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## DESCRIPTION OF THE LARVA OF *MONOMMA RESINORUM* HOPE 1842 (COLEOPTERA, ZOPHERIDAE), WITH REMARKS ON THE COMPOSITION OF THE FAMILY

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The late-instar larva of *Monomma resinorum* Hope 1842, from India, is described in due detail for the first time, including data on the chaetotaxy and structure of the thoracic endoskeleton. A comparison with other known monommatid larvae is provided to point out their specific features and clarify the taxonomic position of this group. Based on larval characters, a transfer of monommatid beetles from Zopheridae to Monommatidae **stat. rest.** is proposed. In the course of an analysis of original and previously published morphological data on the known larvae of Zopheridae sensu Ślipiński, Lawrence 1999, the composition of the family is reconsidered through dividing it into Monommatidae, Zopheridae and Colydiidae **stat. rest.** Moreover, the systematic position of certain disputable taxa of Zopheridae and Colydiidae is also discussed.

**Keywords:** Coleoptera, larva, morphology, taxonomy, *Monomma*, Zopheridae

**DOI:** 10.1134/S0044513418110089

Monommatid beetles, now considered as a tribe in the large and diverse family Zopheridae Solier 1834, is a group of 14 genera and about 225 species worldwide, mostly distributed in tropical and subtropical regions with greatest diversity in Africa and Madagascar (Freude, 1958; Ślipiński, Lawrence, 1999). The systematic position of monommatids, as well as some other taxa of Zopheridae is uncertain (Ślipiński, Lawrence, 1999; Ivie et al., 2016). First described as a family by Blanchard (1845) this group was later transferred to an expanded Zopheridae by Ślipiński and Lawrence (1999), and became the tribe Monommatini Blanchard 1845 in subfamily Zopherinae Solier 1834, although the authors themselves noted that it is “a very distinctive group” in both larval and imaginal characters (Ślipiński, Lawrence, 1999). Larvae are described for only 3 genera: *Hyporhagus* Thomson 1860 (*H. texanus* Linnell 1899 and *Hyporhagus* sp. from Brasil), *Inscutomonomma* Pic 1951 (*I. hessei* Freude 1958) and *Monomma* Klug 1833 (*M. brunneum* Thomson 1860) (Fletcher, 1916; Peterson, 1951; Freude, 1958; Costa et al., 1988). The description of *M. brunneum* larva by Fletcher is rather formal, because no specific characters of the genera were pointed out, and the description could equally describe the larvae of many other families of Coleoptera (elongated larva with brown head and yellow body, 2 upturned urogomphi and 3 pairs of thoracic legs).

In this paper we provide first description of the late-instar larva of *Monomma resinorum* Hope 1842,

compare it with other known monommatid larvae to point out their specific features and clarify the taxonomic position of this group. Moreover, larvae of some other members of Zopheridae sensu Ślipiński, Lawrence were examined and some remarks on the composition of the family are proposed.

### MATERIAL AND METHODS

Larvae of *M. resinorum* were reared to adult stage, which was identified by the late prof. H. Freude. Material examined: 1 L – India, Rajasthan, Chazri Farm, under bark of *Ficus* sp., 09.09.1989 leg. A. V. Kompantsev, det. H. Freude; 3L, 2A – India, Rajasthan, Jodhpur, under bark of *Calotropis*, 11.10.1989 leg. A. V. Kompantsev, det. H. Freude; 5L, 5A – India, Rajasthan, Beawar, in *Euphorbia* 21.10.1989 leg. A. V. Kompantsev, det. H. Freude; 8L, 1A – India, Rajasthan, 10 km N of Jodhpur, in *Euphorbia* 27.11.1989 leg. A. V. Kompantsev, det. H. Freude. Additional larval material studied: *Hyporhagus* sp. (Zopherinae, Monommatini); *Phellopsis amurensis* Heyden 1885 (Zopherinae, Phellopsini), *Pycnomerus sulcicollis* Germar 1824 (Zopherinae, Pycnomerini), *Bitoma crenata* Fabricius 1775, *Colobicus hirtus* Rossi 1790, *Endophloeus excelsptus* Germar 1847, *Synchita humeralis* Fabricius 1792 (Colydiinae, Synchitini); *Aulonium trisulcum* Geoffroy 1775, *Colydium elongatum* Fabricius 1787 (Colydiinae, Colydiini).

Habitus photographs were taken with a Canon EOS 40D camera with a MP-E 65 mm macro lens. Photos of slide mounts were taken with Canon EOS 6D camera attached to a Carl Zeiss AXIO Scope.A1 microscope. All photos were processed using Zerene Stacker software. Line drawings were made in Corel Draw 12. The specimens were preserved in 70% ethanol or on slides with Faure's Berlese media and are deposited in Moscow State Pedagogical University, Moscow, Russia (MSPU).

## RESULTS

### The Description of Late-Instar Larva

Maximum body length about 18 mm; head length 0.8 mm; urogomphi length 0.5 mm; maximum width of thorax 2 mm; maximum width of abdomen 2.6 mm. Body elongated, cylindrical; widest across abdominal segments II–III, slightly tapering posterad; urogomphi well developed, distinctly upturned. Head yellow with darkened areas near frontal sutures and on clypeus; stemmata dark brown; mandibles brownish, with brown-red apices; antennae, maxillae and labium yellow. Thoracic and abdominal sclerites light, pale-yellow; asperities on thoracic segment III and abdominal segments I–VI brownish. Legs light-yellow, with yellow-brown claws. Abdominal segment IX dark-yellow, with darker tubercles; anterior margin of urogomphal pit red-brown, posterior margin and apices of urogomphi dark-brown. Dorsal surface of thoracic segment III and abdominal segment I with transverse row of heavilysclerotized asperities; abdominal segments II–VI with 2 such rows, forming ovals; ventral surfaces membranous, covered with short setae (Fig. 1A–1C).

Head (Figs 2, 3): prognathous, slightly retracted, posterior edge of head capsule moderately emarginated at the middle; epicranial suture very short, about 0.04 as long as head capsule; frontal sutures lyriform, their bases contiguous. Endocarina paired, lying between frontal sutures, 0.2 as long as head capsule (Fig. 2A). Frontal sclerite with 6 setae and 2 pores on each side (Fig. 2A): 1 microseta and 1 pore close to the inner margin of the frontal suture, approximately in its middle part; 1 micro- and 1 macroseta between the antennal socket and dorsal mandibular articulation point; 1 microseta close to the midpoint of the clypeolabral suture; 1 macroseta and 1 mesoseta close to the arc of the frontal suture, 1 pore located outside the macroseta. Each parietal sclerite dorsally with 15 setae and 7 pores (Fig. 2A): 1 macroseta close to the outer margin of the frontal suture, approximately in its middle part; 1 macroseta, 1 mesoseta and 2 microsetae as well as 1 pore on the outer edge of the sclerite, near two anterior stemmata; 1 macro-, 1 microseta and 1 pore located within; 1 macro-, 1 microseta and 1 pore near the outer edge of the sclerite, approximately in its medial part; 4 microsetae and 2 pores forming a row from the medial part of the posterior margin of the sclerite; 2 microsetae and 2 pores near the outer edge of the sclerite in its posterior part. Ventrally each parietal sclerite with 8 setae and 3 pores (Fig. 3A): 2 macrosetae,

2 mesosetae and 1 pore near its inner edge; 1 macroseta, 2 mesosetae and 2 pores near the outer edge; 1 macroseta near the ventral mandibular articulation point. Frontal and parietal sclerites bear numerous small sensilla dorsally. Hypopharyngeal rods well-developed, extend posteriorly towards the margin of the head capsule, almost parallel (Fig. 3A).

Stemmata (Fig. 3B) 5 on each side, forming two vertical rows, with 2 and 3 stemmata accordingly.

Frontoclypeal suture distinct, complete. Clypeus (Fig. 2A) trapezoidal, about 0.3 as long as wide; its posterior part more sclerotized than the anterior, each side with 1 macroseta, 1 mesoseta and 1 pore located laterally. Clypeolabral suture distinct; labrum (Fig. 2B–2C) rectangular, 0.5 as long as wide; rounded laterally, widest at medial part, slightly narrowing anteriorly and posteriorly; its anterior margin with small notch. Dorsally on each side it bears 6 setae (Fig. 2B): 1 macroseta located slightly outer from the midpoint; 3 macrosetae and 2 mesosetae forming a row on the anterior margin. There are a pair of mesal campaniform sensilla as well as 5 smaller sensilla located on each side of the dorsal surface of the labrum. Ventrally each side of the labrum bears 4 broad mesosetae, 1 conical sensillum and 1 campaniform sensillum on the anterior margin. Epipharynx (Fig. 2C) with numerous small spines and 2 groups of campaniform sensilla: distal and proximal, each with 10 sensilla; also there are 2 lateral campaniform sensilla on each side of the posterior part of the epipharynx. Tormae present, well developed (Fig. 2C); leiotorma and dexiotorma symmetrical and connected to each other approximately at the level of their posterior thirds; almost reaching anterior margin of the labrum. A small heavy sclerotized area located near the outer margin of the anterior part of each torma (Fig. 2C).

Antenna (Fig. 2D–2E) with 3 antennomeres, 0.3 as long as greatest head width. Antennomere I 1.2 as long as wide, with 4 campaniform and 1 smaller sensilla. Antennomere II almost as long as antennomere I and 1.6 as long as wide, with 1 campaniform sensillum; its apical part with 3 mesosetae and 1 microseta, as well as conical sensorium (Fig. 2D) which is 0.3 as long as antennomere III. Antennomere III 0.8 as long as antennomere II and 3.3 as long as wide, with 1 campaniform sensillum; its apical part with a group of 1 medial macroseta, 3 mesosetae and 1 microseta.

Mandible (Fig. 2F–2G) 1.4 as long as basal width, bidentate; incisor edge with rather broad subapical tooth. Prosthema absent. Mola represented by two rows of small teeth shifted ventrally (Fig. 2F). At the base of the mesal edge of each mandible a row of well-developed hyaline teeth situated (Fig. 2F–2G). Ventral surface of the mandible in basal part with a group of small cuticular spines and tubercles (Fig. 2F). Dorsally each mandible bears 1 macroseta, 1 microseta, 1 pore and a group of 5 sensilla on the outer edge, as well as 1 medial pore.

