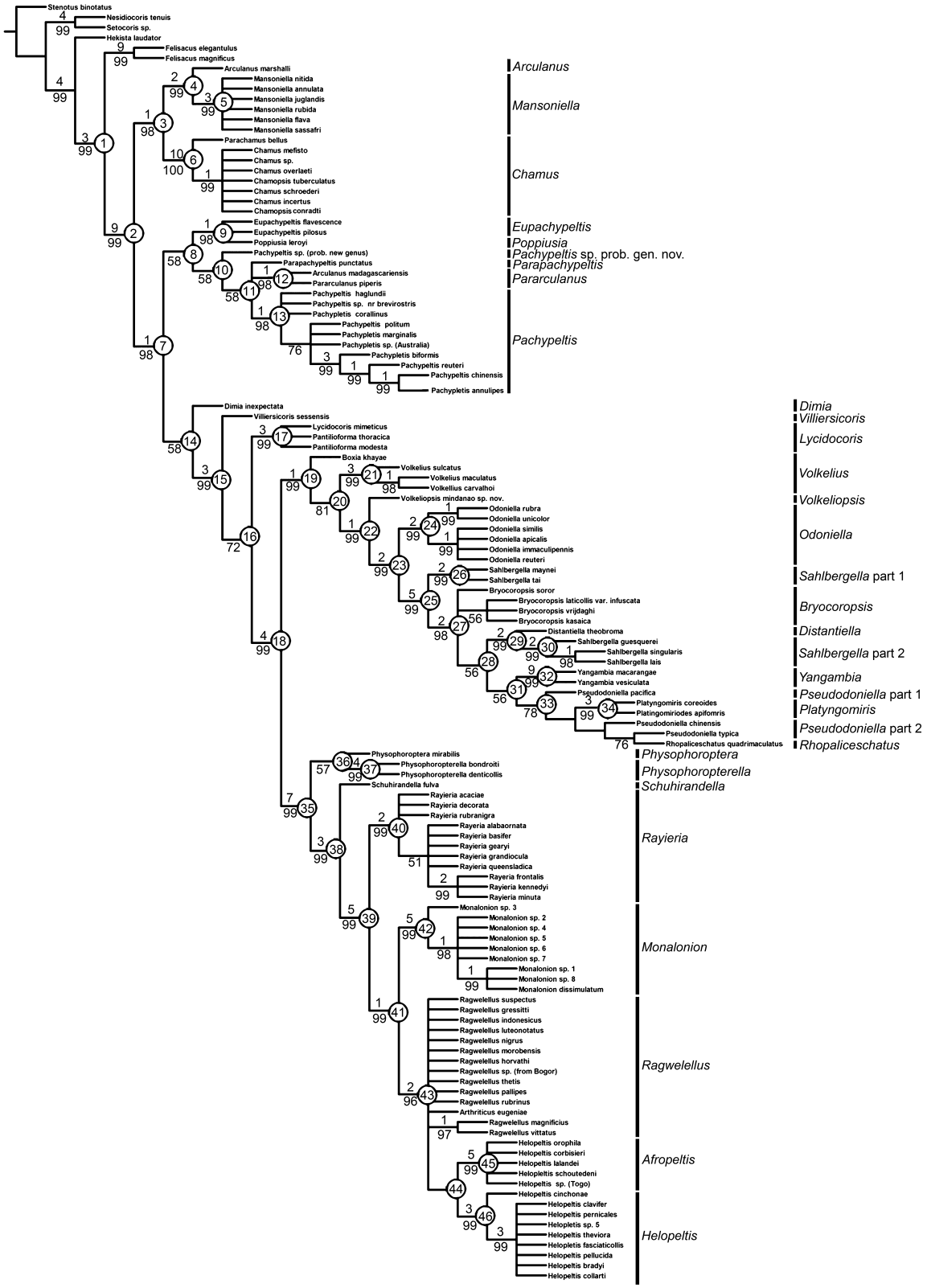

Figure 2. Strict consensus tree for the tribe Monaloniini, implied weights analysis, K = 7. Number of nodes is given in circles, Bremer support values above nodes and bootstrap support values below nodes.

Figure 3. Optimization of characters on one of the shortest trees for the tribe Monaloniini with implied weights. Part 1, nodes 1–13. Number of nodes is given in circles.

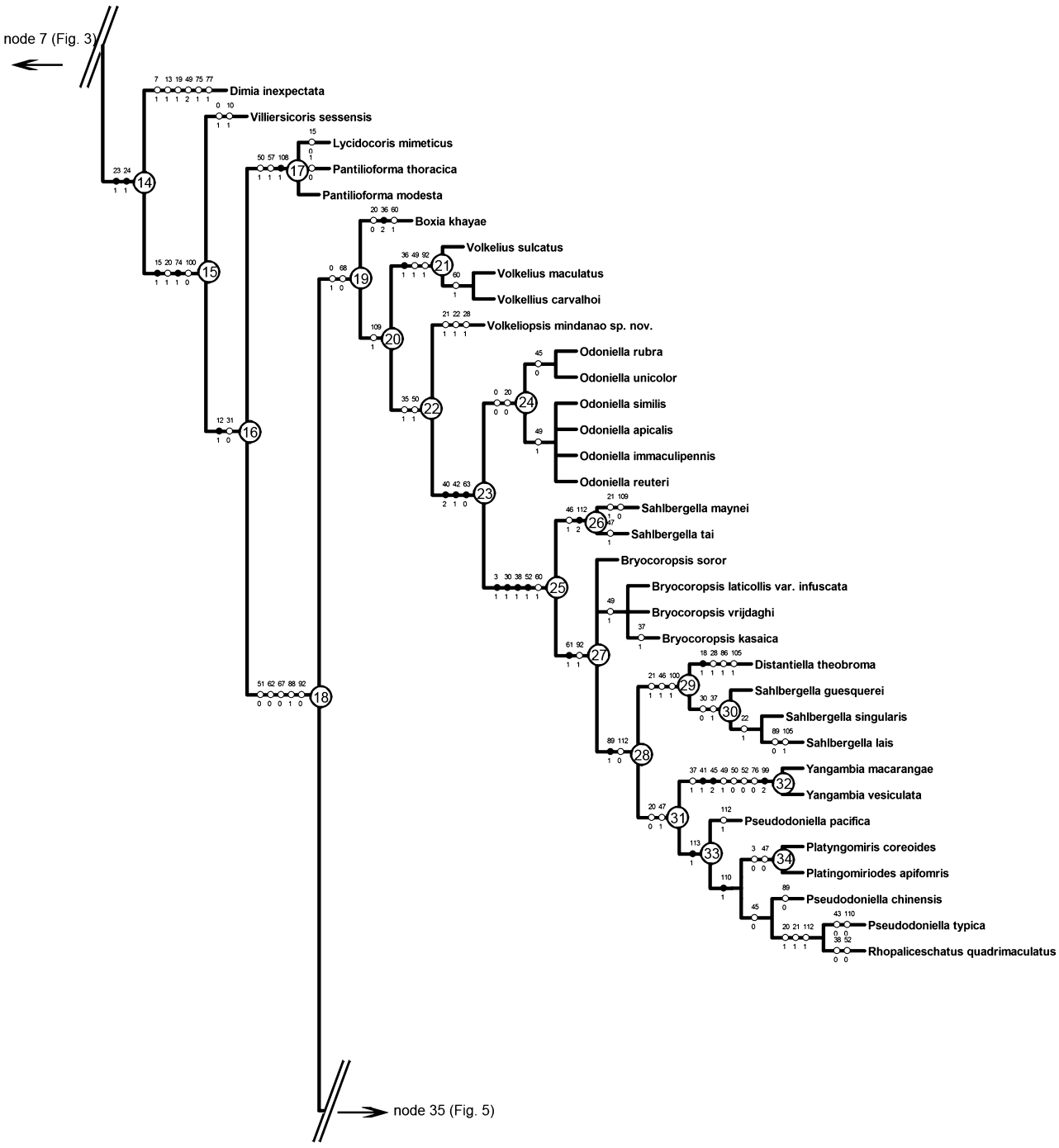

Figure 4. Optimization of characters on one of the shortest trees for the tribe Monaloniini with implied weights. Part 2, nodes 14–34. Number of nodes is given in circles.
30

supported by a single contradicted apomorphy: head removed from pronotum at distance subequal to or longer than eye diameter (1–2) (for more synapomorphies and discussion of this clade, also see Namyatova *et al*., in press).

Node 2. Monaloniini (BS = 9, Bsv = 99). The non-contradicted apomorphies for this clade are as follows: metepimeron posteriorly prominent (56-1) (Fig. 13A–E); metasternum with medial projection on abdominal segment II (fig. 16A in Namyatova *et al*., in press)

Figure 5. Optimization of characters on one of the shortest trees for the tribe Monaloniini with implied weights. Part 3, nodes 34–43. Number of nodes is given in circles.

(58-1); membrane cell surpassing apex of cuneus (fig. 13A–C in Namyatova *et al*., in press, fig. 9G in Namyatova & Cassis, 2013b) (76-1); supragenital bridge on genital capsule present (Figs 14–18) (96-1); dorsal side of theca sclerotized much more strongly than ventral part, broad apically (106-1). This clade is also supported by four contradicted apomorphies: opening of metathoracic scent gland placed almost ventrally (Fig. 13E) (54-0); microsculpture of metathoracic scent gland area absent (Fig. 13E) (55-0), outgrowths on phallobase from lateral margins of ductus seminis present (100-1); sclerotization around secondary gonopore absent (105-0). The taxa within this clade do not split into monaloniines and odoniellines, as was previously proposed (Carvalho, 1952, 1955; Schuh, 1995). Namyatova *et al*. (in press) also discussed the phylogeny and classification of the Monaloniini, albeit based on more limited taxon sampling.

Node 3. *Arculanus marshalli* Distant, 1904 + *Mansoniella* Poppius, 1915 + *Chamus*-complex (BS = 1, Bsv = 88). This clade is supported by the non-contradicted apomorphy: costal margin of hemelytron in male distinctly widened near posterior margin of corium (71-1); and a single contradicted apomorphy, costal margin of hemelytron in female distinctly widened near posterior margin of corium (72-1). Diagnostically, these taxa are also similar to each other in coloration, usually having white or yellow body with red or bright yellow markings on hemelytron (Fig. 6).

Node 4. *Arculanus marshalli+Mansoniella* (BS = 1, Bsv = 98). This clade is supported by four contradicted apomorphies: depression delimiting occipital region distinct (10-1) (Fig. 10A); collar at least slightly swollen (29-1), pair of punctures on depression delimiting calli present (34-1) (Fig. 10A); setae on pronotum absent or very scarce (43-0). This clade has a basal position within Monaloniini, and it also possesses symplesiomorphies with *Felisacus*, including semitransparent hemelytron and medial pair of punctures on the pronotum, anteriorly placed beyond the depression delimiting the calli (fig. 4E in Namyatova *et al*., in press). Although *Arculanus marshalli* and *Mansoniella* are similar to each other externally (Fig. 6 and see discussion for the genus *Arculanus* Distant, 1904) and apart from the listed synapomorphies including similarity of the structure of the ductus seminis, which is very narrow (Figs 14I, 16A, E), we have ongoing doubts about the position of *Arculanus*.

Node 5. *Mansoniella* (BS = 3, Bsv = 99). This genus is supported by two contradicted apomorphies: apex of ASI swollen (fig. 8C in Namyatova *et al*., in press) (16-1), calli fused with each other (32-1) (Fig. 10A). Although there are no non-contradicted apomorphies for this clade, the species examined are very similar to each other externally and possess a unique structure of ASI, which is shorter than the head width and is swollen apically.

Node 6. *Chamus*-complex (BS = 10, Bsv = 100). This clade is supported by three non-contradicted apomorphies: three long outgrowths on frons present (8-1) (Fig. 10C, K), wrinkles on lateral side of head present (11-1) (Fig. 4B in Namyatova *et al*., in press), flattened and elongate setae on ASI present (18-2). It is also supported by six contradicted apomorphies: eye not embedded to head (2-1) (Fig. 10C), margins of antennal fossa distinctly tuberculate (13-1) (Fig. 10L, M), wide longitudinal depression on scutellum present (49-2); flattened setae on hemelytron present (60-1); R + M not reaching posterior margin of hemelytron (68-0); coils on ductus seminis absent or faint and indistinct (102-0) (Fig. 14T, X, AB). Here we synonymize *Chamopsis* Reuter & Poppius, 1911 and *Parachamus* Schouteden, 1946 with *Chamus* Distant, 1904. This clade is highly autapomorphic, and groupings within it are uncertain (see also discussion for *Chamus*). The genera of the *Chamus*-complex were previously treated within the subtribe Odoniellina *sensu* Schuh. The current analysis shows that they are not related to the *Odoniella*-complex, which includes most species previously assigned to Odoniellina *sensu* Schuh.

Node 7. (BS = 1, Bsv = 98). This node is supported by a single contradicted apomorphy: eye removed from pronotum at distance shorter than eye diameter (Fig. 10B, D, F–J) (1-1). The node includes all monaloniine genera except for *Arculanus*, *Chamus*-complex and *Mansoniella*. This clade is not well supported, and it is possible that some genera, such as *Eupachypeltis* Poppius, 1915 and *Poppiusia* China, 1944, are more closely related to node 3 (*Arculanus*, *Mansoniella* and *Chamus*-complex). Those two genera have the ridges on the frons, which are similar to outgrowths of the *Chamus*-complex, but are much shorter. *Eupachypeltis* also possesses similar coloration to taxon representatives of node 3, which is yellow with pale brown marking on the hemelytron (Fig. 6).

Node 8. (**Bsv = 58**). This node is supported by a single contradicted apomorphy: coils on ductus seminis absent, faint or indistinct (Figs 15I, 16T, X, AB, AF, 17I) (102-0). This node includes *Arculanus madagascariensis* Poppius, 1912, *Eupachypeltis*, *Pachypeltis* Signoret, 1858, *Parapachypeltis punctatus* Hu & Zheng, 2001, *Pararculanus piperis* Poppius, 1912 and *Poppiusia leroyi* (Schouteden, 1943). This node is not recovered in the unweighted strict consensus cladogram, and has neither Bremer or > 50% bootstrap support. *Eupachypeltis* and *Poppiusia* might be phylogenetically closer to node 3 (see discussion for node 7).

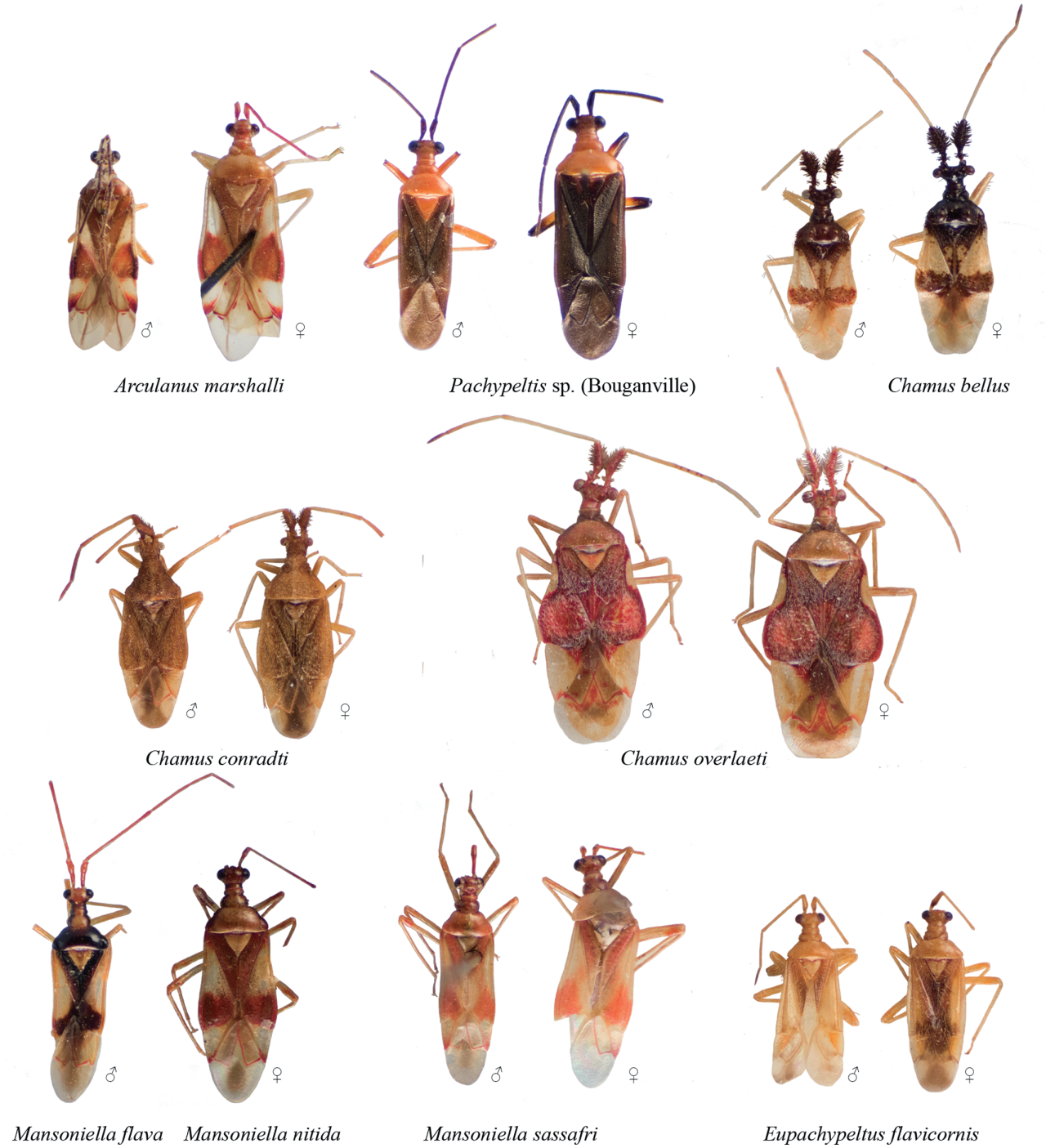

Figure 6. Habitus photographs. *Arculanus marshalli* ♂ AMNH_PBI 5102, ♀ AMNH_PBI 19290; *Pachypeltis* sp. ♂ AMNH_PBI 46046, ♀ AMNH_PBI 34149; *Chamus bellus* ♂ AMNH_PBI 19050, ♀ AMNH_PBI 5223; *Chamus conradti* ♂ AMNH_PBI 19048, ♀ AMNH_PBI 19046; *Chamus overlaeti* ♂ AMNH_PBI 5123, ♀ AMNH_PBI 5123; *Mansoniella flava* ♂ AMNH_PBI 19270; *Mansoniella nitida* ♀ AMNH_PBI 45968; *Mansoniella sassafri* ♂ AMNH_PBI 19276, ♀ AMNH_PBI 19067; *Eupachypeltis flavicornis* ♂ LT AMNH_PBI 19128, ♀ PT AMNH_PBI 19641.

Node 9. *Eupachypletis+Poppiusia leroyi*. (BS = 1, Bsv = 98). This node is supported by two contradicted apomorphies: three shallow ridges on frons present (Fig. 10M) (7-1); margins of antennal fossa distinctly tuberculate (Fig. 10L, M) (13-1). *Eupachypeltis* and *Poppiusia* are similar to each other in structure, but the former is much smaller in size and inhabits South Asia, whereas the latter is known from the Congo and Ghana. The ridges on the frons of these genera are very similar, but this character is not unique to them as it is also present in *Dimia*. Although the species of *Eupachypeltis* do not form a clade in this analysis, they are very similar to each other and have near identical male genitalia (see also discussion *Eupachypeltis*).

Node 10. (Bsv = 58). This node is supported by a single contradicted apomorphy only, calli fused (32-1) (fig. 3A in Namyatova *et al*., in press). This clade includes *Arculanus madagascariensis*, *Pararculanus piperis*, *Pachypeltis* and *Parapachypeltis punctatus*, it does not appear on the unweighted strict consensus cladogram and has non-significant bootstrap support. The unidentified species of *Pachypeltis* from Bougainville analysed in this work is basal within this clade but is not nested within the monophyletic group that comprises the other *Pachypeltis* species. Although this species is externally similar to other *Pachypeltis* species, it differs from them in many respects (see discussion of the genus *Pachypeltis*), and may represent a different genus. However, we refrain from the description of a new genus to accommodate it, pending a thorough revision of *Pachypeltis*.

Node 11. (Bsv = 58). This node is supported by a single contradicted apomorphy: membrane cell forming a sharp angle (fig. 13A in Namyatova *et al*., in press) (77-1). This node does not appear in the unweighted strict consensus cladogram. It includes African taxa (*Arculanus madagascariensis*, *Pararculanus piperis*) and South Asian taxa (*Parapachypeltis punctatus*, *Pachypeltis*). The relationships of the taxa in this node are mostly unresolved.

Node 12. *Pararculanus piperis+Arculanus madagascariensis* (BS = 2, Bsv = 91). This node is supported by two contradicted apomorphies: eyes removed from pronotum at a distance subequal to or longer than eye diameter (as in Fig. 10A) (1–2), small tubercles in posterior wall of bursa copulatrix absent (Fig. 20N, P) (114-0). Based on this analysis, we transfer *Arculanus madagascariensis* to *Pararculanus*, although it is different from other species in this genus (see discussion for *Pararculanus*).

Node 13. *Pachypeltis* (BS = 1, Bsv = 91). The monophyly of this group is supported by two contradicted apomorphies: posterior margin of metepimeron wider than long, bifurcate (Fig. 13D) (57-1), sclerotization of DLP in shape of medial circle (Fig. 20A) (109-1).

Node 14. (Bsv = 58). This node is supported by two non-contradicted apomorphies: ASIII widened apically or clavate (fig. 8F, G in Namyatova *et al*., in press) (23-1) and ASIV clavate (fig. 8F, G in Namyatova *et al*., in press) (24-1). This clade includes *Dimia inexpectata* Kerzhner, 1988, *Villiersicoris sessensis* Odhiambo, 1962, *Lycidocoris* Reuter & Poppius, 1911, *Pantilioforma* China, 1944, *Odoniella*-complex and *Monalonion*-complex. The position of *Dimia* Kerzhner, 1988 in this clade is questionable, as its ASIII–IV are only slightly clavate, and it also possesses three shallow ridges on the frons, which are similar to those found in *Eupachypeltis* and *Poppiusia* (Fig. 10M), and its scutellum has a longitudinal depression similar to that found in *Chamus*.

Node 15. (BS = 3, Bsv = 99). This clade is supported by two non-contradicted apomorphies: ASI very short and stout, *c*. 1.5× as long as wide (Fig. 10F–H) (15-1); cuneus as long as or shorter than scutellum (74-1). It is also supported by two contradicted apomorphies: ASII distantly incrassate apically (fig. 8E in Namyatova *et al*., in press) (20-1); outgrowths on phallobase on from lateral margins of ductus seminis absent (100-0). This node includes *Villiersicoris sessensis*, *Lycidocoris*, *Pantilioforma*, *Odoniella*-complex and *Monalonion*-complex. *Villiersicoris* Dellatre, 1950 and *Lycidocoris* were previously treated within the tribe Odoniellina *sensu* Schuh, as soon as they have wide antennae and more or less robust body. According to the current analysis they form the clade with the *Odoniella*-complex+*Monalonion*-complex.

Node 16. *Lycidocoris mimeticus* Reuter and Poppius, 1911 + *Pantilioforma+Odoniella*-complex+*Monalonion*-complex (Bsv = 72). This node is supported by two contradicted apomorphies: antennal fossa oval, longer than half of eye height (fig. 3B in Namyatova *et al*., in press, fig. 6D–F in Namyatova & Cassis, 2013b) (12-1), depression delimiting calli laterally absent (31-1). *Lycidocoris* and *Pantilioforma* together form the sister group to *Monalonion*-complex+*Odoniella*-complex.

Node 17. *Lycidocoris mimeticus+Pantilioforma* (BS = 3, Bsv = 99). This clade is supported by three synapomorphies: punctures on scutellum present (50-1), posterior part of metepimeron higher than wide, bifurcate (as in Fig. 13D) (57-1), outgrowth of phallotheca from left-hand side present (Fig. 15V, Z) (108-1). The latter state is non-contradicted. We synonymize *Pantilioforma* with *Lycidocoris*, as species of these genera are monophyletic, but the relationships within this group are doubtful (see discussion for *Lycidocoris*).

Node 18. ***Odoniella*-complex+*Monalonion*-complex (BS = 4, Bsv = 99)**. This clade is supported by five contradicted apomorphies: pair of punctures between mesoscutum and scutellum absent (51-0), row of punctures on clavus absent (62-0), row of punctures on R + M absent (67-0), small black spinules on tibiae placed irregularly (88-1), basal tooth on claw short and triangular (92-0) (fig. 10H in Namyatova & Cassis, 2013b). All the states are unique within Monaloniini. Those two groups form a well-supported monophyletic group, although their typical representatives are very different externally, which supports the phylogeny in Namyatova *et al*. (in press). Typical *Odoniella*-complex species are oval and robust bugs with shortened appendages (Fig. 8), whereas *Monalonion*-complex species are usually elongate bugs with very long antennae (Fig. 9) (see also Namyatova *et al*., in press for discussion). This clade was also revealed and discussed in Namyatova *et al*. (in press).

Node 19 *Odoniella*-complex (BS = 1, Bsv = 99). This clade is supported by two contradicted characters: head more than 2.5× as long as wide (Fig. 10F–I) (0–1); R + M far not reaching posterior margin of corium (68-0). Representatives of the *Odoniella*-complex are all very similar to each other, having robust and oval body, widened antennae, hemelytron without row of punctation on clavus and R + M. See also Namyatova *et al*. (in press) for a discussion. This clade was also revealed and discussed in Namyatova *et al*. (in press).

Node 20. *Odoniella complex less Boxia khayae* China, 1943 (Bsv = 81). This clade does not appear on the strict consensus unweighted cladogram. The clade is characterized by a single contradicted apomorphy: presence of sclerotization on DLP in shape of medial circle (109-1) (Figs 18G, I, R, 19P, R, 21A, C, E, P, R, S). Although the genus *Boxia* China, 1943 is different from other genera of the *Odoniella*-complex and shows many plesiomorphic characters for this clade, e.g. scutellum only slightly raised, rather thin antennae, absence of punctures on pronotum and scutellum, and absence of sclerotized circle on dorsal labial plate, its sister-group relationships with other species of the *Odoniella*-complex are not very well supported and warrant further verification. The genus *Boxiopsis* is synonymized with *Boxia* in this work (see also redescription of *Boxia* for further discussion).

Node 21. ***Volkelius* Distant, 1904 (BS = 3, Bsv = 99)**. This Australian genus is supported by three synapomorphies: presence only of wide and longitudinal wrinkles on pronotum (36-1), presence of narrow longitudinal depression on scutellum (49-1), basal tooth on claw longer than wide (fig. 3F, H, I in Namyatova & Cassis, 2014) (92-1). The state 36-1 is non-contradicted. Species of *Volkelius* represent a well-defined group, possessing similar wrinkled texture of the pronotum and scutellum, pattern of endosomal sclerotization, as well as other similarities. See Namyatova & Cassis (2014) for a revision of the genus.

Node 22. ***Odoniella*-complex species with punctate pronotum and scutellum (BS = 1, Bsv = 99)**. The clade is supported by two contradicted apomorphies: pronotum punctate (35-1), scutellum punctate (50-1). *Yangambia* Schouteden, 1942 is also within this group, although its scutellum is not punctate.

Node 23. ***Odoniella*-complex species with distinctly swollen scutellum (BS = 2, Bsv = 99)**. The clade is supported by three non-contradicted apomorphies: humeral angles of pronotum dilate (Fig. 10G, I) (40-2), posterior margin of pronotum distinctly concave, angulate at sides of scutellum (Fig. 11D, F–J) (42-1), claval commissure distinctly shorter than scutellum (fig. 12E in Namyatova *et al*., in press) (63-0). This clade is also characterized by the distinctly swollen scutellum (Fig. 11D–J), which we did not code as a separate state, as the scutellum is more or less inflated in some other representatives of Monaloniini. *Volkeliopsis mindanao* sp. nov. forms the sister-group to this clade. It is similar externally, except for the only slightly swollen scutellum.

Node 24. ***Odoniella* Haglund, 1985 (BS = 2, Bsv = 99)**. This clade is supported by two contradicted apomorphies: head 1.2–2.3× as long as wide (Fig. 10G) (0-0) and ASII straight, not swollen or incrassate apically (20-0). Although the clade is not very well supported, species of *Odoniella* are similar to each in body shape and coloration. For further discussion see redescription of this genus

Node 25 (BS = 5, Bsv = 99). This clade is supported by five synapomorphies: tubercles on head dorsally present (Fig. 10F) (3-1), four tubercles on collar present (30-1), tumescences on pronotum present (Fig. 10I, fig. 4C in Namyatova *et al*., in press) (38-1), tumescences of scutellum present (Fig. 11F, G, H, J) (52-1), flattened setae on hemelytron present (Fig. 60-1). Only the last state is contradicted. This clade includes eight closely related genera, namely *Bryocoropsis* Schumacher, 1917, *Distantiella* China, 1944, *Sahlbergella* Haglund, 1895, *Pseudodoniella* China & Carvalho, 1951, *Platyngomiriodes* Ghauri, 1963, *Platyngomiris* Kirkaldy, 1902, *Rhopaliceschatus* Reuter, 1903 and *Yangambia*. The relationships between those groupings are obscure. Although the monophylies of the genera *Bryocoropsis*, *Sahlbergella* and *Pseudodoniella* are not supported, we refrain from any taxonomical decision pending a thorough revision of this clade.

Node 26. *Sahlbergella maynei* Schuteden, 1935 and *S. tai* Schmitz, 1987 (BS = 2, Bsv = 99). The clade

is supported by two states: scutellum divided into upper and lower parts (as in Fig. 12B) (46-1), spermathecal gland placed from left-hand side (Fig. 22Q) (112-2). The former state is contradicted and the latter is non-contradicted. Those two species together form the sister-group to the rest of the species of clade 25. Their position is uncertain and they can also form a group with the remaining *Sahlbergella* species and *Distantiella*, as they all have the unique structure of scutellum, divided into upper and lower parts. For a further discussion of the characters within *Sahlbergella* see the redescription of this genus.

Node 27. (BS = 2, Bsv = 88). The clade is supported by two synapomorphies: flattened setae on hemelytron mostly dark colored (61-1), basal tooth on claw longer than wide (as in fig. 3F, H, I in Namyatova & Cassis, 2014) (92-1). The former state is non-contradicted and the latter is contradicted. This clade includes all species of clade 22 except *Sahlbergella maynei* and *S. tai*, and its status is doubtful (see discussion for clade 26).

Node 28. (Bsv = 56). The clade is supported by two synapomorphies: swellings on hind tibiae present (88-1), spermathecal gland on DLP placed medially (112-0) (Figs 18R, 21C, E). The former state in non-contradicted, and the latter is contradicted. This clade includes *Distantiella theobroma*, *Sahlbergella guesquierei* Schuteden, 1935, *S. lais* Linnavuori, 1973, *S. singularis*, *Platyngomiris*, *Platyngomiriodes*, *Pseudodoniella*, *Rhopaliceschatus* and *Yangambia*. This clade does not appear on the strict consensus unweighted cladogram and has low support.

Node 29. ***Distantiella theobroma*, *Sahlbergella guesquierei*, *S. singularis* and *S. lais* (BS = 2, Bsv = 99)**. This group is supported by three contradicted apomorphies: swellings on ASII present (fig. 8E in Namyatova *et al*., in press) (21-1), scutellum divided into lower and upper parts (Fig. 12B) (46-1), outgrowths on phallobase from lateral margins of ductus seminis present (Fig. 14P, fig. 23E in Namyatova *et al*., in press) (100-1). Although the species of this clade are very similar to each other, we refrain from any formal synonymy, as there are doubts regarding the monophyly of *Sahlbergella* (see also discussion of nodes 26 and 30).

Node 30. *Sahlbergella guesquierei*, *S. singularis* and *S. lais* (BS = 2, Bsv = 99). This node is supported by two contradicted apomorphic states: four tubercles on collar present (30-1), paired tubercles behind calli laterally present (as in Fig. 10I) (37-1). The three species of *Sahlbergella* that form this clade differ from *Sahlbergella maynei* and *S. tai* by many salient and genitalic characters, and the monophyly of the genus requires further investigation. See description of *Sahlbergella* for a discussion.

Node 31. (Bsv = 56). This node is supported by two contradicted apomorphies: ASII straight, not swollen apically (20-0), anterior margin of scutellum distinctly covering posterior margin of pronotum (Fig. 11F-I) (47-1). This clade includes *Pseudodoniella*, *Platyngomiris*, *Platyngomiriodes*, *Rhopaliceschatus* and *Yangambia*. The African genus *Yangambia* is the sister-group to the remaining taxa of this clade, with the latter taxa distributed in South Asia and Australasia. *Yangambia* is very different in appearance to the others and all other taxa of the *Odoniella*-complex. Although the phylogenetic position of *Yangambia* in this complex is not in question, the exact sister-taxon relationship(s) of *Yangambia* is in doubt.

Node 32. ***Yangambia* (BS = 9, Bsv = 99).** This genus is supported by three non-contradicted apomorphies: humeral angles on pronotum serrate (Fig. 10I) (41-1), scutellum subdivided into six parts (Fig. 11I) (45-2); lateral outgrowths on genital capsule on both sides present (Fig. 17A, H) (99-2). The clade is also supported by five contradicted apomorphies: tumescence behind calli laterally present (Fig. 10I) (37-1), narrow longitudinal depression on scutellum present (Fig. 11I) (49-1); punctures on scutellum absent (Fig. 11I) (50-0); tumescences on scutellum absent (52-0); membrane cell not surpassing apex of scutellum (76-0). There are only two species described in *Yangambia*, and they are very similar to each other.

Node 33. (Bsv = 78). This node is supported by a single non-contradicted apomorphy: paired sclerotized areas on posterior wall of bursa copulatrix present (Fig. 21B, F) (113-1). The clade comprises *Platyngomiriodes*, *Platyngomiris*, *Pseudodoniella* and *Rhopaliceschatus*, which are known from South Asia and Australasia, whereas all other species of the *Odoniella*-complex that have a strongly inflated scutellum are known only from Africa (see Node 23). The species within this clade are similar to each other morphologically (see discussion for *Platyngomiris*). Although the support for this node is weak, it is likely that the genera within it are closely related or even congeneric.

Node 34. *Platyngomiris coreoides* Kirkaldy, 1902 and *Platyngomiriodes apiformis* Ghauri, 1963 (BS = 3, Bsv = 99). This node is supported by two contradicted apomorphies: tubercles on head dorsally absent (3-0), anterior margin of scutellum not covering pronotum (47-0). The two species are so similar that we propose a new synonymy for both genera and species. See the description of *Platyngomiris* for justification.

Node 35. *Monalonion*-complex (BS = 7, Bsv = 99). This node is supported by seven characters: metasternum without projection on abdominal

segment II (fig. 17B in Namyatova *et al*., in press) (58-0); margins of claval commissure concave (fig. 11G in Namyatova *et al*., in press, fig. 9A, B in Namyatova & Cassis, 2013b) (64-1); medial fracture subparallel to R + M (figs 11G, 12F in Namyatova *et al*., in press, fig. 9A in Namyatova & Cassis, 2013b) (70-1); forecoxae separate (fig. 17B in Namyatova *et al*., in press, fig. 9A in Namyatova & Cassis, 2013b) (79-0); femora distinctly swollen apically (fig. 18A in Namyatova *et al*., in press) (81-1); tarsal segment I longer than segments II and III each (fig. 19B in Namyatova *et al*., in press, fig. 7F in Namyatova & Cassis, 2013b) (90-1); ventral wall of genital capsule shortened anteriorly (Fig. 15Q) (98-1). Only 58-0 is contradicted. This node includes *Arthriticus*, *Monalonion*, *Physophoroptera*, *Physophoropterella*, *Ragwelellus*, *Rayieria* and *Schuhirandella*. The clade was also recovered in the phylogenies of Namyatova & Cassis (2013b) and Namyatova *et al*. (in press).

Node 36. *Physophoroptera+Physophoropterella* (Bsv = 57). This node is supported by three synapomorphies: eye not embedded into head (2-0) (Fig. 10E, fig. 4D in Namyatova *et al*., in press); setae on ASI absent (17-0), swelling on corium posteriorly present (fig. 12F in Namyatova *et al*., in press) (66-1). The last apomorphy is non-contradicted. Additionally, the genera have a similar colour pattern and both possess an exaggerated scutellum. Although this clade has non-significant resampling support, we are confident that *Physophoroptera* and *Physophoropterella* are sister-taxa (also see diagnoses for both genera). This clade was also revealed by Namyatova & Cassis (2013b) and Namyatova *et al*. (in press).

Node 37. ***Physophoropterella* (BS = 4, Bsv = 99)**. This node is supported by three characters: head more than 2.5× as wide as long (Fig. 10E) (0-1); humeral angle of pronotum acute (Fig. 10E) (40-1), bifurcate spine on scutellum present (Figs 11K, 12D) (48-1). Only 40-1 is contradicted. We examined only *P. bondroiti* Poppius, 1914 and *P. denticollis* (Reuter & Poppius, 1911) of the four described species of *Physophoropterella*. However, based on the descriptions of the two species which we did not examine, we have no doubt that they are congeneric (Schumacher, 1917; Schouteden, 1942c) (see also discussion for *Physophoropterella*).

Node 38. ***Monalonion*-complex less *Physophoroptera and Physophoropterella* (BS = 3, Bsv = 99)**. This node is supported by two non-contradicted apomorphies: single furrow on lateral margin of scutellum from each side present (fig. 9H in Namyatova & Cassis, 2013b) (53-2), posterior margin of metepimeron higher than long, with rounded margin (fig. 9C in Namyatova & Cassis, 2013a) (57-3). It is also supported by three contradicted apomorphies: ASII more than 1.5× as long as head and pronotum combined (19-1), collar at least slightly swollen (fig. 7A, C, D in Namyatova & Cassis, 2013b) (29-1), cuneus longer than scutellum (74-0). This clade includes *Schuhirandella fulva*, which is the sister-group to the rest of the taxa, all of which have an elongate body and long appendages. *Schuhirandella* is much shorter than the other taxa, and has thickened antennal segments, similar to those taxa found in the *Odoniella*-complex. However, it shares many characters unique for the *Monalonion*-complex (see also Namyatova & Cassis, 2013a for a discussion of characters and description of *Schuhirandella*; and Namyatova & Cassis, 2013b, for additional discussion of characters of this clade). This clade was also revealed by Namyatova & Cassis (2013b).

Node 39. (BS = 7, Bsv = 97). **Elongate monaloniines**. This node is supported by five contradicted apomorphies: antennal subequal to or longer than body (14-1); ASII straight, not incrassate apically (20-0); ASIII not widened or clavate (23-0); ASIV not clavate (24-0); inner margin of cuneus distinctly concave (fig. 13C in Namyatova *et al*., in press) (73-2). State 14-1 is unique within Monaloniini. The node includes all elongate monaloniines with long antennae and legs. See also Namyatova & Cassis (2013b) for additional discussion. This clade was also revealed by Namyatova & Cassis (2013b).

Node 40. ***Rayieria* (BS = 2, Bsv = 99)**. The monophyly of the genus is supported by two single contradicted apomorphies: ASI slightly longer than head and pronotum combined (15-2), metepimeron not prominent, broadly rounded (56-0) (fig. 9C in Namyatova & Cassis, 2013b). The species of the genus are diverse morphologically, but represent the well-defined group, which is mainly characterized by the structure of the antenna and shape of the claw (fig. 10A, B in Namyatova & Cassis, 2013b) (see Namyatova & Cassis, 2013b for diagnosis and discussion).

Node 41. *Monalonion* Herrich-Schaeffer, 1850 + *Arthriticus* Bergroth, 1923 + *Ragwelellus* Odhiambo, 1962 +*Helopeltis* Signoret, 1858 (BS = 1, Bsv = 99). This clade is supported by a single non-contradicted apomorphy only: margins of corial commissure curved (fig. 9E in Namyatova & Cassis, 2013b) (65-1). This node includes all elongate monaloniines with long appendages, except for *Rayieria*. Although in this work the clade is supported with only a single apomorphy, its species differ from other members of the *Monalonion*-complex in shape of head, labium and antennae (see Namyatova & Cassis, 2013a,b for additional characters).

Node 42. ***Monalonion* (BS = 5, Bsv = 99)**. The monophyly of the genus is supported by five contradicted apomorphies: distinct depression delimiting

occipital region (10-1), setae on ASI absent (17-0), forecoxae contiguous (79-1), sclerotization on DLP present as medial circle (Fig. 19N) (109-1), base of second valvula with bifurcate outgrowth (Fig. 19O) (116-1).

Node 43. ***Arthriticus+Ragwelellus+Helopeltis* (BS = 2, Bsv = 96)**. This node is supported by three non-contradicted apomorphies: ASI more than 1.5× as long as head and pronotum combined (15-3), fore and middle femora curved (fig. 18A in Namyatova *et al*., in press) (82-1), foretibia distinctly longer than head and pronotum combined (85-1). The species of this clade form a well-defined group, but the relationships within this clade are unclear. *Ragwelellus* is not monophyletic in the weighted and unweighted consensus trees, and we did not find any synapomorphies to support it. Species of this genus are more or less uniform externally, but the male and female genitalia vary considerably within the genus. *Ragwelellus* is similar to *Helopeltis* subgen. *Helopeltis* in structure, except for lack of a scutellar spine, which is characteristic for both subgenera of *Helopeltis*. As noted by Stonedahl (1991), it might be possible that *Helopeltis* is not a monophyletic genus, and the subgenus *Helopeltis* is a sister-group to *Ragwelellus*, or part thereof. The monotypic genus *Arthriticus* is also very similar externally to representatives of *Ragwelellus*. However, it is not as yet clear if *Arthriticus eugeniae* is closer to any subgroup of *Ragwelellus* species or represents a sister group to all of them; its male and female genitalia are different from all species of *Ragwelellus* that we examined (see discussion for *Arthriticus*). This clade was also revealed by Namyatova & Cassis (2013b).

Node 44. *Helopeltis* + *Afropeltis*. The node is supported by a single apomorphy: spine on scutellum present, not bifurcate (Fig. 21D, E) (48-2); it has no Bremer support and the bootstrap value was non-significant. We have raised *Afropeltis* Stonedahl, 1991 to full generic rank, thereby restricting the composition and definition of *Helopeltis* (see Schmitz, 1968 and Stonedahl, 1991 for subgeneric classification). See discussion for *Afropeltis*.

Node 45. *Afropeltis* (BS = 5, Bsv = 99). This node is supported by two non-contradicted apomorphies: posterior part of metepimeron with narrow outgrowth rounded apically (Fig. 3B) (57-2), apex of genital capsule curved apically (Fig. 14D) (97-1). It is also supported by a single contradicted apomorphy: sclerotized rings on DLP present (Fig. 18A) (111-1).

Node 46. ***Helopeltis* (BS = 3, Bsv = 99).** This genus is supported by three contradicted apomorphies: frons not swollen, almost flat (5-0), collar flat (29-0), basal tooth on claw elongate, longer than wide (92-1) (Fig. 10D). *Helopeltis cinchonae* Mann, 1907 is a sister-group to all other *Helopeltis* species and differs significantly from them in external and genital characters. For further discussion of characters, see discussion for *Helopeltis*, as well as Schmitz (1968) and Stonedahl (1991).

TAXONOMY

Tribe Monaloniini

Monalonionaria Reuter, 1892: 398 (division nov.);

Eucerocoraria Kirkaldy, 1902: 294 (division nov.); Reuter, 1910: 123 (disc.)

Monaloniaria Reuter, 1910: 123 (disc.);

Odoniellaria Reuter, 1910: 123 (disc.); Oshanin, 1912: 70 (as tribe, cat.)

Monaloniini Carvalho, 1952: 33, 35, 40, 41, 59 (as tribe, disc., key to tribes, cat.); Carvalho, 1955: 16, 38 (key to tribes, key to gen.); Carvalho, 1957: 131 (cat.); Odhiambo, 1962: 313 (review of some African genera); Schmitz, 1968: 7 (descr., disc., key to Ethiopian fauna); Schuh, 1975: 9, 17 (trichobothria); Carayon, 1977: 21 (key to tribes); Lavabre, 1977a: 57 (desc., review of cocoa pest genera); Carvalho, 1981: 5, 7 (list of spp. for Papua New Guinea, key to gen.); Kerzhner, 1988a: 792 (key to spp. of Far East USSR); Cassis and Gross, 1995: 141 (cat.); Kerzhner and Konstantinov, 1999: 122 (male genitalia).

Odoniellini Carvalho, 1952: 33, 35, 40, 41, 60 (disc., key to tribes, cat.); Carvalho, 1955: 15, 40 (key to tribes, key to gen.); Miller and China, 1957: 430 (key to gen.); Carvalho, 1957: 143 (cat.); Odhiambo, 1962: 271 (generic review, in part); Schuh, 1975: 9, 17 (trichobothria); Carayon, 1977: 21 (key to tribes); Lavabre, 1977a: 48 (descr., key to gen.; review of cocoa pest genera); Carvalho, 1981: 5, 6 (list of spp. for Papua New Guinea, key to gen.); Kerzhner and Konstantinov, 1999: 122 (male genitalia).

Monaloniina Schuh, 1976: 23 (as subtribe, pretarsus, disc.); Schuh, 1995: 508 (cat.); Schuh and Slater, 1995: 176 (disc.)

Odoniellina Schuh, 1976: 32 (as infratribes, pretarsus, disc.); Schuh, 1995 (cat.); Schuh and Slater, 1995: 176 (disc.)

Diagnosis: The Monaloniini differ from other bryocorine suprageneric groups by the unique structure of the thoracic pleura, with the opening of the scent glands obscure, ventrally positioned and without evaporative bodies (fig. 14A in Namyatova *et al*., in press; see also Cassis, 1986 and Cassis & Schuh, 2012 where this character was initially mentioned), the suture between mesopleuron and metapleuron incomplete (fig. 14A in Namyatova *et al*., in press), and the metepimeron in many species with a distinct lobe (Fig. 13A–C, fig. 14A in Namyatova *et al*., in press). Other important diagnostic characters for the Monaloniini are: LSI–II more

than twice as long as wide (fig. 9A in Namyatova *et al*., in press); LSIV usually the longest, rarely subequal to LSIII (fig. 8A-E in Namyatova & Cassis, 2013b; fig. 2F in Namyatova & Cassis, 2014; fig. 19A in Namyatova *et al*., in press), collar weakly separated, usually delimited laterally, hemelytron membrane with single cell, with cell often elongate, surpassing apex of cuneus; basal tooth on claw present (fig. 9A, B in Namyatova & Cassis, 2013b; fig. 21F, I Namyatova *et al*., in press); parempodia symmetrical (fig. 10 in Namyatova & Cassis, 2013b; fig. 20F in Namyatova *et al*., in press); unguitractor plate with three contiguous rows of tiles, tiles of middle row straight (fig. 10B in Namyatova & Cassis, 2013b; fig. 20F in Namyatova *et al*., in press). See also diagnosis of Monaloniini in Namyatova *et al*. (in press).

Description: Body size 4.5–14 mm, usually ranging between 8 and 11 mm. COLORATION (Figs 6–9, figs 2–4 in Namyatova & Cassis, 2013b). Colour usually bright, varying from uniformly pale yellow (e.g. *Yangambia vesiculata*) to dark brown (e.g. *Sahlbergella singularis*) or bright red (e.g. *Physophoroptera mirabilis*). Body usually multicoloured with markings and spots, sometimes with braconid-mimicking (e.g. *Rayieria basifer*) or bee-mimicking (*Platyngomiris apiformis*) colour pattern. TEXTURE. Head impunctate, usually with short medial sulcus, which sometimes is very indistinct; some genera with flattened area on vertex near or behind each eye (fig. 4B, C in Namyatova *et al*., in press); pronotum and scutellum impunctate or punctuate, sometimes punctures mixed with wrinkles or only wrinkles present; pair of punctures on depression delimiting calli and pair of punctures between mesoscutum and scutellum absent or present (fig. 10A in Namyatova *et al*., in press); small tubercles or tumescences on pronotum and scutellum absent or present (Figs 10I, 11D, F–H, J, L, fig. 4B, C in Namyatova *et al*., in press); lateral margin of scutellum usually with row of punctures or striations (fig. 11C, D in Namyatova *et al*., in press), except genera from the *Monalonion*-complex (see discussion and node 35); sulcus between mesoscutum and scutellum with pair of medial punctures in many genera, except the *Monalonion*-complex and *Odoniella*-complex (fig. 11C,D in Namyatova *et al*., in press); hemelytron generally impunctate, but in many genera bearing rows of punctures on clavus and R + M (fig. 11C, D in Namyatova *et al*., in press); pleura smooth, impunctate. VESTITURE. Body often clothed with simple setae; in many species of *Chamus* and some genera of the *Odoniella*-complex ASI and hemelytra mostly or entirely with flattened setae, sometimes those setae darkened (many genera of the *Odoniella*-complex); sometimes vestiture scarce, pronotum, scutellum and hemelytron almost without setae; rarely vestiture dense; legs sometimes covered with very long and dense setae (*Sahlbergella theobroma*, *Platyngomiris apiformis*); small black setae on tibia usually placed in irregular rows (as in fig. 18D in Namyatova *et al*., in press), sometimes irregularly distributed, present only apically or absent. STRUCTURE. *Head*. Dorsal view (Fig. 10A-J, fig. 2D in Namyatova & Cassis, 2013a, fig. 5A–F in Namyatova & Cassis, 2013b, fig. 2A–D in Namyatova & Cassis, 2014, fig. 4A–D in Namyatova *et al*., in press). Eye often removed from pronotum at a distance at least equivalent to half eye diameter or sometimes placed closer to pronotum; occipital region delimited or not delimited by depression; eye stylate or not stylate; distance between antennal fossa varying from as long as to twice as long as antennal fossa diameter; frons often swollen, sometimes straight, sometimes with paired tubercles or more or less bifurcate outgrowth (many representatives of *Odoniella*-complex), three outgrowths (*Chamus*), or with three shallow ridges (*Eupachypeltis*, *Dimia*, *Poppiusia*). Anterior view (Fig. 10K, fig. 2B in Namyatova & Cassis, 2013a, fig. 6 in Namyatova & Cassis, 2013b, fig. 2B, E in Namyatova & Cassis, 2014, fig. 3A, B in Namyatova *et al*., in press). Varying from as wide as long to almost twice as wide as long; from anterior view eye oval, higher than wide or roundish; eye height varying from distinctly longer to slightly shorter than distance between eye and apex of clypeus; antennal fossa round distinctly shorter than eye height or oval, varying from subequal to half of eye height to almost subequal to eye height; inferior margin of antennal fossa slightly above inferior margin of eye, but sometimes at the same level or below inferior margin of eye; base of clypeus placed below, slightly above or at half eye height, often distinctly delimited basally, sometimes not delimited. Lateral view (Fig. 10L, fig. 2A in Namyatova & Cassis, 2013a, fig. 7 in Namyatova & Cassis, 2013b, fig. 2C in Namyatova & Cassis, 2014, fig. 6A-C in Namyatova *et al*., in press). Head swollen of almost flat; in lateral view eye oval, margin of eye surpassing clypeus, but not reaching maxillary plate; maxillary and mandibular plates subrectangular; buccula shortened, almost as long as wide or elongate; gula usually longer than buccula or shortened, straight or convex. *Labium* (fig. 8A, E in Namyatova & Cassis, 2013b, fig. 9A in Namyatova *et al*., in press). Length varying from very short, slightly surpassing anterior margin of prosternum to reaching abdominal segments III–IV; LSI–III usually longer than wide, more or less subequal in length, sometimes LSIII shortened, LSIV usually elongate, longer than each of previous segments; sometimes LSIV as long as LSIII or all segments shortened, almost as long as wide. *Antenna*. Shape and length varying from short and wide, distinctly shorter than body, to long and filiform, distinctly longer than body. *Thorax*. Pronotum (Fig. 10A-E, G-J, fig. 2D in Namyatova & Cassis, 2013a, fig. 5A–E in Namyatova & Cassis, 2013b, fig. 4A–D in

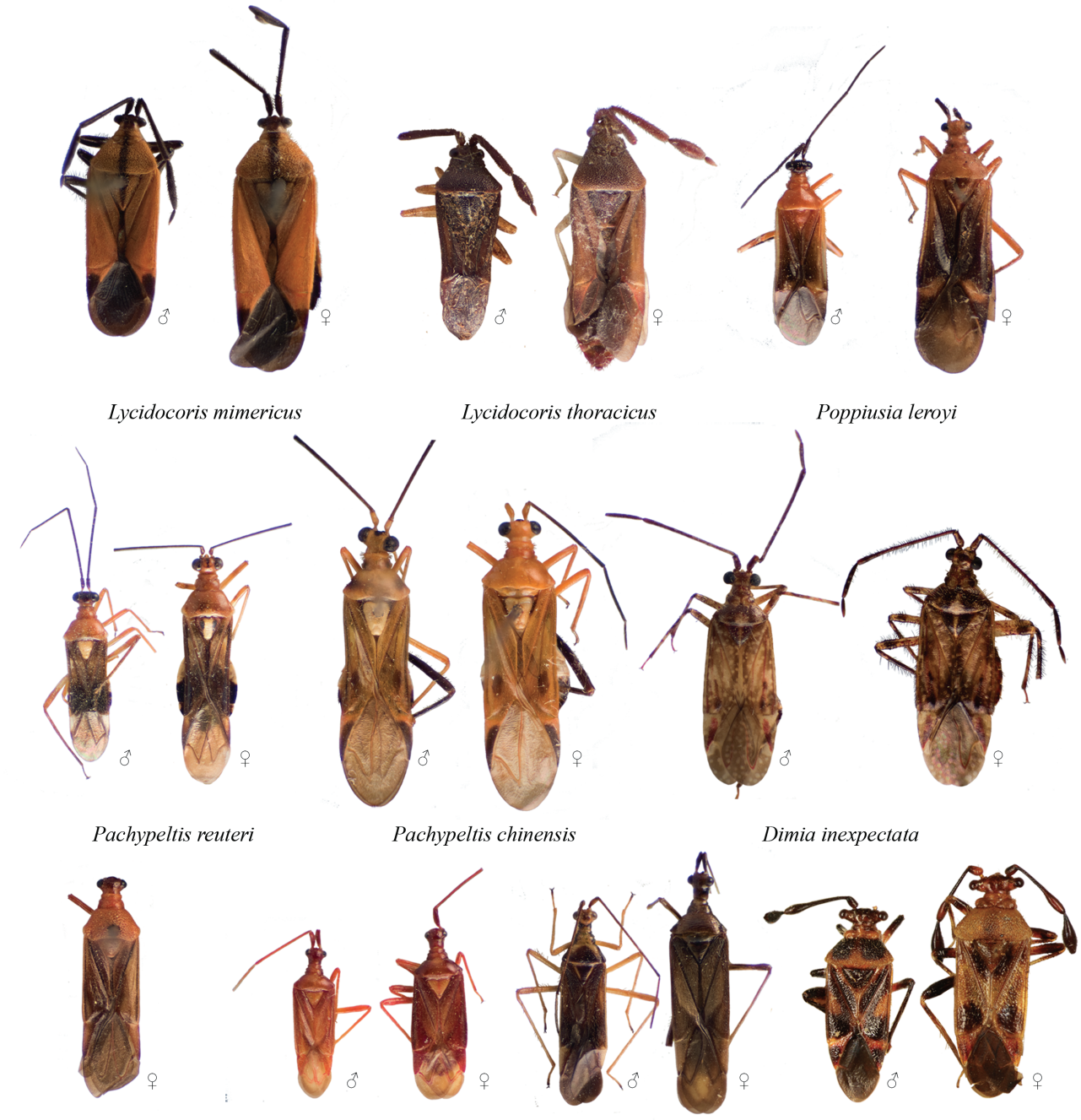

Figure 7. Habitus photographs. *Lycidocoris mimeticus* ♂ AMNH_PBI 5076, ♀ AMNH_PBI 5085; *Lycidocoris thoracicus* ♂ AMNH_PBI 5105, ♀ AMNH_PBI 5044; *Poppiusia leroyi* ♂ AMNH_PBI 19314, ♀ AMNH_PBI 5048; *Pachypletis reuteri* ♂ AMNH_PBI 5224, ♀ AMNH_PBI 271339; *Pachypeltis chinensis* ♂ AMNH_PBI 19285, ♀ AMNH_PBI 19304; *Dimia inexpectata* ♂ PT AMNH_PBI 271336, ♀ PT 19313; *Parapachypeltis punctatus* ♀ PT AMNH_PBI 19331; *Pararculanus madagascariensis* ♂ HT AMNH_PBI 271337, ♀ AMNH_PBI 271333; *Pararculanus piperis* ♂ AMNH_PBI 5060, ♀ AMNH_PBI 5062; *Villiersicoris sessensis* ♂ no USI label (BMNH), ♀ type AMNH_PBI 19435.

