

## Review of larval morphology of beetles of the suborder Archostemata (Insecta: Coleoptera), including first-instar chaetotaxy

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**Key words.** *Distocupes*, *Tenomerga*, *Rhipsideigma*, *Priacma*, *Omma*, *Micromalthus*, Cupedidae, Micromalthidae, Ommatidae, Archostemata, Coleoptera, larvae, morphology, chaetotaxy, phylogeny

**Abstract.** This paper presents a synthesis of morphological information on larvae of the beetle suborder Archostemata. Larvae of the following families and species were studied: Ommatidae: *Omma* sp.; Micromalthidae: *Micromalthus debilis* LeConte, 1878; Cupedidae: *Priacma serrata* LeConte, 1861, *Distocupes varians* (Lea, 1902), *Rhipsideigma raffrayi* (Fairmaire, 1884), *Tenomerga cinerea* (Say, 1831) and *Tenomerga mucida* (Chevrolat, 1829). Morphological characters of the suborder and three families are described. Monophyly of the suborder is strongly supported by more than 10 larval autapomorphies. A close relationship between Micromalthidae and Cupedidae is confirmed. New larval characters are introduced, including chaetotaxy of first instar larvae of *Micromalthus* LeConte, 1878, *Priacma* LeConte, 1874 and *Distocupes* Neboiss, 1984. An identification key to families and subfamilies of Archostematan larvae is provided, along with a checklist of extant Archostemata taxa. The work is illustrated with 120 morphological drawings.

### INTRODUCTION

This is an overview of the external larval morphology of members of the coleopteran suborder Archostemata. This suborder has a rich paleontological history and a diverse extinct fauna (see references in Ponomarenko, 1969, 1995; Lawrence, 1999), but only 40 extant species arranged in five families (see Appendix). The first and only representative of the family Crowsoniellidae was described as recently as in 1976 based on a single collection of three endogean beetles from Central Italy (Pace, 1976; Crowson, 1976). Another family, the Sikhotealinidae, was described in 1996 based on a specimen, without reliable biological data, from the Russian Far East (Lafer, 1996), whose archostematan affinities are doubtful (Lawrence, 1999). Kirejtshuk (1999) attributed this species to the long extinct family Jurodidae. Consequently, the scope of this paper is restricted to the three remaining families for which larvae are known: Ommatidae, Cupedidae and Micromalthidae.

The family Ommatidae consists of two monogeneric subfamilies: Ommatinae and Tetraphalerinae. The genus *Omma* Newman, 1839 includes four species from Australia. A supposedly older-instar *Omma* larva was recently discovered in the collection of the Western Australian Museum in Perth and described by Lawrence (1999). Larvae of the two South American species of the genus *Tetraphalerus* Waterhouse, 1901 are unknown.

The family Micromalthidae includes only one species: *Micromalthus debilis* LeConte, 1878, which is possibly the most remarkable coleopteran as it is parthenogenetic, viviparous, and has a unique life cycle with morphologically different types of larvae (Barber, 1913a, b; Pringle, 1938; Scott, 1936, 1941; Pollock & Normark, 2002). Morphological descriptions of the larvae of this species

can be found in several publications (Barber, 1913a, b; Böving, 1929; Böving & Craighead, 1931; Pringle, 1938; Scott, 1936, 1938, 1941; Peterson, 1960; Costa et al., 1988; Lawrence, 1991; Lawrence et al., 1999; Philips & Young, 2000), with the most recent one including internal structures (Beutel & Hörnschemeyer, 2002a).

The family Cupedidae is the most diverse of the recent Archostemata. One of its two subfamilies is the monogeneric Priacminae erected for *Priacma serrata* LeConte, 1861 from North America. First instar larvae of this species were reared ex ovo and described by Ross & Pottery (1970). The second subfamily, the Cupedinae, consists of eight genera known from all zoogeographical regions of the World (with the exception of New Zealand and Europe). Of these genera larvae are known for *Tenomerga cinerea* (Say, 1831) (see: Böving, 1929; Böving & Craighead, 1931; Lawrence 1991; Young, 2000) and *T. mucida* (Chevrolat, 1829) (see: Fukuda, 1938), *Distocupes varians* (Lea, 1902) (see: Neboiss, 1968) and *Rhipsideigma raffrayi* (Fairmaire, 1884) (see: Beutel & Hörnschemeyer, 2002b). Larvae of the cupedine genera *Adinolepis* Neboiss, 1984, *Ascioplaga* Neboiss, 1984, *Prolixocupes* Neboiss, 1984, *Cupes* Fabricius, 1801 and *Paracupes* Kolbe, 1898 are unknown.

The aim of the present paper is to provide a morphological overview of the Archostematan larvae by re-examining all previously described species, including the chaetotaxy of the first instar larvae. Archostematan larvae are rare in entomological collections and, therefore, not readily available for study by morphologists. Therefore, particular emphasis is placed on providing detailed morphological drawings of previously unknown morphological characters of these animals. To facilitate identification a key is included to all the taxa of the suborder for which larvae are known. A checklist of extant

archostematan taxa is provided. Phylogenetic affinities based on larval morphology of some archostematan taxa discussed, however no formal cladistic analysis was performed. Some peculiar morphological characters are discussed in detail and new larval synapomorphies of the suborder suggested.

## MATERIAL AND METHODS

This study is based on examination of Archostemata larvae kept in the following collections (names of curators in parentheses):

ANIC – Australian National Insect Collection, Canberra, Australia (J.F. Lawrence, S.A. Ślipiński)

CAS – California Academy of Sciences, San Francisco, USA (D.H. Kavanaugh, R. Brett)

IECR – Institute of Entomology, České Budějovice, Czech Republic (P. Švácha)

MVMA – Museum of Victoria, Melbourne, Australia (C. McPhee)

NHML – The Natural History Museum, London, UK (S. Hine, M. Kerley)

NMNH – National Museum of Natural History, Washington DC, USA (D.G. Furth, N. Adams)

VGC – V.V. Grebennikov Collection, Pretoria, South Africa

WAMP – Western Australian Museum, Perth, Australia (T.F. Houston)

Larvae were disarticulated, macerated in hot KOH and mounted on microscope slides either temporarily in glycerine, or permanently in Euparal. A compound microscope, MBI-2, with up to X900 magnification was used to study the larval morphology. Drawings were made with the aid of a camera lucida. Morphological terms used in this work are those explained by Lawrence (1991: 147–177). The concept of the order and families follows Lawrence & Newton (1982, 1995). The use of the terms “seta” and “pore” follows that of Bousquet & Goulet (1984) for Carabidae; Alarie & Balke (1999) for Dytiscidae; Ashe & Watrous (1984) and Thayer (2000) for Staphylinidae; Kovarik & Passoa (1993) for Histeridae; Grebennikov & Beutel (2002) for Ptiliidae; Delgado & Soler (1996, 1997) for Hydraenidae and Wheeler (1990) and Kilian (1998) for Leiodidae.

## MORPHOLOGY OF ARCHOSTEMATAN LARVAE

### Description

**First-instar larvae:** Like older instars, except general appearance is more of the “campodeiform” type. Head fully protracted. Frontal sclerite separated from epicranial plates by clear frontal suture (*Priacma*) or frontal sclerite fully united with epicranial plates and frontal suture not detectable (*Micromalthus*, *Distocupes*). First instar larvae of *Rhipsideigma* and *Omma* are unknown. Lateral sides of cranium with or without single stemma. Egg-bursters absent. Frontoclypeal suture not detectable. Body segments similar in shape, with (*Distocupes*) or without (*Micromalthus*, *Priacma*) transverse membranous folds dorsally and ventrally. **Chaetotaxy** (most full set of sensilla is indicated, reductions are common and noted for each genus separately): Cranium with setae 1–24 and pores A–R; prothorax with setae 1–21 and pores A–B; mesothorax with setae 1–23 and pores A–B; abdominal segments I–VIII with setae 1–16 and pores A–B; abdominal segment IX with setae 1–17 and pores A–C; abdominal segment X with setae 1–4. **Older-instar lar-**

**vae:** Body cerambycoid (less so in *Omma*), with tergal ampullae on thorax and abdomen. Body elongate, straight, slightly flattened dorso-ventrally, more or less parallel-sided, lightly sclerotized, whitish. Integument relatively smooth with scattered simple setae. Body surface without setiferous tubercles, granules, frayed setae or gland openings. Cranium transverse, symmetrical, sclerotized, prognathous, with deep posterior dorsal triangular median emargination, widened posteriorly, partly retracted (except in *Micromalthus*). Clypeus trapezoidal, usually with unpigmented area posterior to labrum. Median endocarina present, well developed, straight or forked. Epicranial stem and frontal arms not detectable. Hypostomal rods extending into basal half of cranium. Antennae short, not or only slightly protruding beyond level of clypeal apex. Single conical sensorium located ventro-apically on penultimate antennomere. Mandibles short, markedly sclerotized, nearly symmetrical, with relatively wide bases. Mandibles with three apical teeth. Incisor area without teeth or, rarely, with retinaculum (*Omma*). Stridulatory teeth, prostheca, penicillus, dorsal and ventral carinae, and accessory ventral process absent. Mola markedly developed. Ventral mouthparts slightly retracted. Maxilla with transversely oriented cardo and relatively wide antero-mesally directed stipes. Cardo divided into sclerotized mesal and membranous lateral parts. Two basal maxillary palpomeres subequal in shape, third apical palpomere markedly shorter and narrower. Galea and lacinia subequal or lacinia slightly shorter, fused at base and separated apically, both fused to stipes. Galea with group of setae apically, lacinia with numerous articulated spines and setae apically, and along mesal side. Medial surface of lacinia flattened, and delimited dorsally and ventrally by lines of stout setae. Labium with mentum, prementum and postmentum fused, and constricted between maxillary grooves. Prementum with large wedge-shaped sclerotized ligular sclerome extending apically beyond apices of labial palp. Dorsal surface of ligular sclerome co-joined with flat sclerotized surface of hypopharynx. Labial palps 2-segmented (1-segmented in *Micromalthus* and first instar of *Priacma*), widely separated, anteriorly divergent. Labrum transverse, clearly separated dorsally from cranium by clypeolabral suture (except first instar *Priacma* larvae); with setae along straight anterior edge. Epipharynx bearing pores and setae, not clearly delimited posteriorly. Legs normally present (absent in older instars of *Micromalthus*), widely separated, 6-segmented consisting of coxa, trochanter, femur, tibia, tarsus and normally two claws (one of which is markedly reduced or apparently absent in first instar of *Distocupes* and *Priacma*). Abdominal segments I–III combined longer than thorax. Urogomphi absent. Respiratory system of peripneustic type with annular functional spiracles present on mesothorax and abdominal segments I–VIII; thoracic spiracles larger than those on abdomen. Spiracular closing apparatus present.

**KEY TO FAMILIES AND SUBFAMILIES OF  
ARCHOSTEMATA LARVAE**

- 1 Abdominal apex sclerotized, terminated by one (Figs 19, 20, 34, 35, 71, 76, 77) or two (Figs 9, 10, 64, 65) apical projections; cranium with dorsal endocarina straight, not forked (Figs 11, 21, 58, 69, 78, 97) ..... 2
- Abdominal apex membranous, without sclerotized apical projection; cranium with dorsal endocarina anteriorly forked (Fig. 36) ..... Ommatidae (*Omma*)
- 2 Sclerotized apical projection of abdomen consists of two vertically separated parts originating respectively from tergum and sternum, and slightly curved towards each other (Figs 9, 10, 64, 65); legs absent or, if present, not shorter than maximum width of body (Fig. 8) .....  
..... Micromalthidae (*Micromalthus*)
- Sclerotized apical projection of abdomen consists of single straight projection originating from tergum (Figs 19, 20, 34, 35, 71, 76, 77); legs always present and markedly shorter than maximum width of body (Figs 18, 33, 106, 107) ..... 3
- 3 Cranium dorsally with markedly developed frontal suture separating frontal sclerite from parietal sclerites (Fig. 11); sclerotized apical projection of abdomen with 4 separate apical rounded sub-elements (Figs 19, 20); north-western part of North America .....  
..... Cupedidae: Priacminae (*Priacma*)
- Cranium dorsally without frontal suture and frontal sclerite completely fused with parietal sclerites (Figs 21, 69, 78, 97); sclerotized apical projection of abdomen not subdivided apically into separate sub-elements (Figs 34, 35, 71, 76, 77, 108, 109); any region of the World, except New Zealand and Europe ..... Cupedidae: Cupedinae

**FAMILY OMMATIDAE**

**Diagnosis**

**First instar:** unknown. **Older instars** (Figs 36–57): Body evenly narrowing posteriorly. Cranium with median endocarina forked with both apical arms additionally forked; two additional endocarinae present lateral of median line; frontoclypeal suture absent; 4 stemmata present; cranium nearly parallel-sided. Antenna short, slightly extending beyond clypeal apex; with 4 antennomeres, basal antennomere not reduced in size; apical antennomere not longer than half the length of the rest of antenna. Mandibles with retinaculum; dorsal tooth shortest and ventral longest; transverse ridges on mola absent; dorsal surface of left mandible with non-sclerotised short appendage. The shape of mola deformed in the specimen examined. Maxillary palpifer clearly delimited; sensory spot on lateral surface of apical maxillary and labial palpomeres present, medium sized; apical maxillary and labial palpomeres with single palpal sensorium about half as long as respective apical palpomeres; non-articulated apical cuticular projections present mesally on first and second maxillary palpomeres; narrow and anteriorly oriented sclerotized fixed process present on ventral surface of lacinia; dorsal membranous projection with about 20 cuticular non-articulated teeth present on labio-maxillary articulation membrane; ventral surface of ligular sclerome with 2 setae in transverse line; labial palps 2-segmented. Prothorax ventrally without field of asperities; legs present; claws 2, subequal in length; coxa

with 1 tooth anteriorly. Lateral bulge on abdomen absent; abdominal segment IX without asperities; abdominal segment IX membranous and rounded, not pointed; anal opening located apically; abdominal segment X reduced, not visible externally.