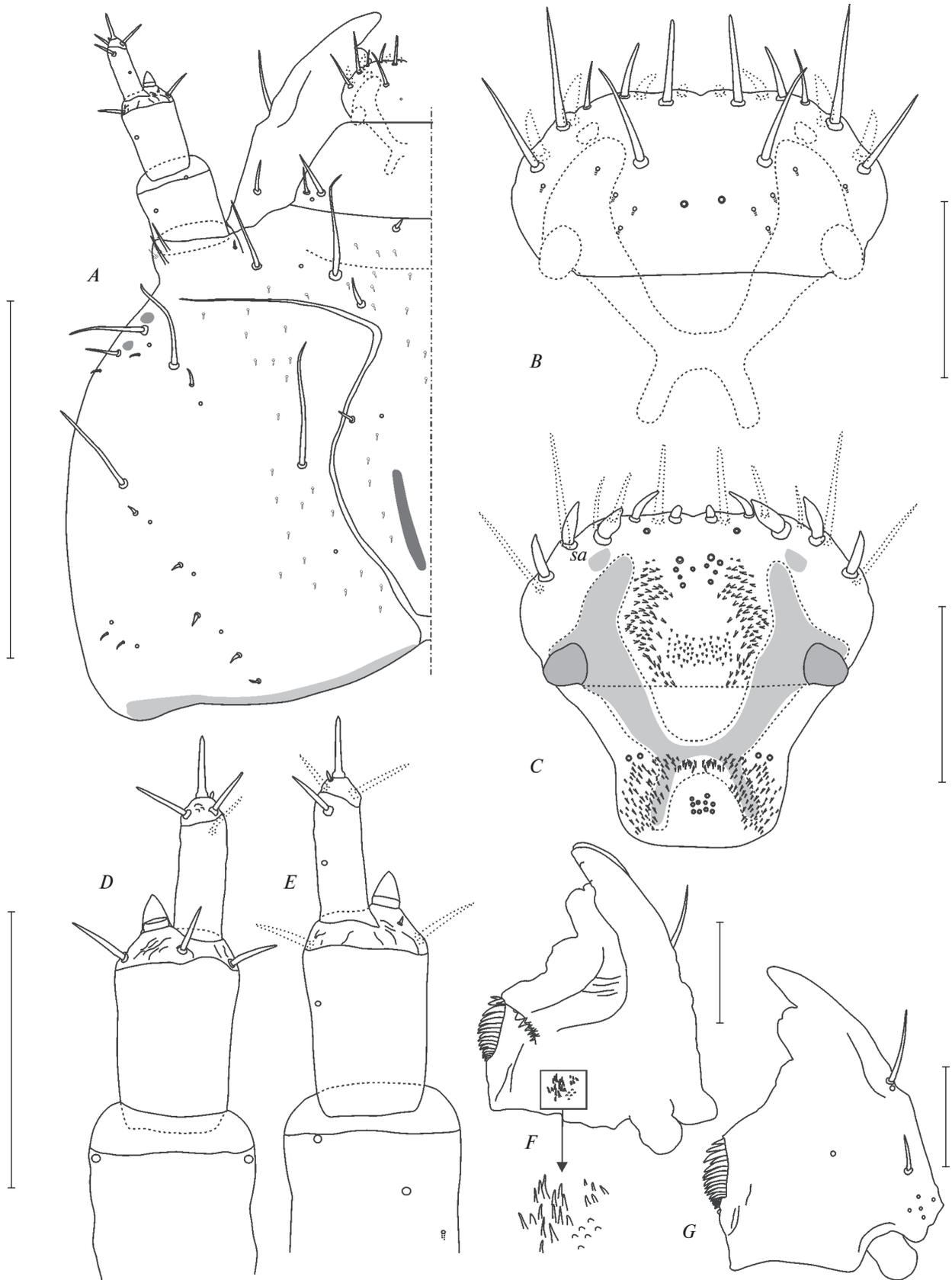
Ventral mouthparts retracted; maxillary articulating area (Fig. 3C) large, dorsally with 2 microsetae and 4 campaniform sensilla. Cardo (Fig. 3A, 3C) not di-



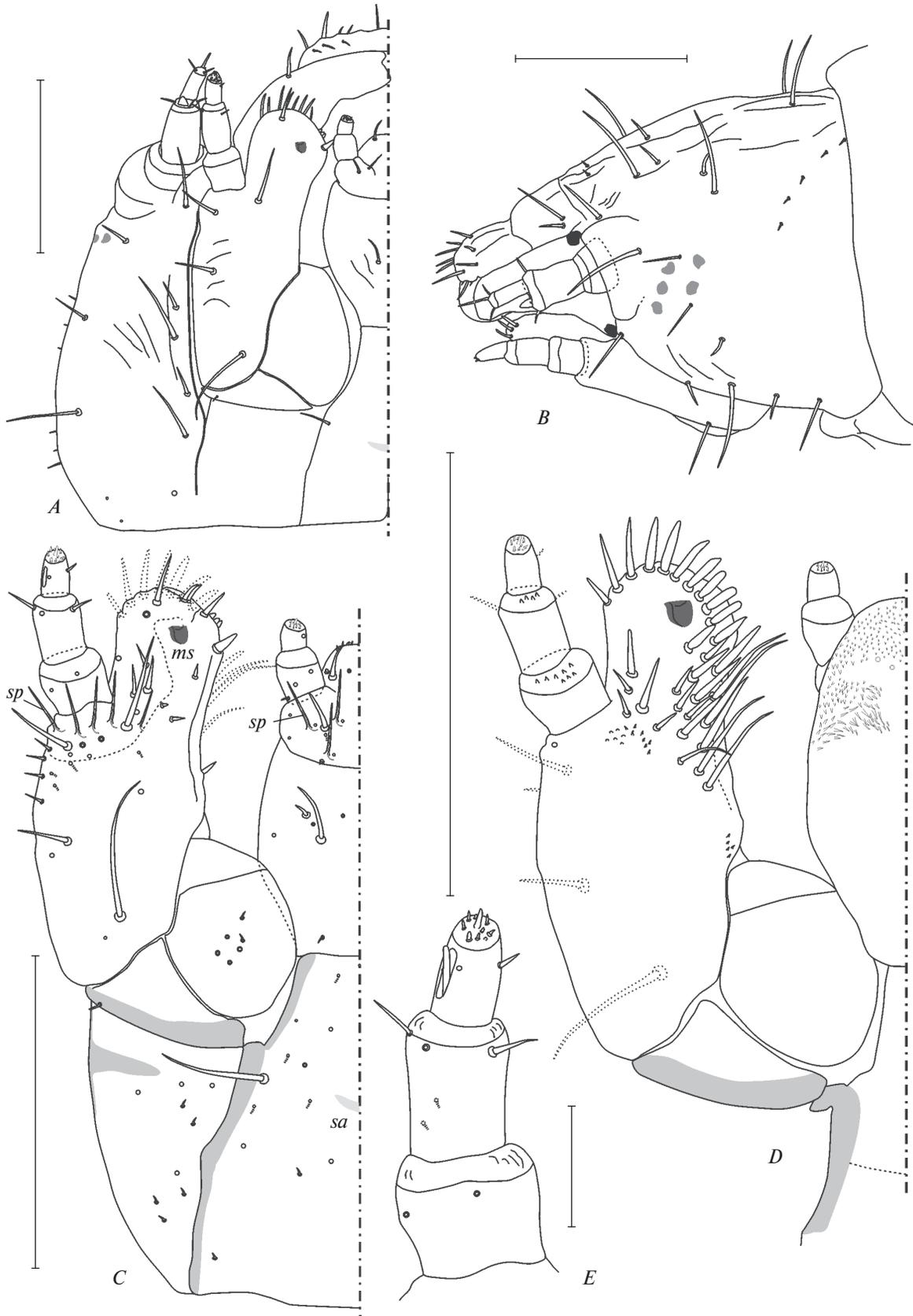
Fig. 1. Larva of *Monomma resinorum*, habitus (A–C): A – Dorsal; B – Lateral; C – Ventral. Scale bar: 3 mm.

vided by the internal sclerotization, transverse, of triangular shape; dorsally with 1 microseta on the distal part. Stipes (Fig. 3C–3D) 2.5 as long as wide; proxistipes dorsally with 1 macroseta and 1 pore; mesal part of sti-

pes with 1 macroseta, 3 mesosetae, 1 pore and 3 sensilla on the outer edge; 1 medial pore and 1 conical sensillum on the inner edge. Dististipes dorsally with 2 macrosetae, 1 microseta, and 5 pores, as well as 5 long



**Fig. 2.** Larva of *Monomma resinorum* (A–G): A – Head, dorsal. Scale bar: 0.8 mm; B – Labrum and tormae, dorsal; C – Labrum, epipharynx and tormae, ventral; D – Right antenna, ventral; E – Right antenna, dorsal; F – Right mandible, ventral; G – Left mandible, dorsal. Scale bars: 0.15 mm. Abr.: sa – sclerotized area.



**Fig. 3.** Larva of *Monomma resinorum* (A–E): A – Head, ventral; B – Head, lateral; C – Labio-maxillary complex and paragular area, dorsal; D – Labio-maxillary complex, ventral. Scale bars: 0.5 mm; E – Maxillary palpi, dorsal. Scale bar: 0.3 mm. Abr.: *ms* – malar scleroma; *sa* – sclerotised area; *sp* – spines.

spines with visible internal channels, forming horizontal row (Fig. 3C). Ventrally dististipes with 1 pore near the outer edge just before the maxillary palp I, and with the field of about 15 small cuticular asperities (Fig. 3D). Mala (Fig. 3C–3D) truncate, cleft, its inner apical angle with 3 small teeth. Dorsally proximal part of mala with 5 mesosetae and 1 microseta, as well as 1 pore near the outer margin; distal part of mala dorsally with 1 macroseta, 3 mesosetae, 1 pore and 1 elongated conical sensillum. Malar scleroma well-developed (Fig. 3C). Ventrally mala with 2 macrosetae and 3 mesosetae just anterior to the field of asperities; anterior margin of mala with a row of 10 macrosetae, inner margin with a group of 14 macrosetae and 3 mesosetae (Fig. 3D). Maxillary palps 3-jointed (Fig. 3C–3E). Palpomere I 0.9 as long as wide, with 2 campaniform sensilla; its apex ventrally with several asperities. Palpomere II 1.1 as long as palpomere I and 1.4 as long as wide, with 2 campaniform sensilla, 2 mesosetae and 1 pore on the apical part; apex of palpomere II ventrally with several asperities. Palpomere III 0.7 as long as palpomere II and 1.6 as long as wide, with digitiform sensillum and 1 pore near it as well as 1 microseta. Apex of palpomere III with a group of about 10 conical sensilla, the medial one is the largest (Fig. 3E).

Labium (Fig. 3C–3D) free to the base of mentum. Ligula present, with 1 macroseta, 1 pore and 1 conical sensillum on each side (Fig. 3C). Each side of prementum dorsally with 1 macroseta; 1 microseta near the posterior margin, and 6 pores as well as 3 long spines similar to those on the dististipes. Labial palps 2-jointed. Palpomere I 1.2 as long as wide, with 1 basal microseta on the outer edge and 2 pores. Palpomere II 0.7 as long as palpomere I and 1.2 as long as wide, with 1 pore; its apex with a group of 8 short conical sensilla (Fig. 3C). Hypopharynx with numerous small asperities and 2 campaniform sensilla on each side (Fig. 3D). Hypopharyngeal sclerome absent. Mentum distinctly separated from gulamentum; each side with 1 mesal macroseta, 1 mesoseta and 3 pores as well as 1 microseta near the posterior margin. Submentum fused with gula, thus forming gulamentum; on each side with 1 macroseta near the anterior part of gular suture, 2 microsetae, 5 pores, and 4 campaniform sensilla (Fig. 3C). Approximately in the middle of gulamentum small sclerotized area present. Each paragular area with 5 microsetae and 4 pores (Fig. 3C).