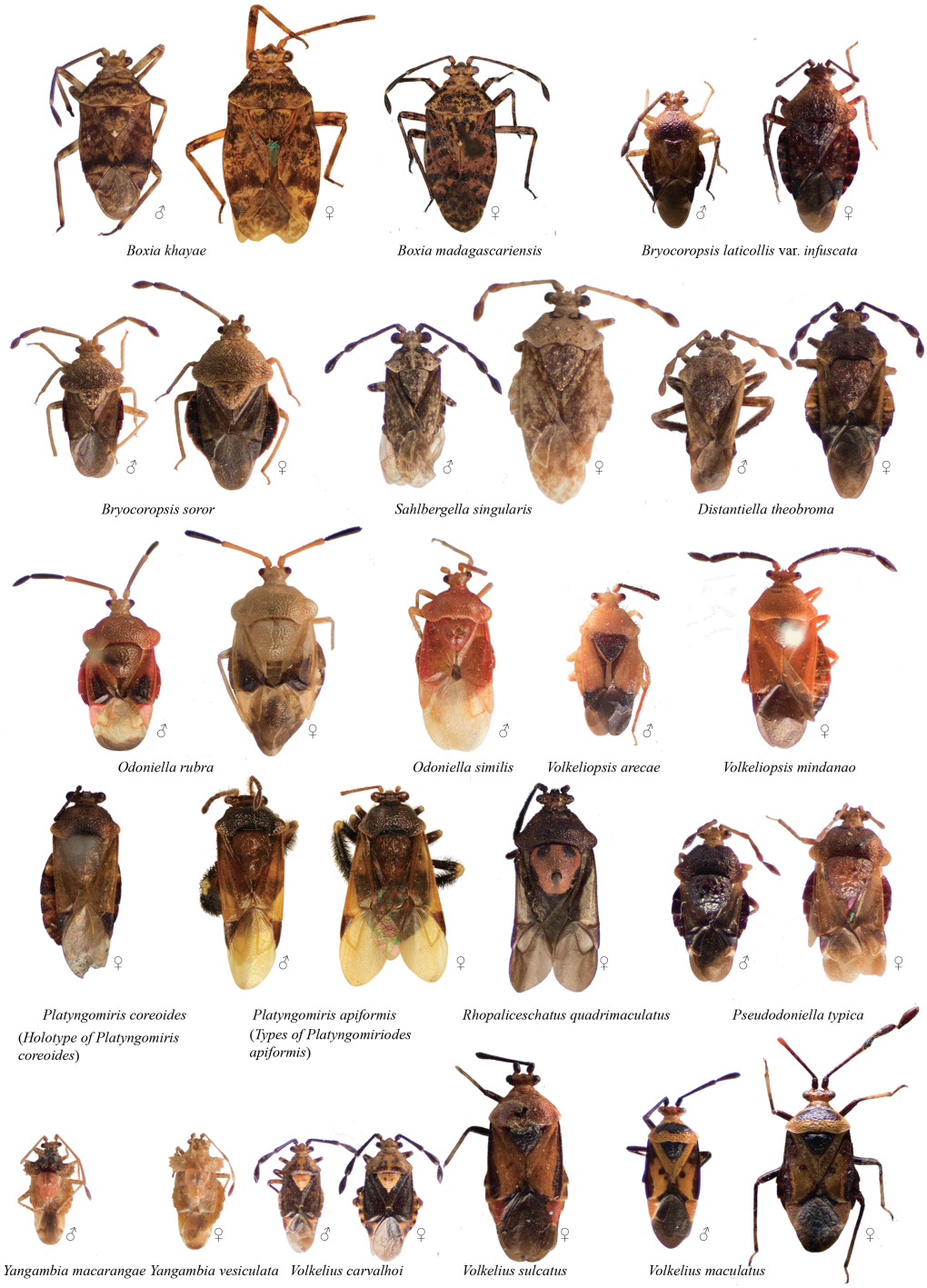

Figure 8. Habitus photographs. *Boxia khayae* ♂ AMNH_PBI 5065, ♀ type 19448; *Boxia madagascariensis* ♀ AMNH_PBI 19532; *Bryocoropsis laticollis* var. *infuscata* ♂ AMNH_PBI 18947, ♀ AMNH_PBI 18946; *Bryocoropsis soror* ♂ AMNH_PBI 5115, ♀ AMNH_PBI 5117; *Sahlbergella singularis* ♂ AMNH_PBI 19118, ♀ AMNH_PBI 19057; *Distantiella theobromae* ♂ AMNH_PBI 5016, ♀ AMNH_PBI 5019; *Odoniella rubra* ♂ AMNH_PBI 18951, ♀ AMNH_PBI 18958; *Odoniella similis* ♂ AMNH_PBI 5036; *Volkeliopsis arecae* ♂ HT AMNH_PBI 19516; *Volkeliopsis mindanao* ♀ AMNH_PBI 5237; *Platyngomiris coreoides* ♀ HT of *P. coreoides* AMNH_PBI 19643; ♂ HT of *Platyngomiriodes apiformis* AMNH_PBI 19471, ♀ PT of *P. apiformis* no USI label (BMNH); *Platyngomiris quadrimaculatus* ♀ AMNH_PBI 20253; *Platyngomiris typicus* ♂ AMNH_PBI ♀; *Yangambia macarangae* ♂ AMNH_PBI 34057, ♀ AMNH_PBI 20192; *Yangambia vesiculata* ♂ AMNH_PBI 19079, ♀ AMNH_PBI 19086; *Volkelius carvalhoi* ♂ AMNH_PBI 19309, ♀ AMNH_PBI 20197; *Volkelius sulcatus* ♀ PLT AMNH_PBI 5047; *Volkelius maculatus* ♂ AMNH_PBI 19043, ♀ AMNH_PBI 19386.

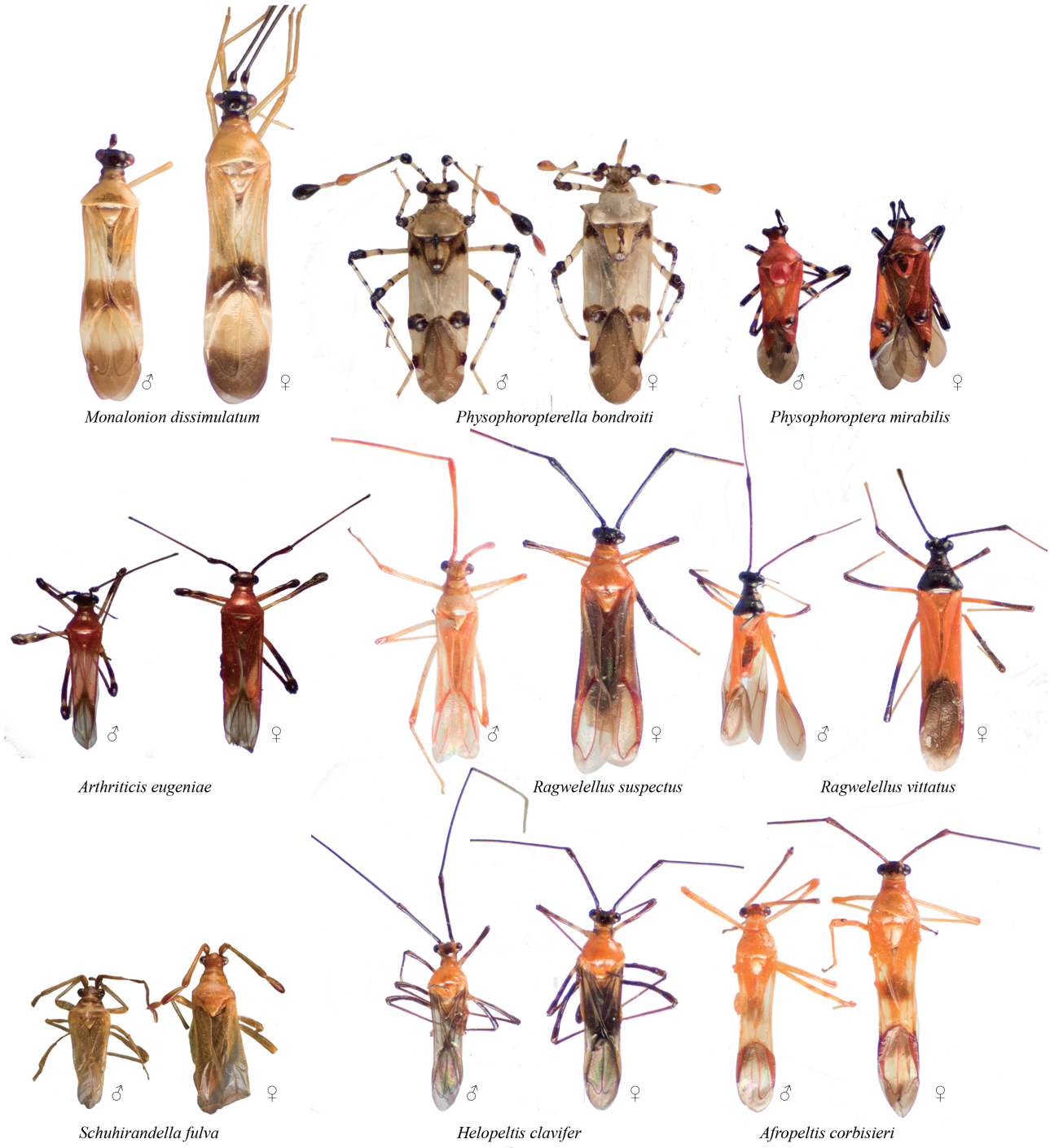

Figure 9. Habitus photographs. *Monalonion dissimulatum* ♂ AMNH_PBI 19564, ♀ AMNH_PBI 5258; *Physophoropterella bondroiti* ♂ AMNH_PBI 400348, ♀ AMNH_PBI 5037; *Physophoroptera mirabilis* ♂ AMNH_PBI 5070, ♀ AMNH_PBI 5083; *Arthriticus eugeniae* ♂ AMNH_BPI 19573, ♀ AMNH_PBI 19575; *Ragwelellus suspectus* ♂ AMNH_PBI 34153, ♀ AMNH_PBI 34154; *Ragwelellus vittatus* ♂ AMNH_PBI 34152, ♀ AMNH_PBI 45821; *Schuhirandella fulva* ♂ PT AMNH_PBI 400345, ♀ PT AMNH_PBI 19576; *Helopeltis clavifer* ♂ AMNH_PBI 40416, ♀ AMNH_PBI 202016; *Afropeltis corbisieri* ♂ AMNH_PBI 5133, ♀ AMNH_PBI 5216.

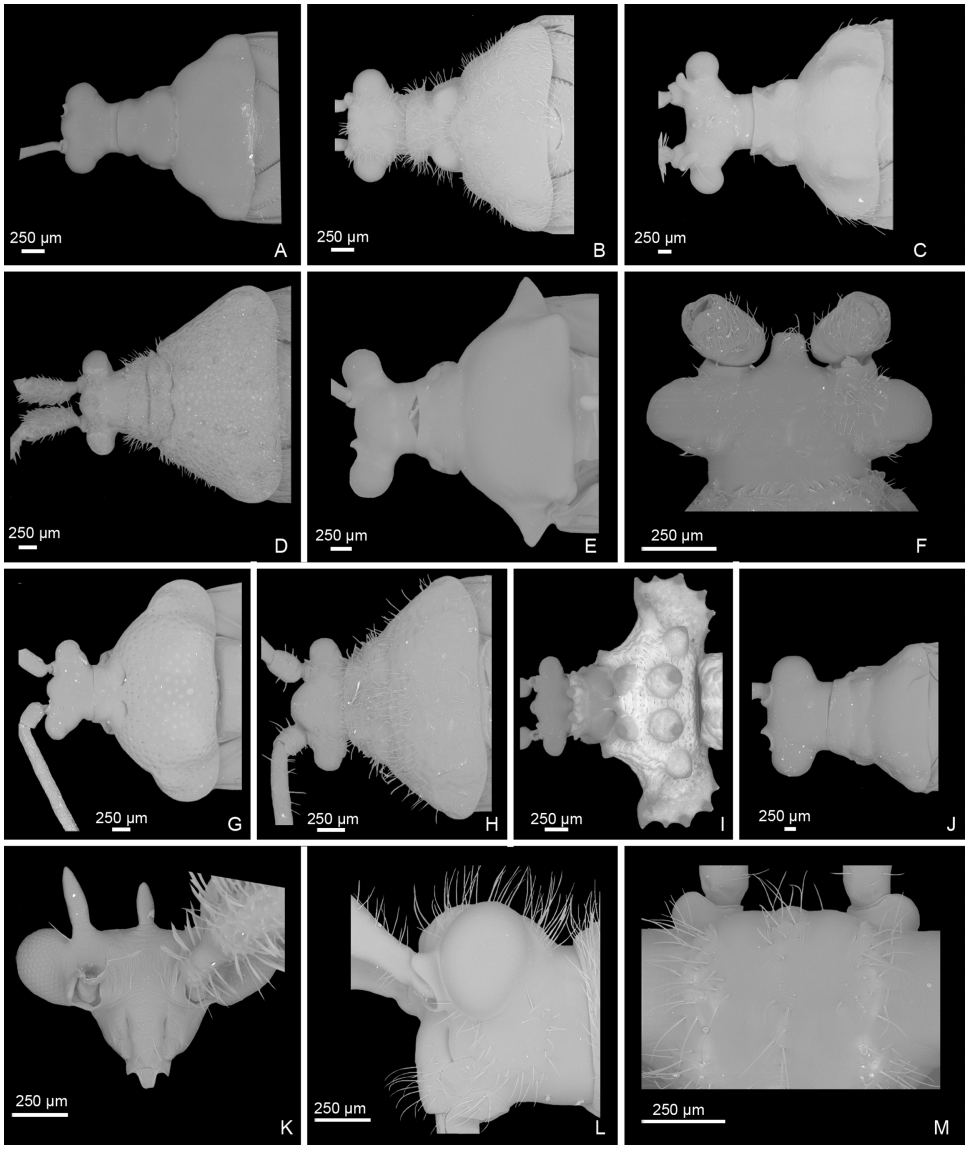

Figure 10. Scanning electron micrographs. Head and pronotum, dorsal view. A, *Mansoniella nitida* ♀ AMNH_PBI 46067; B, *Poppiusia leroyi* ♀ AMNH_PBI 5838; C, *Chamus bellus* ♀ AMNH_PBI 5223; D, *Lycidocoris mimeticus* ♀ AMNH_PBI 5043; E, *Physophoropterella bondroiti* ♂ AMNH_PBI 19110; G, *Odoniellia reuteri* ♂ AMNH_PBI 19090; H, *Volkelius carvalhoi* ♀ PT AMNH_PBI 19630; I, *Yangambia vesiculata* ♀ AMNH_PBI 19084; J, *Ragwelellus suspectus* ♂ AMNH_PBI 19629. Head, dorsal view. F, *Sahlbergella tai* ♀ AMNH_PBI 5106. Head, anterior view. K, *Parachamus bellus* ♀ AMNH_PBI 5837. Head, lateral view. L, *Poppiusia leroyi* ♀ AMNH_PBI 5838. Frons, dorsal view. M, *Poppiusia leroyi* ♀ AMNH_PBI 5838.

Namyatova *et al*., in press). Collar often delimited only laterally, fused with callosite area medially, sometimes delimited posteriorly with shallow depression, flat or swollen; calli varying from flat to distinctly raised, sometimes fused with each other, delimited or not delimited by sulcus posteriorly; humeral angles of pronotum dilated or flat, sometimes acute; posterior margin of pronotum varying from almost straight to distinctly concave. Scutellum (Figs 11A-K, 12, fig. 9H in Namyatova & Cassis, 2013b, figs 11C, D, G, 12E, F in Namyatova *et al*., in press). Varying from flat to distinctly swollen of different shape, sometimes with longitudinal depression, in some with elongate vertical process (*Afropeltis*, *Helopeltis*, *Physophoropterella*). Pleura (Fig. 13A–E, fig. 9C in Namyatova & Cassis, 2013b, fig. 3d in Namyatova & Cassis, 2014, fig. 14A in Namyatova *et al*., in press). Mesothoracic apodeme round, open. Metathoracic spiracle oval, open, without

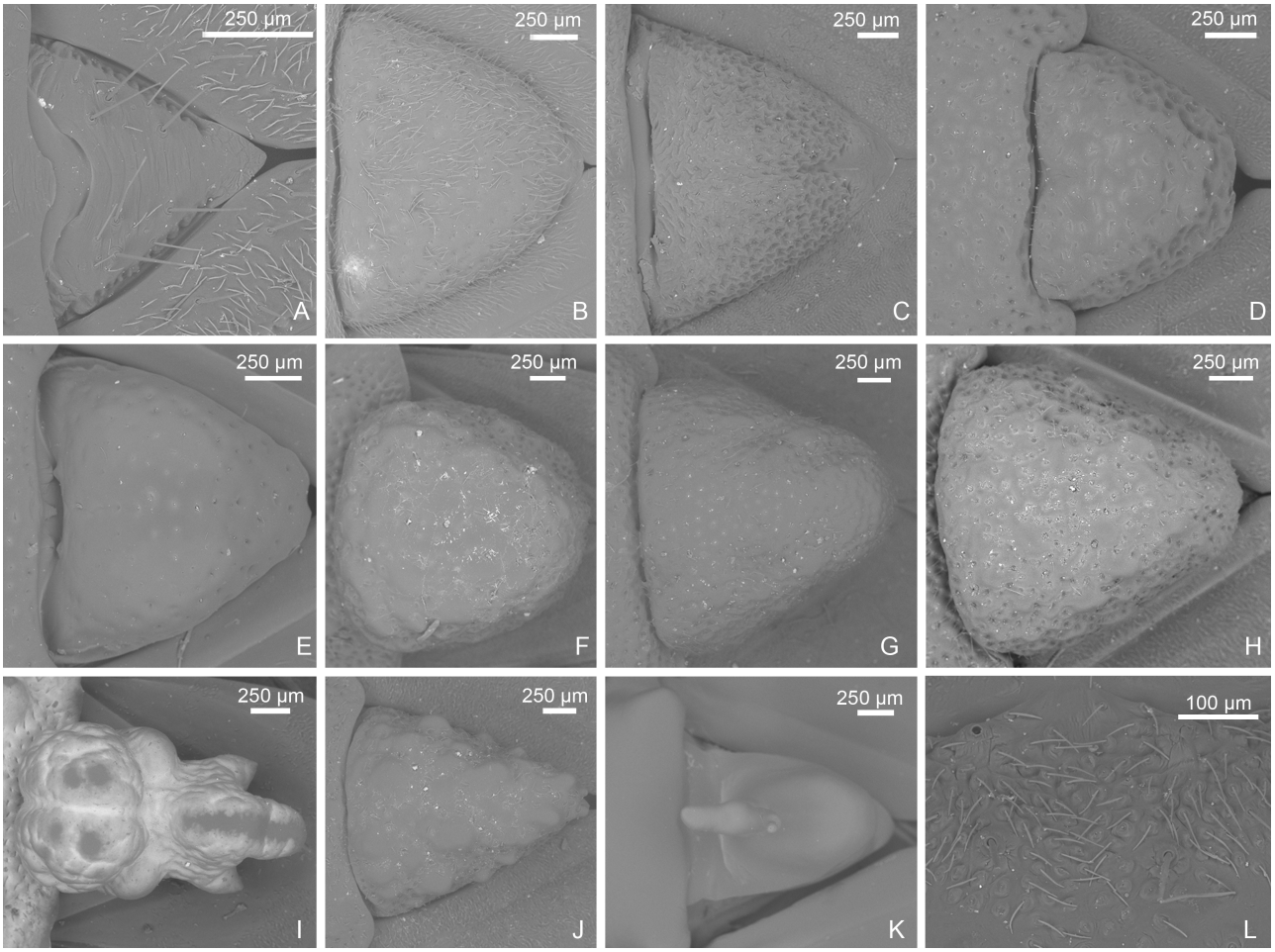

Figure 11. SEM images. Scutellum, dorsal view. A, *Chamus tuberculatus* ♂ AMNH_PBI 5025; B, *Volkeliopsis mindanao* ♀ PT AMNH_PBI 45979; C, *Boxia khayae* ♂ AMNH_PBI 5065; D, *Bryocoropsis soror* ♂ AMNH_PBI 5115; E, *Odoniella reuteri* ♂ AMNH_PBI 19090; F, *Pseudodoniella typical* ♂ AMNH_PBI 45978; G, *Sahlbergella tai* ♀ AMNH_PBI 5106; H, *Pseudodoniella pacifica* ♂ AMNH_PBI 46080; I, *Yangambia vesiculata* ♀ AMNH_PBI 19084; J, *Sahlbergella singularus* ♂ AMNH_PBI 19053; K, *Physophoropterella bondroiti* ♂ AMNH_PBI 19110. Small tubercules on pronotum. L, *Chamus tuberculatus* ♂ AMNH_PBI 5025.

evaporative bodies bounding it. Metathoracic gland ostiole placed ventrally, indistinct, evaporative area absent; suture between meso- and metapleuron incomplete; metepimeron often enlarged or narrow with lobe or elongate projection, sometimes angulate, rarely rounded. Posterior margin of metasternum rounded (fig. 17B in Namyatova *et al*., in press) or with medial projection on to abdomen (fig. 17A in Namyatova *et al*., in press). *Hemelytron* (Figs 6–9, figs 2–4, fig. 9A, B, D–G in Namyatova & Cassis, 2013b, figs 12C–F, 13E, F in Namyatova *et al*., in press). Costal margin straight or concave; hemelytron sometimes tapering towards apex; claval commissure of different length, its margins straight or curved; R + M distinct, reaching or not reaching posterior margin of corium; medial fracture distinctly inclined towards midline or subparallel to costal margin of hemelytron; corium rarely with swelling posteriorly (*Physophoroptera* and *Physophoropterella*) (Fig. 13F); length of cuneus varying from 2 to 6 times as long as its base, medial margin of cuneus straight or concave; membrane with single cell, cell often surpassing apex of scutellum, rarely only reaching or almost reaching apex of cuneus, of different length, its apex acute or rounded. *Legs*. Length varying from very short to elongate. Coxae short, length varying from almost as long as wide to twice as long as wide; forecoxae contiguous (fig. 17A in Namyatova *et al*., in press) or separated (fig. 17B in Namyatova *et al*., in press); hind and middle coxae separated (fig. 17A, B in Namyatova & Cassis, in press). Femora (13G, H, fig. 18A, C in Namyatova *et al*., in press). Straight or curved, sometimes only hind femur

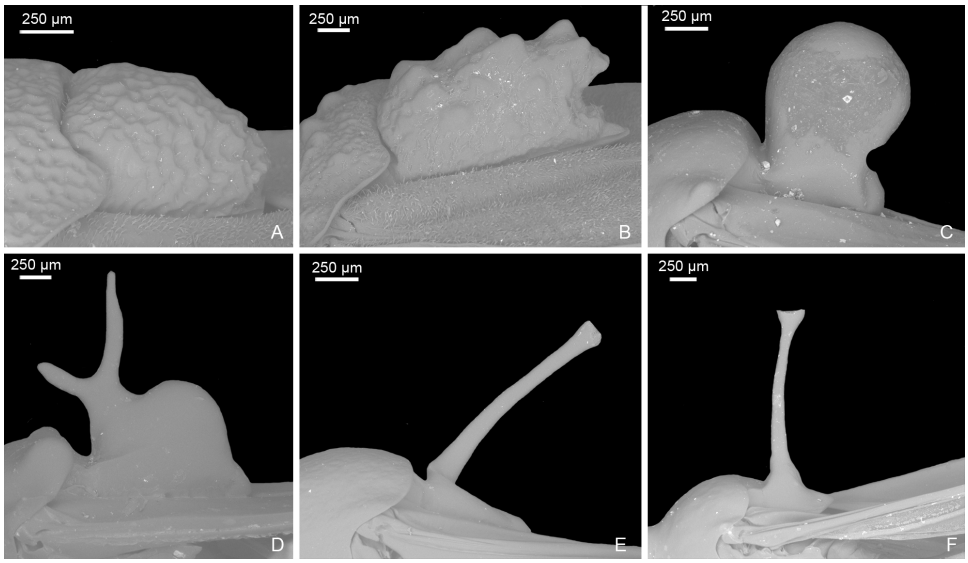

Figure 12. Scanning electron micrographs. Scutellum, lateral view. A, *Bryocoropsis soror* ♂ AMNH_PBI 5115; B, *Sahlbergella singularis* ♂ AMNH_PBI 19053; C, *Physophoroptera mirabilis* ♀ AMNH_PBI 20202; D, *Physophoropterella bondroiti* ♂ AMNH_PBI 19112; E, *Afropeltis lalandei* ♂ AMNH_PBI 5272; F, *Helopeltis pellucida* sex unknown AMNH_PBI 19628.

slightly curved, sometimes with swellings apically and medially. Tibiae straight or slightly curved, as long as or longer than femora, sometimes with swellings. Hind tarsus (Fig. 13I, fig. 2C in Namyatova & Cassis, 2013a, fig. 8F in Namyatova & Cassis, 2013b, fig. 3H in Namyatova & Cassis, 2014, fig. 19A, B in Namyatova *et al*., in press) with segments subequal in length, or segment I longer than others; tarsal segment III incrassate; guard setae long. Pretarsus (Fig. 13J–L, fig. 20F in Namyatova *et al*., in press, fig. 2F in Namyatova & Cassis, 2013a, fig. 10 in Namyatova & Cassis, 2013b, fig. 3f, i in Namyatova & Cassis, 2014); unguitractor plate with three contiguous rows of tiles, with lateral rows wider than middle row; claw with basal tooth short triangular or subrectangular, sometimes concave or subdivided into basal and apical parts; parempodia present, symmetrical; pseudopulvilli present, as long as or shorter than claw. *Male genitalia* (Figs 14–17, fig. 3A–D in Namyatova & Cassis, 2013a, figs 11–13 in Namyatova & Cassis, 2013b, fig. 4 in Namyatova & Cassis, 2014, fig. 22A–H in Namyatova *et al*., in press). Genital capsule variable in shape, sometimes ventral wall shortened anteriorly; supragenital bridge present; left paramere 2–4× as long as right paramere, r-shaped or almost straight; right paramere reduced; phallobase sclerite of primary gonopore of different shape, sometimes with outgrowth in front of ductus seminis attachment place (*Helopeltis*) or with pair of outgrowths supporting ductus seminis; length of ductus seminis variable, with or without coils, attached medially or on left-hand side; ductus seminis sometimes with sclerite around secondary gonopore, rarely base of secondary gonopore also sclerotized (*Monalonion*); phallotheca of aedeagus distinctly sclerotized dorsally and membranous laterally and ventrally, sometimes only very narrow area of phallotheca sclerotized; endosoma membranous, not subdivided, often with elongate spicules or fields of small spicules. *Female genitalia* (Figs 18–21, fig. 3E–F in Namyatova & Cassis, 2013a, fig. 14 in Namyatova & Cassis, 2013b, fig. 5 in Namyatova & Cassis, 2014, fig. 23H in Namyatova *et al*., in press). DLP with one or two sclerotized bands, sometimes with medial sclerotized circle or with paired sclerotized rings, sometimes also with sclerotized ridge medially or small additional sclerites medially, sometimes entirely membranous; DLP sometimes with dense striations, especially around places of attachment of lateral oviducts; attachment of lateral oviducts varying; spermathecal gland usually attached medially, in anterior or posterior part of DLP, rarely at midpoint, sometimes shifted to right- or left-hand side; posterior wall of bursa copulatrix often with small tubercles, sometimes with outgrowths or sclerotization, rarely with posterior wall entirely membranous; base of second valvula concave, straight or convex, sometimes with bifurcated outgrowth; ventral wall of bursa copulatrix with or without sclerotization bounding vulva.

Distribution: Circumtropical. Most diverse in Africa and Indo-Pacific, with some genera known from Australia, Eastern Palaearctic and South America (Figs 22–24).

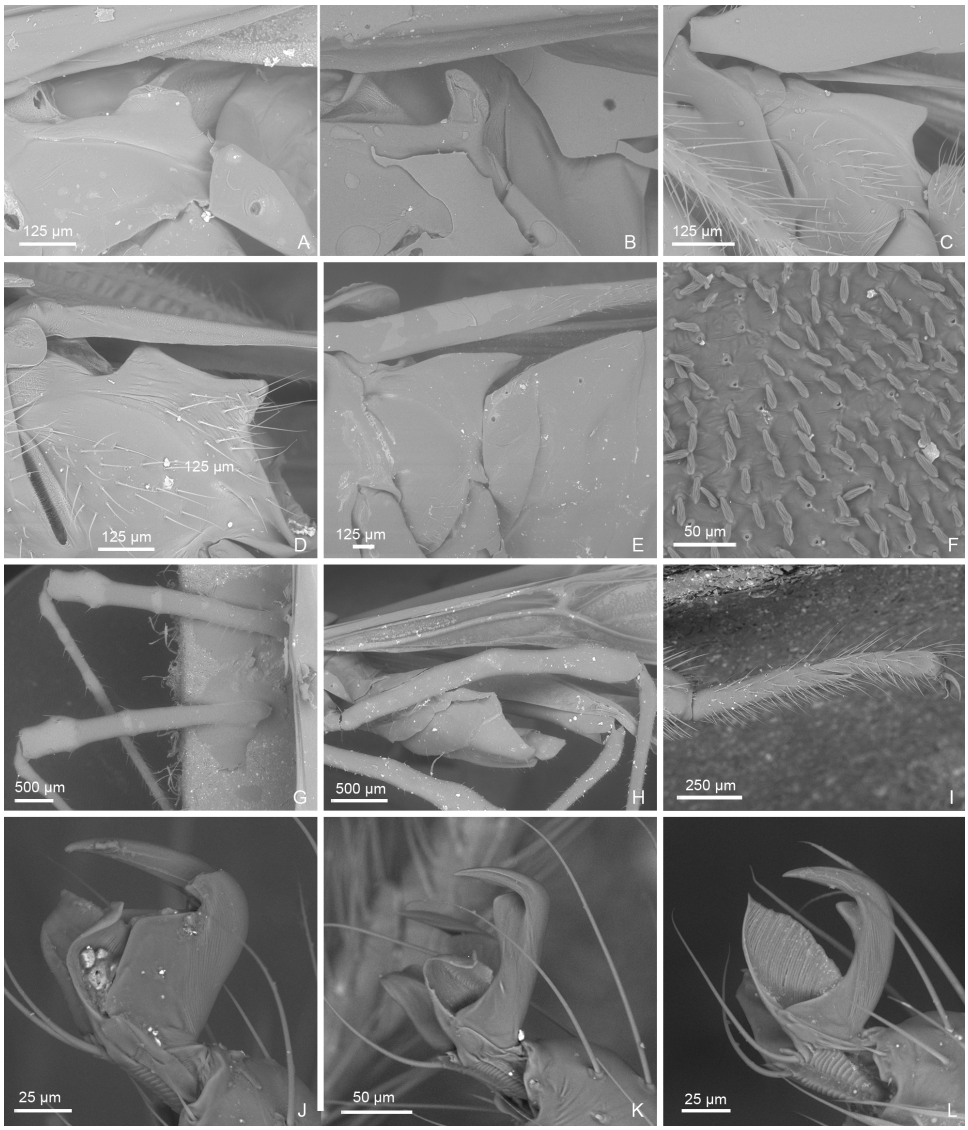

Figure 13. Scanning electron micrographs. Metepimeron. A, *Helopletis pellucida* sex unknown AMNH_PBI 19628; B, *Afropeltis hyalospilosus* ♂ AMNH_PBI 5137; C, *Poppiusia leroyi* ♀ AMNH_PBI 5838; D, *Pachypeltis reuteri* ♂ AMNH_PBI 45980; E, *Odoniella reuteri* ♂ AMNH_PBI 19194. Setae on hemelytron. F, *Boxia khayae* ♂ AMNH_PBI 5065. Fore- and middle femora. G, *Physophoropterella bondroiti* ♂ AMNH_PBI 19110. Hind femur. H, *Helopeltis pellucida* sex unknown AMNH_PBI 19628. Hind tarsus. I, *Physophoropterella bondroiti* ♂ AMNH_PBI 19110. Claw, lateral view. J, *Chamus* sp. sex unknown, not databased; K, *Pachypeltis brevirostris* sp. nov. sex unknown, not databased; L, *Helopeltis bradyi* sex unknown, not databased.

Host plants: Monaloniines are known to feed on a wide range of plants, with some of them being pests of cocoa, tea, cashew and other cultivated plants (e.g. Schmitz, 1968; de Abreu, 1977; Lavabre, 1977a,b; Piart, 1977; Hill, 1983; Stonedahl, 1991).

Discussion: The position of the Monaloniini within the Bryocorinae was discussed by Namyatova *et al*. (in press). Previous to this study, the Monaloniini included 21 genera, all of which were listed in Schuh (1995: 1995–2013), aside from our recent description of *Schuhirandella* (Namyatova & Cassis, 2013a). *Felisacus* was transferred to the tribe Felisaciini by us (Namyatova *et al*., in press).

We have removed *Onconotellus* Knight, 1935 and *Pachypeltopsis* Poppius, 1912 from the Monaloniini. Knight (1935) initially placed *Onconotellus* within the subfamily Dicyphini. Cassis (1986) tentatively transferred *Onconotellus* to the tribe Monaloniini based on the original description. Knight's illustrations showed

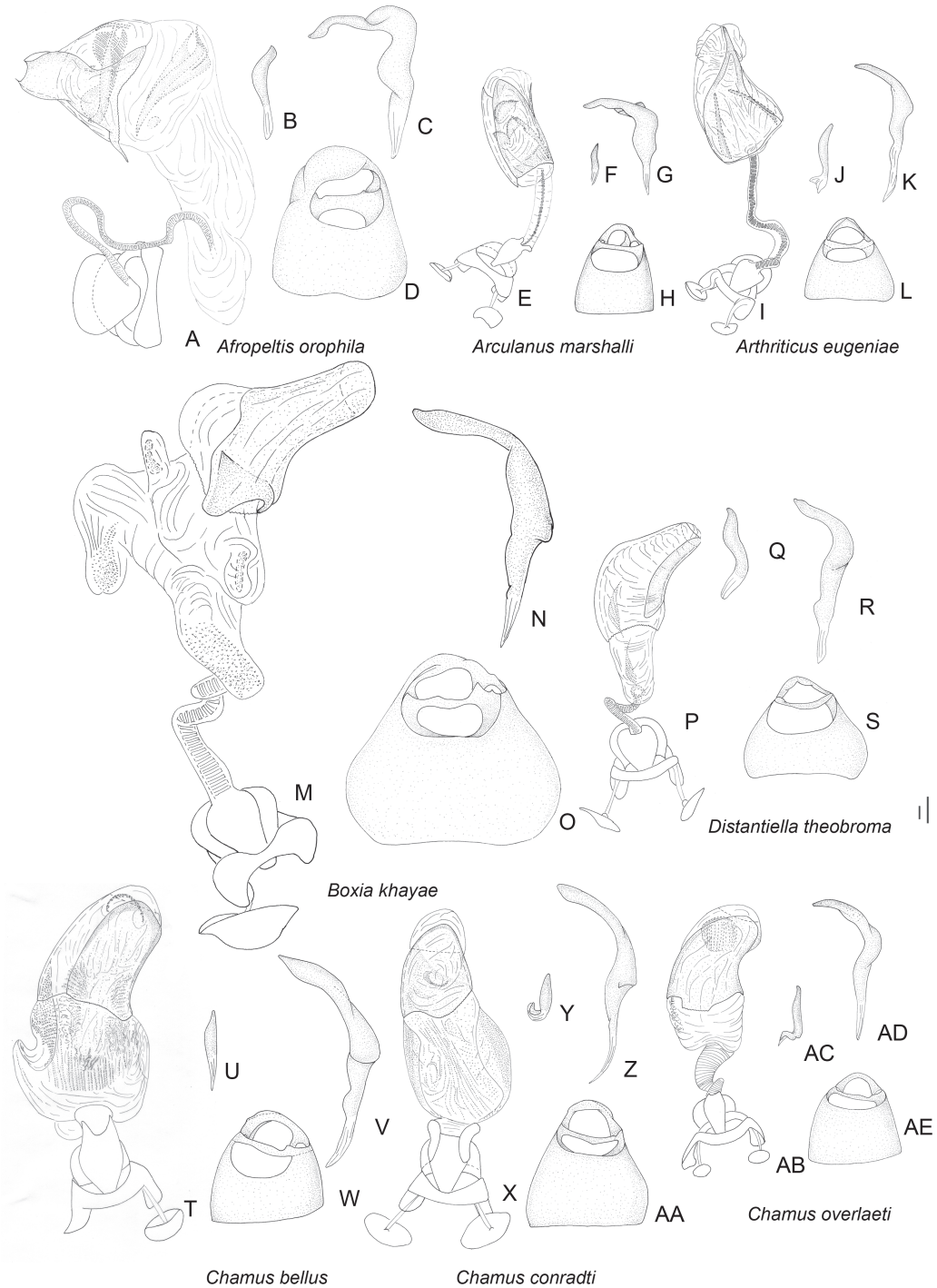

Figure 14. Male genitalia, dorsal view. *Afropeltis hyalospilosus* AMNH_PBI 5137. A, aedeagus; B, right paramere; C, left paramere; D, genital capsule. *Arculanus marshalli* AMNH_PBI 5102. E, aedeagus; F, right paramere; G, left paramere; H, genital capsule. *Arthriticus eugeniae* AMNH_PBI 19573. I, aedeagus; J, right paramere; K, left paramere; L, genital capsule. *Boxia khayae* AMNH_PBI 5065. M, aedeagus; N, left paramere; O, genital capsule. *Distantiella theobromae* AMNH_PBI 19056. P, aedeagus; Q, right paramere; R, left paramere; S, genital capsule. *Chamus bellus* AMNH_PBI 19059. T, aedeagus; U, right paramere; V, left paramere; W, genital capsule. *Chamus conradti* AMNH_PBI 19048. X, aedeagus; Y, right paramere; Z, left paramere; AA, genital capsule. *Chamus overlaeti* AMNH_PBI 19073. AB, aedeagus; AC, right paramere; AD, left paramere; AE, genital capsule. The smaller scale is for genital capsule, the larger scale is for aedeagi and paramers.

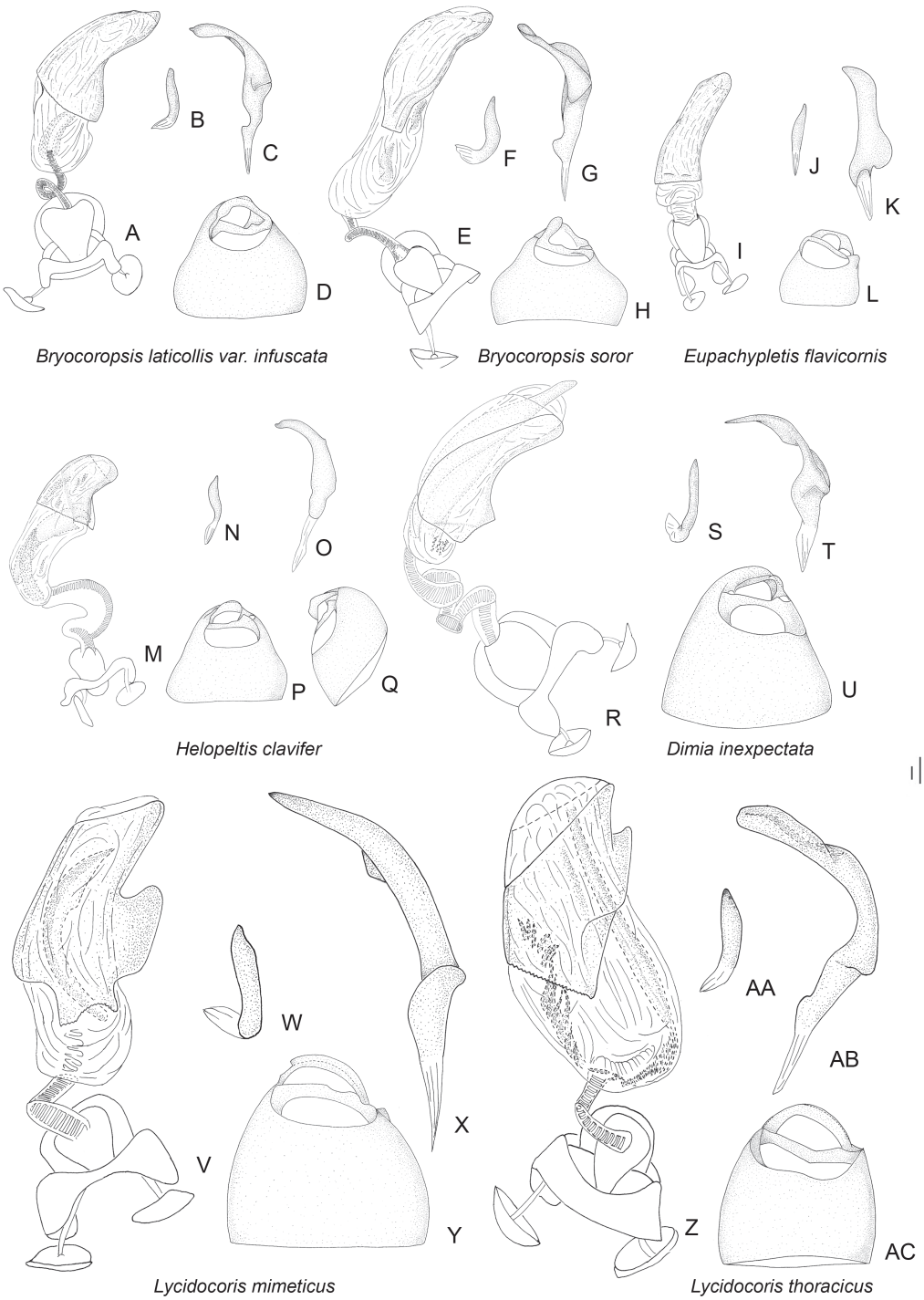

Figure 15. Male genitalia. Dorsal view. *Bryocoropsis laticollis* var. *infuscata*. AMNH_PBI 18942. A, aedeagus; B, right paramere; C, left paramere. AMNH_PBI 5108. D, genital capsule. *Bryocoropsis soror* AMNH_PBI 19072. E, aedeagus; F, right paramere; G, left paramere; H, genital capsule. *Eupachypeltis flavicornis* LT AMNH_PBI 19128. I, aedeagus; J, right paramere; K, left paramere; L, genital capsule. *Helopeltis clavifer* AMNH_PBI 34191. M, aedeagus; N, right parameres; O, left paramere; P, genital capsule. *Dimia inexpectata* PT AMNH_PBI 271336. R, aedeagus; S, right paramere; T, left paramere; U, genital capsule. *Lycidocoris mimericus* AMNH_PBI 5066. V, aedeagus; W, right paramere; X, left paramere; Y, genital capsule. *Lycidocoris thoracicus* no USI. Z, aedeagus; AA, right paramere; AB, left paramere; AC, genital capsule. Lateral view. *Helopeltis clavifer* AMNH_PBI 34191. Q, genital capsule. The smaller scale is for genital capsule, the larger scale is for aedeagi and parameres.

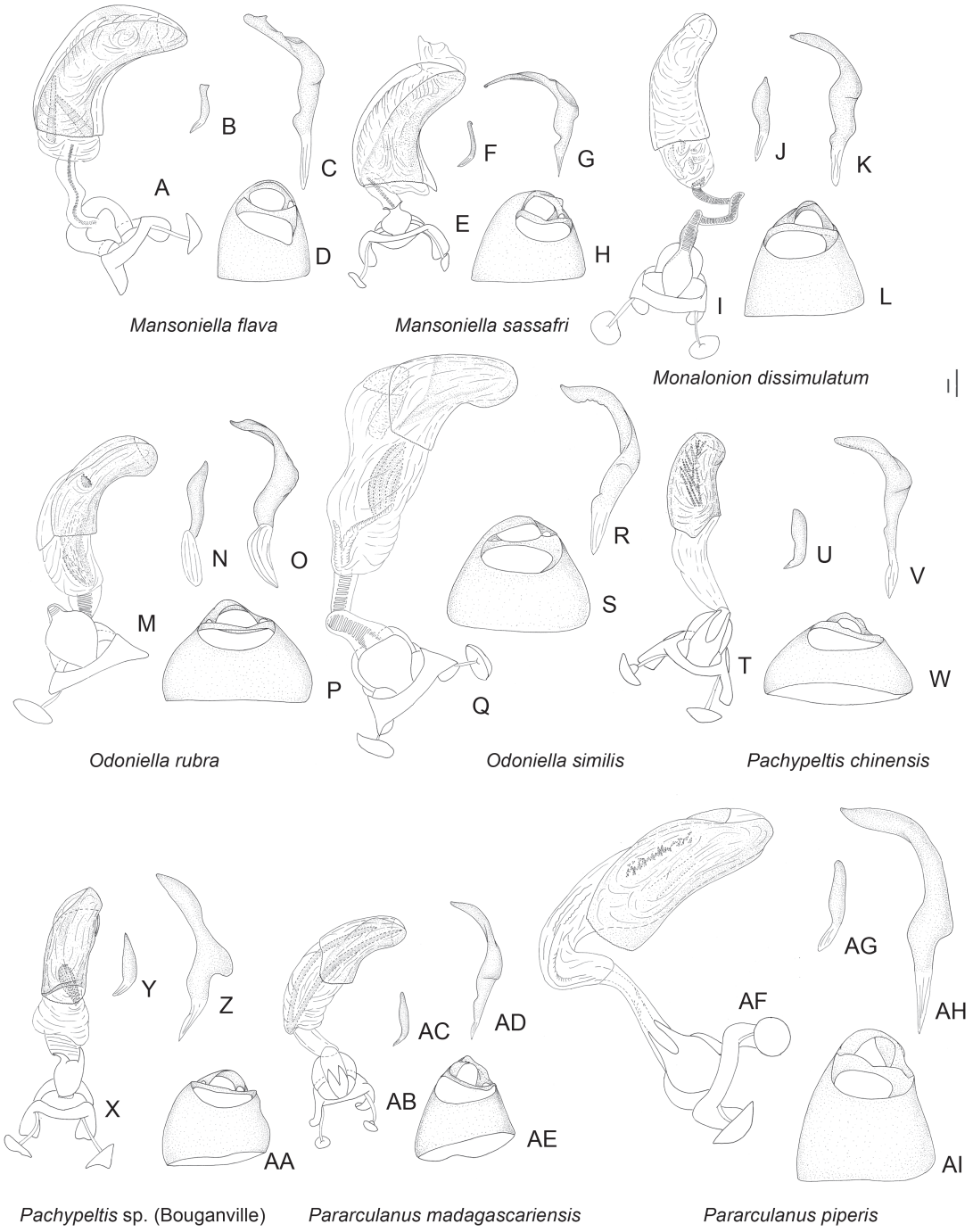

Figure 16. Male genitalia, dorsal view. *Mansoniella flava* AMNH_PBI 19270. A, aedeagus; B, right paramere; C, left paramere; D, genital capsule. *Mansoniella sassafti* AMNH_PBI 19276. E, aedeagus; F, right paramere; G, left paramere; H, genital capsule. *Monalonion dissimulatum* no USI. I, aedeagus; J, right paramere; K, left paramere; L, genital capsule. *Odoniellia rubra* AMNH_PBI 18951. M, aedeagus. AMNH_PBI 18950. N, right paramere; O, left paramere; P, genital capsule. *Odoniellia similis* AMNH_PBI 5036. Q, aedeagus; R, left paramere; S, genital capsule. *Pachypeltis chinensis* no USI. T, aedeagus; U, right paramere; V, left paramere; W, genital capsule. *Pachypeltis* sp. (Bouganville) AMNH_PBI 46046. P, aedeagus; Q, right paramere; R, left paramere; S, genital capsule. *Pararculanus madagascariensis* no USI. X, aedeagus; Y, right paramere; Z, left paramere; AA, genital capsule. *Pararculanus piperis* AMNH_PBI 18979. AB, aedeagus; AC, right paramere; AD, left paramere; AMNH_PBI 271336. AE, genital capsule. The smaller scale is for genital capsule, the larger scale is for aedeagi and parameres.