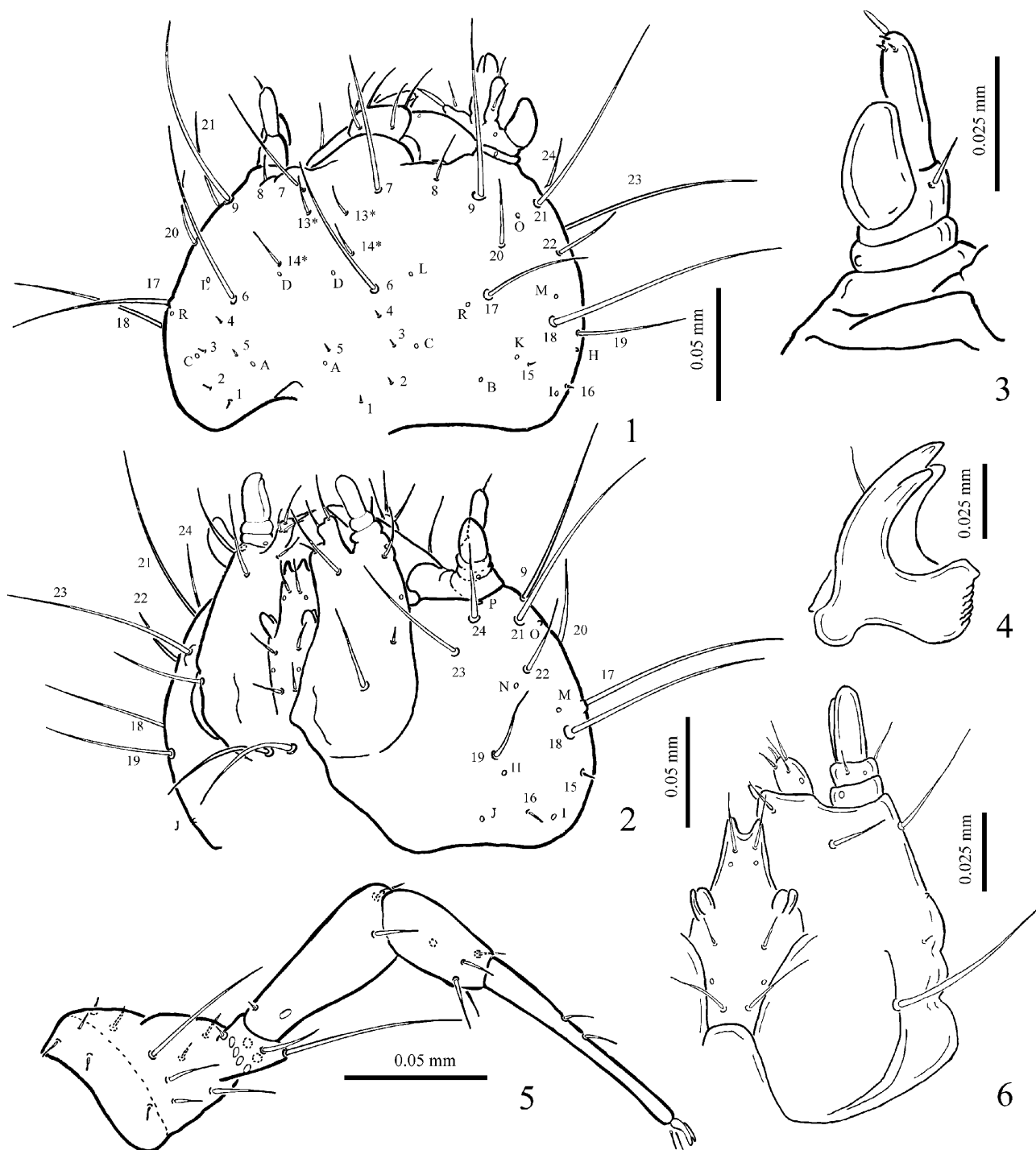
**Genus *Omma* Newman, 1839**

**MATERIAL EXAMINED.** *Omma* sp. (supposedly *O. rutherfordi* Lawrence, 1999 or *Omma sagitta* Neboiss, 1989; for details see Lawrence, 1999: 377), one older-instar larva (head and left legs dissected and cleaned; body studied without prior maceration in KOH). Western Australia, Red Hill, 29.ix.1964, L.E. Koch (WAMP). Head width: 1.69 mm (n = 1; older instar larva).

**FAMILY MICROMALTHIDAE**

**Diagnosis**

**First instar** (Figs 1–10): like older instars, except for the following: smaller, legs present and fairly long; chaetotaxy different. Other characters are: clypeolabral suture present and labrum clearly separated from cranium; frontal suture absent; dorsal medial emargination of cranium markedly developed, deep; projection of cranium dorsad of antennifer absent; stemma absent (presence of single stemma was reported for the specimens collected in Hong Kong. I studied two larvae from Hong Kong collected in 1956 and found no trace of stemmata; specimens, however, were markedly degraded); antenna with 3 antennomeres, basal one markedly reduced; mandibles with 3 apical teeth and without additional ventral and basal smaller tooth; anterior edge of labrum straight; labial palps with 1 palpomere; thorax and abdominal segments I–VIII without transverse membranous folds dorsally and ventrally; abdomen terminates with tergal and sternal toothed and curved opposite processes. **Chaetotaxy:** cranium (Figs 1, 2) with setae 1–9, 13–24 and pores A–D, H–P, R; prothorax (Figs 7, 8) with setae 1–9, 11–15, 17, 19–21 and pores A–B; mesothorax (Figs 7, 8) with setae 1–23 and pores A, B; abdominal segments I–VIII (Figs 9, 10) with setae 1–5, 7–16 and pores A, B; abdominal segment IX (Figs 9, 10) with setae 1–15 and pores A–C; abdominal segment X absent. **Older instars** (Figs 58–68): Body parallel-sided. Cranium with straight median endocarina; two additional dorsal endocarinae lateral of median line absent; frontoclypeal suture absent; stemmata absent; cranium markedly rounded laterally. Antenna markedly shortened, not extending beyond clypeal apex; antenna with 4 antennomeres, basal one highly reduced and antenna appearing 3-segmented; apical antennomere markedly elongated, about as long as the rest of antenna. Mandibles without retinaculum; dorsal and ventral tooth about same length, middle one longest; transverse ridges present on mola; dorsal surface of left mandible without non-sclerotised short appendage. Maxillary palpifer poorly delimited; sensory spot on lateral surface of apical maxillary and labial palpomeres absent; each apical maxillary and labial palpomeres with one long palpal sensorium as long as respective apical palpomere, which therefore appear subdivided into one wider and one narrower substructure (represented by palpal sensorium); non-articulated apical cuticular projec-



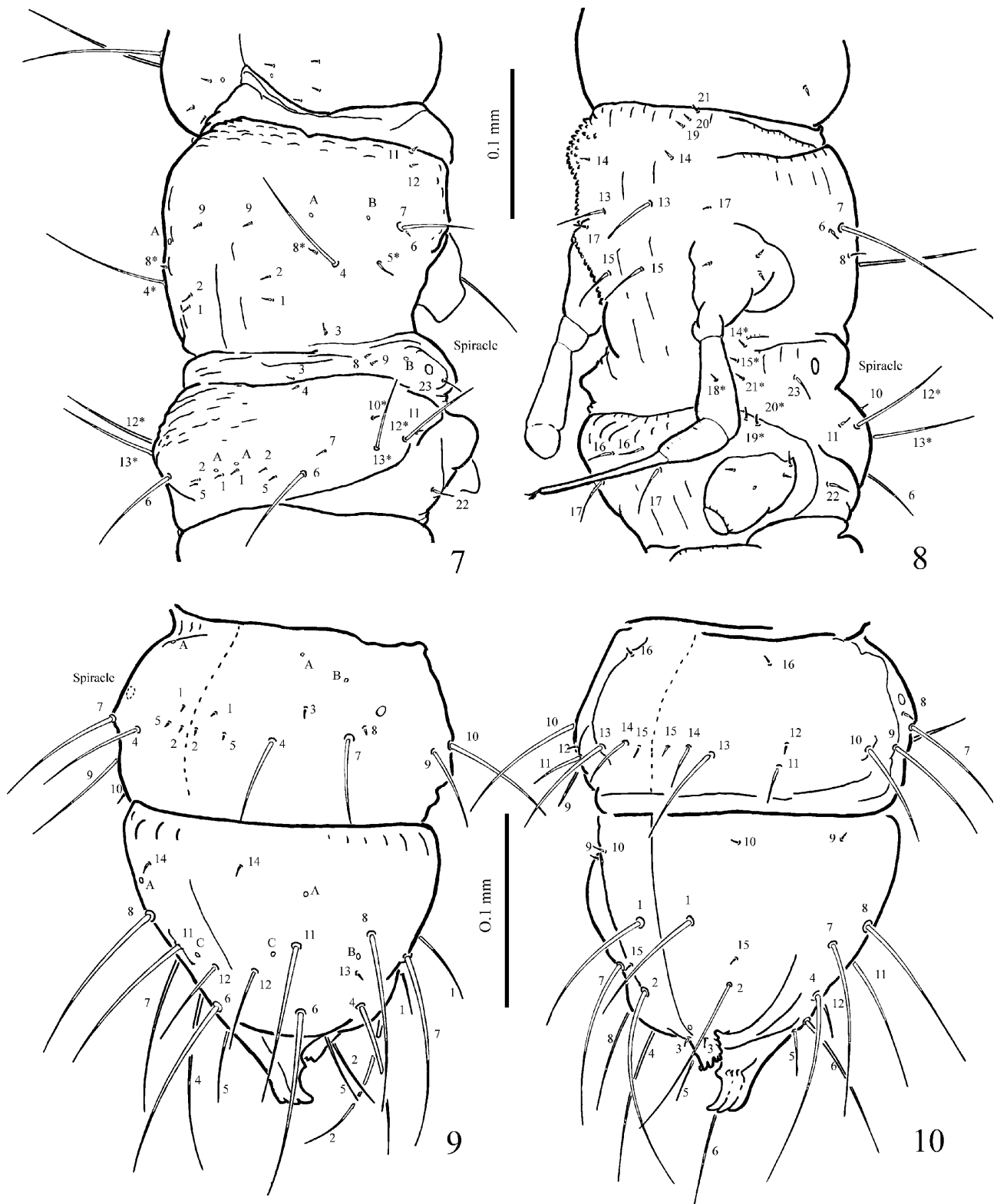
Figs 1–6. First instar larva of *Micromalthus debilis*, details. 1, 2 – head, dorsolateral (1) and ventrolateral (2); 3 – right antenna, ventral; 4 – right mandible, ventral; 5 – fore leg, anterior; 6 – left maxilla and labium, ventral.

tions mesally on first and second maxillary palpomeres absent; narrow and anteriorly oriented sclerotized fixed process on ventral surface of lacinia absent; dorsal membranous projection on labio-maxillary articulation absent; ventral surface of ligular sclerome with 2 setae in transverse line; labial palps 1-segmented. Prothorax ventrally without field of asperities; legs absent. Lateral bulge on abdomen absent; abdominal segment IX without asperities; abdominal segment IX with sclerotized, toothed and

curved tergal and sternal processes; anal opening located apically; abdominal segment X not visible externally.

#### Genus *Micromalthus* LeConte, 1878

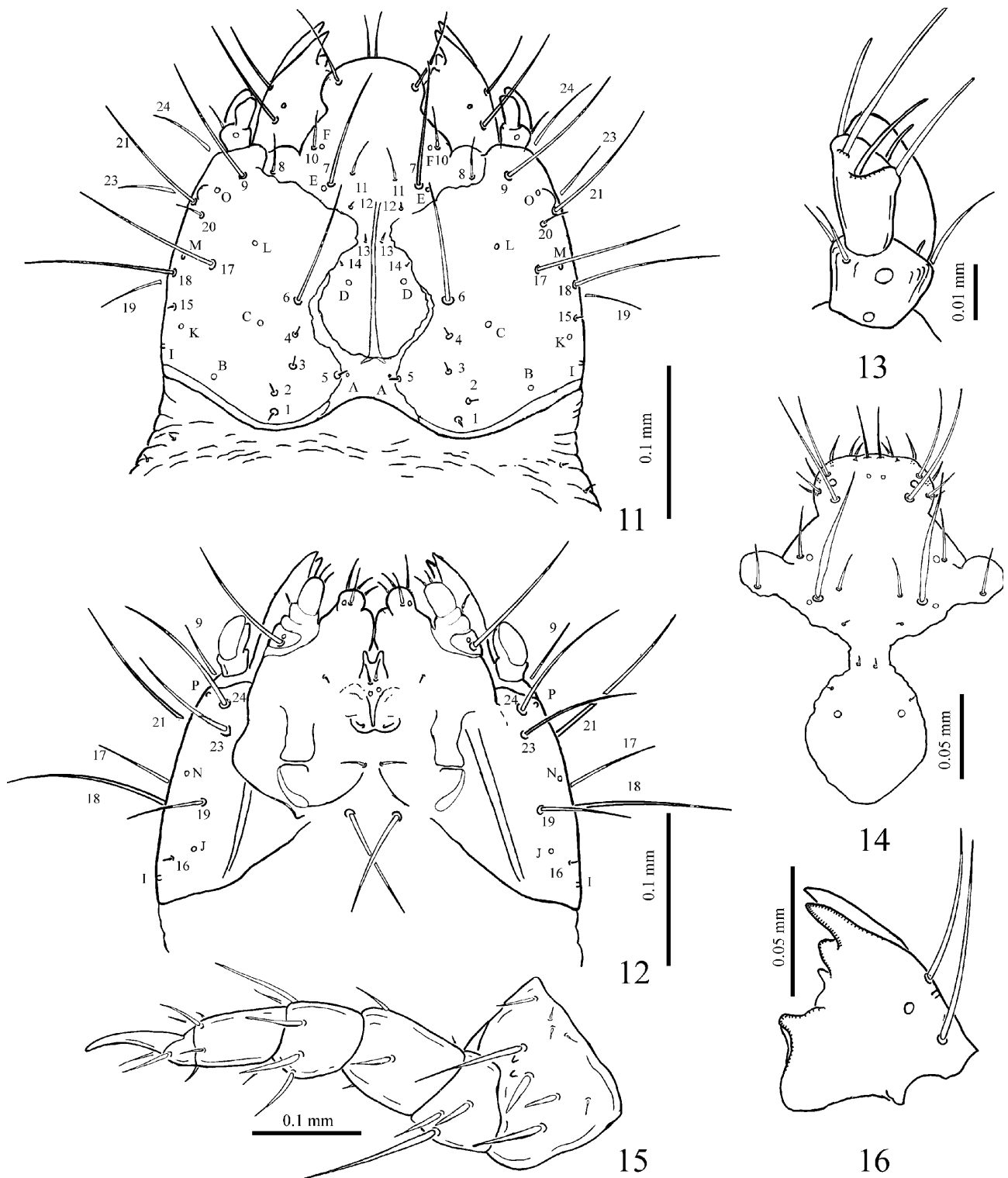
**MATERIAL EXAMINED.** *Micromalthus debilis* LeConte, 1878. Four “caraboid” and five “cerambycoid” larvae (two “caraboid” and two “cerambycoid” larvae were macerated in KOH and mounted in Euparal), 1970’s, reared by “Bundesanstalt für Materialprüfung, Berlin” but originally from USA, no further data available (VGC). Two “cerambycoid” larvae (cleared in KOH and mounted in Euparal), with the label: “*Micromalthus debilis* Lec. (H.S.B. det 1911), in rotting base of Chestnut tele-



