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

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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 endogeain beetles from Central Italy ( Pace, 1976; Crowson, 1976). Another family, the Sikkotealiniidae, 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 monogenic 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 &raighead, 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 monogenic Priacminae erected for Priacma serrata LeConte, 1861 from North America. First instar larvae of this species were reared ex ovo and described by Ross & Potheary (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 taxa is provided.
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. Śliwiński)
- CAS – California Academy of Sciences, San Francisco, USA (D.H. Kavanaugh, R. Brett)
- ECR – Institute of Entomology, České Budějovice, Czech Republic (P. Švacha)
- MVMA – Museum of Victoria, Melbourne, Australia (C. McPhee)
- NHML – The Natural History Museum, London, UK (S. Hine, M. Kerley)
- 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 glycine, 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.


**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, Distocopes). First instar larvae of *Rhipsideigma* and *Onnma* are unknown. Lateral sides of cranium with or without single stemma. Egg-bursters absent. Frontoclypeal suture not detectable. Body segments similar in shape, with (Distocopes) 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 larva**: Body cerambycid (less so in *Onnma*), 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. Hyposcutal 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 sharp, markedly sclerotized, nearly symmetrical, with relatively wide bases. Mandibles with three apical teeth. Incisor area without teeth or, rarely, with retinaculum (*Onnma*). Stridulatory teeth, prostheca, penicillus, dorsal and ventral carinae, and accessory ventral process absent. Mola markedly developed. Ventral mouthparts slightly retracted. Maxilla with transversely oriented carido and relatively wide antero-mesally directed stipes. Cardo divided into sclerotized mesal and membranous lateral parts. Two basal maxillary palpomere 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 *Distocopes* 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) ........................................... 2
   – 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 ........................................... 2
   – 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 Australia .......................... 2

FAMILY OMMATIDIAE

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 sensillum 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 MICROMALTHIDIAE

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 sensillum 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-
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 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.
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 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).
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 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.
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 & Pothecary (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 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).
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
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; pro-thorax (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 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).
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.
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


*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

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

**Genus Rhipsideigma Neboiss, 1984**


**DISCUSSION**

**Monophyly of Archostemata**

Beutel & Hörschemeyer (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
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 posterom edian 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 (*Onnea, Micro- malthus*; 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 & Hönschemeyer (2002a), but the inclusion of the lyneyxilid genus *Hylecoetus* Latreille, 1806 in the outgroup 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 *Onnea*; Figs 36, 37), this character was interpreted by Beutel & Hönschemeyer (2002a) as a synapomorphy for Cupedidae and Micro- malthidae); (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 palpmere 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 Neuroptera 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,
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 & Hörnschemeyer, 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; Kukalová-Peck & Lawrence, 1993; Beutel & Haas, 2000). However, Baehr (in: Hennig, 1981: 308) considered this genus to be a simplified member of Cantharoida 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 & Hörnschemeyer (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 & Hörnschemeyer (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 & Hörnschemeyer, 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
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*, *Rhipsideigma* 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).
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 metastomum). 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 sensilla 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 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.
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 sensilla 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 *Tetrapteralus* 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 majority are types series, and in the case of *Sikhotealinia* it is a single beetle.

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APPENDIX


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
Omna mastersi Macleay, 1871 (Eastern Australia)
Omna rutherfordi Lawrence, 1999 (South-western Australia)
Omna sagitta Neboiss, 1989 (South-western Australia)
Omna stanleysi Newman, 1839 (Eastern Australia)

Crawsoniellidae Iablokoff-Khnzorian, 1983
Genus Crawsoniella Pace, 1976
Crawsoniella reticata 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 mathesonea (Neboiss, 1960) (Eastern Australia)
  Adinolepis scalena Neboiss, 1984 (Eastern Australia)
  Adinolepis youanga (Neboiss, 1960) (Eastern Australia)
Genus Ascioiplaga Neboiss, 1984
  Ascioiplaga mimeta Neboiss, 1984 (New Caledonia)
  Ascioiplaga sciama 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 la treillei (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 (Sey, 1831) (Eastern USA and Canada)
  Tenomerga favela Neboiss, 1984 (Borneo)
  Tenomerga japonica (Tamanuki, 1928) (Japan, ?China)
  Tenomerga kapnodes Neboiss, 1984 (Papua New Guinea)
  Tenomerga kuroswai Miyatake, 1986 (Southern Japan)
  Tenomerga leucophaca (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)
Genus Sikhotealinia Lafer, 1996
  Sikhotealinia zhilzovae Lafer, 1996 (Russian Far East)

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