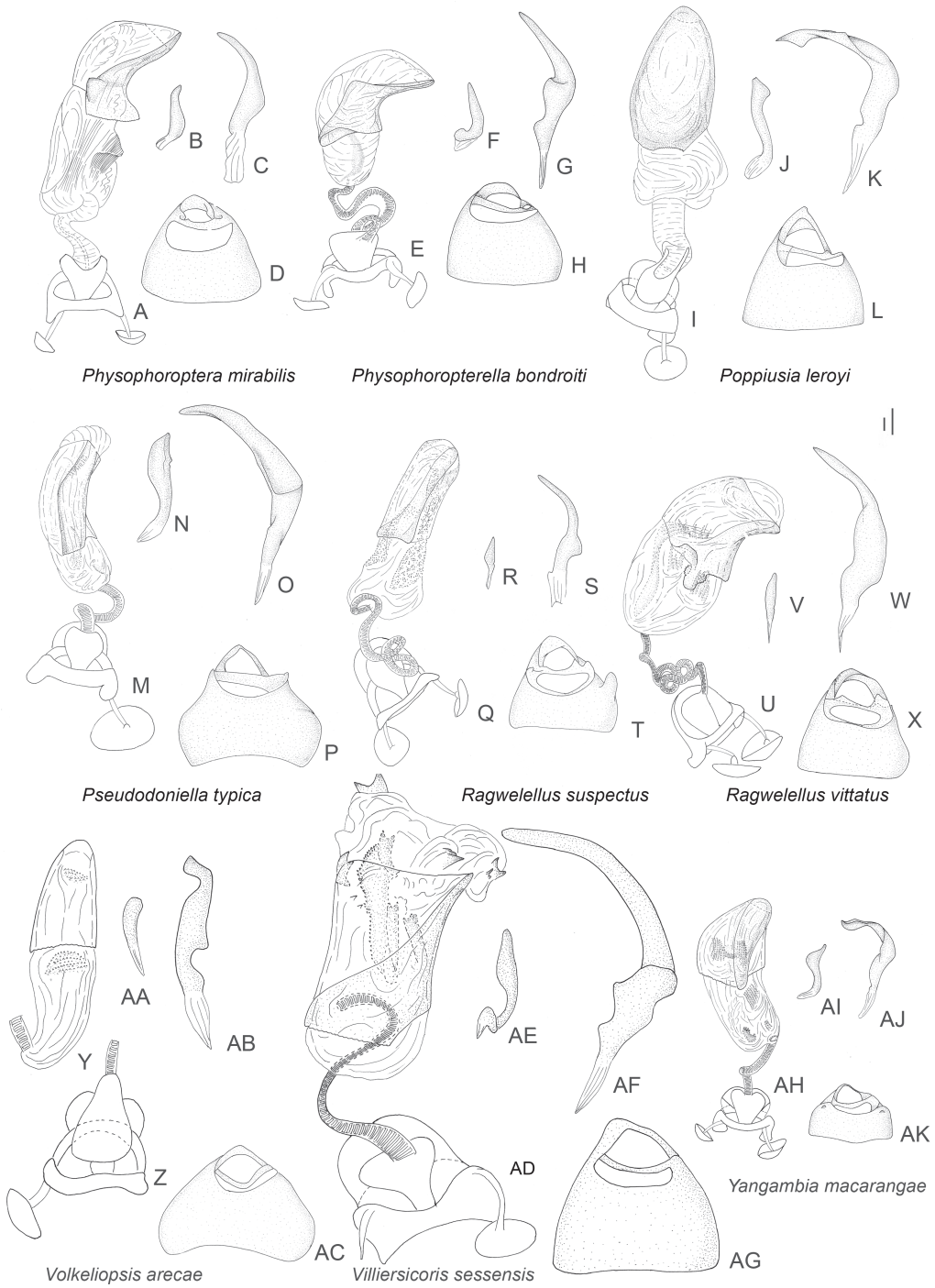

Figure 17. Male genitalia, dorsal view. *Physophoroptera mirabilis* AMNH_PBI 5070. A, aedeagus; B, right paramere; C, left paramere; D, genital capsule. *Physophoropterella bondroiti* no USI. E, aedeagus; AMNH_PBI 5072. F, right paramere; G, left paramere; H, genital capsule. *Poppiusia leroyi* AMNH_PBI 19314. I, aedeagus; J, right paramere; K, left paramere; L, genital capsule. *Pseudodoniella typica* no USI. M, aedeagus; N, right paramere; O, left paramere; P, genital capsule. *Ragwelellus suspectus* no USI. Y, aedeagus; Z, right paramere; AA, left paramere; AB, genital capsule. *Ragwelellus vittatus* no USI. U, aedeagus; V, right paramere; W, left paramere; X, genital capsule. *Volkeliopsis arecae* AMNH_PBI 19427. I, phallobase; J, endosoma and theca; K, right paramere; L, left paramere; M, genital capsule. *Villiersicoris sessensis* AMNH_PBI 19458. Q, aedeagus; R, right paramere; S, left paramere; T, genital capsule. The smaller scale is for genital capsule, the larger scale is for aedeagi and parameres. *Yangambia macarangae* AMNH_PBI 5006. AG, aedeagus. no USI. AH, right paramere; AI, left paramere; AJ, genital capsule. The smaller scale is for genital capsule, the larger scale is for aedeagi and parameres.

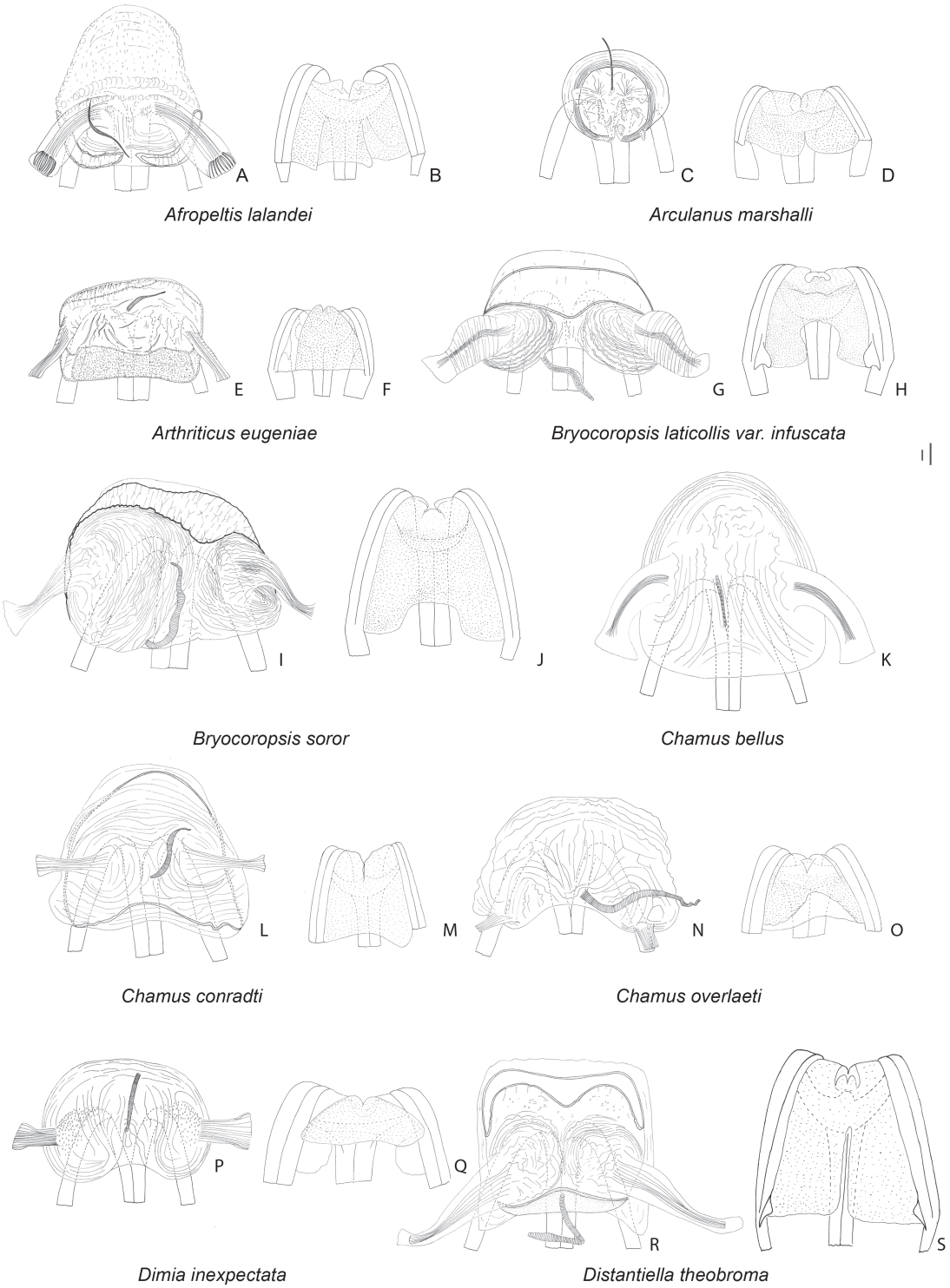

Figure 18. Female genitalia, bursa copulatrix. *Afropeltis lalandei* AMNH_PBI 5261. A, dorsal labiate plate; B, posterior wall. *Arculanus marshalli* AMNH_PBI 19290. C, dorsal labiate; D, posterior wall. *Arthriticus eugeniae* no USI. E, dorsal labiate plate; F, posterior wall. *Bryocoropsis laticollis* var. *infuscate* AMNH_PBI 29096. G, dorsal labiate plate; H, posterior wall. *Bryocoropsis soror* AMNH_PBI 5144. I, dorsal labiate plate; J, posterior wall. *Chamus bellus* AMNH_PBI 19290. K, dorsal labiate plate. *Chamus conradti* AMNH_PBI 19046. L, dorsal labiate plate; M, posterior wall. *Chamus overlaeti* AMNH_PBI 19073. N, dorsal labiate plate; O, posterior wall. *Dimia inexpectata* AMNH_PBI 271341. P, dorsal labiate plate; Q, posterior wall. *Distantiella theobromae*. R, dorsal labiate plate; S, posterior wall.

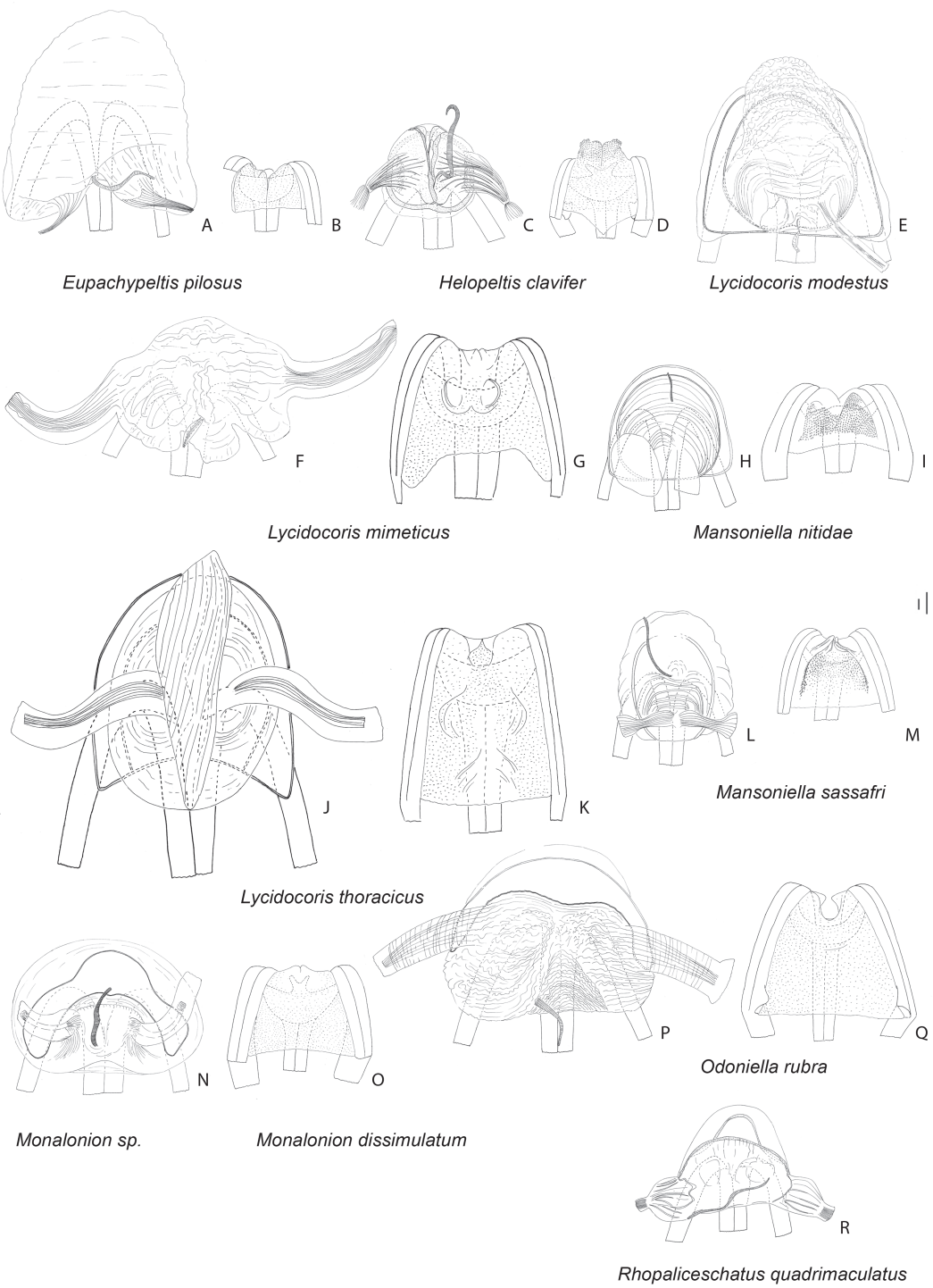

Figure 19. Female genitalia, bursa copulatrix. *Eupachypletis pilosus* AMNH_PBI 46068. A, dorsal labiate plate; B, posterior wall. *Helopletis clavifer* AMNH_PBI 74192. C, dorsal labiate; D, posterior wall. *Lycidocoris modestus* AMNH_PBI 5099. E, dorsal labiate plate. *Lycidocoris mimeticus* AMNH_PBI 5086. F, dorsal labiate plate; G, posterior wall. *Mansoniella nitida* AMNH_PBI 45970. H, dorsal labiate plate; I, posterior wall. *Lycidocoris thoracicus* AMNH_PBI 5096. G, dorsal labiate plate; K, posterior wall. *Mansoniella sassafri* AMNH_PBI 19067. L, dorsal labiate plate; M, posterior wall. *Monalonion* sp. AMNH_PBI 19632. N, dorsal labiate plate. *Monaloion dissimulatum* no USI. O, posterior wall. *Odoniella rubra* AMNH_PBI 18952. P, dorsal labiate plate; Q, posterior wall. *Rhopaliceschatus quadrimaculatus* AMNH_PBI 20523. R, dorsal labiate plate.

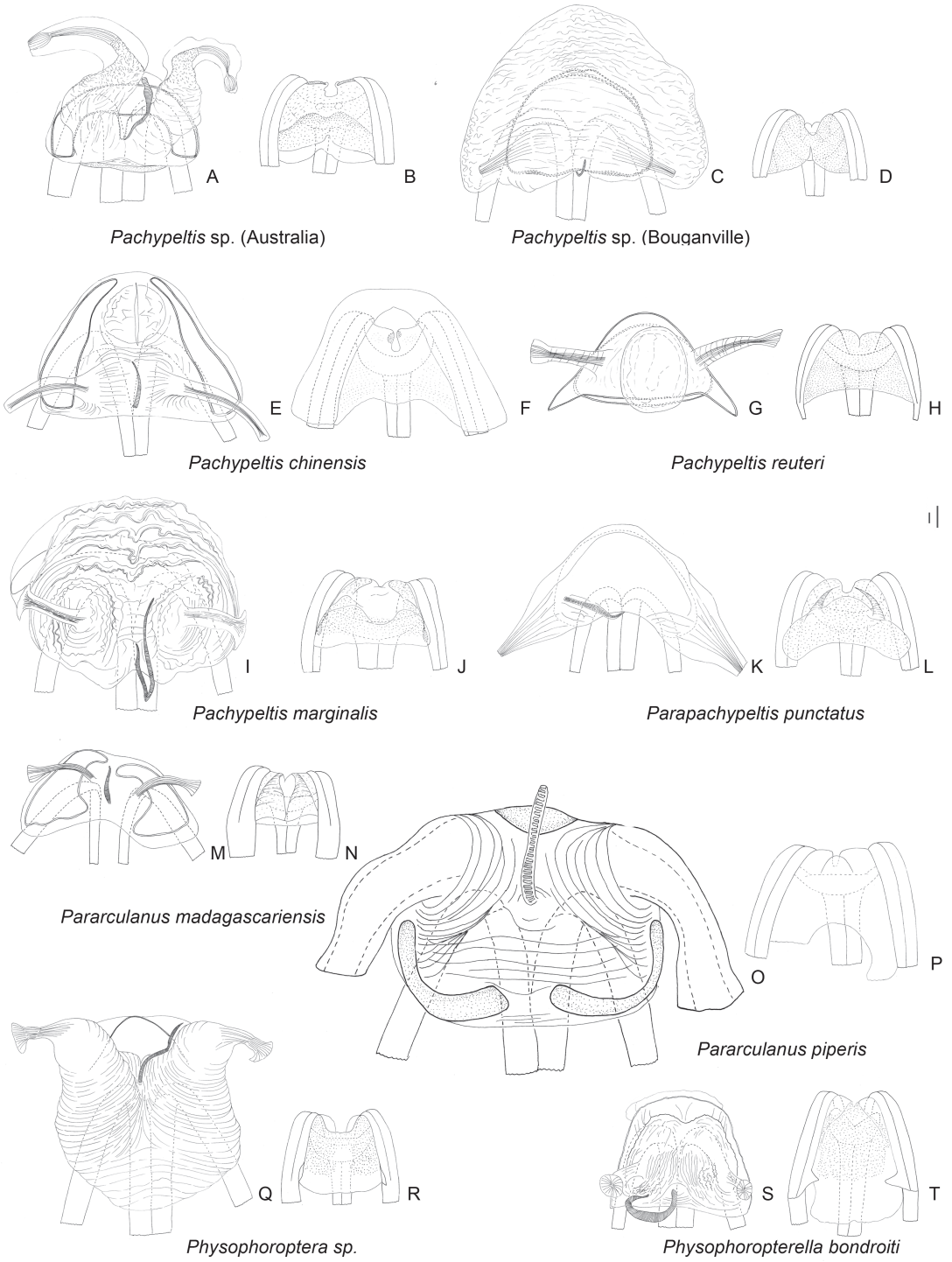

Figure 20. Female genitalia, bursa copulatrix. *Pachypletis* sp. (Australia) AMNH_PBI 19328. A, dorsal labiate; B, posterior wall. *Pachypeltis* sp. (Bouganville) AMNH_PBI 34149. C, dorsal labiate plate; D, posterior wall. *Pachypletis chinensis* AMNH_PBI 19593. E, dorsal labiate plate; F, posterior wall. *Pachypletis reuteri* AMNH_PBI 20215. G, dorsal labiate plate; H, posterior wall. *Pachypeltis marginalis* AMNH_PBI 20214. I, dorsal labiate plate; J, posterior wall. *Parapachypeltis punctatus* PT AMNH_PBI 21342. K, dorsal labiate plate; L, posterior wall. *Pararculanus madagascariensis* AMNH_PBI 271333. M, dorsal labiate plate; N, posterior wall. *Pararculanus* sp. AMNH_PBI 5062. O, dorsal labiate plate; P, posterior wall. *Physophoroptera* sp. AMNH_PBI 5083. Q, dorsal labiate plate; R, posterior wall. *Physophoropterella bondroiti* AMNH_PBI 5037. S, dorsal labiate plate; T, posterior wall.

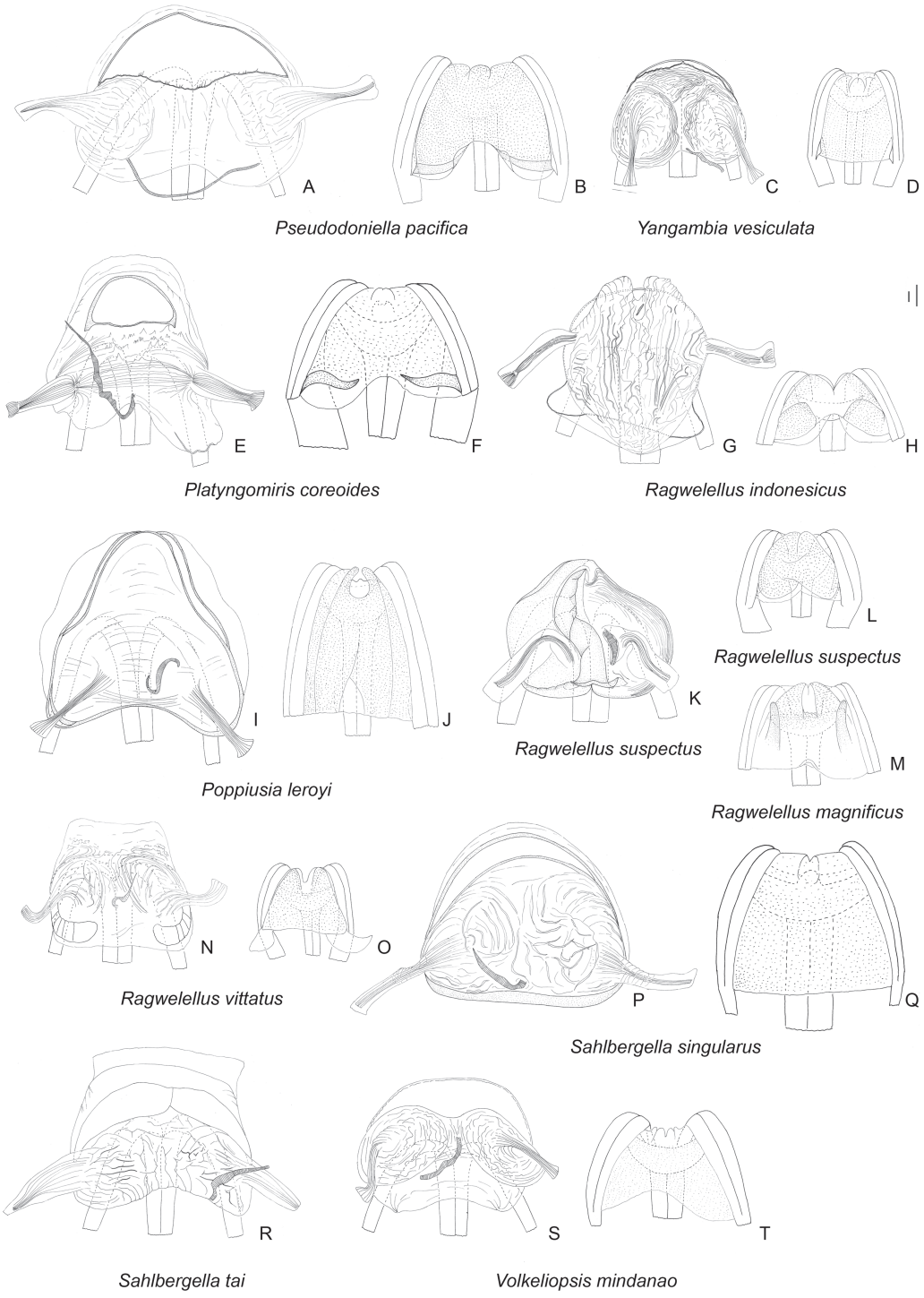

Figure 21. Female genitalia, bursa copulatrix. *Pseudodoniella pacifica* AMNH_PBI 45974. A, dorsal labiate plate. AMNH_PBI 20192. B, posterior wall. *Yangambia vesiculata* AMNH_PBI 19084. C, dorsal labiate plate; D, posterior wall. *Platyngomiris coreoides* AMNH_PBI 19643. E, dorsal labiate plate; F, posterior wall. *Ragwelellus indonesicus* AMNH_PBI 46074. G, dorsal labiate plate; H, posterior wall. *Poppiusia leroyi* AMNH_PBI 5049. I, dorsal labiate plate; J, posterior wall. *Ragwelellus suspectus* no USI. K, dorsal labiate plate; L, posterior wall. *Ragwelellus magnificus* AMNH_PBI 19384. M, posterior wall. *Ragwelellus vittatus* no USI. N, dorsal labiate plate; O, posterior wall. *Sahlbergella singularis* AMNH_PBI 20212. P, dorsal labiate plate; Q, posterior wall. *Sahlbergella tai* PT AMNH_PBI 5106. R, dorsal labiate plate. *Volkeliopsis mindanao* AMNH_PBI 5237. S, dorsal labiate; T, posterior wall.

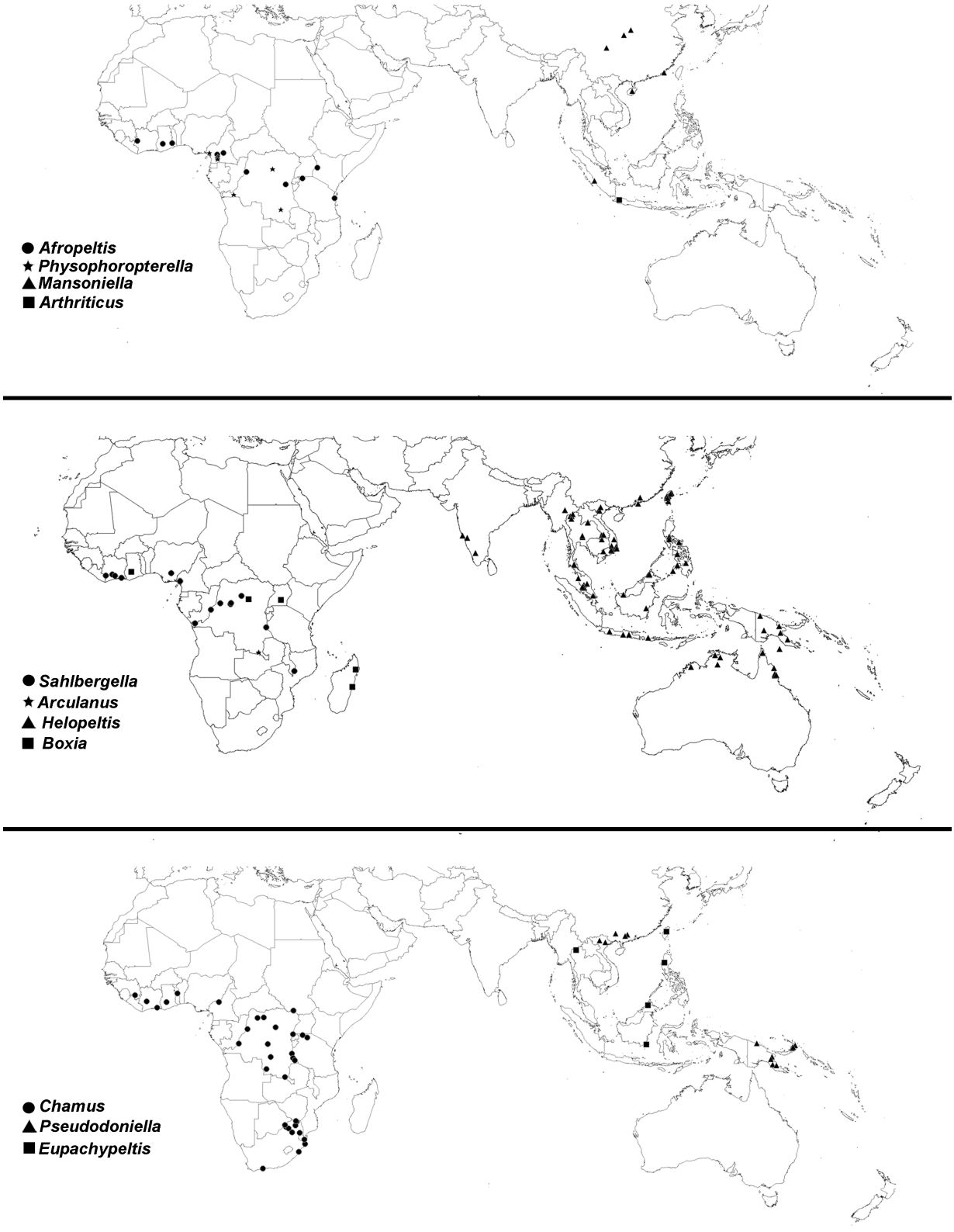

Figure 22. Distribution maps of *Afropeltis*, *Arculanus*, *Arthriticus*, *Boxia*, *Chamus*, *Eupachypeltis*, *Helopeltis*, *Mansoniella*, *Physophoropterella*, *Pseudodoniella* and *Sahlbergella*.

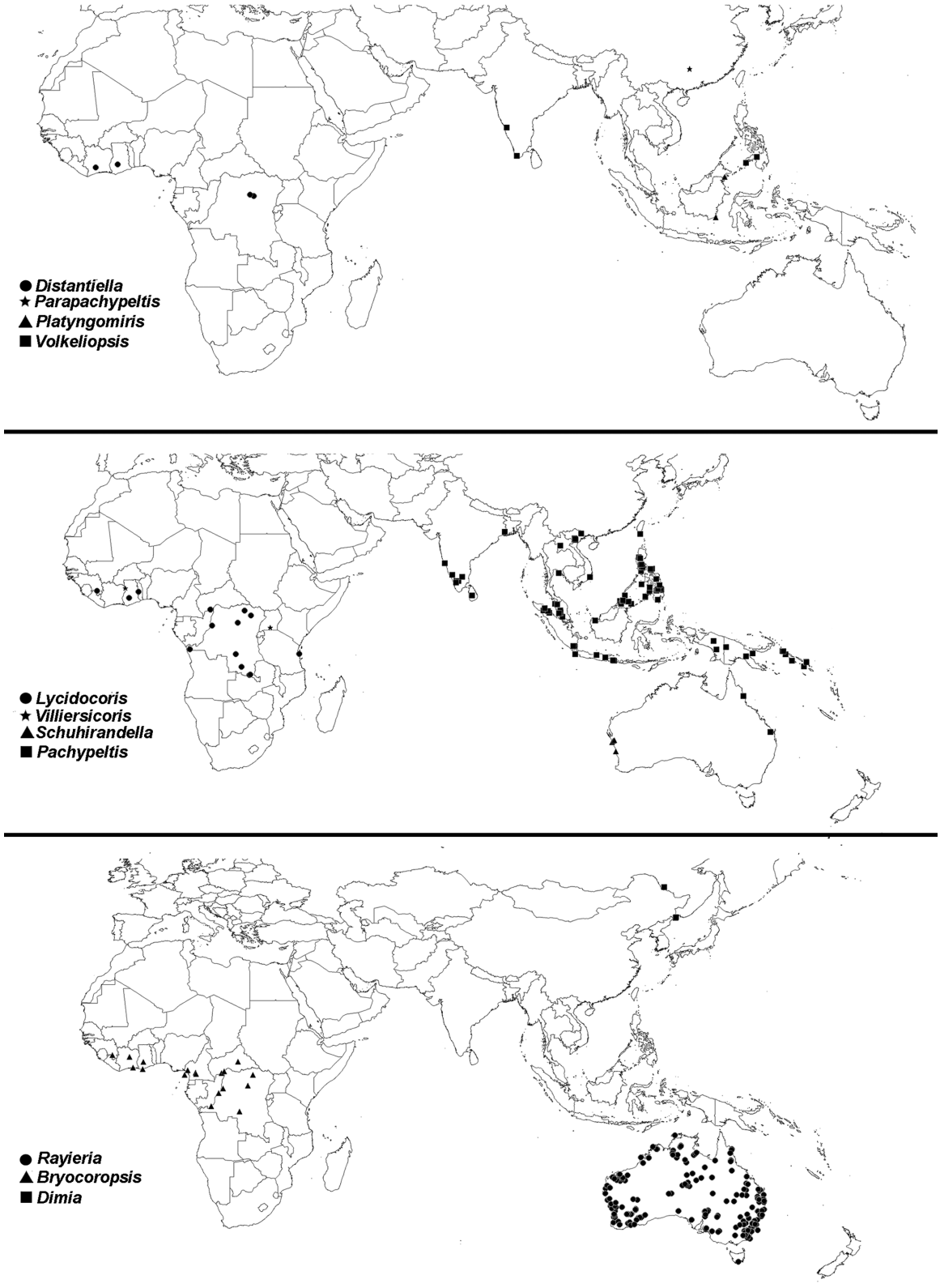

Figure 23. Distribution maps of *Bryocoropsis*, *Dimia*, *Distantiella*, *Lycidocoris*, *Pachypeltis*, *Parapachypeltis*, *Platyngomiris*, *Rayieria*, *Schuhirandella*, *Villiersicoris* and *Volkeliopsis*.

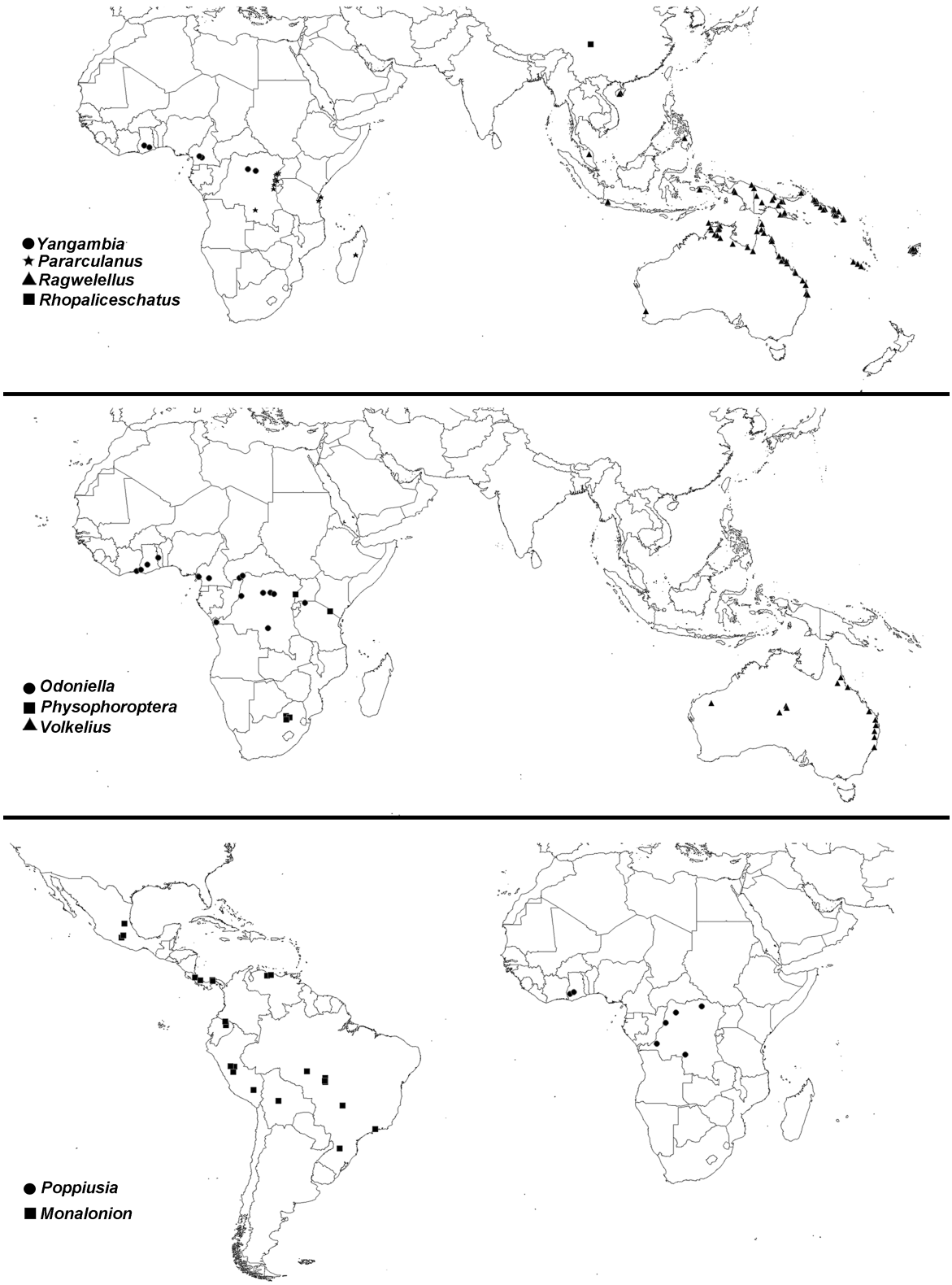

Figure 24. Distribution maps of *Monalonion*, *Odoniella*, *Pararculanus*, *Physophoroptera*, *Poppiusia*, *Ragwelellus*, *Rhopaliceschatus*, *Volkelius* and *Yangambia*.

two membrane cells, and convergent flattened parempodia without pseudopulvilli. These characters are common for the subfamily Orthotylinae, and we transfer *Onconotellus* to it (see Schuh, 1976 for a discussion of the pretarsus). Poppius (1912) described the monotypic bryocorine genus *Pachypeltopsis*, and Carvalho (1952) placed it in the tribe Monaloniini. We examined the holotype of *Pachypeltopsis australicus*, and observed a distinct collar, delimited by a deep sulcus, two membrane cells, and setiform parempodia and no pseudopulvilli. On the basis of these characters we transfer this genus to the tribe Saturniomirini. One of us (A.N.N.) also examined the monotypic genus *Felisacoris* Carvalho, 1956, and found that it is very similar to *Felisacus* in external view and genitalia and most probably it is nested within this genus. Based on this observation, we transfer *Felisacoris* to the tribe *Felisacini*, and the full revision of the groups will be provided in a subsequent paper.

Our phylogenetic analysis resulted in the recognition of two major clades within a redefined tribe, namely the *Monalonion*-complex and *Odoniella*-complex (see Namyatova & Cassis, 2013a,b, Namyatova *et al*., in press). These complexes comprise more than half of the monaloniine genera, and correspond in part to Carvalho's (1952, 1955) notions of Monaloniini and Odoniellini (see also nodes 12–14 in Namyatova *et al*., in press). We have refrained from redefining these subtribes, as it would require us to erect new and less supported subtribes for the remaining monaloniine genera, and we prefer the use of informal groups pending further phylogenetic analysis. These two complexes comprise the following genera:

1) The *Monalonion*-complex includes *Afropeltis*, *Helopeltis*, *Monalonion*, *Physophoroptera*, *Physophoropterella*, *Rayieria*, *Ragwelellus*, *Physophoroptera*, *Physophoropterella*, *and Schuhirandella* (node 35). The group of species is characterized by the following set of characters: pronotum and scutellum without punctures or wrinkles, punctures on R + M and clavus absent, forecoxae separated from each other, outgrowth on metepisternum absent. The representatives of this group are usually elongate bugs with long antennae and legs, although some genera are more oval with relatively short appendages (*Schuhirandella*, *Physophoroptera*).
2) The *Odoniella*-complex includes *Boxia*, *Bryocoropsis*, *Distantiella*, *Odoniella*, *Platyngomiris*, *Pseudodoniella*, *Rhopaliceschatus*, *Sahlbergella*, *Volkeliopsis* Poppius, 1915, *Volkelius* and *Yangambia* (node 19). Representatives of this group and oval bugs, with more or less swollen scutellum, pronotum and scutellum with distinct punctures or wrinkles, R + M and clavus without punctures, antennal segments III and IV clavate or incrassate apically.

Checklist of genera of tribe Monaloniini

(Names in bold italics are valid names; names in regular italics are junior synonyms or genera, transferred to other tribes).

Afropeltis Stonedahl, 1991 status nov., this work
Arculanus Distant, 1904 = *Tetanophleps* Bergroth, 1922 syn. by China, 1944
Arthriticus Bergroth, 1923
Aspicelus A. Costa, 1864; see *Helopeltis* Signoret, 1858
Boxia China, 1943 = *Boxiopsis* Lavabre, 1960 syn. nov., this work
Boxiopsis Lavabre, 1960; see *Boxia* China, 1943
Bryocoropsis Schumacher, 1917
Chamus Distant, 1904 = *Chamopsis* Reuter and Poppius, 1911 syn. nov., this work = *Parachamus* Schouteden, 1946 syn. nov., this work
Chamopsis Reuter and Poppius, 1911; see *Chamus* Distant, 1904
Deimatostages Kuhlgatz, 1906; see *Sahlbergella* Haglund, 1895
Dimia Kerzhner, 1988
Disphinctus Stål, 1871; see *Pachypeltis* Signoret, 1858
Distantiella China, 1944
Ealincola Schouteden, 1942; see *Lycidocoris* Reuter and Poppius, 1911
Eucerocoris Westwood, 1837
Eupachypeltis Poppius, 1915
Helopeltis Signoret, 1858 = *Aspicelus* Costa, 1864 syn. by Atkinson, 1890a
Idioaspis China, 1944; see *Yangambia* Schouteden, 1942
Felisacus Distant, 1904; transferred to tribe Felisacini, see Namyatova *et al*., in press
Felisacoris Carvalho, 1956; transferred to tribe Felisacini, this work
Lycidocoris Reuter and Poppius, 1911 = *Pantilioforma* Schumacher, 1917 syn. nov., this work = *Ealincola* Schouteden, 1942 syn. by China, 1944
Mandragora Schumacher, 1917; see *Physophoropterella* Poppius, 1914
Mansoniella Poppius, 1915
Mircarvalhoia Kerzhner and Schuh, 1998; see *Volkeliopsis* Poppius, 1915
Miomonalonion Sailer and Carvalho, 1957
Monalonion Herrich-Schaeffer, 1850
Odoniella Haglund, 1859
Onconotellus Knight, 1935; transferred to subfamily Orthotylinae, tribe Orthotylini, this work
Pachypeltis Signoret, 1858 = *Disphinctus* Stål, 1871 syn. by Reuter, 1910
Pachypeltopsis Poppius, 1912; transferred to subfamily Deraeocorinae, tribe Saturniomirini, this work

Pantilioforma Schumacher, 1917; see *Lycidocoris* Reuter and Poppius, 1911
Parabryocoropsis China and Carvalho, 1951; see *Platyngomiris* Kirkaldy, 1902
Parachamus Schouteden, 1946; see *Chamus* Distant, 1904
Parapachypeltis Hu and Zheng, 2001
Pararculanus Poppius, 1912
Physophoroptera Poppius, 1910
Physophoropterella Poppius, 1914 = *Mandragora* Schumacher, 1917 syn. by Bergroth, 1922
Platyngomiriodes Ghauri, 1963; see *Platyngomiris* Kirkaldy, 1902
Platyngomiris Kirkaldy, 1902 = *Platyngomiriodes* Ghauri, 1963 syn. nov., this work
Pseudodoniella China and Carvalho, 1951
Poppiusia China, 1943
Ragwelellus Odhiambo, 1962
Rayieria Odhiambo, 1962
Rhopaliceschatus Reuter, 1903
Sahlbergella Haglund, 1895 = *Deimatostages* Kuhlgatz, 1906 syn. by Reuter, 1907
Schuhirandella Namyatova and Cassis, 2013
Tetanophleps Bergroth, 1922 see *Arculanus* Distant, 1904
Villiersicoris Delattre, 1950
Volkeliopsis Poppius, 1915 = *Mircarvalhoia* Kerzhner and Schuh, 1998; syn. nov., this work
Volkelius Distant, 1904
Yangambia Schouteden, 1942 = *Idioaspis* China, 1944 syn. by Schouteden, 1945

AFROPELTIS STONEDAHL STAT. REV.

Figures 9, 12E, 13B, 14A–D, 18A, B, 22

Afropeltis Schmitz, 1968: 1 (subgen. nov.; name unavailable, no designated type species); Stonedahl, 1991: 470 (subgen. nov.; type species *Eucerocoris westwoodi* White, 1842 by original designation); Schuh, 1995: 512 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Afropeltis belongs to the *Monalonion*-complex (see discussion for the tribe), and among other genera of this group it can be recognized by: elongate body and antennae longer than body, all femora arcuate (as in fig. 18A in Namyatova *et al*., in press); antennae distinctly longer than body; ASI longer than head and pronotum combined; collar distinctly swollen (as in fig. 7D in Namyatova & Cassis, 2013b); base of clypeus not delimited with depression; metepimeron with process, rounded apically (Fig. 13B); claw without apical tooth (as in fig. 10C, E in Namyatova & Cassis, 2013b); attachment of ductus seminis on phallobase distinctly shifted to left; ductus seminis entirely membranous; endosoma with two large spicules (Fig. 14A); DLP with pair of sclerotized rings (Fig. 18A).

Redescription: Male: Length ranges from 5 to 12 mm, usually 7–9 mm. COLORATION (Fig. 9). Varying from yellow to dark brown, often with dorsal side of head, frons and clypeus dark brown to black. TEXTURE. Body mostly smooth, without punctures, tubercles or wrinkles; vertex without flattened areas; semicircular depression between scutellum and mesoscutum absent; striations on scutellum laterally absent; only small depression on anterior angle of scutellum present (as in fig. 9H in Namyatova & Cassis, 2013b). VESTITURE. Setae on dorsum and thoracic pleura absent; very short, adpressed pale setae present on antennae, apex of femora, tibiae and tarsi and genital segment; setae also rarely distributed on clypeus and labium; black spinules on femora absent, those on tibiae present only apically. STRUCTURE. *Head*. Distance from eye and pronotum shorter than eye diameter (as in Fig. 10J); occipital region not delimited with depression; longitudinal depression distinct, longer than eye diameter; eyes not stylate, in line with contour of head, *c*. 0.2–0.25× as wide as head; distance between antennal fossae subequal or slightly longer than antennal fossa diameter; frons straight, without ridges, outgrowths or longitudinal depression (as in Fig. 10J); anterior view of head *c*. 1.6–1.8× as wide as high; eye height *c*. 1.4–2× as long as distance between eye and apex of clypeus; antennal fossa round, only slightly shorter than eye height, not raised, inferior margin placed above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, not delimited or delimited with shallow depression; head almost flat or slightly swollen in lateral view; gula *c*. 1.5–2× as long as buccula, almost straight. *Labium*. Length varying from reaching middle of metasternum to reaching abdominal segment IV; LSI *c*. 3× as long as wide; LSII *c*. 4× as long as wide, subequal to LSI; LSIII *c*. 4–6× as long as wide, subequal to or slightly longer than LSII; LSIV *c*. 5–8× as long as wide, *c*. 1.2–1.5× as long as LSIII. *Antenna*. About 1.6–3× as long as body; ASI *c*. 4–4.5× as long as head, swollen apically (as in fig. 8I in Namyatova *et al*., in press); ASII *c*. 1.4–1.5× as long as ASI, *c*. 2.8–3× as long as head and pronotum combined; ASIII *c*. 0.9× as long as ASII; ASII–IV filiform. *Thorax*. Collar convex, delimited posteriorly; calli separated, flat, depression delimiting calli posteriorly absent (as in Fig. 10J); humeral angles of pronotum rounded, not dilated (as in Fig. 10J); posterior margin of pronotum straight or slightly concave (as in Fig. 10J); scutellum only slightly swollen, with elongate spine-like process with expanded apex (Fig. 12E), with smooth medial ridge behind spine, without medial depression; scutellum with rounded apex; metepimeron narrow, *c*. 3× as high as long, with process (Fig. 13B); metasternum rounded posteriorly, without medial projection on to abdominal segment II (as in fig. 18B in Namyatova *et al*., in press). *Hemelytron*. Costal margin

KEY TO GENERA OF TRIBE MONALONIINI

This work is the fifth paper we have produced concerning the systematics of Bryocorinae, particularly of the monaloniines (Namyatova & Cassis, 2013a [description of the genus *Schuhirandella*], Namyatova & Cassis, 2013b [revision of the genus *Rayieria*], Namyatova & Cassis, 2014 [revision of the genus *Volkelius*] and Namyatova *et al*., in press [phylogeny of the subfamily Bryocorinae, including Monaloniini]). We refer to figures from these papers in the following key, as well as illustrations given in this work.

