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Larval morphology and phylogenetic position of *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae)

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Abstract. External and internal structures of the cerambycoid and triungulin larvae of *Micromalthus debilis* are described and compared to features found in larvae of other groups of Coleoptera. The morphological data are evaluated with respect to the systematic position of Micromalthidae. A cladistic analysis was carried out with fifty characters. Micromalthidae are not closely related to Lymexylidae (Polyphaga: Cucujiformia) but belong to Archostemata, which is confirmed as a monophyletic unit. Micromalthidae are specialized in terms of morphology and life cycle and are characterized by a considerable number of larval autapomorphies. Their sister-group relationship with Cupedidae is supported by several apomorphic features, which are probably correlated with xylobiontic habits: head transverse and strongly rounded laterally, absence of stemmata, shortened antennae, presence of sternal asperities and presence of eversible lobes of segment IX. Cupedidae is monophyletic and *Priamca* is the sister group of the remaining genera of Cupedidae included in the analysis. A closer relationship between *Tenomerga* and *Rhipsideigma* is supported by several larval synapomorphies. The ancestral life style of larvae of Archostemata was probably xylobiontic. This is suggested by derived groundplan features of the suborder, which are also found in larvae of non-related, wood-associated families.

Introduction

Micromalthus debilis LeConte is probably the most spectacular beetle species in terms of life cycle and morphology. It is the only known species of Micromalthidae and has a natural range restricted to northeastern North America (Lawrence, 1991). However, it was apparently introduced with timber to different parts of the world, such as Burgenland (southeastern Austria) (Jäch & Komarek, 2000), British Columbia, New Mexico, Cuba, Brazil (Minas Gerais, São Paulo), South Africa (Witwatersrand, Johannesburg), Hawaii (Oahu), Hong Kong and Gibraltar (Lawrence, 1991). In contrast to all other known micromalthid triungulins, those found in Hong Kong possess a pair of stemmata (Marshall & Thornton, 1963) and may therefore belong to a separate species. Differences between adults from South Africa and North America were pointed out by Patterson (1938). However, they were not considered as sufficient evidence for description of a new species.

The highly complex life cycle of *M. debilis* is characterized by active, first-instar triungulins, different types of larviform reproductive stages, vivipary and parthenogenesis (Barber, 1913a,b; Pringle, 1938; Lawrence, 1991). This reproductive system is unparalleled in Coleoptera and other groups of insects.

The systematic position of Micromalthidae has been the subject of a long controversy. The species was described by LeConte (1878), who emphasized that the adults (Fig. 1) are 'feeble and ill developed'. He included it in Lymexylidae. This was supported by Hubbard (1878), who provided the first larval description and pointed out similarities in antennae and mouthparts of micromalthid and lymexylid larvae. A close relationship with Lymexylidae was also suggested by Jeannel & Paulian (1949), whereas affinities with Adephaga were discussed by van Emden (1932). Micromalthidae was placed with Cupedidae (Archostemata) based on the wing venation and larval mouthparts by Forbes (1926)

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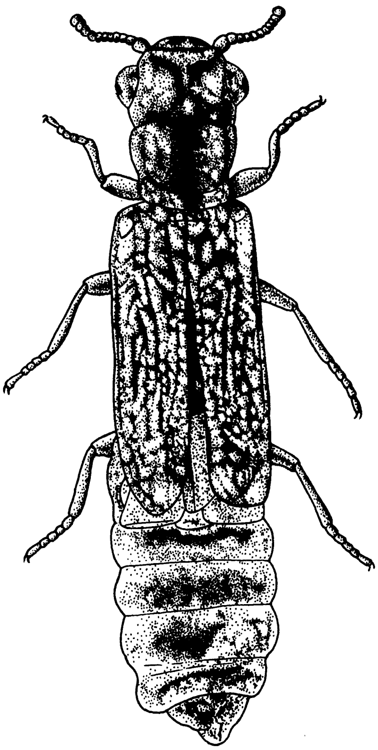

Fig. 1. *Micromalthus debilis*: adult habitus. Specimen from Austria (Burgenland), drawn after photograph, no scale available. Length of specimen approximately 2.5 mm.

and Böving & Craighead (1931), respectively. This view was adopted by Crowson (1955). Machatschke (1962) and Hennig (1969) rejected this placement, and the family was tentatively transferred to Cantharoidea by Arnett (1968). Archostematan affinities were also clearly rejected by Klausnitzer (1975): 'die Archostemata im Sinne Crowson's sind zweifellos paraphyletisch'. The concept of Micromalthidae as an archostematan family was again strongly supported in several systematic studies (e.g. Lawrence, 1982; Lawrence & Newton, 1982, 1995; Kukalová-Peck & Lawrence, 1993). Nevertheless, Barlet (1996) decidedly advocated a position close to Lymexylidae (Polyphaga: Cucujiformia) based on an examination of thoracic features of adults.

If *Micromalthus* belongs to the oldest suborder of Coleoptera (Lawrence, 1999), a profound knowledge of the morphology of its immature stages is important for understanding the evolution of beetles. Nevertheless, little information on micromalthid, cupedid and ommatid larvae is presently available. Larvae of species of Tetraphalerinae, Crowsoniellidae and several genera of Cupedidae are unknown. The descriptions of larvae of *M. debilis* (Hubbard, 1878; Pringle, 1938; Costa *et al.*, 1988), *Omma* sp. (one known specimen; Lawrence, 1999), *Tenomerga cinereus* (Say) (Böving, 1929; Böving & Craighead, 1931), *T. mucida* (Chevrolat) (Fukuda, 1938), *Distocupes varians* (Lea) (Neboiss, 1968) and first-instar larvae of *Priacma serrata* (LeConte) (Ross & Pothecary, 1970) are concise and largely or completely restricted to external structures.

The main purpose of this study was to give a detailed account of the larval morphology of *M. debilis*. Cladistic analyses were carried out in order to clarify the archostematan affinities of Micromalthidae and to reconstruct the ancestral life style of this suborder. Features of archostematan larvae are compared to those of immature stages of other xylobiontic groups, and correlations of structural features to specialized wood-boring habits are examined.

Materials and methods

Material and morphology

Larvae of *M. debilis* (one first-instar triungulin larva, one second-instar cerambycoid larva, seven third-instar cerambycoid larvae, two damaged fourth-instar cerambycoid larvae) were collected from wood in the laboratory and fixed in Bouin's solution. The body segments of the larvae were less well preserved than the head. The triungulin and two third-instar cerambycoid larvae were imbedded in Historesin medium, cut into 3–5 μm sections with a rotation microtome (Microm GmbH, Walldorf, Germany) and stained with methylene-blue and acid fuchsin. Drawings were made using an ocular grid or a camera lucida (cross-sections). For scanning electron microscopy, two third-instar cerambycoid larvae were cleaned with ultrasonic sound, critical-point dried and coated with gold.

The concept of the order and families follows Lawrence & Newton (1995). von Kéler's (1963) nomenclature for muscles is used in the text, and the corresponding numbers are used in the illustrations. The following material was examined.

