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# Jumping plant-lice of the Paurocephalinae (Insecta, Hemiptera, Psylloidea): systematics and phylogeny

Daniel Burckhardt & David Mifsud

## ABSTRACT

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Much confusion exists with respect to the content and definition of the psyllid subfamily Paurocephalinae. Based on a cladistic analysis of 22 morphological characters (16 adult and 6 larval), the subfamily is redefined to comprise the following five valid genera: *Aphorma* (3 species), *Camarotoscena* (12 valid species, with 1 new synonymy), *Diclidophlebia* (= *Aconopsylla*, *Haplaphalara*, *Paraphalaroida*, *Sinuonemopsylla* and *Woldaia*; 24 species), *Paurocephala* (52 species) and *Syntomoza* (= *Anomoterga* and *Homalocephala*; 7 species). The tribe Diclidophlebiini is synonymised with the subfamily Paurocephalinae. The seven new generic synonymies produce 25 new species combinations. A key to genera for adults and fifth instar larvae is presented. In their revised definitions the genera exhibit relatively restricted distributions and host ranges: *Aphorma*: Palaearctic, Oriental - Ranunculaceae; *Camarotoscena*: Palaearctic - Salicaceae; *Diclidophlebia*: pantropical - Tiliaceae, Malvaceae, Sterculiaceae, Melastomataceae, Rhamnaceae, Ulmaceae and Euphorbiaceae; *Paurocephala*: Old World tropics - Moraceae, Urticaceae, Ulmaceae (all Urticales), Malvaceae, Sterculiaceae (all Malvales) and Clusiaceae (Theales); *Syntomoza*: Oriental, Afrotropical, Palaearctic - Flacourtiaceae, Salicaceae. The following taxa which have been referred to the Paurocephalinae are transferred to other taxa: *Atmetocranium* to the Calophyidae and *Primascena* to the Aphalaroidinae; *Pseudaphorma* is synonymised with *Aphalara*, and *P. astigma* with *A. polygoni*; the position of *Strophingia* is confirmed in the Strophingiinae.

## Introduction

Phytophagy is widespread among insects. Coevolution with their host plants contributed probably much to the present enormous species diversity of phytophagous insects. Coevolution can be seen as association by descent of the phytophages with their host plants. In this respect coevolution, or cospeciation

as it is termed more aptly in this context, is similar to historical biogeography and can be analysed with the methods of this field (Humphries et al. 1986; Brooks & McLennan 1991; Page 1993a, 1993b, 1995; Burckhardt 2003). A prerequisite for cospeciation studies is the availability of independently derived explicit phylogenetic hypotheses for the phytophages and the plants.

In this respect, a potentially significant taxon is the superfamily Psylloidea or jumping plant lice, comprising some 3000 described species of plant-sap feeding bugs (Burckhardt & Basset 2000). Psylloids are usually highly specific to their almost exclusively angiosperm hosts both at lower and higher taxonomic levels. A major drawback in using psylloids in cospeciation studies is the absence of a well-corroborated phylogenetic base in several groups. One taxon with a particularly confused history is the subfamily Paurocephalinae. Its content varies between authors, and there is no explicit phylogenetic hypothesis available of its internal relationships.

The confusion started when Crawford (1914a) erected *Paurocephala* for *P. psylloptera*, a species developing on *Ficus ulmifolia* (Moraceae), and noted a resemblance to *Pauropsylla* RÜBSAAMEN, also associated with *Ficus* spp. In his monograph of the Psyllidae of the New World, Crawford (1914b) assigned both *Paurocephala* and *Pauropsylla* to the subfamily Pauropsyllinae. He added the two species *Paurocephala magnifrons* CRAWFORD (currently placed in *Platycorypha* TUTHILL, Psyllidae, possibly Psyllinae/Arytaininae) and *Psylla ilicis* ASHMEAD (currently placed in *Gyropsylla* BRETHERS, Psyllidae, Aphalarinae). In the same year Enderlein (1914) described *Agonosцена* and included *Agonosцена sauteri* ENDERLEIN from Taiwan. Crawford (1920) suggested that *Agonosцена sauteri* might be synonymous with *Paurocephala psylloptera* but that *Agonosцена* might be a valid genus, as Enderlein had fixed *Psylla targionii* LICHTENSTEIN as type species, which is not closely related to *P. psylloptera*.

In the following decades additional species have been added, usually characterised by the lack of genal processes and the presence of a pterostigma in the forewing. This combination of characters, however, does not indicate phylogenetic relationships, thus producing an extremely artificial classification. Several authors removed species from *Paurocephala* to other genera (e. g. Heslop-Harrison 1952, Loginova 1972, Hollis 1984, Brown & Hodkinson 1988) trying to make *Paurocephala* more homogenous. The subgenus *Thoracocorna* was established for *Paurocephala chonchaiensis* BOSELLI by Klimaszeski (1970) and later synonymised with *Paurocephala* CRAWFORD by Loginova (1972). Hodkinson (1983, 1986a) concluded that *Paurocephala* is a large Old World genus, and that the few New World species probably belong to a separate genus. For diagnosing *Paurocephala*, Brown & Hodkinson (1988) used the presence of weakly sclerotised apical metatibial spurs, the basally thickened portion of the

distal segment of the aedeagus and the lack of basimetatarsal spurs. In this revised definition, *Paurocephala* included also a few New World species. Burckhardt (1996) in adding two species from Paraguay concluded that the phylogenetic significance of these characters is difficult to assess, and that the monophyly of *Paurocephala* remains debatable. Mifsud & Burckhardt (2002) redefined *Paurocephala* to include 51 named Old World species and, thus, confirmed Hodkinson's (1983, 1986a) view.

Similarly confusing are the discussions on the phylogenetic relationships of *Paurocephala*. Crawford (1914b) assigned *Paurocephala* together with *Pauropsylla*, *Heteropsylla* CRAWFORD (now placed in Psyllidae, Ciriacreminae) and *Calophya* LÖW (now placed in Calophyidae), to the Pauropsyllinae. Several authors including Mathur (1975) followed this concept. Vondráček (1957) included the Pauropsyllinae in the Aphalaridae, whereas Loginova (1972) treated the Pauropsyllini as tribe of the Carsidaridae. Heslop-Harrison (1952), in contrast, removed *Paurocephala* from the Pauropsyllinae to the Aphalarinae. Vondráček (1963a), who followed Heslop-Harrison's (1952) view, treated the aphalarids as a family and erected the tribe Paurocephalini for *Paurocephala* and *Camarotoscena* HAUPT, the latter as subgenus of the former, in the subfamily Aphalaroidinae. Klimaszewski (1964) adopted a similar view but raised the group to subfamily level, Paurocephalinae, of the Aphalaridae. He included in the subfamily, among other genera, *Atmetocranium* TUTHILL and *Syncoptozus* ENDERLEIN.

Based on much sounder evidence, Hollis (1984) and White & Hodkinson (1985) confirmed the assignment of *Paurocephala* to the Aphalaridae. White & Hodkinson (1985) assigned *Paurocephala* and *Camarotoscena* to the Paurocephalinae. In a closely related subfamily, the Euphyllurinae, they included the Diclidophlebiini with *Diclidophlebia* CRAWFORD, *Paraphalaroida* LOGINOVA and *Haplaphalara* UICHANCO, in addition to the tribes Euphyllurini with six genera including *Syntomoza* ENDERLEIN, and the Ctenarytainini. The Euphyllurini are identical with the concept of Loginova (1973). Burckhardt (1991) synonymised the Ctenarytainini with the Spondylaspidini.

The genus *Aphorma* HODKINSON, according to Heslop-Harrison (1949), “fitted” between *Aphalaroida* CRAWFORD and *Paurocephala*. Burckhardt (1983), Burckhardt & Lauterer (1989) and Burckhardt & Bänziger (1995) suggested a close relationship to *Camarotoscena*. *Anomoterga* KLYVER, *Aconopsylla* TUTHILL & TAYLOR and *Homalocephala* YANG & LI were all referred to the Paurocephalinae, however, without detailed evidence (Hodkinson 1983; Morgan 1984; Yang & Li 1987). Conci & Tamanini (1985) erected the genus *Pseudaphorma* for a single male which they felt belongs to the Aphalaridae, Rhinocolinae or Paurocephalinae.

Brown & Hodkinson (1988) suggested that the monophyly of the subfamily Paurocephalinae sensu White & Hodkinson (1985) is doubtful and that it may ultimately prove necessary to include the Diclidophlebiini (genera *Diclidophlebia*, *Paraphalaroida* and *Haplaphalara*) and Togepsyllinae (*Togepsylla* KUWAYAMA and *Syncoptozus*). They transferred *Haplaphalara* to the Paurocephalinae, and concluded that Neotropical *Haplaphalara* form a homogeneous group, which may be generically distinct from the Old World species. *Woldaia* BROWN & HODKINSON was put close to *Diclidophlebia* (Euphyllurinae, Diclidophlebiini). Burckhardt & Brown (1992) transferred *Woldaia* to the Paurocephalinae.

Using differences in the hindwing venation, Klimaszeski (1993) subdivided the family Aphalaridae sensu White & Hodkinson (1985) into the Aphalaridae (with Aphalarinae and Togepsyllinae) and Rhinocolidae (with Rhinocolinae, Aphalaroidinae, Bharatianinae (spelt Bhrtianinae) and Strophingiinae (spelt Strophinginae)). Liviinae, Paurocephalinae and some Euphyllurinae are probably included in the latter family. Burckhardt & Lauterer (1997) showed that the characters for this family separation are trivial and synonymised the two.

Klimaszewski (1998) erected the genus *Primascena* for a fossil species in Dominican amber which he assigned to the Rhinocolidae, Paurocephalinae. According to the original drawings and the description, the taxon lacks genal processes and metabasitarsal spurs. Finally the genus *Sinuonemopsylla* LI & YANG (1991), which was referred to the Rhinocolinae, is included in the following considerations as it lacks basimetatarsal spurs.

The present paper revises and cladistically analyses the Paurocephalinae with the following aspects addressed in particular: monophyly, definition and content of Paurocephalinae; internal relationships of Paurocephalinae; relationships of Paurocephalinae with Togepsyllinae, Euphyllurinae sensu White & Hodkinson (1985), *Atmetocranium*, *Strophingia*, *Pseudaphorma* and *Primascena*. Host plants and distributions are examined to search for general patterns.

## Material and Methods

Morphological terminology follows mostly Ossiannilsson (1992). Hollis (1976) is followed here in the usage of the terms “spurs” and “spines” in relation to the metatibia.

Material from following collections was examined: AMNH, American Museum of Natural History, New York; BAUC, Beijing Agricultural University, Beijing, China; BMNH, The Natural History Museum, London, UK; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; MHNG, Muséum d'histoire naturelle, Geneva, Switzerland; NCHU, National Chung Hsing University, Taiwan; NHMB,

Naturhistorisches Museum, Basel, Switzerland; OMNH, Osaka Museum of Natural History, Osaka, Japan; TULE, Tokyo University of Agriculture, Laboratory of Entomology, Japan; USNM, National Museum of Natural History, USDA, Beltsville, MD, USA.