Thorax (Fig. 1A–1C): about 0.2 as long as total body length, widest across prothorax. Prothorax is 0.6 as long as wide, as long as mesothorax and 0.8 as long as metathorax. Anterior part of metathorax with a transverse row of small heavy sclerotized asperities.

Chaetotaxy of thorax (Fig. 4A): pronotum on each side with 6 macrosetae, 1 mesoseta, 7 microsetae and about 15 small cuticular spines. Anterior part of mesonotum on each side with 4 microsetae; posterior part with 3 macrosetae, 4 mesosetae, 6 microsetae and a few small cuticular spines. Anterior part of metanotum on each side with 4 microsetae; posterior part have similar chaetotaxy as on mesonotum. Prosternite on each side with 1 mesoseta and 3 microsetae; stern-

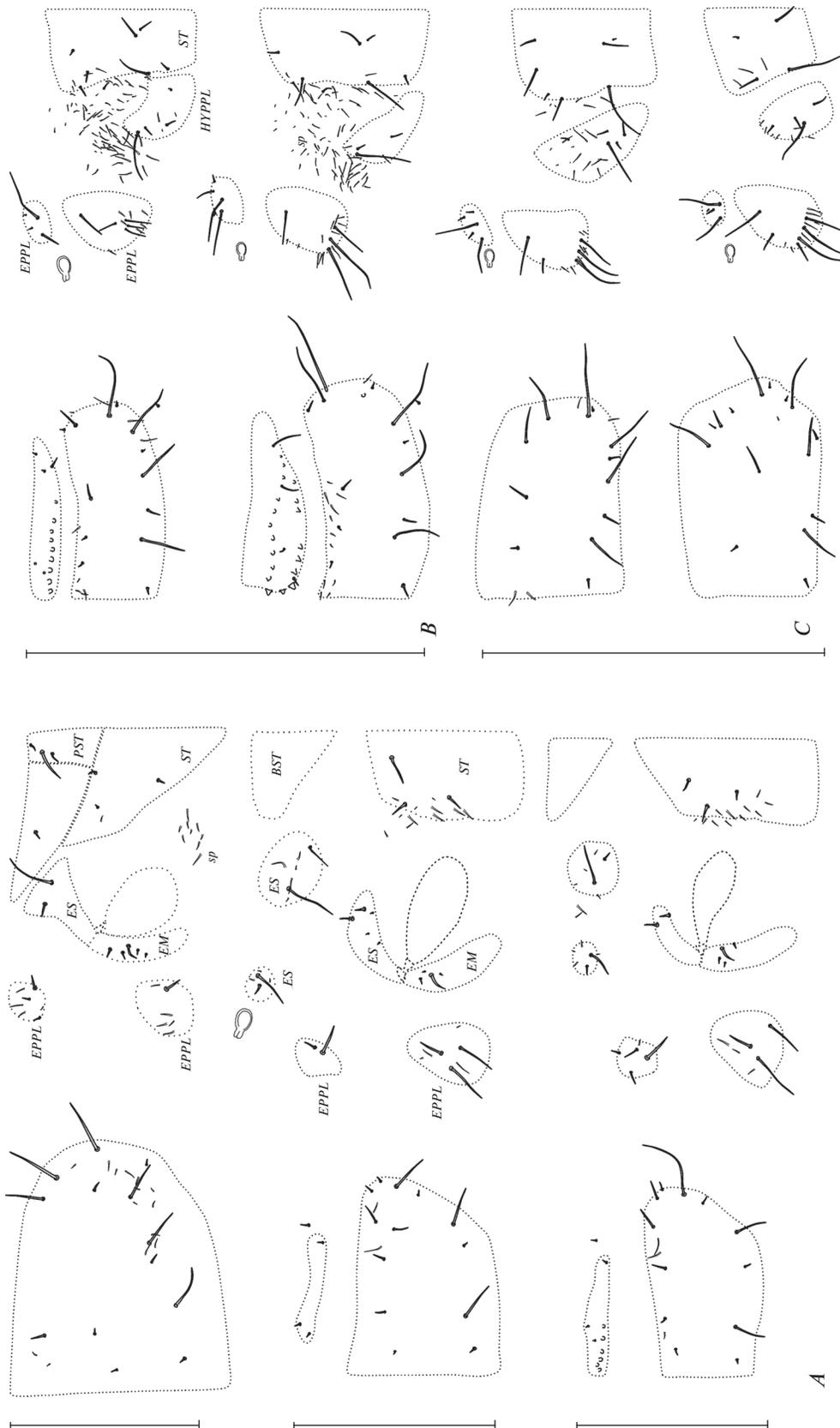
ellum I with 3 microsetae; a group of cuticular spines located between sternellum I and coxal cavity. Basisternites II–III without setae, sternellum II–III with 3 mesosetae and about 10 cuticular spines on each side. Anterior prothoracic epipleurite on each side with 3 microsetae and several cuticular spines; posterior epipleurite on each side with 1 mesoseta and several cuticular spines; episternum with 1 macroseta and 1 mesoseta; epimeron with 1 mesoseta and 4 microsetae. Anterior mesothoracic epipleurite on each side with 1 mesoseta and 1 microseta; posterior epipleurite with 2 macrosetae, 1 mesoseta and few cuticular spines; episternum with 1 macroseta, 2 mesosetae and 6 microsetae; epimeron with 1 mesoseta and 3 microsetae. Chaetotaxy of metathoracic pleurite similar in general with mesothoracic pleurite, the major difference is in anterior epipleurite with additional 2 microsetae.

Thoracic spiracles annular-biforous (Fig. 6A). Legs 5-jointed; length ratio of its joints to coxa is 0.8 : 0.8 : 0.7 : 0.5. Coxa with 1 macroseta, about 25 stout mesosetae, about 10 microsetae and 5 pores; trochanter with 4 macrosetae, 13 stout mesosetae, 7 pores and 5 long cuticular spines; femur with 5 macrosetae, 20 mesosetae, 4 pores and 3 long cuticular spines; tibiotalarsus with 3 macrosetae, 4 mesosetae, 8 microsetae and 2 pores; a single long and sharp claw with 2 mesosetae (Fig. 5A–5B).

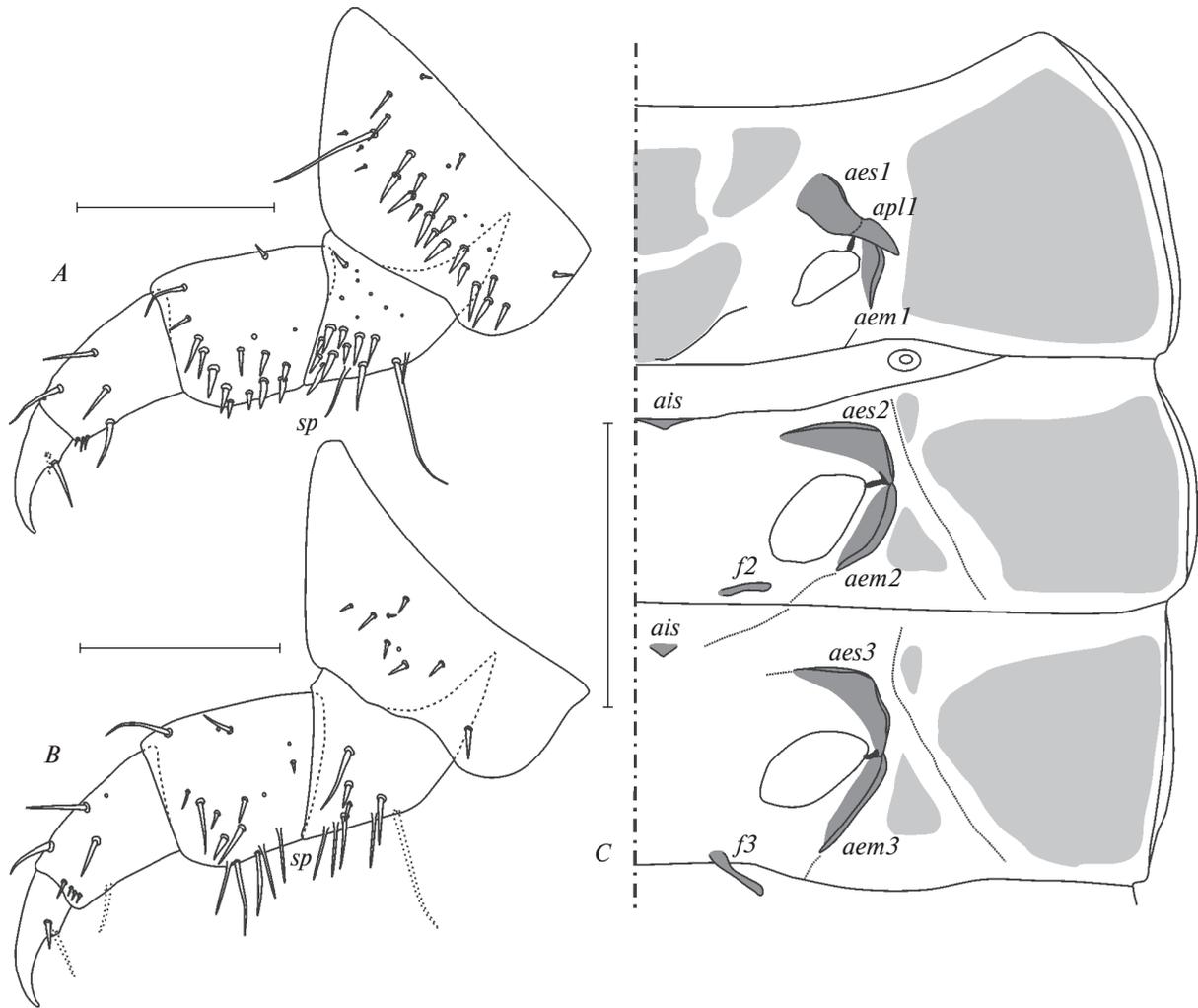
Thoracic endoskeleton (Fig. 5C): prothorax with well-developed episternal and epimeral apodemes; pleural apodeme triangular, narrowed apically. Meso- and metathorax with well-developed episternal and epimeral apodemes; pleural apodemes reduced; meso- and metathoracic furcae present, rather long, mesothoracic furca about 1.5 smaller than metathoracic furca; meso- and metathoracic spinae rather small, triangular, with broad bases. Such structure of the thoracic endoskeleton is nearly identical to those of *Hyporhagus* sp., but differs from the most of other Zopheridae sensu Ślipiński, Lawrence by the lack of prothoracic furcae and by the size and shape of spinae, which was pointed out before (Zaitsev, 2009).