Megaloptera, Sialidae. Larvae: *Sialis* sp. (fixed in FAE = formol-ethanol-acetic acid; diss. = dissection). Adults: *Sialis lutaria* (Linnaeus) (FAE; diss.).

Archostemata, Micromalthidae. Larvae: *M. debilis* (Bouin's solution, micr. = microtome sections, SEM) (from decaying wood, collected in south-central Wisconsin by D. K. Young; material deposited in collection of R.G.B). Adults: *M. debilis* (dried, SEM).

Cupedidae. Larvae: *Rhipsideigma raffrayi* Neboiss (Pampel's fluid, ethanol), *Tenomerga cinereus* (Westwood) (ethanol; examined at the Australian National Insect Collection, Canberra = ANIC), *Distocupes varians* (Lea) (ethanol, micr.). Adults: *Priacma serrata* LeConte (diss., micr., SEM), *Prolixocupes latreillei* (Solier) (dried), *Distocupes varians* (dried, SEM).

Ommatidae. Larvae: *Omma* sp. (ethanol; at ANIC). Adults: *Omma stanleyi* Newman (diss.; SEM), *Tetraphalerus* sp. (dried).

Adephaga, Trachypachidae. Larvae and adults: *Trachypachus holmbergi* Mannerheim (FAE, diss., micr., SEM).

Myxophaga, Torridincolidae. Larvae and adults: *Satonius kurosawai* Satô (ethanol, micr., SEM).

Polyphaga, Lymexylidae. Larvae and adults: *Hylecoetus* sp. (FAE, micr.). Adults: *Hylecoetus* sp. (Bouin's solution, diss.), *Lymexylon navale* (Linnaeus) (Bouin's solution, diss.).

Coccinellidae. Larvae and adults: *Coccinella septempunctata* Linnaeus (FAE, micr.).

Melandryidae. Larvae: *Orchesia* sp. (FAE, micr., SEM).

Cladistic analysis

Most parsimonious cladograms were generated with PAUP version 3.1 (Swofford, 1991). Branch and bound search was applied (thirteen taxa and fifty characters; Appendix 1: data matrix). Analysis of character evolution was conducted using MacClade version 3 (Maddison & Maddison, 1992). *Sialis* sp. (larva), *Sialis lutaria* (adults) (Megaloptera), *Trachypachus holmbergi* (Adephaga), *Satonius kurosawai* (Myxophaga), *Hylecoetus* sp. and *Coccinella septempunctata* (Polyphaga) were used as outgroup taxa. The outgroup taxa were treated as all other groups in the analysis (simultaneous analysis; Nixon & Carpenter, 1993). All characters were weighted equally and not ordered.

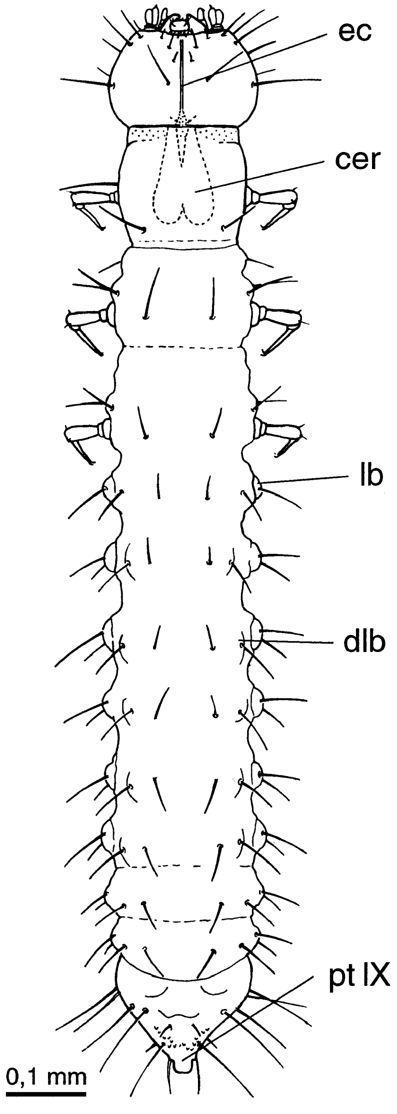

Fig. 2. *Micromalthus debilis*: triungulin larva, dorsal view. cer = cerebrum, ec = endocarina, dlb = dorsolateral bulge, lb = lateral bulge, pt IX = process of tergum IX.

Morphological observations

Cerambycoid larvae are described in detail from specimens prepared for scanning electron microscopy (SEM), microtome sections and dissection. A more concise description of the triungulin or caraboid larva is given, mainly pointing out differences with subsequent stages and with the description presented by Costa *et al.* (1988).

Cerambycoid larva (third instar)

General appearance. Length of larva 2.7–3.3 mm. The head is of a light brown colour and markedly sclerotized. The cuticle of the thorax and abdomen is unpigmented except for the tergum and sternum of segment IX. The body is slender and elongate, parallel-sided and cylindrical, with dorsal and ventral ampullae and lateral bulges on most segments. The thorax is shorter than the abdominal segments I–III together. Legs are absent.

Head capsule (Fig. 3). The maximum width of the head is 0.5 mm. It is prognathous and not retracted into the prothorax but connected with it by a fairly broad and thick cervical membrane (Figs 3, 5). The head capsule is distinctly broader than long, and it is broader than the protergum. It is strongly rounded laterally, and widened posteriorly. A well defined neck is absent. However, the head is strongly narrowed anterad the foramen occipitale. Distinct, triangular, posteromedian emarginations are present on the dorsal and ventral sides. The distribution of setae is shown in Fig. 3. Stemmata are absent. The labrum is not fused with the head capsule (Figs 3A, 5). The unpigmented clypeus is clearly separated from the anterior margin of the frontal area (not visible on SEM micrographs, see Figs 3, 4A). The frons is completely fused with the adjacent parts of the head capsule. The frontal and coronal sutures are absent. The median endocarina is present, unforked and nearly reaches the anterior and posterior margins of the head capsule. The ventral side of the head is shorter than the dorsal side. The maxillary grooves are deep and separated from each other by the narrow posterior part of the labium. Faintly impressed lines corresponding with high internal ridges are present posterior to the insertion of the cardo, and they enclose the gula, which is fused with the submento-mentum anteriorly and completely divided into two halves by the triangular ventromedian emargination (Figs 3B, 4B). The emargination is closed