Figs 7–10. First instar larva of *Micromalthus debilis*, details. 7, 8 – pro- and mesothorax dorso-lateral (7) and ventro-lateral (8); 9, 10 – abdominal segments VIII and IX, dorso-lateral (9) and ventro-lateral (10).

phone pole underground, Coll. Feb. 1911, T.E. Snyder. – Washington D.C. Hopk. U.S. no. 9242” (NMNH). Four “caraboid” larvae: USA: WI: Richland Co., 43°11'44"N; 90° 14'31"W, Oct. 07, 2001, near red-rot *Quercus* log, Daniel K. Young leg. (VGC). One “caraboid”, four “cerambycoid” larvae: “USA, Michigan, Clinton Co., Rose Lake Wildlife Exp. Station, RSW, RIW, Sec 23, 1 km E of Burke Lake, 6 May 1974, in oak-

Hickory woods, *Micromalthus debilis*” (CAS). Three “caraboid” larvae, mounted on two microscope slides in Canada Balsam: Hong Kong, May 31, 1956 from floor boards in house, J.D. Romer (NHML). One “cerambycoid” larva mounted on microscope slide in Canada Balsam with label: “Pretoria, 1934, Dr. N. Paterson” (NHML). Head width: 0.18 mm (n = 1; L1); 0.43–0.44 mm (n = 2; presumably second instar).



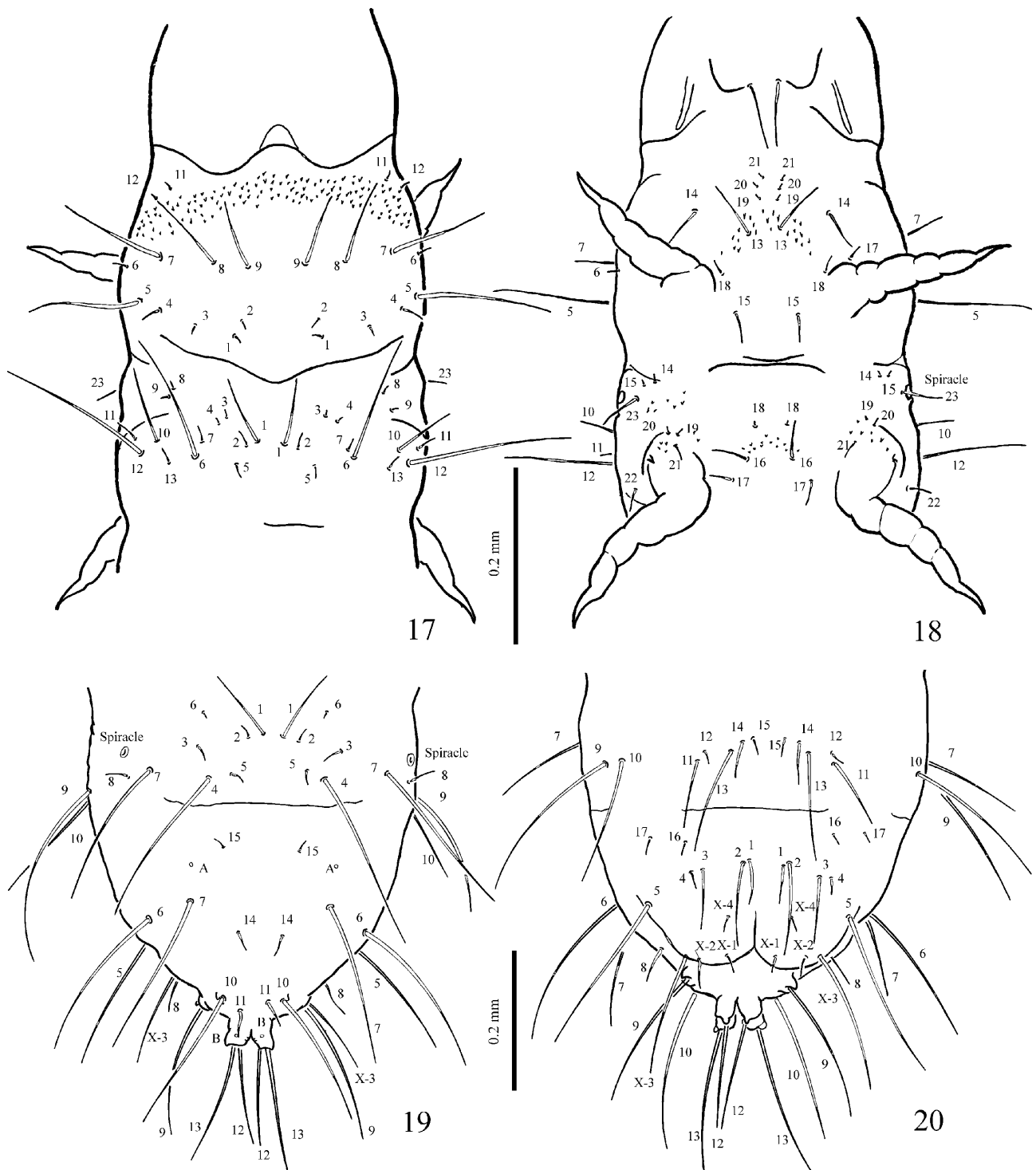
Figs 11–16. First instar larva of *Priacma serrata*, details. 11, 12 – head, dorsal (11) and ventral (12); 13 – right antenna, dorsal; 14 – frontal sclerite, dorsal; 15 – fore leg, anterior; 16 – right mandible, dorsal.

**FAMILY CUPEDIDAE: PRIACMINAE**

**Diagnosis**

**First instar** (Figs 11–20): Clypeolabral suture absent, labrum fully incorporated with frontal sclerite; frontal suture present, frontal sclerite clearly demarcated; dorsal medial emargination of cranium poorly developed; projection of cranium dorsad of antennifer absent; cranium

with single stemma on each side; antenna with 2 antennomeres; mandibles with 3 apical teeth and with additional ventral and basal smaller tooth; anterior edge of labrum rounded; labial palps with 1 palpomere; thorax and abdominal segments I–VIII without transverse membranous folds dorsally and ventrally; abdomen terminates with tergal process with 4 separate apical rounded sub-

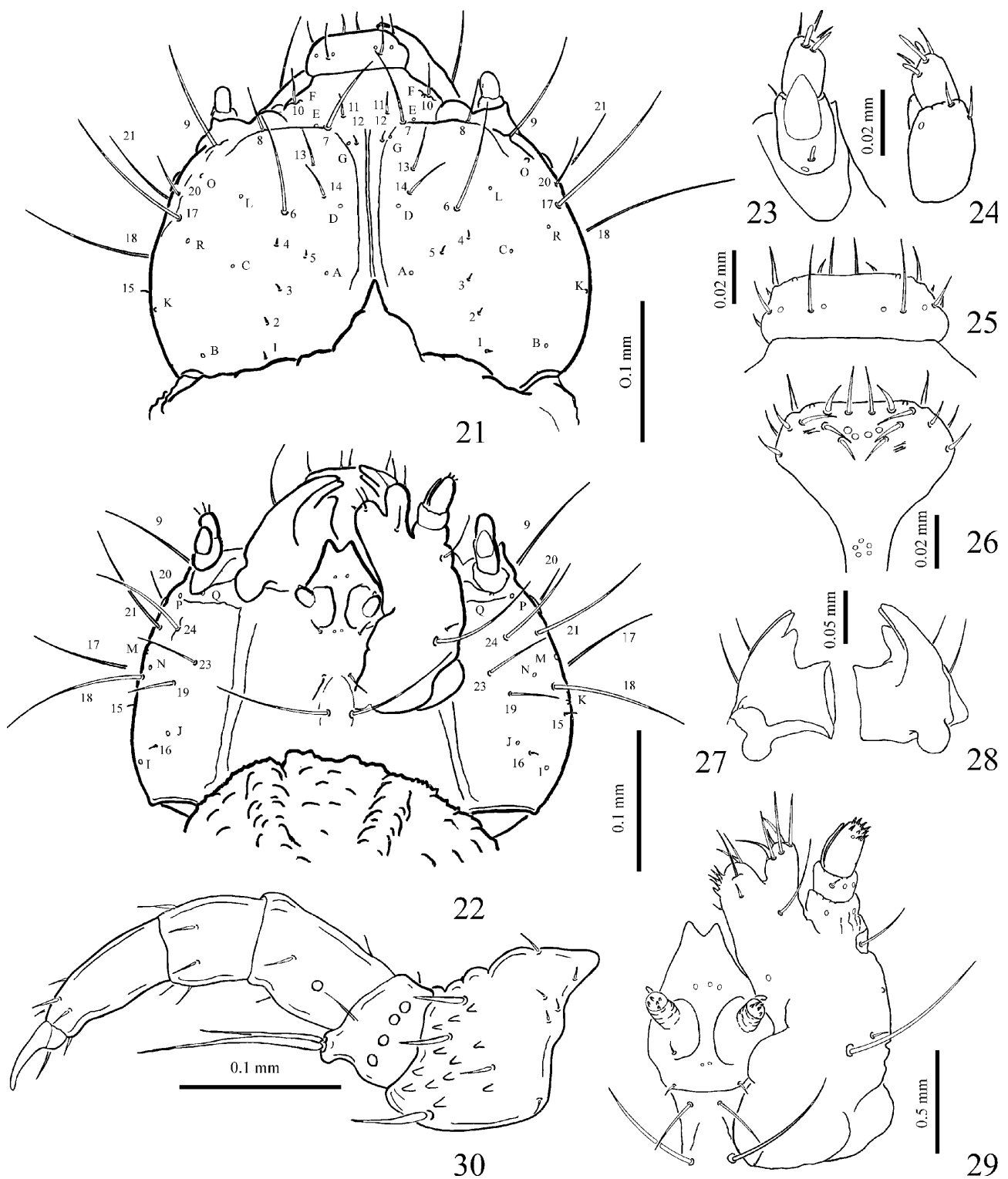


Figs 17–20. First instar larva of *Priacma serrata*, details. 17, 18 – pro- and mesothorax dorsal (17) and ventral (18); 19, 20 – abdominal segments VIII, IX, and X dorsal (19) and ventral (20).

elements. **Chaetotaxy:** cranium (Figs 11, 12) with setae 1–21, 23, 24 and pores A–F, I–P; prothorax (Figs 17, 18) with setae 1–9, 11–15, 17, 19–21 and pore A; mesothorax (Figs 17, 18) with setae 1–23; abdominal segments I–VIII (Figs 19, 20) with setae 1–15; abdominal segment IX (Figs 19, 20) with setae 1–17 and pores A, B; abdominal segment X (Fig. 20) with setae 1–4 (indicated on Fig. 20 as X-1, X-2, X-3 and X-4 to distinguish them from setae on abdominal segment IX). **Older instars:** unknown.

#### Genus *Priacma* LeConte, 1874

**MATERIAL EXAMINED.** *Priacma serrata* LeConte, 1861. Six first-instar larvae mounted on three slides with labels: “*P. serrata*, inst. 1, 29.VII.68” (ANIC). Head width: L1: 0.28–0.30 mm (n = 5; first instar, heads of larvae on these microscope slides are somewhat squashed). **Remarks.** The six larval specimens of *Priacma* I have studied originated from those reared by Ross & Potchecary (1970) from a single female collected on June 5, 1968 in British Columbia, Canada. These authors noted that no other *Priacma* female was seen, but over 830 males were caught



Figs 21–30. First instar larva of *Distocupes varians*, details. 21, 22 – head, dorsal (21) and ventral (22); 23, 24 – left antenna, ventral (23) and dorsal (24); 25, 26 – labrum, dorsal (25) and ventral (26); 27, 28 – left mandible, dorsal (27) and ventral (28); 29 – left maxilla and labium, ventral; 30 – fore leg, anterior.