Abdomen (Fig. 1A–1C): abdominal tergite I with anterior transverse row of heavy sclerotized asperities; abdominal tergites II–VI with 2 such rows, forming paired ovals (Fig. 1A–1B).

Chaetotaxy of abdomen (Figs 4B–4C, 7A–7B): anterior part of abdominal tergites I–VI on each side with 3 setae; posterior part with 5 macrosetae, 4 mesosetae, 5 microsetae and several small cuticular spines. Tergites VII–VIII on each side with few small cuticular spines, 5 macrosetae, 5 mesosetae and 2 and 6 microsetae respectively (Fig. 4B–4C). Tergite IX dorsally covered with numerous heavier sclerotized tubercles, most of which bear 1 microseta; dorsal chaetome on each side consists of 13 macrosetae, 3 mesosetae and about 55 microsetae; ventral chaetome on each side consists of 7 macrosetae, 4 mesosetae, 13 microsetae and 9 long cuticular spines (Fig. 7A–7B). Sternites I–VII with 1 macroseta and 6 setae on each side. Sternite VIII with 1 macroseta, 2 mesosetae and 1 microseta on



**Fig. 4.** Larva of *Monomma resinorum*, chaetotaxy (A–C): A – Pro-, meso- and metathorax. Scale bars: 1 mm; B – Abdominal segments I–II; C – Abdominal segments VII–VIII. Scale bars: 1.5 mm. Setae drawn in thick lines, spines drawn in thin lines. Abr.: *BST* – basisternum; *EM* – epimeron; *EPPL* – epipleurite; *ES* – episternum; *HYPPL* – hypopleurite; *PST* – prosternum; *ST* – sternellum; *sp* – spines.



**Fig. 5.** Larva of *Monomma resinorum* (A–C): A – Mesothoracic leg, anterior; B – Mesothoracic leg, posterior. Scale bars: 0.3 mm; C – Thoracic endoskeleton. Scale bar: 2 mm. Abr.: *aem 1–3* – epimeral apodeme of pro-, meso, and metathorax; *aes 1–3* – episternal apodeme of pro-, meso, and metathorax; *ais* – intersegmental apodeme; *apl 1* – pleural apodeme of prothorax; *f2–3* – furca of meso- and metathorax; *sp* – spines.

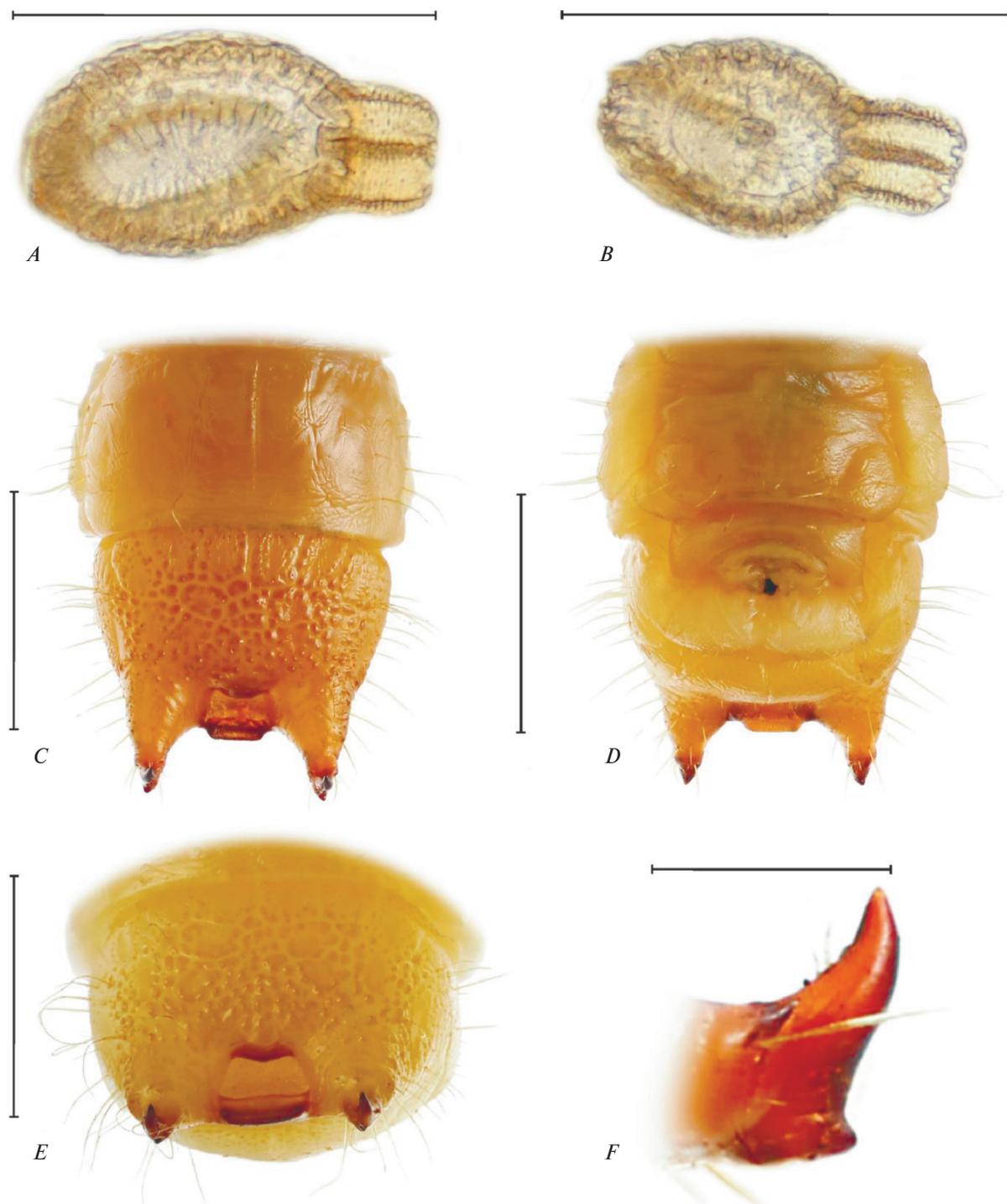
each side (Fig. 4B–4C). Sternite IX on each side with 1 macroseta, 1 mesoseta, 3 microsetae and 2 long cuticular spines (Fig. 7B). Pleurites I–VIII have anterior epipleurite with 2 macrosetae and 2–3 microsetae; posterior epipleurite with 4 macrosetae, 1–2 microsetae and several small cuticular spines; hypopleurite with 1 macroseta, 3–4 microsetae and several small cuticular spines. Anterior to hypopleurites I–VI numerous small cuticular spines located (Fig. 4B–4C).

Abdominal spiracles similar to those on thorax, annual-biforous (Fig. 6B). Urogomphi well developed, widely separated, distinctly upturned; heavy sclerotized apically; their surface mostly smooth; with 1 ventral and 1 lateral processes (Fig. 6C–6F). Each urogomphi dorsally with about 15 basal microsetae, 3 macrosetae and 2 mesosetae; ventrally with about 10 basal microsetae, 4 macrosetae, 3 mesosetae and a group of 3 mesosetae and 3 microsetae near the ventral process (Fig. 7A–7B). Urogomphal pit well-developed, trapezoidal, covered in numerous microsetae

(Figs 6E, 7A). Segment X short, considerably retracted and directed posteroventrally, with 1 macroseta, 3 mesosetae, 2 microsetae and numerous long cuticular spines (Fig. 7B).

### Biology of monommatid larvae

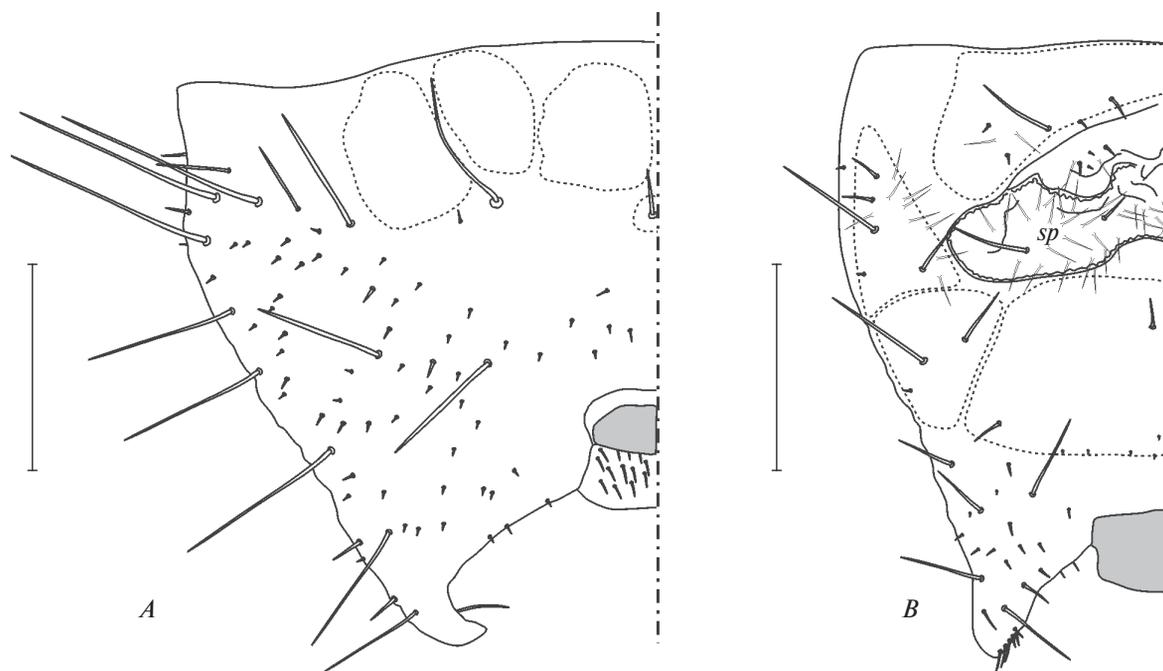
In arid regions of Northwest India larvae are associated with shrubs and usually inhabit *Euphorbia caducifolia* Haines 1914 (Euphorbiaceae) and *Calotropis procera* (Aiton) Dryand 1811 (Apocynaceae). The development of larvae take place in moribund shoots, usually on the border with their living part. Larvae fed on rather moist subcortical tissue, gnawing out horizontal areas. Pupation takes place under cortex or in medullary part of the shoot; on this stage feeding substrate becomes darkened and structureless. Low pigmented imagoes were also found under the feeding plant, suggesting that this species can also pupate in the soil.



**Fig. 6.** Larva of *Monomma resinorum* (A–F): A – Thoracic spiracle; B – Fifth abdominal spiracle. Scale bars: 0.3 mm; C – Abdominal segments VIII–IX, dorsal; D – Abdominal segments VIII–X, ventral; E – Abdominal segment IX, showing urogomphal pit, anterior. Scale bars: 1.3 mm; F – Apical part of right urogomphus, lateral. Scale bar: 0.3 mm.