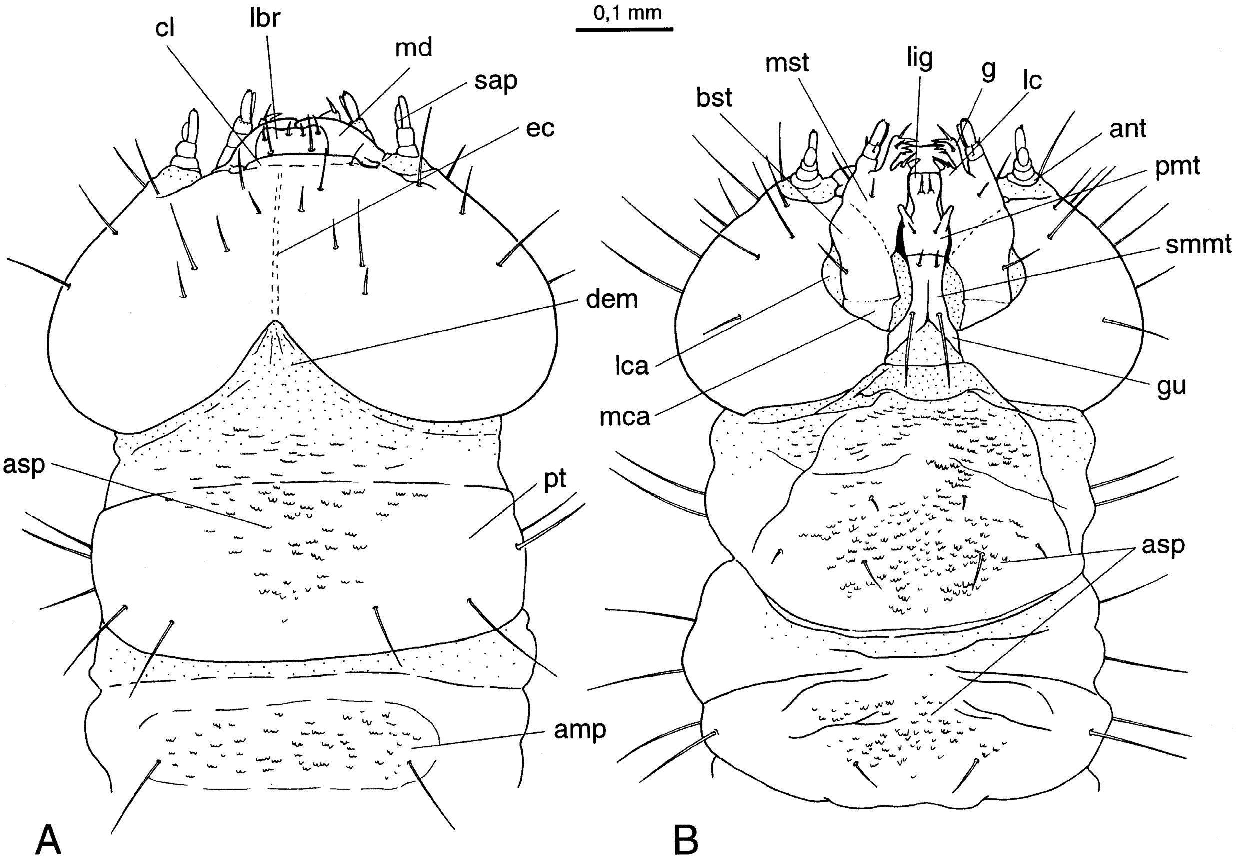

Fig. 3. *Micromalthus debilis*: head, prothorax and mesothorax of cerambycoid larva (third instar). A, Dorsal view; B, ventral view. amp = ampullae, ant = antenna, asp = asperities, bst = basistipes, cl = clypeus, dem = dorsal emargination, ec = endocarina, g = galea, gu = gula, lbr = labrum, lc = lacinia, lca = lateral part of cardo, lig = ligula, mca = mesal part of cardo, md = mandible, mst = mediostipes, pmt = prementum, pt = protergum, sap = sensorial appendage, smmt = submento-mentum.

by a triangular semi-membranous area and a posteriorly adjacent broader trapezoid membranous fold (Figs 3B, 4B).

Internal skeletal structures (Figs 5–7). The hypostomal rods are not visible externally but are represented by fairly high and strongly sclerotized internal longitudinal ridges. The gula is laterally enclosed by well developed gular ridges. They are connected with the unsclerotized posterior tentorial arms, which arise between the bases of the maxillae and the posterior part of the submento-mentum. The apical part of the posterior arms is attached to the anatomical mouth, below the attachment of the frontohypopharyngeal muscle. The tentorial bridge and the dorsal and anterior arms are absent. A strong, sclerotized transverse bar is present in the anterior head region. It separates the upper part of the maxillae from the head interior and the prementum from the posterior hypopharynx. Musculature: the gular ridges are connected with each other by a large transverse muscle with unclear homology.

Labrum (Figs 3A, 4A, 5, 6A). The roughly quadrangular labrum is connected with the anterior clypeal margin by an interior fold. It is fairly broad, moderately long and rounded laterally. The anterior margin is almost straight and strongly sclerotized (Figs 3A, 4A). The position of the labrum is horizontal in relation to the longitudinal body axis. Four distinct setae are present along the anterior margin and an additional pair posterolaterally (Fig. 4A). In cross-sections, the labrum is triangular except for the flattened anterior margin (Fig. 6A). A pair of internal paramedian sclerotizations is present on the ventral side and the ventromedian edge is sharp and strongly sclerotized (Fig. 6B). Musculature (Figs 5, 6): M 7 (M. labroepipharyngalis) absent. M 9 (M. frontoepipharyngalis) is a strong pair of muscles, parallel and very closely adjacent along the median line: origin is the posterior margin of the median endocarina and the posterodorsal part of the postoccipital ridge; insertion is medially on the posterior epipharynx by means of a tendon.

Antenna (Figs 3, 4A,B). The antennae are inserted on semi-membranous, anterolateral areas and are composed of vestigial, extremely short antennomeres I and distinct antennomeres II-IV. Antennomere II is wider than long. The penultimate antennomere is slightly longer and narrower than antennomere II; it is protracted dorsally and set with several short setae around its apical part. A large sensorial appendage is inserted ventrally on antennomere III, below antennomere IV. The latter is more than twice as long as antennomere II, parallel-sided and narrower than