1. Punctures on clavus and R + M present (fig. 11C in Namyatova *et al*., in press); pair of punctures present between mesoscutum and scutellum, sometimes shallow (Fig. 11C, D in Namyatova *et al*., in press).2 (clades 3, 8, *Dimia*, *Lycidocoris*, *Villiersicoris*)
   – Punctures on clavus and R + M absent; pair of punctures between mesoscutum and scutellum lacking……12 (clade 18)
2. ASII incrassate apically; ASIII–IV distinctly clavate; pronotum punctate……3
   – ASII straight; ASIII–IV filiform; sometimes ASII slightly incrassate and ASIII and IV slightly clavate (*Dimia*); pronotum impunctate ……4
3. ASIV distinctly shorter than ASIII; eyes not stylate (Fig. 10D); calli flat (Fig. 10D); scutellum punctate; left-hand outgrowth on phallotheca present (Fig. 15V, Z)……*Lycidocoris* (Fig. 7)
   – AS IV only slightly shorter than ASIII; eyes stylate; calli swollen; scutellum impunctate; phallotheca without outgrowths (Fig. 17D)……*Villiersicoris* (Fig. 7)
4. Frons with three prominent outgrowths (Fig. 10K); lateral margins of head with wrinkles (fig. 6B in Namyatova *et al*., in press); ASI clothed with flattened setae; R + M very short, not reaching middle of corium……*Chamus* (Fig. 6)
   – Frons straight or swollen, without distinct outgrowths, sometimes only three shallow ridges present; ASI without flattened setae; R + M reaching or almost reaching posterior margin of corium……5
5. Frons with three distinct ridges (Fig. 10B, M); labium reaching or slightly surpassing anterior margin of metasternum.6
   – Frons smooth, without ridges; sometimes three indistinct tubercles present, if so labium surpassing anterior margin of metasternum……7
6. Head distinctly convex in lateral view (Fig. 10B, L); occipital region distinctly delimited with depression (Fig. 10B, L); phallobase outgrowths, supporting ductus seminis long (Fig. 17I); sclerotized bands on DLP present (Fig. 21I)……*Poppiusia* (Fig. 7)
   – Head almost flat in lateral view; occipital region delimited with very shallow depression or flat; phallobase outgrowths, supporting ductus seminis, short (Fig. 15I); sclerotized bands on DLP absent (Fig. 19A)……*Eupachypeltis* (Fig. 6)
7. Metasternum rounded, not extending on to abdomen (as in Fig. 17B in Namyatova *et al*., in press), LSIII and IV almost as long as wide each and subequal in length; long auxiliary vein on membrane present.*Arculanus* (Fig. 6)
   – Metasternum extending on to abdomen (fig. 17B in Namyatova *et al*., in press); at least LSIV longer than wide, longer than LSIII; auxiliary vein absent or very short ……8
8. ASI swollen apically (fig. 8C in Namyatova *et al*., in press); ductus seminis with distinct coils, forming narrow tube (Fig. 16A, E); with pair of punctures on depression delimiting calli posteriorly (Fig. 10A); hemelytron often whitish yellow, semitransparent with yellow, red or brown to dark brown markings on posterior part of corium……*Mansoniella* (Fig. 6)
   – ASI swollen medially (fig. 8B in Namyatova *et al*., in press); ductus seminis without coils (e.g. Fig. 16T, X, AB, AF) or coils present and forming wide tube (Fig. 15R); without pair of punctures on depression delimiting calli posteriorly; coloration of hemelytron variable, mostly brown or red……9
9. ASIII–IV slightly clavate; LSI *c*. 4× as long as wide; labium surpassing anterior margin of metasternum; antennal fossa distinctly tuberculate; ductus seminis with coils, forming broad tube (Fig. 15R)……*Dimia* (Fig. 7)
   – ASIII–IV filiform; LSI at most 3× as long as wide; labium reaching middle of metasternum at most; and ductus seminis shorter than phallotheca length, without coils (e.g. Fig. 16T, X, AB, AF)……10
10. Distance between eye and pronotum subequal to or slightly longer than eye diameter; metepimeron subtriangular with apex undivided (as in Fig. 13C); posterior wall of bursa copulatrix without tubercles (Fig. 20N, P)……*Pararculanus* (Fig. 7)
    – Distance between eye and pronotum shorter than eye diameter; metepimeron bifurcate (Fig. 13D); posterior wall of bursa copulatrix with tubercles (Fig. 20B, D, F, H, J, L)……11
11. Pronotum punctate (Fig. 7) ……*Parapachypeltis*
    – Pronotum impunctate (Fig. 7) ……*Pachypeltis*

12. Pronotum and scutellum with distinct punctures or wrinkles; R + M mostly indistinct and not reaching posterior margin of corium; medial fracture distinctly inclined towards midline; cuneus shorter than scutellum; segment I of hind tarsus subequal to segment III (as in fig. 19A in Namyatova *et al*., in press); metasternum with medial projection on to abdomen (fig. 17A in Namyatova *et al*., in press); ventral wall of genital capsule not shortened anteriorly ..... 13 (*Odoniella*-complex, node 19)
– Pronotum and scutellum glabrous, without punctures, rarely with indistinct wrinkles; R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M (figs 11G, 12F in Namyatova *et al*., in press); cuneus longer than scutellum; segment I of hind tarsus longer than segment III (Fig. 13I); metasternum without medial projection on to abdominal segment II (fig. 17B in Namyatova *et al*., in press); ventral wall of genital capsule shortened anteriorly (Fig. 15Q) ..... 23 (*Monalonion*-complex, node 35)
13. Pronotum with tumescences distinctly raised (Fig. 10I); humeral angles of pronotum serrate (Fig. 10I); scutellum dorsally divided into six parts (Fig. 11I); setae on hemelytron forming patches; genital capsule with pair of outgrowths laterally (Fig. 17AK) ..... *Yangambia* (Fig. 8)
– Pronotum without tumescences (Fig. 10G, H) or with shallow tumescences (fig. 4C in Namyatova *et al*., in press); humeral angles of pronotum not serrate; scutellum dorsally not divided into parts; setae on hemelytron uniformly scattered; genital capsule without pair of outgrowths laterally 14
14. Pronotum with wrinkles 15
– Pronotum with distinct deep punctures (Fig. 10G, fig. 4C in Namyatova *et al*., in press) 16
15. Wrinkles on pronotum and scutellum shallow, mostly transverse; scutellum with longitudinal depression; LSIII *c*. 1.5× as long as wide; pronotum clothed with simple setae or elongate flattened setae (fig. 3C in Namyatova & Cassis, 2014); ..... *Volkelius* (Fig. 8, Fig. 1 in Namyatova & Cassis *et al*.)
– Wrinkles on pronotum and scutellum upraised, transverse and longitudinal (Fig. 11C); scutellum without longitudinal depression; LSIII *c*. 4× as long as wide; pronotum clothed short small flattened setae ..... *Boxia* (Fig. 8)
16. Head *c*. 2–2.3× as long as wide (Fig. 10G); coloration mostly orange, reddish or yellow, sometimes with dark markings on pronotum, scutellum and hemelytron; dorsal surface of scutellum rounded (Fig. 13E, fig. 12E in Namyatova *et al*., in press); pair of tubercles on frons absent (Fig. 10G) ..... *Odoniella* (Fig. 8)
– Head *c*. 2.5–5× as long as wide (Fig. 10F); coloration mostly brown; pair of tubercles on frons often present (Fig. 10F); sometimes coloration orange and tubercles on frons absent, if so scutellum flat (*Volkeliopsis*) 17
17. Head and pronotum orange; surface of scutellum flat (Fig. 11B); LSIV as long as LSIII; body clothed with simple setae only ..... *Volkeliopsis* (Fig. 8)
– Head and pronotum pale brown to dark brown; surface of scutellum often convex (Fig. 11D, F-H, J); LSIV mostly longer than LSIII; rarely surface of scutellum flat or LSIV subequal to LSIII, coloration of body brown to dark and hemelytron clothed with flattened setae 18
18. Scutellum subdivided into lower and upper parts (Fig. 12B) 19
– Scutellum not subdivided into lower and upper parts (Fig. 12A) 20
19. Hind tibia with dense setation ..... *Distantiella* (Fig. 8)
– Hind tibia with rare regular setation *Sahlbergella* (Fig. 8)
20. Scutellum not surpassing height of pronotum from lateral view, subtriangular or trapeziform; often with longitudinal depression at least anteriorly, if absent, surface of scutellum flat; hemelytron clothed with flattened setae; posterior wall of bursa copulatrix without pair of elongate sclerites posteriorly (Fig. 18H, J) ..... *Bryocoropsis* (Fig. 8)
– Scutellum surpassing height of pronotum from lateral view, without longitudinal depression, mostly rounded or oval (Fig. 11F) or subtriangular (Fig. 11G), in the latter case setae on hemelytron simple; posterior wall of bursa copulatrix often with pair of elongate sclerites posteriorly (Fig. 21B, F), if absent scutellum distinctly rounded and setae on hemelytron flattened 21
21. Hind tibia covered with long and dense setae ..... *Platyngomiris* (Fig. 8)
– Setae on hind tibiae regular, not very long and dense 22
22. Tubercles on pronotum and scutellum present, distinct (as in Fig. 11H); scutellum unicolorous ..... *Pseudodoniella* (Fig. 8)
– Tubercles on pronotum and scutellum absent; scutellum orange with four dark markings ..... *Rhopaliceschatus* (Fig. 8)
23. Swelling on posterior part of corium present (fig. 12F in Namyatova *et al*., in press); eyes stylate (fig. 4D in Namyatova *et al*., in press) 24
– Swelling on posterior part of corium absent or slightly upraised; eyes not stylate 22

24. Coloration yellow with dark brown to black areas; bifurcate process on scutellum present (Figs 11K, 12D); ASI slightly longer than head and pronotum combined; ASII distinctly swollen apically (fig. 8G in Namyatova *et al*., in press); posterior part of pronotum with pair of swellings (Fig. 10E); femora with swellings in middle part (Fig. 13G).....*Physophoropterella* (Fig. 9)
    – Coloration red with dark brown to black areas; scutellum with rounded outgrowth (Fig. 12C, fig. 12F in Namyatova *et al*., in press); ASI distinctly shorter than head and pronotum combined; ASII only slightly swollen apically; posterior part of pronotum without swellings; femora without swellings medially.....*Physophoroptera* (Fig. 9)
25. ASI shorter than head width.....26
    – ASI longer than head width.....27
26. Body more or less oval, relatively small, 3–5 mm, clothed with simple setae; ASII incrassate towards apex, ASIII and IV clavate; ductus seminis entirely membranous, attached to phallobase on left-hand side (fig. 3A in Namyatova & Cassis, 2013a).....*Schuhirandella* (Fig. 9)
    – Body elongate, usually more than 10 mm long, mostly without setae; ASII–IV filiform; ductus seminis sclerotized basally and apically, attached medially (Fig. 16I).....*Monalonion* (Fig. 9)
27. Vertical process on scutellum present (Fig. 12E, F).....28
    – Vertical process on scutellum absent.....29
28. Collar distinctly swollen; scutellum v-shaped, with ridge behind process; femora without swellings medially; metepimeron with elongate process (Fig. 13B); pretarsal claw without subapical tooth; endosoma with two large spicules (Fig. 14A); DLP with sclerotized rings (Fig. 18A).....*Afropeltis* (Fig. 9)
    – Collar almost flat or only slightly swollen; scutellum broadly rounded posteriorly, without ridge behind process; metepimeron with small rounded or subrectangular outgrowth (as in Fig. 13A); pretarsal claw with subapical tooth (Fig. 13L, fig. 10D in Namyatova & Cassis, 2013b); endosoma with single large spicule and often with fields of small tubercles (as in fig. 15M, see also Stonedahl, 1991); DLP without sclerotized rings, often sclerotized bands present (Fig. 19C, see also Stonedahl, 1991) .....*Helopeltis* (Fig. 9)
29. Frons often distinctly swollen, at least in lateral view (fig. 5A–F in Namyatova & Cassis, 2013b); foretibia as long as or slightly longer than head and pronotum combined; ASI often subequal or only slightly longer than head and pronotum combined; claw mostly straight, apically curved only (fig. 10A, B in Namyatova & Cassis, 2013b) .....*Rayieria* (figs 2–4 in Namyatova & Cassis, 2013b)
    – Frons mostly straight or only slightly swollen (Fig. 10J); foretibia distinctly longer than head and pronotum combined; ASI often almost twice as long as head and pronotum combined; claw broadly rounded (fig. 10C, E in Namyatova & Cassis, 2013b) 30
30. ASI curved; distance between antennal fossa distinctly longer than antennal fossa diameter; apices of femora wider than eye diameter; phallotheca distinctly tapering towards apex (Fig. 14I).....*Arthriticus* (Fig. 9)
    – ASI straight or only slightly curved (fig. 8I in Namyatova *et al*., in press); distance between antennal fossa as long as or slightly longer than antennal fossa diameter (Fig. 10J); diameter of apices of femora subequal to shorter than eye diameter; phallotheca broad or narrow, but only slightly tapering apically (Fig. 17Q, U)..... .....*Ragwelellus* (Fig. 9)

straight or slightly concave, hemelytra tapering posteriorly; claval commissure *c*. 2.8–4.5× as long as scutellum, concave; R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M; corium without swelling posteriorly (as in fig. 11G in Namyatova *et al*., in press); cuneus *c*. 6–7× as long as wide, *c*. 1.2–1.4× as long as pronotum, its medial margin distinctly concave; membrane cell distinctly surpassing apex of cuneus, *c*. 1.5–2× as long as pronotum, rounded or acute (as in fig. 13C in Namyatova *et al*., in press); auxiliary vein absent or short; distance between cell and apex of membrane *c*. 0.2–0.3× as long as cell (as in fig. 13C in Namyatova *et al*., in press). *Legs*. Forecoxae separated (as in fig. 17B in Namyatova *et al*., in press); femora swollen apically (as in fig. 17A in Namyatova *et al*., in press), without additional swelling medially; femora distinctly curved (as in fig. 18A in Namyatova *et al*., in press); foretibia longer than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus longer than segments I and II each, segment II slightly shorter than segment III (as in fig. 19B in Namyatova *et al*., in press); claw broadly rounded (as in fig. 10C, E in Namyatova & Cassis, 2013b), basal tooth short, triangular, apical tooth absent (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 14A–D). Genital capsule almost twice as long as wide, without outgrowth(s); ventral wall of genital capsule shortened anteriorly; left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore subtriangular, without outgrowth(s); ductus seminis longer than phallotheca length, with coils, forming wide tube, without sclerotization basally or apically, attached to left-hand side of phallobase near base; sclerotized part of phallotheca broad occupying

entire dorsal side, rounded apically, without outgrowth(s) or ridges; endosoma with two large spicules.

Female: Similar to male, body usually generally large. Length ranges from 6 to 12 mm, usually 8–10 mm. *Genitalia* (Fig. 18A, B). DLP with pair of sclerotized rings posteriorly, without any additional sclerotization, striation present only medially; lateral oviducts attached posteriorly, distance between them shorter, than distance from lateral oviduct to lateral margin; spermathecal gland attached near posterior margin medially; posterior wall of bursa copulatrix with small tubercles, without spinose lobes; base of second valvula concave.

Distribution: Widely distributed in Tropical Africa (Fig. 22).

Host plants: Feeds on a wide range of cultivated and wild plants. The species of *Afropeltis* are pests of cocoa, tea, cotton, cashew, quina and castor oil (Schmitz, 1968; Hill, 1983).

Included species

Afropeltis alluaudi (Reuter, 1905) **comb. nov.**
Afropeltis anacardii (Miller, 1954) **comb. nov.**
Afropeltis basilewskyi (Schmitz, 1968) **comb. nov.**
Afropeltis bergevini (Poppius, 1914) **comb. nov.**
Afropeltis bergrothi (Reuter, 1892) **comb. nov.**
Afropeltis carayoni (Schmitz, 1968) **comb. nov.**
Afropeltis corbisieri (Schmitz, 1968) **comb. nov.**
Afropeltis couturieri (Schmitz, 1988) **comb. nov.**
Afropeltis gerini (Carayon, 1949) **comb. nov.**
Afropeltis ghesquièrei (Schmitz, 1968) **comb. nov.**
Afropeltis hyalospilosus (Schmitz, 1988) **comb. nov.**
Afropeltis labaumei (Poppius, 1911) **comb. nov.**
Afropeltis lalandei (Carayon, 1949) **comb. nov.**
Afropeltis lemosi (Ghesquière, 1922) **comb. nov.**
Afropeltis maynei (Ghesquière, 1922) **comb. nov.**
Afropeltis mayumbensis (Ghesquière, 1922) **comb. nov.**
Afropeltis melanescens (Schmitz, 1988) **comb. nov.**
Afropeltis orophila (Ghesquière, 1939) **comb. nov.**
Afropeltis plebejus (Poppius, 1911) **comb. nov.**
Afropeltis poppiusi (Schmitz, 1968) **comb. nov.**
Afropeltis pseudomaynei (Schmitz, 1968) **comb. nov.**
Afropeltis rauwolfiae (Ghesquière, 1948) **comb. nov.**
Afropeltis schoutedeni (Reuter, 1906) **comb. nov.**
Afropeltis seredensis (Schmitz, 1968) **comb. nov.**
Afropeltis villiersi (Delattre, 1947) **comb. nov.**
Afropeltis waterhousei (Kirkaldy, 1902) **comb. nov.**
Afropeltis westwoodii (White, 1842) **comb. nov.**

Discussion: Afropeltis is a speciose genus that is distributed in Africa. The above description is based on only five species that were available to us for study, including one unidentified species. The species are similar and it was beyond the scope of this study to re-examine Schmitz's (1968) revision.

Schmitz (1968) described *Afropeltis* as a new subgenus of *Helopeltis* to accommodate all African species of *Helopeltis*. However, he did not designate a type species, which according to the Code of Zoological Nomenclature makes *Afropeltis* unavailable. Stonedahl (1991) validated the *Afropeltis* name, and designated *Eucerocoris westwoodi* White as the type species. Diagnostic characters for those two closely related groups can be found in Schmitz (1968: 219–220) and Stonedahl (1991: 470–473). We agree with the views of these authors, and we consider that the two supraspecific groups are distinctive. The undivided scutellar spine is the only unambiguous synapomorphy for the genus *Helopeltis* in its original sense.

On the basis of external characters, as well as male and female genitalia characters, we raise *Afropeltis* to generic rank. *Helopeltis* differs from *Afropeltis* by the following characters: base of clypeus more or less delimited with depression; metepimeron rounded or slightly angulate (as in Fig. 13A); claw with apical tooth (fig. 10D in Namyatova & Cassis, 2013b); endosoma with single large spicule, and sometimes also with sclerotized areas, or entirely membranous (Fig. 15M); and DLP with sclerotized bands and sclerotized ridge medially (Fig. 19C, see also Stonedahl, 1991).

Schmitz (1968) reported that the labium reaches the posterior margin of the pronotum in *Helopeltis* and the anterior margin of the metasternum in *Afropeltis*. According to our observations, the labium in both genera is long and can reach abdominal segments in some species.

We have not been able to report on the morphology of ASIV as it is lost in all specimens that we examined.

Arculanus Distant

Figures 6, 14F–H, 18C, D, 22

Arculanus Distant, 1904a: 198 (gen. nov.; type species: *Arculanus marshalli* Distant, 1904 by monotypy); Kirkaldy, 1906 (list); Reuter, 1910: 157 (cat.); Poppius, 1912: 176, 190 (key, description); Bergroth, 1922: 56 (cat.) China, 1944: 173 (key); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 39 (key); Carvalho, 1957: 131 (cat.); Schmitz, 1968: 11 (key to gen.); Schuh, 1995: 509 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Tetanophleps Bergroth, 1922: 56 (gen. nov.; type species: *Tetanophleps gibbifrons* by monotypy; syn. by China, 1944: 172); Carvalho, 1957: 131 (cat.)

Diagnosis: Arculanus can be diagnosed by the following characters: presence of punctures on clavus and R + M (as in fig. 11C, D in Namyatova *et al*., in press); corium semitransparent with reddish marking posteriorly; hemelytra broadened posteriorly; metasternum rounded, not extending to abdomen (as in fig. 17C in Namyatova *et al*., in press); ASI subequal to half of head width, swollen medially; LSIII as long as wide, LSIV as long as LSIII; gula almost as long as buccula; calli separated (as in Fig. 10B); presence of two punctures on that depression near calli (as in Fig. 10A); setae on pronotum absent or very rare; presence of long auxiliary vein on membrane emanating from closed cell; ductus seminis with distinct coils, forming narrow tube (Fig. 14E); DLP with lateral oviducts placed medially (Fig. 18C).

*Redescription:*Male: Length *c*. 5 mm. COLORATION (Fig. 6). Mostly whitish yellow to yellow, with reddish and brown markings, the largest reddish marking placed on hemelytron. TEXTURE. Body smooth; head without tubercles, wrinkles or flattened areas, vertex without flattened areas; pronotum and scutellum mostly impunctate, without tumescences or wrinkles, only pair of punctures on depression delimiting calli and between mesoscutum and scutellum; striations on lateral margin of scutellum, and rows on punctures on clavus and on R + M present (as in fig. 11C in Namyatova *et al*., in press); semicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with pale short simple setae, very rare or absent on head, pronotum and pleura, dense and adpressed on hemelytron; mostly suberect on appendages, setae on legs and thorax sometimes not very dense, slightly longer than width of hind tibia; black spinules on femora absent; rows of small black spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum subequal to eye diameter (as in Fig. 10A); occipital region distinctly delimited with transverse depression; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head (as in Fig. 10A), *c*. 0.33× as wide as head; distance between antennal fossa twice as long as antennal fossa diameter; frons distinctly swollen, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.3× as wide as high; eye almost twice as high as distance from eye to apex of clypeus; antennal fossa round, diameter subequal to quarter of eye height (as in fig. 4A in Namyatova *et al*., in press), only slightly raised; inferior margin of fossa placed slightly above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with depression; head distinctly swollen dorsally in lateral view; gula straight, almost as long as buccula length. *Labium*. Reaching or almost reaching posterior margin of prosternum; LSI and II each twice as long as wide; LSIII–IV each almost as long as wide, slightly shorter than LSII. *Antenna*. Slightly surpassing base of cuneus; ASI subequal to half of head width, widened medially (as in fig. 8C in Namyatova *et al*., in press); ASII *c*. 3× as long as ASI, subequal in length to head and pronotum combined; ASIII *c*. 0.7–0.8× as long as ASII; ASIV *c*. 0.5× as long as ASIII, ASII–IV filiform. *Thorax*. Collar distinct, fused with calli posteriorly (as in Fig. 10A), distinctly swollen; calli separated, tuberculate (as in Fig. 10B), depression delimiting callosite region posteriorly indistinct medially; humeral angles of pronotum rounded, not dilated (as in Fig. 10A); posterior margin of pronotum concave; scutellum almost flat, acute apically, without outgrowth, ridge or medial depression; metepimeron slightly widened, *c*. 4–5× as high as long, slightly angulate; metasternum rounded posteriorly, without medial projection on to abdominal segment II (as in fig. 17C in Namyatova *et al*., in press). *Hemelytron*. Widened posteriorly, its costal margin convex near posterior margin of corium; claval commissure *c*. 1.5× as long as scutellum, straight (as in fig. 11C in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium without swelling posteriorly; cuneus *c*. 2.5× as long as wide, subequal to pronotum length, medial margin almost straight (as in fig. 13A in Namyatova *et al*., in press); membrane cell not surpassing or only slightly surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), slightly longer than pronotum; distance from cell to apex of membrane subequal to length of cell; auxiliary vein present, very long, almost reaching posterior margin of membrane. *Legs*. Forecoxae contiguous (as in fig. 17C in Namyatova *et al*., in press); fore and middle femora only indistinctly swollen apically, hind femur distinctly swollen apically; femora not curved or only indistinctly curved (as in fig. 18C in Namyatova *et al*., in press); foretibia shorter than head and pronotum combined; swellings on tibae absent; segments of hind tarsus subequal in length (as in fig. 19A in Namyatova *et al*., in press); claw mostly straight, apical third curved; basal tooth on claw more than twice as long as wide, concave (as in Fig. 13K). *Genitalia* (Fig. 14E–H). Genital capsule longer than wide, without outgrowth(s), its ventral wall not shortened anteriorly; left paramere distinctly r-shaped, *c*. 2.5× as long as right paramere; phallobase sclerite of primary gonopore bowl-shaped, with short outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, as long as phallotheca length, with coils forming narrow tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowths or ridge; endosomal spicules with or without serrations, varying in shape.

Female: Length *c*. 6–7 mm. Similar to male, body usually generally larger. *Genitalia* (Fig. 18C, D). DLP with two sclerotized bands; membrane encircled by inner sclerotized band, not striated, without membranous outgrowths, with small sclerites; lateral oviducts separated, at mid-length of DLP, equidistant from lateral margins of DLP; spermathecal gland placed slightly above midpoint of DLP; posterior wall covered with small tubercles, without sclerites or outgrowths; base of second valvula slightly convex; ventral wall of bursa copulatrix membranous.

Distribution: Democratic Republic of Congo (Elisabethville) (Fig. 22).

Host plants: No information.

Included species

Arculanus marshalli Distant, 1904
Arculanus gibbifrons (Bergroth, 1922)

Discussion: Arculanus was previously placed in the Monaloniina *sensu* Schuh (1995). It is most similar to *Mansoniella*, particularly in coloration, with a semitransparent corium and a contrasting marking posteriorly (Fig. 6), hemelytra broadened posteriorly, with a pair of punctures on the depression delimiting calli posteriorly (Fig. 10A), pronotum almost devoid of setae, and the coils of the ductus seminis forming a narrow tube (compare Figs 14E, 16A, E). However, *Mansoniella* can be separated from *Arculanus* by several structural characters, including metasternum produced on to abdomen as a triangular outgrowth (as in fig. 17A in Namyatova *et al*., in press), the calli undivided (Fig. 10A), ASI is subequal to the head width, and swollen apically, LSIV is longer than LSIII, and absence of auxiliary vein on the hemelytral membrane.

Species of *Poppiusia* were initially described in *Arculanus*, as they also possess calli separated from each other (Fig. 10B). However, the former genus is readily differentiated by the metasternum extending to the abdomen as a triangular outgrowth (fig. 18A in Namyatova *et al*., in press). In addition, ASI is as long as or only slightly shorter than head width, there are no punctures on the depression delimiting calli posteriorly (Fig. 10B), pronotum covered with setae; and the coils of the ductus seminis are indistinct (Fig. 17I).

This redefinition of *Arculanus* results in it being composed of *Arculanus marshalli* and *A. gibbifrons* only; the latter is the type species, and for which one of us (A.N.N.) examined the holotype and two additional specimens.

We could not locate the holotype of *A. gibbifrons*, and it is presumably lost. On the basis of the original description of Bergroth (1922), it is very similar to *A. marshalli*. Bergroth originally described this species in his monotypic genus *Tetanophleps*, which was subsequently synonymized with *Arculanus* by China (1944), although without any justification. Bergroth claimed that *Tetanophleps* has affinities with *Arculanus*, *Mansoniella* and *Eupachypeltis*, but distinguished it by the structure of the head, pronotum and the supernumerary vein on the hemelytral membrane. He also noted the presence of chitinized calli on the hemelytral membrane, which he also reported as occurring in *Chamus*; however, we could not find this structure in any of the specimens of the latter genus. According to Bergroth's description, *Tetanophleps* possesses a distinct auxiliary vein on the hemelytral membrane (= venam supernumeriam), which is darker than the membrane cell. Among all Monaloniini *rev. stat*. genera that we examined, this character is present only in *Arculanus*. In other genera it is either absent or at most very short, and if present it is concolorous with the cell. *Tetanophleps* is also similar to *Arculanus* in a few more generalized characters, such as the short labium, swollen frons, the calli separated and the presence of a large red marking on the corium. Aside from tubercles on the hemelytral membrane, only two characters differentiate *Tetanophleps* from *Arculanus*; i.e. ASI is subequal to the length of the head and the calli are slightly tuberculate in the former, whereas in comparison, *Arculanus* has the ASI shorter than the head length and distinctly tuberculate calli. We conclude these differences are slight and not worthy of generic status, and support China's (1944) synonymy.

This revised definition of *Arculanus* requires the transfer of *A. madagascariensis* to *Pararculanus* (see discussion of *Pararculanus*).

Arthriticus Bergroth

Figures 9, 14I–L, 18E, F, 22

Arthriticus Bergroth, 1923: 413 (gen. nov.; type species *Arthriticus eugeniae* Bergroth, 1923 by monotypy); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 38 (key to gen.); Carvalho, 1957: 132 (cat.); Schuh, 1995: 509 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Arthriticus belongs to the *Monalonion*-complex (see discussion for tribe) and among the genera of this group it be recognized by: elongate body and appendages (Fig. 9), ASI and femora distinctly swollen apically; ASI longer than head and pronotum combined; frons not swollen on only slightly convex (as in Fig. 10J); distance between antennal fossa longer than antennal fossa width; antenna distinctly longer than body; forefemur curved; scutellum without spine-like projection; claw broadly rounded (fig. 10C in Namyatova & Cassis, 2013b); sclerotized part of phallotheca wide

basally and distinctly tapering apically (Fig. 14I); DLP with two sclerotized bands (Fig. 18E).

*Redescription:*Male: Length *c*. 5 mm. COLORATION (Fig. 9). Body mostly red, with brown markings, mostly on appendages. TEXTURE. Body mostly smooth, without punctures, wrinkles and tubercles; vertex without flattened areas; semicircular depression between scutellum and mesoscutum absent; striations on scutellum laterally absent; only single depression at each side of scutellum anteriorly, present (as in fig. 9H in Namyatova & Cassis, 2013b). VESTITURE. Setae on dorsum and thoracic pleura absent; pale simple setae on clypeus, labium, appendages and abdomen present; setae on lateral margins of head, labium and abdomen mostly adpressed and short, setae on abdomen very rare, present apically only; setae on antenna mostly short, suberect or adpressed, sometimes setae on ASII longer than width of hind tibia; setae on femora present only apically, adpressed; setae on tibiae short, mostly spine-like, suberect, not very dense; apex of tibia and tarsi with adpressed short setae; black spinules on femora and tibiae absent. STRUCTURE. *Head*. Distance from eye and pronotum slightly shorter than eye diameter (as in Fig. 10J); occipital region not delimited by transverse depression; longitudinal depression distinct, almost as long as or longer than eye diameter; eyes not stylate, in line with contour of head, *c*. 0.25× as long as head width (as in Fig. 10J); distance between antennal fossa longer than antennal fossa diameter; frons slightly convex, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.3× wide as high; eye height *c*. 1.5× as long as distance between eye and apex of clypeus; antennal fossa oval *c*. 0.7× as long as eye height, not raised, inferior margin placed distinctly above inferior margin of eye; base of clypeus placed slightly below than margin of antennal fossa, basally not delimited with depression; head more or less swollen in lateral view; gula *c*. 2–3× as long as buccula, convex. *Labium*. Length slightly surpassing posterior margin of metasternum; LSI twice as long as wide; LSII *c*. 3× as long as wide, subequal to LSI; LSIII *c*. 3× as long as wide, subequal to LSII; LSIV *c*. 6× as long as wide, twice as long as LSIII. *Antenna*. About 1.8× as long as body; ASI *c*. 2.3× as long as head width, swollen apically; ASII *c*. 1.7× as long as ASI, *c*. 2.5× as long as head and pronotum combined; ASIII 0.8× as long as ASII; ASIV *c*. 0.5× as long as ASIII; ASII–IV filiform. *Thorax*. Collar slightly swollen (as in fig. 7A in Namyatova & Cassis, 2013b), faintly delimited posteriorly; calli separated, almost flat; depression delimiting calli posteriorly absent (as in Fig. 10J); humeral angles of pronotum rounded, not dilated; posterior margin of pronotum straight or slightly concave (as in Fig. 10J); scutellum flat, rounded apically; without outgrowth, ridge or medial depression; metepimeron narrow, *c*. 2.5–3× as high as long, with subrectangular outgrowth (as in Fig. 13A); metasternum rounded posteriorly, without medial projection on to abdominal segment II (as in fig. 17B in Namyatova *et al*., in press). *Hemelytron*. Costal margin concave or straight; claval commissure *c*. 2.3× as long as scutellum, concave (as in fig. 11G in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M (as in fig. 11G in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus *c*. 5× as long as wide, subequal to pronotum, medial margin distinctly concave (as in fig. 13C in Namyatova *et al*., in press); membrane cell distinctly surpassing apex of cuneus, *c*. 1.75× as long as pronotum, acute apically (as in fig. 14C in Namyatova *et al*., in press); short auxiliary vein present; distance between cell and apex of membrane *c*. 0.14× as long as cell. *Legs*. Forecoxae separated (as in fig. 17B in Namyatova *et al*., in press); femora distinctly swollen apically and medially, apically as wide as eye, curved; foretibia longer than head and pronotum combined; swelling on tibiae absent; segment I of hind tarsus distinctly longer than segment II, segment II and III subequal in length (as in fig. 19B in Namyatova *et al*., in press); claw broadly rounded (fig. 10C in Namyatova & Cassis, 2013b); basal teeth short and triangular (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 14I–L). Genital capsule slightly longer than wide, with ventral wall shortened anteriorly (as in Fig. 15Q); left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore subtriangular, concave, without outgrowth(s); ductus seminis slightly longer than phallotheca, with coils, forming broad tube, without sclerotization basally or apically, attached to phallobase medially; sclerotized part of phallotheca broad basally and tapering apically; endosoma with pair of symmetrical elongate spicules.

Female: Length *c*. 6–7 mm. Coloration, surface, vestiture and structure as in male, but body generally larger (Fig. 9). *Genitalia* (Fig. 18E, F). DLP membranous, with two narrow sclerotized bands, some striations present; lateral oviduct placed slightly anteriorly to midline of DLP, close to lateral margin of DLP; spermathecal gland shifter anteriorly from midpoint; posterior wall of bursa copulatrix with distinct tubercles, without outgrowths or sclerotization; base of second valvula with swelling; ventral wall with sclerites around vulva.

Distribution: Bogor (Indonesia) (Fig. 22).

Host plants: Known from *Eugenia* sp. (Myrtaceae) (Bergroth, 1923).

INCLUDED SPECIES

Arthriticus eugeniae Bergroth, 1923

Discussion: Arthriticus was described by Bergroth (1923), where he noted that this genus differs from *Eucerocoris*, in the following way: 'principally in the structure of the rostrum and legs'.

In our cladogram, *Arthriticus* is nested within *Ragwelellus* and is similar to this genus externally. However, we have for now maintained its generic status as the monophyly of *Ragwelellus* is not supported (see node 43). In the *Ragwelellus* species that we have examined, the length of the labium varies distinctly, and reaches at least the posterior margin of the mesosternum. The structure of the legs in *Ragwelellus* is similar to that of *Arthriticus*; femora always swollen apically and usually also swollen medially; however, in *Ragwelellus* apices of the femora are usually narrower than eye diameter, but sometimes almost as wide as eye diameter. *Ragwelellus* can be also separated by the straight ASI, and longer cuneus, which is at least 6× as long as wide as the base, the cuneus at least slightly longer than the pronotum, and the phallotheca is not tapering or only slightly tapering apically (Fig. 17Q, U).

Boxia China

Figures 8, 11C, 13F, 14M-O, 22

Boxia China, 1943b: 287 (gen. nov.; type species: *Boxia khayae* China, 1943 by monotypy); China, 1944: 179 (key to gen.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 143 (cat.); Lavabre, 1977a: 50 (key to gen); Schuh, 1995: 526 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Boxiopsis Lavabre, 1960: 715 (gen. nov.; type species *Boxiopsis madagascariensis* Lavabre, 1960 by monotypy); Lavabre, 1960: 716 (key to gen.); Decazy, 1977: 124 (disc.); Lavabre, 1977a: 52, 60 (key to gen., descr.); Schuh, 1995: 526 (cat.); syn. nov., this work.

Diagnosis: Boxia belongs to the *Odoniella*-group (see discussion for the tribe), and can be separated from other genera of this group by the following characters: ASII straight; ASIII incrassate towards apex; ASIV only slightly clavate, spotted coloration (Fig. 8); pronotum and scutellum impunctate, with dense longitudinal and transverse raised wrinkles (Fig. 11C); posterior margin of pronotum almost straight; body clothed with very small rounded setae (Fig. 13F); spermathecal gland placed near middle of posterior margin of DLP.

Redescription: Male: Length 7–8 mm. COLORATION (Fig. 8). Mainly yellow, orange or pale brown with brown to dark brown markings, sometimes with reddish tinge; pronotum and hemelytron with dense brown to dark brown markings, hemelytron also with large dark brown marking posteriorly. TEXTURE. Body without tubercles; flattened areas or on vertex absent, head without wrinkles laterally; pronotum and scutellum impunctate, with dense longitudinal and transversal upraised wrinkles (Fig. 11C); pair of punctures between mesoscutum and scutellum, punctures on clavus and on R + M absent; striations on lateral margins of scutellum present; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Head, pronotum anteriorly, thoracic pleura and hemelytra clothed with short rounded setae (Fig. 13F), most part of pronotum without setae, those on thoracic pleura very rare; appendages clothed with short, adpressed dark simple setae, not very dense; black spinules on femora and tibiae present, irregularly distributed. STRUCTURE. *Head*. Distance between eye and pronotum very short, distinctly shorter than eye diameter (as in Fig. 10H); occipital region not delimited with depression; longitudinal depression on vertex absent or very short; eyes stylate (as in Fig. 10H), directed outwards, *c*. 0.2–0.25× as wide as head; distance between antennal fossa *c*. 1.5–2× as long as antennal fossa diameter; frons distinctly swollen, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.7× as wide as high; eye *c*. 1.2× as high as distance between eye and apex of clypeus; antennal fossa oval, diameter subequal to half of eye height, not raised (as in fig. 3B in Namyatova *et al*., in press); inferior margin of fossa placed near inferior margin of eye; base of clypeus placed slightly above inferior margin of antennal fossa, distinctly delimited with depression; head flat in lateral view; gula shorter than buccula, straight or convex. *Labium*. Reaching posterior margin of mesosternum; LS I *c*. 4× as long as wide; LSII *c*. 5× as long as wide, subequal to LSII in length; LSIII *c*. 4× as long as wide, slightly longer than LSII; LSIV *c*. 6× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 1.5× times as long as wide, subequal to quarter of head width, widened basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 5–6× as long as ASI, as long as head and pronotum combined, slightly widened towards apex; ASIII *c*. 0.6–0.7× as long as ASII, incrassate towards apex, without swellings basally or medially; ASIV 0.7–0.8× as long as ASIII, clavate. *Thorax*. Collar distinct, contiguous with calli posteriorly, flat; calli separated, flat (as in Fig. 10H); depression delimiting callosite region absent; humeral angles of pronotum rounded, not dilated (as in Fig. 10H); posterior margin of pronotum straight or sinuate (as in Fig. 10H); scutellum moderately swollen, triangular, not covering posterior margin of pronotum, acute apically, without outgrowth, ridge or medial depression (Fig. 11C); metepimeron enlarged, twice as high as long, angulate, subtriangular (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin slightly rounded, slightly concave

anteriorly; claval commissure *c*. 0.5–0.7× as long as scutellum, straight (as in fig. 12E in Namyatova *et al*., in press); R + M distinct only anteriorly, not reaching middle of corium (as in fig. 12E in Namyatova *et al*., in press); medial fracture strongly inclined towards midline; corium without swelling posteriorly; cuneus *c*. 1.2–1.3× as long as wide, as long as half of pronotum, medial margin almost straight (as in fig. 13B in Namyatova *et al*., in press); membrane cell slightly surpassing apex of cuneus, forming right angle, *c*. 0.7–0.8× as long as pronotum (as in fig. 13B in Namyatova *et al*., in press); auxiliary vein absent; distance from cell to apex of membrane *c*. 0.8× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, straight; foretibia shorter than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus slightly longer than segment II and subequal to segment III; claw broadly rounded (as in fig. 10C in Namyatova & Cassis, 2013b); basal tooth on claw short and triangular (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 14M, N). Genital capsule as long as wide, without outgrowth(s), its ventral wall not shortened anteriorly; left paramere distinctly r-shaped; phallobase sclerite of primary gonopore subtriangular, straight apically, without outgrowths supporting ductus seminis; ductus seminis not sclerotized basally or apically, slightly longer than phallotheca, with coils, forming wide tube, attached to phallobase medially; sclerotized part of phallotheca wide, occupying entire dorsal part, rounded apically, with subtriangular uprising basally, without ridge or outgrowths; endosoma with two elongate spicules and two fields of small spicules, one of them placed close to secondary gonopore.

Female: Length varying from 6 to 10 mm. Coloration, texture, vestiture and structure as in male (Fig. 8). *Genitalia*. DLP without sclerotized bands, with distinct paired areas of striations at sides; lateral oviducts attached at middle of striated areas, widely separated, placed near lateral margin of DLP, at half way of DLP; spermathecal gland placed in posterior part half of DLP, at equal distance from each lateral oviducts.

Distribution: Ghana, Madagascar (Fig. 22).

Host plants: Both species are known to feed on cocoa (Lavabre, 1960; Leston, 1970; Decazy, 1977; Entwistle, 1977). *Boxia khayae* is also affiliated with *Khaya grandifoliola* C.DC. (China, 1943) and *Entandrophragma* sp. (Meliaceae) (Piart, 1977).

Included species

Boxia khayae China (1942)
Boxia madagascariensis (Delattre, 1960) **comb. nov.**

Discussion: China (1943) described *Boxia* for a single species from Ghana. Lavabre (1960) described *Boxiopsis* as a monotypic genus from Madagascar. Lavabre (1977a) reported that the frons is pointed and the hemelytron is rugose in *Boxia*, and that the frons is rounded and the hemelytron more or less smooth in *Boxiopsis*.

We examined the female holotype and a non-type male specimen of *Boxia khayae*. We could not locate the type material of *Boxiopsis madagascariensis*, but examined a number of non-type female specimens from Madagascar, which fit the original description (Fig. 8). We found that the female genitalia of the two species are very similar. *Boxiopsis madagascarinesis* possesses an elongate and convex gula, as opposed to being very short and straight in *Boxia khayae*. We regard these as nothing more than species-level differences, and propose a new synonymy of these two genera.

Boxia was previously placed in the subtribe Odoniellina *sensu* Schuh because of its short and stout ASI (as in fig. 8E in Namyatova *et al*., in press) and a raised scutellum (Fig. 11C). It can be confused with *Bryocoropsis* because both taxa have brownish coloration, and some species of the latter genus also have a spotted hemelytron (Fig. 8), and the claw has a basal tooth (as in fig. 10B in Namyatova & Cassis, 2013b). *Bryocoropsis* can be separated from *Boxia* by the following characters: ASII incrassate apically, ASIII–IV clavate, broad medially, absence of small rounded setae, presence of long flattened setae and spermathecal gland orientated to the right-hand side (Fig. 15A, E).

Boxia is also similar to *Volkelius*, with both taxa sharing the following characters: scutellum only slightly swollen and not vesiculate (cf. Fig. 11C, fig. 3A in Namyatova & Cassis, 2014), impunctate and wrinkled pronotum and scutellum (Figs 10H, 11C, figs 2A, D, 3A in Namyatova & Cassis, 2014). In contrast, *Volkelius* is differentiated from *Boxia* by the following characters: ASII distinctly incrassate towards apex, wrinkles on pronotum and scutellum shallow and longitudinal (Fig. 10H, figs 2A, D, 3A in Namyatova & Cassis, 2014), tooth on claw elongate and subrectangular (fig. 3F, I in Namyatova & Cassis, 2014), and spermathecal gland on right-hand side of DLP (Fig. 18G, I).

Bryocoropsis Schumacher

Figures 8, 10H, 11D, 12A, 15A–H, 18G–J, 23

Bryocoropsis Schumacher, 1917: 453 (gen. nov.; type species *Bryocoropsis laticollis* by monotypy); Bergroth, 1922: 53 (cat.); China, 1944: 179 (key to gen.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 41 (key to gen.); Carvalho, 1957: 143 (cat.); Odhiambo, 1962: 298 (disc.); Lavabre, 1977a: 51 (key to gen.); Schuh, 1995: 526 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Bryocoropsis belongs to the *Odoniella*-complex and can be distinguished from other genera in this group by the following characters: coloration mostly brown, body oval (Fig. 8), ASII distinctly incrassate towards apex, with tip not swollen or only slightly swollen; ASIII–IV distinctly clavate (as in fig. 9F in Namyatova *et al*., in press); eyes stalked, distinctly directed laterally (as in Fig. 10H); pronotum and scutellum often with shallow tumescences (Fig. 11D); setae on pronotum very rare; long and flattened setae on hemelytron; scutellum distinctly swollen, not exceeding pronotum height, nor divided into lower and upper regions (as in Fig. 12A); spermathecal gland attached to right of midline (Fig. 18G, I).

*Redescription:*Male: Length *c*. 5–7 mm. COLORATION (Fig. 8). Mostly brown to dark brown with yellow markings on pleura and appendages, sometimes abdomen and legs with reddish tinge. TEXTURE. Vertex often with two pairs of tubercles on vertex anteriorly and a third pair near posterior margin of eye, sometimes some or all tubercles indistinct; flattened areas on vertex often distinct, sometimes indistinct; wrinkles on head laterally absent; ASI without tubercles; pronotum and scutellum covered with distinct punctures, sometimes mixed with wrinkles; collar with two pairs of tubercles; shallow tubercles on posterior part of pronotum and scutellum often present, sometimes those tubercles more or less upraised or indistinct; pair of punctures between mesoscutum and scutellum, punctures on clavus and on R + M absent; striations on lateral margins of scutellum indistinct or present only anteriorly; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with setae shorter than width of hind tibia; head, pronotum, scutellum, thoracic pleura and abdomen clothed with simple short suberect setae, those setae on dorsal side of head, pronotum, scutellum and thoracic pleura very rare; hemelytron clothed with dark and pale flattened setae, sometimes only slightly flattened; ASI with rare pale or darkened adpressed setae, sometimes flattened; ASII–IV and legs with more or less dense semiadpressed spine-like setae, setae on ASII–IV dark, setae on legs usually pale, sometimes dark; black spinules on femora and tibiae irregularly distributed (as in fig. 18F in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (as in Fig. 10F, H); occipital region not delimited with depression; longitudinal depression on vertex absent or very short and shallow; eyes stylate, directed outwards (as in Fig. 10F, H), *c*. 0.15–0.2× as wide as head; distance between antennal fossa twice as long as antennal fossa width; frons distinctly swollen with paired outgrowths (as in fig. 4C in Namyatova *et al*., in press), without ridges or longitudinal depression; anterior view of head *c*. 1.7–1.9× as wide as high; eye as long as or slightly longer than distance between eye and apex of clypeus; antennal fossa oval, diameter *c*. 0.5–0.7× as long as eye height, not raised (as in fig. 3B Namyatova *et al*., in press); inferior margin of fossa placed near inferior margin of eye; base of clypeus placed at halfway of antennal fossa height; delimited with depression; head flat form lateral view; gula as long as or shorter than buccula length, slightly convex. *Labium*. Almost reaching or slightly surpassing anterior margin of metasternum; LSI *c*. 2–2.5× long as wide; LSII *c*. 3–4× as long as wide, subequal or slightly longer than LSI; LSIII *c*. 3–4× as long as wide, subequal to LSII; LSIV 5–6× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching apex of clavus; ASI *c*. 1.5× as long as wide, *c*. 0.25–0.35× as long as head width, widened basally (as in Fig. 10F–H); ASII *c*. 5–6× as long as ASI, *c*. 0.7–0.9× as long as head and pronotum combined, widened towards apex or swollen apically, without any swellings basally and medially (as in fig. 8E in Namyatova *et al*., in press); ASIII *c*. 0.6–0.7× as long as ASII, widened towards apex; ASIV *c*. 0.6–0.8× as long as ASIII, clavate (as in fig. 8F in Namyatova *et al*., in press). *Thorax*. Collar fused with callosite region or rarely delimited medially, flat; calli separated, flat; depression delimiting calli posteriorly absent (as in fig. 4C in Namyatova *et al*., in press); humeral angles of pronotum slightly or distinctly dilated, not serrate; posterior margin of pronotum distinctly concave, forming right angles (as in Fig. 10G, fig. 4C in Namyatova *et al*., in press); scutellum swollen, not covering base of pronotum, trapeziform, not divided into parts, obtuse apically (Figs 11D, 12A) with or without longitudinal depression medially, without outgrowth or ridge; metepimeron enlarged, *c*. 1.5–2× as high as long, angulate, subtriangular (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in Fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin straight or slightly rounded; claval commissure *c*. 0.5–0.7× as long as scutellum, straight (as in Fig. 12E in Namyatova *et al*., in press); R + M distinct only anteriorly, not reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium without swelling posteriorly; cuneus *c*. 1.8–2.5× as long as wide, *c*. 0.4–0.7× as long as pronotum, medial margin slightly concave (as in fig. 13B in Namyatova *et al*., in press); membrane cell slightly or distinctly surpassing apex of cuneus, forming right angle, *c*. 0.7–0.9× as long as pronotum (as in fig. 13B in Namyatova *et al*., in press); auxiliary vein absent or very short present; distance from cell to apex of membrane *c*. 0.7× as long as cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora barely swollen apically, straight; foretibia shorter than head and pronotum combined; tibiae without swellings; segment I of hind tarsus slightly longer than

segment II, subequal to segment III; claw curved in apical half; basal tooth of claw elongate, slightly concave (as in fig. 3F, I in Namyatova & Cassis, 2014). *Genitalia* (Fig. 15A–H). Genital capsule as long as wide or slightly longer than wide, without outgrowth(s), ventral wall not shortened anteriorly; left paramere r-shaped, *c*. 2–2.5× as long as right paramere; phallobase sclerite of primary gonopore subtriangular or heart-shaped, without outgrowth(s); ductus seminis not sclerotized basally, with or without elongate sclerite bounding secondary gonopore, shorter or as long as phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying almost entire dorsal portion, slightly tapering, rounded apically, without ridge or outgrowths(s); endosoma with or without suboval sclerites.

Females: Length *c*. 7–8 mm. Coloration, surface, vestiture and structure as in male, but females slightly larger than males (Fig. 8). *Genitalia* (Fig. 18G–J). DLP with a single sclerotized ring anteriorly, more than 3× as long as wide; two large areas of striations present, equal in diameter or right one distinctly larger than left; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin and at midpoint of DLP; spermathecal gland placed posteriorly, orientated slightly to right-hand side; posterior wall with small tubercles, without outgrowths and sclerotization; base of second valvula straight or slightly curved; ventral wall membranous.

Distribution: Known from tropical Africa (Fig. 23).

Host plants: Species of this genus are known to feed on cocoa (Leston, 1970; Entwistle, 1977), as well as from some species of the family Annonaceae (Piart, 1977).

Included species

Bryocoropsis cotterelli China, 1929
Bryocoropsis kasaica Schouteden, 1942
Bryocoropsis laticollis Schumacher, 1917
Bryocoropsis laticollis var. *infuscata* Schouteden, 1942
Bryocoropsis soror Schouteden, 1935
Bryocoropsis vrijdaghi (Schouteden, 1942)

Discussion: The monophyly of the genus *Bryocoropsis* is doubtful, and externally its species are similar to those of *Sahlbergella*, *Distantiella*, *Platyngomiris*, *Pseudodoniella* and *Rhopaliceschatus*. Species of *Sahlbergella* and *Distantiella* differ from *Bryocoropsis* in the scutellum being divided into lower and upper parts (Fig. 12B) and the spermathecal gland being placed medially or to the left-hand side on the DLP (Figs 18R, 21P, R). *Pseudodoniella* and *Rhopaliceschatus* differ from *Bryocoropsis* in that the scutellum covers the base of the pronotum (as in Fig. 11F–H). *Platyngomiris* differs from *Bryocoropsis* in having only simple setae.

Bryocoropsis also shares features with *Boxia*, with both having brown and often spotted hemelytra (see discussion for *Boxia*).

We examined the types of all species of *Bryocoropsis*, except for the type species. One of us (A.N.N.), however, examined the holotype of *B. laticollis infuscata*, as well as specimens from the Royal Museum of Central Africa (Tervuren, Belgium) and American Museum of Natural History (New York, USA) identified as *B. laticollis*, but all of them are conspecific with either *B. soror* or *B. laticollis infuscata*. We retain the subspecies status of *B. laticollis infuscata*.

All species of *Bryocoropsis* are consistent with the original description of the genus and are very similar to each other, except for *B. soror*. This last species possesses a flattened scutellum, humeral angles of pronotum only slightly dilated, and the DLP with right-hand striated area larger than the left. In all other species the scutellum is distinctly swollen, the humeral angles of the pronotum are distinctly dilated, and the DLP has striated areas that are subequal in diameter, either side of the midline.

Our description of the male genitalia is based on dissections of *Bryocoropsis cotterelli*, *B. laticollis infuscata* and *B. soror*. Female genitalia were described from *B. kasaica*, *B. laticollis infuscata*, *B. soror* and *B. vrijdaghi*.

Chamus Distant

Figures 6, 10C, K, 11A, 14T–AE, 18K–O, 22

Chamus Distant, 1904a: 197 (gen. nov.; type species: *Chamus wealei* Distant, 1904 by monotypy); Kirkaldy, 1906: 134 (cat.); Reuter, 1910: 152 (cat.); Reuter and Poppius, 1911: 413 (descr.); Poppius, 1912: 176, 192, 193 (key to gen., descr., key to spp.); Bergroth, 1922: 57 (cat.); China, 1944: 174 (key to gen.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 41 (key to gen.); Carvalho, 1957: 144 (cat.); Odhiambo, 1962: 271, 272, 274 (disc., descr., key to spp.); Schuh, 1995: 527 (cat.); Schuh, 2002–2013 (cat.).

Chamopsis Reuter and Poppius, 1911: 415 (gen. nov.; type species: *Chamopsis conradti* Reuter & Poppius, 1911 by monotypy); Poppius, 1912: 176, 195 (key to gen., descr.); Bergroth, 1922: 57 (cat.); China, 1944: 174 (key to gen.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 40 (key to gen.); Carvalho, 1957: 144 (cat.); Odhiambo, 1962: 271, 282 (disc., descr.); Schuh, 1995: 527 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny), syn. nov., this work.

Parachamus Schouteden, 1946: 282 (gen. nov.; type species *Parachamus bellus* Distant, 1918 by monotypy); Villiers, 1952: 187 (descr.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 40 (key to gen.); Carvalho, 1957: 147

(cat.); Odhiambo, 1962: 271, 285 (disc., descr.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.), syn. nov., this work.

Diagnosis: Chamus is diagnosed by a number of unique characters, including: three frontal spines (Fig. 10K, fig. 4B in Namyatova *et al*., in press), presence of long flattened setae on ASI, presence of wrinkles on lateral side of head (fig. 6B in Namyatova *et al*., in press), and R + M very short, not reaching middle of corium. It can also be separated by: row of punctures on R + M and clavus present (as in fig. 12C, D in Namyatova *et al*., in press), distance between antennal fossa longer than antennal fossa diameter; calli separated (fig. 4B in Namyatova *et al*., in press), hemelytra widened posteriorly, membrane cell forming right angle (as in fig. 13B in Namyatova *et al*., in press), endosoma with semicircular or semioval spicule apically (Fig. 14T, X, AB).

*Description:*Male: Length 5–7.5 mm. COLORATION (Fig. 6). Ground colour varying from yellow to dark brown to black, appendages whitish yellow to yellow, sometimes with reddish tinge or pale brown areas; hemelytron often whitish yellow to yellow, transparent, with pale brown to dark brown markings, including large marking on posterior margin of corium, sometimes hemelytron mostly reddish or pale brown, not transparent. TEXTURE. Body mostly impunctate, only pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum, and rows on punctures on clavus and on R + M present (as in Fig. 11C, D in Namyatova *et al*., in press); head dorsally smooth or rugose, with wrinkles laterally (fig. 6B in Namyatova *et al*., in press); vertex with pair of tubercles anteriorly on depression delimiting neck and single depression between eyes; tubercles on ASI absent or present; semicircular depression between scutellum and mesoscutum present (Fig. 11A); pronotum impunctate, often with small tubercles (fig. 4B in Namyatova *et al*., in press), sometimes mostly smooth with tubercles only laterally; scutellum often with wrinkles and tubercles, rarely smooth (Fig. 11A); hemelytron often with tubercles at base of setae, sometimes smooth. VESTITURE. Dorsum, ASII–IV, legs and abdomen clothed with pale or dark long erect setae often longer than tibia width, sometimes those setae spine-like; legs regularly setose; hemelytra also with short flattened setae, sometimes only basally; pleura clothed with pale short simple setae; ASI clothed with dense long flattened setae; spinules on femora absent; spinules on tibia in rows (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum subequal or slightly longer then eye diameter (fig. 4B in Namyatova *et al*., in press); depression delimiting occipital region indistinct or rarely distinct; longitudinal depression on vertex present, short; eye often not stylate, sometimes substylate, not embedded into head (Fig. 10K, fig. 4B in Namyatova *et al*., in press), *c*. 0.2–0.25× as wide as head; distance between antennal fossa almost as long as or slightly longer than antennal fossa diameter; frons straight or concave, with three distinct outgrowths (Fig. 10K, fig. 4B in Namyatova *et al*., in press), sometimes middle outgrowth shorter than lateral; anterior view head *c*. 1.4–1.6× as wide as high (Fig. 10K); eye as long as or slightly longer than distance from eye to apex of clypeus; antennal fossa round, its diameter subequal to or slightly shorter than half of eye height (Fig. 10K), distinctly tuberculate (fig. 6B in Namyatova *et al*., in press), its inferior margin placed slightly above to or on the same level with inferior half of eye; base of clypeus placed on the same level with inferior margin of antennal fossa, delimited with depression; in lateral view head often almost flat, rarely convex dorsally; gula *c*. 1.5–2× as long as buccula. *Labium*. Length varying from slightly surpassing anterior margin of mesosternum to reaching middle of metasternum; LSI–II twice as long as wide, almost subequal in length; LSIII *c*. 1.5–2× as long as wide, slightly shorter than LSII, LSIV *c*. 3–5× as long as wide, *c*. 1.5–2× as long as LSIII. *Antenna*. Almost reaching apex of cuneus; ASI as long as, slightly longer or slightly shorter than head width, widened medially; ASII *c*. 1.6–2.0× as long as ASI, as long as or slightly longer than head and pronotum combined; ASIII *c*. 0.6–0.7× as long as ASII, ASIV *c*. 0.4–0.7× as long as ASIII; ASII–IV filiform. *Thorax*. Collar distinct, fused with calli, flat (fig. 4B in Namyatova *et al*., in press); calli distinctly separated, rounded, depression delimiting calli posteriorly indistinct distinct only laterally (fig. 4B in Namyatova *et al*., in press); humeral angles of pronotum rounded, not dilated (fig. 4B in Namyatova *et al*., in press), posterior part of pronotum sometimes with two protuberances (Fig. 10C); posterior margin of pronotum straight or sinuate (fig. 4B in Namyatova *et al*., in press); scutellum almost flat or slightly swollen anteriorly, without outgrowth, with wide medial depression, without ridge (Fig. 11A); metepimeron more or less enlarged, *c*. 2–3× as high as long, more or less angulate and subtriangular (as in Fig. 13C); metasternum extending to abdominal segment II in triangular outgrowth (fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margins convex; hemelytra broadened posteriorly; claval commissure *c*. 1.6–2× as long as scutellum, straight (as in fig. 11C in Namyatova *et al*., in press); R + M shortened, not reaching posterior margin of corium; medial fracture inclined towards midline; posterior margin of corium slightly or moderately raised, but without swelling; cuneus *c*. 1–1.8× as long as wide, as long as, shorter or slightly longer than pronotum, medial margin almost straight; membrane cell slightly to distinctly surpassing apex of cuneus, forming

almost right angle (as in fig. 13B in Namyatova *et al*., in press), as long as or longer than pronotum; auxiliary vein absent; distance from cell to apex of membrane 0.5–0.6× as long as cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, straight; foretibia shorter than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus subequal to or slightly longer than segment II, subequal to or slightly shorter than segment III; claw with apical half or third part curved; basal tooth on claw 2–3× as long as wide, concave or almost straight (Fig. 13J). *Genitalia* (Fig. 14, T-AE). Genital capsule at least slightly longer than wide, without outgrowth(s), its ventral wall not shortened anteriorly; left paramere *c*. 3.5–5× as long as right paramere, shape varying from almost straight to distinctly curved; sclerite around primary gonopore bowl-shaped, with short or long outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, distinctly shorter than phallotheca length, without coils, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowths or ridges; endosoma with oval or semioval dentate sclerite apically, and sometimes also with large field of small spicules.