The cladistic analyses were performed with WinClada 1.0 (Nixon 2002) and Hennig86 (Farris 1988), using the mh and bb\* search options and successive weighting. A consensus tree was calculated with the nelsen command.

The aim of the analysis was to find monophyletic groupings among the species referred to the genera *Aconopsylla*, *Anomoterga*, *Aphorma*, *Camarotoscena*, *Diclidophlebia*, *Haplaphalara*, *Homalocephala*, *Paraphalaroida*, *Paurocephala*, *Paurocephala* (*Thoracocorna*), *Sinuonemopsylla* and *Woldaia*. The genera *Atmetocranium*, *Ctenarytaina*, *Euphyllura*, *Strophingia*, *Syncoptozus*, *Syntomoza* and *Togepsylla* were included in the analysis to see whether they exhibit close cladistic relationships to any of the above genera. *Rhinocola aceris* served as out-group. The species selected for the analysis are listed in Table 1. If possible the type species was selected (indicated with an asterisk in Table 1). In the few cases where the data for the type species were incomplete (e.g. missing larvae), a species closely related to the type species was selected.

The characters used in the present analyses have partly been used previously to delimit genera or higher level taxa. Other characters come from an extensive morphological comparative analysis which is detailed in Mifsud (2001) and Mifsud & Burckhardt (2002). Characters, which are treated as unordered, are taken from adults (Table 2, characters 1–16) and the last larval instar (Table 2, characters 17–22).

## Cladistics

The cladistic analysis resulted, after 2 iterations, in 18 most parsimonious trees (weighted characters: length 218, consistency index 72, retention index 91; unweighted characters: length 46, consistency index 58, retention index 85). Fig. 9 shows the consensus with character states mapped onto the tree with the fast character optimisation.

A monophyletic clade, which is defined here as the Paurocephalinae, is supported by characters 13 and 15. Character 13, a sclerotised patch with spines on the first visible abdominal tergite, is particularly noteworthy as it is unique within Psylloidea. The Paurocephalinae clearly split into 5 clades which are given generic rank here. *Aphorma* is the only of the five genera whose definition agrees with previous concepts. Both *Camarotoscena* and *Paurocephala* become more restricted, *Camarotoscena africana* and *C. unicolor* are more closely rela-

ted to species assigned to the genera *Syntomoza*, *Anomoterga* and *Homalocephala*, rather than to the remainder of *Camarotoscena*, and *Paurocephala* becomes restricted to Old World species. The content of *Syntomoza* and *Diclidophlebia*, on the other hand, is broadened to include species previously assigned to 4 and 7 genera respectively. Except for *Paurocephala*, which includes 4 monophyletic species groups (Mifsud & Burckhardt 2002), there is no resolution within the five genera. *Diclidophlebia* as defined here is diverse with respect to adult morphology (head, forewing, hind legs) which is in contrast to its homogenous larval morphology. Despite the wide range of adult morphology in *Diclidophlebia*, no infrageneric groupings are supported by the present analysis, in particular there is no support for a separation of the Old World from the New World taxa. Further studies will be necessary to elucidate the phylogenetic relationships within this genus of which, at most, half of the existing species are described up to now.

The cladistic analysis suggests a basal position of *Aphorma*, and a sister-group relationship of *Camarotoscena* with an unresolved clade of *Syntomoza* + *Paurocephala* + *Diclidophlebia* (Fig. 9). The support of this grouping is, however, weak. A consequence of the phylogeny discussed here is the synonymy of Paurocephalinae and Diclidophlebiini.

The cladistic analysis places *Strophingia*, *Ctenarytaina*, *Euphyllura*, *Atmetocranium*, *Togepsylla* and *Syncoptozus* clearly outside the monophyletic Paurocephalinae. These genera are probably not close to the Paurocephalinae and more work is required to investigate their phylogenetic relationships.

## Subfamily Paurocephalinae

Paurocephalini VONDRAČEK, 1963a: 277. Type-genus: *Paurocephala* CRAWFORD, 1914a.

Paurocephalinae; Klimaszewski 1964: 92; Bekker-Migdisova 1973: 108.

Diclidophlebiini BEKKER-MIGDISOVA, 1973: 100. Type-genus: *Diclidophlebia* CRAWFORD, 1920. **Syn. n.**

**Diagnosis. Adult.** Genal cones absent; frons developed, exposed in *Camarotoscena* with parallel-sided margins, small trapezoidal in *Aphorma* and *Syntomoza*, small to moderately sized trapezoidal in *Paurocephala* and small to relatively large trapezoidal in *Diclidophlebia*. Coronal suture fully developed. Metacoxa rounded, with distinct meracanthus, small and apically rounded (Fig. 2E, F) to long, marginally curved or straight laterally (Fig. 2D) or horn-shaped (Fig. 2G); metatibia without basal spine, with an incomplete crown of 4–12 apical spurs (Fig. 2H–N), with (Fig. 2K) or without (Fig. 2M) apical widening. Basal metatarsus without black spurs. First visible abdominal tergite, laterally bearing a

patch with spinule-like microsculpture varying from relatively small and indistinct (Fig. 5F–I) to very large forming a finger-like anteriorly directed process (in some *Paurocephala* spp.). Forewing with costal break developed (Figs. 1, 2 A–C); pterostigma usually developed (absent in *Aphorma*, Fig. 1A). Male proctiger 1-segmented (Fig. 3E–I). Aedeagus 2 or sometimes indistinctly 3-segmented, apex of proximal portion more or less distinctly inflated with folds on the anterior face (Figs. 3I, 4H), apex of distal portion bulbous (Fig. 5H–N).

**Fifth instar larva.** Margin of forewing pads (Fig. 6E–G) and caudal plate (Fig. 7J–L) with sectasetae. Tarsal arolium short triangular to fan shaped (Fig. 7E–I). Outer circumanal ring usually consisting of a single row of pores (Fig. 7M–O) but in some *Paurocephala* species the circumanal ring is subdivided at irregular intervals or consists of multiple pores laterally. Additional pore fields present in all genera (Figs. 7M–O, 8) except for *Paurocephala* CRAWFORD.

*Discussion.* The combination of the above listed characters diagnoses the subfamily Paurocephalinae within the superfamily Psylloidea. The following two characters are considered to be autapomorphies for the subfamily (Table 2, Fig. 9): first visible abdominal tergite bearing lateral patch of spinules, sometimes forming process (character 13-1), apex of proximal portion of aedeagus inflated with folds on the anterior face (character 15-1).

## Key to Paurocephalinae genera

### Adult

- 1 Forewing membrane with plate-like surface structures (Fig. 1A). Head angular anteriorly, vertex clearly delimited from genae. Frons elongate, parallel-sided. *Aphorma*
- Forewing membrane without plate-like surface structures. Head rounded anteriorly, vertex passing smoothly into genae. Frons rhomboidal or elliptical. 2
- 2 Head strongly inclined at about 90° to longitudinal body axis. *Syntomoza*
- Head almost horizontal or inclined but always at less than 90° to longitudinal body axis. 3
- 3 Head weakly inclined, at most, 45° to longitudinal body axis. Metascutellum forming a distinct horn. Hind legs long and slender. Old World. *Paurocephala*
- Character combination different. 4
- 4 Antenna about as long as head width. *Camarotoscena*
- Antenna at least 1.5 times as long as head width. *Diclidophlebia*



## Fifth instar larva

- 1 Additional pore fields lacking. *Paurocephala*
- Additional pore fields present (Figs. 7M–O, 8). 2
- 2 Tibiae with massive peg-like spurs (Fig. 7D). *Syntomoza*
- Tibiae lacking peg-like spurs (Fig. 7A–C). 3
- 3 Antenna 9-segmented, flagellum bearing sectasetae (Fig. 6C). Extra pore fields on caudal plate widely distant from outer circumanal ring (Fig. 8). *Diclidophlebia*
- Antenna 7-segmented, flagellum lacking sectasetae (Fig. 6A, B). Extra pore fields on caudal plate near circumanal ring (Fig. 7M, N). 4
- 4 Sectasetae on abdominal dorsum relatively sparse (Fig. 7K). *Aphorma*
- Sectasetae on abdominal dorsum forming dense rows (Fig. 7L). *Camarotoscena*

## **Aphorma** HODKINSON

*Aphorma* HODKINSON, 1974: 76. Type species: *Aphalara bagnalli* LAING, 1929, by original designation.

**Description. Adult.** Head weakly inclined from longitudinal body axis, directed forwards, without genal processes; vertex large subtrapezoidal, anteriorly more or less delimited to genae, sometimes anterior margin with tubercle, frons small trapezoidal. Frontal ocellus slightly hidden from above; genae strongly expanded at base on either side of clypeal apex, with transverse suture, separating each a subrectangular sclerite from the remainder of genae. Antennae about as long as head width; with each a subapical rhinarium on segments 4, 6, 8, and 9; segment 9 strongly inflated (Fig. 3D). Thorax flattened dorsally, pronotum relatively long and flat; propleurites rectangular, higher than wide, divided by diagonal suture. Parypterae forming large plates extending to posterior pronotal margin. Forewing membrane coriaceous (Fig. 1A), covered by tubercular surface structures, sometimes also with spinules; pterostigma lacking. Metacoxa with horn-shaped meracanthus. Metatibia relatively short and stout (Fig. 2H), without basal spine, slightly widening apically, bearing an incomplete crown of 6–9 sclerotised apical spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, more or less straight posteriorly (Fig. 3E); male paramere lamellar and simple (Fig. 4A); distal portion of aedeagus relatively short with rounded apical dilatation. Female genitalia cuneate (Fig. 5A).

**Fifth instar larva.** Antenna 7-segmented (Fig. 6A), rhinaria formula as 3577. Tarsal arolium large, triangular, petiolate with developed unguitactor (Fig. 7E).

Sectasetae present behind eye, sparse on wing pad margins and on abdomen laterally and dorsally. Anus ventral, outer circumanal ring consisting of a single row of pores, additional pore fields developed (Fig. 7M).

*Comments.* The genus has been revised by Burckhardt & Bänziger (1995) who recognised three valid described species in the Palaearctic and Oriental regions. Species develop, as far as known, on Ranunculaceae.

### ***Camarotoscena* HAUPT**

*Camarotoscena* HAUPT, 1935: 228. Type species: *Rhinocola speciosa* FLOR, 1861a, by original designation.

*Description. Adult.* Head down-curved, without genal processes; vertex subtrapezoidal and anteriorly passing smoothly into genae; frons developed, exposed, with parallel-sided margins. Frontal ocellus situated on anterior margin of head; genae small and rounded. Antennae slightly longer than head width; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3C); thorax curved dorso-laterally, pronotum relatively long and flat. Forewing membrane coriaceous (Fig. 1B, C), covered with surface spinules, often bearing dark pattern (Fig. 1B), pterostigma present. Metacoxa with horn-shaped meracanthus. Metatibia relatively short and stout (Fig. 2I), without basal spine, weakly widening apically, bearing an incomplete crown of 8–12 sclerotised apical spurs and 2–3 small unsclerotised spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, curved posteriorly (Fig. 3F); male paramere lamellar and simple (Fig. 4B); distal portion of aedeagus relatively short with rounded apical dilatation (Fig. 4H). Female genitalia cuneate (Fig. 5B, G).