In sylvan regions of India larvae of *M. resinorum* inhabit rotten bast under the bark of *Ficus* sp. (pers. comm.); larvae of *M. brunneum* are also known to live in rotten *Papaya* sp. stems (Fletcher, 1916).

The development of the African species, *I. hessei*, also connected with *Euphorbia* sp. Larvae were found in its rotten stem, feeding on decaying tissue; pupation takes place in the soil (Freude, 1958).



**Fig. 7.** Larva of *Monomma resinorum*, chaetotaxy (A, B): A – Abdominal segment IX, dorsal; B – Abdominal segments IX–X, ventral. Setae drawn in thick lines, spines drawn in thin lines. Scale bars: 0.5 mm. Abr.: *sp* – spines.

Larvae of *Hyporhagus gilensis* Horn 1872 were found in *Yucca* sp. stems in Arizona (Lawrence, 1991); larvae of *H. texanus* considered to be root-borers of *Agave lechuguilla* Torrey 1858 in Texas and Florida (Peterson, 1951); larvae of *Hyporhagus* sp. from Brasil were collected under the bark and in rotten wood of fallen trees (Costa et al., 1988).

## DISCUSSION

### Comparison with other known monommatid larvae

Larvae of *M. resinorum* can be easily distinguished from those of *Hyporhagus* sp. (Figs 8A, 9A–9G) by a number of characters, the most important are represented below:

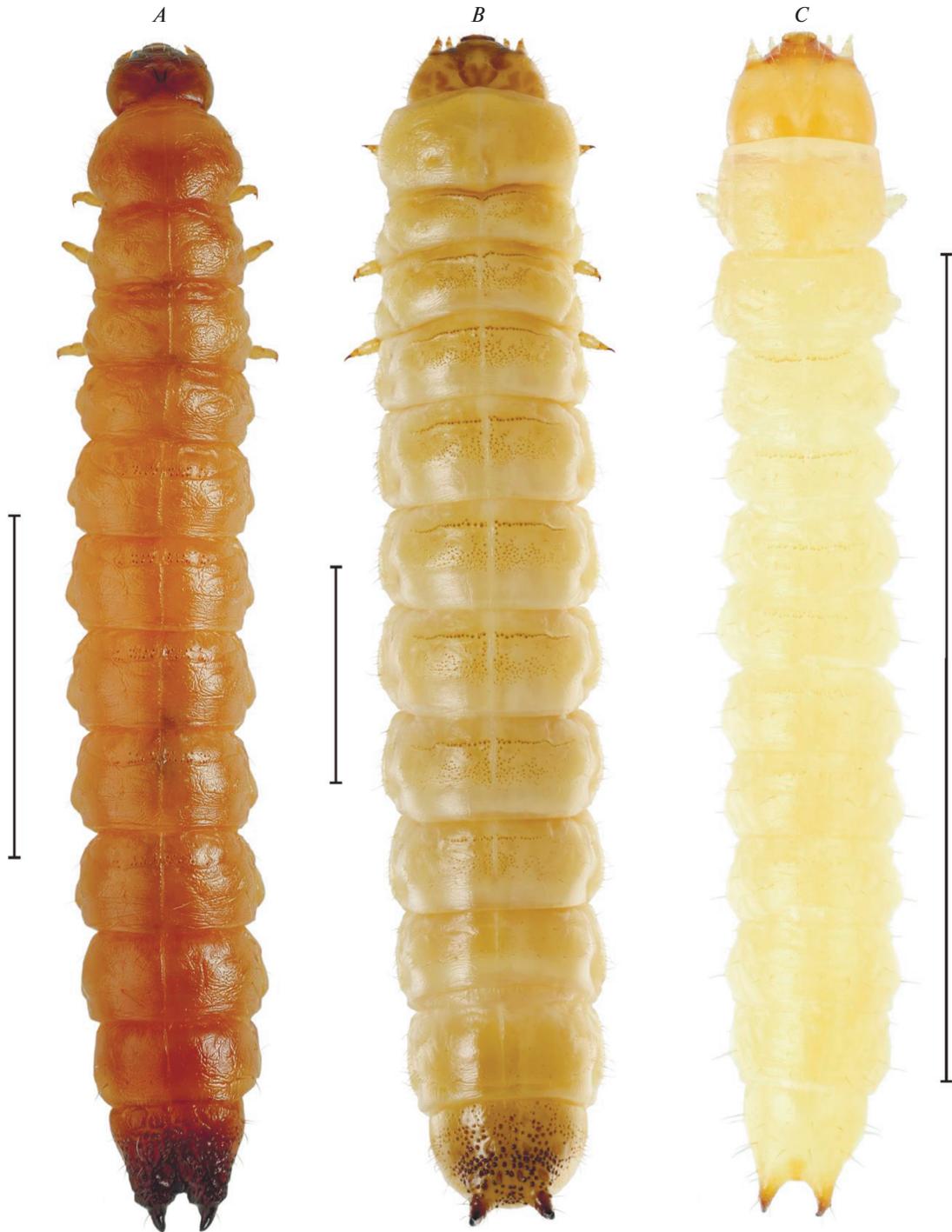
Characters	<i>M. resinorum</i>	<i>Hyporhagus</i> sp.
Tergites, rows of asperities	Metanotum, AT I–VI	AT II–VI
Antennomere III, setae	None	2 setae
Mandibles, ventral molar teeth	2 rows	1 row
Mala, inner apical angle	With 3 small processes	Smooth
Labrum, dorsal setae	4 macro- and 2 mesosetae	4 macro-, 2 meso-, 1 microsetae
Urogomphi, shape	Uniformly narrowed	Bloated at base
Urogomphi, processes	1 ventral, 1 lateral	None

Comparison of *M. resinorum* and *I. hessei* larvae is somewhat complicated due to the rather superficial description of the latter. In general, they look very similar to each other and the only major difference is the lack of ventrally shifted molar teeth on mandibles in *I. hessei*, which were most likely overlooked by the author, or just worn down.

### Systematic position of the monommatid beetles, basing on larval characters

Larvae of *M. resinorum*, *Hyporhagus* sp. and *I. hessei* share a considerable amount of synapomorphies,

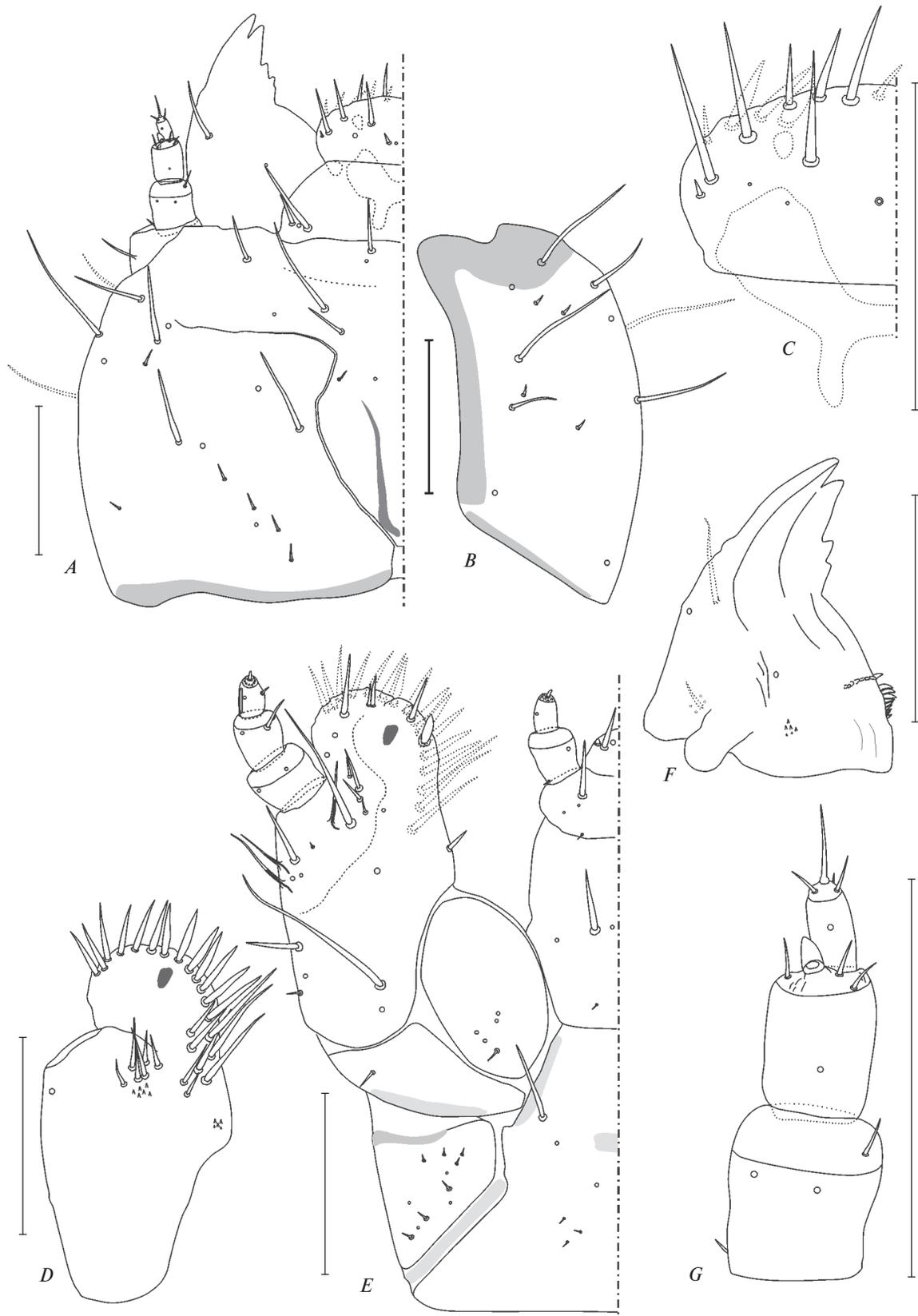
distinguishing them from other larvae of Zopheridae sensu Ślipiński, Lawrence. 1) Mandibles of a peculiar structure: 1 (*Hyporhagus*) or 2 (*Monomma* and, most likely, *Inscutomonomma*) rows of the molar teeth shifted ventrally; ventral surface with a group of small cuticular spines and tubercles in basal part; a row of hyaline teeth situated at the base of the mesal edge (Figs. 1F, 9F). 2) Absence of hypopharyngeal sclerome. 3) Presence of elongated cuticular spines with visible internal channels on dististipes, prementum (all known monommatid larvae) as well as on trochanter, tibia and abdominal segment X (Figs. 2C, 5A–5B, 7B, 9E) (not described for *Inscutomonomma*, but most likely



**Fig. 8.** Larvae of Zopheridae sensu Ślipiński & Lawrence, dorsal (A–C): A – *Hyporhagus* sp.; B – *Phellopsis amurensis*; C – *Pycnomerus (Dechomus) sulcicollis*. Scale bars: 5 mm.

present, too). It can be one of the most important autapomorphy of the group, cause such structures, as far as we know, were not described before for any Tenebrionoidea larva. 4) Paired endocarinae, located between frontal sutures (Figs. 2A, 9A). 5) Presence of small sclerotized area approximately in the middle of gulamentum (Figs. 3C, 9E). 6) Labrum with well developed paired scleroma located near the outer margin of

the anterior part of each torma (Figs 2C, 9C). 7) Transverse rows of asperities on abdominal segments II–VI, forming ovals (Figs 1A, 8A). 8) Numerous small cuticular spines on ventrites, and significantly less on tergites (Fig. 4A–4C). Based on these numerous larval characters, we rule out the possibility that monommatids are just highly modified Zopheridae. Thus we propose to return the family status for monommatid bee-



**Fig. 9.** Larva of *Hyporhagus* sp. (A–G): A – Head, dorsal; B – Left parietal sclerite, ventral; C – Labrum and tormae, dorsal; D – Stipes and mala, ventral; E – Labio-maxillar complex and paragular area, dorsal; F – Right mandible, ventral; G – Right antenna, ventral. Scale bars: 0.4 mm.