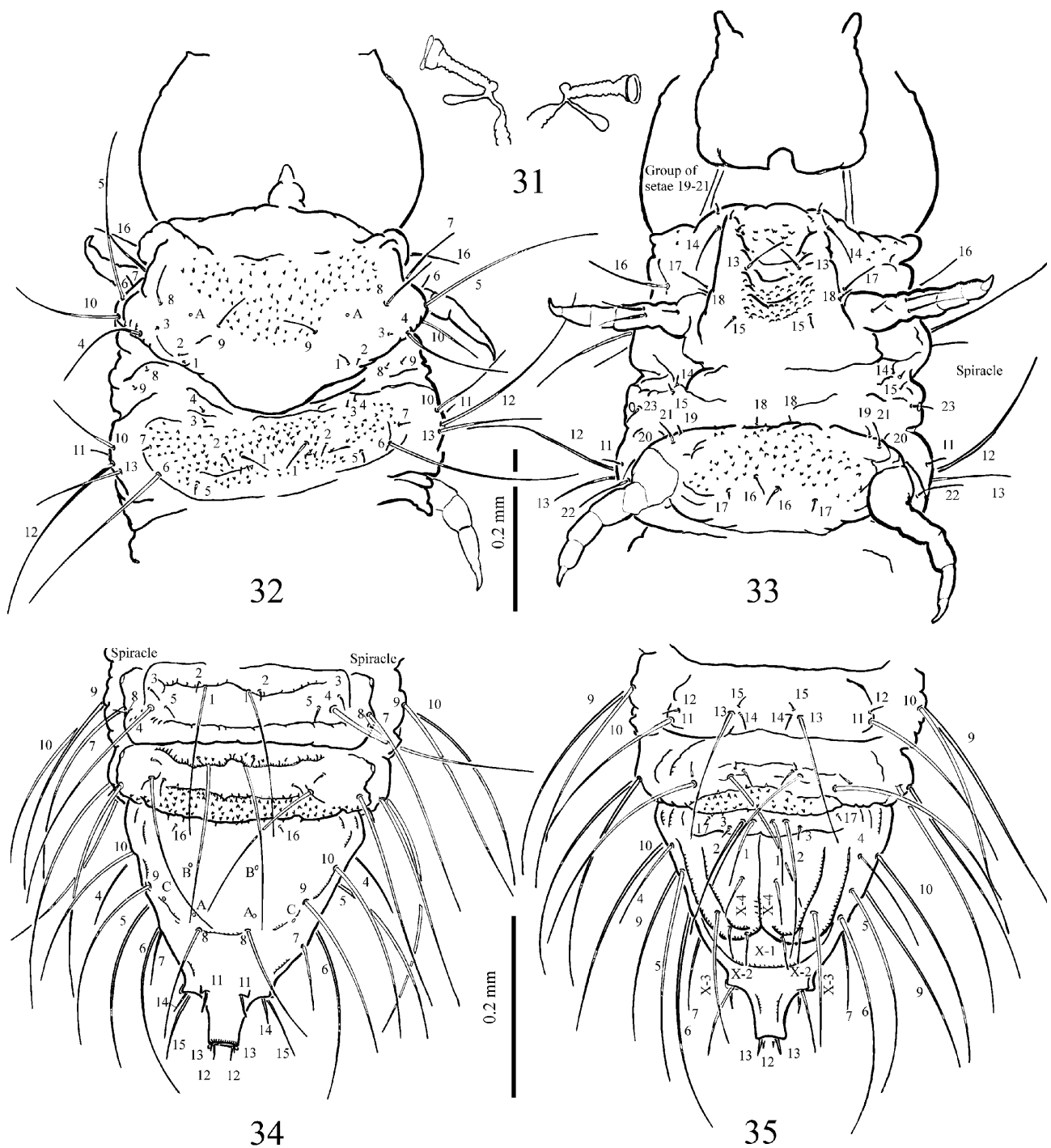
flying nearby by means of window traps during the same season. This female laid in total 1,463 eggs during 63 days in captivity and more than 800 first-instar larvae hatched 28–40 days later. All of them died prior to moulting to the second instar.

**FAMILY CUPEDIDAE: CUPEDINAE**

**Diagnosis**

**First instar** (Figs 21–35): like older instars, except for the following: smaller, body almost parallel-sided; palpal sensorium represented by single structure and not by compact group of sensoria; different chaetotaxy. Other

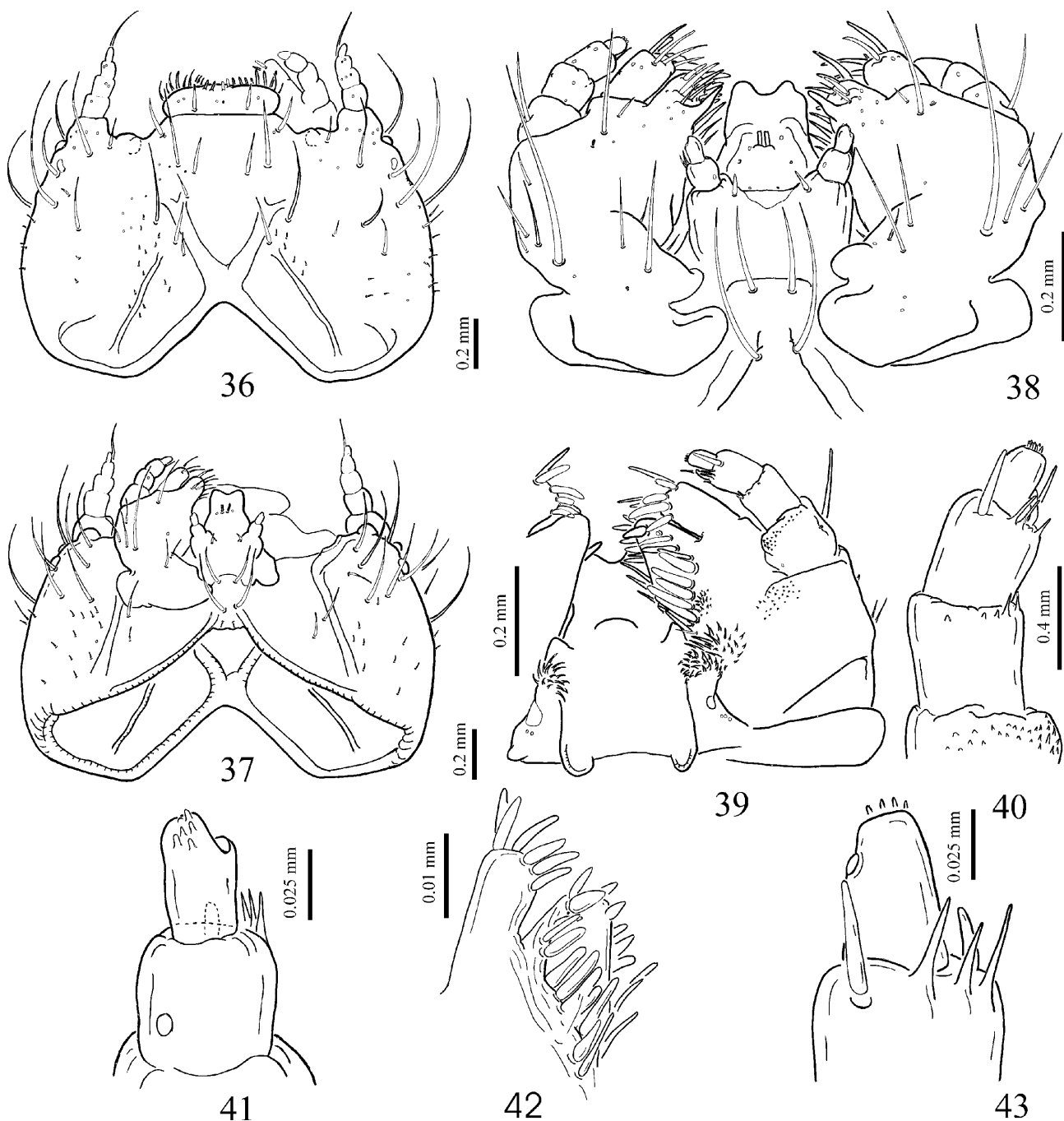




Figs 31–35. First instar larva of *Distocupes varians*, details. 31 – spiracle and spiracular closing apparatus, lateral; 32, 33 – pro- and mesothorax dorsal (32) and ventral (33); 34, 35 – abdominal segments VII–X dorsal (34) and ventral (35).

characters of first instar larvae are: clypeolabral suture present, labrum clearly separated from cranium; frontal suture absent; dorsal medial emargination of cranium markedly developed, deep; projection of cranium dorsad of antennifer present; cranium with single stemma on each side; antenna with 2 antennomeres; mandibles with 3 apical teeth and without additional ventral and basal smaller tooth; anterior edge of labrum straight; labial palps with 2 palpomeres; thorax and abdominal segments I–VIII with transverse membranous folds dorsally and ventrally; abdomen terminates with complete and not-

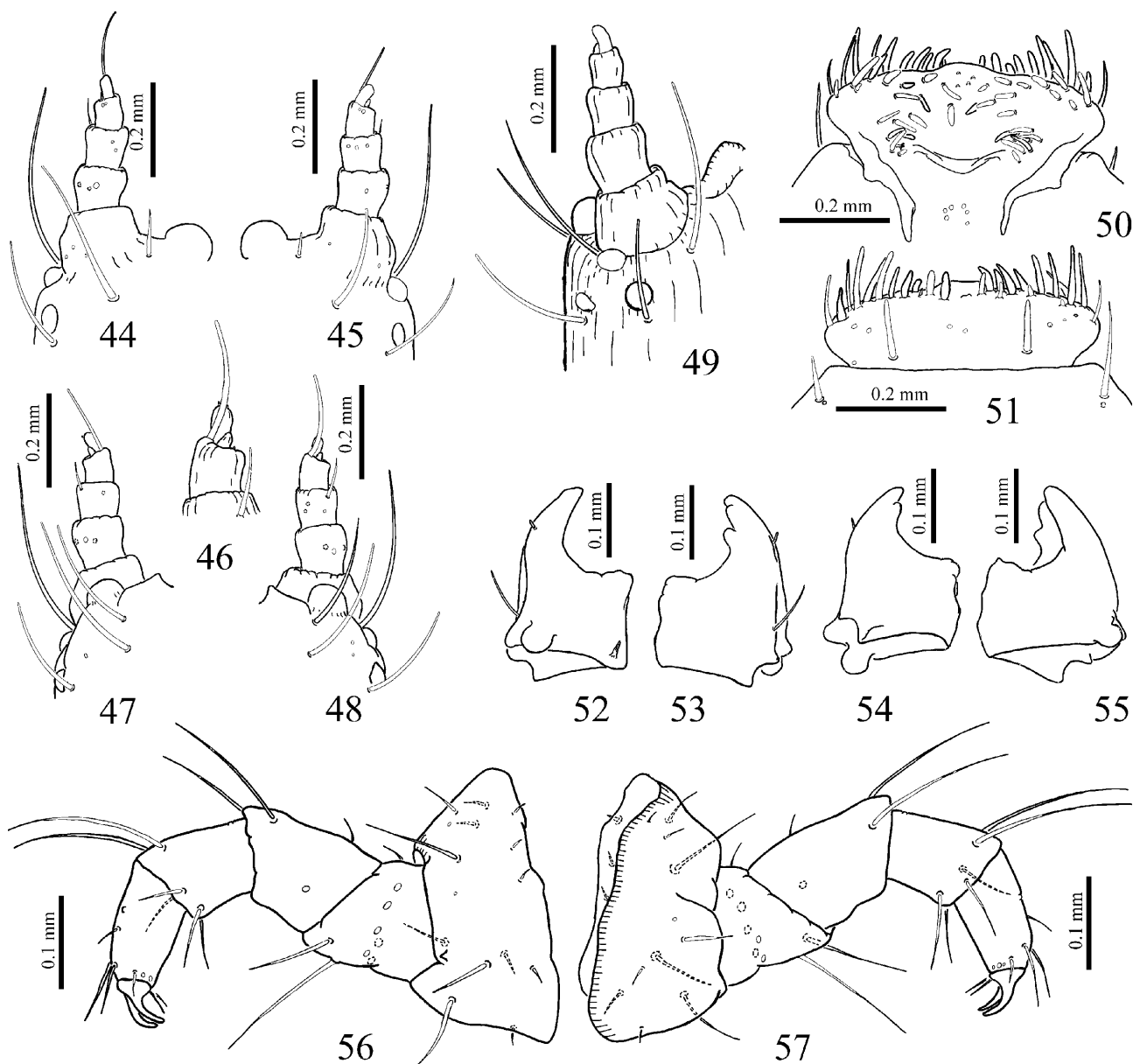
subdivided tergal process. **Chaetotaxy:** cranium (Figs 21, 22) with setae 1–21, 23, 24 and pores A–G, I–R; prothorax (Figs 32, 33) with setae 1–10, 13–21 and pore A; mesothorax (Figs 32, 33) with setae 1–23; abdominal segments I–VIII (Figs 34, 35) with setae 1–5, 7–15; abdominal segment IX (Figs 34, 35) with setae 1–17 and pores A–C; abdominal segment X (Fig. 35) with setae 1–4 (indicated on Fig. 35 as X–1, X–2, X–3 and X–4 to distinguish them from setae on abdominal segment IX). **Older instars** (Figs 69–120): Body widest at segment VIII. Cranium with straight median endocarina; two addi-



Figs 36–43. Older instar larva of *Omma* sp., details. 36, 37 – head (mandibles and left maxilla removed), dorsal (36) and ventral (37); 38 – maxillae and labium, ventral; 39 – right maxilla, labium and mesal part of left maxilla, dorsal; 40 – left maxillary palp, dorsal; 41 – right apical labial palpomeres, ventral; 42 – apex of mesal surface of left stipes and galea; dorso-mesal; 43 – apical and part of pre-apical left maxillary palpomeres, ventral.

tional endocarinae lateral of median line absent; fronto-clypeal suture weakly developed; stemmata absent; cranium markedly rounded laterally. Antenna not extending beyond clypeal apex; antenna with 4 (in *Rhysideigma* more) antennomeres, basal one not reduced in size; apical antennomere not longer than half the length of rest of antenna. Mandibles without retinaculum; dorsal tooth shortest and ventral longest; transverse ridges on mola absent; dorsal surface of left mandible without unsclerotised short appendage. Maxillary palpifer clearly delimited; sensory spot on lateral surface of apical maxillary

and labial palpomeres present, large; apical maxillary and labial palpomeres with palpal sensorium represented by compact group of about 3–15 narrow sensoria; unarticulated apical cuticular projections mesally on first and second maxillary palpomeres absent; narrow and anteriorly oriented sclerotized fixed process on ventral surface of lacinia absent; dorsal membranous projection on labio-maxillary articulation membrane absent; ventral surface of ligular sclerome with 2–6 setae in transverse line; labial palps 2-segmented. Prothorax ventrally with field of asperities; legs present; posterior claw variably reduced



Figs 44–57. Older instar larva of *Omma* sp., details. 44, 49 – left antenna, dorsal (44) and ventral (49); 45, 47 – right antenna, dorsal (45) and ventral (47); 46 – two left apical antennomeres and sensorium, ventral; 48 – four stemmata on left side of cranium, dorso-lateral; 50, 51 – labrum, ventral (50) and dorsal (51); 52, 53 – right mandible, ventral (52) and dorsal (53); 54, 55 – left mandibles, dorsal (54) and ventral (55); 56, 57 – fore leg, anterior (56) and posterior (57).

in size; coxa with more than 1 tooth. Lateral bulge on abdomen absent or present; abdominal segment IX with asperities; abdominal segment IX with sclerotized, toothed and straight tergal process; anal opening located ventrally; abdominal segment X represented by two ventral eversible lobes.