**Last instar larva.** Antenna 7-segmented (Fig. 6B), rhinaria formula as 3577. Tarsal arolium relatively short triangular, petiolate with developed unguitactor (Fig. 7F). Sectasetae present on head and thorax dorsally, abdomen laterally and dorsally and reduced on wing pad margin. Caudal plate and wing pads with numerous long simple setae. Anus terminal or ventral, outer circumanal ring consisting of a single row of pores, additional pore fields developed (Fig. 7N).

*Comments.* The genus contains 12 Palaearctic species associated with *Populus* spp. (Salicaceae). Loginova (1975) revised the recent taxa and included *C. africana* and *C. unicolor* which are transferred here to *Syntomoza*.

### **Species catalogue**

*badia* LOGINOVA, 1965: 198. Distribution: Tajikistan. Host plant: *Populus tadjikistanicus* (Salicaceae).

- bianchii* LOGINOVA, 1975: 56. Distribution: Kyrgyzstan, Mongolia, Russia (East Siberia), Uzbekistan, Tajikistan. Host plant: *Populus laurifolia* (Salicaceae).
- fulgidipennis* LOGINOVA, 1975: 57. Distribution: Armenia, Azerbaijan, Iran, Turkey. Host plant: *Populus* sp. (Salicaceae).
- hoberlandti* VONDRAČEK, 1953: 445. Distribution: Iran, Iraq, Turkey, Turkmenistan. Host plant: *Populus nigra*, *P. sp.* (Salicaceae).
- lauta* LOGINOVA, 1975: 56. Distribution: Azerbaijan. Host plant: *Populus* sp. (Salicaceae).
- libera* LOGINOVA, 1975: 59. Distribution: Azerbaijan. Host plant: *Populus* sp. (Salicaceae).
- pamirica* BAEVA, 1983: 256. Distribution: Tajikistan. Host plant: *Populus* sp. (Salicaceae).
- personata* LOGINOVA, 1975: 58; *huashana* LI & YANG, 1989: 74, **syn. n.** Distribution: China (Shaanxi Province), Russia (East Siberia, Far East). Host plant: *Populus* sp. (Salicaceae). *Comment:* The examination of a ♀ paratype of *C. huashana* (BAUC) showed that this species is characterised by the long apical process of the female subgenital plate which is diagnostic for *C. personata*. The two species are, therefore, synonymised.
- speciosa* (FLOR, 1861a: 526). Distribution: From Spain to Central Asia. Host plant: *Populus alba*, *P. nigra*, *P. pyramidalis* (Salicaceae).
- subrubescens* (FLOR, 1861b: 411). Distribution: Croatia, France, Italy, Spain, Turkey. Host plant: *Populus robusta* (Salicaceae).
- trjapitzini* LOGINOVA, 1968: 282. Distribution: Armenia. Host plant: *Populus* sp. (Salicaceae).
- ujenci* KLIMASZEWSKI, 1982: 3. Distribution: Mongolia. Host plant: *Populus diversifolia* (Salicaceae).

### ***Diclidophlebia* CRAWFORD**

- Heteroneura* CRAWFORD, 1919: 152; nec FALLÉN, 1810. Type species: *Heteroneura oceanica* CRAWFORD, 1919, by original designation and monotypy.
- Diclidophlebia* CRAWFORD, 1920: 355; replacement name for *Heteroneura* CRAWFORD.
- Gyroza* ENDERLEIN, 1921: 122; replacement name for *Heteroneura* CRAWFORD; objective junior synonym of *Diclidophlebia*.
- Haplaphalara* UICHANCO, 1921: 260. Type species: *Aphalara dahli* RÜBSAAMEN, 1905, by original designation. **Syn. n.**
- Aconopsylla* TUTHILL & TAYLOR, 1955: 247. Type species: *Psylla sterculiae* FROGGATT, 1901, by original designation. **Syn. n.**
- Paraphalaroida* LOGINOVA, 1972: 851. Type species: *Paurocephala fremontiae* KLYVER, 1930, by original designation. **Syn. n.**
- Woldaia* BROWN & HODKINSON, 1988: 49. Type species: *Woldaia nebulosa* BROWN & HODKINSON, 1988, by original designation and monotypy. **Syn. n.**
- Sinuonemopsylla* LI & YANG, 1991: 11. Type species: *Sinuonemopsylla excetrodendri* LI & YANG, 1991, by original designation and monotypy. **Syn. n.**

*Description. Adult.* Head weakly inclined from longitudinal body axis directed forwards, without genal processes; vertex subrectangular, smoothly passing into genae; frons small to relatively large. Antennae longer than head width; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3B),

sometimes a small subapical rhinarium present on segment 3. Thorax flattened to marginally curved dorsally, pronotum weakly inclined; propleurites narrow. Forewing membrane smooth (Fig. 1D–K), covered with surface spinules, sometimes forming distinct cellular pattern (Fig. 1H); forewing often with colour pattern (Fig. 1D, E, G); pterostigma developed, as long as or longer than half Rs vein. Metacoxa with short meracanthus almost straight laterally and rounded apically (Fig. 2E). Metatibia moderately long, without basal spine; with or without apical widening, bearing a crown of 4–12 often sclerotised apical spurs arranged as 3 + 1 (Fig. 2L), 4 + 2 and 8 slender unsclerotised setae (Fig. 2K), an incomplete crown of 7–9 black spurs (Fig. 2J) or 10–12 hardly sclerotized spurs (Fig. 2M). Metabasitarsus without black spurs. Male proctiger simple tubular, straight to globular posteriorly (Fig. 3G, H); male paramere robust, often short and complex (Fig. 4C, D, G); aedeagus 2 or 3-segmented with the terminal segment varying from relatively simple to complex (Fig. 4I–L). Female genitalia short (Fig. 5D), sometimes upturned apically (Fig. 5C).

**Last instar larva.** Antenna 9-segmented (Fig. 6C), rhinaria formula as 3578. Tarsal arolium triangular, distinctly petiolate with long unguitractor (Fig. 7H, I). Sectasetae present on antenna, behind eye, on wing pad margins, on legs, on abdomen laterally; dorsal sclerites with short lanceolate setae. Anus terminal, outer circumanal ring consisting of a single row of pores, additional pore fields developed forming semicircular to oval patterns (Fig. 8).

*Comments.* The genus *Diclidophlebia* contains 24 described species but numerous undescribed species are present in collections. The genus has a pan-tropical distribution and is associated with a variety of host families (Tiliaceae, Malvaceae, Sterculiaceae, Melastomataceae, Rhamnaceae, Ulmaceae and Euphorbiaceae).

## Species catalogue

*adelaidae* (BRAZA & CALILUNG, 1981: 344), **comb. n.** from *Paurocephala*; *Haplaphalara*, NAVASERO & CALILUNG, 1998: 14. Distribution: Philippines. Host plant: *Diplodiscus paniculatus* (Tiliaceae).

*crassiflagellata* (BURCKHARDT, 1996: 79), **comb. n.** from *Paurocephala*. Distribution: Paraguay. Host plant unknown, perhaps *Luehea paniculata* (Tiliaceae).

*dahli* (RÜBSAAMEN, 1905: 23), **comb. n.** from *Aphalara*; *Haplaphalara*, Uichanco 1921: 261; *Strophingia*, Crawford 1925: 40. Distribution: Bismark Archipelago, New Caledonia, Papua New Guinea, Philippines (Luzon). Host plant: *Thespesia* spp. (Malvaceae).

*eastopi* VONDRAČEK, 1963b: 289. Distribution: Cameroon, Nigeria. Host plant: *Triplochiton scleroxylon* (Sterculiaceae).

*excetrodendri* (LI & YANG, 1991: 11), **comb. n.** from *Sinuonemopsylla*. Distribution: China (Guangxi). Host plant: *Excetrodendron hsienmu* (Tiliaceae).

- fava* (BROWN & HODKINSON, 1988: 44), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Miconia argentea* (Melastomataceae).
- fremontiae* (KLYVER, 1930: 111), **comb. n.** from *Paurocephala*; *Paraphalaroida*, Loginova 1972: 851. Distribution: USA (California). Host plant: *Fremontodendron californica* (Sterculiaceae).
- grewiae* (KANDASAMY, 1986: 61) **comb. n.** from *Paurocephala*. Distribution: India. Host plant: *Grewia rotundifolia* (Tiliaceae).
- harrisoni* OSISANYA, 1969: 71. Distribution: Central African Republic, Nigeria. Host plant: *Triplochiton scleroxylon* (Sterculiaceae).
- heterotrichi* (CALDWELL & MARTORELL, 1952: 605), **comb. n.** from *Paurocephala*; *Haplaphalara*, Brown & Hodkinson 1988: 40. Distribution: Puerto Rico. Host plant: *Heterotrichum cymosum* (Melastomataceae).
- lanceomedia* (BROWN & HODKINSON, 1988: 37), **comb. n.** from *Paurocephala*. Distribution: Panama. Host plant unknown.
- longitarsata* (BROWN & HODKINSON, 1988: 42), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Miconia argentea* (Melastomataceae).
- maculata* (CRAWFORD, 1919: 151), **comb. n.** from *Paurocephala*; *Haplaphalara*, Loginova 1972: 841. Distribution: Malaysia (Sabah), Singapore. Host plant unknown.
- maculipennis* (BROWN & HODKINSON, 1988: 47), **comb. n.** from *Haplaphalara*. Distribution: Panama, Trinidad. Host plant: *Trema micrantha* (Ulmaceae).
- menoni* (MATHUR, 1975: 50), **comb. n.** from *Paurocephala*; *Haplaphalara*, Hollis 1984: 28. Distribution: India. Host plant: *Grewia asiatica* (Tiliaceae).
- nebulosa* (BROWN & HODKINSON, 1988: 49), **comb. n.** from *Woldaia*. Distribution: Panama. Host plant: *Luehea seemannii* (Tiliaceae).
- oceanica* (CRAWFORD, 1919: 152). Distribution: Malaysia (Sabah), Philippines (Basilan, Luzon), Singapore. Host plant unknown.
- paucivena* (BROWN & HODKINSON, 1988: 39), **comb. n.** from *Paurocephala*. Distribution: Guatemala, Panama. Host plant unknown.
- paucipunctata* (BROWN & HODKINSON, 1988: 40), **comb. n.** from *Haplaphalara*. Distribution: Panama. Host plant: *Conostegia xalapensis* (Melastomataceae).
- setinervis* (BURCKHARDT, 1996: 78), **comb. n.** from *Paurocephala*. Distribution: Paraguay. Host plant unknown.
- sterculiae* (FROGGATT, 1901: 255), **comb. n.** from *Psylla*; *Aconopsylla*, TUTHILL & TAYLOR 1955: 247. Distribution: Australia (NSW, SA). Host plant: *Brachychiton* spp. (Sterculiaceae).
- trimaculata* (MATHUR, 1975: 69), **comb. n.** from *Paurocephala*; *Haplaphalara*, Hollis 1984: 28. Distribution: India. Host plant: *Zizyphus jujuba* (Rhamnaceae).
- tuxtlaensis* (CONCONI, 1972: 51), **comb. n.** from *Paurocephala*; *Haplaphalara*, Brown & Hodkinson 1988: 40. Distribution: Mexico. Host plant: *Conostegia xalapensis*, *Miconia* sp. (Melastomataceae).
- xuani* MESSI in Messi et al., 1998: 233; *Camarotoscena* sp., Vondráček 1963a: 278. Distribution: Cameroon, Nigeria. Host plant: *Ricinodendron heudelotii* (Euphorbiaceae).