**Table 1.** Composition of Zopheridae sensu Ślipiński, Lawrence 1999 with list of described larvae

Tribe	Genera	Species	Authors
Latometini Ślipiński, Lawrence 1999	Larvae unknown		
Phellopsini Ślipiński, Lawrence 1999	<i>Phellopsis</i> LeConte 1862	<i>Ph. amurensis</i> Heyden 1885 <i>Ph. obcordata</i> Kirby 1837	Keleinikova, Mamaev, 1971; Böving, Craighead, 1931
Usechini Horn 1867	<i>Usechus</i> Motschulsky 1845	<i>U. lacerta</i> Motschulsky 1845	Doyen, Lawrence, 1979
Pycnomerini Erichson 1845	<i>Pycnomerus</i> Erichson 1842	<i>P. (Dechomus) sulcicollis</i> Germar 1824 <i>P. (Penthelispa) vilis</i> Sharp 1885 <i>P. fuliginosus</i> Erichson 1842 <i>P. terebrans</i> Olivier 1790 <i>P. secutus</i> Pascoe 1860	Mamaev, 1975 Hayashi, 1972 Dajoz, 1971 Nikitski, Belov, 1980 Ślipiński, Lawrence, 1999
	<i>Cotulades</i> Pascoe 1860	<i>C. bindabellae</i> Ślipiński, Lawrence 1999	Ślipiński, Lawrence, 1999
Zopherini Solier 1834	<i>Noserinus</i> Casey 1907b	<i>Noserinus dormeanus</i> Fairmaire 1889	Costa et al., 1988
	<i>Nosoderma</i> Solier 1841	<i>Nosoderma</i> sp.	Doyen, Lawrence, 1979
	<i>Phloeodes</i> LeConte 1862	<i>Ph. diabolicus</i> LeConte 1851	Doyen, 1976
	<i>Zopherus</i> Gray 1832	<i>Z. nodulosus</i> Solier 1831, <i>Z. granicollis</i> Horn 1885	Doyen, Lawrence, 1979

tles, placing them in Monommatidae Blanchard 1845 **stat. rest.** and remove this group from Zopheridae sensu Ślipiński, Lawrence.

#### Notes on the composition of Zopheridae sensu Ślipiński, Lawrence

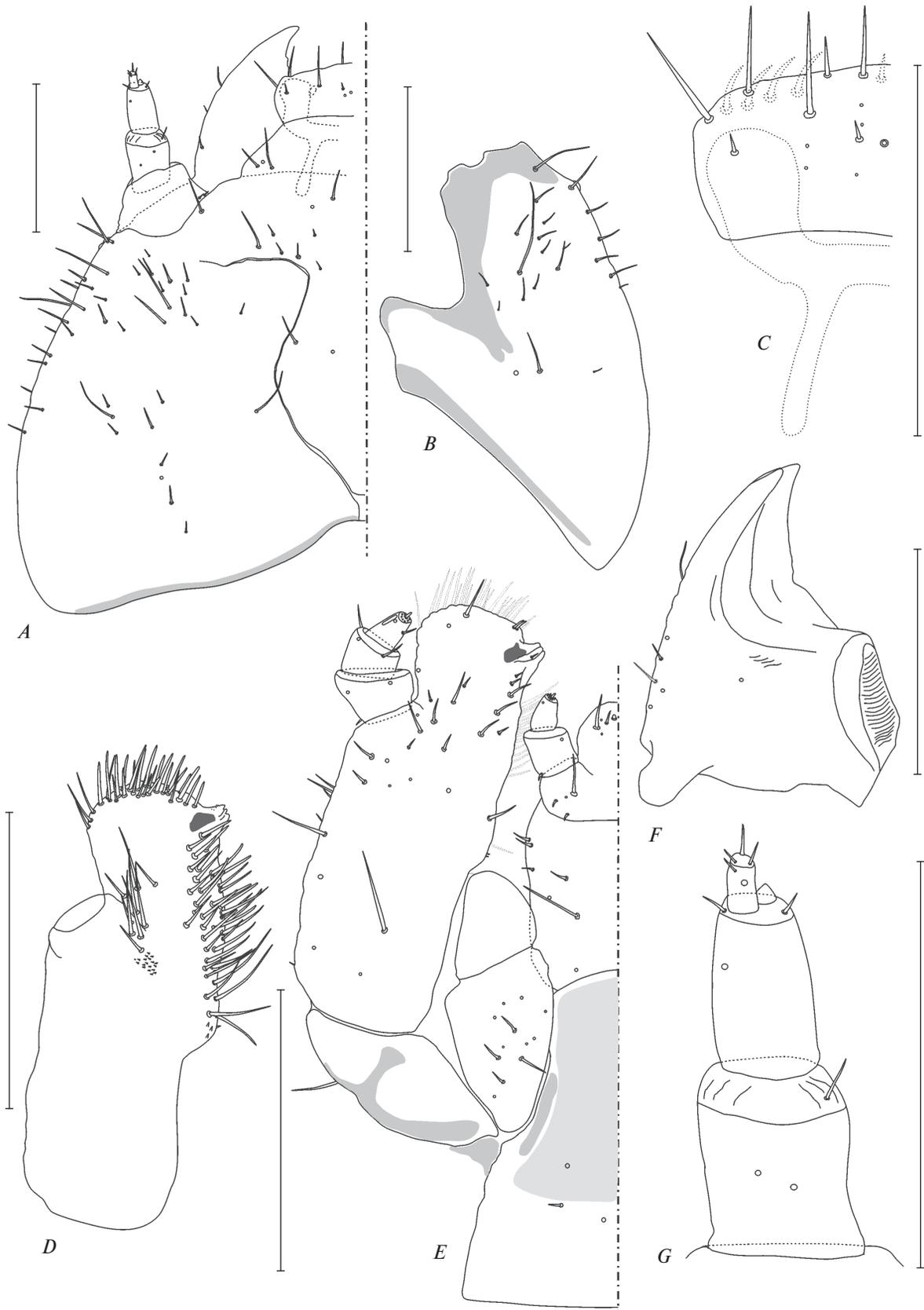
With the exclusion of monommatid beetles, Zopherinae sensu Ślipiński, Lawrence consists of 5 tribes and 18 genera with larvae described for 8 of them (see the table below).

Known larvae of Zopherinae (except of Pycnomerini and Usechini, which will be discussed further) can be distinguished from Monommatidae and Colydiinae Erichson 1842 by the complex of following autapomorphies (Figs 8B, 10A–10G): 1) internal sclerotization of the cardo, which makes it look partially or almost fully divided (Fig. 10E); 2) very small antennomere III, usually about 0.3 as long as antennomere II (Fig. 10A, 10G); 3) urogomphal pit always absent (Fig. 8B); 4) mala with numerous macro- and mesosetae on anterior and inner margin, and usually with large and broad teeth on inner apical angle (Fig. 10D, 10E); 5) mandibles always with transversely ridged mola (Fig. 10F). Larvae of some zopherine genera are not described, but it's highly probable that they will share the same characters, as was proposed by Doyen (1976). So, based on the larval autapomorphies mentioned above it is possible to restrict Zopheridae **stat. rest.** to Phellopsini and Zopherini, with possible inclusion of Usechini (see below) and Latometini (depends on the characters of still unknown larvae).

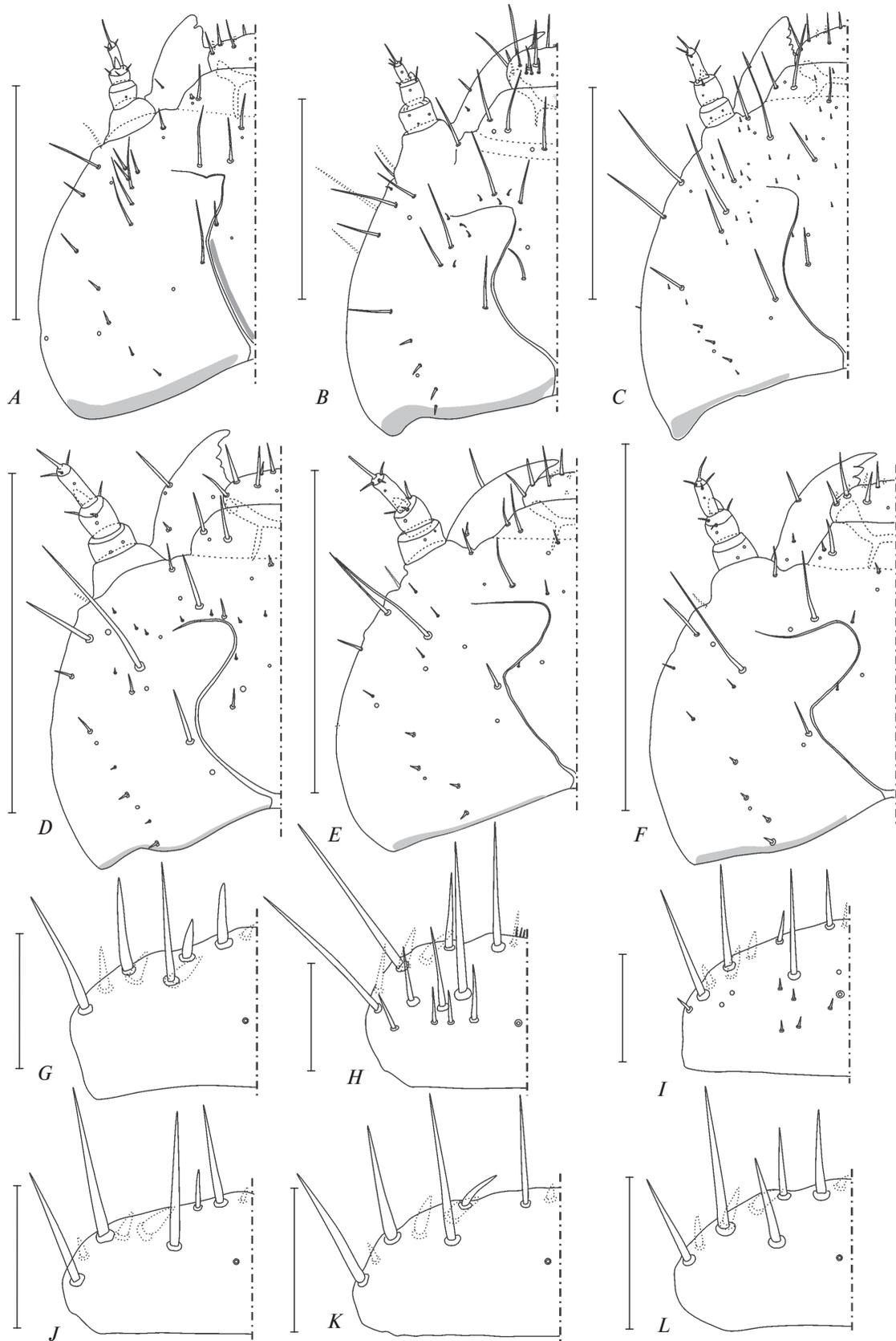
With the composition of Zopheridae proposed above and separation of Monommatidae, it becomes evident that Colydiinae should also retain family rank, Colydiidae Erichson 1842 **stat. rest.** It's rather hard to point out specific characters of this group because of the great variety in both adult and larval forms. All described colydiid larvae have an undivided cardo, antennomere III about 1–1.5 as long as antennomere II, and the vast majority has a urogomphal pit. These characters separate them from Zopheridae; differences from Monommatidae were pointed out earlier in this paper.