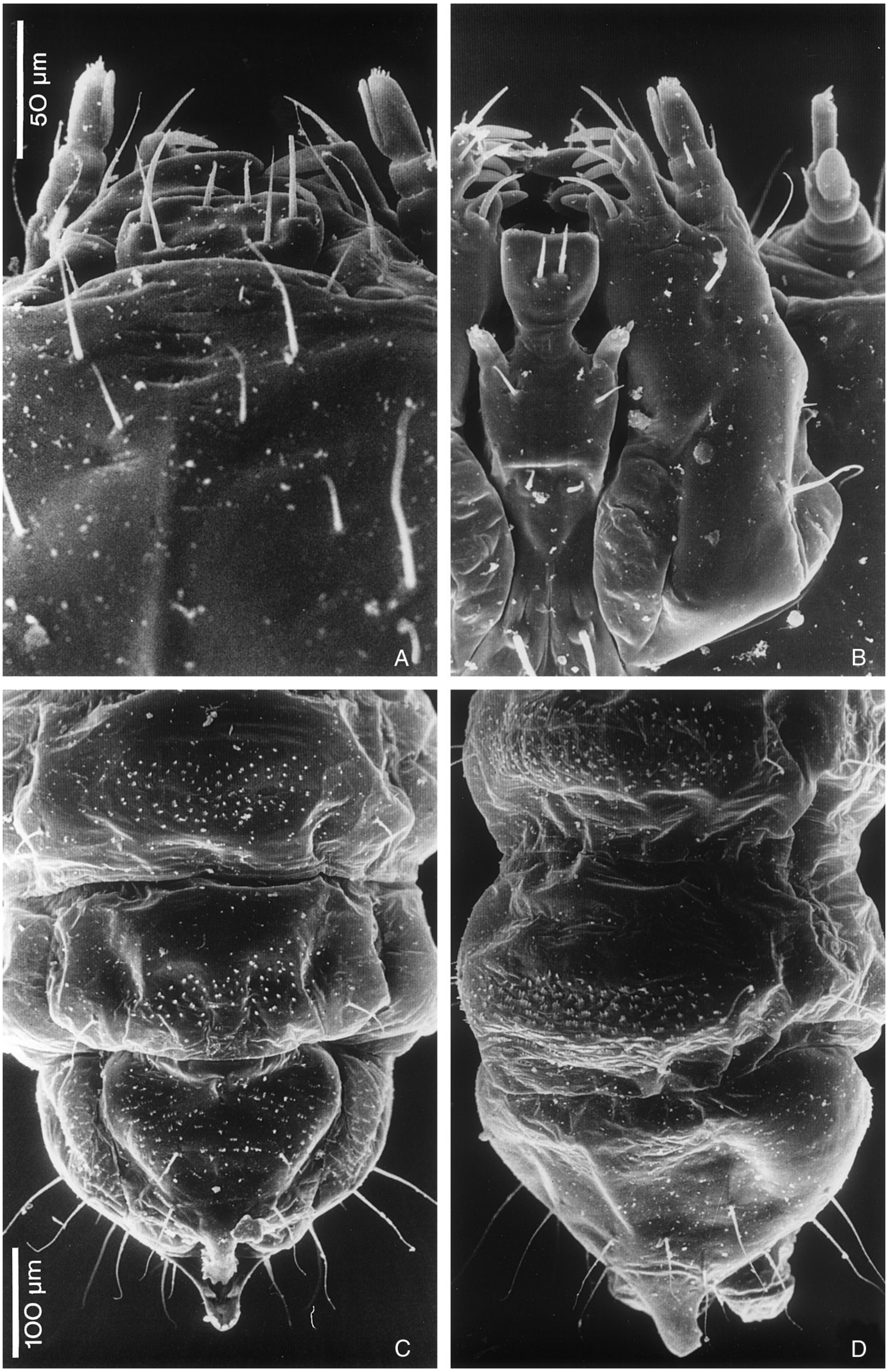

Fig. 4. *Micromalthus debilis*: third instar, SEM micrographs. A, Mouthparts, dorsal view; B, mouthparts, ventral view; C, posterior abdomen, dorsal view; D, posterior abdomen, ventral view.

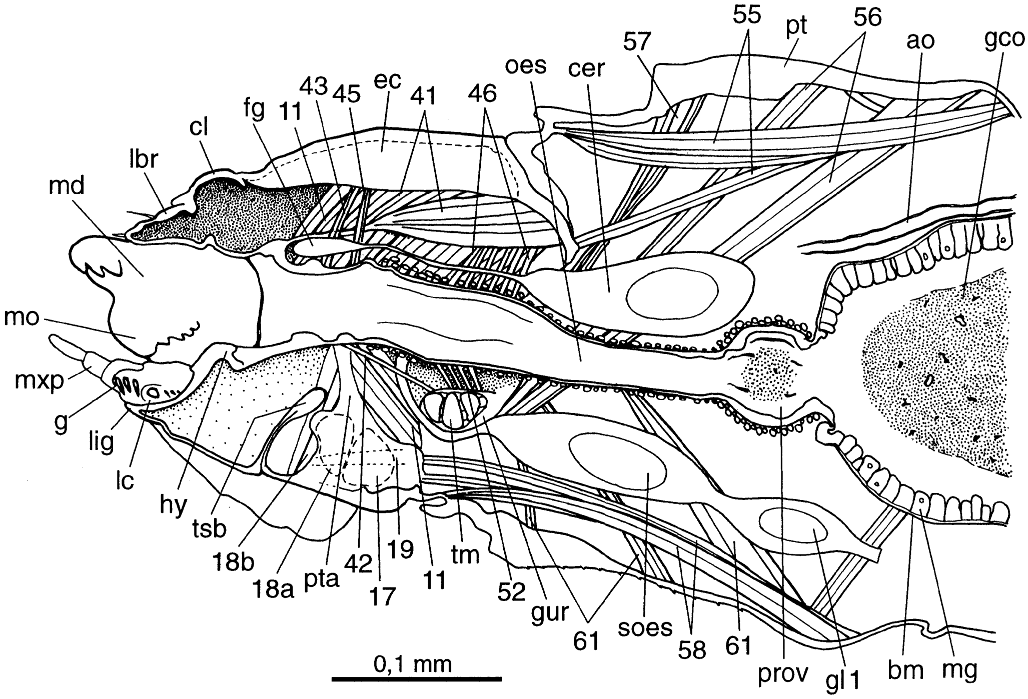

Fig. 5. *Micromalthus debilis*: cerambycoid larva, third instar, head and prothorax, sagittal section. ao = aorta, bm = basement membrane, cer = cerebrum, cl = clypeus, ec = endocarina, fg = frontal ganglion, g = galea, gco = gut contents, gl1 = prothoracic ganglion, gur = gular ridge, hy = hypopharynx, lbr = labrum, lc = lacinia, lig = ligula, md = mandible, mg = midgut, mo = mola, mxp = maxillary palp, oes = oesophagus, prov = proventriculus, pt = protergum, pta = posterior tentorial arm, soes = suboesophageal gangion, tm = transverse muscle, tsb = transv. sclerotized bar, 11 = M. craniomandibularis internus, 17 = M. tentoriocardinalis, 18 = M. tent.-stipitalis, 19 = M. craniolacinialis, 41 = M. frontohypopharyngalis, 42 = M. tentoriohypophar., 43 = M. clypeopalatalis, 45 = M. frontobuccalis anterior, 46 = M. frontobucc. posterior, 52 = M. tentoriopharyngalis, 55 = M. praephragmapostoccipitalis medialis, 56 = M. praephr.-postocc. lateralis, 57 = M. pronotopostocc. medialis, 58 = M. profurcatentorialis, 61 = M. cervicopostocc.

the sensorium. Antennomere IV bears several minute apical sensilla. Musculature (Fig. 6C): M. tentorioscapalis (M 1, 2 or 4) is the only muscle attached to the antennal base: origin on anterior frontal region; insertion on base of antennomere I.

Mandible (Figs 3A, 4A, 6). The mandibles are short and compact, with three strong apical teeth and distinctly delimited, roughly quadrangular and strongly sclerotized molae. A retinaculum and a moveable appendage are not developed. Two setae are inserted dorsolaterally. Musculature (Figs 5–7): M 11 (M. craniomandibularis internus) is the largest muscle of the head: origin on extensive parts of the dorsal, dorsolateral, lateral and ventrolateral areas of the head capsule; insertion by adductor tendon. M 12 (M. craniomandibularis externus) is moderately large: origin on the anterolateral part of the head capsule; insertion by abductor tendon.