#### Genus *Tenomerga* Neboiss, 1984

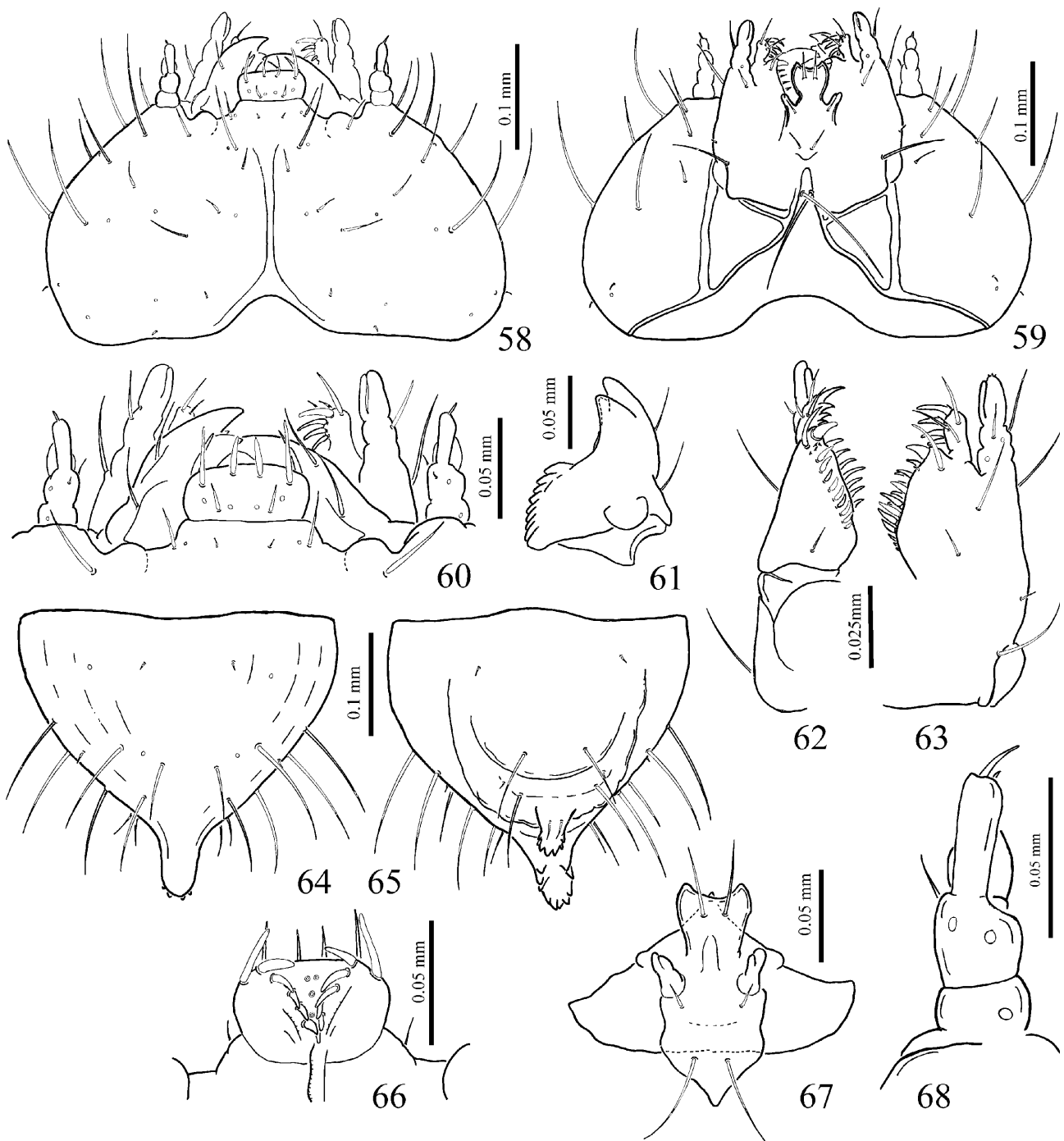
**MATERIAL EXAMINED.** *Tenomerga cinerea* (Say, 1831) [= *T. concolor* (Westwood, 1835)]. Two older-instar larvae (one larva cleared in KOH and mounted in glycerine), with the label: “*Cupes*, in rotten oak, Dead Run, Va. Opposite Plummera Isl. Md. Apr. 18, 1915, Schaeffer & Barber” (NMNH). Six apparently mature larvae “Michigan, Ingham Co. East Lansing 29 Apr. ’62 S.E. Chang” (ANIC). **Head width:** 1.54 mm. (*T. cinerea*, n = 1; older instar). **Remarks.** Bousquet (1993) pointed out

that the name *Tenomerga cinerea* (Say, 1831) has priority over *Tenomerga concolor* (Westwood, 1835).

*Tenomerga mucida* (Chevrolat, 1829). One older-instar larva mounted on slide in Canada Balsam from Roy Crowson’s collection (currently kept in NHML), with the label: “*Cupedidae: Cupes clathratus*, Japan, M. Chûjo leg. R.A.C.”. **Head width:** 1.94 mm (*T. mucida*, n = 1; older instar).

#### Genus *Distocupes* Neboiss, 1984

**MATERIAL EXAMINED.** *Distocupes varians* (Lea, 1902). Two apparently mature larvae and two pupae: “Puckapunyal nr. Seymour, Vic., 15 Oct. 1963, *Cupes varians* Lea – larvae” “*Cupes varians* Lea det. A. Neboiss 1963” (MVMA). 10 older- and 2 intermediate-instar larvae” Lyons, Canberra A.C.T. 10 July 1979, R. John, white-rotted structural timber” (ANIC). 11 first-instar larvae, eggs: O’Connor, A.C.F. 6 Feb. 1989 W.W.K. Houston” (ANIC). **Head width:** 1.98–2.02 (n = 2; older instar).



Figs 58–68. Second (cerambycoid) instar larva of *Micromalthus debilis*, details. 58, 59 – head, dorsal (58) and ventral (59); 60 – anterior part of cranium and mouthparts, dorsal; 61 – left mandible, ventral; 62 – right maxilla, ventro-mesal; 63 – left maxilla, ventral; 64, 65 – abdominal segment IX, dorsal (64) and ventral (65); 66 – labrum, ventral; 67 – labium, ventral; 68 – right antenna, dorsal.

**Remarks.** First-instar larvae of *Distocupes* were previously undescribed.

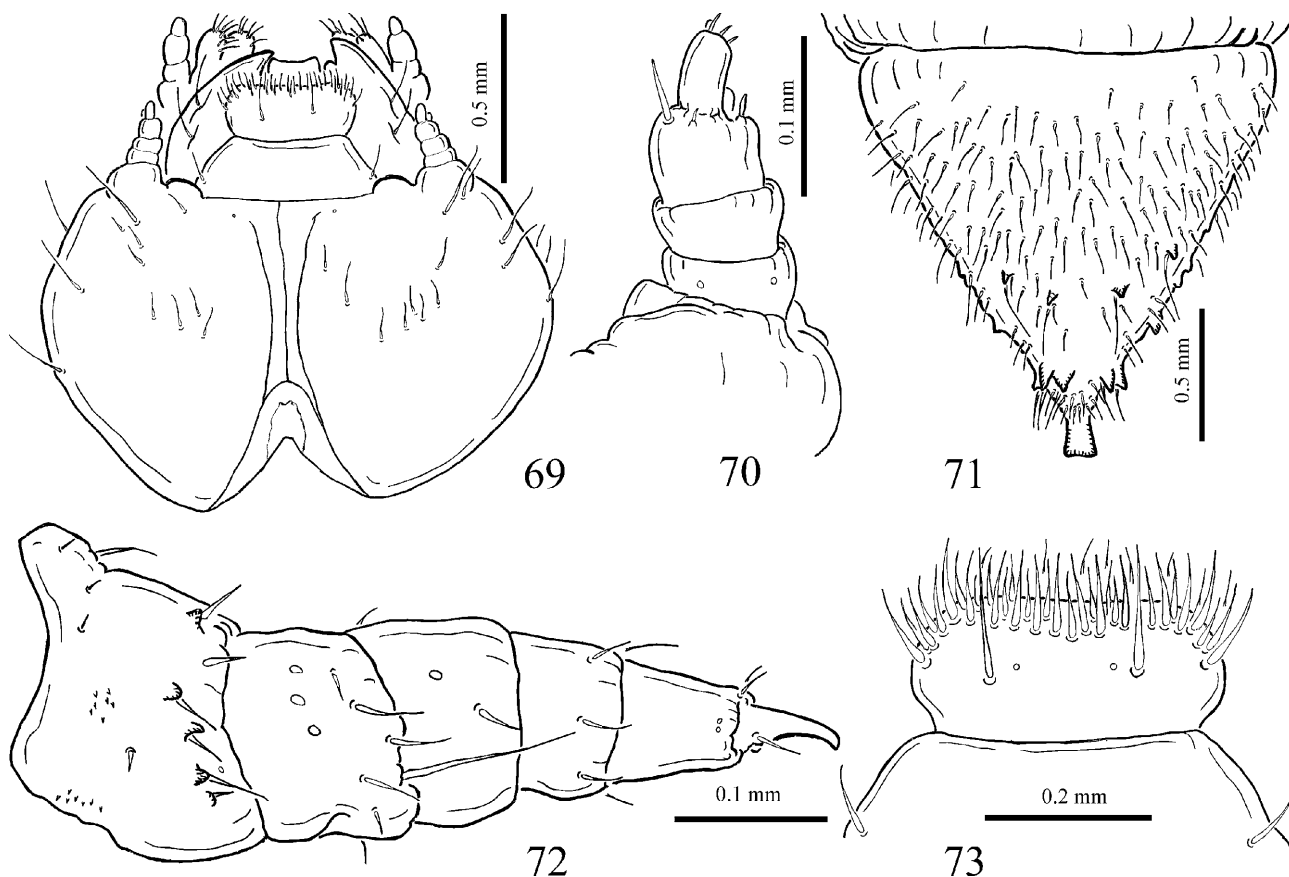
#### Genus *Rhysideigma* Neboiss, 1984

**MATERIAL EXAMINED.** *Rhysideigma raffrayi* (Fairmaire, 1884): three older-instar larvae (one larva is macerated in KOH and mounted in glycerol), Madagascar, Manankazo env., Ambohitantely Nat. Res., 21–22.xi.1996, Petr Švácha (IECR). Head width: 3.1 mm (exact instar unknown).