Following species probably also belongs to *Diclidophlebia*:

*Haplaphalara durio* HESLOP-HARRISON, 1952: 974; nomen nudum, Malaysia.

## ***Paurocephala* CRAWFORD**

*Paurocephala* CRAWFORD, 1914a: 293. Type species: *Paurocephala psyллоptera* CRAWFORD, 1914a, by original designation.

Subgenus *Thoracocorna* KLIMASZEWSKI, 1970: 427. Type species: *P. chonchaiensis* BOSELLI, 1929, by original designation; synonymised with *Paurocephala* by Loginova 1972: 842.

**Description. Adult.** Head down-curved, without genal processes; frons small to moderate-sized trapezoidal. Antenna 8- to 10-segmented, shorter to longer than head width; with each a subapical rhinarium on segments 3, 4, 6, 7, segments 3, 5, 7, 8, or segments 4, 6, 8, 9. Thorax curved dorso-laterally, pronotum relatively long; metascutellum produced into horn-shaped structure. Forewing membrane smooth, often covered with surface spinules, rarely with dark pattern, pterostigma developed. Metacoxa with short to long meracanthus, margin curved or straight laterally. Metatibia short to moderately long, without basal spine, weakly widening apically, bearing an incomplete crown of 6–8 unsclerotised apical spurs. Metabasitarsus without black spurs. Male proctiger simple, tubular, often with distinct lateral plates posteriorly; male paramere lamellar to simple, often with stout or peg-like setae on inner surface; distal portion of aedeagus relatively short with rounded apical dilatation. Female genitalia cuneate, sometimes up-turned apically.

**Last instar larva.** Antenna 3-segmented, sometimes subdivided, flagellum rarely with distinct subdivisions; rhinaria formula, when 3-segmented, 3333. Tarsal arolium relatively short triangular to fan-shaped, basally expanded, petiolate with developed unguitactor. Sectasetae present on head, antenna, dorsal sclerites and wing pads. Anus ventral or terminal, circumanal ring simple without additional pore fields, if present, laterally connected to outer circumanal ring.

**Comments.** The genus has been revised by Mifsud & Burckhardt (2002) who recognised 51 species, and one species has been added by Navasero & Calilung (2001). *Paurocephala* is restricted to the Old World and is most diverse in the Oriental region (43 spp.) with some Afrotropical species. Host records include: Moraceae, Urticaceae, Ulmaceae (all Urticales), Malvaceae, Sterculiaceae (all Malvales) and Clusiaceae (Theales).

## ***Syntomoza* ENDERLEIN**

*Syntomoza* ENDERLEIN, 1921: 117. Type species: *Euphyllura magna* KUWAYAMA, 1907, by original designation and monotypy.

*Anomoterga* KLYVER, 1932: 93. Type species: *Anomoterga tahuata* KLYVER, 1932, by original designation and monotypy. **Syn. n.**

*Homalocephala* YANG & LI, 1987: 54. Type species: *Homalocephala homali* YANG & LI, 1987, by original designation and monotypy. **Syn. n.**

**Description. Adult.** Head down-curved, without genal processes; vertex passing smoothly into genae; frons small trapezoidal. Frontal ocellus clearly visible from above. Antennae slightly longer than head width, segment 3 very long; with each a subapical rhinarium on segments 4, 6, 8, and 9 (Fig. 3A); thorax curved dorso-laterally, pronotum relatively long and flat. Forewing membrane smooth to rugose (Fig. 2A–C), covered with surface spinules, pterostigma developed, longer than half Rs vein. Metacoxa with short robust to horn-shaped meracanthus (Fig. 2G). Metatibiae relatively short and stout, slightly widening apically, without basal spine, bearing an incomplete crown of 9–11 sclerotised apical spurs and 2–3 small black stout setae (Fig. 2N). Metabasitarsus without black spurs. Male proctiger simple, tubular, curved posteriorly, bearing few setae on inner surface (Fig. 3I); male paramere lamellar to complex, widened apically (Fig. 4E, F); distal portion of aedeagus relatively short with rounded apical dilatation (Fig. 4M, N); male subgenital plate produced apically. Female genitalia long (Fig. 5E).

**Last instar larva.** Antenna 7-segmented (Fig. 6D), rhinaria formula as 3577. Tarsal arolium short fan-shaped with developed unguitractor (Fig. 7G). Setae present on abdominal margin and on dorsum of caudal plate. Legs with massive spurs (Fig. 7D). Anus ventral, outer circumanal ring consisting of a single row of pores, additional pore fields forming oval patches (Fig. 7L, O).

**Comments.** The genus contains 7 species occurring in the Oriental, Afrotropical and Palearctic regions. Host plants include Flacourtiaceae with one species associated with *Populus* (Salicaceae).

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*africana* (LOGINOVA, 1975: 55), **comb. n.** from *Camarotoscena*. Distribution: Ethiopia, Kenya, Uganda. Host plant: *Dovyalis abyssinica* (Flacourtiaceae).

*homali* (YANG & LI, 1987: 54), **comb. n.** from *Homalocephala*. Distribution: China (Fujian, Guangdong, Guangxi). Host plant: *Homalium hainanense* (Flacourtiaceae).

*hsenpinensis* (FANG & YANG, 1986: 137), **comb. n.** from *Anomoterga*. Distribution: (China (Fujian), Hong Kong, Taiwan, Vietnam). Host plant: *Homalium cochinchinensis* (Flacourtiaceae).

*magna* (KUWAYAMA, 1907: 151), from *Euphyllura*, Enderlein 1921: 117. Distribution: Korea, Japan. Host plant: *Idesia polycarpa*, *Xylosma congestum* (Flacourtiaceae); Klimaszewski (1973) and Loginova (1973) report also *Myroxylon japonicum* (Fabaceae) which is an unlikely host.

*scolopiae* YANG, 1984: 23. Distribution: Taiwan. Host plant: *Scolopia oldhamii* (Flacourtiaceae).

*tahuata* (KLYVER, 1932: 94), **comb. n.** from *Anomoterga*. Distribution: Marquesas Islands. Host plant unknown.

*unicolor* (LOGINOVA & PARFENTIEV, 1958: 99), **comb. n.** from *Camarotoscena*. Distribution: Afghanistan, Armenia, Iran, Kazakhstan, Kyrgyzstan, Mongolia, Uzbekistan, Tajikistan. Host plant: *Populus diversifolia*, *P. pruinosa* (Salicaceae).

Following species should be excluded from *Syntomoza* and the Paurocephalinae: *Syntomoza lebezia* HODKINSON, 1986b: 149. Distribution: Belize. In the head shape *S. lebezia* resembles *Metapsylla* spp. with which it may be related.

## Phylogenetic implications

The Paurocephalinae can be diagnosed within the Psylloidea with adult and larval characters. The present revised definition differs from previous classifications. Based on the compact adult body form (Loginova 1973), and the presence of additional pore fields on the caudal plate in larvae respectively (White & Hodkinson 1985), *Syntomoza* and *Diclidophlebia* were assigned to the Euphyllurini/Euphyllurinae. These characters are clearly homoplasies. Our results confirm, in part, the suggestion of Brown & Hodkinson (1988) that the inclusion of the Diclidophlebiini (*Diclidophlebia*, *Paraphalaroida* and *Haplaphalara*) and Togepsyllinae (*Togepsylla* and *Syncoptozus*) may render the subfamily Paurocephalinae sensu White & Hodkinson (1985) more natural. The Diclidophlebiini are part of the Paurocephalinae in our analysis, the Togepsyllinae, however, are not. Similarities between the two subfamilies could not be substantiated with genuine synapomorphies. The position of Togepsyllinae as well as Euphyllurinae remains doubtful. Hodkinson (1986b) has pointed out that the Euphyllurini comprise a fairly heterogeneous collection of genera. The group may not be monophyletic even after removal of *Syntomoza*.

Four other taxa have been related to the Paurocephalinae: *Atmetocranium*, *Primascena subita*, *Pseudaphorma astigma* and *Strophingia*.

The monotypic New Zealand genus *Atmetocranium* has a highly autapomorphic morphology which makes it difficult to relate to other psylloid groups. The metatibia with an internal comb of apical spurs and the 1-segmented asymmetric larval antenna suggest a relationship with the Calophyidae to which it is transferred here.

*Primascena subita* KLIMASZEWSKI, 1998: 21, was described from a single male from Dominican amber. According to Klimaszewski's description the taxon lacks metabasitarsal spurs and exhibits a clypeus which is markedly pointed downwards. The examination of the holotype (AMNH) revealed that neither is true. The alleged clypeus is in fact part of the fore leg, the head being partly



destroyed. Both metabasitarsi have two sclerotised spurs. This clearly puts *Primascena* outside the Paurocephalinae. The metatibia has a crown of spaced apical spurs similar to those of some Aphalaroidinae to which it may belong.

*Pseudaphorma astigma* CONCI & TAMANINI, 1985: 350, was erected for a single male specimen which appears to be lost now (C. Conci pers. comm., M. Daccordi pers. comm.). From the description it is quite clear that the abdomen and genitalia do not belong to the same animal as the remaining parts. The description of the head, antenna, forewing, distribution of surface spinules and hind leg fits perfectly well *Aphalara polygoni* FOERSTER, the abdomen belongs without doubt to *Trioza remota* FOERSTER. Here we suggest following synonymies *Aphalara* = *Pseudaphorma*, **syn. n.**, and *Aphalara polygoni* FOERSTER = *Pseudaphorma astigma*, **syn. n.**

*Strophingia* is a small West Palaearctic genus which lacks autapomorphies of the groups such as Paurocephalinae, Rhinocolinae or Aphalaroidinae to which it has been related to. Our analysis is not informative in this respect.

## Biogeography and host plants

The subfamily Paurocephalinae is predominantly pantropical with *Diclidophlebia* as sole New World representative. *Aphorma* and *Camarotoscena* are mostly Palaearctic with a few Oriental species restricted to Ranunculaceae and *Populus* spp. (Salicaceae) respectively. *Diclidophlebia* has 12 New World, 8 Indo-Australian, 3 Afrotropical and 1 Australian species. Host plant records are within the Malviflorae: Malvales (Malvaceae, Sterculiaceae, Tiliaceae), Urticales (Ulmaceae), Rhamnales (Rhamnaceae), Euphorbiales (Euphorbiaceae) and Myrtiflorae: Myrtales (Melastomataceae). *Syntomoza* includes 7 described species, 4 of which are Oriental, 2 Palaearctic and 1 Afrotropical. Host plants are within the family Flacourtiaceae, except for *S. unicolor* which is associated with *Populus* spp. (Saliaceae).