Female: Length 5.5–8.5 mm. Similar to male, generally only slightly larger than males (Fig. 6). *Genitalia* (Fig. 18K–O). DLP often without sclerotized bands, sometimes with single band, with many striations, without sclerotizations; lateral oviducts placed in posterior half of DLP or at midpoint, equidistant between them and lateral margins of DLP; spermathecal gland often placed in posterior part of DLP, sometimes almost at midpoint; posterior wall of bursa copulatrix with small tubercles, without any sclerotizations; base of second valvula slightly concave; ventral wall membranous.

Distribution: Broadly distributed in central and southern Africa (Fig. 22).

Host plants: Chamus species are known from non-crop plants, such as *Alchornea* sp. (Euphorbiaceae), *Tetracera potatoria* (Dilleniaceae), *Erythrina* sp. (Fabaceae) (Odhiambo, 1962) and *Combretum* spp. (China, 1944; Odhiambo, 1962). *Chamus tuberculatus* was collected from guava (Odhiambo, 1962).

Included species

Chamus bellus Distant, 1918, **comb. rev.** {*Parachamus*}
Chamus conradsianus Schouteden, 1942
Chamus conradti (Reuter & Poppius, 1911), **comb. nov.** {*Chamopsis*}
Chamus incertus Reuter and Poppius, 1911
Chamus mefisto Reuter and Poppius, 1911
Chamus overlaeti Schouteden, 1942
Chamus reuteri Poppius, 1914
Chamus schroederi Poppius, 1912
Chamus tuberculatus Distant, 1918 **comb. nov.** {*Chamopsis*}
Chamus wealei Distant, 1914

Discussion: Chamus was placed in the subtribe Odoniellina *sensu* Schuh (2002–2013), but it is not closely related to the other genera previously assigned to that tribe. It possesses a number of autapomorphic characters and cannot be confused with any monaloniine genus (see above *Chamus* diagnosis).

Distant (1904a) described *Chamus* as possessing three long outgrowths on the frons that are directed upwardly. Reuter & Poppius (1911) described *Chamopsis* as having lateral outgrowths on the frons that are directed laterally. Schouteden (1946) described the monotypic genus *Parachamus* for *Chamus bellus*.

Odhiambo (1962) diagnosed these genera from each other. *Chamus* differs from *Chamopsis* by the following characters: lateral spines on head directed upwardly, hairs on ASII–IV at least twice as long as width of antennal segments, tarsal claw without prominent basal claw; whereas *Chamopsis* has: lateral spines on head directed outwards, hairs on head about as long as or a bit longer than width of antennal segments, tarsal claw with prominent basal tooth. *Parachamus* differs from the other two genera by: pronotum shiny, very sparsely pubescent, with two protuberances near basal lateral margins, calli on pronotum tuberculate, conical in shape, ASI with the broad area without setae, and foretibia without distinct spur.

Seven species have been assigned to *Chamus*, two species to *Chamopsis* and *Parachamus* is a monotypic genus. We have examined four *Chamus* species (*C. incertus*, *C. mefisto*, *C. overlaeti* and *C. schroederi*), three species of *Chamopsis* (*C. conradti* and *C. tuberculatus*, and one undescribed species) and *Parachamus bellus*. *Chamus* and *Chamopsis* differ in the direction of the frontal spines. The setae on ASII are generally longer in *Chamus*, although in *C. overlaeti* they are only slightly longer than the width of ASII. There is a prominent basal tooth in the pretarsal claw of all species of the above genera; however, it is often narrow and concave, except *Chamus mefisto* and *C. overlaeti*, where it is broader and straight. The male genitalia of *Chamopsis* are distinct having numerous minute spicules, which cover most of the endosoma, whereas in *Chamus* only large sclerotization is present.

Parachamus is distinguished from the other two genera by two protuberances on the pronotum (Fig. 10C). However, the other character, noted by Schouteden as diagnostic for *Parachamus*, also occurs in *Chamus* and *Chamopsis*; that is, the latter genera also have an area

on ASI without setae, which may be broader in some species than in others; the spur on the foretibia is present on *Parachamus bellus*, but a little shorter than in other genera; and a glabrous pronotum is also present in *C. incertus*. The male genitalia of *P. bellus* are very similar to those of *Chamopsis* species, although all the spines on the frons are directed upwards, as in *Chamus*.

As the monophyly of the group, containing *Chamus*, *Chamopsis* and *Parachamus*, is well defined and has high support on the cladogram and the relationships within this clade and diagnoses of those genera are obscure, we synonymize *Chamopsis* and *Parachamus* with *Chamus*.

Dimia Kerzhner

Figures 7, 15R–U, 18P, Q, 23

Dimia Kerzhner, 1988a: 779 (gen. nov.; type species: *Dimia inexpectata* Kerzhner, 1988 by monotypy); Kerzhner, 1988a: 779, 792 (key for gen.); Kerzhner, 1988b: 7 (descr., disc); Schuh, 1995: 509 (cat.); Kerzhner and Josifov, 1999: 14 (cat.); Schuh, 2002–2013 (cat.); Lin, 2006: 407 (disc.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Dimia differs from other monaloniine genera that have a row of punctures on the clavus and R + M, in the following characters: labium slightly surpassing anterior margin of metasternum; LSI–III more than three times as long as wide; ASII twice as long as head and pronotum combined; ASIII–IV slightly clavate; three shallow ridges on frons present (as in Fig. 10M); head flat in lateral view; anterior fossa tuberculate (as in Fig. 10L); distance between them longer than anterior fossa width; metepimeron subtriangular (as in Fig. 13C); calli separated (as in fig. 4B in Namyatova *et al*., in press); membrane cell distinctly elongate and acute (as in fig. 13A in Namyatova *et al*., in press); distance from cell to apex subequal to quarter of cell length; ductus seminis longer than phallotheca, with coils, forming wide tube (Fig. 15R).

Redescription: Male: Length 8–9 mm. Coloration (Fig. 7). Mainly brown or reddish brown, dorsum with dark brown markings, head, pronotum and scutellum also with whitish yellow, yellow, reddish or dark brown markings, labium and appendages mostly yellow to pale brown. Texture. Body without tubercles; head without flattened areas, scutellum with wrinkles; body mostly impunctate, but pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum and row of punctures on clavus and R + M present (as in fig. 11C, D in Namyatova *et al*., in press); punctures on depression delimiting calli posteriorly absent; semicircular depression between scutellum and mesoscutum absent; hemelytron smooth, without swelling posteriorly; femora with shallow tubercles at base of setae. Vestiture. Body clothed with pale or dark simple setae; head, pronotum, scutellum, appendages and abdomen with long and suberect setae; hemelytron mostly with semiadpressed short setae, with protuberance posteriorly with dense setae; thoracic pleura with rarely distributed short pale adpressed setae; femora without spinules; rows of spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). Structure. *Head*. Distance between eye and pronotum distinctly shorter than eye diameter; transverse depression delimiting occipital region very shallow; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head, *c*. 0.25× as wide as head; distance between antennal fossa *c*. 1.5× as long as antennal fossa diameter; frons distinctly swollen, with three very shallow longitudinal ridges (as in Fig. 10M), without outgrowth or longitudinal depression; anterior view of head *c*. 1.7–1.8× as wide as high; eye *c*. 3× as high as distance between eye and apex of clypeus; antennal fossa round, diameter subequal to third part of eye height, tuberculate; inferior margin of fossa placed above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with depression; head flat in lateral view; gula convex, *c*. 3× as long as buccula length. *Labium*. Long, slightly surpassing anterior margin of metasternum; each of LSI–II *c*. 4× as long as wide, subequal in length; LSIII *c*. 5× as long as wide, slightly longer than LSIII, LSIV *c*. 6–7× as long as wide, slightly longer than LSIII. *Antenna*. Slightly surpassing base of cuneus; ASI subequal to half of head width, widened medially (as in fig. 8D in Namyatova *et al*., in press); ASII *c*. 5× as long as ASI, twice as long as head and pronotum combined, slightly incrassate towards apex; ASIII *c*. 0.35× as long as ASII, slightly clavate with shallow swellings; ASIV subequal to half of ASIV, slightly clavate. *Thorax*. Collar distinct, fused with calli posteriorly, flat (as in fig. 4B in Namyatova *et al*., in press); calli separated, rounded (as in fig. 4B in Namyatova *et al*., in press); depression delimiting callosite region posteriorly indistinct medially; humeral angles of pronotum rounded, not dilated (as in fig. 4B in Namyatova *et al*., in press); posterior margin of pronotum slightly sinuate; scutellum slightly swollen, acute apically, without outgrowth or ridge, with wide medial depression; metepimeron enlarged, *c*. 1.5× as high as long, angulate, subtriangular (as in Fig. 13E); metasternum with medial projection to abdominal segment II (fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin straight; claval commissure twice as long as scutellum, straight (as in fig. 11C in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium with shallow oval swelling posteriorly; cuneus twice as long as wide,

slightly longer than pronotum, medial margin almost straight; membrane cell elongate, distinctly surpassing apex of scutellum, forming acute angle (as in fig. 13A in Namyatova *et al*., in press), twice as long as pronotum; auxiliary vein present, short; distance from cell to apex of membrane subequal to quarter of cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora weakly swollen apically, straight; foretibia shorter than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus subequal in length to segments II and III each (as in fig. 19A in Namyatova *et al*., in press); apical half of claw curved; basal tooth on claw more than twice as long as wide, straight (as in Fig. 13J). *Genitalia* (Fig. 15R–U). Genital capsule slightly longer than wide, without outgrowth(s), ventral wall not shortened anteriorly; left paramere distinctly r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore bowl-shaped, concave apically, without outgrowth(s); ductus seminis not sclerotized basally or apically, longer than phallotheca, with coils, forming wide tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal side, slightly tapering towards apex, rounded apically, without outgrowth(s) or ridge; endosoma with two large partly sclerotized areas and area of small spicules basally.

Female: Length 9–10 mm. Coloration, surface, vestiture and structure as in male (Fig. 7). *Genitalia* (Fig. 18P, Q). DLP without sclerotization, with distinct striations; lateral oviducts widely separated, placed near lateral margins and slightly below midline of DLP; spermathecal gland placed slightly below midpoint; posterior wall of bursa copulatrix with tubercles very indistinct, without sclerites or outgrowths; base of second valvula slightly concave; ventral wall of bursa copulatrix membranous.

Distribution: Restricted to Russian Far East, China, Taiwan (Fig. 23).

Host plants: Dimia inexpectata was recorded from *Quercus dentata* Thunb. (Fagaceae) (Kerzhner, 1988b).

Included species

Dimia formosana Lin, 2006
Dimia inexpectata Kerzhner, 1988

Discussion: Dimia is a very distinct genus, formerly included in the subtribe Monaloniina *sensu* Schuh. *Eupachypeltis* and *Poppiusia* also possess three ridges on frons (Fig. 10M), but they differ in ASII subequal to length of head and pronotum combined, filiform, ASIII–IV not clavate, labium slightly surpassing posterior margin of prosternum, LSI–II only twice as long as wide; membrane cell forming right angle (as in fig. 13B as in Namyatova *et al*., in press), distance from cell to apex of membrane subequal to half of cell length; ductus seminis shorter than phallotheca, without coils (Fig. 15R).

Pachypeltis is similar to *Dimia* in the following characters: the membrane possessing an acute cell (fig. 13A in Namyatova *et al*., in press), but differs in the frons smooth, without tubercles, ASIII–IV filiform, each of LSI–II at most three times as long as wide, labium reaching at most middle of mesosternum, metepimeron with two apices (as in Fig. 13D); and ductus seminis shorter than phallotheca length, without coils (Fig. 16T, X).

There are two species described in *Dimia* and we only examined the type species, *D. inexpectata*. Lin (2006) proposed that *Dimia formosana* is very close to *D. inexpectata* and differs slightly in: coloration, length of ASII and number of small spicules at the base of the endosoma.

Distantiella China

Figures 8, 14P–S, 18R, S, 23

Distantiella China, 1944: 188 (gen. nov.; type species *Sahlbergella theobroma* Distant, 1909 by original designation); China, 1944: 179 (key to gen.); Schouteden, 1945: 116 (note); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 145 (cat.); Lavabre, 1977a: 50, 53 (key to gen., descr.); Lotode, 1977: 188 (ecol.); Schmitz, 1987: 1 (disc.); Schuh, 1995: 528 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Distantiella belongs to the *Odoniella*-complex (see discussion for the tribe), and it differs from other genera of this group by: apex of ASII distinctly swollen (fig. 8E in Namyatova *et al*., in press); and ASIII–IV distinctly clavate (fig. 8F in Namyatova *et al*., in press); scutellum triangular (as in Fig. 11J), divided into lower and upper parts (as in Fig. 12B); frons with undivided or bifurcated outgrowth (as in Fig. 10F, fig. 4C in Namyatova *et al*., in press); pronotum and scutellum punctuate, bearing tumescences (Fig. 4C in Namyatova *et al*., in press); hemelytron with pale or dark flattened setae; hind tibiae densely setate with distinct tumescences.

Redescription: Male: Length 6–8.5 mm. Coloration (Fig. 8). Mostly dark brown with brown markings. Texture. Tubercles on vertex indistinct; flattened areas on vertex more or less distinct; ASII and hind tibia with tumescence medially; pronotum and scutellum covered with distinct punctures, collar with paired tubercles at sides; tubercles on pronotum and scutellum present, upraised (as in Fig. 11J); row of punctures on clavus and on R + M and punctures on depression delimiting calli posteriorly absent; striations on lateral margins of scutellum indistinct or present only

anteriorly; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Head, pronotum and scutellum clothed mostly with short simple adpressed pale setae, sometimes very rare, sometimes setae on head and anterior part of pronotum flattened; thoracic pleura with simple or flattened adpressed pale setae; hemelytron mostly with pale or dark flattened setae, cuneus and often posterior margin of corium with simple adpressed setae; ASI with adpressed short pale simple setae, ASII–IV with simple pale or dark suberect setae, some of them spine-like, shorter than width of hind tibia; legs with very dense dark setae, shorter than width of hind tibia; abdomen often clothed with short pale adpressed setae; black spinules on femora and tibiae not clear because of the dense setation. STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (as in Fig. 10F); occipital region not delimited with depression; longitudinal depression on vertex present, shorter than eye diameter; eye stylate, directed outwards, *c*. 0.15× as wide as head; distance between antennal fossa twice as long as antennal fossa width; frons distinctly swollen (as in Fig. 10F), with paired outgrowths (as in fig. 4C in Namyatova *et al*., in press), without longitudinal depression or ridges; anterior view of head *c*. 2.1× as wide as high; eye height as long as distance from eye to apex of clypeus; antennal fossa oval, its width *c*. 0.6× as long as eye height, not raised (as in fig. 3B in Namyatova *et al*., in press); inferior margin placed near inferior margin of eye; base of clypeus placed above inferior margin of eye, distinctly delimited basally; in lateral view head flat, gula shorter than buccula length, convex. *Labium*. Length reaching middle of metasternum; LSI *c*. 2× as long as wide; LSII *c*. 3× as long as wide, subequal to LSI; LSIII *c*. 3× as long as wide, subequal to LSII; LSIV *c*. 4× as long as wide, slightly longer than LSIII. *Antenna*. Slightly surpassing base of scutellum; ASI *c*. 1.5× as long as wide, subequal to quarter of head width, swollen basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 4× as long as ASI, *c*. 0.6× as long as head and pronotum combined, swollen apically; ASIII *c*. 0.6× as long as ASII, swollen apically; ASIV *c*. 0.8× as long as ASIII, clavate (as in fig. 8F in Namyatova *et al*., in press). *Thorax*. Collar not delimited posteriorly, flat (as in fig. 4C in Namyatova *et al*., in press); calli separated, flat (as in fig. 4C in Namyatova *et al*., in press); depression delimiting calli posteriorly absent; humeral angles of pronotum slightly dilated, not serrate (as in fig. 4C in Namyatova *et al*., in press); posterior margin of pronotum distinctly concave, forming right angles (as in Fig. 11J); scutellum swollen (as in Fig. 11J), not covering or rarely covering base of pronotum, triangular (as in Fig. 11J), divided into lower and upper parts (as in Fig. 12B), lower part obtuse apically, without outgrowth, ridge or longitudinal depression medially; metepimeron enlarged, *c*. 1.5× as long as wide, angulate (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Slightly tapering anteriorly; costal margins straight; claval commissure *c*. 0.2× as long as scutellum, straight; R + M distinct only anteriorly, sometimes also medially, not reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E in Namyatova *et al*., in press); cuneus *c*. 1.5× as long as wide, *c*. 0.4× as long as pronotum, medial margin almost straight (as in Fig. 13B); corium without swelling posteriorly; membrane distinctly surpassing apex of cuneus, forming acute angle, *c*. 0.7× as long as pronotum; auxiliary vein absent or very short; distance from cell to apex of membrane subequal to cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight; foretibia shorter than head and pronotum combined; tibia with distinct tumescences; segment I of hind tarsus as long as segment II and shorter than segment III; claw broadly rounded, basal tooth on claw more or less concave. *Genitalia* (Fig. 14R, S). Genital capsule slightly wider than long, without outgrowth, ventral wall not shortened anteriorly; left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore subtriangular, with anterior distinctly concave; without outgrowth(s); ductus seminis not sclerotized basally, with sclerotized ring around secondary gonopore, ductus seminis shorter than phallotheca with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca narrow wider basally, rounded apically, occupying half of dorsal side, without ridge or outgrowth; endosoma with sclerotized areas.

Female: Length 7.5–8.5 mm. Coloration, surface, vestiture and structure as in male, but females slightly larger than males (Fig. 8). *Genitalia* (Fig. 18R, S). DLP with medial sclerotized circle, *c*. 4× as long as wide, also with sclerotization along posterior margin; two large areas of striations present, contiguous; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin and at a halfway of DLP; spermathecal gland placed posteriorly, medially or on left-hand side; posterior wall with small tubercles, without outgrowth or sclerotization; base of second valvula with distinct swelling; ventral wall membranous.

Distribution: Distributed in Tropical Africa (Fig. 23).

Host plants: Distantiella is known to be a major pest of cocoa (Entwistle, 1977). It is also known from some other species of *Malvaceae* and *Citrus* sp. (Piart, 1977).

INCLUDED SPECIES

Distantiella collarti (Schouteden, 1935)
Distantiella theobroma (Distant, 1909)

Discussion: Species of *Distantiella* are very similar to each other externally. *Distantiella* is most similar to the genus *Sahlbergella*, and the latter genus differs in hind tibia regularly setate with tumescences (see discussion for the genus *Sahlbergella* for details).

EUCEROCORIS WESTWOOD

Eucerocoris Westwood, 1837: 21 (gen. nov.; type species *Eucerocoris nigriceps* Westwood, 1837 by monotypy); Signoret, 1858: 501 (note); Walker, 1873 (cat.); Atkinson, 1890a: 49 (cat.); Kirkaldy, 1906: 134 (list.); Reuter, 1910: 153 (cat.); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 39 (key to gen.); Carvalho, 1957: 132 (cat.); Odhiambo, 1962: 313 (descr., key to spp.); Odhiambo, 1965: 20 (descr., disc.); Carvalho, 1976: 54 (disc.); Cassis and Gross, 1995: 141 (cat.); Schuh, 1995: 509 (cat.); Schuh, 2002–2013 (cat.), rev. stat., this work.

Description: See Westwood (1837) for original description.

INCLUDED SPECIES

Eucerocoris nigriceps Westwood, 1937

Discussion: Westwood (1837) described *Eucerocoris* as a monotypic genus, from a single specimen without exact locality. Odhiambo (1962) erected *Rayieria* as a new genus, and included three species of *Eucerocoris* within it, and further divided species in the newly established subgenus *Eucerocoris* (*Ragwelellus*) and the nominotypical *Eucerocoris* (*Eucerocoris*). He stated that he examined the type specimen of the type species *Eucerocoris nigriceps* Westwood, 1837, preserved in the Hope Museum, University of Oxford. He reported the spine on the scutellum, which is absent in all other species included in this genus, but is characteristic for *Helopeltis* Signoret. On this basis, Odhiambo (1965) raised *Ragwelellus* to generic rank and described a new subgenus, *Ragwelellus* (*Narinellus*), where he placed all the species previously included in the subgenus *Eucerocoris* (*Eucerocoris*). He did not synonymize *Eucerocoris* with *Helopeltis*, but treated it as a monotypic genus.

Carvalho (1976) reported that the holotype of *E. nigriceps* was lost, and the specimen thought of as the holotype by Odhiambo (1965) was in fact a specimen of *Helopeltis bergrothi* Reuter, 1892. He also proposed to disregard *Eucerocoris* and to transfer all the species previously included within it to *Ragwelellus* and *Rayieria*. However, Schuh (1995) followed Odhiambo's (1965) opinion, and Cassis & Gross (1995) treated *Ragwelellus* as a synonym of *Eucerocoris*, and accepted Odhiambo's *Rayieria*.

According to the original description of *Eucerocoris nigriceps* the types of many species described in that paper were preserved in the Hope Museum ('Mus. Dom. Hope'). *Eucerocoris nigriceps* was reported to be preserved in 'Mus. nostr.', which, we suggest, should be translated as 'in author's own collection'. According to Zoe Simmons (pers. comm.), the curator of the collection of the Hope Museum, the specimen mentioned by Odhiambo (1965) and Carvalho (1976) is present in the Hope collection, and there is no other specimen that can be treated as the type of *E. nigriceps*.

We follow Carvalho's (1976) opinion that this specimen is not a type of *Eucerocoris*, as the spine on the scutellum is a very obvious character and would be unlikely to be overlooked. The specimen as depicted by Westwood (1837) has a single elongate cell, common for many groups of Bryocorinae, and has the overall elongate monaloniine body shape. It is not *Helopeltis*, because it does not have a scutellar spine, and the antennae in his illustration is almost twice as long as the body, which is not what is found in most monaloniine species, where they are much shorter, except for species included in *Eucerocoris*, *Ragwelellus* and *Helopeltis*. Based on this evaluation we regard the species described by Westwood as belonging to or being very close to *Ragwelellus*.

We also follow Odhiambo's (1965) treatment of *Eucerocoris* as a monotypic genus. From the literature it is best to assume that no one except Westwood observed the type specimen and all opinions about the systematic position of *Eucerocoris nigriceps* are not reliable, being based on the original short description and single illustration.

EUPACHYPELTIS POPPIUS

Figures 6, 15I–L, 19A, B, 22

Eupachypeltis Poppius, 1915: 79 (gen. nov.; type species: *Eupachypeltis pilosus* Poppius, 1915 by monotypy); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 39 (key); Carvalho, 1957: 133 (cat.); Schuh, 1995: 510 (cat.); Kerzhner and Josifov, 1999: 14 (cat.); Lin, 2000a: 119 (disc., key to spp.); Hu and Zheng, 2001: 415 (key to gen., key to spp.); Schuh, 2002–2013 (cat.).

Diagnosis: The main diagnostic characters of *Eupachypeltis* are: presence of punctures on clavus and R + M (as in fig. 11C, D in Namyatova *et al*., in press); presence of three tubercles on frons (as in Fig. 10B, M); head almost flat dorsally in lateral view; antennal fossa tuberculate (as in Fig. 10L); distance between antennal fossae longer than antennal fossa diameter; ASI swollen medially (as in fig. 9D in Namyatova *et al*., in press); ASII subequal to head and pronotum combined, filiform; labium slightly surpassing posterior margin of pronotum; LSI–II only twice as long as wide; metepimeron distinctly enlarged, subtriangular, twice

as long as wide (as in Fig. 13E); costal margins straight, corium not broadened posteriorly; membrane cell forming right angle (fig. 13B in Namyatova *et al*., in press); distance from cell to apex of membrane subequal to half of cell length; outgrowths on phallobase supporting ductus seminis very short; ductus seminis shorter than phallotheca length, without coils (Fig. 15I); DLP without sclerotized bands (Fig. 19A).

*Description:*Male: Body length 5.5–8 mm. COLORATION (Fig. 6). Body mainly whitish yellow to pale brown with pale brown to brown or reddish markings or areas; corium, embolium, cuneus and membrane semitransparent, corium often with pale brown to brown marking posteriorly. TEXTURE. Dorsum smooth; vertex without tubercles or flattened areas; pronotum and scutellum mostly impunctate, without tubercles or wrinkles, only pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum, and rows on punctures on clavus and on R + M present (as in fig. 12C, D in Namyatova *et al*., in press); punctures on depression delimiting calli posteriorly absent; semicircular depression between scutellum and mesoscutum present (as in Fig. 11A). VESTITURE. Body mostly clothed with suberect pale setae, often as long as or shorter than hind tibia width, setae on legs and abdomen sometimes twice as long as tibia width, not very dense; setae on thoracic pleura short and adpressed; spinules on femora absent; rows of spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE AND MEASUREMENTS. *Head*. Distance between eye and pronotum subequal to or slightly shorter than eye diameter; occipital region delimited with very shallow depression or almost not delimited; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head, *c*. 0.2–0.25× as wide as head; distance between antennal fossa as long as or slightly longer than antennal fossa diameter; frons swollen, with three longitudinal ridges (as in Fig. 10M), without longitudinal depression; anterior view of head *c*. 1.3–1.5× as wide as high; eye almost twice as long as distance from eye to apex of clypeus; antennal fossa round (as in fig. 3A in Namyatova *et al*., in press), its diameter subequal to third part of eye height, tuberculate (as in Fig. 10L, M), its inferior margin placed slightly above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with depression; in lateral view head mostly flat or slightly convex dorsally; gula *c*. 1.5× as long as buccula length, straight or slightly convex. *Labium*. Reaching or slightly surpassing anterior margin of mesosternum; LSI–II twice as long as wide, almost subequal in length; LSIII *c*. 1.5× as long as wide, slightly shorter than LSII, LSIV *c*. 3–4× as long as wide, *c*. 2–2.5× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 0.7–0.8× as long as head width, widened medially (as in fig. 8D in Namyatova *et al*., in press); ASII *c*. 2.5–3× as long as ASI, subequal to or slightly longer than head and pronotum combined length; ASIII *c*. 0.6× as long as ASII, ASIV subequal to half of ASIII; ASII–IV filiform. *Thorax*. Collar distinct, fused with calli posteriorly, almost flat; calli more or less separated from each other (as in fig. 5B in Namyatova *et al*., in press), rounded, depression delimited calli posteriorly distinct between calli; humeral angles of pronotum rounded, not dilated; posterior margin of pronotum straight or slightly sinuate; scutellum almost flat, acute apically, without outgrowth, ridge or medial depression; metepimeron enlarged twice as high as long, angulate, subtriangular (as in Fig. 13C); metasternum extending to abdominal segment II in triangular outgrowth (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margins of hemelytron subparallel; claval commissure almost twice as long as scutellum, straight; R + M distinct, reaching posterior margin of corium; medial fracture inclined towards midline; corium without swelling posteriorly; cuneus *c*. 1.5× as long as wide, slightly shorter than pronotum, its medial margin almost straight; membrane cell distinctly surpassing apex of scutellum, forming right angle, as long as or slightly longer than pronotum; auxiliary vein absent; distance from cell to apex of membrane slightly shorter than cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, straight; foretibia shorter than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus subequal to segment II and slightly shorter than segment III; apical half of claw curved; basal tooth on claw three times as long as wide, almost straight (as in Fig. 13J). *Genitalia* (Fig. 15I–L). Genital capsule slightly longer than wide, with swelling on left-hand side; ventral wall of genital capsule not shortened anteriorly, left paramere *c*. 3× as long as right paramere, almost straight; sclerite around primary gonopore suboval, with short outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, distinctly shorter than phallotheca length, without coils, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowths or ridge; endosoma without spicules.

Female: Body length 5.8–8 mm. Similar to male, but generally darker. Texture and vestiture as in male (Fig. 6). Structure as in male, but females generally larger. *Genitalia* (Fig. 19A, B). DLP without sclerotized bands and without striations or sclerites, lateral oviducts and spermathecal gland placed posteriorly, lateral oviducts proximal to each other; posterior wall of bursa copulatrix with small tubercles, without sclerites or outgrowths; base of second valvula distinctly swollen; ventral wall membranous.

Distribution: Known from China (Hainan), Taiwan, Indonesia (Kalimantan), Philippine Islands (Luzon) (Fig. 22).

Host plants: Unknown.

Included species

Eupachypeltis flavicornis Poppius, 1915
Eupachypeltis immanis Lin, 2000
Eupachypeltis pilosus Poppius, 1915
Eupachypeltis unicolor Hu and Zheng, 2001

Discussion: Eupachypeltis is closely related to *Poppiusia*; both have three ridges on the frons (as in Fig. 10M). They also share many external characters, such as: distance between antennal fossa distinctly longer than antennal fossa diameter, corium in males with straight outer margins, not broadened posteriorly, metepimeron subtriangular (as in Fig. 13C, E), and membrane cell forming right angle (as in fig. 13B in Namyatova *et al*., in press). External characters that separate these two genera are relatively minor. Representatives of *Poppiusia* are generally larger and can be separated by: head distinctly swollen in lateral view with distinct depression delimiting occipital region, and metepimeron *c*. 3–4× as long as wide (Fig. 13C). There are also differences in the genitalia; in *Poppiusia* outgrowths on the phallobase are elongate (Fig. 17I) and distinct sclerotized bands on DLP are present (Fig. 21I).

Dimia also possess three shallow ridges on the frons (as in Fig. 10M). See the discussion for *Dimia* for diagnostic differences between these two genera.

Four species are included in *Eupachypeltis*. We examined male and female syntypes of *E. flavicornis* Poppius and the female syntype and additional specimens of *E. pilosus* Poppius. Specimens of *E. pilosus* are generally larger and darker, and its corium has a brownish marking posteriorly. However, the male genitalia of those two species are the same. Two other species, *E. unicolor* Hu and Zheng 2001 and *E. immanis* Lin 2000, were described from Hainan (mainland China) and Taiwan, respectively (Lin, 2000; Hu & Zheng, 2001) and, according to the respective descriptions, both possess three ridges on the frons and are very close to the other described *Eupachypeltis* species.

Helopeltis Signoret

Figures 9, 12F, 13A, H, 15M–Q, 19C, D, 22

Helopeltis Signoret, 1858: 502 (gen. nov.; type species *Helopeltis antonii* Signoret, 1858 by monotypy); Walker, 1873: 165 (cat., syn.); Atkinson, 1890a: 51 (cat.); Atkinson, 1890b: 175 (descr.); Watt & Mann, 1898: 247 (bibliography, history, biology, etc.); Distant, 1904b: 439 (descr.); Kirkaldy, 1906: 134 (list.); Mann, 1907: 277 (descr., disc.); Reuter, 1910: 153 (cat.); Poppius, 1911: 39 (key to spp.); Poppius, 1912: 175 (key to gen., descr., key to spp.); Bergroth, 1922: 54 (list); Ghesquière, 1922: 281 (disc., key to spp.); China, 1944: 144 (key to gen.); Ghesquière & Carayon: 1948: 59 (note); Carayon & Delattre, 1948: 185 (note, key to spp.); Villiers, 1952: 191 (descr.); Carvalho, 1952: 59 (cat,); Carvalho, 1955: 38 (key to gen.); Carvalho, 1957: 133 (cat.); Schmitz, 1968: 1 (disc., descr., diag.; key to gen., key to spp.); Steyskal: 1973: 206 (correction); Lavabre, 1977a: 51 (descr., disc.); Lavabre, 1977b: 107 (note); Carvalho, 1981: 39 (key to gen.); Stonedahl, 1991: 465 (descr., diag., key to spp.); Cassis & Gross, 1995: 142 (cat.); Schuh, 1995: 511 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Aspicellus Costa, 1864: 146 (gen, nov.; type species *Aspicellus podagricus* A. Costa, 1864 by monotypy, synonymized by Walker, 1873: 165); Schuh, 1995: 512 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Helopeltis belongs to the *Monalonion*-complex (see discussion for tribe), and can be separated from other genera in this complex by: long, undivided spinelike projection on scutellum (Fig. 12F); antenna distinctly longer than body; femora curved (as in fig. 18A in Namyatova *et al*., in press); collar flat; base of clypeus delimited with depression; metepimeron with rounded or rectangular outgrowth (as in Fig. 13A); claw with apical tooth (as in fig. 10D in Namyatova & Cassis, 2013b); place of attachment of ductus seminis on phallobase only slightly to left of midline (Fig. 15M); DLP with two sclerotized bands (Fig. 19C).

*Redescription (partly based on Stonedahl, 1991):*Male: Body length 5–8 mm. Coloration (Fig. 9). Variable, from pale brown to dark brown or almost black, sometimes reddish, often with paler or darker markings. Texture. Body mostly smooth, without punctures and tubercles; vertex without flattened areas; semicircular depression between scutellum and mesoscutum absent; striations on scutellum laterally absent; only small depression on anterior angle of pronotum present (as in fig. 9H in Namyatova & Cassis, 2013b). Vestiture. Setae on dorsum and thoracic pleura absent; very short, pale or dark simple suberect setae present on clypeus, labium, antenna, apices of femora, tibiae, tarsi, genital segment and often on scutellar process; ASI sometimes almost without setae; setae on clypeus sometimes flattened; tibiae regularly setose; small black spinules on femora absent, spinules on tibia apically absent or present. Structure. *Head*. Distance between eye and pronotum slightly shorter or subequal to eye diameter (as in Fig. 10J); occipital region delimited with shallow depression; longitudinal depression distinct, as long as or longer than eye diameter, sometimes extending on frons; eyes not stylate, in line with contour of head, *c*. 0.2× as long as head width

(as in Fig. 10J); distance between antennal fossae subequal or slightly longer than antennal fossa diameter; frons straight, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.6–1.9× wide as high; eye height *c*. 1–2× as long as distance between eye and apex of clypeus; antennal fossa oval, only slightly shorter than eye height, not raised, inferior margin placed above inferior margin of eye; base of clypeus placed slightly below than or near inferior margin of antennal fossa delimited with depression; head swollen or almost flat in lateral view; gula *c*. 1.5–2.5× as long as buccula, convex. *Labium*. Length varying from reaching posterior margin of mesosternum to reaching abdominal LSII; LSI *c*. 3–4× as long as wide; LSII *c*. 4–6× as long as wide, subequal to or slightly longer than LSI; LSIII *c*. 3–6× subequal to or slightly longer than LSII; LSIV *c*. 5–8× as long as wide, *c*. 1.2–1.5× as long as segment III. *Antenna*. Twice as long as body, rarely only 1.5× as long as body (*H. cinchonae*); ASI *c*. 2–2.5× as long as head width, rarely subequal to head width (*H. cinchonae*), swollen apically (as in fig. 8I in Namyatova *et al*., in press); ASII *c*. 1.6–3.5× as long as ASI, *c*. 2.2–3.2× as long as head and pronotum combined; AS III *c*. 0.7–1× as long as ASII; ASIV *c*. 0.3–0.5× as long as ASIII, ASII–IV filiform. *Thorax*. Collar flat, delimited posteriorly; calli separated (as in Fig. 10J), flat, almost indistinct; depression delimiting calli posteriorly absent; humeral angles of pronotum rounded, not dilated (as in Fig. 10J); posterior margin of pronotum straight or concave; scutellum swollen, with elongate spine-like process with expanded apex (Fig. 12F); scutellum distinctly rounded apically, without ridge or medial depression; metepimeron narrow, *c*. 3–4× as high as long, rounded or with small subrectangular outgrowth (Fig. 13A); metasternum rounded posteriorly, without medial projection on to abdominal segment II (fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin straight; hemelytra tapering posteriorly; margins of claval commissure *c*. 3× as long as scutellum, curved; R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M; corium without swelling posteriorly; cuneus *c*. 4–7× as long as wide, *c*. 1.2–1.4× as long as pronotum, medial margin distinctly concave (as in fig. 13C in Namyatova *et al*., in press); membrane cell *c*. 1.6–3× as long as pronotum, rounded or acute apically; auxiliary vein absent or short present; distance between cell and apex of membrane *c*. 0.2–0.3× as long as cell. *Legs*. Forecoxae separated (as in fig. 17B in Namyatova *et al*., in press); femora swollen apically, with additional swelling medially, distinctly curved (Fig. 13H); foretibia longer than head and pronotum combined; swellings on tibiae absent; segment I of hind tarsus distinctly longer than segments II and III each, segment II slightly shorter than segment III; claw broadly rounded, tooth subdivided into basal and subapical parts (Fig. 13L). *Genitalia* (Fig. 15M–Q). Genital capsule slightly longer than wide, without outgrowth(s); ventral margin of genital capsule shortened anteriorly; left paramere r-shaped or only slightly curved, *c*. 3× as long as right paramere; phallobase sclerite of primary gonopore subtriangular, often with outgrowth in front of ductus seminis attachment place; ductus seminis longer than phallotheca length, with coils, forming wide tube, without sclerotization basally or apically, attached to phallobase on left-hand side or almost medially; sclerotized part of phallotheca broad occupying entire dorsal side, rounded apically, without outgrowth(s) or ridges; endosoma usually with lobal sclerite and fields of small spicules, sometimes endosoma without sclerotization (see also illustrations of Stonedahl, 1991).

Female: Body length 6–9 mm. Similar to male, but coloration sometimes paler and body larger (Fig. 9). *Genitalia* (Fig. 19C, D). DLP mostly membranous with two sclerotized bands, sometimes fused; DLP often with medial ridge and sclerotization around it, sometimes without ridge (*H. cinchonae*); striations absent or present only at base of lateral oviducts; lateral oviducts attached at halfway of DLP, removed from each other, placed close to lateral margins of DLP; spermathecal gland placed in posterior half, slightly below midline or close to posterior margin, not shifted right or left; posterior wall of bursa copulatrix covered with small tubercles and with pair of spinose lobes; base of second valvula with bifurcate outgrowth or straight (*H. cinchonae*); posterior wall of bursa copulatrix membranous, not bearing sclerites around vulva (see also illustrations from Stonedahl, 1991).

Distribution: Widely distributed in South-East Asia, Pacific Islands, Australia (Fig. 22).

Host plants: The host plants are known for many species of *Helopeltis*; some *Helopeltis* species are serious pests of cocoa, tea and cashew (see Stonedahl, 1991 for details).

Included species

Helopeltis antonii Signoret, 1858
Helopeltis bakeri Poppius, 1915
Helopeltis bradyi Waterhouse, 1886
Helopeltis cinchonae Mann, 1907
Helopeltis clavifer (Walker, 1871)
Helopeltis collaris Stål, 1871
Helopeltis cuneata Distant, 1903
Helopeltis fasciaticollis Poppius, 1915
Helopeltis insularis Kirkaldy, 1902
Helopeltis obscuratus Poppius 1915

Helopeltis pellucida Stål, 1871
Helopeltis pernicalis Stonedahl, Malipatil and Houston, 1995
Helopeltis podagricus (Costa, 1864)
Helopeltis sulawesi Stonedahl, 1991
Helopeltis sumatranus Roepke, 1916
Helopeltis theivora Waterhouse, 1886

Discussion: Helopeltis is one of the more species-rich genera in the tribe, previously included in the subtribe Monaloniina *sensu* Schuh. We examined nine described species.

Stonedahl (1991) subdivided all *Helopeltis* species, except *H cinchonae*, into two groups, based on the structure of the genital chamber. We did not evaluate these groups and verification of Stonedahl's division is a matter for further research and infrageneric phylogenetic analysis.

Helopeltis cinchonae is an enigmatic species, as it possesses: shortened ASI, only slightly longer than head width, very simple DLP without medial sclerotized ridge, and base of second valvula straight. In contrast, in all other *Helopeltis* species examined, the ASI is distinctly longer than the head and pronotum combined, DLP has a medial sclerotized ridge, and the base of the second valvula has a bifurcate outgrowth. The last character was not discussed by Stonedahl (1991) and also occurs in *Monalonion* and *Schuhirandella*.

Stonedahl (1991) noted that the subgenus *Ragwelellus* (*Narinellus*) is closely related to the subgenus *Helopeltis* based on the DLP bearing a medial ridge and sclerites, and that as a consequence *Ragwelellus* and *Helopeltis* could be non-monophyletic. Our investigations indicate that the sclerotized ridge is present only in *Ragwelellus suspectus* (Fig. 21K), whereas all species of *Ragwelellus* (*Narinellus*) examined are lacking this ridge (Fig. 21G, N). Stonedahl also noted that 'those two subgenera also have unbroken, ribbonlike sclerotized rings that fully encircle the genital chamber'. However, in all species of *Ragwelellus* (*Narinellus*) that we examined, the sclerotized circle, if present, is broken posteriorly and there are no sclerotized rings (Fig. 21G, N). As a consequence we conclude that a close relationship between these two subgenera is not well supported. See also discussion for *Ragwelellus* for further notes on this genus.

Also see discussion of *Afropeltis* for notes on its relationships with *Helopeltis*.

Lycidocoris Reuter and Poppius

Figures 7, 10D, 15V–AC, 19E–G, J, K, 23

Lycidocoris Reuter & Poppius, 1911: 409 (gen. nov.; type species: *Lycidocoris mimeticus* Reuter & Poppius, 1911 by monotypy); Poppius, 1912: 175, 182 (key to gen., descr.); Bergroth, 1922: 53 (cat.); Schouteden, 1942a: 1, 3 (disc., key to spp.); China, 1944: 174 (key to gen.); Schouteden, 1945: 117 (note); Villiers, 1952: 188 (descr.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 40 (key to gen.); Carvalho, 1957: 145 (cat.); Odhiambo, 1962: 287, 288 (descry., key to spp.); Schuh, 1995: 528 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Pantilioforma Schumacher, 1917: 447 (gen. nov.; type species *Pantilioforma impressopunctata* Schumacher, 1917 by monotypy); Bergroth, 1922: 53 (cat.); China, 1944: 173, 179, 180 (key to gen., disc., key to spp.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 40 (key to gen.); Schouteden, 1946: 274 (note); Carvalho, 1957: 147 (cat.); Odhiambo, 1962: 297 (descr.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.), syn. nov., this work.

Pantiliomorfa Mayné & Ghesquière, 1934: 25 (error pro *Pantilioforma* Schumacher, 1917).

Ealincola Schouteden, 1942a: 4 (gen. nov.; type species *Pantilioforma modesta* Distant, 1918 by original designation); China, 1944: 172, 179 (syn., disc.); Schouteden, 1946: 275 (note); Carvalho, 1957: 147 (cat.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Lycidocoris is diagnosed by the following characters: presence of row of punctures on clavus and R + M (as in fig. 11C, D in Namyatova *et al*., in press); antennal fossa oval, subequal half of eye height (as in fig. 3B in Namyatova *et al*., in press); ASII incrassate apically; ASIII and IV clavate, ASIV subequal to quarter of ASIII; eyes not stylate; calli flat (as in Fig. 10D); pronotum and scutellum punctuate (Fig. 10D); claval commissure subequal to scutellum length (Fig. 10D); membrane cell short, forming right angle (as in fig. 13B in Namyatova *et al*., in press), distance between cell and apex of membrane subequal to cell; phallotheca with outgrowth from left-hand side, wide basally and distinctly tapering towards apex (Fig. 15V, Z).

*Redescription:*Male: Body length 8–12 mm. Coloration (Fig. 7). Main coloration yellow, reddish, brown or reddish brown, with dark brown markings; legs whitish yellow or mostly or entirely dark brown; abdomen pale brown or reddish, sometimes with dark brown areas. Texture. Body without tubercles; flattened areas on head absent or present; pronotum and scutellum punctate, without wrinkles; pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum and row of punctures on clavus and R + M present; punctures on depression delimiting calli posteriorly absent; semicircular depression between scutellum and mesoscutum absent; hemelytron rugose, without swelling posteriorly. Vestiture. Body clothed with dark or pale simple setae, usually dense; head, pronotum, appendages and abdomen with suberect setae, usually short; setae on abdomen and legs longer than width of hind tibia; setae

on scutellum and hemelytron short and adpressed; setae on thoracic pleura suberect, short and rare; tibiae regularly setose; spinules on femora apically present or absent; rows of black spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum absent or distinctly shorter than eye diameter (Fig. 10D); occipital region not delimited with depression; longitudinal depression on vertex absent or very short; eyes not stylate, in line with contour of head, *c*. 0.2–0.25× as wide as head; distance between antennal fossae as long as or slightly longer than antennal fossa diameter; frons distinctly swollen (Fig. 10D), without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.5–1.8× as wide as high; eye 1.5–2× as high as distance between eye and apex of clypeus; antennal fossa oval, diameter subequal to half of eye height, not raised (as in fig. 3B in Namyatova *et al*., in press); inferior margin of fossa placed slightly above inferior margin of eye; base of clypeus placed near inferior half of eye, delimited with distinct or shallow depression; head flat in lateral view; gula as long as or slightly longer than buccula length, almost straight or convex. *Labium*. Length varying from almost reaching middle of mesosternum to reaching posterior margin of mesosternum; LSI *c*. 2–3× as long as wide; LSII *c*. 2–4× as long as wide, almost subequal or slightly longer than LSI; LSIII *c*. 1.5–3× as long as wide, slightly shorter than LSII; LSIV *c*. 3–5× as long as wide, *c*. 1.5–2× as long as LSIII. *Antenna*. Almost reaching base of clypeus; ASI *c*. 0.3–0.6× as long as head width, *c*. 2–4× as long as wide, widened basally; ASII *c*. 4–6× as long as ASI, *c*. 0.9–1.3× as long as head and pronotum combined, incrassate towards apex; ASIII *c*. 0.6–0.7× as long as ASII, distinctly clavate; ASIV *c*. 0.2–0.3× as long as ASIII, clavate. *Thorax*. Collar distinctly delimited or fused with callosite region posteriorly, flat or upraised (Fig. 10D); calli separated, flat; depression delimiting callosite region posteriorly distinct medially, distinct laterally and distinct or indistinct medially (Fig. 10D); humeral angles of pronotum rounded, not dilated (Fig. 10D); posterior margin of pronotum straight or slightly concave (Fig. 10D); scutellum flat or slightly swollen, slightly rounded apically, without outgrowth, ridge or medial depression; metepimeron enlarged twice as high as long, angulate, with two apices (as in Fig. 13D); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight or slightly rounded, hemelytra not widened or rounded; margins of claval commissure *c*. 0.6–0.8× as long as scutellum, straight; R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium without swelling posteriorly; cuneus *c*. 0.7–1× as long as wide, *c*. 0.6–0.8× as long as pronotum, its medial margin straight; membrane cell distinctly surpassing apex of cuneus, forming right angle, almost subequal to or slightly shorter than pronotum (as in fig. 13B in Namyatova *et al*., in press), auxiliary vein short or absent; distance from cell to apex subequal to cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, straight; foretibia shorter than head and pronotum combined; swellings on tibiae absent; segments of hind tarsus subequal on length or segment III slightly longer than each of segments I and III (as in fig. 19A in Namyatova *et al*., in press); apical third part of claw curved; basal tooth on claw elongate and concave (as in Fig. 13K). *Genitalia* (Fig. 15, V-AC). Genital capsule as long as wide or slightly longer than wide, without outgrowth(s), its ventral side not shortened anteriorly; left paramere distinctly r-shaped or only slightly curved, *c*. 4–5× as long as right paramere; phallobase sclerite of primary gonopore subtriangular or suboval, rounded apically, without outgrowth(s); ductus seminis not sclerotized basally or apically, shorter than phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal side, acute apically, with outgrowth on left-hand side, without ridge; endosoma with long spicule, sometimes also with elongate area of small spicules; sometimes without any sclerotization.

Female: Body length 9–14 mm. Coloration, surface and vestiture as in male (Fig. 7). Structure similar to male, but females generally larger. *Genitalia* (Fig. 19E–G, J, K). DLP with sclerotized bands, sometimes covered with membrane, with striations, sometimes with distinct membranous outgrowth medially, without additional sclerites; lateral oviducts widely separated or close to each other, placed in posterior part or at halfway of DLP, near lateral margins or at distance from them; spermathecal gland placed near posterior margin of DLP, centrally; posterior wall of bursa copulatrix with small tubercles, with or without pair of depressions anteriorly; base of second valvula slightly concave; ventral wall of bursa copulatrix membranous.

Distribution: Tropical Africa (Fig. 23).

Host plants: The genus was collected from different species of the family Rubiaceae, including *Coffea arabica* L. (coffee) and *Cinchona* sp. (quina) (Distant, 1918; Mayné & Ghesquière, 1934; China, 1944; Odhiambo, 1962).

INCLUDED SPECIES

Lycidocoris crinatus Odhiambo, 1962
Lycidocoris ghanaensis Odhiambo, 1962

Lycidocoris impressopunctatus (Schumacher, 1917) **comb. nov.** {*Pantilioforma*}
Lycidocoris infulatus Odhiambo, 1962
Lycidocoris mimeticus Reuter and Poppius, 1911
Lycidocoris mimeticus var. *dispar* Shouteden, 1942
Lycidocoris mimeticus var. *impictus* Shouteden, 1942
Lycidocoris mimeticus var. *lineatus* Schouteden. 1942
Lycidocoris mimeticus var. *minor* Schouteden, 1942
Lycidocoris mimeticus var. *soror* Schouteden, 1942
Lycidocoris mimeticus var. *uniformis* Schouteden, 1942
Lycidocoris mimeticus var. *vittatus* Schouteden, 1942
Lycidocoris modestus Distant, 1918 **rev. stat.** {*Pantilioforma*}
Lycidocoris simulans Odhiambo, 1962
Lycidocoris thoracicus Distant, 1918 **rev. stat.** {*Pantilioforma*}
Lycidocoris tumidus Odhiambo, 1962

Discussion: Lycidocoris is a distinct and highly autapomorphic genus, within those genera that possess a row of punctures on the clavus and R + M (as in fig. 11C, D in Namyatova *et al*., in press). It is closely allied to *Villiersicoris*, as they both possess: punctate pronotum, claval commissure subequal to scutellum length; ASII incrassate towards apex and ASIII–IV clavate; membrane cell forming right angle, and sclerotized part of phallotheca wide basally and distinctly tapering apically (Figs 15V, Z, 17A, D). *Villiersicoris* differs in: eyes stylate, calli distinctly swollen, ASIV only slightly shorter than ASIII, scutellum impunctate and phallotheca smooth, without an outgrowth on left-hand side (Fig. 17A, D).

One of us (A.N.N.) has examined the type specimen of the type species, *L. mimeticus*, and numerous specimens now included in the genus. We have the digital images of the types of all other species. All of them are similar externally, with the same orange coloration, with dark brown appendages, and most of them have a dark brown longitudinal stripe on the pronotum and scutellum, and the collar is distinctly delimited posteriorly. The type of *L. uniformis* does not have a stripe on the pronotum and scutellum and one of us (A.N.N.) also has observed a specimen of an undescribed species, which possesses two stripes and raised collar, which is unique within the genus.