#### DISCUSSION

##### Monophyly of Archostemata

Beutel & Hörnschemeyer (2002a) listed 10 autapomorphies of Archostemata, nine of which are in larval morphology: (01.) dorsal and ventral posteromedian emarginations of cranium present; (02.) frontal suture absent in older instars (Figs 36, 58, 69, 78, 97); (03.) mandibles with three apical teeth (Figs 4, 16, 27, 28, 52–55, 61, 88–91, 99); (04.) cardo with separate lateral



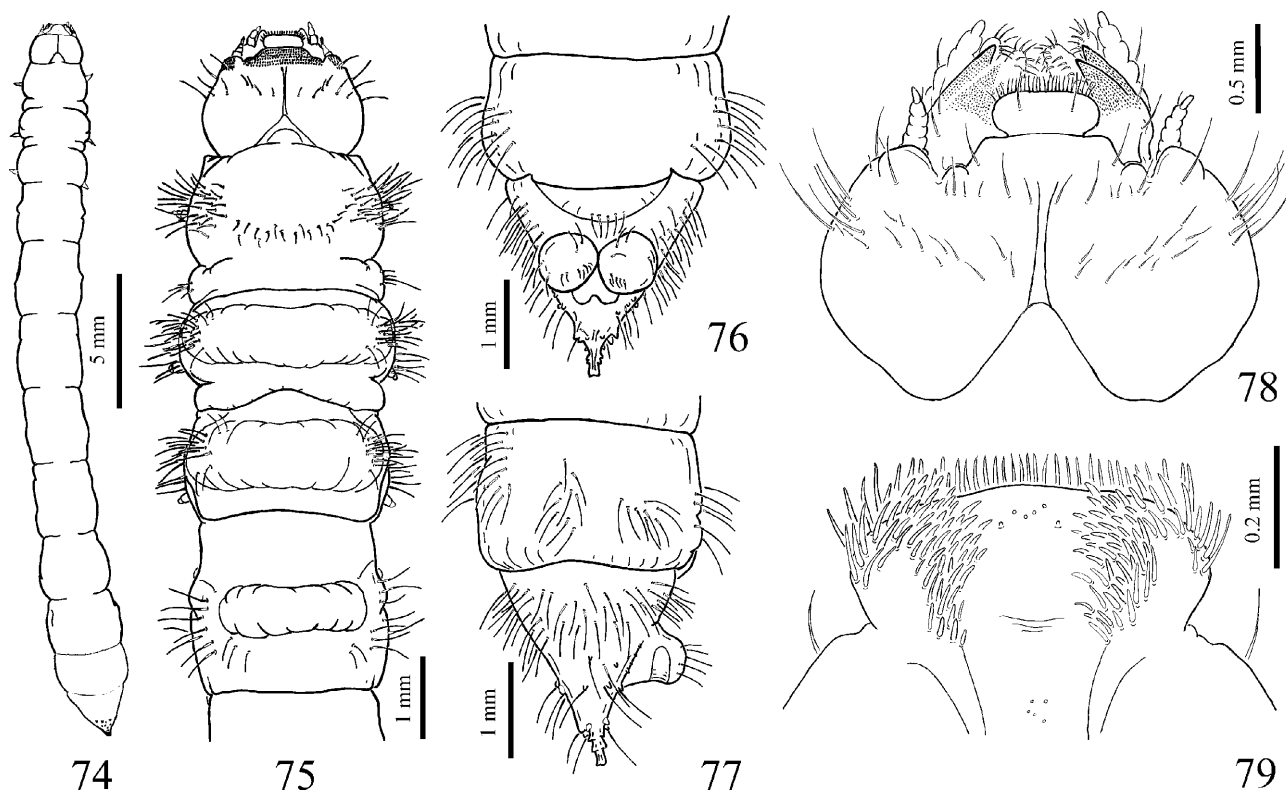
Figs 69–73. Older instar larva of *Tenomergera cinerea*, details. 69 – head, dorsal; 70 – right antenna, dorsal; 71 – abdominal segment IX, dorsal; 72 – fore leg, antero-ventral; 73 – labium, dorsal.

piece; (05.) ligula sclerotized, enlarged and wedge-shaped; (06.) submentum fused to mentum and constricted between maxillary grooves (Figs 6, 12, 29, 37, 38, 59, 98); (07.) abdominal segments I–III combined longer than prothorax in older instar larvae (Fig. 75); (08.) tergal ampullae present in older instar larvae (Figs 75, 105–108) and (09.) segment X not visible externally. Of these characters I would suggest slightly re-wording the following: (01.) only the dorsal posteromedian emargination of cranium is distinctly detectable (Figs 1, 11, 21, 36, 37, 58, 59, 69, 75, 79, 97, 98); (05.) labium with sclerotized, enlarged, and wedge-shaped ligula and markedly separated palps (Figs 6, 12, 29, 37, 38, 67, 92, 93, 100, 101); (09.) segment X highly reduced, absent (*Omma*, *Micromalthus*; Figs 9, 10, 64, 65) or reduced to two ventral eversible lobes not visible dorsally (Cupedidae; Figs 19, 20, 34, 35, 71, 76, 77, 108, 109).

Other larval characters are also characteristic of Archostemata and might eventually be shown to be autapomorphies: (10.) cranium with dorsal median endocarina (Figs 11, 21, 36, 58, 69, 78, 97; character used by Beutel & Hörnschemeyer (2002a), but the inclusion of the lymexylid genus *Hylecoetus* Latreille, 1806 in the out-group resulted in the final cladogram not showing this character as an Archostematan synapomorphy; likely an artefact); (11.) hypostomal rods extending well into basal half of cranium (Figs 12, 22, 37, 59, 98); (12.) antennae short (Figs 1, 2, 11, 12, 21, 22, 36, 37, 58, 59, 69, 78, 97,

98), not or only slightly protruding beyond the level of clypeal apex (slightly longer in *Omma*; Figs 36, 37), this character was interpreted by Beutel & Hörnschemeyer (2002a) as a synapomorphy for Cupedidae and Micromalthidae); (13.) medial surface of lacinia flattened and delimited dorsally and ventrally by lines of stout articulated spines and setae (Figs 42, 62); (14.) apical labial and maxillary palps with characteristic palpal sensorium (see below).

Archostemata larvae are characterised by the peculiar structure of apices of the labial and maxillary palps. In all larvae the penultimate palpomere bears a palpal sensorium, which is represented either by a single relatively large structure (Figs 6, 29, 40, 41, 43, 62, 63) or, in older instar larvae of Cupedinae, by a compact group of smaller and similar sensoria (Figs 85, 86, 92, 100, 102, 103). I am not aware of similar structures in other Coleopteran or Neuropteran larvae and, therefore, this sensorium on the labial and maxillary palps might be an autapomorphic character for Archostemata. Additionally, the Archostemata larvae studied are characterised by marked similarities in epipharynx, maxillae and antennae, which, however, currently can hardly be put in a phylogenetic context due to the difficulties of distinguishing discrete and independent characters in these structures. Moreover, first instar larvae of Archostemata (*Micromalthus*, *Priacma* and *Distocupes*) have a markedly similar chaetotaxy on cranium, thorax and abdominal segments I–VIII,



Figs 74–79. Older instar larva of *Distocupes varians*, details. 74 – habitus, dorsal; 75 – head, thorax and abdominal segment I, dorsal; 76, 77 – abdominal segments VIII–X, ventral (76) and lateral (77); 78 – head, dorsal; 79 – labrum, ventral.

which also might eventually provide additional autapomorphies for the group (see also below).

#### Position of *Micromalthus*

When described, the genus *Micromalthus* was assigned to Lymexylidae and since then many authors have discussed the taxonomic position or phylogenetic affinities of this remarkable taxon (see Beutel & Hörschemeyer, 2002a for more details). Forbes (1926) was apparently the first to propose archostematan relationships of *Micromalthus* based on a study of wing-folding patterns; this view was corroborated by Böving & Craighead (1931) based on larval morphology. This hypothesis dominates in publications of recent authors (Crowson, 1955, 1981; Lawrence, 1982, 1991; Lawrence & Newton, 1982, 1995; Kukulová-Peck & Lawrence, 1993; Beutel & Haas, 2000). However, Baehr (in: Hennig, 1981: 308) considered this genus to be a simplified member of Cantharoidea or Lymexyloidea based primarily on the characters of adults. Barlet (1996) corroborated this view giving reasons why *Micromalthus* is a lymexylid. Recent revision of Lymexylidae by Wheeler (1986) does not treat *Micromalthus* as a member. The most recent work by Beutel & Hörschemeyer (2002a) on the larval morphology and anatomy of *Micromalthus* clearly supports archostematan affinities of the genus and indicates that the family Cupedidae is a sister-group to Micromalthidae, and the present work supports their conclusions. Following features are potential synapomorphies: cranium is posteriorly widened and laterally rounded; number of stemmata is reduced to one or stemmata absent; antennae are markedly shortened

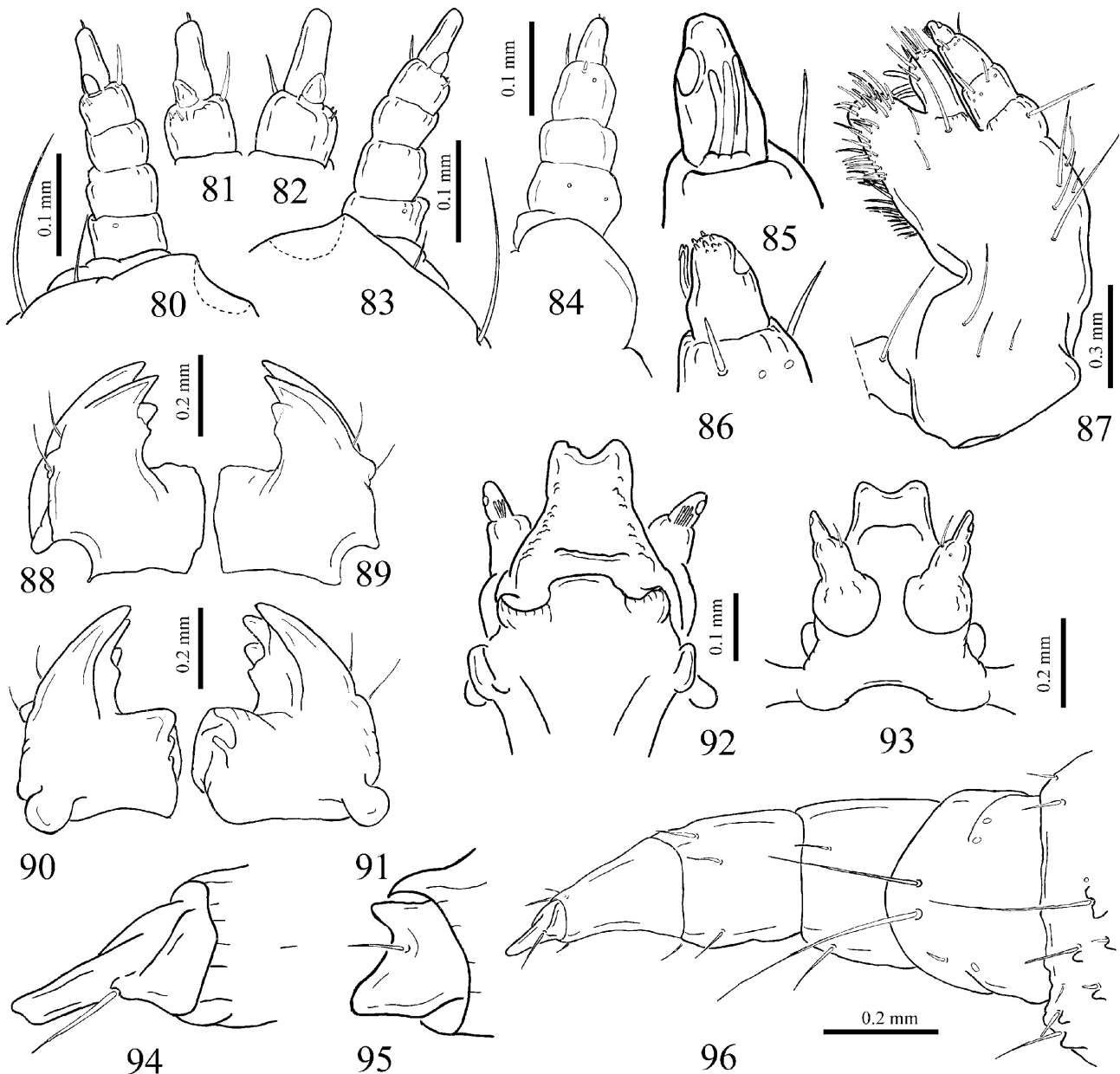
and do not extend beyond clypeal apex; see also Beutel & Hörschemeyer (2002a: 185–186).

#### Cupedidae larvae

Older instar Cupedinae larvae are remarkably similar. I was unable to provide reliable diagnostic characters to distinguish the genera based on external morphology because of the limited number of specimens. Larvae of *Tenomerga* and *Rhipsideigma*, however, differ from those of *Distocupes* by having a lateral longitudinal bulge on each side of the abdominal segments I–VIII (Figs 105–107; character noted by Beutel & Hörschemeyer, 2002a), while some *Distocupes* larvae have more than four antennomeres (Figs 78, 80, 83; Lawrence, 1991). There are differences in number of sub-elements in maxillary palpal sensorium varying within the subfamily from three to 15 (Figs 85, 102) with *Rhipsideigma* having the highest number. Larvae of this genus have most of setae on body, most notably on dorsal surface of cranium (Fig. 97). Otherwise older instar larvae of the subfamily Cupedinae are generally similar. A basal position of *Priacma* within Cupedidae is suggested by the following presumptive autapomorphic character of Cupedinae: cranium dorsally is without frontal sutures and therefore frontal sclerites are completely fused with parietal sclerites.