Maxilla (Figs 3B, 4B, 5). The maxillae are inserted in a deep fossa maxillaris and are composed of cardo, stipes, galea, lacinia and a palp with three palpomeres. The cardo is divided into a short, sclerotized mesal and a semimembranous lateral part. The stipito-cardinal hinge is present but indistinct on SEM micrographs. An indistinct line divides the stipes into a proximal basistipes and a distal mediostipes. The palpifer is obsolete. The fingerlike galea is set with several setae and mesally directed, articulated spines. The lacinia bears a strong distal spine and a pediculate seta is inserted dorsally. Palpomeres I and II are fairly short. Palpomere III is about twice as long as II and bears a slender, elongate appendage. Musculature (Figs 5–7): M 15 (M. craniocardinalis) is absent. M 17 (M. tentoriocardinalis): origin on basal part of posterior tentorial arm; insertion on ventral surface of cardo. M 18 (M. tentoriostipitalis) is composed of two subcomponents, M 18a with origin on the basal part of the posterior tentorial arm, close to M 17, and M 18b with origin on the apical part of the posterior tentorial arm, which is attached to the anatomical mouth; both parts insert on the ventral stipital surface. M 19 (M. craniolacinialis): origin on head capsule, between gula and hypostomal rods; insertion dorsally on base of lacinia, without tendon. M 22, 23 (M. stipitopalpalis externus and internus) are both represented by one moderately strong bundle: origin ventrolaterally on mediostipes; insertion mesally on base of palpomere I. A strong oblique muscle connects the mesal and ventral sides of the mediostipes.

Labium (Figs 3B, 4B, 5–7). The submentum and mentum are fused and are posteriorly continuous with the medially divided gula. The submento-mentum is distinctly narrowed

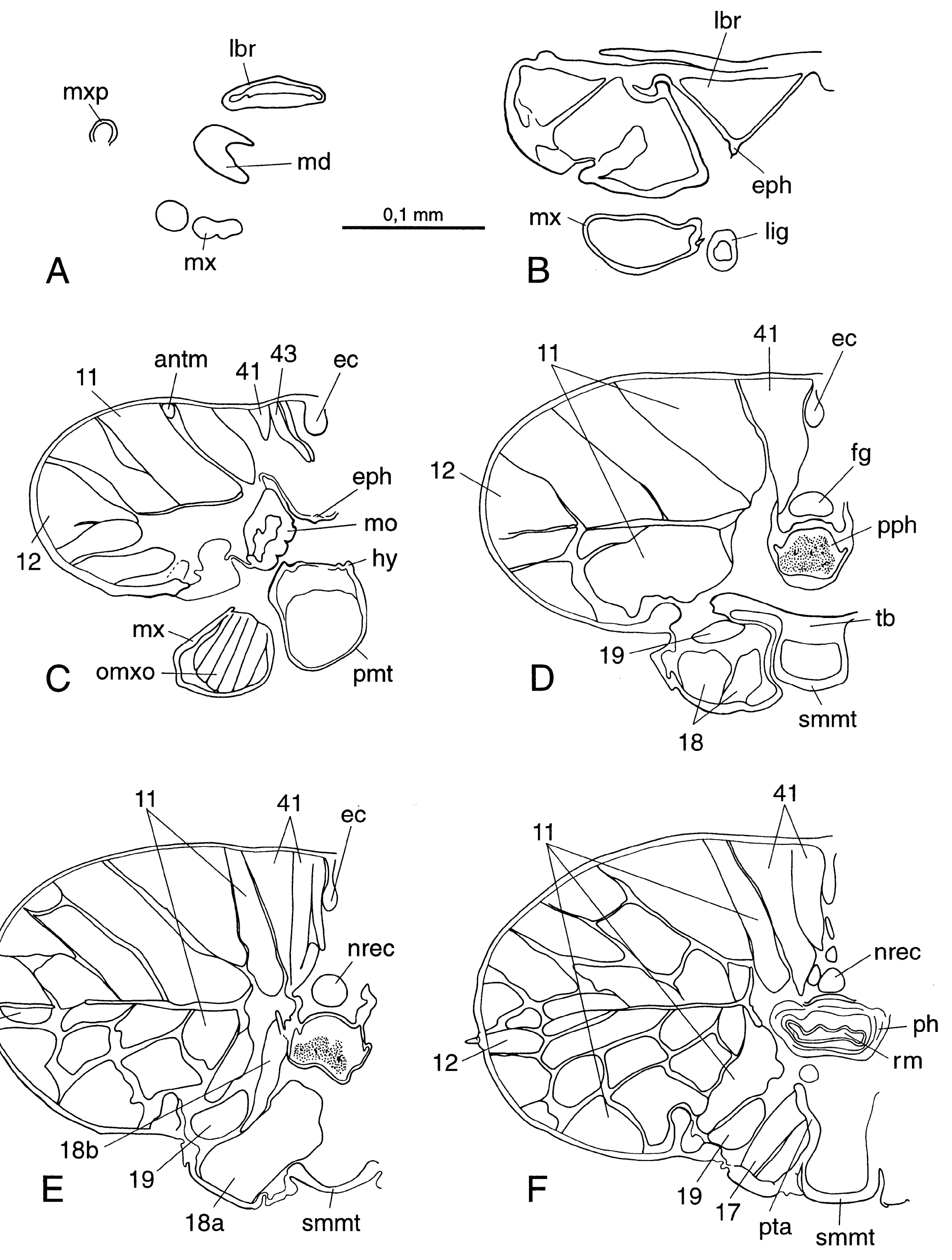

Fig. 6. *Micromalthus debilis*: cerambycoid larva, third instar, head, cross-sections. A, Anterior labral region; B, posterior labral region; C, posterior epipharyngeal region; D, anatomical mouth region; E, attachment of M. tentoriostipitalis b; F, anterior pharyngeal region. antm = antennal muscle, ec = endocarina, eph = epipharynx, fg = frontal ganglion, hy = hypopharynx, lbr = labrum, lig = ligula, md = mandible, mo = mola, mx = maxilla, mxp = maxillary palp, nrec = nervus recurrens, omo = oblique maxillary muscle, ph = pharynx, pmt = prementum, pph = prepharynx, pta = posterior tentorial arm, rm = ring muscle, smmt = submento-mentum, tsb = transverse sclerotized bar, 11 = M. craniomandibularis internus, 12 = M. craniomandibularis externus, 17 = M. tentoriocardinalis, 18a, b = M. tentoriostipitalis, 19 = M. craniolacinialis, 41 = M. frontohypopharyngalis, 43 = M. clypeopalatalis.