One of us (A.N.N.) has also examined two of the three species previously placed in *Pantilioforma*: *L. modesta* and *L. thoracica*. They are very similar to each other, more so than to the other *Lycidocoris* species, as they possess: similar coloration without dark brown stripes and with legs whitish yellow, and collar not delimited or only indistinctly delimited posteriorly. In contrast, all species of *Lycidocoris* possess: appendages mostly dark brown to black and collar distinctly delimited posteriorly. *Lycidocoris modesta* has the head removed from the pronotum as in other species of *Lycidocoris*, whereas it is very close to the pronotum in *L. thoracicus*. In addition, *P. thoracicus* and *P. mimeticus* have an endosomal spicule, whereas in *P. modesta* the endosoma is entirely membranous. We could not locate the type species of *Pantilioforma*, *P. impressopunctata*. However, according to the description, it has similar antenna with ASII incrassate and ASIII–IV clavate, and a punctate pronotum and scutellum. It also has the same coloration as *L. thoracica*, mostly brownish with red antenna and yellow legs. In contrast to the latter species, *L. impressopunctata* also has a 'neck', which is absent in *L. thoracica*, but is present in all *Lycidocoris*, including *L. modesta*, with the collar distinctly delimited posteriorly, which is common for most *Lycidocoris* species. Based on this we synonymize *Pantilioforma* with *Lycidocoris*.

There are eight varieties described for *Lycidocoris mimeticus*. We did not have an opportunity to examine all of them, and thus we treat them as separate pending revision of the genus.

Mansoniella Poppius

Figures 6, 10A, 16A–H, 19H, I, L, M, 22

Mansoniella Poppius, 1915: 77 (gen. nov.; type species: *Mansoniella nitida* Poppius, 1915 by monotypy); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 40 (key); Carvalho, 1957: 137 (catalogue); Carvalho, 1981: 41 (descry., disc.); Schuh, 1995: 517 (cat.); Lin, 2000b: 1 (disc., key to spp.), Lin, 2001: 377 (disc., key to spp.); Hu & Zheng, 2001: 415, 420 (key to gen., key to spp.); Lin, 2002 (disc., key to spp.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Mansoniella can be separated from other genera with rows of punctures on clavus and R + M by: ASI swollen apically (fig. 8C in Namyatova *et al*., in press), its length subequal to head diameter. It also can be recognized by hemelytron semitransparent with reddish, pale brown or dark brown marking on corium posteriorly; distance between eye and pronotum slightly longer than eye diameter; frons distinctly swollen (Fig. 10A); distance between antennal fossa subequal to antennal fossa diameter; gula *c*. 1.5–2× as long as buccula; LSIV *c*. 1.5–2× as long as LSIII; calli fused (Fig. 10A); pronotum almost without setae; depression delimiting calli posteriorly distinct medially, bearing pair of punctures (Fig. 10A); metasternum extending to abdominal segment II in triangular outgrowth (fig. 17A in Namyatova *et al*., in press); posterior part of corium broadened; membrane cell forming right angle (as in fig. 13B in Namyatova *et al*., in press); auxiliary vein on membrane absent; coils on ductus seminis

distinct, forming narrow tube; outgrowths on phallobase supporting ductus seminis very short or absent (Fig. 16A, E), and posterior wall of bursa copulatrix with small tubercles (Fig. 19I, M).

*Redescription:*Male: Body length 5.4–8.8 mm. COLORATION (Fig. 6). *Head*. Ground colour mostly yellow to pale brown, with reddish or brown marking on hemelytron, dorsum, sides and appendages often with reddish or brown markings. TEXTURE. Body smooth; head without tubercles or flattened areas; pronotum and scutellum mostly impunctate, without tubercles or wrinkles, only pair of punctures on depression delimiting calli and between mesoscutum and scutellum present (Fig. 10A); striations on lateral margin of scutellum, rows of punctures on clavus and on R + M present (as in fig. 11C, D in Namyatova *et al*., in press); hemelytron without swelling posteriorly; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with pale short simple setae, those setae very rare or absent on head, pronotum and scutellum, dense and adpressed on hemelytron, setae on appendages dense and suberect, sometimes slightly longer than hind tibia length; setae on abdomen suberect, of varying length; black spinules on femora absent; spinules on tibia in rows (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum slightly longer than or subequal to eye diameter (Fig. 10A); occipital region delimited with transverse depression; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head, *c*. 0.25–0.33× as wide as head; distance between antennal fossa almost subequal to or slightly longer than antennal fossa diameter; frons distinctly swollen (Fig. 10A), without swellings or outgrowths, without longitudinal depression; anterior view of head *c*. 1.2–1.3× as wide as high; eye almost twice as long as distance between eye and apex of clypeus; antennal fossa round, diameter subequal to third part of eye height (as in fig. 3A in Namyatova *et al*., in press), only slightly raised, its inferior margin placed slightly above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with depression; in lateral view head distinctly bulged dorsally; gula *c*. 1.5–2× as long as buccula, straight. *Labium*. Reaching middle of prosternum, sometimes slightly surpassing anterior margin of metasternum; LSI–II twice as long as wide, subequal in length; LSIII *c*. 1.5–2× as long as wide, subequal to or slightly shorter than LSII; LSIV *c*. 3–5× as long as wide, *c*. 1.5–2× as long as LSIII. *Antenna*. Reaching apex of cuneus; ASI subequal to or slightly shorter head width, swollen apically (fig. 8C in Namyatova *et al*., in press); ASII *c*. 2–3× as long as ASI, subequal to or slightly longer than head and pronotum combined; ASIII slightly shorter than ASII; ASIV *c*. 0.3–0.4× as long as ASIII; ASII–IV filiform. *Thorax*. Collar distinct, fused with calli posteriorly, upraised; calli fused with each other, distinctly separated posteriorly by depression (Fig. 10A); humeral angles of pronotum rounded, not dilated (Fig. 10A); posterior margin of pronotum straight or slightly concave or sinuate; scutellum almost flat, acute apically, without outgrowth, ridge or medial depression; metepimeron enlarged, *c*. 3–4× as high as long, rounded or angulate and subtriangular; metasternum extending to the abdominal segment II in triangular outgrowth (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margins of hemelytra convex near posterior margin of corium, hemelytra widened posteriorly; claval commissure twice as long as scutellum, straight; R + M distinct, reaching posterior margin of corium; medial fracture inclined towards midline; corium without swelling posteriorly; cuneus *c*. 2–2.5× as long as wide, as long as or slightly shorter than pronotum, medial margin almost straight; membrane cell slightly surpassing apex of scutellum, forming right angle (as in fig. 13B in Namyatova *et al*., in press), slightly longer than pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 1.5× as short as length of membrane cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); fore- and middle femora slightly swollen apically, hind femur distinctly swollen apically; femora straight or only indistinctly curved; tibiae without swellings; foretibia shorter than head and pronotum combined; segment I of hind tarsus slightly longer than segment II, and subequal to or slightly shorter than segment III (as in fig. 19A in Namyatova *et al*., in press); most part of claw straight, apical third part curved; basal tooth on claw more than twice as long as wide, concave (as in Fig. 13K). *Genitalia* (Fig. 16A–H). Genital capsule as wide as or wider than long, without any outgrowths; left paramere three times as long as right paramere, distinctly r-shaped; sclerite around primary gonopore heart-shaped or bowl-shaped, sometimes with short outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, distinctly shorter than phallotheca length, with coils forming narrow tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowth or ridge; endosoma with or without spicules at base, areas of small spicules absent.

Female: Body length 5.7–9.4 mm. Coloration, surface and vestiture as in male (Fig. 6). Structure similar to male, eyes slightly larger, *c*. 0.2–0.33× as wide as head. *Genitalia* (Fig. 19H, I, L, M). DLP with one or two sclerotized bands; membrane encircled by the inner sclerotized band striated, sometimes with small sclerites; lateral oviducts placed close to each other, near posterior margin, almost medially; spermathecal gland

placed in around midpoint of DLP or slightly above it; posterior wall with small tubercles, sometimes they absent apically, without any sclerotization; base of second valvula straight or concave; ventral wall membranous.

Distribution: Known from South-East Asia, mostly from China, Taiwan, Vietnam. *Mansoniella minuta* was described from Papua New Guinea (Fig. 22).

Host plants: The genus has been recoded from *Liquidambar formosana* Hance (Altingiaceae), *Cinnamomum camphora* (L.) J.Presl. (Lauraceae) and *Sassafras tzumu* Hemsl. (Lauraceae) (Zheng & Liu, 1992; Lin, 2001, 2002).

Included species

Mansoniella annulata Hu and Zheng, 1999
Mansoniella cervivirga Lin, 2000
Mansoniella cinnamomi (Zheng & Liu, 1992)
Mansoniella cristata Hu and Zheng, 1999
Mansoniella flava Hu and Zheng, 1999
Mansoniella formosana Lin, 2002
Mansoniella juglandis Hu and Zheng, 1999
Mansoniella kungi Lin, 2001
Mansoniella minuta Carvalho, 1981
Mansoniella nitida Poppius, 1915
Mansoniella rosacea Hu and Zheng, 1999
Mansoniella rubida Hu and Zheng, 1999
Mansoniella sassafri (Zheng & Liu, 1992)
Mansoniella shihfanae Lin, 2000
Mansoniella wuyishana Lin, 2002
Mansoniella yafanae Lin, 2000
Mansoniella wangi (Zheng & Li, 1992)

Discussion: Mansoniella is a distinct genus, whose main diagnostic characters is the ASI subequal to the head width and widened apically (fig. 8C in Namyatova *et al*., in press). It is most closely related to *Arculanus* (see also discussion for *Arculanus*).

Mansoniella is also similar to *Pararculanus* in the following characters: distance between antennal fossa subequal to antennal fossa diameter; swollen frons (Fig. 10A); long gula; and ASI subequal the head width, but the former genus can be separated by the ASI swollen medially (as in fig. 9D in Namyatova *et al*., in press); corium straight, membrane cell forming acute angle (as in Fig. 13A in Namyatova *et al*., in press), depression delimiting calli without pair of punctures, coils on ductus seminis indistinct, outgrowths on phallobase supporting ductus seminis long (Fig. 16AB, AF), and posterior wall of bursa copulatrix without small tubercles (Fig. 20P, R).

We examined only six of the 17 described *Mansoniella* species. However, there are also detailed original descriptions for *Mansoniella cervivirga*, *M. cristata*, *M. formosana*, *M. kungi*, *M. rosacea*, *M. shihfanae*, *M. wuyishana*, *M. yafanae* and *M. wangi*, and on our reading of these descriptions, they are all very similar to the species that we examined.

Hu & Zheng (2001) described *Pachypeltis cinnamomi* and *P. sassafri* and Zheng & Li (1992) described *P. wangi*. Lin (2002) transferred all of these species to *Mansoniella* without discussion. One of us (A.N.N.) examined paratypes of *P. sassafri* and this species possesses the diagnostic generic characters for *Mansoniella*. In contrast, other *Pachypeltis* species possess the following characters: ASI subequal to half of head width or shorter, swollen medially, pair of punctures on the depression delimiting calli posteriorly absent, anterior part of corium as broad as posterior part, and coils in ductus seminis indistinct. Based on these above observations, we support the new combinations of Lin (2002).

One of us (A.N.N.) also examined the type of *Mansoniella minuta*, which is from Papua New Guinea and preserved in the Bernice P. Bishop Museum, and we conclude that is it very similar to the species described from east Asia.

Miomonalonion Sailer and Carvalho

Miomonalonion Sailer and Carvalho, 1957: 257 (gen. nov.; type species: *Miomonalonion conoidifrons* Sailer & Carvalho, 1957 by monotypy); Schuh, 1995: 517 (cat.); Schuh, 2002–2013 (cat.).

Description: The description of Sailer & Carvalho (1957) is as follows: 'Head, with frons connately produced between antennae, but projected little beyond anterior margin of eyes; vertex immarginate, smooth; neck distinct; eyes pedunculate, projected laterally; antennae with first segment incrassate; clypeus vertical, scarcely prominent; rostrum with second segment thickened towards apex and with bilateral papilliform projections near middle of inner surface. Pronotum smooth; calli not visible; disc of posterior lobe convexly declivous. Scutellum smooth (shape distorted). (Hemelytra badly damaged.) Embolium very narrow; cuneus apparently much longer than wide. (Abdomen and legs fragmentary), one visible tibia incrassate towards apex and distinctly pilose.'

See also plate 33, figs 8, 9 in Sailer & Carvalho (1957).

Included species

Miomonalonion conoidifrons Sailer and Carvalho, 1957

Discussion: We did not examine this genus and species. It was placed by Sailer & Carvalho (1957) in the

Monaloniini, between *Monalonion* and *Felisacus*, based on the presence of a neck-like anterior pronotal lobe. They also stated that it does not fit with any other mirid subfamily. The characters that are important for diagnosing Monaloniini, such as the structure of the genitalia, efferent system of metathoracic gland and membrane cell morphology, are not discernible from the description. Nonetheless, based on the description, the head is very similar to that found in Monaloniini, and it is most likely to be related to the Australian genera *Schuhirandella*, *Rayieria* and the African genus *Physophoroptera*, as all of them possess: distinctly swollen frons (fig. 4D in Namyatova *et al*., in press, fig. 5A–F in Namyatova & Cassis, 2013b, fig. 2D in Namyatova & Cassis, 2013a), shortened labial segments (as in fig. 8A–D in Namyatova & Cassis, 2013b) and elongate incrassate apically ASI. In contrast, *Monalonion* has the labial segments usually distinctly longer than wide, frons straight or only slightly convex, and ASI shortened and not incrassate. In *Miomonalonion* the eyes are stylate, which is only found in *Physophoroptera* amongst the abovementioned genera (fig. 5D in Namyatova *et al*., in press). However, in *Physophoroptera* the scutellum has rounded outgrowth (Fig. 12C), which is absent in *Schuhirandella*, *Rayieria*, *Miomonalonion* and *Monalonion*.

MONALONION HERRICH-SCHAEFFER

Figures 9, 16I–L, 19N, O, 24

Monalonion Herrich-Schaeffer, 1850: 168 (gen. nov.; type species *Monalonion parviventre* Herrich-Schaeffer, 1859 by monotypy); Fieber, 1858: 300 (key to gen.); Signoret, 1858: 500 (descr.); Walker, 1873: 161 (cat.); Distant, 1883: 246 (descr.); Atkinson, 1890a: 49 (cat.); Kirkaldy, 1906: 134 (list); Kuhlgatz, 1906: 29 (key to gen.); Reuter, 1908: 150 (descr.); Reuter, 1910: 153 (cat.); Bondar, 1939: 1 (note); Knight, 1939: 226 (note); Carvalho, 1952: 59 (cat.): Carvalho, 1955: 39 (key to gen.); Carvalho, 1957: 138 (cat.); Carvalho, 1972: (diag., key to spp.); Lavabre, 1977a: 65 (diag.); de Abreu, 1977: 85 (desc., distrib., ecol.); Schuh, 1995: 517 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Among genera of the *Monalonion*-group, *Monalonion* can be separated by: ASI very short, *c*. 1.5–3× as long as wide; elongate body (Fig. 9), ASII–IV filiform; collar distinctly swollen (as in fig. 7D in Namyatova & Cassis, 2013b); scutellum without spine; forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); foretibia almost straight; secondary gonopore surrounded with small sclerite (Fig. 16I); ductus seminis slightly sclerotized basally; and DLP with sclerotized circle (Fig. 19N).

Redescription: Male: Body length 7–12 mm. COLORATION (Fig. 9). Variable, mostly brown to dark brown or yellow, sometimes with reddish areas; antennae and legs usually dark colored, legs sometimes with yellow or pale brown band on femur or mostly yellow. TEXTURE. Body mostly smooth, without punctures, wrinkles and tubercles; vertex without flattened areas; semicircular depression between scutellum and mesoscutum absent; striations on scutellum laterally absent; only small depression on anterior angle of pronotum present (as in fig. 9H in Namyatova & Cassis, 2013b). VESTITURE. Setae on dorsum and thoracic pleura absent; only short simple suberect setae on ASII–IV, legs and abdomen present; setae on ASII sometimes slightly longer than width of hind tibia; setae on tibia and hind femur sometimes very dense, shorter or longer than width of hind tibia; setae on abdomen pale, short and adpressed and very rare; black spinules on femora and tibiae absent. STRUCTURE. *Head*. Distance between eye and pronotum subequal to half of eye diameter (as in Fig. 10J), sometimes subequal to eye diameter; occipital region delimited with distinct depression; longitudinal depression on vertex as long or slightly longer than eye diameter; eyes not stylate, in line with contour of head, *c*. 0.2–0.3× as long as head width; distance between antennal fossae oval as long as or slightly longer than antennal fossa diameter; frons straight or slightly convex, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.4–1.7× as wide as high; eye *c*. 1.7–2.8× as long as distance between eye and apex of clypeus; antennal fossa oval *c*. 0.5–0.7× as long as eye height, not raised (as in fig. 6D–F in Namyatova & Cassis, 2013b), inferior margin placed distinctly above inferior margin of eye; position of base of clypeus varying from distinctly below inferior margin of antennal fossa to near halfway of antennal fossa height, not delimited with depression; head swollen in lateral view; length of gula varies from slightly longer to almost twice as long as buccula. *Labium*. Length varying from reaching middle of mesosternum to slightly surpassing posterior margin metasternum; *c*. 2–3× as long as wide; LSIII *c*. 3–4× as long as wide, varying from slightly shorter to distinctly longer than LSI; LSIII *c*. 2–5× as long as wide, varying from slightly shorter to distinctly longer than LSII; LSV *c*. 4–8× as long as wide, from slightly longer almost twice as long as long as LSIII. *Antenna*. Slightly shorter or longer than body; ASI *c*. 2–3× as long as wide, *c*. 0.3–0.7× as long as head width, widened basally; ASII *c*. 4–6× as long as ASI, *c*. 1.4–2× as long as head and pronotum combined; ASIII *c*. 0.7–0.9× as long as ASII; ASIV *c*. 0.2–0.3× as long as ASIII; ASII–IV filiform. *Thorax*. Collar distinctly delimited laterally and posteriorly, swollen; calli separated, flat almost indistinct (as in Fig. 10J); depression delimiting calli posteriorly absent (as in

Fig. 10J); humeral angles of pronotum rounded, not dilated (as in Fig. 10J); posterior margin of pronotum slightly sinuate (as in Fig. 10J); scutellum flat, rounded apically; without outgrowth or medial depression; metepimeron *c*. 3–4× as high as long, rounded (as in fig. 9C in Namyatova & Cassis, 2013b); metasternum rounded posteriorly, without medial projection on to abdominal segment II (as in fig. 17B in Namyatova *et al*., in press). *Hemelytron*. Costal margin concave or almost straight, hemelytron almost not tapering posteriorly; claval commissure *c*. 2–5× as long as scutellum, concave (as in fig. 11G in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M; corium without swelling posteriorly; cuneus *c*. 3–4× as long as wide, *c*. 0.7–1.2× as long as pronotum, medial margin distinctly concave (as in fig. 13C in Namyatova *et al*., in press); membrane cell *c*. 1.4–2.2× as long as pronotum, rounded or acute apically; auxiliary vein absent; distance between cell and apex of membrane *c*. 0.2–0.4× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora more or less swollen apically (as in fig. 18A in Namyatova *et al*., in press); forefemur almost straight, middle and hind femora distinctly curved, hind tibia sometimes with medial part widened; foretibia slightly shorter, as long as or slightly longer than head and pronotum combined; tibiae without swellings; segment I of hind tarsus distinctly longer than segment II and subequal to or slightly longer than segment III (as in fig. 19A in Namyatova *et al*., in press); claw broadly rounded (fig. 10F in Namyatova & Cassis, 2013b); basal tooth on claw triangular, short (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 16I–L). Genital capsule slightly longer than wide, without outgrowth(s); ventral wall shortened anteriorly; left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore suboval, without outgrowths supporting ductus seminis; ductus seminis longer than phallotheca, with coils forming wide tube, sclerotized basally and with narrow sclerite around secondary gonopore, attached to phallobase medially; sclerotized part of phallotheca occupying entire dorsal side, rounded apically, without ridge or outgrowth(s); endosoma with small sclerites or sclerotized areas.

Female: Body length 8–12.5 mm. Coloration, surface, vestiture and structure as in male, generally larger than males and eye usually smaller than in male (Fig. 9). *Genitalia* (Fig. 19N, O). DLP with sclerotized ring, sometimes indistinct, mostly without striations or with some medially, especially at base of lateral oviducts; lateral oviducts placed at halfway of or in posterior half of DLP, removed from each other and from lateral margins of DLP; spermathecal gland placed in posterior half, medially; posterior wall of bursa copulatrix with tubercles, without outgrowths or sclerotizations; base of second valvula with bifurcate outgrowth; ventral wall of bursa copulatrix membranous.

Distribution: Widely distributed in Latin America, including Mexico (Fig. 24).

Host plants: Many species of *Monalonion* are known to damage cocoa pods (Distant, 1917; Costa Lima, 1938; Bondar, 1939; Carvalho, 1972; de Abreu, 1977; Entwistle, 1977). *Monalonion schaefferi* was also recorded from cashew (Piart, 1977), and *M. velenzagi* is known from avocado (Carvalho & Costa, 1988). Species are also known from *Ficus* sp., *Cercopia adenopsis* (Moraceae), *Hamelia patens* (Rubiaceae) and *Begonia* spp. (Begoniaceae) (Costa Lima, 1938; Bondar, 1939; Carvalho, 1972; Piart, 1977).

Included species

Monalonion annulipes Signoret, 1858
Monalonion atratum Distant, 1883
Monalonion bahiense Costa Lima, 1938
Monalonion bicolor Carvalho and Costa, 1988
Monalonion bondari Costa Lima, 1938
Monalonion columbiensis Carvalho, 1984
Monalonion decoratum Monte, 1942
Monalonion dissimulatum Distant, 1883
Monalonion incaicus Carvalho, 1972
Monalonion itabunensis Carvalho, 1972
Monalonion paraensis Carvalho, 1985
Monalonion parviventre Herrich-Schaeffer, 1850
Monalonion peruvianus Kirkaldy, 1907
Monalonion schaefferi Stål, 1860
Monalonion velezangeli Carvalho and Costa, 1988
Monalonion versicolor Distant, 1883

Discussion: Monalonion is distinctive with the Monaloniini. It differs from other members of the *Monalonion*-complex by the elongate body in combination with ASI distinctly shorter than the width of the head (Fig. 9). This genus also has the ductus seminis sclerotized basally and apically (Fig. 16I), which is unique within this complex.

Twenty-nine species have been described in *Monalonion*, 13 of which have been designated as junior synonyms. We have examined types of 15 of the available names of *Monalonion*; six of these represent valid species. The type of *M. schaefferi* is preserved in the Swedish Museum of Natural History (Stockholm). The information on four types of this genus is available on the website of the National Museum of Natural History (Washington, DC) (http://collections.nmnh.si.edu/

search/ento/). We could not locate the type of *M. parviventre*, which is the type species of the genus. The original description of this species is brief, although Carvalho (1972) redescribed the species based on additional specimens, and noted that it is similar to *M. schaefferi*.

ODONIELLA HAGLUND

Figures 8, 10G, 11E, 16M–P, 19P, Q, 24

Odoniella Haglund, 1895: 468 (gen. nov.; type species *Odoniella reuteri* Haglund, 1895 by monotypy); Reuter, 1905: 2 (disc.); Kirkaldy, 1906: 134 (list); Reuter, 1910: 153 (cat.): Reuter & Poppius, 1911: 411 (descr.); Poppius, 1912: 176, 185, 186 (key gen., descr., key to spp.); Bergroth, 1922: 51 (cat.); China, 1944: 179 (key to gen.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 43 (key to gen.); Carvalho, 1957: 146 (cat.); Odhiambo, 1962: 298 (key to spp.); Lavabre, 1977a: 51 (key to gen.); Schuh, 1995: 529 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Among other genera of the *Odoniella*-complex, *Odoniella* itself is recognized by ASII only slightly incrassate apically; ASIV distinctly clavate; yellow to reddish coloration (Fig. 8); humeral angles of pronotum distinctly flattened, pronotum and scutellum without tumescences (Fig. 10G); scutellum distinctly swollen (Fig. 11E, fig. 12E in Namyatova *et al*., in press), not divided into lower and upper parts (as in Fig. 12A); without tubercles or bifurcated outgrowth on frons; eye directed distinctly outwards and forwards (Fig. 10G); and body clothed with simple setae only.

Redescription: Male: Body length 7–10 mm. COLORATION (Fig. 8). Ground colour varying from mostly yellow to reddish, pronotum, scutellum and hemelytron sometimes with dark brown to black markings and areas, antennae and abdomen also often with brown to black markings. TEXTURE. Body without tubercles and wrinkles; flattened areas on vertex indistinct; pronotum and scutellum covered with distinct dense punctures; pair of punctures between calli, pair of punctures between mesoscutum and scutellum, punctures on clavus and on R + M absent (fig. 12E in Namyatova *et al*., in press); striations on lateral margins of scutellum present; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with simple setae; adpressed pale setae on dorsum, thoracic pleura and abdomen present; setae on head, pronotum, scutellum and pleura often very rare; setae on antennae mostly dark and adpressed, often pale on ASI- II; setae on legs mostly pale and adpressed, not very dense, setae on tibia spine like and suberect; black spinules on femora and tibiae irregularly distributed (as in fig. 18F in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum as long as or slightly longer than eye diameter (Fig. 10G); occipital region not delimited with depression; longitudinal depression on vertex absent or very short and shallow; eyes stylate, directed outwards and forwards (Fig. 10G), *c*. 0.17–0.22× as long as head width; distance between antennal fossa as long as or slightly longer than antennal fossa diameter; frons distinctly swollen, without ridges, outgrowth(s) or longitudinal depression (Fig. 10G); anterior view of head *c*. 1.5–1.8× as wide as high; eye as long as or slightly longer than distance between eye and apex of clypeus; antennal fossa oval, diameter subequal to or slightly longer than half of eye height, not raised; inferior margin of fossa placed slightly above inferior margin of eye; base of clypeus placed near or slightly above inferior margin of eye, delimited with depression (fig. 3B in Namyatova *et al*., in press); head almost flat in lateral view; gula shorter than buccula length, straight. *Labium*. Slightly surpassing middle of mesosternum or almost reaching posterior margin of mesosternum; LSI *c*. 2.5–3× as long as wide, LSII *c*. 2–2.5× as long as wide, as long as or slightly shorter than LSI; LSIII *c*. 2.5–3× as long as wide, as long as or slightly longer than LSIII; LSIV *c*. 4× as long as wide, *c*. 1.5–2× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 1.5–2× as long as wide, subequal to one third of head width, swollen basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 5× as long as ASI, *c*. 0.8–0.9× as long as head and pronotum combined, slightly incrassate towards apex, without swellings; ASIII *c*. 0.7–0.9× as long as ASII, widened towards apex; ASIV *c*. 0.7× as long as ASIII, clavate. *Thorax*. Collar distinct, fused with callosite region medially, flat; calli separated; depression delimiting calli posteriorly absent; humeral angles of pronotum distinctly dilated, not serrate; posterior margin of pronotum distinctly concave, often forming right angles (Fig. 11E); scutellum distinctly swollen, not covering base of pronotum (Fig. 11E, fig. 12R in Namyatova *et al*., in press), not divided into lower and upper parts (as in Fig. 12A), trapeziform or round, obtuse apically, with or without longitudinal depression medially, without outgrowth or ridge (Fig. 11E, fig. 12R in Namyatova *et al*., in press); metepimeron enlarged *c*. 1–1.5× as high as long, subtriangular (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron slightly rounded; claval commissure *c*. 0.3–0.7× as long as scutellum, straight; R + M distinct only anteriorly and medially, not reaching posterior margin of corium (fig. 12E in Namyatova *et al*., in press); medial fracture strongly inclined towards midline; cuneus *c*. 1.7–2.4× as long as wide, *c*. 0.7–0.9× as long as pronotum, medial margin slightly

concave (fig. 13B in Namyatova *et al*., in press); membrane cell slightly or distinctly surpassing apex of cuneus, forming right angle, as long as or slightly longer than pronotum (fig. 13B in Namyatova *et al*., in press); auxiliary vein absent; distance from cell to apex of membrane *c*. 1.7–1.9× as long as cell length. *Legs*. Forecoxae contiguous (fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight; foretibia shorter than head and pronotum combined; tibia without swellings; segment I of hind tibia of as long as segment II and distinctly shorter than segment III; apical half ore third part curved or claw broadly rounded; basal tooth on claw very short, triangular, or elongate, straight or slightly concave (as in Fig. 13J). *Genitalia* (Fig. 16M–S). Genital capsule as long as or slightly shorter than wide, without outgrowth(s), ventral wall not shortened anteriorly; left paramere r-shaped, *c*. 1.5–2× times as long as right paramere; phallobase sclerite of primary gonopore subtriangular or suboval, without outgrowth(s); ductus seminis not sclerotized basally or apically, shorter than phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca broad, occupying almost entire dorsal portion, rounded apically, without ridge or outgrowths(s); endosoma with single or a number of serrate spicules.

Female: Body length 9–12.5 mm. Coloration, surface, vestiture and structure as in male (Fig. 8). *Genitalia* (Fig. 19P, Q). DLP with sclerotized ring, with pair of symmetrical striated areas; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin and at a halfway of DLP; spermathecal gland placed posteriorly, slightly shifted right, posterior wall with small tubercles, without outgrowths and sclerotization; base of second valvula concave; ventral wall membranous.

Distribution: Distributed in tropical Africa (Fig. 24).

Host plants: Odoniella reuteri and *O. rubra* have been recorded from cocoa (Leston, 1970; Entwistle, 1977). *Odoniella apicalis* and *O. rubra* are also known from *Piper* spp. (Piperaceae), *Odoniella camerunesis* was recorded from *Culcasia parviflora* (Araceae), and *Odoniella similis* is known from *Smilax* sp. (Smilaceae) (Odhiambo, 1962; Hill, 1983).

Included species

Odoniella apicalis Reuter and Poppius, 1911
Odoniella camerunensis Schumacher, 1917
Odoniella immaculipennis Poppius, 1914
Odoniella reuteri Haglund, 1895
Odoniella rubra Reuter, 1905
Odoniella similis Poppius, 1914
Odoniella unicolor Poppius, 1912

Discussion: Our description of the male genitalia of *Odoniella* is based on observations of all species, except for *Odoniella camerunensis*. The female genitalia were described based on our dissections of *O. apicalis* and *O. rubra*.

Odoniella is similar to *Volkeliopsis* in coloration and presence of simple setae only, but the latter differs in the following characters: scutellum only slightly swollen, not exceeding height of scutellum; humeral angles of pronotum not flattened; and spermathecal gland on DLP placed on right-hand side (Fig. 21S).

Some species of *Odoniella* are reminiscent of many species of *Bryocoropsis* by the presence of a trapeziform shaped scutellum (Fig. 11E), which is not divided into lower and upper parts (Fig. 12A). Also, see *Bryocoropsis* for further discussion.

Odoniella comprises seven species. We examined type specimens of *O. apicalis*, *O. immaculipennis*, *O. similis*, *O. reuteri* and *O. unicolor*. We could not locate the types of *O. rubra* and *O. camerunensis*. However, we have examined specimens that fit the description of *O. rubra*. Based on the original description of *O. camerunensis*, it is apparently congeneric with the other assigned species. All the examined species are very similar to each other, and in *O. rubra* and *O. unicolour* the scutellum is round and the phallobase sclerite of the primary gonopore is suboval; whereas in all other species the scutellum is more or less triangular and the phallobase sclerite is subtriangular. In addition, *O. rubra* has the basal tooth of the claw elongate and slightly concave, whereas in specimens of *O. unicolor* all the tarsi are lost, and the remaining species have the claw with the basal tooth short and triangular.

Pachypeltis Signoret

Figures 7, 13D, K, 16T–AA, 20A–J, 23

Pachypeltis Signoret, 1858: 501 (gen. nov.; type species: *Pachypeltis chinensis* Signoret, 1858 by monotypy); Walker, 1873: 164 (cat.); Atkinson, 1890a: 51 (cat.); Reuter, 1903: 2 (descr.); Kirkaldy, 1906: 134 (list); Kuhlgatz, 1906: 29 (key to gen.); Reuter, 1910: 153 (cat.); Hsiao, 1942: 250 (key to gen., list.); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 40 (key to gen.); Carvalho, 1957: 140 (cat.); Steyskal, 1973: 206 (correction); Carvalho, 1981: 41 (descr., disc., key to spp.); Schuh, 1995: 520 (cat.); Hu and Zheng, 2001: 421 (key to spp.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Disphinctus Stål, 1871: 668 (gen. nov.; type species *Disphinctus sahlbergii* Stål, 1858 by consequent designation Kirkaldy, 1902: 294); Walker, 1873: 161 (cat.); Atkinson, 1890a: 50 (cat.); Distant, 1904b: 443 (descr.);

Kirkaldy, 1906: 134 (list); Reuter, 1910: 166 (syn.); Carvalho, 1957: 140 (cat.); Schuh, 1995: 520 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Pachypeltis is diagnosed by the following characters: row of punctures on clavus and R + M (fig. 11C, D in Namyatova *et al*., in press); calli merged (fig. 4A in Namyatova *et al*., in press); apex of scutellum often rounded (fig. 12C, D in Namyatova *et al*., in press); distance between head and pronotum subequal to half of eye diameter (fig. 4A in Namyatova *et al*., in press); frons without ridges or spines, without depression medially; LSI–II only twice as long as wide, LSII often more than twice as long as wide; ASII–IV filiform; scutellum often rounded apically; hind femur often distinctly curved (fig. 18C in Namyatova *et al*., in press); hemelytra with outer margins straight or slightly concave; membrane cell distinctly acute (fig. 13A in Namyatova *et al*., in press), distinctly longer than pronotum; ductus seminis shorter than phallotheca, without coils; and, outgrowths on phallobase supporting ductus seminis present, long or short (Fig. 16T, fig. 22A in Namyatova *et al*., in press).

*Redescription:*Male: Body length 7–9 mm. COLORATION (Fig. 7). Usually bright-colored, coloration varies from yellow with dark markings to dark brown to black with paler markings, sometimes orange or red; antennae, or, at least, ASII–IV, usually darker than body, brown to dark brown, corium sometimes with dark marking or darkened posteriorly. TEXTURE. Body smooth, without tubercles; head without wrinkles and flattened areas; pronotum impunctate, without wrinkles; scutellum impunctate, smooth or with transverse wrinkles; pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum, and punctures on clavus and R + M present (fig. 11C, D in Namyatova *et al*., in press), pair of punctures on depression delimiting callosite region andsemicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with dense pale or dark simple setae, usually suberect, adpressed hemelytron and thoracic pleura, setae on abdomen suberect and adpressed; setae usually shorter, sometimes longer than width of hind tibia, tibia regularly setose; black spinules on femora absent, rows of black spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum shorter or subequal to eye length dorsally (fig. 4A in Namyatova *et al*., in press); occipital region not delimited or distinctly delimited with transverse depression; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head, *c*. 0.2–0.3× as wide as head; distance between antennal fossae slightly longer than antennal fossae diameter; frons from only slightly to distinctly swollen, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.3–1.4× as wide as high; eye *c*. 1.3–2× as high as distance from eye to apex of clypeus; antennal fossae round, diameter of fossa ca.0.25–0.35× as long as eye diameter, only slightly raised (fig. 3A in Namyatova *et al*., in press), inferior margin placed above of inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with more or less distinct or very shallow depression (fig. 3A in Namyatova *et al*., in press); head from slightly to distinctly swollen dorsally in lateral view; gula straight or slightly convex, *c*. 1.5–2× as long as buccula length. *Labium*. Length varying from slightly surpassing anterior margin of mesosternum to almost reaching middle of mesosternum; LSI twice as long as wide, LSII *c*. 2–3.5× as long as wide, as long as or longer than LSII; LSIII ca.1.5–3.5× subequal to or slightly shorter than LSII; LSIV *c*. 2.5–6× as long as wide, *c*. 1.5–2× as long as LSIII. *Antenna*. Length varying from reaching base of cuneus to surpassing apex of cuneus; LSI *c*. 0.5–0.7× as long as head width, widened medially (fig. 8D in Namyatova *et al*., in press), LSII *c*. 3.5–5.8 times as long as LSI, *c*. 1.1–2× as long as head and pronotum combined; LSIII *c*. 0.5–0.7× as long as LSIII; LSIV *c*. 0.4–0.7× as long as LSIII; LSII–IV filiform. *Thorax*. Collar fused with callosite region posteriorly, flat or swollen; calli fused with each other; callosite region delimited posteriorly with depression (fig. 4A in Namyatova *et al*., in press); humeral angles of pronotum not dilated; posterior margin of pronotum slightly concave or sinuate (fig. 4A in Namyatova *et al*., in press); scutellum almost flat or moderately swollen (fig. 11C, D in Namyatova *et al*., in press), often obtuse apically, rarely acute, without outgrowth or ridge, with or without shallow medial depression; metepimeron enlarged, *c*. 2–4× as long as wide, usually bifurcate (Fig. 13D); metasternum with medial projection on to the abdominal segment II (fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight or slightly concave medially; claval commissure *c*. 1–2× as long as scutellum, its margins straight (fig. 11C, D in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium not raised posteriorly; cuneus *c*. 1–4× as long as wide, *c*. 0.6–1.3× as long as pronotum, its medial margin straight or slightly concave (fig. 13A in Namyatova *et al*., in press); membrane cell elongate, distinctly surpassing apex of cuneus, forming acute angle (fig. 13A in Namyatova *et al*., in press), *c*. 1–2× as long as pronotum; auxiliary vein often present, short; distance from cell to membrane *c*. 0.3–0.6× as long as cell length. *Legs*. Forecoxae contiguous (fig. 17A in Namyatova *et al*., in press); femora

slightly swollen apically (fig. 18C in Namyatova *et al*., in press); fore- and middle femora straight, hind femur often distinctly curved, sometimes almost straight; tibia without swellings; foretibia shorter than head and pronotum combined; segments of hind tarsus subequal in length (fig. 29A in Namyatova *et al*., in press), sometimes segment I longer than segments I and II each and segments I and II subequal in length, or segment I slightly longer than segment II and as long as segment III; apical third part of claw curved; basal tooth on claw elongate, concave (Fig. 13K). *Genitalia* (Fig. 16T–AA, fig. 22A–D in Namyatova *et al*., in press). Genital capsule longer or shorter than wide, without outgrowth(s), its ventral wall not shortened anteriorly; left paramere *c*. 3.5–4 times as long as right paramere, distinctly r-shaped; phallobase sclerite of primary gonopore bowl-shaped or oval, with long or short outgrowth(s), supporting ductus seminis; ductus seminis not sclerotized basally or apically, distinctly shorter than phallotheca, without coils; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowth or ridge; endosoma with fields of small spicules, sometimes with number of elongate spicules, sometimes with both.

Female: Body length 6–12 mm. Coloration, surface, vestiture and structure as in male (Fig. 7). *Genitalia* (Fig. 20A–J, fig. 23H in Namyatova *et al*., in press). DLP with sclerotized ring anteriorly, sometimes covered with membrane, or with two sclerotized bands, or with two sclerotized rings; DLP with or without striations, without additional sclerites; lateral oviduct widely separated, placed in posterior half of DLP, sometimes slightly below midline; spermathecal gland placed in posterior half of DLP, medially, sometimes almost at posterior margin; posterior wall covered with small tubercles, sometimes with outgrowths and small sclerites; base of second valvula slightly concave; ventral wall of bursa copulatrix membranous.

Included species

Pachypeltis anadyomene (Kirkaldy, 1902)
Pachypeltis annulipes Poppius, 1912
Pachypeltis biformis Hu and Zheng, 1999
Pachypeltis brevirostris Poppius, 1912
Pachypeltis chinensis Signoret, 1858
Pachypeltis corallinus Poppius, 1915
Pachypeltis dudgeoni (Kirkaldy, 1902)
Pachypeltis elegans (Distant, 1904)
Pachypeltis fallenii (Stål, 1871)
Pachypeltis gigas Carvalho, 1981
Pachypeltis haglundii (Stål, 1871)
Pachypeltis humerale (Walker, 1873)
Pachypeltis javanus Poppius, 1914
Pachypeltis maesarum (Kirkaldy, 1902)
Pachypeltis marginalis Poppius, 1912
Pachypeltis philippinensis (Distant, 1910)
Pachypeltis politum (Walker, 1873)
Pachypeltis reuteri (Stål, 1871)
Pachypeltis sahlbergii (Stål, 1871)
Pachypeltis stahli (Distant, 1910)
Pachypeltis sumatrator (Kirkaldy, 1902)
Pachypeltis vittiscutis (Bergroth, 1894)

Distribution: Widely distributed in South Asia and Pacific Islands (Fig. 23).

Host plants: Information on the host plants of *Pachypeltis* is limited. *Pachypeltis maesarum* has been recorded as a pest of cashew (Bhat & Srikumar, 2012) and tea (Remamony & Abraham, 1977) in India. It has also been recorded from *Piper* sp. (Piperaceae), *Acalypha hispida* (Euphorbiaceae) and *Maesa indica* (Primulaceae) (Kirkaldy, 1902; Remamony & Abraham, 1977; Bhat & Srikumar, 2012). *Pachypeltis gigas* is known from *Piper* sp. (Piperaceae) (Carvalho, 1981). *Pachypeltis dudgeoni* was recorded from *Maesa* spp. (Primulaceae) (Kirkaldy, 1902). *Pachypeltis politum* is known from *Peperomia* sp. (Piperaceae), *Solanum* sp. (Solanaceae), *Acalypha* sp. (Euphorbiaceae) and guava (Kirkaldy, 1902).

Discussion: Pachypeltis is similar to the African genus *Pararculanus* on the basis of the following characters: calli merged (fig. 4A in Namyatova *et al*., in press), frons without tubercles or outgrowths, labium slightly surpassing anterior margin of mesosternum or reaching middle of mesosternum and LS III often more than twice as long as wide. However, *Pararculanus* differs in: distance between head and pronotum subequal to eye diameter (as in Fig. 10A) and small tubercles on dorsal wall of bursa copulatrix absent (Fig. 20N, P).

Pachypeltis can be confused with *Dimia*. See discussion for *Dimia* for characters distinguishing these two genera.

Twenty-two described species have been assigned to *Pachypeltis*. We conclude that the genus may include many synonymies and some new species, and because *Pachypeltis* is widely distributed in South Asia and is reported as pest for some crops, a revision of the genus is essential. We examined specimens of 11 species, including the types of *P. annulipes*, *P. biformis*, *P. chinensis* and *P. corallinus*. We also have examined images of the type specimens of *P. anadyomene*, *P. elegans*, *P. falleni*, *P. gigas*, *P. haglundii*, *P. humerale*, *P. marginalis*, *P. philippinensis*, *P. politum*, *P. reuteri*, *P. sahlbergi* and *P. stali*. We consider all these species to be congeneric. Some species are apparently very closely related and may turn out to be conspecific. In particular, *P.*

humerale, *P. philippinensis*, *P. reuteri*, *P. sahlbergi* and *P. stali* are very similar in external morphology. We have examined many specimens of *P. reuteri* from South Asia, which are variable in coloration but possess identical male genitalia. We have also identified specimens as *P. haglundii*, and based on a comparison of a provided photograph of *P. elegans*, conclude that they are very similar. We also conclude that *Pachypeltis chinensis*, *P. gigas* and *P. sumatrator* are also very similar externally, although our knowledge of *P. sumatrator* is based on the original description alone.

We could not locate type specimens of *Pachypeltis brevirostris*, *P. dudgeoni*, *P. maesarum* or *P. vittiscutis*. Based on the original description, *P. brevirostris* is similar to an unidentified species of the genus that we codified in our phylogenetic analysis; we have tentatively identified it as *Pachypeltis* nr. *brevirostris*, based on their similar dark coloration. *Pachypeltis dudgeoni* was originally described from the Himalayas and its affinities are unclear. The type of *P. maesarum* is supposedly preserved in the Natural History Museum (London), but we did not find it in this collection. We have photographs of non-type specimens of this species housed in the Natural History Museum (London), and we tentatively treat them as very close to *P. reuteri*. However, without an examination of the type we refrain from a formal synonymy. According to the original description, *P. vittiscutis* is also very similar to *P. reuteri*.

The unidentified species from Bougainville found in the B.P. Bishop collection is similar to *Pachypeltis* externally, but differs in some important characters, such as the subtriangular and not bifurcate metepimeron (as in Fig. 13C), collar distinctly demarcated posteriorly, and hemelytron membrane cell forming a right angle (as in fig. 13B in Namyatova *et al*., in press). Based on our phylogenetic analysis, a relationship between the species from Bougainville and other *Pachypeltis* species is not strongly supported. Therefore, we do not include this species in the present description of *Pachypeltis* pending a taxonomic revision of the genus (see also node 10 of the phylogenetic analysis).

Parapachypeltis Hu and Zheng

Figures 7, 20K, L, 23

Parapachypeltis Hu and Zheng, 2001: 26 (gen. nov.; type species: *Parapachypeltis punctatus* Hu and Zheng by monotypy); Schuh, 2002–2013 (cat.).

Diagnosis: Parapachypeltis can be separated by the following characters: punctate pronotum; impunctate scutellum, presence of row of punctures on clavus and R + M; metepimeron enlarged, rounded, calli distinctly separated laterally.

*Redescription:*Female: Body length 8.5–9.2. Coloration (Fig. 7) (partly based on figures in Hu & Zheng, 2001). The main colors are reddish and brown. Texture. Body without tubercles; head without wrinkles and flattened areas; pronotum punctate, without wrinkles; scutellum impunctate; pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum, and punctures on clavus and R + M present (as in fig. 11C, D in Namyatova *et al*., in press), pair of punctures on depression delimiting callosite region and semicircular depression between scutellum and mesoscutum absent. Vestiture. Body clothed with dense semiadpressed setae. Structure. *Head*. Distance between eye and pronotum subequal to eye length dorsally (fig. 4A in Namyatova *et al*., in press); occipital region not delimited with transverse depression; longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head, *c*. 0.2× as wide as head; distance between antennal fossae slightly longer than antennal fossae diameter; frons more or less swollen, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.4× as wide as high; diameter of fossa ca.0.3× as long as eye diameter, only slightly raised (fig. 4A in Namyatova *et al*., in press), inferior margin placed above of inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, head slightly swollen dorsally in lateral view. *Labium*. Length reaching forecoxae, LSI twice as long as wide, LSII twice as long as wide, as long as LSII; LSIII twice as long as wide slightly shorter than LSII; LSIV *c*. 3× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. ASI *c*. 0.4× as long as head width, widened medially (fig. 8D in Namyatova *et al*., in press), ASII *c*. 5× as long as ASI, *c*. 1.1–2× as long as head and pronotum combined; ASIII *c*. 0.5–0.7× as long as ASIII; ASIV *c*. 0.4–0.7× as long as ASIII; ASII–IV filiform. *Thorax*. Collar fused with callosite region posteriorly, flat or swollen; calli fused with each other; callosite region delimited posteriorly with depression (fig. 4A in Namyatova *et al*., in press); humeral angles of pronotum not dilated; posterior margin of pronotum slightly concave or sinuate (fig. 4A in Namyatova *et al*., in press); scutellum almost flat or moderately swollen (fig. 11C, D in Namyatova *et al*., in press), often obtuse apically, rarely acute, without outgrowth or ridge, with or without shallow medial depression; metepimeron enlarged, projected and rounded; metasternum with medial projection on to the abdominal segment II (fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight medially; claval commissure twice as long as scutellum, its margins straight (fig. 11C, D in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium not raised posteriorly; cuneus *c*. 3× as long as wide, *c*. 0.8× as long as pronotum, its medial margin straight; membrane cell elongate, distinctly surpassing apex of cuneus, forming acute angle (fig. 13A in Namyatova *et al*., in

press), *c*. twice as long as pronotum; auxiliary vein often present, short; distance from cell to membrane *c*. 0.3× as long as cell length. *Legs*. Forecoxae contiguous (fig. 17A in Namyatova *et al*., in press). *Genitalia* (Fig. 20K, L). DLP without visible sclerotization or striations; DLP with or without striations, without additional sclerites; lateral oviduct widely separated, placed in posterior half of DLP, spermathecal gland placed in posterior half of DLP placed at posterior margin of DLP, medially; posterior wall covered with small tubercles, base of second valvula concave; ventral wall of bursa copulatrix membranous.

Distribution: Known from mainland China only (Fig. 23).

Host plants: Unknown.

Included species

Parapachypeltis punctatus Hu and Zheng, 2001

Discussion: One of us (A.N.N.) examined a single female of the genus, which had all its appendages damaged. *Parapachypeltis* is very close to *Pachypeltis*, as it has very similar body ratios and external morphology. The latter genus mainly differs in the bifurcate metepimeron and impunctate pronotum. Those differences are slight, and it is possible that *Parapachypeltis* is nested within *Pachypeltis*. However, a revision of *Pachypeltis* and examination of additional material of *Parapachypeltis* is required to resolve this question.

Pararculanus Poppius

Figures 7, 16AB–AI, 20M–P, 24

Pararculanus Poppius, 1912: 189 (gen. nov.; type species: *Pararculanus piperis* Poppius, 1912 by monotypy); Poppius, 1912: 176 (key to gen.); Bergroth, 1922: 56 (cat.); China, 1944: 175 (key to gen.); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 39 (key to gen.); Carvalho, 1957: 139 (cat.); Schmitz, 1968: 101 (key to gen.); Schuh, 1995: 522 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Pararculanus can be separated from genera with a row of punctures on clavus and R + M by the following characters: the structure of head, i.e. distance between eye and pronotum subequal to eye diameter; distance between antennal fossae subequal to diameter of antennal fossa; frons swollen, not bearing tubercles or outgrowths (as in Fig. 10A); gula three times as long as buccula; LS III three times as long as wide; calli fused with each other; outer margins of hemelytra straight; metasternum protruding to abdominal segment II in triangular outgrowth (fig. 17A in Namyatova *et al*., in press); coils in ductus seminis indistinct; phallobase with pair of long outgrowths supporting ductus seminis (Fig. 16AB, AF); and absence of small tubercles on posterior wall of bursa copulatrix (Fig. 20PN, P).

Redescription: Male: Body length 6–8 mm. Coloration (Fig. 7). Three species, placed in this genus, differ in coloration. *P. ghesquierei* mostly pale brown with reddish or pale brown areas, *P. piperis* mostly brown to dark brown, with pale cuneus and markings on head and pronotum, pleura and abdomen yellow to pale brown, ASI sometimes reddish; *P. madagascariensis* mostly reddish with yellow areas. Texture. Body mostly smooth; head without wrinkles, tubercles or flattened areas; pronotum and scutellum impunctate, without tubercles, sometimes with wrinkles; pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum and rows of punctures on clavus and on R + M present (as in fig. 11C, D in Namyatova *et al*., in press); semicircular depression between scutellum and mesoscutum absent. Vestiture. Body clothed with simple setae, mostly pale, dark on appendages; head and pronotum with suberect setae, sometimes very rare; thoracic pleura with rare short and adpressed setae; hemelytron densely covered with short adpressed setae; appendages and abdomen with suberect setae, some of them as long as width of hind tibia; femora without rows of small black spinules; tibiae regularly setose; rows of spinules on tibia present (as in fig. 18D in Namyatova *et al*., in press). Structure. *Head*. Distance between eye and pronotum slightly longer than or subequal to eye diameter (as in Fig. 10A); transverse depression delimiting occipital region distinct or indistinct; longitudinal depression on vertex absent or very short; eyes not stylate, in line with contour of head, *c*. 0.25× as wide as head; distance between antennal fossa almost subequal to or slightly longer than antennal fossa diameter; frons distinctly swollen, without ridges, outgrowths or longitudinal depression (as in Fig. 10A); anterior view of head *c*. 1.3–1.4× as wide as high; eye almost twice as long as distance from eye to apex of clypeus; antennal fossa round, diameter subequal to third part of eye height, only slightly raised (as in fig. 3A in Namyatova *et al*., in press); inferior margin of fossa placed above inferior margin of eye; base of clypeus placed near inferior margin of antennal fossa, delimited with depression; head slightly to distinctly swollen dorsally in lateral view; gula slightly convex, *c*. 3–4× times as long as buccula length. *Labium*. Length varying from reaching anterior margin of mesosternum to reaching middle of mesosternum; LSI twice as long as wide; LSII *c*. 2.5–4× as long as wide, as long as or slightly longer than LSI; LSIII *c*. 2–3× as long as wide, slightly shorter or longer than LSII; LSIV *c*. 4–6× as long as wide, *c*. 1.5–3× as long as LSIII. *Antenna*. Slightly surpassing base of cuneus or reaching apex of cuneus;

ASI *c*. 0.7–0.9× as long as head width, widened medially (as in fig. 8D in Namyatova *et al*., in press); ASII *c*. 3–4× as long as ASI, *c*. 1.3–1.6× as long as length of head and pronotum combined; ASIII *c*. 0.5–0.6× as long as ASII, ASIV subequal to half of ASIII length; ASII–IV filiform. *Thorax*. Collar distinct, fused or not fused with calli posteriorly, flat (as in Fig. 10A); calli fused with each other, depression, delimiting callosite region posteriorly distinct medially (as in Fig. 10A); humeral angles of pronotum rounded, not dilated (as in Fig. 10A); posterior margin of pronotum slightly concave or sinuate; scutellum almost flat, acute apically, without outgrowth, medial ridge or depression; metepimeron enlarged, twice as long as wide, angulate and subtriangular (as in Fig. 13E); metasternum with medial projection on to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Almost not tapering posteriorly, costal margin straight; claval commissure *c*. 1.7–2.2× as long as scutellum, straight; R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium not raised posteriorly; cuneus twice as long as wide, subequal to or slightly longer than pronotum length, its medial margin almost straight; membrane cell distinctly surpassing apex of scutellum, forming right or acute angle (as in fig. 13A in Namyatova *et al*., in press), *c*. 1.3–1.4× as long as pronotum length; auxiliary vein absent or very short; distance from cell to apex of membrane subequal to or slightly shorter than half of cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora slightly swollen apically, straight; tibiae without swellings; foretibia as long as head and pronotum combined; segment I of hind tarsus slightly longer than segment II and subequal to segment III, or all segments subequal in length (as in fig. 19A in Namyatova *et al*., in press); apical third of claw curved; basal tooth on claw more than twice as long as wide, concave (as in Fig. 13K). *Genitalia* (Fig. 16AB–AI). Genital capsule longer than wide, without outgrowth(s); left paramere distinctly r-shaped, *c*. 2.5–3× as long as right paramere; phallobase sclerite of primary gonopore bowl-shaped, with long outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, as long as phallotheca length, without coils, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowths or ridge; endosoma with single long v-shaped spicule or with field of small spicules.