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|     |  |                         |
|-----|--|-------------------------|
| RHI | * <i>Rhinocola aceris</i> (LINNAEUS)             | 0100010001100000000001  |
| SPO | <i>Ctenarytaina eucalypti</i> (MASKELL)          | 2000400000100000100002  |
| EUP | <i>Euphyllura olivina</i> (COSTA)                | 2000400000000000000001  |
| STR | * <i>Strophingia ericae</i> (CURTIS)             | 00000100000000000210000 |
| CAL | * <i>Atmetocranium myersi</i> (FERRIS & KLYVER)  | 3121411001110000200000  |
| TOG | <i>Togepsylla matsumurana</i> KUWAYAMA           | 1020?11001110000100000  |
| TOG | <i>Syncoptozus mexicana</i> HODKINSON            | 1020???001110000100000  |
| PAU | * <i>Aconopsylla sterculiae</i> (FROGGATT)       | 0001311000011011110002  |
| PAU | <i>Anomoterga hsenpinensis</i> FANG & YANG       | 2001111000011010001001  |
| PAU | <i>Aphorma clematidis</i> BURCKHARDT & BÄNZIGER  | 1000000000011010000001  |
| PAU | <i>A. lichenoides</i> (PUTON)                    | 1000000000011010??????? |
| PAU | <i>Camarotoscena africana</i> LOGINOVA           | 2001111000011010001001  |
| PAU | <i>C. fulgidipennis</i> LOGINOVA                 | 0001100000011010000101  |
| PAU | <i>C. speciosa</i> (FLOR)                        | 0001100000011010000101  |
| PAU | <i>C. unicolor</i> LOGINOVA & PARFENTIEV         | 2001111000011010001001  |
| PAU | <i>Diclidophlebia eastopi</i> VONDRAČEK          | 0001311000011011110002  |
| PAU | * <i>Haplaphalara dahli</i> (RÜBSAAMEN)          | 0001311000011011110002  |
| PAU | * <i>Homalocephala homali</i> YANG & LI          | 2001111000011010?01001  |
| PAU | * <i>Paraphalaroida fremontiae</i> (KLYVER)      | 0001311000011011110002  |
| PAU | <i>Paurocephala artocarpae</i> BRAZA & CALILUNG  | 1001201010011010210000  |
| PAU | <i>P. crassiflagellata</i> BURCKHARDT            | 0001311000011011??????? |
| PAU | <i>P. gossypii</i> RUSSELL                       | 1001201010011010210000  |
| PAU | <i>P. lanceomedia</i> BROWN & HODKINSON          | 0001311000011011??????? |
| PAU | <i>P. paucivena</i> BROWN & HODKINSON            | 0001311000011011??????? |
| PAU | * <i>P. psylloptera</i> CRAWFORD                 | 1001201010011010210000  |
| PAU | <i>P. pterospermi</i> MIFSUD & BURCKHARDT        | 1001201010011010210000  |
| PAU | * <i>P. (Thoracocorna) chonchaiensis</i> BOSELLI | 1001201010011010210010  |
| PAU | * <i>Sinuonemopsylla excetrodendri</i> LI & YANG | 0001311000011011110002  |
| PAU | <i>Syntomoza scolopiae</i> YANG                  | 2001111000011010001001  |
| PAU | * <i>Woldaia nebulosa</i> BROWN & HODKINSON      | 0001311000011011110002  |

**Table 1. Matrix for adult and larval characters of selected members of Paurocephalinae (PAU), Euphyllurinae (EUP), Rhinocolinae (RHI), Spondyliaspidaenae (SPO), Strophingiinae (STR), Togepsyllinae (TOG) (all Psyllidae) and Calophyidae (CAL) (Table 2, Fig. 9) (subfamilies as in present review, genera as previous to review). Asterisks indicate type species.**

1. Head inclination 45–90° (0); 0–45° (1); 90° (2); >90° (3).
2. Rhinaria present on apex of antennal segments 4, 6, 8, and 9 (0); 4, 5, 6, 7, 8, 9 (1).
3. Coronal suture fully developed (0); largely reduced (1); completely reduced (2).
4. Vertex and genae separated by angle, lobes or processes (0); vertex passing smoothly into genae (1).
5. Frons elongate, parallel-sided (0); moderately wide, rhomboidal (1); elliptical (2); very wide, rhomboidal (3); reduced (4).
6. Clypeus pear-shaped (0); flattened (1).
7. Terminal setae on antennal segment 10 short (0); very long (1).
8. Pro- and mesothorax flat (0); with large conspicuous horns (1).
9. Metascutellum flat or weakly raised (0); horn-shaped (1).
10. Metacoxae with meracanthus (0); without meracanthus (1).
11. Metacoxae without (0); with a membranous process near trochanteral insertion (1).
12. Metabasitarsus with 2 sclerotised spurs (0); without spurs (1).
13. First visible abdominal tergite without (0); with sclerotised patch of spinules laterally (1).
14. Paramere simple (0); cleft apically (1).
15. Proximal portion of aedeagus simple apically (0); with a rim-like inflation apically (1).
16. Distal portion of aedeagus simple (0); complex (1).
17. Fifth instar larva with antenna 7- or 8-segmented (0); 9- or 10-segmented (1); 3-segmented (2).
18. Larva without sectasetae or lanceolate setae on antennal flagellum (0); with (1).
19. Larval mid and hind legs without (0); with massive peg-like setae (1).
20. Last instar larva with precaudal tergites not (0); bearing a row of densely spaced setae (incl. sectasetae) (1).
21. Last instar larva with outer circumanal ring consisting of a single row of pores (0); consisting of one row of pores which is expanded laterally (1).
22. Last instar larva without additional pore fields (0); with additional pore fields present, which are close to circumanal ring (1); with additional pore fields present, which are widely distant from circumanal ring (2).

**Table 2. Characters of adult (1–16) and last instar larva (17–22) with character states of matrix in Table 1.**



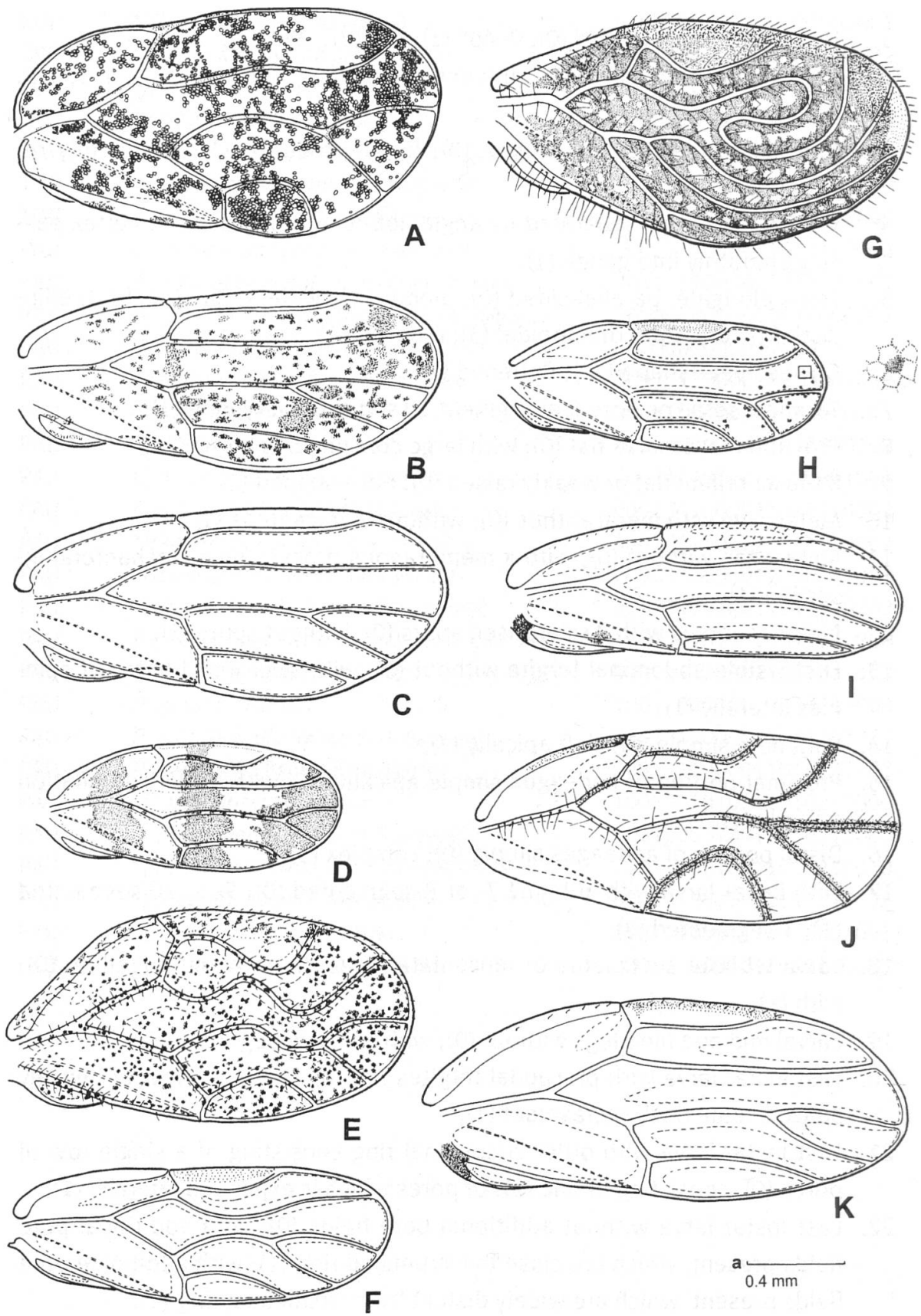


Fig. 1. Forewing. A, *Aphorma lichenoides*; B, *Camarotoscena personata*; C, *C. subrubescens*; D, *Diclidophlebia dahli*; E, *D. excetridendri*; F, *D. lanceomedia*; G, *D. oceanica*; H, *D. paucipunctata*; I, *D. paucivena*; J, *D. setinervis*; K, *D. xuani*. Scale bar a: A–K.