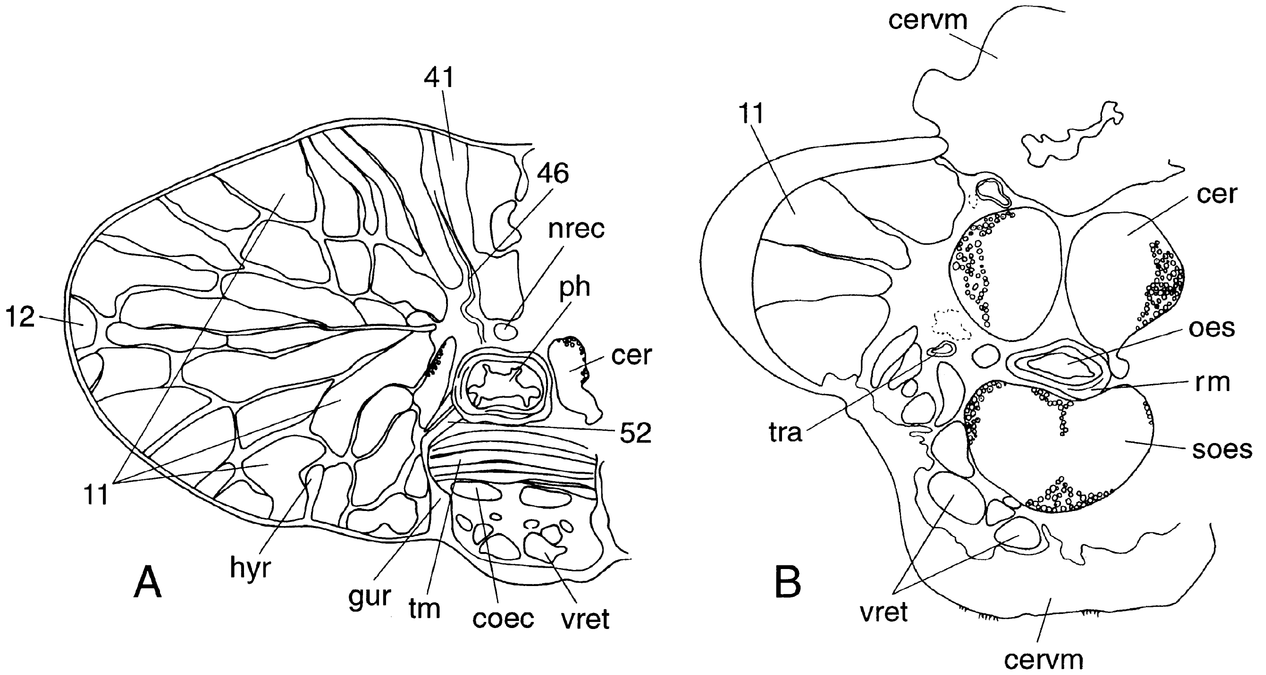

Fig. 7. *Micromalthus debilis*: cerambycoid larva, third instar (specimen 3), posterior head region, cross-sections. A, Posterior pharyngeal region; B, cervical region. cer = cerebrum, cervm = cervical membrane, coec = circumoesophageal connective, gur = gular ridges, hyr = hypostomal ridges, nrec = nervus recurrens, oes = oesophagus, ph = pharynx, rm = ring muscle, soes = suboesophageal ganglion, tm = transverse muscle, tra = trachea, vret = ventral retractors of the head, 11 = M. craniomandibularis internus, 12 = M. craniomandibularis externus, 41 = M. frontohypopharyngalis, 46 = M. frontobuccalis posterior, 52 = M. tentoriopharyngalis.

between the maxillary grooves. A pair of short setae are present on the anterior mental region and a pair of long posteriorly directed setae are present on the posterior submental part. The prementum is markedly developed. It bears a pair of short, one-segmented palps and a very strongly extended, sclerotized, wedge-shaped ligula. A pair of short setae are present proximad the palps and a pair of strong, anteriorly directed setae are present on the ventral side of the ligula. Musculature (Figs 5, 6): M. 28 (M. submentopraementalis), M 29 (M. tentoriopraementalis inferior), M 30 (M. tentoriopraementalis superior), M 34 (M. praementopalpalis ext.) and transverse muscle absent.

Epipharynx (Figs 5, 6; see also labrum). The anterior part, i.e. ventral labral wall, is described above. The intermediate part forms the dorsal wall of a short and wide preoral chamber which is ventrally delimited by the dorsal wall of the hypopharynx and laterally by the mandibular bases (Fig. 6C). The posterior part is laterally fused with the posterior hypopharynx thus forming a very short prepharyngeal tube (Fig. 6D). Musculature (Fig. 5): M 43 (M. clypeopalatalis) is composed of one bundle: origin on anterior frontal region, anterad to M. frontopharyngalis and laterad to the anterior end of the median endocarina; insertion dorsolaterally on the roof of the prepharynx. Transverse epipharyngeal muscles are absent.

Hypopharynx (Figs 5, 6). The hypopharynx is fused with the anterior part of the labium. Most parts of the dorsal side, especially the lateral edges are strongly sclerotized. Hairs, bristles or densely pubescent areas are absent. The posterior part is laterally fused with the posterior part of the epipharynx (Fig. 6; see above). Musculature (Figs 5, 6): M 41 (M. frontohypopharyngalis) is an unusually large muscle: origin on dorsal postoccipital ridge, dorsomedian part of frons and vertex, and on median endocarina; insertion on lateral edge of hypopharyngeal tube with a strong tendon. M 42 (M. tentoriohypopharyngalis) is composed of one thin bundle: origin on anterior margin of gular ridge; insertion ventral to anatomical mouth (it cannot be fully excluded that this muscle is an anteroventral pharyngeal dilator, M 50).

Pharynx (Figs 5–7). The pharynx is moderately wide and slightly flattened anteriorly. The shape of the posterior part is rather irregular in cross-section. Folds are present dorsally, laterally and ventrolaterally. Musculature (Fig. 5): M 45 (M. frontobuccalis anterior) is a moderately large bundle: origin on anterior part of frontal region, mesal to M 41 and posterior to M 43; insertion is dorsolaterally on the pharynx, immediately posterior to the anatomical mouth. M 46 (M. frontobuccalis posterior) is composed of six thin bundles: origin on posterodorsal part of head capsule, between M 41 and dorsolateral components of M 11; insertion is successively on dorsal folds of the pharynx. M 51 (M. verticopharyngalis) absent. M 52 (M. tentoriopharyngalis) is composed of four thin bundles: origin on gular ridges; insertion is ventrolaterally and laterally on the posterior pharynx. Ring muscles are well developed.

Cerebrum and suboesophageal ganglion (Figs 5, 7). The elongate, pear-shaded hemispheres of the cerebrum and the suboesophageal ganglion are shifted to the anterior prothorax.

Cephalic glands. Tubelike labial glands or subantennal glands are not developed in the head.

Prothorax (Figs 3, 5). The prothorax is slightly longer than the meso- and metathorax. It is connected with the head by a broad cervical membrane. Legs are absent. The protergum is unpigmented but recognizable as a separate, lightly sclerotized area. Dense fields of asperities cover its anterior and central area. A pair of dorsal setae is inserted close to the posterior margin and an additional seta is present laterally. Other setae are arranged as shown in Fig. 3. The protergum is connected with the dorsal mesothorax by a moderately broad unsclerotized area. A pleural sclerite or a distinct lateral bulge are absent. The sternum is unpigmented and appears sclerotized on SEM micrographs. The broad semi-membranous fold connecting the prosternum and the gular area is covered with asperities. The asperities are less densely arranged on the central region of the sternum. Internally, the prothorax is separated from the mesothorax by thick membranous folds. Sclerotized endoskeletal structures are absent. Musculature (Fig. 5): The exact origin and insertion of several muscles could not be identified in the specimens available for microtome sectioning. Well developed groups of dorsal and ventral retractors of the head are present in the prothorax. Dorsoventral muscles function as rotators, depressors or levators, respectively (Fig. 5). The posterior margin of the gula is marked by the attachment of the median subcomponents of the ventral retractors (Fig. 5: M 58).