Female: Body length 8–10 mm. Mostly similar to male, but body generally larger (Fig. 7). *Genitalia* (Fig. 20M–P). DLP with two longitudinal sclerotized rings or with pair of concave sclerites close to posterior margin and single suboval sclerite anteriorly; membrane with or without striations, without additional sclerites; lateral oviducts widely separated, placed in anterior half of DLP, close to or at distance from lateral margins of DLP; spermathecal gland placed slightly above or slightly below midpoint of DLP; posterior wall of bursa copulatrix without tubercles or they very shallow, without sclerites, membrane on posterior wall flat or raised at each side; base of second valvula straight or slightly concave; and, ventral wall membranous.

Distribution: Known from tropical Africa and Madagascar (Fig. 24).

Host plants: The type specimens were recorded from *Piper capense* (Piperaceae) (Poppius, 1912).

Included species

Pararculanus guesquierei Schouteden, 1943
Pararculanus piperis Poppius, 1912
Pararculanus madagascariensis (Poppius, 1912) **comb. nov.** {*Arculanus*}

Discussion: Pararculanus is similar to *Mansoniella* on the basis of head structure, but differs from it in many other characters (see discussion for *Mansoniella*).

Pararculanus is also similar to *Poppiusia* and *Pachypeltis* in external and male genitalia characters, but *Poppiusia* differs by: distance between eye and pronotum shorter than eye diameter (Fig. 10B), gula 1–1.5× as long as buccula length and presence of small tubercles on dorsal wall of bursa copulatrix (Fig. 21J), presence of three small tubercles on frons (Fig. 10M), and calli separated (Fig. 10M). For the characters distinguishing *Pararculanus* from *Pachypeltis* see the discussion of *Pachypeltis*.

One of us (A.N.N.) examined the type specimens of *Pararculanus guesquierei* and *P. piperis* and determined that they are closely related. We tentatively transfer *Arcualnus madagascariensis* to *Pararculanus* in this work based on the examination of type specimens and position in phylogenetic analysis. Although it differs from other species of *Paraculanus* in many characters and might represent a new genus, we refrain from this taxonomic decision. Establishing the new genus in this case involves the revision and clear understanding the limits of the genus *Pachypeltis* (see clade 10), as it is closely related to *Pararculanus*. The type species of *Arculanus*, *A. marshalli*, does not share many diagnostic characters with *Pararculanus*, e.g. distance between antennal fossa distinctly longer than antennal fossa diameter, gula almost as long as buccula, calli separated (as in Fig. 10M), metasternum not protruding to abdominal segment II in triangular outgrowth (as in fig. 18C in Namyatova *et al*., in press), two punctures on depression delimiting calli present

(as in Fig. 10A) and auxiliary vein on membrane present and long, hemelytron broadened posteriorly, coils on ductus seminis distinct forming narrow tube (Fig. 14E), and small tubercles on dorsal labiate place present (Fig. 18D).

P. guesquierei and *P. piperis* differ from *Pararculanus madagascariensis* in more elongate body (Fig. 7), the head swollen dorsally in lateral view, ASII *c*. 1.5–2× as long as length of head and pronotum combined, labium reaching middle of mesosternum, collar not delimited posteriorly, pronotum almost without vestiture, endosoma only with fields of small spicules (Fig. 16AF). In contrast, *P. madagascariensis* can be recognized by: body more robust (Fig. 7), head almost flat dorsally in lateral view; ASII almost as long as long as head and pronotum combined, labium reaching only anterior margin of mesosternum, collar delimited posteriorly, pronotum with long setae, endosoma with v-shaped elongate spicule and without fields of small spicules (Fig. 16AB).

Despite these differences we treat *P. guesquierei*, *P. madagascarinesis* and *P. piperis* as congeneric, but the status of *P. madagascariensis* is more doubtful and will require further research.

Physophoroptera Poppius

Figures 9, 12C, 17A–D, 20Q, R, 24

Physophoroptera Poppius, 1910: 26 (gen. nov. type species *Physophoroptera mirabilis* Reuter, 1910 by monotypy); Reuter, 1910: 153 (cat.); Reuter & Poppius, 1911: 208 (descr.); Poppius, 1912: 175, 184 (key to gen., descr.); Bergroth, 1922: 52 (cat.); China, 1944: 174 (key to gen.); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 38 (key to gen.); Carvalho, 1957: 142 (cat.); Schmitz, 1968: 10 (key to gen.); Schuh, 1995: 522 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Physophoroptera belongs to the *Monalonion*-complex (see discussion for tribe), but among genera of this group it differs by: distinctly swollen scutellum with round swelling on it (Fig. 12C, fig. 12F in Namyatova *et al*., in press); swelling on corium posteriorly (fig. 12F in Namyatova *et al*., in press); ASII with apex swollen, without any tubercles, ASIII–IV distinctly swollen (fig. 8G in Namyatova *et al*., in press); eyes stylate (fig. 4D in Namyatova *et al*., in press); sclerotized part of phallotheca wide basally and distinctly tapering towards apex; ductus seminis without coils (Fig. 17A).

*Redescription:*Male: Body length 5 mm. Coloration (Fig. 9). *Head*. Reddish with brown to black markings. Texture. Body mostly smooth, without punctures, wrinkles and tubercles; vertex without flattened areas; striations on scutellum laterally absent; semicircular depression between scutellum and mesoscutum absent. Vestiture. Setae mostly absent, only short dark adpressed simple setae on ASII–IV and legs present; black spinules on femora and tibiae absent. Structure. *Head*. Distance between eye and pronotum slightly longer than eye diameter (fig. 4D in Namyatova *et al*., in press); occipital region not delimited with transverse depression; longitudinal depression on vertex indistinct; eyes stylate, directed outwards and forward, subequal to fifth part of head width (fig. 4D in Namyatova *et al*., in press); distance between antennal fossa twice as long as antennal fossa diameter; frons distinctly swollen, without ridges, outgrowths or longitudinal depression (fig. 4D in Namyatova *et al*., in press); anterior view of head *c*. 1.3–1.5× as long as wide; eye *c*. 0.8× as high as distance from eye to apex of clypeus; antennal fossa oval, subequal to 2/3 of eye height, not raised (as in fig. 6D–F in Namyatova & Cassis, 2013b), inferior margin on the same level with inferior margin of eye; base of clypeus placed at the same level with inferior margin of antennal fossa, distinctly delimited with depression; head convex dorsally in lateral view; gula almost subequal to buccula length, straight. *Labium*. Reaching posterior margin of mesosternum or slightly surpassing it; LS I twice as long as wide; LSII *c*. 3× as long as wide, subequal to LSI; LSIII *c*. 1.5× as long as slightly shorter than LSII; LSIV *c*. 3–4× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching base of cuneus or slightly surpassing it; ASI distinctly longer than wide, length subequal to head width, swollen apically (fig. 8G in Namyatova *et al*., in press); ASII *c*. 1.2–1.3× as long as ASI, *c*. 0.6× as long as head and pronotum combined, swollen apically; ASIII subequal to half of ASII, clavate; ASIV subequal to or slightly longer than ASIII, clavate (fig. 8G in Namyatova *et al*., in press). *Thorax*. Collar weekly delimited, fused with callosite region posteriorly, flat (fig. 4D in Namyatova *et al*., in press); calli separate, flat, almost indistinct (fig. 4D in Namyatova *et al*., in press); humeral angles of pronotum not dilated, rounded or acute (fig. 4D in Namyatova *et al*., in press); depression delimiting calli posteriorly absent; posterior margin of pronotum slightly concave (fig. 4D in Namyatova *et al*., in press); scutellum distinctly swollen with round swelling medially (fig. 12F in Namyatova *et al*., in press), distinctly rounded apically, without longitudinal depression or ridge medially; metepimeron enlarged, *c*. 1.5× as long as wide, angulate and subtriangular (as in Fig. 13E); metasternum rounded, without medial projection on to abdominal segment II (as in fig. 17B in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight; hemelytra tapering apically; margins of claval commissure *c*. 0.8–1× as long as scutellum, curved posteriorly (fig. 12F in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial

fracture subparallel to R + M; corium with distinct swelling posteriorly (fig. 12F in Namyatova *et al*., in press); cuneus twice as long as wide, *c*. 0.8× as long as pronotum, medial margin concave; membrane cell distinctly surpassing apex of cuneus, forming right angle, *c*. 1.1–1.3× as long as pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 0.5–0.7× as long as membrane. *Legs*. Forecoxae separated (as in fig. 17B in Namyatova *et al*., in press); femora distinctly swollen apically, forefemora almost straight, middle and hind femora distinctly curved; tibia without swellings; foretibia shorter than head and pronotum combined; segment I of hind tarsus distinctly longer than segment II and slightly longer than segment III (as in fig. 19A in Namyatova *et al*., in press); apical half of claw curved; basal tooth on claw elongate, straight (fig. 10H in Namyatova *et al*., in press). *Genitalia* (Fig. 17A–D). Genital capsule slightly longer than wide, without outgrowth(s), ventral wall shortened anteriorly; left paramere only slightly curved, twice as long as right paramere; phallobase sclerite of primary gonopore heart-shaped, without outgrowth(s); ductus seminis not sclerotized basally or apically, shorter than phallotheca, without coils, attached to phallobase medially; sclerotized part of phallotheca wide basally tapering towards apex, acute apically, with swelling on right-hand side; endosoma without sclerotization.

Female: Body length 5–7 mm. Coloration, surface, vestiture and structure as in males. *Genitalia* (Fig. 20Q, R). DLP without sclerotized rings or bands, only with curved sclerite anteriorly; DLP entirely striated; lateral oviducts placed anteriorly near lateral margins of DLP, distinctly removed from each other; spermathecal gland in anterior half, above midpoint; posterior wall of bursa copulatrix with small tubercles, without outgrowths or sclerites; ventral wall of bursa copulatrix membranous; base of second valvula concave.

Distribution

Belgian Congo, Tanzania, South Africa (Fig. 24).

Host plants

Unknown.

INCLUDED SPECIES

Physophoroptera mirabilis Poppius, 1910

Discussion:Physophoroptera was previously placed in the subtribe Monaloniina *sensu* Schuh and it is similar only to *Physophoropterella*, which also has: ASII swollen apically, ASIII–IV clavate; scutellum swollen with outgrowth, swellings on corium posteriorly, eyes stylate, and sclerotized part of phallotheca tapering. The latter genus differs by the following characters: frons straight (Fig. 10E), ASII with tubercles basally; foretibia longer than head and pronotum combined; outgrowth on scutellum narrow and bifurcating (Figs 11K, 12D), and ductus seminis with distinct coils (Fig. 17E).

Physophoropterella Poppius

Figures 9, 10E, 11K, 12D, 13G, I, 17E–H, 20S, T, 22

Physophoropterella Poppius, 1914: 128 (gen. nov.; type species: *Physophoropterella bondroiti* Poppius, 1914 by monotypy); Bergroth, 1922: 54 (cat., syn.); China, 1944: 174 (key to gen.); Carvalho, 1952: 59 (cat.); Carvalho, 1955: 39 (key to gen.); Carvalho, 1957: 142 (cat.); Schmitz, 1968: 10 (key to gen.); Schuh, 1995: 522 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Mandragora Schumacher, 1917: 449 (gen. nov.; type species *Mandragora venefica* Schumacher, 1914 by initial designation, synonymized by Bergroth, 1922: 54); Carvalho, 1957: 142 (cat.); Schuh, 1995: 522 (cat.).

Diagnosis:Physophoropterella belongs to the *Monalonion*-complex, and is distinguished by the following characters: distinctly swollen scutellum with bifurcated outgrowths on it (Figs 11K, 12D); swelling on corium posteriorly (as in fig. 12F in Namyatova *et al*., in press); ASII swollen apically, with tubercles also basally; ASIII–IV distinctly clavate; eyes stylate (Fig. 10E); medial margin of clavus as long as scutellum length; foretibia longer than head and pronotum combined; sclerotized part of phallotheca wide basally and distinctly tapering towards apex; ductus seminis with distinct coils (Fig. 17E).

*Redescription:*Male: Body length 7–9 mm. Coloration (Fig. 9). *Head*. Mostly yellow with brown to black markings, with reddish markings on antennae. Texture. Body mostly smooth, without punctures, wrinkles and tubercles; vertex without flattened areas; striations on scutellum laterally present; semicircular depression between scutellum and mesoscutum absent. Vestiture. Setae mostly absent, only present on costal margin of hemelytron anteriorly, antenna, legs and abdomen with short simple adpressed or suberect setae; black spinules on femora absent, spinules on tibia irregularly distributed (as in fig. 19F in Namyatova *et al*., in press). Structure. *Head*. Distance between eye and pronotum slightly shorter than eye diameter (Fig. 10E); occipital region delimited with shallow depression; longitudinal depression on vertex almost subequal to eye diameter, often shallow; eyes stylate, directed

outwards and forward, subequal to forth part of head width (Fig. 10E); distance between antennal fossae subequal to or slightly longer than antennal fossa diameter; frons straight or only slightly convex, without ridges, outgrowths or longitudinal depression (Fig. 10E); anterior view of head *c*. 1.3–1.5× as wide as high; eye height subequal to distance from eye to apex of clypeus; antennal fossa oval, almost subequal to eye height, not raised (as in fig. 6D–F in Namyatova & Cassis, 2013b), inferior margin placed slightly above inferior margin of eye; base of clypeus placed slightly below inferior margin of eye; delimited with very shallow depression; head convex dorsally in lateral view; gula subequal to buccula length, straight. *Labium*. Reaching middle of mesosternum; LSI *c*. 1.5× as long as wide; LSII twice as long as wide, subequal to LSII, LSIII *c*. 1.5× as long as wide subequal to or slightly shorter than LSII; LSIV *c*. 2–3× as long as wide, slightly longer than LSIII. *Antenna*. Reaching or almost reaching apex of membrane; ASI distinctly longer than wide, *c*. 1.8× as long as head width, swollen apically with additional swelling medially; ASII *c*. 0.9× as long as ASI, *c*. 1.1–1.2× as long as head and pronotum combined, swollen apically and with small tubercle near base; ASIII *c*. 0.6× as long as ASII, distinctly swollen, but narrow basally; ASIV *c*. 0.6× as long as ASIII, clavate (fig. 8G in Namyatova *et al*., in press). *Thorax*. Collar not delimited; calli separated, flat, almost indistinct (Fig. 10E); depression delimiting calli posteriorly absent (Fig. 10E); humeral angles of pronotum acute (Fig. 10E); posterior margin of pronotum straight, with paired large swellings (Fig. 10E); scutellum distinctly swollen with bifurcate outgrowth, distinctly obtuse apically, without longitudinal outgrowth or ridge medially (Figs 11K, 12D); metepimeron enlarged, twice as long as wide, angulate and subtriangular (as in Fig. 13E); metasternum rounded posteriorly, without medial projection on to abdominal segment II (fig. 17B in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight, hemelytra slightly tapering posteriorly; claval commissure *c*. 0.9–1× as long as scutellum, slightly concave; R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M (as in fig. 12F in Namyatova *et al*., in press); corium with distinct swelling posteriorly (as in fig. 12F in Namyatova *et al*., in press); cuneus *c*. 2.2–2.3× as long as wide, *c*. 1.1–1.2× as long as pronotum, medial margin slightly concave (as in fig. 13C in Namyatova *et al*., in press); membrane cell *c*. 1.5× as long as pronotum, forming acute angle (as in fig. 13C in Namyatova *et al*., in press); auxiliary vein absent; distance from cell to apex of membrane subequal to half of cell length. *Legs*. Forecoxae separated (as in fig. 17B in Namyatova *et al*., in press); femora distinctly swollen apically, fore- and middle femora almost straight, hind femora curved; swellings on femora in apical half and on tibiae in basal part present (Fig. 13G); foretibia longer than head and pronotum combined; segment I of hind tarsus *c*. 3× as long as segment II and III each, segment II subequal to segment III (Fig. 13I); claw broadly rounded (fig. 10H in Namyatova & Cassis, 2013b); basal tooth on claw short, triangular (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 17E–H). Genital capsule as long as wide, without outgrowth(s), its ventral wall shortened anteriorly; left paramere only slightly curved, *c*. 2.5× as long as right paramere; phallobase sclerite of primary gonopore subtriangular or suboval, without outgrowth(s); ductus seminis longer than phallotheca, not sclerotized basally or apically, with distinct coils forming wide tube, attached to phallobase on left-hand side; sclerotized part of phallotheca wide basally, tapering towards apex and acute apically, without outgrowths or ridges; endosoma with sclerotized area basally.

Female: Body length 10–11 mm. Coloration, surface, vestiture and structure as in males (Fig. 9). *Genitalia* (Fig. 20S, T). DLP with sclerotized bands thin, indistinct posteriorly; DLP with some striations medially and posteriorly; lateral oviducts placed in posterior half near lateral margins, distinctly removed from each other, spermathecal gland placed close to posterior margin, medially; posterior wall of bursa copulatrix with small tubercles; without outgrowths or sclerotizations; base of second valvula distinctly concave; ventral wall of bursa copulatrix membranous.

Distribution: Known from tropical Africa (Fig. 22).

Host plants: Physophoropterella denticollis and *P. poppiusi* were recorded damaging *Dacryodes edulis* H.J.Lam (Burseraceae) (China, 1945; Ndindeng *et al*., 2006).

Included species

Physophoropterella bondroiti Poppius, 1914
Physophoropterella denticollis (Reuter & Poppius, 1911)
Physophoropterella poppiusi Schouteden, 1942
Physophoropterella venefica (Schumacher, 1917)

Discussion: Physophoropterella was previously included in the subtribe Monaloniina *sensu* Schuh and is similar to *Physophoroptera* (see discussion of latter genus). Amongst species included in *Physophoropterella*, we examined the types and additional material of *P. bondroiti* and *P. denticollis*, which are very similar to each other, differing only slightly in the structure of the antenna and male genitalia. We did not examine specimens of *P. poppiusi* or *P. venefica*, but based on the original descriptions, we consider them to be also congeneric.

PLATYNGOMIRIS KIRKALDY

Figures 8, 21E, F, 23

Platyngomiris Kirkaldy, 1902: 258 (gen. nov.; type species: *Platyngomiris coreoides* Kirkaldy, 1902 by monotypy); Kirkaldy, 1906: 134 (list); Reuter, 1910: 153 (cat.): Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 148 (cat.); Miller & China, 1957: 430 (key to gen.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.).

Platyngomiriodes Ghauri, 1963 (gen. nov.; type species *Platyngomiriodes apiformis* Ghauri, 1963 by monotypy); Lavabre, 1977a: 51, 54 (key to gen., descr.); Lavabre, 1977b: 108 (disc.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.), syn. nov., this work.

Diagnosis: Platyngomiris belongs to the *Odoniella*-complex (see discussion for the tribe) and is recognized by the following characters: ASIII distinctly incrassate apically, ASIV clavate (as in fig. 8E in Namyatova *et al*., in press); frons with paired tubercles; scutellum distinctly swollen (as in Fig. 11H), exceeding height of pronotum, subtriangular, not subdivided into lower and upper parts (as in Fig. 12A), hemelytron clothed simple setae only, hind tibiae with tumescences and clothed with long and extremely dense setae.

*Redescription:*Female: Body length 9.5 mm. COLORATION (Fig. 8). Coloration mainly brown, hemelytron mostly pale, almost yellow, but cuneus brown. TEXTURE. Tubercles on vertex and flattened areas indistinct; wrinkles on head absent; ASII without tubercles; pronotum and scutellum punctate; tubercles on collar very shallow; shallow tumescences on pronotum and scutellum present; row of punctures on clavus and on R + M and punctures on depression delimiting calli posteriorly absent; striations on lateral margins of scutellum indistinct or present only anteriorly; hind tibia with tumescences; semicircular depression between scutellum and mesoscutum absent; hemelytron smooth, without tubercles. VESTITURE. Body clothed with pale or dark simple adpressed setae, those setae pale on dorsum and dark on appendages; setae on hind tibia extremely long and dense; flattened setae on hemelytron absent. STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (as in Fig. 10F); occipital region not delimited with depression; longitudinal depression on vertex indistinct or very short; eyes stylate, directed outwards (as in Fig. 10H), *c*. 0.25× as long as head width; distance between antennal fossa *c*. 3× as long as antennal fossa diameter; frons distinctly swollen, with paired tubercles, without longitudinal depression or ridges; anterior view of head *c*. 1.5× as wide as high; eye height *c*. 0.8× as distance from eye to apex of clypeus; antennal fossa oval, *c*. 0.3× as long as eye height, not raised (as in fig. 3B in Namyatova *et al*., in press), its inferior margin placed near inferior margin of eye and base of clypeus; base of clypeus distinctly delimited basally; in lateral view head flat; gula shorter than buccula length, straight. *Labium*. Reaching posterior margin of metasternum; LSI *c*. 2–3× as long as wide; LSII *c*. 4× as long as wide, slightly longer than LSI; LSIII *c*. 4× subequal to LSII; LSIV *c*. 6× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 1.5–2× as long as wide, subequal to quarter of head width, swollen basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 5× as long as ASII, *c*. 0.8× as long as head and pronotum combined, slightly incrassate apically, without tumescences; *Thorax*. Collar not delimited, flat; calli separated, flat; depression delimiting calli posteriorly absent (as in fig. 4C in Namyatova *et al*., in press); humeral angles of pronotum dilated; posterior margin of pronotum distinctly concave, forming right angles, scutellum distinctly swollen, triangular (as in Fig. 11H), not covering base of pronotum, not divided into parts (as in Fig. 12A), obtuse apically, without longitudinal depression, ridge or outgrowth; metepimeron *c*. 1.5× as high as long, angulate (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Tapering posteriorly; costal margin straight (as in fig. 12E in Namyatova *et al*., in press); claval commissure *c*. 0.2× as long as scutellum, straight; R + M almost reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus *c*. 1.7× as long as wide, *c*. 0.6× as long as pronotum, medial margin slightly concave; membrane cell distinctly surpassing apex of cuneus, forming acute angle, *c*. 0.9× as long as pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 0.79× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight, hind tibia often slightly curved; foretibia shorter than head and pronotum combined. *Genitalia* (Fig. 21E, F). DLP with a single sclerotized ring anteriorly, *c*. 1.5× as long as wide; with paired areas of striations, placed at base of lateral oviducts; lateral oviducts in posterior half of DLP; spermathecal gland placed medially at posterior margin; posterior wall with small tubercles, without outgrowths with paired sclerotization posteriorly; base of second valvula concave; ventral wall membranous.

Distribution: Known from Borneo only (Fig. 23).

Host plants: The genus is known as a pest of cocoa (Ghauri, 1963; Leston, 1970; Azhar, 1989; Keane & Putter, 1992; Schaefer & Panizzi, 2000).

Included species

Platyngomiris coreoides Kirkaldy, 1902 = P. apiformis (Ghauri, 1963), syn. nov., this work.

Discussion: Our treatment of this taxon is based on a single female, and images of types from the Natural History Museum, London. It is, however, apparently widely distributed in Sabah (Azhar, 1989).

Platyngomiris is similar to *Pseudodoniella* and *Rhopaliceschatus*, and they can be separated by the setation on the hind tibia not being densely and regularly distributed. Additionally, in *Rhopaliceschatus* the tumescences on the pronotum and scutellum are absent, the scutellum has four dark markings and the hemelytron has flattened setae.

The latter three genera form a clade based on the weighted strict consensus tree (Figs 2, 4); they are also all distributed in the South-East Asia. However, the only unique character for the clade is the presence of sclerotization on the posterior region of the posterior wall of the bursa copulatrix (as in Fig. 21B, F), although we did not find it in *Rhopaliceschatus*. However, our observation for *Rhopaliceschatus* is, based on a single specimen that one of us (A.N.N.) examined, that the posterior wall of the bursa copulatrix was too cleared and the sclerites could not be distinguished.

The phylogenetic relationships of the species within this group of genera are obscure, and there is some doubt as to whether *Pseudodoniella* is monophyletic. There are also some characters that infer closer relationships between some of the species within genera of the *Odoniella*-complex. *Platyngomiris coreoides* and *Platyngomiriodes apiformis* are very similar externally and both are from Borneo. We compared their female genitalia and found the bursa copulatrix of these two species to be identical, and propose *P. apiformis* as a junior synonym of *P. coreoides* (Fig. 8). This species is also clothed with simple setae only, whereas many allied species are clothed with flattened setae, except for *Pseudodoniella pacifica*.

Pseudodoniella pacifica differs from *Pseudodoniella chinensis* and *Pseudodoniella typica* in the following characters: elongate body, scutellum subtriangular, and hemelytron clothed only with simple setae; whereas in species of the latter two species the body is shorter, scutellum is round, and hemelytron is clothed mainly with flattened dark setae. The external characters of *Pseudodoniella pacifica*, including coloration, setation and subtriangular scutellum, are very similar to those of *Platyngomiris*.

Pseudodoniella chinensis and *P. typica* are similar to *Rhopaliceschatus quadrimaculatus*, with the last named differing in the absence of tumescences on the pronotum and scutellum. Specimens of *P. typica* also differ from *R. quadrimaculatus* in having thicker antennae.

In *Pseudodoniella chinensis*, *Platyngomiris coreoides* and *Rhopaliceschatus quadrimaculatus* the sclerotized circle on the DLP is very short, almost as long as wide (Figs 19R, 21E), which never occurs in other monaloniine groups. However, in *Psedodoniella typica* and *P. pacifica* it is 2.5× as long as wide (Fig. 21A). The latter structure is similar to many other genera formerly placed in the Odoniellini. In *P. chinensis* and *P. coreoides* the spermathecal gland is placed medially (Fig. 21E), whereas in all other species it is positioned to the right of the midline (Figs 19R, 21A).

Although the characters show that the genera *Platyngomiris*, *Pseudodoniella* and *Rhopaliceschatus* are closely related to each other, the morphological characters do not resolve their relationships, and we refrain from any nomenclatorial changes pending further revision of this group.

Pseudodoniella Kirkaldy

Figures 8, 11F, H, 17M–P, 21A, B

Pseudodoniella China & Carvalho, 1951: 465 (gen. nov.; type species *Pseudodoniella pacifica* China & Carvalho, 1951 by monotypy); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 148 (cat.); Miller & China, 1957: 430 (key to gen.); Miller, 1958: 57 (disc., key to spp.); Odhiambo, 1962: 303, 305 (syn., key to spp.); Lavabre, 1977a: 51, 55 (key to gen., descry.); Lavabre, 1977b: 109 (key to spp., descr.); Carvalho, 1981: 36, 37 (key to gen., descr.); Schuh, 1995: 530 (cat.); Schuh, 2002–2013 (cat.).

Parabryocoropsis China & Carvalho, 1951: 468 (gen. nov.; type species *Parabryocoropsis typicus* China & Carvalho, 1951 by monotypy, synonymized by Odhiambo, 1962: 303); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 147 (cat.); Miller, 1958: 57 (disc); Steyskal, 1973: 206 (correction); Carvalho, 1981: 36 (key to gen., descr.); Schuh, 1995: 531 (cat.).

Diagnosis: Pseudodoniella belongs to the *Odoniella*-complex and is distinguished by the following characters: ASIII distinctly incrassate apically, ASIV clavate (as in Fig. 8E in Namyatova *et al*., in press); frons with bifurcate outgrowth or paired tubercles (as in fig. 4C in Namyatova *et al*. in press); pronotum and scutellum with tumescences (Fig. 11F, H, as in Fig. 4C in Namyatova *et al*. in press); scutellum distinctly swollen (Fig. 11F, H) and uniformly colored, not subdivided into lower and upper parts (as in Fig. 12A), tibiae without distinct tumescences and with regular setation, not very dense.

Redescription: Male: Body length 7–10 mm. Coloration (Fig. 8). Body varying from pale brown, to dark brown, sometimes mostly orange or reddish, can be brown with orange markings or orange with dark

markings, or uniformly colored. TEXTURE. Two pairs of tubercles on vertex between eyes medially more or less distinct, sometimes indistinct, flattened areas on vertex indistinct; wrinkles on head absent; tumescences on ASII absent or present; pronotum and scutellum covered with punctures (as in fig. 4C in Namyatova *et al*. in press); collar with two pairs of shallow tubercles, sometimes indistinct; shallow tumescences on pronotum and scutellum present (as in fig. 4C in Namyatova *et al*. in press); row of punctures on clavus and on R + M and punctures on depression delimiting calli posteriorly absent; striations on lateral margins of scutellum indistinct or present only anteriorly; semicircular depression between scutellum and mesoscutum absent; hemelytron smooth, without tubercles. VESTITURE. Head, pronotum scutellum, thoracic pleura and abdomen clothed with pale or dark simple adpressed setae, sometimes those setae very rare; hemelytron mostly clothed with flattened dark setae, with cuneus clothed with simple setae; sometimes hemelytron clothed with pale short simple adpressed setae only; antenna with pale or dark simple setae, long or short; setae on legs adpressed or suberect pale or dark, of variable length, not very dense, spinules on femora present or absent apically; spinules on tibia irregularly distributed (as in fig. 18F in Namyatova *et al*. in press). STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (as in Fig. 10F); occipital region not delimited with depression; longitudinal depression on vertex indistinct or very short; eyes stylate, directed outwards (as in Fig. 10F), *c*. 0.16–0.25× as long as head width; distance between antennal fossa *c*. 2–3× as long as antennal fossa diameter; frons distinctly swollen, with paired outgrowths (as in fig. 4C in Namyatova *et al*., in press), sometimes only shallow paired tubercles present, without longitudinal depression or ridges; anterior view of head *c*. 1.6–2.1× as wide as high; eye height *c*. 0.8–1.5× as distance from eye to apex of clypeus; antennal fossa oval, *c*. 0.5–0.7× as long as eye height, not raised (as in fig. 3B in Namyatova *et al*., in press), its inferior margin placed near inferior margin of eye; or base of clypeus placed slightly above or near inferior margin of eye, distinctly delimited basally; in lateral view head flat; gula shorter than buccula length, straight. *Labium*. Reaching posterior margin of metasternum; LSI twice as long as wide; LSII *c*. 3–4× as long as wide, subequal to or slightly longer than LSI; LSIII *c*. 4× as long as wide, subequal to LSII; LSIV *c*. 4–5× as long as wide, *c*. 1–1.5× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 1.5–2× as long as wide, subequal to quarter of head width, swollen basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 5–6× as long as ASII, *c*. 0.8–1× as long as head and pronotum combined, slightly or distinctly incrassate apically; ASIII *c*. 0.6–0.8× as long as ASII; widened towards apex or swollen apically; ASIV *c*. 0.7–0.9× as long as ASIII, clavate (as in fig. 8E in Namyatova *et al*., in press). *Thorax*. Collar not delimited or delimited posteriorly, flat (as in fig. 4C in Namyatova *et al*., in press); calli separated, flat; depression delimiting calli posteriorly absent; humeral angles of pronotum distinctly dilated (as in fig. 4C in Namyatova *et al*., in press); posterior margin of pronotum distinctly concave, forming right angles (Fig. 11F, H) scutellum distinctly swollen, often covering, rarely not covering base of pronotum, round or subtriangular (Fig. 11F, H), not divided into parts (as in Fig. 12A), obtuse apically, without longitudinal depression, ridge or outgrowth; metepimeron *c*. 1–1.5× as long as wide, angulate (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Tapering posteriorly; costal margin straight; claval commissure *c*. 0.3× as long as scutellum, straight; R + M almost reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus *c*. 1.5–2.3× as long as wide, *c*. 0.5–0.6× as long as pronotum, its medial margin slightly concave; membrane cell slightly or distinctly surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), *c*. 0.7–1× as long as pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 0.7–1.0× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight, hind tibia often slightly curved; foretibia shorter than head and pronotum combined; tibia without tumescences; segments of hind tibia subequal in length or segments I subequal to segment III and longer than segment II; apical half or third part of claw curved; basal tooth on claw elongate, straight or slightly concave (as in Fig. 13J). *Genitalia* (Fig. 17M–P). Genital capsule as wide as long or slightly wider than long, without outgrowth, ventral wall not shortened anteriorly; left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore subtriangular, with anterior margin concave, without outgrowths; ductus seminis not sclerotized basally or apically; shorter than or as long as phallotheca, with coils forming wide tube, attached to phallobase medially; phallotheca narrow, occupying half of dorsal side, only slightly tapering apically; without ridge or outgrowths; endosoma with sclerotized areas.

Female: Body length 8–10.5 mm. Coloration, surface, vestiture and structure as in male, but females slightly larger than males (Fig. 8). *Genitalia* (Fig. 21A, B). DLP with a single sclerotized ring anteriorly, *c*. 2–2.5× as long as wide; with two large areas of striations, mostly subequal in diameter,; lateral oviducts attached at middle of those striated areas, widely

separated, placed near lateral margin and at a halfway of DLP or in posterior half; spermathecal gland placed on right-hand side; posterior wall with small tubercles, without outgrowths with paired sclerotization posteriorly; base of second valvula concave; ventral wall membranous.

Distribution: Known from China and New Guinea (Fig. 22).

Host plants: Pseudodoniella pacifica and *P. typica* are pests of cocoa (Leston, 1970; Entwistle, 1977; Lavabre, 1977b; Carvalho, 1981; China & Carvalho, 1951). *Pseudodoniella pacifica* was also recorded from *Ficus pungens* (Carvalho, 1981) (Moraceae) and *P. typicus* is the pest of *Cinnamomum cassia* (Lauraceae) (Zheng, 1992). Unidentified representatives of *Pseudodoniella* were also recorded from *Ficus* sp. (Hill, 1983).

Included species

Pseudodoniella chinensis Zheng, 1992)
Pseudodoniella pacifica China and Carvalho, 1951
Pseudodoniella typica (China and Carvalho, 1951)

Discussion: Miller & China (1957) described two new genera, *Pseudodoniella* and *Parabryocoropsis*. They compared *Pseudodoniella* with *Odoniella*, *Volkelius* and *Rhopaliceschatus*, noting that it differs from them by 'the frontal tubercle and shape of scutellum'. China and Miller (1957) compared *Parabryocoropsis* only with *Bryocoropsis* and *Distantiella*. Odhiambo (1962) synonymized *Parabryocoropsis* with *Pseudodoniella* with a detailed explanation of his decision. Carvalho (1981) followed his own initial views and Schuh (1995) supported the views of Odhiambo (1962).

We confirm that *P. pacifica* is different from *P. typica* and *P. chinensis*, having only simple setae on hemelytron, subtriangular scutellum and yellow to orange coloration, whereas two other species are brown, with round scutellum and flattened setae on hemelytron. However, we also follow the opinion of Odhiambo (1962) pending a thorough revision of the group, which includes *Pseudodoniella* and closely related genera, *Pseudodoniella* and *Rhopaliceschatus* (see discussion for *Platyngomiris* for further explanation and comparison of those genera).

Poppiusia China

Figures 7, 10B, L, M, 13C, 17I–L, 21I, J, 24

Poppiusia China, 1944: 184 (gen. nov.; type species: *Poppiusia combretorum* China, 1944 jun. syn. of *Poppiusia leroyi* (Schouteden, 1943) by monotypy); China, 1944: 176 (key); Schouteden, 1945: 116 (disc); Schouteden, 1946: 285 (disc); Carvalho, 1952: 59 (cat.), Carvalho, 1955: 39 (key); Carvalho, 1957: 143 (cat.); Schmitz, 1968: 11 (key to gen.); Schuh, 1995: 522 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Among species with row of punctures on clavus and R + M, *Poppiusia* differs in following: presence of three small ridges on frons (Fig. 10M); head distinctly swollen in lateral view (Fig. 10L); ASII subequal to head and pronotum combined, filiform; ASIII–IV not clavate; labium slightly surpassing posterior margin of prosternum, its segments I-II only twice as long as wide; pair of punctures on depression delimiting calli absent; calli separated (Fig. 10B); setae on pronotum present; metepimeron *c*. 3–4× as long as wide, subtriangular (Fig. 13C); membrane cell forming right angle; ductus seminis shorter than phallotheca, without coils; outgrowths supporting ductus seminis long (Fig. 17I).

*Redescription:*Male: Body length 7–9 mm. Coloration (Fig. 7). Body mostly orange to pale brown with brown to dark brown or reddish areas, antennae uniformly dark brown; hemelytra often mostly dark with yellow to pale brown areas. Texture. Body smooth; vertex without wrinkles, tubercles or flattened areas; pronotum and scutellum mostly impunctate, without tubercles, only pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum, and rows on punctures on clavus and on R + M present (as in fig. 11C, D in Namyatova *et al*., in press); punctures on depression delimiting calli posteriorly absent (fig. 11D in Namyatova *et al*., in press); semicircular depression between scutellum and mesoscutum present (as in Fig. 11A). Vestiture. Body clothed with suberect dark or pale setae, setae on tibiae and abdomen longer than those on dorsum and pleura some of them twice as long as hind tibia width; black spinules on femora absent; tibiae regularly setose; spinules on tibiae organized in rows (as in fig. 18D in Namyatova *et al*., in press). Structure. *Head*. Distance between eye and pronotum subequal to eye diameter (Fig. 10B); depression delimiting occipital region distinct (Fig. 10L); longitudinal depression on vertex indistinct; eyes not stylate, in line with contour of head (Fig. 10B), *c*. 0.3× as wide as head; distance between antennal fossa twice as long as antennal fossa diameter; frons swollen, with three longitudinal ridges (Fig. 10M), without longitudinal depression; anterior view of head *c*. 1.3–1.4× as wide as high; eye almost twice as long as distance from eye to apex of clypeus; antennal fossa round, its diameter subequal to third part of eye height (as in fig. 3A in Namyatova *et al*., in press), tuberculate (Fig. 10L), its inferior margins placed slightly above inferior margin of eye; base of clypeus placed on the same level with inferior margin of antennal fossa, delimited with

depression; in lateral view head distinctly swollen dorsally (Fig. 10L); gula *c*. 1.5× as long as buccula length, straight. *Labium*. Reaching or slightly surpassing anterior margin of mesosternum; LSI and II twice as long as wide, almost subequal in length or LSII slightly longer than LSI; LSIII *c*. 1.5× as long as wide, slightly shorter than LSII; LSIV *c*. 2.5× as long as wide, twice as long as LSIII. *Antenna*. Reaching apex of cuneus; ASI only slightly shorter than head width, widened medially (fig. 9D in Namyatova *et al*., in press); ASII *c*. 3× as long as ASI, subequal to length of head and pronotum combined; ASIII *c*. 0.6–0.7× as long as ASII; ASIV slightly longer than half of ASIII length; ASII–IV filiform. *Thorax*. Collar distinct, fused with calli posteriorly, slightly swollen; calli separated from each other, rounded, not conical; depression delimiting calli posteriorly distinct laterally, but indistinct between calli; humeral angles of pronotum rounded, not dilated; posterior margin of pronotum concave (Fig. 10B); scutellum almost flat, acute apically, without outgrowth; metepimeron enlarged 3× as long as wide, angulate (Fig. 13C); metasternum extending to abdominal segment II in triangular outgrowth (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margins subparallel, hemelytron not tapering; claval commissure almost twice as long as scutellum, straight (as in fig. 11C in Namyatova *et al*., in press); R + M distinct, reaching posterior margin of corium; medial fracture inclined towards midline; corium without swelling posteriorly; cuneus *c*. 1.7–2× as long as wide, *c*. 0.8× as long as pronotum; its medial margin straight; membrane cell distinctly surpassing apex of scutellum, forming almost right angle (as in fig. 13A in Namyatova *et al*., in press), slightly longer than pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 0.6–0.7× as long as cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, fore- and middle femora straight, hind femur moderately curved; swellings on tibiae absent; foretibia shorter than head and pronotum combined; segment I of hind tarsus subequal to segment II and slightly shorter than segment III; apical third of claw curved; basal tooth on claw three times as long as wide, distinctly concave (as in Fig. 13K). *Genitalia* (Fig. 17I–L). Genital capsule slightly longer than wide, without outgrowths, ventral wall not shortened anteriorly; left paramere r-shaped, *c*. 1.5× as long as right paramere; sclerite around primary suboval, with long outgrowths, supporting ductus seminis; ductus seminis not sclerotized basally or apically, slightly shorter than phallotheca length, without coils, attached to phallobase medially; sclerotized part of phallotheca broad, occupying entire dorsal part, rounded apically, without outgrowths and ridges; endosoma without spicules.

Female: Body length 9–10 mm. Coloration similar to male, abdomen reddish (Fig. 7). Surface and vestiture as in male, setae on abdomen dark and suberect of different length, sometimes twice as long as hind tibia width. Structure similar to male, but body generally larger, pronotum wider than in male, and hemelytron slightly widened posteriorly. *Genitalia* (Fig. 21I, J). DLP with two distinct sclerotized bands, without striations or sclerites, lateral oviducts and spermathecal gland placed posteriorly, not shifted right or left, lateral oviducts distinctly removed from each other, but placed far from lateral margins of DLP; posterior wall of bursa copulatrix with small tubercles, without sclerites; base of second valvula distinctly swollen; ventral wall membranous.

Distribution: Known from Ghana and Democratic Republic of Congo (Fig. 24).

Host plants: Poppiusia leroyi was recorded from *Combretum* sp. and *Combretorum racemosum* (Combretaceae) (China, 1944; Leston, 1980).

Included species

Poppiusia leroyi (Schouteden, 1943)
Poppiusia kapangensis (Schouteden, 1943)

Discussion: Dimia and *Eupachypeltis* also possess three ridges on the frons (as in Fig. 10M). See the discussion sections for *Dimia* and *Eupachypeltis* on characters distinguishing them from *Poppiusi*a.

Poppiusia is composed of two described species: *P. leroyi* and *P. kapangensis*. They were originally described in the genus *Arculanus*, but are demonstrably not members of it (see discussion for *Arculanus*). We have examined type material of both species, as well as additional specimens, and determined that they are very closely related to each other.

Ragwelellus Odhiambo

Figures 9, 10J, 17Q–X, 21G, H, K–O, 24

Ragwelellus Odhiambo, 1962: 314 (subgen. nov.; type species *Eucerocoris peregrinus* Odhiambo, 1962 by original designation, jun. syn. of. *Eucerocoris vittatus* Odhiambo, 1962); Carvalho, 1976: 54 (disc.); Odhiambo, 1965: 22 (descr., disc., changed status); Schuh, 1995: 523 (cat.); Schuh, 2002–2013 (cat.); Namyatova & Cassis, 2013a: 101 (disc.); Namyatova & Cassis, 2013b: 706 (disc., phylogeny); Namyatova *et al*., in press (phylogeny); rev. status, this work.

Ragwelellus (*Narinellus*) Odhiambo, 1965: 22 (subgen nov.; type species *Ragwelellus thetis* (Kirkaldy, 1908) by original designation); syn. nov., this work.

Diagnosis: Ragwelellus belongs to the *Monalonion*-complex (see discussion for the tribe), and it is differentiated from other genera of this group by: ASI longer than head and pronotum combined; frons not swollen or only slightly convex (Fig. 10J); forefemora curved; scutellum without spine-like projection; pretarsal claw broadly rounded (fig. 10E in Namyatova & Cassis, 2013b); phallotheca usually more or less rounded or only slightly tapering apically (Fig. 17Q, U).

Redescription: Male: Body length 4–10 mm. COLORATION (Fig. 9). Variable, mostly pale brown, brownish or reddish, often not uniformly colored with head and pronotum at least partly darker than hemelytron or with markings on hemelytron. TEXTURE. Body mostly smooth, without punctures and tubercles; vertex without flattened areas; semicircular depression between scutellum and mesoscutum absent; striations on scutellum laterally absent; only small depression on anterior angle of pronotum present (as in fig. 9H in Namyatova & Cassis, 2013b). VESTITURE. Setae on dorsum and thoracic pleura absent; pale simple setae on sides of head, labium, appendages and abdomen present; setae on sides on head, labium and abdomen mostly adpressed and short, setae on abdomen very rare, present apically only; setae on antenna mostly short, suberect or adpressed, sometimes setae on antenna segment II longer than hind tibia width; setae on femora rare and adpressed, often present apically only; setae on tibiae short, mostly spine-like, suberect, not very dense; apex of tibia and tarsi with adpressed short setae; black spinules on femora absent, spinules on tibiae absent or present only apically. STRUCTURE. *Head*. Distance between eye and pronotum subequal to half of eye diameter (Fig. 10J); occipital region delimited with depression, sometimes very shallow; longitudinal depression distinct, almost as long as or longer than eye diameter; eyes not stylate, in line with contour of head (Fig. 10J), *c*. 0.2–0.33× as long as head width; distance between antennal fossa subequal to or slightly longer than antennal fossa diameter; frons straight or only slightly convex (Fig. 10J), without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.4–1.5× wide as high; eye height *c*. 1.6–2.2× as long as distance between eye and apex of clypeus; antennal fossa oval *c*. 0.5–0.7× as long as eye height, not raised (as in fig. 6D–F in Namyatova & Cassis, 2013b), its inferior margin placed distinctly above inferior margin of eye; base of clypeus placed slightly below than or near inferior margin of antennal fossa, slightly delimited or not delimited basally with depression; head more or less swollen in lateral view; gula *c*. 2–3× as long as buccula, convex. *Labium*. Length varying from slightly surpassing posterior margin of mesosternum to reaching abdominal LSII; LSI *c*. 2–3× as long as wide; LSII *c*. 2.5–5× as long as wide, subequal to, slightly shorter or longer than LSI; LSIII *c*. 3–4× as long as wide, subequal to, slightly shorter or longer than LSI; LSIV *c*. 6–12× as long as wide, *c*. 1.5–3× as long as LSIII. *Antenna*. About 1.5–2× as long as body; ASI *c*. 2–4× as long as head width, swollen apically (fig. 9I in Namyatova *et al*., in press); ASII *c*. 1.1–1.8× as long as ASI, *c*. 2–3× as long as head and pronotum combined; ASIII 0.6–0.9× as long as ASII; ASIV *c*. 0.3–0.5× as long as ASIII; ASII–IV filiform. *Thorax*. Collar flat or slightly swollen, slightly delimited or not delimited posteriorly; calli separated, slightly swollen or almost flat; depression delimiting calli posteriorly absent; humeral angles of pronotum rounded, not dilated; posterior margin of pronotum straight or slightly concave (Fig. 10J); scutellum flat, obtuse apically; without outgrowths, medial ridge or depression (as in fig. 9H in Namyatova & Cassis, 2013b); metepimeron narrow, *c*. 2.5–3× as long as wide, with roundish or subrectangular outgrowth (as in Fig. 13A); metasternum rounded posteriorly, without medial projection on to abdominal segment II (fig. 17B in Namyatova *et al*., in press). *Hemelytron*. Costal margin concave or straight; claval commissure *c*. 2–3.5× as long as scutellum, curved medially; R + M distinct, reaching posterior margin of corium; medial fracture subparallel to R + M (as in fig. 11G in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus *c*. 6–11× as long as wide, *c*. 1.1–1.4× as long as pronotum (as in fig. 13C in Namyatova *et al*., in press), medial margin distinctly concave; membrane cell distinctly surpassing apex of cuneus, *c*. 2–2.5× as long as pronotum, acute apically (as in fig. 13C in Namyatova *et al*., in press); auxiliary vein absent or short present; distance between cell and apex of membrane *c*. 0.1–0.2× as long as cell. *Legs*. Forecoxae separated (as in fig. 17A in Namyatova *et al*., in press); femora more or less swollen apically (fig. 18A in Namyatova *et al*., in press), apices as wide as or narrower than eye diameter; femora curved, forefemora sometimes only slightly curved; foretibia longer than head and pronotum combined; additional swellings on tibia absent; segment I of hind tarsus distinctly longer than segment II, segment II and III subequal in length (fig. 19B in Namyatova *et al*., in press), sometimes segments I and III almost subequal in length and longer than segment II; claw broadly rounded (fig. 10E in Namyatova & Cassis, 2013b); basal teeth short and triangular (as in Fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 17Q–X). Genital capsule almost as long as wide or slightly longer than wide, sometimes with outgrowth on left-hand side; ventral wall of genital capsule shortened anteriorly; left paramere r-shaped or only slightly curved, *c*. 2–3× as long as right paramere; phallobase sclerite of primary gonopore subtriangular or suboval, without outgrowth(s); ductus seminis as long as or slightly longer than phallotheca, with coils, forming wide tube, without

sclerotization basally or apically, attached to phallobase on left-hand; sclerotized part of phallotheca broad occupying entire dorsal side or broad basally and tapering apically; phallotheca sometimes with serrate sclerotization basally and with outgrowth on right-hand side; endosoma with sclerotized areas, areas of small spicules, serrate spicules or elongate spicules.

Female: Body length 5–10 mm. Coloration, texture, vestiture and structure as in male, but larger in size (Fig. 7). *Genitalia* (Fig. 21G, H, K–O). DLP of three types: (1) membranous or partly sclerotized, with membranous or sclerotized ridge medially, sclerotized bands, circle or rings absent; striations present at least on left-hand side; lateral oviducts placed in anterior or posterior part of DLP, slightly or distinctly removed from lateral margins of DLP; spermathecal gland placed on left-hand side at halfway of DLP or near anterior margin medially (Fig. 21K); (2) membranous, with medial sclerotized circle, sometimes with additional sclerites in anterior part; striations present; lateral oviducts placed at halfway of DLP, close to lateral margin of dorsal labiate plat; spermathecal gland placed at midpoint or above midpoint (Fig. 21N); (3) DLP membranous, more or less striated; sclerotized bands present, covered or not covered with membrane; lateral oviducts placed in anterior part or almost at halfway, close to lateral margins of DLP; spermathecal gland placed anteriorly (Fig. 21G).

DLP with distinct tubercles, sometimes with membranous or sclerotized outgrowths posteriorly; base of second valvula slightly or distinctly concave (Fig. 21H, L, M, O); ventral wall membranous or with sclerites around vulva.

Distribution: South-East Asia, Pacific Islands, Australia (Fig. 24).

Host plants: There is very little information on host plant associations for this genus. *Ragwelellus horvathi* is recorded from *Cordamom* sp. (Zingiberaceae) (Carvalho, 1981), *R. festivus* from *Cinchona* sp. (Odhiambo, 1962; Carvalho, 1981) and *Ragwelellus suspectus* is known from *Melaleuca quinquenervia* (Cav.) S.T.Blake (Myrtaceae).

Included species

Ragwelellus bismarkiensis Carvalho and Wallerstein, 1979
Ragwelellus festivus (Miller, 1954)
Ragwelellus gressitti Carvalho and Wallerstein, 1979
Ragwelellus horvathi (Poppius, 1912)
Ragwelellus indonesicus Carvalho and Wallerstein, 1979
Ragwelellus kietae (Odhiambo, 1962)
Ragwelellus luteonotatus Carvalho, 1981
Ragwelellus magnificus Carvalho, 1981
Ragwelellus morobensis Carvalho, 1981
Ragwelellus nigrus Carvalho, 1981
Ragwelellus numanumae (Odhiambo, 1962)
Ragwelellus pallipes (Odhiambo, 1962)
Ragwelellus rubrinus Hu and Zheng, 2001
Ragwelellus similis Carvalho, 1981
Ragwelellus suspectus (Distant, 1904)
Ragwelellus szentivanyi Carvalho and Wallerstein, 1979
Ragwelellus thetis (Kirkaldy, 1908)
Ragwelellus vittatus (Odhiambo, 1962)
Ragwelellus wauensis Carvalho, 1981

Discussion: We retain the generic status of *Ragwelellus*, even though our phylogenetic analysis does not recognize it as a monophyletic taxon. More study is required and at present it can be monophyletic or paraphyletic with respect to *Helopeltis*, *Arthriticus* or both (see node 43).