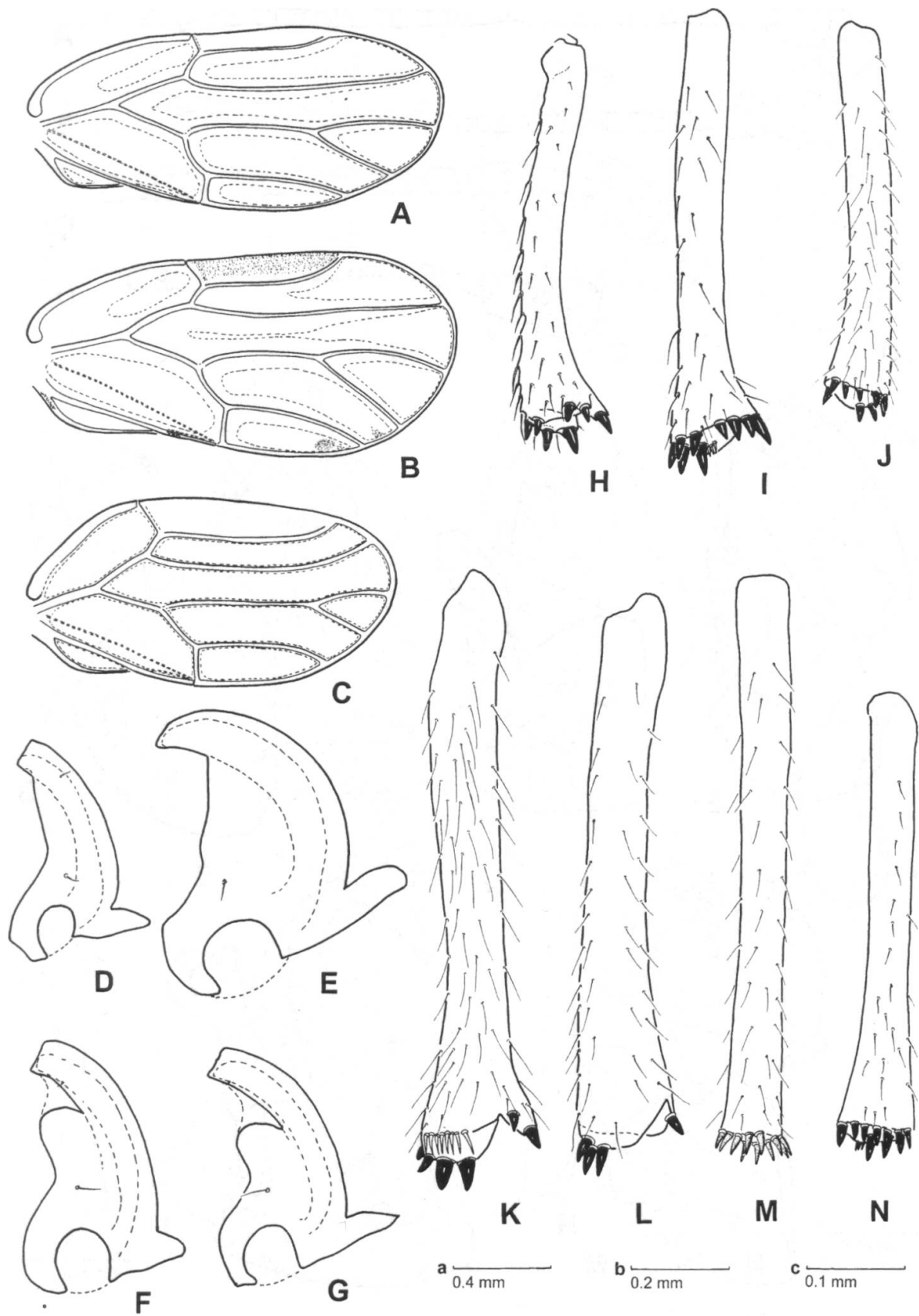


Fig. 2. A–C, Forewing; D–G, metacoxa; H–N, metatibia. A, G, N, *Syntomoza africana*; B, *S. hsenpiniensis*; C, F, *S. scolopiae*; D, I, *Camarotoscena personata*; E, *Diclidophlebia xuani*; H, *Aphorma lichenoides*; J, *Diclidophlebia dahli*; K, *D. oceanica*; L, *D. fremontiae*; M, *D. setinervis*. Scale bar a: A–C; b: D–G; c: H–N.

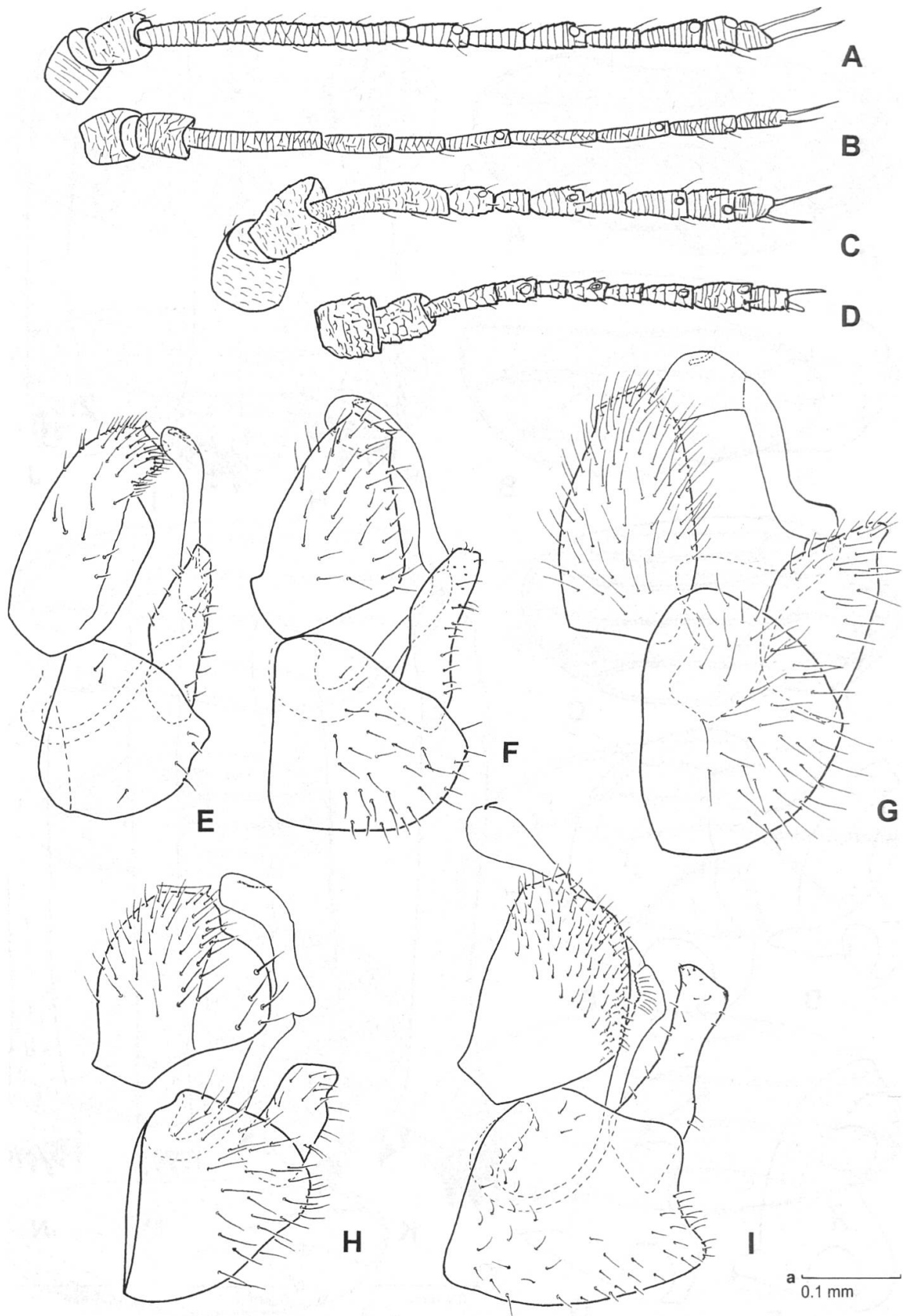


Fig. 3. A–D, Antenna; E–I, male genitalia, lateral view. A, I, *Syntomoza africana*; B, *Diclidophlebia dahli*; C, *Camarotoscena speciosa*; D, E, *Aphorma lichenoides*; F, *Camarotoscena personata*; G, *Diclidophlebia oceanica*; H, *D. xuani*. Scale bar a: A–C; b: D–G; c: H–N.

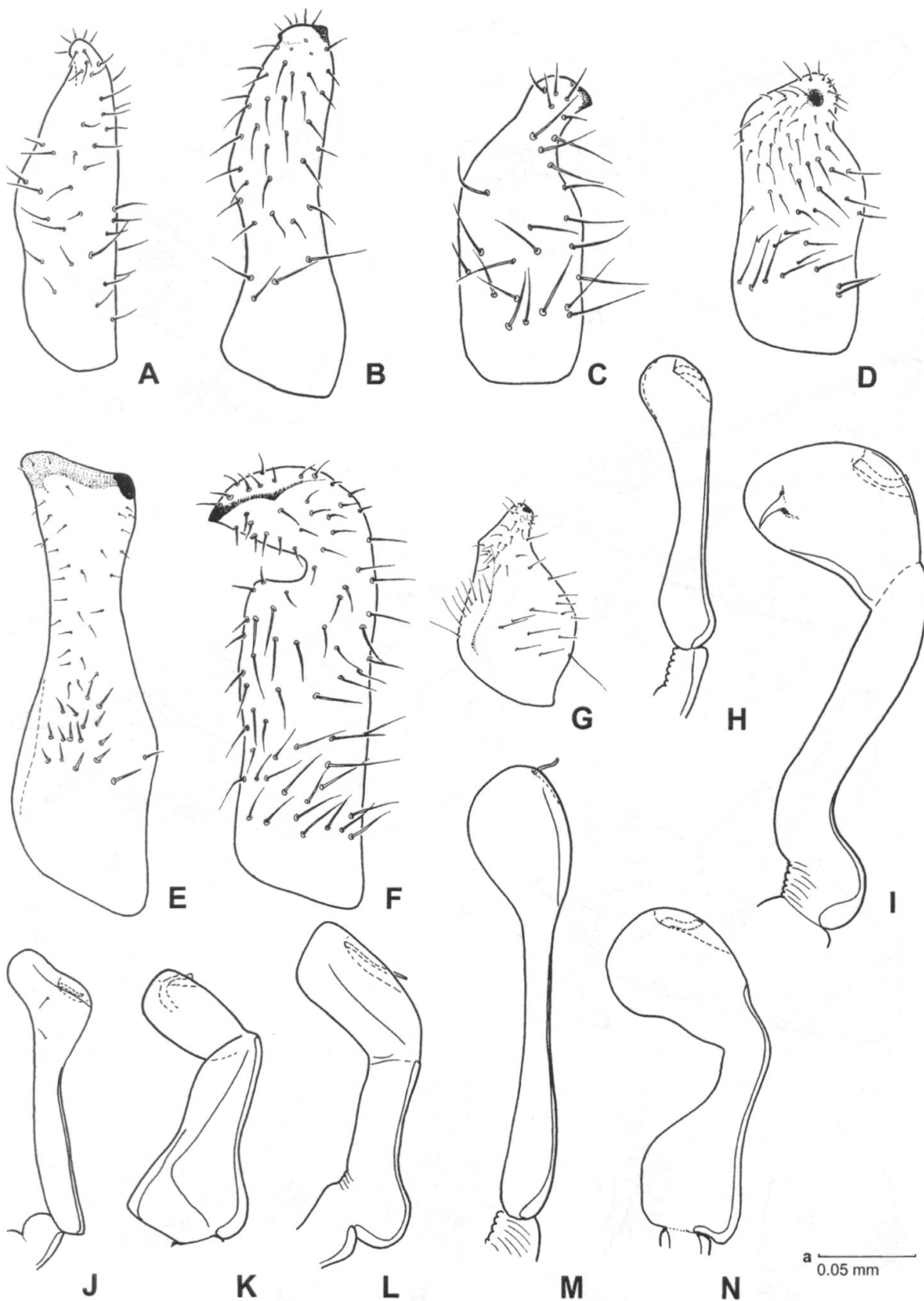


Fig. 4. A–G, paramere, inner surface; H–N, distal portion of aedeagus. A, *Aphorma lichenoides*; B, H, *Camarotoscena personata*; C, K, *Diclidophlebia setinervis*; D, L, *D. xuani*; E, M, *Syntomoza africana*; F, N, *S. hsenpiniensis*; G, J, *Diclidophlebia dahli*; I, *D. oceanica*. Scale bar a: A–N.