#### Noteworthy morphological characters of Archostemata larvae

All Archostemata larvae with the exception of those of *Micromalthus*, have a presumably derived character: a



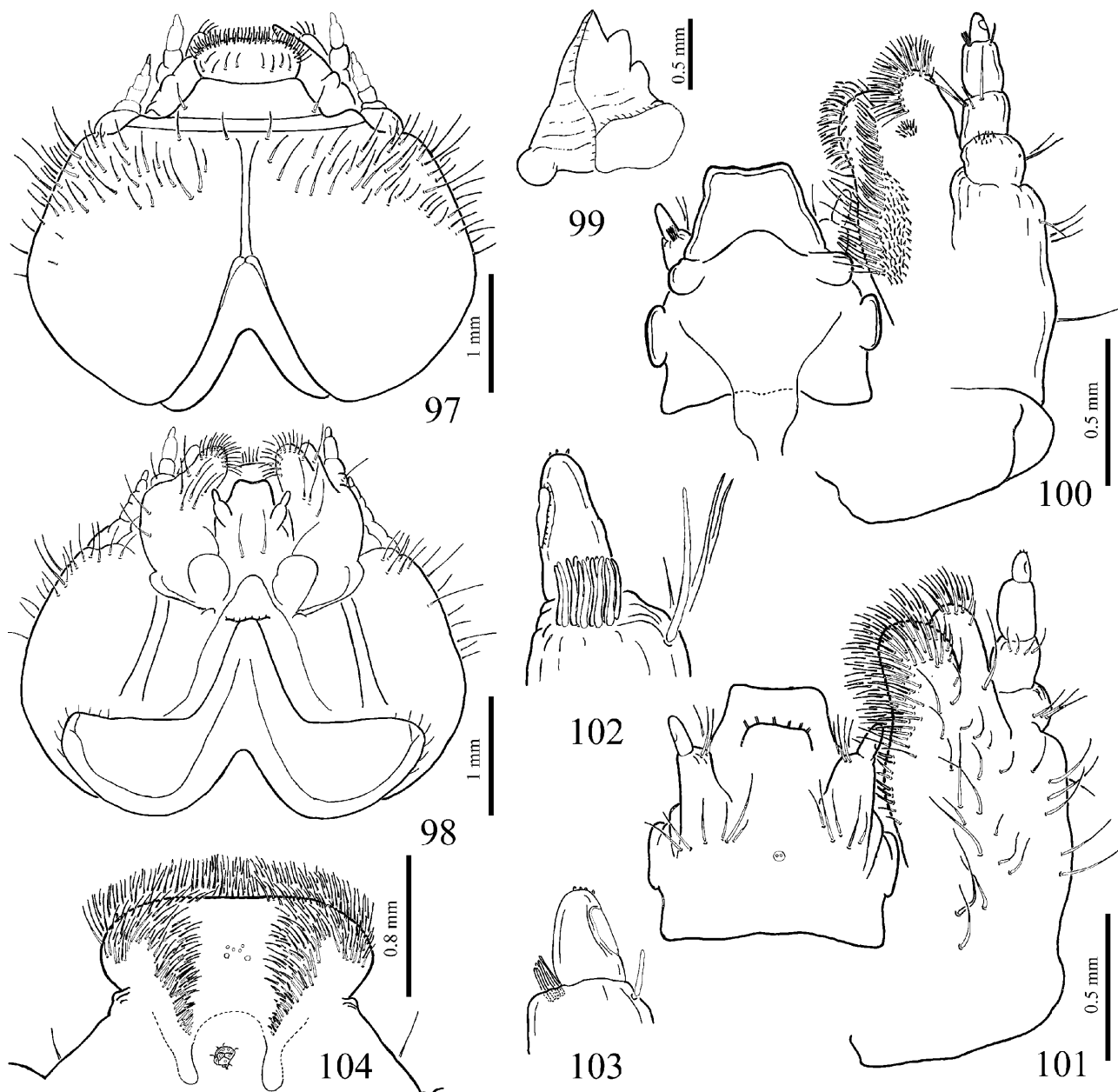
Figs 80–96. Older instar larva of *Distocupes varians*, details. 80, 84 – right antenna, ventral (80) and dorsal (84); 81, 82 – two apical antennomeres and sensorium, ventral, right (81) and left antenna (82); 83 – left antenna, ventral; 85 – right apical maxillary palpomere, dorsal; 86 – right apical labial palpomere, ventral; 87 – left maxilla, ventral; 88, 89 – left mandible, dorsal (88) and ventral (89); 89, 90 – right mandible, dorsal (89) and ventral (90); 92, 93 – hypopharynx and labium, dorsal (92) and ventral (93); 94, 95 – claws; 96 – leg, postero-ventral.

sensory spot on lateral surface of apical labial and maxillary palpomere (43, 85, 86, 102, 103), which may be a potential synapomorphy of Ommatidae + Cupedidae.

First instar larvae of *Priacma* and *Distocupes* have 2-segmented antennae (Figs 11, 13, 21–24), while in *Micromalthus* antennae appear 3-segmented with the basal antennomere markedly reduced in length (Fig. 3). In older instar larvae of *Omma*, *Rhypsodeigma* and *Tenomerga* antennae are clearly 4-segmented (Figs 44–49, 70, 110–113), while in *Micromalthus* they are apparently also 4-segmented (Beutel & Hörnschemeyer, 2002a) with basal antennomere markedly reduced and antennae appearing 3-segmented (Fig. 68). Older instar larvae of *Distocupes* have from four to six antennomeres

(Figs 80, 83, 84), which is rare or even unique in Coleoptera.

All Archostemata larvae are characterised by having a maximum of two claws, and in older instar *Omma* and first instar *Micromalthus* they are of relatively large and equal size (Figs 5, 56, 57). In older instar larvae of Cupedidae, however, the posterior claw is variably reduced (94, 95, 115–117), from equal to the anterior claw to almost reduced. These different degrees of claw reduction might be seen on different legs of the same larva. First instar larvae of Cupedidae have, apparently, the posterior claw completely reduced and the legs, therefore, appear to have only one claw (Figs 15, 30).



Figs 97–104. Older instar larva of *Rhipsideigma raffrayi*, details. 97, 98 – head, dorsal (97) and ventral (98); 99 – right mandible, ventral; 100 – right maxilla and labium, dorsal; 101 – left maxilla and labium, ventral; 102 – right apical labial palpomere, ventral; 103 – left apical maxillary palpomere, ventral; 104 – labrum, ventral.

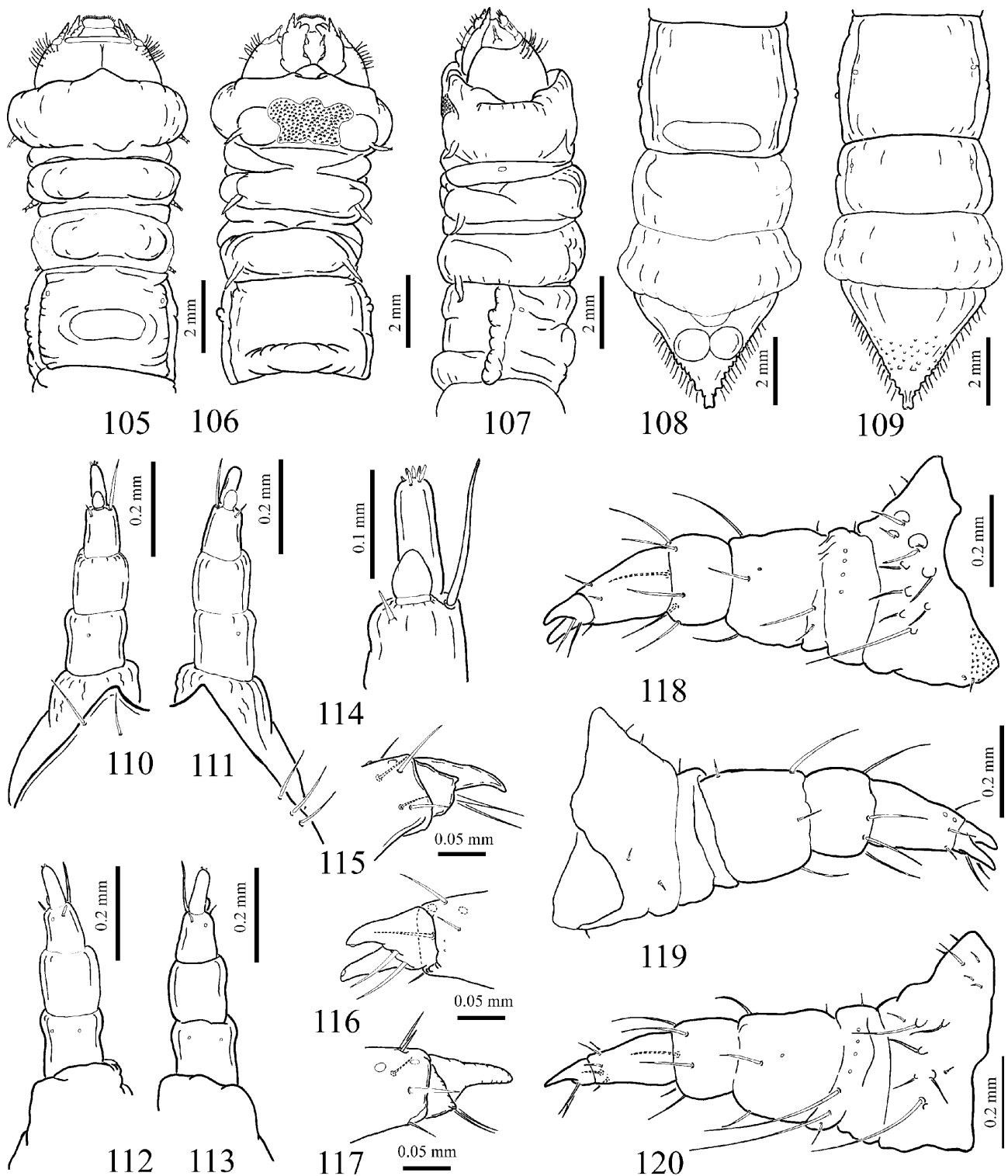
#### Chaetotaxy of first instar larvae of Archostemata.

This paper presents the first attempt to document the diversity of chaetotaxy in first instar Archostemata larvae. Since the chaetotaxy work with first instar Archostemata larvae is hampered by a scarcity of material, the description is restricted to the most easily observed body parts, namely the cranium and body segments (except metanotum). No attempts were made to provide a detailed description of the chaetotaxy of head appendages and legs. No firm homology is postulated between similarly numbered setae and pores on homologous body parts in *Micromalthus*, *Priacma* and *Distocupes*. I believe, however, that the majority of the similarly designated sensillae on cranium, prothorax, mesothorax and abdominal

segments I–VIII are indeed homologous (asterisk (\*) near sensillar number indicates the most ambiguous cases of homology). The chaetotaxy of abdominal segments IX and X were found to be markedly different and consequently their sensory structures are simply numbered without any presumption of homology. The structure and chaetotaxy of the metathorax is similar to that of the mesothorax with the most notable exception of the absence of the spiracle and associated seta 23.

The general practice in coleopteran chaetotaxy is to establish a generalised reference system for a family (see references in Material and Methods). The reference system should include the maximum number of recognisable sensory elements. This reference system does not necessarily have to be the most plesiotypic set of sensilla





Figs 105–120. Older instar larva of *Rhipsideigma raffrayi*, details. 105–109 – head, thorax and abdominal segment I, dorsal (105), ventral (106) and lateral (107); 108, 109 – abdominal segments VI–X, ventral (108) and dorsal (109); 110, 113 – right antenna, ventral (110) and dorsal (113); 111, 112 – left antenna, ventral (111) and dorsal (112); 114 – two right apical antennomeres and sensorium, ventral; 115–117 – claws; 118, 119 – hind leg, anterior (118) and posterior (119); 120 – fore leg, anterior.

similar to that of a larva of a stem species of the group. The only role of this reference system is to name similarly located and presumably homologous sensillae in larvae of related species. Phylogenetic polarisation of differences in chaetotaxy should be done by using an outgroup as in the analysis of Trechitae (Carabidae) larvae (Grebennikov

& Maddison, 2004). Consequently, the absence of a given sensilla does not necessarily imply that this is an apomorphic character, as is sometimes believed.

Establishing a reference system for chaetotaxy requires a relatively large number of representatives of a given group to be studied in order to find the optimal set of sen-

sillae for designation. The optimal criteria imply that this reference system should be relatively similar to the larval chaetotaxy patterns of the majority of species within the group. For Archostemata such an approach is currently hardly possible due to the scarcity of material. In terms of the presence versus absence of sensillae, there are no significant differences between the larvae of the three species studied. The location of sensillae in *Micromalthus*, however, differs markedly from that in *Distocupes* and *Priacma*, and, therefore, it is plausible that the Archostemata larval chaetotaxy reference system will be more similar to that found in the latter two taxa.

#### CONCLUDING REMARKS

Larval morphology strongly suggests that Archostemata is a natural group and that the bizarre *Micromalthus* is indeed a member. Chaetotaxy of first instar archostematan larvae proved to be an informative source of characters, however more larvae have to be studied. Special efforts should be directed towards obtaining larvae of *Tetraphalerus* in South America, *Sikhotealinia* in Russian Far East and *Crowsoniella* in Italy. This might not be an easy task, since for the latter two taxa the only material are type series, and in the case of *Sikhotealinia* it is a single beetle.

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#### REFERENCES

ALARIE Y. & BALKE M. 1999: A study of the larva of Carabdytes upin Balke, Hendrich and Wewalka (Coleoptera: Adephaga: Dytiscidae), with comments on the phylogeny of the Colymbetinae. *Coleopt. Bull.* **53**: 146–154.

ASHE J.S. & WATROUS L.E. 1984: Larval chaetotaxy of Aleocharinae (Staphylinoidea) based on a description of Atheta coriarica Kraatz. *Coleopt. Bull.* **38**: 165–179.

ATKINS M.D. 1963: The Cupedidae of the world. *Can. Entomol.* **95**: 140–162.

BARBER H.S. 1913a: Observations on the life history of *Micromalthus debilis* Lec. (Coleoptera). *Proc. Entomol. Soc. Wash.* **15**: 31–38, pl. 3.

BARBER H.S. 1913b: The remarkable life-history of a new family (Micromalthidae) of beetles. *Proc. Biol. Soc. Wash.* **26**: 185–190.

BARLET J. 1996: Quelques précisions au sujet de *Micromalthus* (Insecta Coleoptera). *Bull. Soc. R. Sci. Liège* **65**: 373–378.

BEUTEL R.G. & HAAS F. 2000: Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* **16**: 103–141.

BEUTEL R.G. & HÖRNSCHEMEYER T. 2002a: Larval morphology and phylogenetic position of *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae). *Syst. Entomol.* **27**: 169–190.

BEUTEL R.G. & HÖRNSCHEMEYER T. 2002b: Description of the larva of *Rhysodius raffrayi* (Coleoptera: Archostemata), with phylogenetic and functional implications. *Eur. J. Entomol.* **99**: 53–66.

BOUSQUET Y. 1993: On Thomas Say's entomological publications printed in New Harmony, Indiana. *Entomol. News* **104**(1): 1–14.

BOUSQUET Y. & GOULET H. 1984: Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Can. J. Zoology* **62**: 573–588.

BÖVING A.G. 1929: On the classification of beetles according to larval characters. *Bull. Brooklyn Entomol. Soc.* **24**: 55–80.

BÖVING A.G. & CRAIGHEAD F.C. 1931: *An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera*. Brooklyn Entomological Society, Brooklyn, N.Y.C., 351 pp.