Ragwelellus can be confused with *Rayieria* by having an elongate body and long ASI, but the latter genus can be separated by the following characters: pretarsal claws only curved apically (fig. 10A in Namyatova & Cassis, 2013b), frons often distinctly swollen (as in fig. 5A–F in Namyatova & Cassis, 2013b), and forefemora straight or only slightly curved.

Ragwelellus is very closely related to *Helopeltis*, and most of their diagnostic characters are shared. However, *Helopeltis* species differ in possessing a scutellar spine-like projection (Fig. 12F). Most species of *Ragwelellus* were previously treated in the genus *Eucerocoris*. Also see discussion of *Eucerocoris* for further details.

Odhiambo (1965) reported that species of the nominotypical subgenus of *Ragwelellus* possess bow-shaped femora and a swollen projection on the genital capsule, whereas in *Ragwelellus* (*Narinellus*) the femora are almost straight and the genital capsule is without projection. Odhiambo included *Ragwelellus kietae*, *R. pallipes*, *R. peregrinus* Odhiambo, *R. propinquus* Odhiambo and *R. vittatus* in the nominotypical subgenus. He placed *R. horvathi*, *R. festivus*, *R. suspectus* and *R. thetis* in *Ragwelellus* (*Narinellus*).

One of us (A.N.N.) examined the male genitalia of the following species: *R. horvathi*, *R. indonesicus*, *R. magnificus*, *R. morobensis*, *R. pallipes*, *R. rubrinus*, *R. suspectus* and *R. thetis*, as well as *Ragwelellus vittatus*, and an unidentified species from Bogor (Indonesia). We could not assign all these species to the two subgenera, based on the characters given by Odhiambo (1965). Among them, only *R. vittatus* and *R. pallipes* correspond to Odhiambo's definition of the nominotypical subgenus of *Ragwelellus*. *Ragwelellus indonesicus*, *R. morobensis*, *R. suspectus*, *R. rubrinus* and *R. thetis* can be assigned to *Ragwelellus* (*Narinellus*). However, *R. magnificus*, which is very closely related to *R. festivus*, has femora only slightly curved, but possesses the

projection on the genital capsule. In contrast, *Ragwelellus horvathi* has distinctly bow-shaped femora, but lacks the projection on the genital capsule.

Species of *Ragwelellus* are similar to each other in all other respects, except in the structure of the phallotheca and DLP, and there is no consistency of these characters with the characters noted by Odhiambo (1965).

Based on this we reject the need for a subgeneric classification, and synonymize *Ragwelellus* (*Narinellus*) with the nominotypical subgenus of *Ragwelellus*. We conclude from our observations that the relationships of the species within the genus are in need of further investigation.

Rayieria Odhiambo

Figure 24

Rayieria Odhiambo, 1962: 236. (subgen. nov.; type species: *Eucerocoris basifer* Walker, 1873 by original designation). Cassis & Gross, 1995: 144 (cat.); Schuh, 1995: 524 (cat.); Schuh, 2002–2013 (cat.); Namyatova & Cassis 2013a: 99, 101 (disc); Namyatova & Cassis 2013b: 689 (rev.); Namyatova *et al*., in press (phylogeny).

Diagnosis: Rayieria belongs to the *Monalonion*-complex *Rayieria* and can be distinguished by the following characters: structure of ASI, which is subequal to head and pronotum combined (fig. 6A–C in Namyatova & Cassis, 2013b), frons often swollen (fig. 5A–F in Namyatova & Cassis, 2013b), scutellum without outgrowth, margin of corial fracture straight (fig. 9D in Namyatova & Cassis, 2013b), foretibia subequal to head and pronotum combined, claw curved apically only (fig. 10A, B in Namyatova & Cassis, 2013b).

Description. See Namyatova & Cassis (2013b).

Distribution: Widespread in Australia (Fig. 24), see Namyatova & Cassis (2013b) for details.

Host plants: The species of *Rayieria* are known from plant species belonging to the families Asparagaceae, Fabaceae, Myrtaceae, Papilionaceae and Proteaceae, and in particular, from numerous species of *Acacia* and *Eucalyptus*. See Namyatova & Cassis (2013b) for additional information on host associations.

Included species

Rayieria acaciae Namyatova and Cassis, 2013
Rayieria albaornata Namyatova and Cassis, 2013
Rayieria basifer (Walker, 1873)
Rayieria decorata Namyatova and Cassis, 2013
Rayieria frontalis Namyatova and Cassis, 2013
Rayieria gearyi Namyatova and Cassis, 2013
Rayieria grandiocula Namyatova and Cassis, 2013
Rayieria kennedyi Namyatova and Cassis, 2013
Rayieria minuta Namyatova and Cassis, 2013
Rayieria queenslandica Namyatova and Cassis, 2013
Rayieria rubranigra Namyatova and Cassis, 2013

Discussion: Rayieria is highly autapomorphic, but is most similar to *Ragwelellus* and *Arthriticus* in shape, although the latter genera differ in having the ASI longer than the head and pronotum combined, and the pretarsal claws are broadly curved (fig. 10C, E in Namyatova & Cassis, 2013b). Some species of *Rayieria* are reminiscent of *Schuhirandella* in size and shape (see discussion for *Schuhirandella* for comparison). Also see Namyatova & Cassis (2013b) for further comparisons of *Rayieria* with other monaloniine genera.

Rhopaliceschatus Reuter

Figures 8, 19R, 24

Rhopaliceschatus Reuter, 1903: 1 (gen. nov.; type species: *Rhopaliceschatus quadrimaculatus* Reuter, 1903 by monotypy); Kuhlgatz, 1906: 29 (key to gen.); Reuter, 1910: 153 (cat.); Oshanin, 1910: 647 (cat.); Hsiao, 1942: 250 (key to gen., list); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Miller & China, 1957: 430 (key to gen.); Carvalho, 1960: 193 (cat.); Schuh, 1995: 574 (cat.); Schuh, 2002–2013 (cat.).

Ropaliceschatus Kirkaldy, 1906: 156a (error pro *Rhopaliceschatus* Reuter, 1903).

Diagnosis: Rhopaliceschatus belongs to the *Odoniella*-complex (see discussion for tribe), and is recognized by the following characters: ASIII distinctly incrassate apically, ASIV clavate (as in fig. 8E in Namyatova *et al*., in press); frons with bifurcate outgrowth (as in fig. 4C in Namyatova *et al*., in press); pronotum and scutellum without tumescences; scutellum distinctly swollen, roundish, exceeding height of pronotum, not subdivided into lower and upper parts (as in Fig. 12A), covering base of pronotum; hemelytron clothed with flattened dark setae; tibiae without distinct tumescences and regularly setate.

*Redescription:*Female: Body length 10 mm. Coloration (Fig. 8). Coloration mostly brown to dark brown, scutellum orange with four brown markings. Vestiture. Head, pronotum scutellum, thoracic pleura and abdomen clothed with pale or dark simple adpressed or erect setae; hemelytron mostly clothed with flattened dark setae, with cuneus clothed with simple setae; antenna with dark simple setae, mostly adpressed and short; setae on legs suberect and long, dark, spinules on femora present or absent apically; spinules on tibia irregularly distributed (as in fig. 18F in Namyatova *et al*.,

in press). STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (as in Fig. 10F); occipital region not delimited with depression; longitudinal depression on vertex indistinct or very short; eyes stylate, directed outwards (as in Fig. 10F), *c*. 0.2× as long as head width; distance between antennal fossa *c*. 3× as long as antennal fossa diameter; frons distinctly swollen, with bifurcate outgrowth (as in fig. 4C in Namyatova *et al*., in press), without longitudinal depression or ridges; anterior view of head *c*. 1.9× as wide as high; eye height *c*. 0.8× as distance from eye to apex of clypeus; antennal fossa oval, *c*. 0.5× as long as eye height, not raised (as in fig. 3B in Namyatova *et al*., in press), inferior margin placed near inferior margin of eye; base of clypeus placed slightly above inferior margin of eye, distinctly delimited basally; in lateral view head flat; gula shorter than buccula length, slightly convex. *Labium*. Reaching posterior margin of metasternum; LSI *c*. 3× as long as wide; LSII *c*. 3× as long as wide, slightly longer than LSI; LSIII *c*. 3× as long as wide, subequal to LSII; LSIV *c*. 5× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching base of cuneus; ASI *c*. 1.5–2× as long as wide, subequal to quarter of head width, swollen basally (as in fig. 8E in Namyatova *et al*., in press); ASII *c*. 7× as long as ASI, subequal to head and pronotum combined, slightly incrassate apically, with shallow tumescences; ASIII *c*. 0.6× as long as ASII; widened towards apex; ASIV *c*. 0.9× as long as ASIII, clavate (as in fig. 8E in Namyatova *et al*., in press). *Thorax*. Collar not delimited posteriorly, flat; calli separated, flat (as in fig. 4C in Namyatova *et al*., in press); depression delimiting calli posteriorly absent (as in fig. 4C in Namyatova *et al*., in press); humeral angles dilated (as in fig. 4C in Namyatova *et al*., in press); posterior margin of pronotum distinctly concave, forming right angles (as in Fig. 11F) scutellum distinctly swollen, often covering, rarely not covering base of pronotum, round or subtriangular (as in Fig. 11F, H), not divided into parts (as in Fig. 12A), obtuse apically, without longitudinal depression, ridge or outgrowth; metepimeron *c*. 1–1.5× as long as wide, angulate (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Tapering posteriorly; costal margin straight; claval commissure *c*. 0.15× as long as scutellum, straight (as in fig. 12E in Namyatova *et al*., in press); R + M almost reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus twice as long as wide, *c*. 0.6× as long as pronotum, medial margin slightly concave (as in fig. 13B in Namyatova *et al*., in press); membrane cell distinctly surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), *c*. 0.8× as long as pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 1.2× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight, hind tibia often slightly curved; foretibia shorter than head and pronotum combined; tibia without swellings; segments of hind tibia subequal in length; apical half or third part of claw curved; basal tooth on claw elongate, slightly concave (as in Fig. 13J).

Genitalia (Fig. 19R). DLP with a single sclerotized ring anteriorly, *c*. 1.5× as long as wide; with two areas of striations surrounding bases of lateral oviducts; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin in posterior half; spermathecal gland placed on right-hand side.

Distribution: Known from Tibet only (Fig. 24).

Host plants: Unknown.

INCLUDED SPECIES

Rhopaliceschatus quadrimaculatus Reuter, 1903

Discussion: Rhopaliceschatus quadrimaculatus was described by Reuter (1903) and he compared it with *Pachypeltis* only. One of us (A.N.N.) examined only two type females of this species from the Museum National d'Histoire Naturelle and Finish Museum of Natural History (Helsinki, Finland). We conclude that it is closely related to *Pseudodoniella* and *Platyngomiris* (see the discussion for *Platyngomiris* for further details). We could not locate any males of this species, but Reuter's original description (Reuter, 1903) was based on both sexes.

SAHLBERGELLA HAGLUND

Figures 8, 10F, 11G, J, 21P–R, 22

Sahlbergella Haglund, 1895: 469 (gen. nov.; type species: *Sahlbergella singularis* Haglund, 1895 by monotypy); Kirkaldy, 1906: 134 (list); Reuter, 1907: 102 (disc., syn.); Reuter, 1910: 153 (cat.); Poppius, 1912: 176, 188 (key to gen., descr.); Bergroth, 1922: 52 (cat.); China, 1944: 179, 188 (key to gen., disc.); Villiers, 1952: 188 (descr.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 148 (cat.); Odhiambo, 1962: 298 (disc.); Linnavuori, 1973: 66 (disc., key to spp.); Lavabre, 1977a: 51, 54 (key to gen., descr.); Lotode, 1977: 188 (ecol.); Schmitz, 1987: 1, 2 (disc., key to spp.); Schuh, 1995: 532 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Deimatostages Kuhlgatz, 1906: 29 (gen. nov.; type species: *Deimatostages contumax* Kuhlgatz, 1906 by

monotypy, synonymized by Reuter, 1907: 102); Carvalho, 1957: 148 (cat.); Schuh, 1995: 532 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Sahlbergella belongs to the *Odoniella*-complex (see discussion after tribe) and is recognized by the following characters: apex of ASII distinctly swollen (as in fig. 9E in Namyatova *et al*., in press); ASIII–IV distinctly clavate (as in fig. 9F in Namyatova *et al*., in press); scutellum triangular or trapeziform (Fig. 11G, J), divided into lower and upper parts (Fig. 12B); frons with undivided or bifurcated outgrowth (Fig. 10F, as in fig. 5C in Namyatova *et al*., in press); pronotum and scutellum punctate, bearing tumescences (Fig. 11G, J); hemelytron with pale or dark flattened setae; hind tibia regularly setate.

*Redescription:*Male: Body length 6–10 mm. COLORATION (Fig. 8). Mostly pale brown to dark brown, with pale or darker markings. TEXTURE. Vertex often with two pairs of tubercles anteriorly and a third pair near posterior margin of eye, sometimes very shallow; flattened areas on vertex distinct or indistinct; ASII with or without tumescences; pronotum and scutellum covered with distinct punctures; collar with more or less distinct tubercles; tumescences on pronotum and scutellum present, shallow or upraised (Fig. 11G, J, fig. 4C in Namyatova *et al*., in press); row of punctures on clavus and on R + M and punctures on depression delimiting calli posteriorly absent; striations on lateral margins of scutellum indistinct or present only anteriorly; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Head, pronotum and scutellum clothed mostly with short simple adpressed pale setae, sometimes very rare, sometimes setae on head and anterior part of pronotum flattened; thoracic pleura with simple or flattened adpressed pale setae; hemelytron mostly with pale or dark flattened setae, cuneus and often posterior margin of corium with simple adpressed setae; ASI with adpressed short pale simple setae, sometimes adpressed, ASII–IV with simple pale or dark suberect setae, some of them spine-like, shorter than width of hind tibia; legs with adpressed pale or dark setae, hind tibia regularly setose, shorter width of hind tibia; abdomen often clothed with short setae; black spinules on femora and tibiae irregularly distributed (as in fig. 18F in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter (Fig. 10F, fig. 4C in Namyatova *et al*., in press); occipital region not delimited with depression; longitudinal depression on vertex present, shorter than eye diameter; eyes stylate, directed outwards, *c*. 0.2–0.25× as wide as head; distance between antennal fossa *c*. 1.7–2× as long as antennal fossa width; frons distinctly swollen, with single or paired outgrowth(s) or not paired outgrowth (Fig. 10F, fig. 4C in Namyatova *et al*., in press), without longitudinal depression or ridges; anterior view of head *c*. 1.8–2.2× as wide as high; eye height *c*. 1.8–2.6× as distance from eye to apex of clypeus; antennal fossa oval, its diameter *c*. 0.3–0.6× as long as eye height, not raised (as in fig. 3B in Namyatova *et al*., in press); inferior margin placed near inferior margin of eye; base of clypeus placed above inferior margin of eye, distinctly delimited basally; in lateral view head flat, gula as long as or shorter than buccula length, straight or convex. *Labium*. Reaching posterior margin of metasternum; LSI *c*. 2–3× as long as wide; LSII *c*. 3–5× as long as wide, subequal or slightly longer than LSI; LSIII *c*. 3–4× as long as wide, subequal to LSII; LSIV *c*. 5–6× as long as wide, *c*. 1.2–1.5× as long as LSIII. *Antenna*. Length varying from reaching apex of scutellum to almost reaching apex of cuneus; ASI *c*. 1.5× as long as wide, subequal to quarter of head width, swollen basally (as in fig. 9E in Namyatova *et al*., in press); ASII *c*. 4.9–5.7× as long as segment I, *c*. 0.9–1.4× as long as head and pronotum combined, swollen apically; ASIII *c*. 0.5× as long as ASII, clavate or swollen apically; ASIV *c*. 0.8–0.9× as long as ASIII, clavate (as in fig. 8F in Namyatova *et al*., in press). *Thorax*. Collar not delimited or slightly delimited posteriorly, flat (fig. 4C in Namyatova *et al*., in press); calli separated, flat (fig. 4C in Namyatova *et al*., in press); depression delimiting calli posteriorly absent; humeral angles of pronotum slightly dilated, not serrate (fig. 4C in Namyatova *et al*., in press); posterior margin of pronotum distinctly concave, forming right angles (fig. 4C in Namyatova *et al*., in press); scutellum swollen (Fig. 11G, J), not covering or rarely covering base of pronotum, triangular or trapeziform (Fig. 11G, J), without outgrowth, divided into lower and upper parts (Fig. 12B), lower part obtuse or acute apically, ridge or longitudinal depression medially; metepimeron enlarged, *c*. 1–1.5× as long as wide, angulate (Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Not tapering or slightly tapering anteriorly; costal margins slightly rounded; claval commissure *c*. 0.3–0.6× as long as scutellum, straight; R + M distinct only anteriorly, sometimes also medially, not reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E Namyatova *et al*., in press); cuneus *c*. 1.5–1.8× as long as wide, *c*. 0.5–1.0× as long as pronotum, medial margin almost straight; corium without swelling posteriorly; membrane cell slightly or distinctly surpassing apex of cuneus, forming acute or almost straight angle, *c*. 0.7–1.2× as long as pronotum; auxiliary vein absent or very short; distance from cell to apex of membrane *c*. 0.8–1.3× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora almost not swollen apically, straight; foretibia

shorter than head and pronotum combined; tibia without tumescences; segment I of hind tarsus as long as segment II and shorter than segment III; apical half or third part of claw curved or claw broadly rounded, basal tooth on claw elongate, slightly concave (as in Fig. 13J) or distinctly concave (as in Fig. 13K), sometimes short and triangular (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (fig. 23A–D in Namyatova *et al*., in press). Genital capsule as wide as long or slightly wider than long, without outgrowth, ventral wall not shortened anteriorly; left paramere r-shaped, twice as long as right paramere; phallobase sclerite of primary gonopore subtriangular, with anterior margin straight or distinctly concave, without outgrowth(s); ductus seminis not sclerotized basally, with sclerotized ring and sclerites around secondary gonopore, or without sclerotization; ductus seminis shorter than phallotheca with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca narrow wider basally, rounded apically, occupying half of dorsal side, without ridge or outgrowth; endosoma with sclerotized areas.

Female: Body length 8–11 mm. Coloration, surface, vestiture and structure as in male, but females slightly larger than males (Fig. 8). *Genitalia* (Fig. 21P–R). DLP with single sclerotized ring, sometimes very thin; sometimes also with sclerotization along posterior margin; two large areas of striations present, separate or contiguous; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin and at a halfway of DLP; spermathecal gland placed at posterior margin, medially or on left-hand side; posterior margin of DLP membranous, with small tubercles, without outgrowth or sclerotization; base of valvula IX with distinct swelling; ventral wall membranous.

Distribution: Distributed in tropical Africa (Fig. 22).

Host plants: Host plants are known for *Sahlbergella singularis* only. It is known to feed on species of the family Malvaceae. It is a major pest of cocoa (Taylor, 1954; Leston, 1970; Entwistle, 1977), and is also known from other species of *Theobroma*, *Cola*, cotton, *Sterculia*, *Ceiba* and *Bombax* (Piart, 1977). There is also a record from *Berria amonilla* (Tiliaceae) (Piart, 1977).

Included species

Sahlbergella qhesquierei Schouteden, 1935
Sahlbergella lais Linnavuori, 1973
Sahlbergella maynei Schouteden, 1935
Sahlbergella singularis Haglund, 1895
Sahlbergella tai Schmitz, 1987

Discussion: Descriptions of the male genitalia were based on dissections of *Sahlbergella lai* and *S. singularis*. Descriptions of the female genitalia were based on dissections of *S. maynei*, *S. singularis* and *S. tai*.

Sahlbergella and *Distantiella* are very similar to each other, and differ mostly by the dense setation and tumescences on the hind tibia of the latter genus.

Haglund (1895) described *Sahlbergella*. China (1944) described *Distantiella* to accommodate *Sahlbergella collarti* and *S. theobroma*. We examined the types of all *Distantiella* and *Sahlbergella* species, except *S. singularis*, for which digital images are available at the website of the Swedish Museum of Natural History (http://www2.nrm.se/en/het_nrm/heteroptera.html).

In our phylogenetic analysis, *Distantiella* species share apomorphic characters with *Sahlbergella*, and are, in particular, closer to *S. singularis*, *S. lais* and *S. qhesquierei* and form a clade with them on the phylogeny (see node 29), in the possession of the following characters: swellings on ASII, LSIV almost as long as LSIII, and spermathecal gland on DLP placed medially (Fig. 21P). We are of the view that these species are very closely related and most probably are congeneric; however, we refrain from synonymizing *Distantiella* with *Sahlbergella* because the monophyly of the latter genus remains doubtful (see nodes 25, 26 and 29).

Schuhirandella Namyatova and Cassis

Figures 9, 23

Schuhirandella Namyatova & Cassis, 2013a: 100 (gen. nov.; type species *Schuhirandella fulva* Namyatova & Cassis, 2013 by monotypy); Namyatova & Cassis, 2013b: 707 (disc., phylogeny); Namyatova *et al*., in press (phylogeny).

Diagnosis: Schuhirandella belongs to the *Monalonion*-complex and is recognized by the following characters: antenna distinctly shorter than body (Fig. 9); ASI distinctly shorter than head width (fig. 2A, D in Namyatova & Cassis, 2013a); ASIII–IV clavate; clypeus delimited with depression; medial fracture subparallel to R + M (as in fig. 11G in Namyatova *et al*., in press); scutellum flat, without outgrowth; dorsum clothed with suberect setae; metepimeron narrow and rounded (as in fig. 9C in Namyatova & Cassis, 2013b); and pretarsal claws broadly rounded (Fig. 2F in Namyatova & Cassis, 2013a).

Description: See Namyatova & Cassis (2013a).

Host plants: Schuhirandella is known from *Calothamnus* sp., *Calothamnus quadrifidus* R.Br. (Myrtaceae) and

Pityrodia bartlingii (Lehm.) Benth. (Lamiaceae) (see Namyatova & Cassis, 2013a for further details).

Included species

Schuhirandella fulva Namyatova and Cassis, 2013

Discussion: Schuhirandella is very distinct within the Monaloniini. It is most closely related to the Australian endemic genus *Rayieria*, as both have the frons and clypeus swollen (fig. 2D in Namyatova & Cassis, 2013a, fig. 5A–F in Namyatova & Cassis, 2013b), and the labium is of similar length and structure. Some species of *Rayieria* are small and show similar body ratios as *Schuhirandella fulva*. However, *Rayieria* can be easily separated in having ASI distinctly longer than width of the head and ASIII–IV filiform, and are not clavate. See also Namyatova & Cassis (2013a) for a description of the genus and included species.

Villiersicoris Delattre

Figures 7, 17AD–AG, 23

Villiersicoris Delattre, 1950: 263 (gen. nov.; type species: *Villiersicoris sessensis* Delattre, 1950 by monotypy); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 42 (key to gen.); Carvalho, 1957: 149 (cat.); Odhiambo, 1962: 311 (descr. disc.); Schuh, 1995: 533 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Villiersicoris is recognized by the following characters: presence of row of punctures on clavus and R + M (as in fig. 11C, D in Namyatova *et al*., in press); eyes stylate; ASII incrassate towards apex; AS III–IV clavate, ASIV only slightly shorter than ASIII; calli upraised; pronotum punctate, scutellum impunctate; claval commissure subequal to scutellum length; membrane cell forming right angle (as in fig. 13B Namyatova *et al*., in press); genital capsule without outgrowth on left-hand side (Fig. 17AG); and sclerotized part of phallotheca wide basally and tapering towards apex (Fig. 17AD).

*Redescription:*Male: Body length 6.9. Coloration (Fig. 7). Ground colour of body is yellow and orange, with brown and reddish markings; antennae dark brown or reddish brown. Texture. Body without tubercles; flattened areas on head absent; pronotum with shallow punctures and wrinkles; scutellum without punctures, with shallow wrinkles; pair of punctures between mesoscutum and scutellum, striations on lateral margin of scutellum and row of punctures on clavus and R + M present (as in fig. 11C, D as in Namyatova *et al*., in press); punctures on depression delimiting calli posteriorly absent; semicircular depression between scutellum and mesoscutum absent; hemelytron rugose. Vestiture. Body clothed with dense suberect pale setae, setae on head, pronotum and legs mostly longer than hind tibia width; femora and tibiae with black spinules, those on tibia placed in rows (as in fig. 18D in Namyatova *et al*., in press); tibiae not very densely setose. Structure. *Head*. Distance between eye and pronotum shorter than eye diameter; occipital region delimited with shallow depression; longitudinal depression on vertex distinct, as long as eye length; eyes stylate, directed outwards, *c*. 0.2× as wide as head; distance between antennal fossa 3× as long as antennal fossa diameter; frons distinctly swollen, without ridges, outgrowths or longitudinal depression; anterior view of head *c*. 1.7–1.8× as wide as high; eye slightly shorter than distance from eye to apex of clypeus; inferior margin of antennal fossa placed near inferior margin of eye; base of clypeus placed near inferior half of eye, delimited with distinct depression; in lateral view head flat dorsally; gula subequal to length of buccula, slightly convex. *Labium*. Reaching posterior margin of mesosternum; LSI distinctly not reaching posterior margin of head; LSII slightly longer than LSI, LSIII slightly longer than LSII. *Antenna*. Reaching apex of clavus; ASI subequal to quarter of head width, twice as long as wide, widened basally; ASII 3–4× as long as ASI, with apical one third swollen, without swellings basally or medially; ASIII *c*. 0.6× as long as ASII, clavate, slightly longer than half of ASII; ASIV clavate, slightly shorter than ASIII. *Thorax*. Collar more or less delimited posteriorly, flat; calli separated, distinctly upraised, rounded; depression delimiting callosite region distinct laterally and medially; humeral angles of pronotum not dilated; posterior margin of pronotum slightly concave; scutellum only slightly upraised, acute apically, without outgrowth, medial ridge or depression; metepimeron enlarged, angulate (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margins straight, subparallel, claval commissure as long as scutellum, straight; R + M distinct, reaching posterior margin of corium; medial fracture strongly inclined towards midline; corium without swelling posteriorly; cuneus *c*. 1.25× as long as wide, *c*. 0.7× as long as pronotum, with medial margin straight (as in fig. 13A in Namyatova *et al*., in press); cuneus shorter than pronotum, base of cuneus slightly longer than half of its length; its medial margin almost straight; membrane cell slightly surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), *c*. 0.8–0.9× as long as pronotum, auxiliary vein absent; distance from cell apex to apex of membrane *c*. 0.7–0.8× as long as cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); forefemora indistinctly swollen, middle and hind femora distinctly swollen; femora straight, not curved; foretibia shorter than head and pronotum

combined; segment I of hind tarsus longer than segments II and III; claw with basal tooth elongate. *Genitalia* (Fig. 17AD–AG). Genital capsule as long as wide, without outgrowth(s); left paramere 3× as long as right paramere, distinctly r-shaped; phallobase sclerite of primary gonopore subtriangular, straight apically, without outgrowth(s); ductus seminis not sclerotized basally or apically, longer than phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca triangular, occupying half of dorsal side, acute apically, without ridge or outgrowth; endosoma with a number of medium-sized spicules, some of them serrate.

Female: Body length 7.6. COLORATION (Fig. 7). Similar to male, but paler. TEXTURE, VESTITURE AND STRUCTURE. As in male. Generally larger than male. *Genitalia*. Spermathecal gland placed close to the midpoint of DLP.

Distribution: Liberia and Uganda (Fig. 23).

Host plants: Unknown.

INCLUDED SPECIES

Villiersicoris holasi Delattre, 1951
Villiersicoris sessensis Odhiambo, 1962

Discussion: One of us (A.N.N.) made observations of these taxa at the Natural History Museum, London. Because these observations were made early on in our study some characters that later proved to be of significance were not recorded. Those characters that were not recorded are as follows: vestiture on thoracic pleura and abdomen, shape and size of antennal fossa; ratio of length and width of labial segments; ratio of length and width of metepimeron; shape of basal tooth on claw; surface of DLP, position of lateral oviducts, shape of base of second valvula, structure of posterior and ventral walls of bursa copulatrix.

Villiersicoris is a very distinct genus and is not easily confused with any other monaloniine taxa. It is phylogenetically close to *Lycidocoris* (also see discussion of *Lycidocoris*).

There are two species described within *Villiersicoris*. Only the female holotype of *V. sessensis* and an identified male species preserved in the Natural History Museum, London, were available for study. Although *V. holasi* and *V. sessensis* were described from different parts of Africa (Liberia and Uganda, respectively), they apparently belong to the same genus. We could not locate the type species of *V. holasi*; however, according to the original description and illustrations, it is very closely related to *V. sessensis*, differing only slightly in coloration.

ASIV is lost in all specimens of *Villiersicoris* that we examined.

VOLKELIOPSIS POPPIUS

Figures 8, 11B, 17Y–AC, 21S, T, 23

Volkeliopsis Poppius, 1915: 81 (gen. nov.; type species: *Volkeliopsis frontalis* Reuter, 1915 by monotypy); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 41 (key); Carvalho, 1957: 149 (cat.); Miller & China, 1957: 430 (key to gen.); Schuh, 1995: 533 (cat.); Schuh, 2002–2013 (cat.)' Sadowska-Woda & Chérot, 2008: 51 (disc.).

Carvalhoia Miller & China, 1957: 429 (gen. nov.; type species *Carvalhoia arecae* Miller & China, 1957 by monotypy, junior homonym of *Carvalhoia* Kormilev, 1951); Miller & China, 1957: 430 (key to gen.); Schuh, 1995: 526 (cat.); Kerzhner & Schuh, 1998: 171 (nom. nov.).

Mircarvalhoia Kerzhner & Schuh, 1998: 171 (nom. nov. for *Carvalhoia* Miller & China, 1957).

Diagnosis: Volkeliopsis belongs to the *Odoniella*-complex and can recognized by the following characters: scutellum moderately swollen, not vesiculate (Fig. 11B); pronotum and scutellum distinctly punctate, humeral angles of pronotum not dilate; hemelytron clothed with simple setae only.

*Redescription:*Male: Body length 4.5–7. COLORATION (Fig. 8). Mostly orange to pale brown with ASIII–IV, cuneus, hemelytral membrane and markings on abdomen posteriorly brown to dark brown, scutellum and inner part of clavus or hemelytron sometimes also brown; sometimes also brown marking on head and reddish tinge on head and pronotum present. TEXTURE. Body without tubercles; flattened areas on vertex absent; pronotum and scutellum densely punctate, without wrinkles (Fig. 11B); pair of punctures behind calli, pair of punctures between mesoscutum and scutellum, punctures on clavus and on R + M absent; striations on lateral margins of scutellum present; semicircular depression between scutellum and mesoscutum absent. VESTITURE. Body clothed with pale or dark simple setae; dorsum and appendages with dense and suberect setae, thoracic pleura with rare and adpressed setae; shorter than ASII width; setae mostly shorter than ASII width, those on dorsum and legs sometimes longer than ASII width, setae on tibiae not very dense; femora and tibiae with black spinules irregularly distributed (as in fig. 18F in Namyatova *et al*., in press). STRUCTURE. *Head*. Distance between eye and pronotum slightly shorter than eye diameter; occipital region not delimited with depression; longitudinal depression on vertex absent or very short; eyes stylate, directed outwards and slightly forwards, *c*. 0.17–0.2× as wide as head; distance between antennal fossa twice as long as antennal fossa

diameter; frons distinctly swollen, without ridges and longitudinal depression, with or without two tubercles, each with long seta apically; anterior view of head almost twice as wide as high; eye almost as high as distance from eye to apex of clypeus; antennal fossa oval, diameter subequal to 2/3rd of eye height, not raised (as in fig. 3B in Namyatova *et al*., in press), inferior margin of fossa placed near inferior margin of eye; base of clypeus placed at the halfway of antennal fossa height; distinctly delimited with depression; head flat in lateral view; gula as long as or shorter than buccula, straight. *Labium*. Length varying from slightly surpassing anterior margin of mesosternum to reaching posterior margin of mesosternum; LSI *c*. 2.5–3× as long as wide; LSII *c*. 3–4× as long as wide, as long as LSI; LSIII *c*. 3–4× as long as wide, slightly shorter or longer than LSII, LSIV *c*. 3× as long as wide, slightly shorter or longer than LSIII. *Antenna*. Reaching base of cuneus; ASI ca.1.5× as long as wide (as in fig. 8E in Namyatova *et al*., in press), subequal to quarter of head width, widened basally; ASII *c*. 4.5–5× as long as ASI, as long as head and pronotum combined, distinctly incrassate towards apex, with shallow swellings basally and medially, ASIII clavate, with shallow swellings. *Thorax*. Collar distinctly delimited laterally and medially, not fused with callosite region posteriorly, flat; calli separated, flat; depression delimiting calli posteriorly absent (as in Fig. 10G); humeral angles of pronotum not dilated; posterior margin of pronotum straight or distinctly concave, forming right angles (as in Fig. 10G); scutellum moderately swollen, flattened dorsally, triangular, acute or slightly obtuse apically, without outgrowth, medial longitudinal depression or ridge (Fig. 11B); metepimeron enlarged, twice as long as wide, angulate, subtriangular (as in Fig. 13E); metasternum with medial projection to abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron straight or slightly rounded; claval commissure *c*. 0.6–0.9× as long as scutellum, straight (as in fig. 12E in Namyatova *et al*., in press); R + M distinct anteriorly and medially, but not reaching posterior margin of corium; medial fracture strongly inclined towards midline (as in fig. 12E in Namyatova *et al*., in press); corium without swelling posteriorly; cuneus *c*. 1.8× as long as wide, *c*. 0.5–0.7× as long as pronotum, medial margin slightly concave (as in fig. 13B in Namyatova *et al*., in press); membrane cell distinctly surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), *c*. 0.8–0.9× as long as pronotum; auxiliary vein absent; distance from cell to apex of membrane *c*. 0.8–0.9× as long as cell. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora only indistinctly swollen apically, straight; tibiae without swellings; foretibia shorter than head and pronotum combined; segment I of hind tarsus distinctly longer than segment II and almost as long than segment III; claw broadly rounded; basal tooth on claw short and triangular (as in fig. 10B in Namyatova & Cassis, 2013b). *Genitalia* (Fig. 17Y–AC). Genital capsule longer than width, without outgrowth(s), ventral wall not shortened anteriorly; left paramere almost straight, not r-shaped, *c*. 2.5× as long as right paramere; phallobase sclerite of primary gonopore pear-shaped, tapering apically, without outgrowth(s); ductus seminis not sclerotized basally or apically, as long as phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca wide, occupying entire dorsal part, rounded apically, without ridge or outgrowth; endosoma with two suboval serrate spicules or six not serrate spicules.

Female: Body length 6–7.5. COLORATION (Fig. 8). Similar to male, specimens with brown to dark brown corium unknown. TEXTURE. As in male. VESTITURE. Similar to male, but setae dark or pale, length and density of setae sometimes as in male or shorter, only few setae on appendages as long as width of hind tibia, adpressed on posterior part of pronotum, scutellum, thoracic pleura, and abdomen and suberect on head, anterior part of pronotum and legs; setae on antennae adpressed and suberect. STRUCTURE. Similar to male, but segment I of hind tarsus slightly longer than segment II and segment II as long as segment III; ASIII *c*. 0.7–0.8× as long as ASII; ASIV *c*. 0.7–0.8× as long as ASIII, clavate; claw broadly rounded and basal tooth on claw short and triangular. *Genitalia* (Fig. 21T, S). DLP with single, long, very indistinct sclerotized ring; with distinct paired areas of striations at sides; lateral oviducts attached at middle of those striated areas, widely separated, placed near lateral margin and at half way of DLP; spermathecal gland placed slightly above or below midpoint; posterior wall with small tubercles, without outgrowth and sclerotization; base of second valvula slightly concave; ventral wall membranous.

Distribution: Philippine Islands and India.

Host plants: Volkeliopsis arecae is known from the palm species *Areca catechu* (Arecaceae) (Miller & China, 1957).

INCLUDED SPECIES

Volkeliopsis arecae (Miller & China, 1957) **comb. nov.**
Volkeliopsis frontalis (Poppius, 1915)
Volkeliopsis mindanao **sp. nov.**

Discussion: The information on length/width ratio of ASIII, characters on ASIV and structure of claw are available for females only; male genitalia were mostly described from the specimen of *V. arecae*.

Information on endosomal spicules was also added from the redescription of *V. frontalis* by Sadowska-Woda & Chérot (2008).

Volkeliopsis was placed in the previously recognized subtribe Odoniellina *sensu* Schuh. It is similar to *Volkelius* (Distant, 1904) on the basis of the following characters: absence of tubercles on frons in *V. arecae*, scutellum only slightly raised (Fig. 11B, D) and acute and absence of flattened setae on dorsum; but the latter genus differs in the following characters: pronotum and scutellum impunctate, with wrinkles (Fig. 10H); tooth on claw long and straight (as in Fig. 13J), and spermathecal gland attached on left-hand side (fig. 5A, C–E in Namyatova & Cassis, 2014).

The coloration of *Volkeliopsis* is reminiscent of that found in species of *Odoniella* (Fig. 8). For differences between those two genera see the discussion of *Odoniella*.

Volkeliopsis was erected by Poppius (1915) for a single specimen from the Philippines. It was redescribed by Sadowska-Woda & Chérot (2008). Miller & China (1957) described the monotypic genus *Carvalhoia*, which was preoccupied, and was subsequently renamed as *Mircarvalhoia* by Kerzhner & Schuh (1998). The holotype and additional male and females are preserved in the Natural History Museum, London. We could not locate the type specimens of *Volkeliopsis frontalis*, which is supposedly housed in the Finish Museum of Natural History, but one of us (A.N.N.) did not find it in this collection. We have made the decision on the status of this genus, primarily on the observations of Sadowska-Woda & Chérot (2008).

Species of *Volkeliopsis* are very similar externally. Miller & China (1957) separated the genera by presence of paired tubercles on frons in *Volkeliopsis* and absence of them in *Carvalhoia*. Apart for this character, *Mircarvalhoia arecae* also differs from *V. frontalis* by labium reaching posterior margin of mesosternum, scutellum dark brown or reddish brown, and corium orange, whereas *V. frontalis* has labium slightly surpassing anterior margin of mesosternum, scutellum yellow to orange, and hemelytron brown to dark brown.

We could not compare male and female genitalia of those two species, because the illustrations of aedeagus given by Sadowska-Woda & Chérot (2008) for *V. frontalis* are given in lateral view only, and females are unknown. However, the genitalia of taxa belonging to the formerly recognized *Odoniellina sensu* Schuh are usually very monomorphic and have few characters of generic value. For this reason, we propose to treat *Mircarvalhoia* as a junior synonym of *Volkeliopsis*.

One of us (A.N.N.) also examined material from the Philippines (Mindanao), which although closely related to the two described species, is a species new to science (see below).

VOLKELIOPSIS MINDANAO SP. NOV.

Figures 8, 11B, 21S, T

Material examined: Holotype. PHILIPPINES: Mindanao: Iligan, Mindanao, 8.22805°N 124.24527°E, Baker, 1♀ (AMNH_PBI_00005237) (AMNH).

Paratype. PHILIPPINES: Mindanao: *Zamboanga Peninsula Co.*: Zamboanga, 7.07136°N 122.12482°E, 465 m, 2999, Baker, 1♀ (AMNH_PBI_00045979) (BPBM).

Diagnosis: Volkeliopsis mindanao can be separated by the following characters: orange head and corium; presence of two tubercles on frons; labium reaching posterior margin of mesosternum; setae on dorsum mostly pale and adpressed; scutellum slightly rounded apically (as in fig. 11B in Namyatova *et al*., in press); spermathecal gland on DLP placed slightly above midpoint (fig. 21S in Namyatova *et al*., in press).

*Description:*Male: Unknown.

Female (Fig. 8): Total length 6.7–7.4. COLORATION. Body mostly orange; ASIII–IV, eye, cuneus, membrane, abdominal segments VII–VIII laterally and segment IX brown to dark brown. TEXTURE. As in generic description. VESTITURE. Body clothed setae, shorter than ASII width, setae mostly adpressed, mostly pale, dark brown on ASII–IV. STRUCTURE AND MEASUREMENTS. Body *c*. 2.4–2.5× as long as pronotum width; frons with paired tubercles; vertex *c*. 3.2× as wide as eye; labium almost reaching posterior margin of mesosternum; LSI; LSI *c*. 3× as long as wide; LSII *c*. 4× as long as wide, as long as LSI; LSIII *c*. 3× as long as wide; ASI *c*. 0.3× as long as head width, *c*. 0.2× as long as pronotum width; ASII *c*. 1.4× as long as head width, *c*. 0.7–0.8× as long as pronotum width; pronotum *c*. 1.8–1.9× as wide as long and *c*. 1.9–2.0× as wide as head; scutellum slightly obtuse apically; claval commissure *c*. 0.8× as long as scutellum, cuneus *c*. 0.6× as long as pronotum. *Genitalia* (Fig. 21S, T). As in generic description.

Distribution: Philippine Islands (Mindanao Is.) (Fig. 23).

Host plants: Unknown.

Etymology: The species is named after Mindanao Island, from where it was collected.

Discussion: Volkeliopsis mindanao is similar to *V. frontalis*, in that it possesses two outgrowths on the frons and the scutellum is orange. However, we treat these Philippine specimens as a new species, because of the following characters: orange corium, labium reaching posterior margin of mesosternum, and setae on

dorsum mostly pale and adpressed. In comparison, *V. frontalis* has the corium brown to dark brown, labium slightly surpassing anterior margin of mesosternum and dorsum clothed with setae mostly dark and suberect.

Volkeliopsis arecae differs from *V. mindanao* by the following characters: absence of paired outgrowths on frons, scutellum acute, dark brown or reddish brown, and LS III slightly shorter than LSII. The female genitalia of *V. arecae* and *V. mindanao* are very similar to each other, differing slightly in the position of the spermathecal gland, which is placed slightly below the midpoint of the DLP in the former species and slightly above the midpoint in the latter species.

Volkelius Distant

Figures 8, 10H, 12A, 24

Volkelius Distant, 1904b: 271 (gen nov.; type species *Volkelius sulcatus* Distant, 1904 by monotypy); Kirkaldy, 1906: 134 (list); Miller & China, 1957: 430 (key to gen.); Reuter, 1910: 154 (cat.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 43 (key to gen.); Carvalho, 1957: 149 (cat.); Odhiambo, 1962: 307 (descr., disc); Cassis & Gross, 1995: 145 (cat.); Schuh, 1995: 533 (cat.); Schuh, 2002–2013 (cat.); Namyatova & Cassis, 2014 (revision); Namyatova *et al*., in press (phylogeny).

Diagnosis: Volkelius belongs to the *Odoniella*-complex and is recognized by the following characters: ASII incrassate towards apex (as in Fig. 8E); ASIII–IV distinctly clavate (as in fig. 8F in Namyatova *et al*., in press); pronotum and scutellum impunctate, with longitudinal and shallow wrinkles (Figs 10H, 12A); scutellum only moderately swollen, not vesiculate; tooth on claw long (fig. 3F, I in Namyatova & Cassis, 2014); DLP with sclerotized circle and spermathecal gland placed on right-hand side (fig. 5 in Namyatova & Cassis, 2014).

Description: See Namyatova & Cassis (2014).

Distribution: Known from Australia (Fig. 24).

Host plants: Volkelius carvalhoi was collected from *Tephrosia* sp. *aff. rosea* (Papilionaceae). *Volkelius maculatus* was collected from *Ficus rubiginosa* (Moraceae) (Namyatova & Cassis, 2014).

Included species

Volkelius carvalhoi Namyatova and Cassis, 2014
Volkelius maculatus Namyatova and Cassis, 2014
Volkelius sulcatus Distant, 1904

Discussion: See Namyatova & Cassis (2014) for a revision of the genus. *Volkelius* was previously placed in the formerly accepted tribe Odoniellina *sensu* Schuh. It is similar to *Volkeliopsis*. For characters delimiting these two genera see discussion for the latter genus.

Yangambia Schouteden

Figures 8, 10I, 11I, 17AH–AK, 21C, D, 24

Yangambia Schouteden, 1942b: 5 (gen. nov.; type species *Yangambia vesiculata* by monotypy); Schouteden, 1945: 116 (syn.); Carvalho, 1952: 60 (cat.); Carvalho, 1955: 41 (key to gen.); Carvalho, 1957:150 (cat.); Odhiambo, 1962: 307 (disc.); Villiers, 1952: 189 (descr.); Schuh, 1995: 533 (cat.); Schuh, 2002–2013 (cat.); Namyatova *et al*., in press (phylogeny).

Idioaspis China, 1944: 186 (gen. nov.; type species *Idioaspis macarangae* by monotypy, syn. by Schouteden, 1945: 116); China, 1944: 174 (key to gen.); Carvalho, 1952: 60 (cat.); (Carvalho, 1957: 150 (cat.); Schuh, 1995: 533 (cat.); Schuh, 2002–2013 (cat.).

Diagnosis: Yangambia belongs to the *Odoniella*-complex (see discussion after tribe) and it can be distinguished from other genera of this group by: scutellum divided into six parts dorsally (Fig. 11I), scutellum impunctate (Fig. 11I), humeral angles of pronotum distinctly flattened and serrate (Fig. 10I); flattened dark setae on hemelytra in parches, and spermathecal gland on DLP placed medially near posterior margin (Fig. 21C).

*Redescription:*Male: Body length 4–5 mm. Coloration (Fig. 8). Mostly whitish yellow to yellow, sometimes with pale brown to brown markings. Texture. Head with two pairs of tubercles between eyes; flattened areas on vertex indistinct; antenna and tibiae with tubercles at base of setae; pronotum with punctures mixed with wrinkles, with four large tubercles on collar and 10 large tubercles on posterior part of pronotum (Fig. 10I); scutellum without tubercles and punctures, with shallow wrinkles (Fig. 11I); pair of punctures between mesoscutum and scutellum, pair of punctures between mesoscutum and scutellum, punctures on clavus and on R + M absent; striations on lateral margins of scutellum present only anteriorly; semicircular depression between scutellum and mesoscutum absent. Vestiture. Body clothed with setae, shorter than with of hind tibia; head with rarely distributed simple or flattened pale setae, dorsal side of head without setae; antenna with mixture of pale adpressed and spine-like suberect setae; setae on pronotum and scutellum absent; thoracic pleura with rarely distributed, short, pale, adpressed setae; setae on hemelytron dark and flattened, forming patches, simple setae on posterior part of corium and on cuneus present; legs mostly with pale spine like suberect setae, not very dense, tarsi with adpressed pale setae; black spinules

on femora absent, tibia with spinules placed irregularly (fig. 19F in Namyatova *et al*., in press); abdomen mostly clothed with short adpressed pale setae and flattened setae on apical segments. STRUCTURE. *Head*. Distance between eye and pronotum shorter than eye diameter; occipital region not delimited with depression; longitudinal depression on vertex absent or very short; eyes stylate, directed outwards and forwards, subequal to 1/6th of head width; distance between antennal fossa twice as long as antennal fossa diameter; frons only slightly swollen (Fig. 10I), without paired outgrowths or only with pair of very shallow tubercles, without ridges or longitudinal depression; anterior view of head *c*. 1.9× as wide as high; eye height subequal to distance from eye to apex of clypeus; antennal fossa oval, diameter subequal to 2/3rd of eye height, not raised (as in fig. 3B in Namyatova *et al*., in press), inferior margin placed near inferior margin of eye; base of clypeus placed near inferior margin of eye, delimited with depression; head flat in lateral view, gula shorter than buccula length, straight. *Labium*. Reaching middle of mesosternum or slightly surpassing it; LSI twice as long as wide; LSII *c*. 2.5× as long as wide, subequal to LSI; LSIII 2.5× as long as wide, subequal to LSII; LSIV *c*. 4× as long as wide, *c*. 1.5× as long as LSIII. *Antenna*. Reaching base of cuneus or slightly surpassing it; ASI *c*. 1.5× as long as wide (as in fig. 8E in Namyatova *et al*., in press), subequal to 1/4th of head width; ASII *c*. 6× as long as segment I, slightly shorter than head and pronotum combined, slightly widened towards apex (as in fig. 8E in Namyatova *et al*., in press), without swelling basally and medially; ASIII *c*. 0.7× as long as ASII, widened towards apex; ASIV *c*. 0.7× as long as ASIII, clavate. *Thorax*. Collar distinct, fused with callosite region medially, flat (Fig. 10I); calli separated, flat; depression delimiting calli posteriorly absent (Fig. 10I); humeral angles of pronotum strongly dilated, serrate, with six lobes (Fig. 10I); posterior margin of pronotum distinctly concave, forming right angles (Fig. 10I); scutellum distinctly swollen, covering base of pronotum, of irregular shape, divided into six parts, obtuse apically (Fig. 11I), covering base of pronotum, with longitudinal depression medially, without outgrowth medially; metepimeron enlarged, twice as high as wide, angulate and subtriangular (as in Fig. 13E); metasternum with medial projection reaching abdominal segment II (as in fig. 17A in Namyatova *et al*., in press). *Hemelytron*. Costal margin of hemelytron slightly rounded; claval commissure *c*. 0.2–0.3× as long as scutellum, straight; R + M distinct only anteriorly, not reaching posterior margin of corium; medial fracture strongly inclined towards midline; cuneus approximately twice long as wide, *c*. 0.7× as long as pronotum, medial margin slightly concave (as in fig. 13B in Namyatova *et al*., in press); membrane cell not surpassing apex of cuneus, forming right angle (as in fig. 13B in Namyatova *et al*., in press), *c*. 0.6–0.7× as long as pronotum; auxiliary vein absent or short; distance from cell to apex of membrane as long as or slightly shorter than cell length. *Legs*. Forecoxae contiguous (as in fig. 17A in Namyatova *et al*., in press); femora not swollen apically, straight; foretibia shorter than head and pronotum combined; tibia without swellings; segment I of hind tibia of as long as segment II and shorter than segment III; apical half of claw curved; basal tooth on claw elongate, slightly concave (as in Fig. 13J). *Genitalia* (Fig. 17AH–AK). Genital capsule wider than long, with small tubercle at each side, ventral wall not shortened anteriorly; left paramere r-shaped, *c*. 1.5–2× times as long as right paramere; phallobase sclerite of primary gonopore heart-shaped, without outgrowths; ductus seminis not sclerotized basally and with narrow circle sclerite around secondary gonopore; ductus seminis as long as phallotheca, with coils forming wide tube, attached to phallobase medially; sclerotized part of phallotheca narrow, occupying half of dorsal part, widened and rounded apically; without ridge or outgrowth(s); endosoma with a number of serrate spicules of irregular shape).

Female: Body length 4–5 mm. COLORATION, TEXTURE, VESTITURE AND STRUCTURE (Fig. 8). As in male. *Genitalia* (Fig. 21C, D). DLP with single sclerotized ring, divided medially, with pair of striated areas; lateral oviducts attached at midpoint of striated areas, widely separated, placed near lateral margins of DLP; spermathecal gland placed posteriomedially, equidistant from lateral oviducts; posterior wall covered with small tubercles, without outgrowths or sclerotizations; base of second valvula slightly concave; ventral wall membranous.

Distribution: Democratic Republic of Congo, Cameroon, Ghana (Fig. 24).

Host plants: Yangambia macarangae is known from *Macaranga horaefolia* (Euphorbiaceae) (China, 1944).

INCLUDED SPECIES

Yangambia macarangae (China, 1944)
Yangambia vesiculata Schouteden, 1942

Discussion: Yangambia was previously placed in the subtribe Odoniellina *sensu* Schuh, and is not similar to any other genera within the tribe Monaloniini. Only *Y. macarangae* (China, 1944) and *Y. vesiculata* Schouteden, 1942 have been assigned to this genus. One of us (A.N.N.) examined the holotypes of both species, which are very similar to each other, but have minor external differences (see Odhiambo, 1962). As

the holotypes of *Y. macarangae* and *Y. vesiculata* are a male and female, respectively, their differentiation is compromised. One of us (A.N.N.) dissected the male genitalia of additional specimens of the latter species and found it to be very similar, although they differ from that of *Y. macarangae* in endosomal sclerotization.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

SI 1. List of specimens used for the study with label data and USI numbers.
SI 2. Taxa examined for phylogenetic analysis, based on the classifications of Schuh (1995), Namyatova *et al*. (in press) and this work. Putative assignments to outgroup or ingroup are shown.