Mesothorax. Shorter than the prothorax, with asperities on the transverse tergal ampulla (Fig. 3A) and on the sternum. Legs are absent. The lateral bulge is distinct and bears two long setae.

Metathorax. Similar to the mesothorax.

Abdominal segments. I–VI Abdominal segments I–III combined are longer than the thorax. Transverse ampullae with asperities are present dorsally and ventrally. A pair of setae are inserted on their lateral edges. The lateral bulges are distinct and bear two setae. One seta is present on a less prominent dorsolateral bulge, and additional setae are present ventrolaterally and ventrally. Distinctly sclerotized notal or sternal areas are not developed. Musculature: These segments have groups of thin dorsal and ventral longitudinal muscles. Well developed lateral muscles connect the upper and lower edges of the lateral bulges.

Abdominal segments VII and VIII (Figs 4C,D, 8). Contrary to Lawrence (1991), transverse ampullae are not only present on the dorsal and ventral side of segment VII but also on segment VIII in the specimens examined (Fig. 4C,D). The lateral and dorsolateral bulges are less distinct than in the preceding segments. The posterodorsal margin of segment VIII is slightly convex. Musculature: similar to anterior abdominal segments.

Abdominal segments IX and X (Figs 4C,D, 9D). Abdominal segment IX is sclerotized dorsally and ventrally in contrast to the other abdominal segments. Asperities are present on the posterior tergal and anterior sternal areas. Distinct, serrate posteromedian tergal and sternal processes are opposed to each other. Eversible, two-segmented processes are present ventrolaterally. Segment X is not visible externally. It is completely enclosed between tergum and sternum IX. Musculature: with strong retractor muscles of the eversible lobes.

Spiracles (Fig. 8D). The spiracles are small and annular. One slightly larger lateral pair is present posterior to the prothorax. The abdominal spiracles on segments I–VIII open laterally and not ventrally (see triungulin described by Costa *et al.*, 1988) in the specimens examined (Fig. 8D; see also Böving & Craighead, 1931).

Postcephalic gut (Figs 5, 8, 9). The oesophagus is difficult to distinguish from the posterior pharynx. Irregular, internally directed folds are present and a well developed ring musculature. A crop is not developed. A short proventriculus with a thick internal cuticle and a strong layer of ring muscles is present between the posterior oesophagus and the midgut. It is equipped with distinct dorsal, dorsolateral and ventrolateral folds but not with separate sclerotized teeth. The midgut is straight and unusually long. Its anterior part is wide and devoid of caeca and regenerative crypts. The midgut cells are fairly low and partly decomposed in the specimens examined. The lumen contains a compact mass of wood material, which is round in cross-section and enveloped by a peritrophic membrane. The hindgut is short. The distinction between ileum and colon is not apparent. The anterior part is characterized by a loop with strongly developed ring musculature. The rectum is hexagonal in cross-section (Fig. 9A,B). It is posteriorly continuous with a short anal canal, which opens between the eversible lobes (Fig. 9D,E).

Malpighian tubules (Fig. 9A,B). Four Malpighian tubules are present. They originate at the mid-hindgut border region and are posteriorly attached to the rectum by a membrane, thus forming a cryptonephric complex.

Postcephalic glands (Fig. 8A). Structures resembling glands with narrow and elongate cells are attached to the ventrolateral wall of all thoracic segments and to the walls of the lateral bulges of the meso- and metathorax (Fig. 8A). No external openings could be identified.

Internal genital organs (Fig. 8C). Paired abdominal structures of about 60 μm length probably represent an early stage of ovaries. They extend from segment IV to the posterior margin of segment V on the right side and from segment V to the posterior margin of segment VI on the left side. The structures were partly decayed in the sectioned specimens.