The systematics of Colydiidae is very complicated, especially for the largest tribe, Synchitini Erichson 1845, which includes about 120 genera worldwide (Burakowski, Ślipiński, 1988). It was suggested by several authors that the composition of Synchitini needs to be reconsidered (Mamaev, 1975; Nikitski, Belov, 1980; Ivie et al., 2016). Within the bounds of this paper we studied several Synchitini larvae (see materials and methods above) and propose some suggestions on the composition of the tribe.

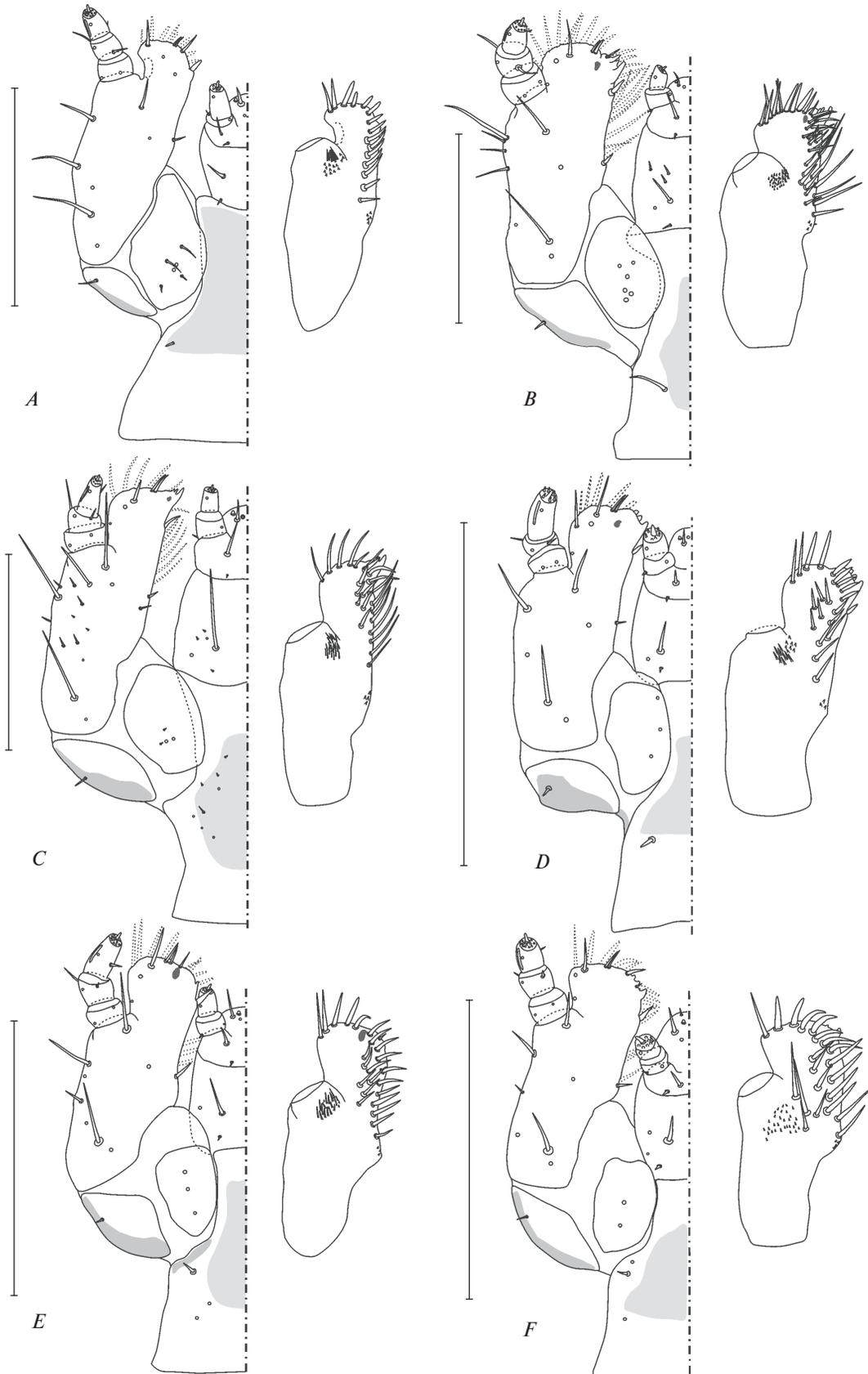
Ślipiński and Lawrence (1997) synonymized *Cicones* Curtis 1827 with *Synchita* Hellwig 1792 based on adult characters. Larvae of *Synchita* s.str. are studied rather well (Craighead, 1920; Mamaev, 1975; Nikitski, Belov, 1980) and share a number of diagnostic characters, not known for any other members of the tribe: prothorax distinctly wider than meso- and metathorax, labial palpomere I very small, about 0.3 as long as palpomere II; outer apical angle of mala with distinct notch (Fig. 12A); thoracic endoskeleton with meso-



**Fig. 10.** Larva of *Phellopsis amurensis* (A–G): A – Head, dorsal; B – Left parietal sclerite, ventral; C – Labrum and torma, dorsal; D – Stipes and mala, ventral; E – Labio-maxillar complex, dorsal; F – Right mandible, ventral; G – Right antenna, dorsal. Scale bars: 0.8 mm.



**Fig. 11.** Larvae of Colydiidae stat. rest. Head, dorsal (A–F); labrum, dorsal (G–L): A, G – *Synchita humeralis*; B, H – *Aulonium trisulcum*; C, I – *Colydium elongatum*; D, J – *Bitoma crenata*; E, K – *Colobicus hirtus*; F, L – *Endophloeus exsculptus*. A–F Scale bars: 0.5 mm. G–L Scale bars: 0.08 mm.



**Fig. 12.** Larvae of Colydiidae stat. rest. Labio-maxillar complex, dorsal (left); stipes and mala, ventral (right) (A–F): A – *Synchita humeralis*; B – *Aulonium trisulcum*; C – *Colydium elongatum*; D – *Bitoma crenata*; E – *Colobicus hirtus*; F – *Endophloeus exsculptus*. Scale bars: 0.3 mm.

**Table 2.** Comparison between two different systems of zopheroid beetles

Authors	Ślipiński, Lawrence, 1999, Ivie et al., 2016		Zaitsev, Kompantsev, 2018				
Family	<b>Zopheridae</b>		<b>Zopheridae</b>		<b>Monommatidae</b>	<b>Colydiidae</b>	
Subfamily	Zopherinae	Colydiinae	Zopherinae	<b>?Usechinae</b>	–	Colydiinae	<b>?Usechinae</b>
Tribes	Latometini* <b>Usechini</b> Monommatini Phellopsini <b>Pycnomerini</b> Zopherini	Acropini* Nematidiini Gempylodini Colydiini Rhagoderini* Rhopalocerini Sarrotrini* <b>Synchitini</b> (over 120 genera)	?Latometini* Phellopsini Zopherini	<b>?Usechini</b>	14 genera not assigned to tribes	?Acropini* Nematidiini Gempylodini Colydiini <b>Pycnomerini</b> ?Rhagoderini* Rhopalocerini ?Sarrotrini* <b>Synchitini</b> ( <i>Synchita</i> s. lato) <b>separate tribe</b> (remaining synchitines)	<b>?Usechini</b>

Principal differences are set off in bold type; taxa with unknown larvae are marked with \*.

and metafurcae absent (Zaitsev, 2009); urogomphi short, closed at basis; urogomphal pit absent.