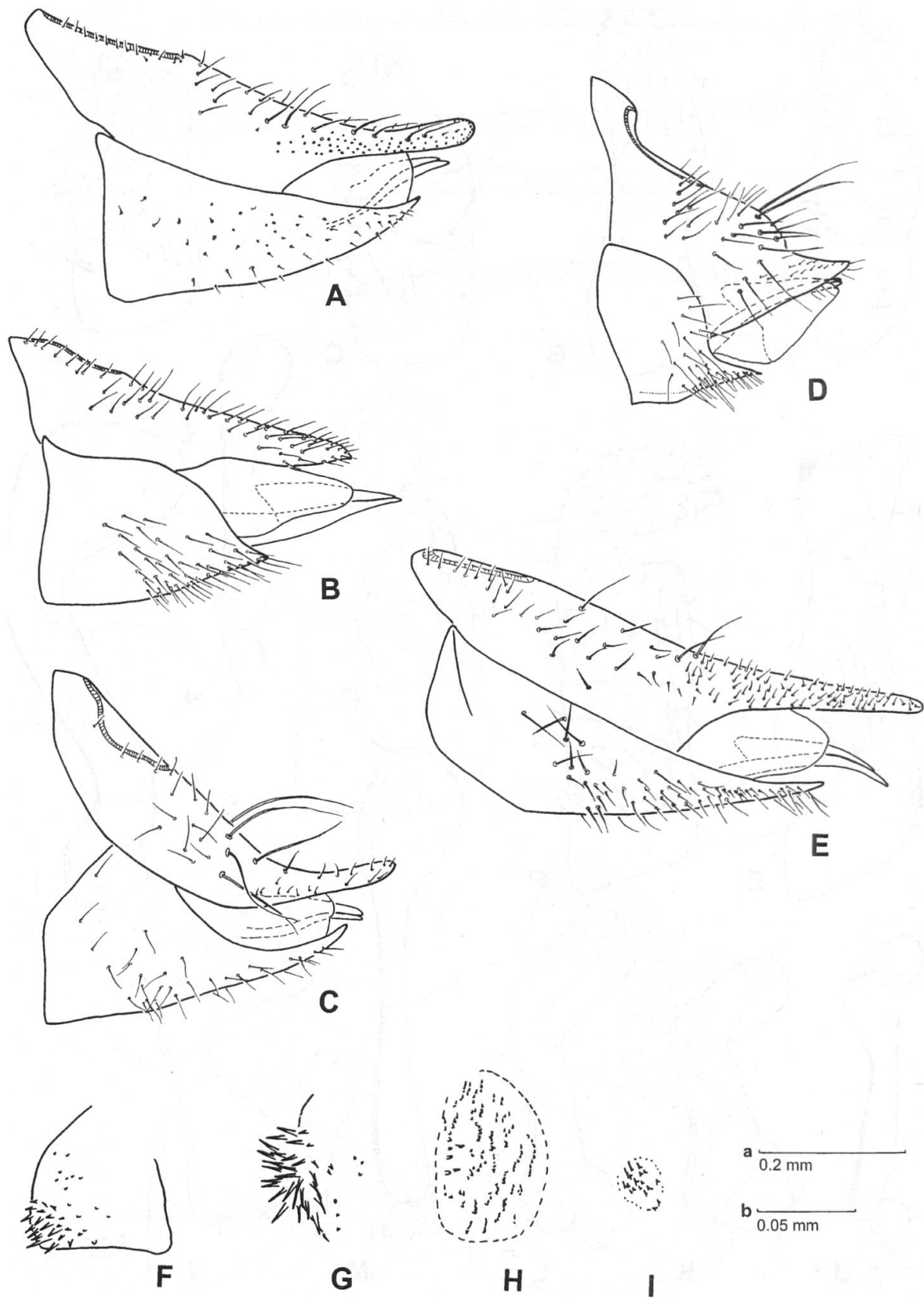


Fig. 5. A-E, Female genitalia, lateral view; F-I, lateral sclerotised patch of spinules on first visible abdominal tergite. A, F, *Aphorma lichenoides*; B, *Camarotoscena speciosa*; C, *Diclidophlebia setinervis*; D, *Diclidophlebia dahli*; E, I, *Syntomoza unicolor*; G, *Camarotoscena subrubescens*; H, *Diclidophlebia exctridendri*. Scale bar a: A-E; b: F-I.

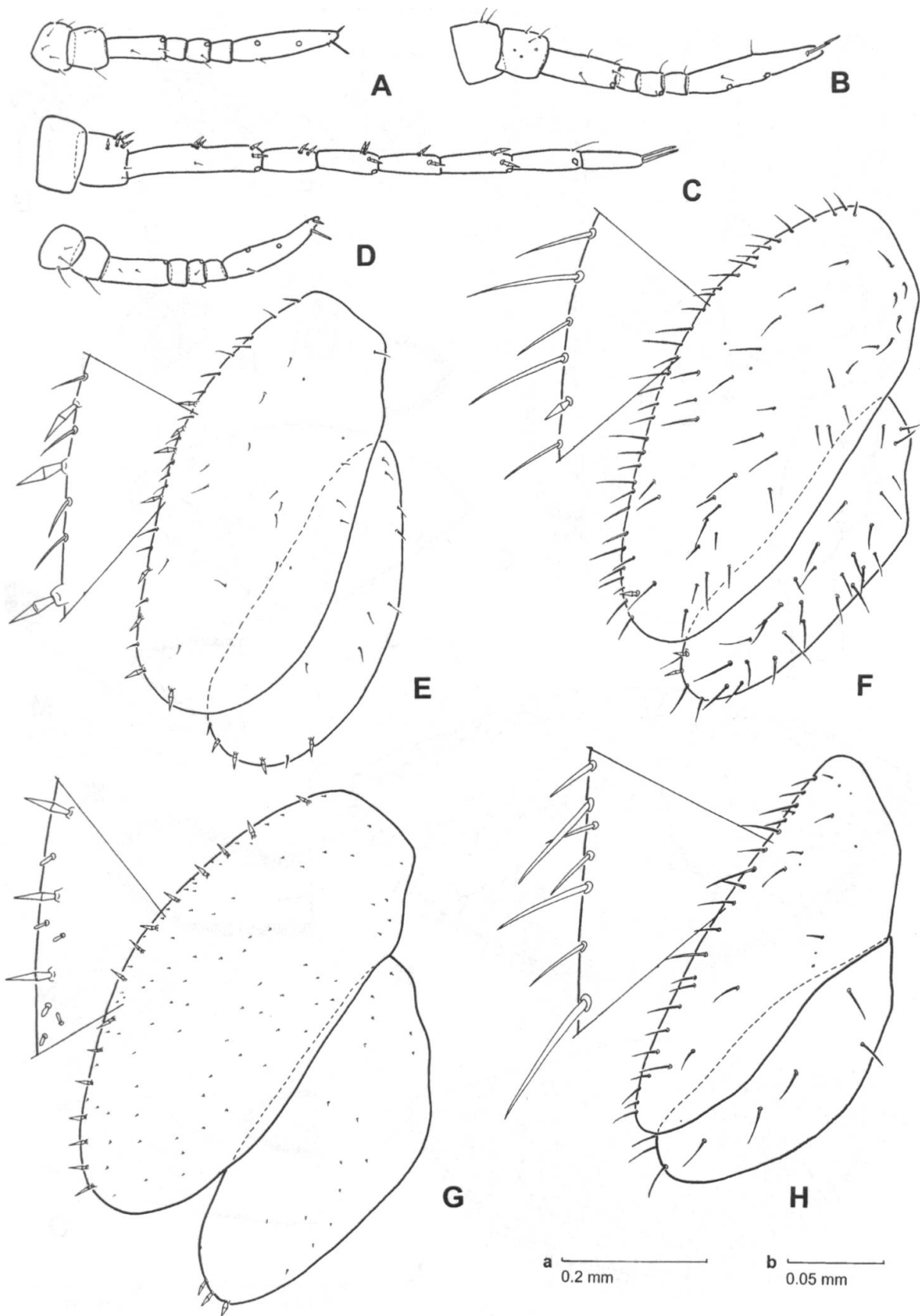


Fig. 6. Fifth instar larva: A–D, antenna; E–H, wing pads. A, E, *Aphorma lichenoides*; B, F, *Camarotoscena fulgidipennis*; C, G, *Diclidophlebia fremontiae*; D, H, *Syntomoza unicolor*. Scale bar a: A–H, b: details of E–H.