CROWSON R.A. 1955: *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd and Co., London, 187 pp.

CROWSON R.A. 1976: The systematic position and implications of *Crowsoniella*. *Boll. Mus. Civ. Stor. Nat. Verona* **2**[1975]: 459–463.

CROWSON R.A. 1981: *The Biology of Coleoptera*. John Murray, London, 802 pp.

COSTA C., VANIN S.A. & CASARI-CHEN S.A. 1988: *Larvas de Coleoptera do Brasil*. Museu de Zoologia, Universidade de São Paulo, São Paulo, 282 pp., 165 pl.

DELGADO J.A. & SOLER A.G. 1996: Morphology and chaetotaxy of the first-instar larva of *Hydraena* (Phoehydraena) *hernandoi* Fresneda and Lagar (Hydraenidae). *Koleopt. Rdsch.* **66**: 147–154.

DELGADO J.A. & SOLER A.G. 1997: Morphology and chaetotaxy of larval Hydraenidae (Coleoptera) I: genus *Limnebius* Leach, 1815 based on a description of *Limnebius cordobanus* d'Orchymont. *Aquat. Insects* **19**: 37–49.

FORBES W.T.M. 1926: The wing-folding pattern of the Coleoptera. *J. N. Y. Entomol. Soc.* **34**: 42–115, 7–18 pls.

FUKUDA A. 1938: Description of the larva and pupa of *Cupes clathratus*. *Trans. Nat. Hist. Soc. Formosa* **28**: 390–393.

GREBENNIKOV V.V. & BEUTEL R.G. 2002: Morphology of the minute larva of *Ptinella tenella*, with special reference to effects of miniaturisation and the systematic position of Ptiliidae (Coleoptera: Staphylinoidea). *Arthropod Struct. Dev.* **31**: 157–172.

GREBENNIKOV V.V. & MADDISON D.R. 2004: Phylogenetic analysis of Trechitae (Coleoptera: Carabidae) based on larval morphology, with description of first-instar *Phrypeus* and a key to genera. *Syst. Entomol.* **29**: (in press).

HENNIG W. 1981: *Insect Phylogeny*. John Wiley & Sons, Chichester, 514 pp.

KILLIAN A. 1998: Morphology and phylogeny of the larval stages of the tribe Agathidiini (Coleoptera: Leiodidae: Leiodinae). *Ann. Zool. Warsz.* **48**: 125–220.

KIREJTSHUK A.G. 1999: *Sikhotealinia zhiltzovae* (Lafer, 1996) – recent representative of the Jurassic coleopterous fauna (Coleoptera, Archostemata, Jurodidae). In Ryss A.Y. & Sinev S.Y. (eds): *Zoological Sessions (Annual Reports 1998). Proceedings of the Zoological Institute of Russian Academy of Sciences* **281**: 21–26 (in Russian).

KOVARIK P.W. & PASSOA S. 1993: Chaetotaxy of larval Histeridae (Coleoptera: Hydrophiloidea) based on a description of

- Onthophilus nodatus* LeConte. *Ann. Entomol. Soc. Am.* **86**: 560–576.
- KUKALOVÁ-PECK J. & LAWRENCE J.F. 1993: Evolution of the hind wing in Coleoptera. *Can. Entomol.* **125**: 181–258.
- LAFER G.SH. 1996: Family Sikhotealiniidae. In Ler P.A. (ed.): *Opredelitel nasekomikh dal'nego vostoka Rossii [Key to the Insects of the Russian Far East]*. Vol. III. Part 3. Dal'nauka, Vladivostok, pp. 390–396.
- LAWRENCE J.F. 1982: Coleoptera. In Parker S. (ed.): *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York, pp. 482–553.
- LAWRENCE J.F. 1991: Order Coleoptera (general discussion, family key, various family treatments). In Stehr F.W. (ed.): *Immature Insects*. Vol. 2. Kendall/Hunt, Dubuque, Iowa, pp. 144–658.
- LAWRENCE J.F. 1999: The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. *Invertebr. Tax.* **13**: 369–390.
- LAWRENCE J.F., HASTINGS A.M., DALLWITZ M.J., PAINE T.A. & ZURCHER E.J. 1999: Beetle larvae of the World: descriptions, illustrations, identification, and information retrieval for families and sub-families. CD-ROM, Version 1.1 for MS-Windows. CSIRO Publishing, Melbourne.
- LAWRENCE J.F. & NEWTON A.F. 1982: Evolution and classification of beetles. *Annu. Rev. Ecol. Syst.* **13**: 261–290.
- LAWRENCE J.F. & NEWTON A.F. 1995: Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In Pakaluk J. & Ślipiński S.A. (eds): *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Vol. 2. Muzeum i Instytut Zoologii PAN, Warsaw, pp. 779–1006.
- MIYATAKE M. 1985: Notes on the genus *Tenomerga* of Japan (Coleoptera: Cupedidae). *Trans. Shikoku Entomol. Soc.* **17**(1–2): 21–26.
- MIYATAKE M. 1986: A new species of *Tenomerga* (Coleoptera: Cupedidae) from Yakushima Island, southwest Japan. In Uéno S.-I. (ed.): *Entomological Papers Presented to Yoshihiko Kurosawa on the Occasion of his Retirement*. Coleopterists' Association of Japan, Tokyo, pp. 111–114.
- NEBOISS A. 1968: Larva and pupa of *Cupes varians* Lea, and some observations on its biology. *Mem. Nat. Mus. Victoria* **28**: 17–19, pl. 7.
- NEBOISS A. 1984: Reclassification of *Cupes* Fabricius (s. lat.), with descriptions of new genera and species (Cupedidae: Coleoptera). *Syst. Entomol.* **9**: 443–477.
- NEBOISS A. 1987: A new species of *Adinolepis* Neboiss from Western Australia (Cupedidae: Coleoptera). *Rec. West. Austr. Mus.* **13**: 323–325.
- NEBOISS A. 1989: New species of Archostemata (Coleoptera: Ommatidae: Cupedidae). *Rev. Fr. Entomol. (N.S.)* **11**(3): 109–115.
- PACE R. 1976: An exceptional endogeous beetle: *Crowsoniella relictata* n. gen. n. sp. of Archostemata Tetraphaleridae from central Italy. *Boll. Mus. Civ. Stor. Nat. Verona* **2**[1975]: 445–458.
- PETERSON A. 1960: *Larvae of Insects. An Introduction to Nearctic Species. Part 2. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera*. Columbus, Ohio, published by the author, 416 pp.
- PHILIPS T.K. & YOUNG D.K. 2000: Micromalthidae Barber, 1913. In Arnett R.H. & Thomas M.C. (eds): *American Beetles*. Vol. 1. CRC Press, Boca Raton, pp. 22–23.
- POLLOCK D.A. & NORMARK B.B. 2002: The life cycle of *Micromalthus debilis* LeConte (1878) (Coleoptera: Archostemata: Micromalthidae): historical review and evolutionary perspective. *J. Zool. Syst. Evol. Res.* **40**: 105–112.
- PONOMARENKO A.G. 1969: Evolution of archostematan beetles. *Trudy Paleontol. Inst.* **125**: 1–235 [in Russian].
- PONOMARENKO A.G. 1995: The geological history of beetles. In Pakaluk J. & Ślipiński S.A. (eds): *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Vol. 1. Muzeum i Instytut Zoologii PAN, Warsaw, pp. 155–171.
- PRINGLE J.A. 1938: A contribution to the knowledge of *Micromalthus debilis* LeC. (Coleoptera). *Trans. R. Entomol. Soc. Lond.* **87**: 271–286.
- ROSS D.A. & POTHECARY D.D. 1970: Notes on adults, eggs, and first-instar larvae of *Priacma serrata* (Coleoptera: Cupedidae). *Can. Entomol.* **102**: 346–348.
- SCOTT A.C. 1936: Haploidy and aberrant spermatogenesis in a coleopteran, *Micromalthus debilis* LeConte. *J. Morphol.* **59**: 485–515.
- SCOTT A.C. 1938: Paedogenesis in the Coleoptera. *Z. Morphol. Ökol. Tiere* **33**: 633–653.
- SCOTT A.C. 1941: Reversal of sex production in *Micromalthus*. *Biol. Bull.* **81**: 420–431.
- THAYER M.K. 2000: *Glypholoma* larvae at last: phylogenetic implications for basal Staphylinidae? (Coleoptera: Staphylinidae: Glypholomatinae). *Invertebr. Tax.* **14**: 741–754.
- VULCANO M.A. & PEREIRA F.S. 1975: Cupesidae (Coleoptera). *Arq. Inst. Biol. São Paulo* **42**: 31–68.
- WHEELER Q.D. 1986: Revision of the genera of Lymexylidae (Coleoptera: Cucujiformia). *Bull. Am. Mus. Nat. Hist.* **183**(2): 113–210.
- WHEELER Q.D. 1990: Morphology and ontogeny of postembryonic larval *Agathidium* and *Anisotoma* (Coleoptera: Leiodiidae). *Am. Mus. Novit.* **2986**: 1–46.
- YOUNG D.K. 2000: Cupedidae Laporte, 1836. In Arnett R.H. & Thomas M.C. (eds): *American Beetles*. Vol. 1. CRC Press, Boca Raton, pp. 19–21.

## APPENDIX

Checklist, present classification and distribution of extant archostematan species (based on Atkins, 1963; Vulcano & Pereira, 1975; Miyatake, 1985, 1986; Neboiss, 1984, 1987, 1989).

### Family Ommatidae Lawrence, 1982

Subfamily Tetraphalerinae Crowson, 1962

Genus *Tetraphalerus* Waterhouse, 1901

*Tetraphalerus bruchi* Heller, 1913 (Argentina)

*Tetraphalerus wagneri* Waterhouse, 1901 (Bolivia, Brazil and Argentina)

Subfamily Ommatinae Sharp and Muir, 1912

Genus *Omma* Newman, 1839

*Omma mastersi* Macleay, 1871 (Eastern Australia)

*Omma rutherfordi* Lawrence, 1999 (South-western Australia)

*Omma sagitta* Neboiss, 1989 (South-western Australia)

*Omma stanleyi* Newman, 1839 (Eastern Australia)

### Crowsoniellidae Iablokoff-Khnzorian, 1983

Genus *Crowsoniella* Pace, 1976

*Crowsoniella relictata* Pace, 1976 (Central Italy)

### Micromalthidae Barber, 1913

Genus *Micromalthus* LeConte, 1878

*Micromalthus debilis* LeConte, 1878 (originally North America; introduced in many countries including Brazil, Hong Kong, Austria, South Africa)

### Cupedidae Laporte, 1836

Genus *Priacma* LeConte, 1874

- Priacma serrata* LeConte, 1861 (Northwestern part of North America)
- Genus *Adinolepis* Neboiss, 1984
- Adinolepis apodema* Neboiss, 1987 (Western Australia)
- Adinolepis eumana* (Neboiss, 1960) (Eastern Australia)
- Adinolepis mathesonae* (Neboiss, 1960) (Eastern Australia)
- Adinolepis scalena* Neboiss, 1984 (Eastern Australia)
- Adinolepis youanga* (Neboiss, 1960) (Eastern Australia)
- Genus *Ascioplaga* Neboiss, 1984
- Ascioplaga mimeta* Neboiss, 1984 (New Caledonia)
- Ascioplaga sciasma* Neboiss, 1984 (New Caledonia)
- Genus *Cupes* Fabricius, 1801
- Cupes capitatus* Fabricius, 1801 (Eastern USA and Canada)
- Genus *Distocupes* Neboiss, 1984
- Distocupes varians* (Lea, 1902) (Eastern Australia, Tasmania)
- Genus *Paracupes* Kolbe, 1898
- Paracupes ascius* Neboiss, 1989 (Ecuador)
- Paracupes brasiliensis* Kolbe, 1898 (Brazil)
- Genus *Prolixocupes* Neboiss, 1960
- Prolixocupes latreillei* (Solier, 1849) (Western South America)
- Prolixocupes lobiceps* (LeConte, 1874) (South-western USA)
- Genus *Rhipsideigma* Neboiss, 1984
- Rhipsideigma adjuncta* Neboiss, 1984 (Madagascar)
- Rhipsideigma anosibensa* Neboiss, 1989 (Madagascar)
- Rhipsideigma cretaceotincta* (Kolbe, 1897) (Eastern Africa)
- Rhipsideigma lugubris* (Fairmaire, 1895) (Madagascar)
- Rhipsideigma raffrayi* (Fairmaire, 1884) (Northern Madagascar)
- Genus *Tenomerga* Neboiss, 1984
- Tenomerga anguliscutis* (Kolbe, 1886) (South-eastern Asia)
- Tenomerga cinerea* (Say, 1831) (Eastern USA and Canada)
- Tenomerga favella* Neboiss, 1984 (Borneo)
- Tenomerga japonica* (Tamanuki, 1928) (Japan, ?China)
- Tenomerga kapnodes* Neboiss, 1984 (Papua New Guinea)
- Tenomerga kurosawai* Miyatake, 1986 (Southern Japan)
- Tenomerga leucophaea* (Newman, 1839) (South Africa)
- Tenomerga moultoni* (Gestro, 1910) (Sarawak)
- Tenomerga mucida* (Chevrolat, 1829) (Russian Far East, Japan, Hawaii, Philippines)
- Tenomerga sibyllae* (Klapperich, 1950) (South-East China)
- Tenomerga trabecula* Neboiss, 1984 (Eastern China and Taiwan)
- Tenomerga yamato* Miyatake, 1985 (Japan)
- Incertae Sedis: **Jurodidae Ponomarenko, 1985** (= **Sikhotealiniidae Lafer, 1996**) (see: Kirejtshuk, 1999)
- Genus *Sikhotealinia* Lafer, 1996
- Sikhotealinia zhiltzovae* Lafer, 1996 (Russian Far East)

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