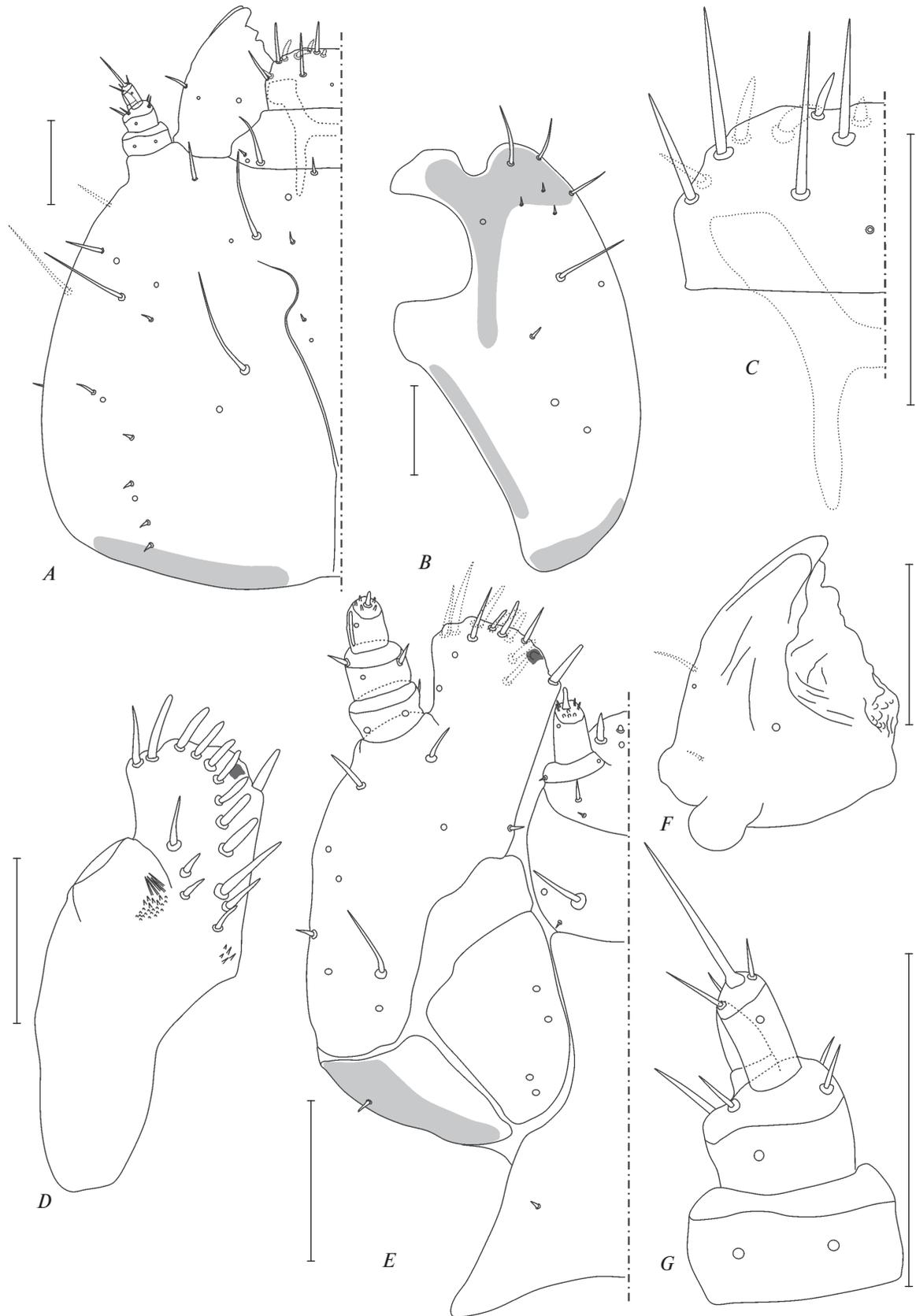
Larvae of certain former *Cicones* share some of these characters, e.g., the shape of prothorax and size of labial palpomere I, but differ clearly in having a mala with simple outer angle, small, spine-like urogomphi and large urogomphal pit (Nikitski, Belov, 1980). Based on larval characters, we propose to revise the composition of *Synchita*, leaving there beetles, whose larvae are of *Synchita*-type, e.g., *Synchita humeralis* (Figs 11A, 11G, 12A), *S. separanda* Reitter 1881, *S. hayashii* Sasaji 1971, and restore the genus *Cicones* for beetles with *Cicones*-type larvae, e.g., *S. (Cicones) pictus* Erichson 1845. Unfortunately, at the present time, larvae of *Synchita* s.lato are described for a limited number of species, but progress in this area can help to clarify the systematic within this genus. Moreover, due to the number of larval synapomorphies mentioned above it is possible to restrict Synchitini to *Synchita* and *Cicones*, at least until similar larvae are described for other genera of the tribe.

Larvae of the rest representatives of Synchitini s. lato directly studied (see Materials and Methods) or known by the description (*Lasconotus jelskii* Wankowicz 1867, *Lastrema verrucicollis* Reitter 1880, *Phloeonemus catenulatus* Horn 1878, *Namunaria picta* Sharp 1885, *Niphopelta imperialis* Reitter 1882) are similar in general: moderately sclerotized body with prothorax almost as wide as meso- and metathorax, urogomphi well developed, urogomphal pit present (Saalas,

1923; Craighead, 1920; Mamaev, 1975; Nikitski, Belov, 1980; Zaitsev, 2016), mala with 1-3 small unci on inner apical angle, labial palpomere I not shortened, about 0.8 as long as palpomere II (Figs 11D–11F, 11J–11L, 12D–12F) and thus can form a single tribe, as was proposed earlier by Mamaev (1975).

Studied larvae of Colydiini Erichson 1842 differ from those of Synchitini s. lato in the chaetotaxy of labrum, structure of mandibles, large tripartite unci on mala (Figs 11C–11D, 11H–11I, 12B, 12C), the structure of abdominal segment IX and other characters, which agreed with their placement in separate tribe Colydiini. Mamaev (1975) proposed to assign *Aulonium* Erichson 1845 and *Colydium* Fabricius 1792b to separate tribes, due to the lack of a urogomphal pit in *Colydium*, but according to our data, the absence or presence of a urogomphal pit itself cannot be the key feature for distinguishing tribes.

*Usechus lacerta*, placed by Ślipiński and Lawrence (1999) in Zopherinae, Usechini has larva which, on the one hand, has only a single row of about 15 setae on anterior and inner margin of mala, mandibular mola without transverse ridges and antennomere III almost equal to antennomere II as in most Colydiidae, but on the other hand has a divided cardo (autapomorphy of Zopheridae) and lacks a urogomphal pit (Doyen, Lawrence, 1979). Unfortunately, this larva was not available for us for the detailed study, so in the present paper we can only state that basing on larval characters *Usechus* (probably with *Usechimorpha* Blaisdell 1929)



**Fig. 13.** Larva of *Pycnomerus (Dechomus) sulcicollis* (A–G): A – Head, dorsal; B – Left parietal sclerite, ventral; C – Labrum and tormaе, dorsal; D – Stipes and mala, ventral; E – Labio-maxillar complex, dorsal; F – Right mandible, ventral; G – Right antenna, dorsal. Scale bars: 0.1 mm.

occupies an intermediate position between Zopheridae and Colydiidae and perhaps deserves rank of separate subfamily in Zopheridae, as was proposed by Doyen and Lawrence (1979), or in Colydiidae.

Genera *Pycnomerus* and *Pycnomerodes* Broun 1886 were traditionally considered as a colydiid tribe Pycnomerini (Dajoz, 1977; Lawrence, 1980; Ślipiński, Burakowski, 1988; Ślipiński, Lawrence, 1997). Ślipiński and Lawrence (1999) moved Pycnomerini (with the addition of *Cotulades* and *Docalis* Pascoe 1860) to Zopherinae basing mostly on adult characters. Ivie (Ivie et al., 2016) pointed out that the systematic position of *Pycnomerus* and *Pycnomerodes* is somewhat uncertain due to the lack of reliable characters, distinguishing them from other colydiines. To find out if *Pycnomerus* belongs to Colydiidae or Zopheridae we studied the larva of *P. (Dechomus) sulcicollis*. It appears that larva itself has practically no one significant common character with those of Zopheridae (except, maybe, with *Usechus*) and seems much more closely related to Colydiidae (Figs 8C, 13A–13G). Thus, the cardo is undivided by the internal sclerotization (Fig. 13E); the length of antennomere III is typical for colydiid, about 0.9 as long as antennomere II, (Fig. 13G); urogomphal pit (Fig. 8C) mostly present (rather poorly developed in *P. sulcicollis*, but distinct in *P. fuliginosus* (Dajoz, 1971)); chaetome of labrum and mala is of colydiid type (Fig. 13C–13E); mandibles with tuberculate mola, and without transverse ridges (Fig. 13F). In the paper of Ślipiński and Lawrence (1999), the characters that separate *Pycnomerus* from *Bitoma* (Colydiidae) larvae are: longer epicranial stem, presence of endocarina, ratio of antennal length to head width and presence of transverse rows of asperities on thoracic and abdominal tergites. The first three characters may vary greatly even in the range of the same genera (e.g., see larval description of *Synchita humeralis* and *S. separanda* (Nikitski, Belov, 1980) and thus cannot be considered as reliable. Moreover, all larvae of *B. crenata* we have studied have transverse rows of asperities on meso- and metanotum and abdominal tergites I–VI (Zaitsev, 2016). The superficial resemblance of larvae of some *Pycnomerus* species with those of Zopheridae can be due to the poorly developed urogomphal pit, which sometimes can be seen only as sclerotized area between urogomphi, and distinct transverse rows of asperities which are better developed than in other colydiid larvae (Fig. 8C). Thus, based on larval characters it is rather evident that at least *Pycnomerus* should be transferred from Zopheridae to Colydiidae. A second genus of Pycnomerini with known larva, *Cotulades*, has some zopherid characters, such as a divided cardo and the absence of a urogomphal pit (Ślipiński, Lawrence, 1999), but was

not available for study, so we cannot make any conclusions about its systematic position.

Thus, with the description of the late-instar larva of *M. resinorum* and review of larval characters of other Zopheridae sensu Ślipiński, Lawrence, 1999 we propose changes to the composition of this group of Coleoptera, the most important of which are:

1) Former Zopherinae, Colydiinae and Monommatini each make up a single family: Zopheridae **stat. rest.**, Colydiidae **stat. rest.** and Monommatidae **stat. rest.**, as was considered before Ślipiński and Lawrence (1999).

2) Pycnomerini, probably with the exception of *Cotulades*, should be transferred from Zopheridae back to Colydiidae.

3) The composition of Synchitini should be revised; most likely it includes only *Synchita* s.lato and, any genera found to have similar larvae. The remaining synchitine genera with known larvae should be transferred to a separate tribe.

The classification of Zopheridae sensu Ślipiński, Lawrence, based mostly on adult features, (Ślipiński, Lawrence, 1999, Ivie et al., 2016) and proposed in the present paper, based on larval characters, are compared below.

It is necessary to point out that all taxonomical changes, which are proposed in this paper, are based only on larval characters. However, due to the difficulties in definition of imaginal autapomorphies for higher-rank taxa, these data can be of a certain value in revising the system of this disputable group.

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## ОПИСАНИЕ ЛИЧИНКИ *MONOMMA RESINORUM* HOPE 1842 (COLEOPTERA, ZOPHERIDAE) С ЗАМЕЧАНИЯМИ ПО СИСТЕМАТИКЕ СЕМЕЙСТВА

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Приведено детальное описание личинки последнего возраста *Monomma resinorum* Hope 1842 из Индии, включая данные о хетотаксии и строении эндоскелета грудных сегментов. Проведено сравнение с личинками близких родов с целью выявления общих признаков, характерных для группы. По особенностям морфологии личинок предложено вывести мономматид из состава Zopheridae в отдельное семейство Monommatidae **stat. rest.** В результате обработки оригинальных и литературных данных о морфологии известных личинок Zopheridae *sensu* Ślipiński, Lawrence 1999 предложено пересмотреть систему семейства, разделив его на три семейства (Monommatidae, Zopheridae и Colydiidae **stat. rest.**), а также уточнено систематическое положение некоторых спорных таксонов Zopheridae и Colydiidae.

Ключевые слова: Coleoptera, Zopheridae, *Monomma*, личинка, морфология, таксономия