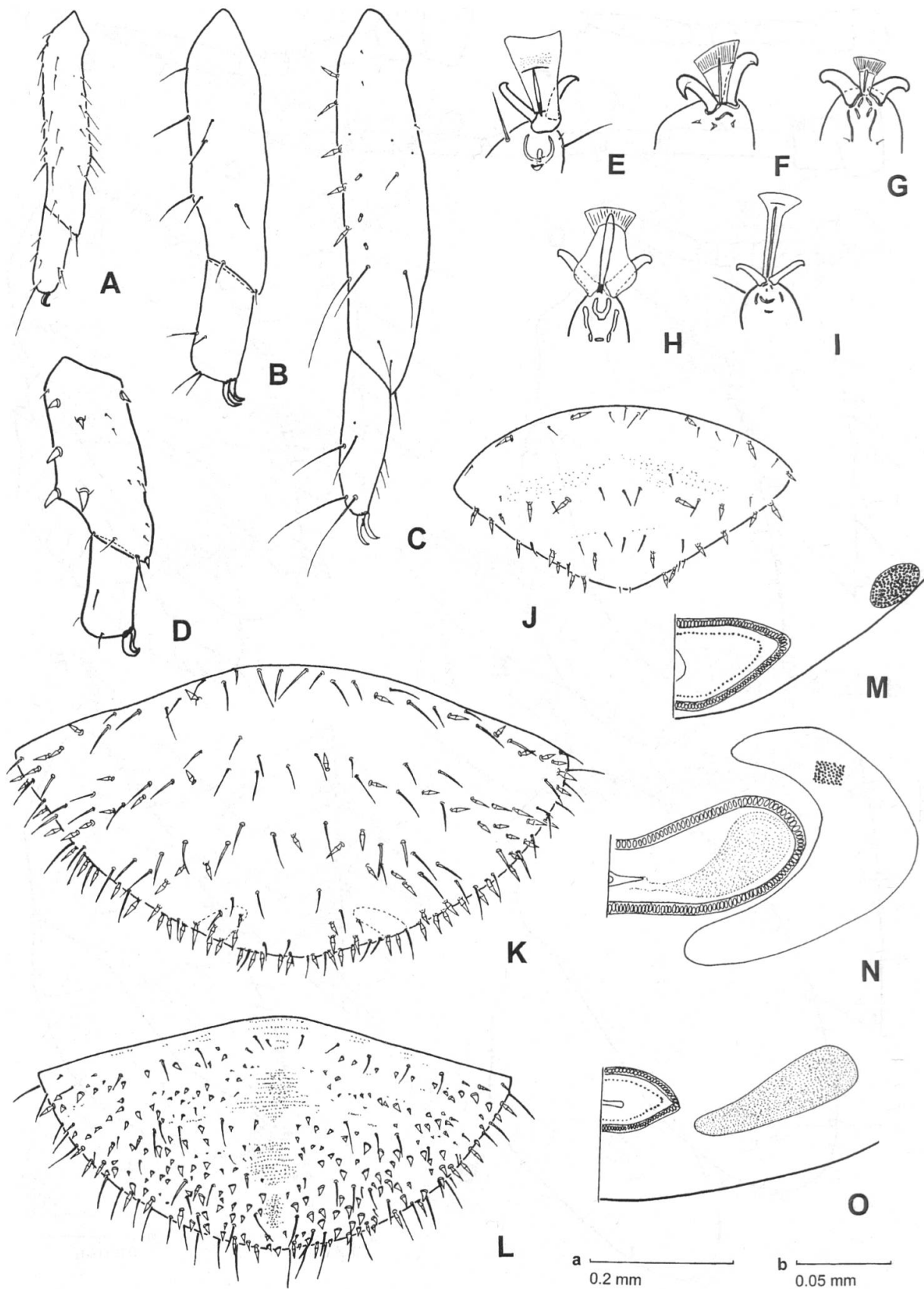
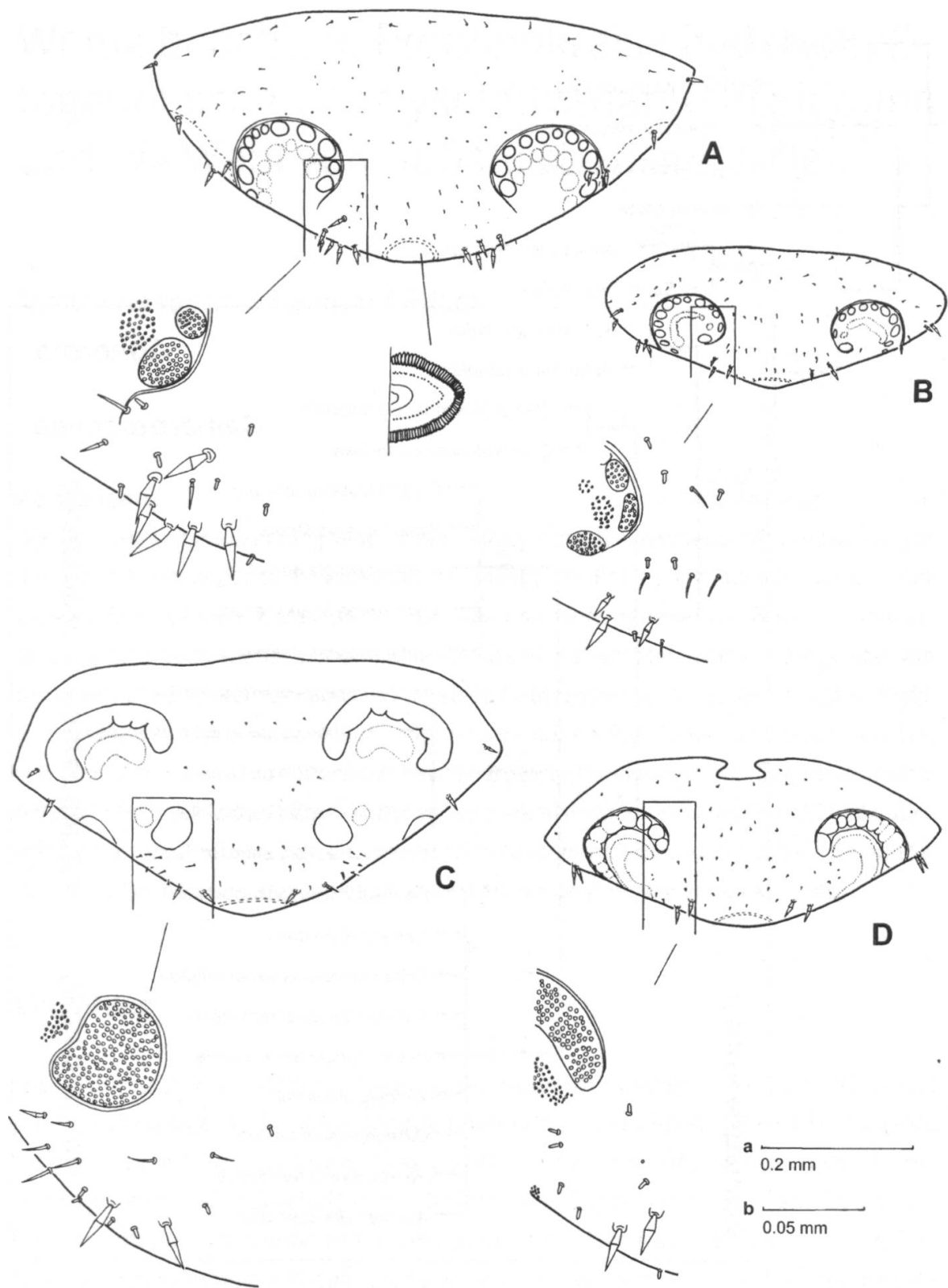


Fig. 7. Fifth instar larva: A–D, tibiotarsus and apical tarsus of hind leg; E–I, apex of tarsus with arolium; J–L, caudal plate, dorsal view; M–O, circumanal ring with additional pore fields, ventral view. A, E, J, M, *Aphorma lichenoides*; B, F, K, N, *Camarotoscena fulgidipennis*; C, H, *Diclidophlebia fremontiae*; D, G, L, *Syntomoza unicolor*; I, *D. dahli*. Scale bar a: A–D, J–L; b: M–O.



**Fig. 8.** Fifth instar larva, caudal plate, dorsal view, with details. A, *Diclidophlebia fremontiae*; B, *D. fava*; C, *D. xuani*; D, *D. dahli*. Scale bar a: A–D; b: details.



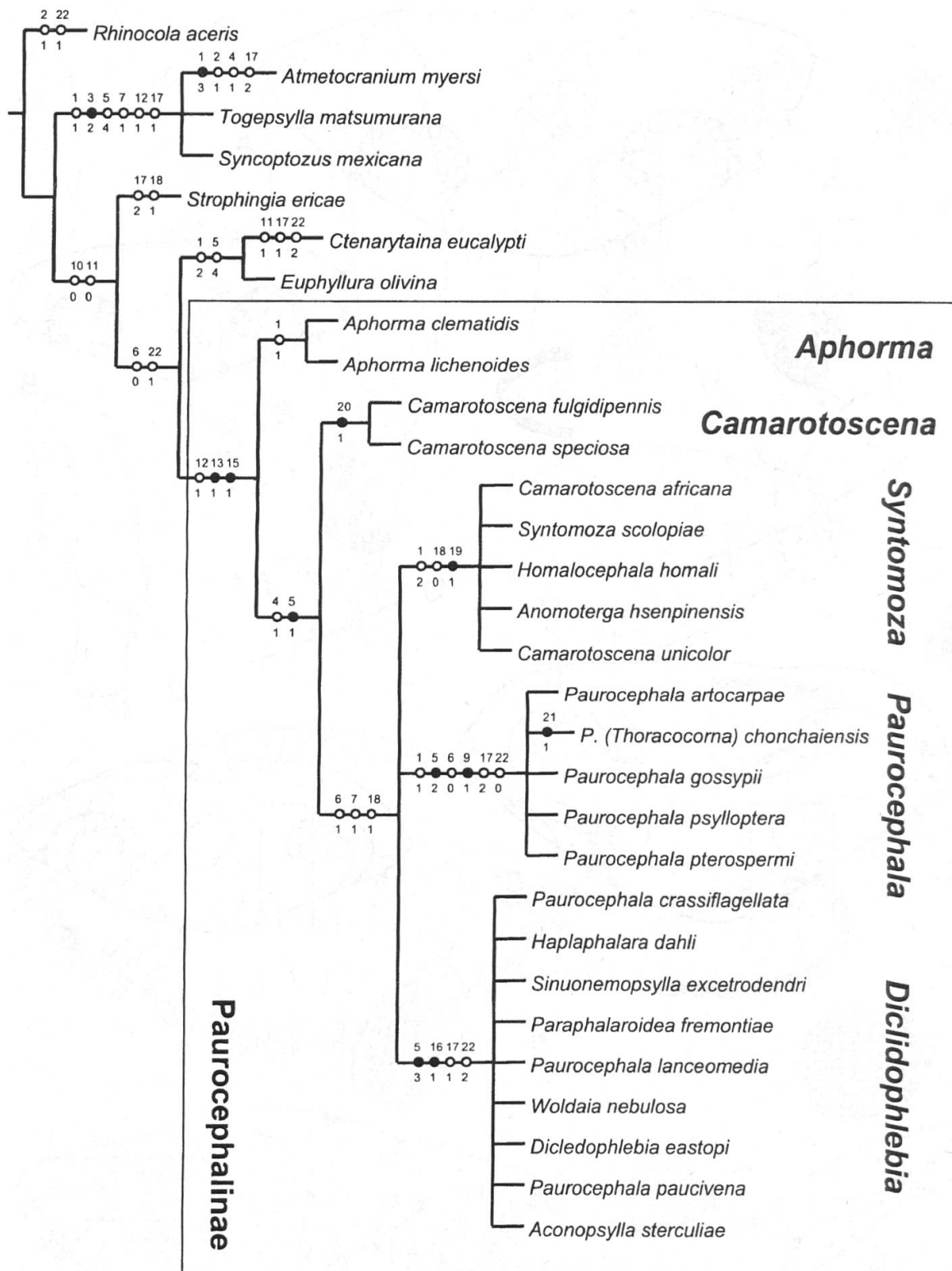


Fig. 9. Cladogram of Paurocephalinae. Nelsen consensus of 18 most parsimonious trees (weighted characters: length 218, consistency index 72, retention index 91; unweighted characters: length 46, consistency index 58, retention index 85). Fast character transformation: full circles = synapomorphies or autapomorphies; open circles homoplasies; numbers above circles = character numbers; numbers below circles = character states. Note that the clade supported by characters 10 and 11 is an artefact of the choice of the out-groups; characters 10 and 11 are, therefore, not genuine synapomorphies.