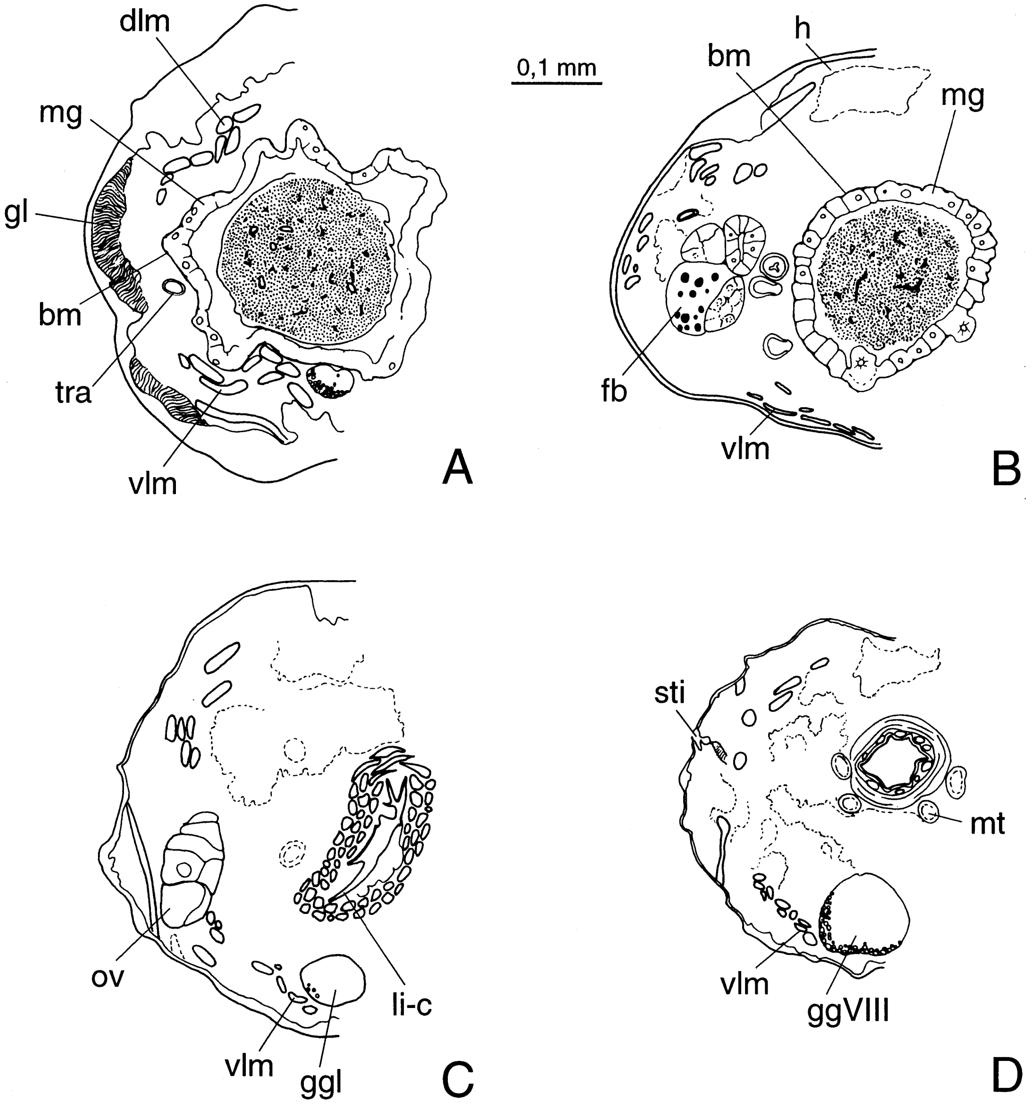

Fig. 8. *Micromalthus debilis*: cerambycoid larva (specimen 3), body, cross-sections. A, Mesothorax, anterior midgut region; B, abdominal segment VI, posterior midgut region, origin of Malpighian tubules; C, abdominal segment VII, loop of anterior hindgut; D, abdominal segment VIII, anterior margin of cryptonephric complex. bm = basement membrane, dlm = dorsal longitudinal muscles, fb = fat body, gg VIII = ganglion, gl = gland (?), h = heart, li-c = loop of ileocolon, mg = midgut, mt = Malpighian tubules, ov = ovary, sti = spiracle, tra = trachea, vlm = ventral longitudinal muscles.

Cerambycoid larva (second-instar larva)

No differences from third-instar larvae are apparent except for a smaller head capsule (greatest width 0.4 mm).

Cerambycoid larva (fourth-instar larva)

The head is larger and more transverse compared to the earlier cerambycoid instars and the body of the two specimens examined is slightly flattened, distinctly broader and slightly shorter than that of third-instar larvae (total length 2.4–2.5 mm).

Triungulin (caraboid larva, first instar)

General appearance (Fig. 2). The single specimen examined is 1.26 mm long. The body shape is similar to that of the cerambycoid larva, but ampullae are very indistinct or absent and the thoracic legs are well developed. Distinct lateral bulges are present in contrast to the specimen described and illustrated by Costa *et al.* (1988) (Fig. 2).

Head (Figs 2, 10A). The head is less strongly rounded laterally and less transverse than that of cerambycoid larvae (Figs 2, 3), but otherwise similar. The cerebrum and the suboesophageal ganglion are almost completely shifted to the prothorax. The two hemispheres of the brain appear

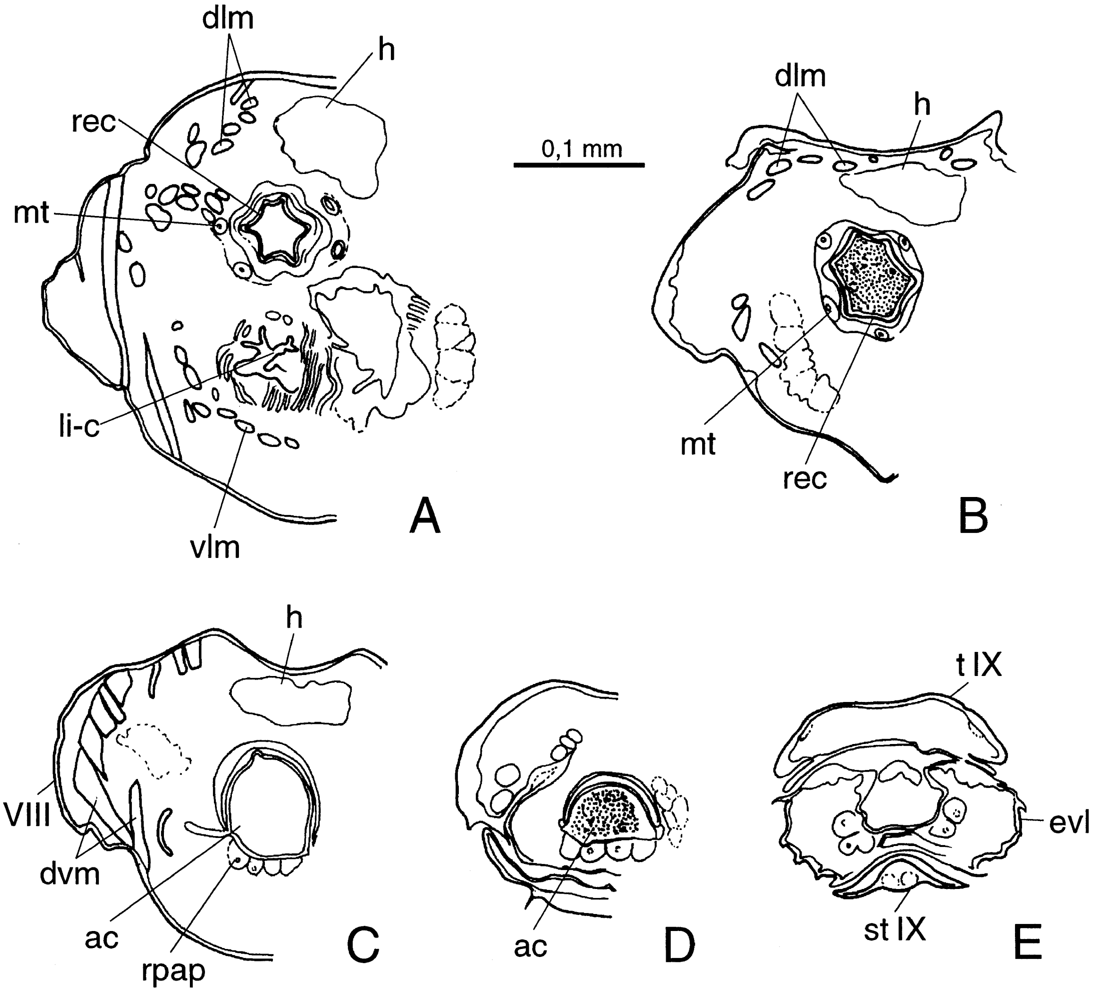

Fig. 9. *Micromalthus debilis*: cerambycoid larva (specimen 4), body, cross-sections. A, Abdominal segment VII, loop of anterior hindgut; B, abdominal segment VIII, cryptonephric complex; C, posterior part of abdominal segment VIII, dorsoventral muscles of ultimate lateral bulge, abdominal segments IX and X, rectum; E–H, apical region of abdomen, eversible lobes. ac = anal canal, dlm = dorsal longitudinal muscles, dvm = dorsoventral muscles of lateral bulge, h = heart, lb VIII = lateral bulge of segment VIII, li-c = loop of ileocolon, mt = Malpighian tubules, rec = rectum, rpap = rectal papillae, vlm = ventral longitudinal muscles.

very narrow and fusiform (Fig. 2). Only a narrow part of the tritocerebrum, which is connected with the circum-oesophageal connective enters the head capsule. Musculature: similar to head musculature of cerambycoid larvae.

Thorax (Figs 2, 10A). The prothorax is slightly longer than the mesothorax. The legs of the thoracic segments are well developed. They are composed of a fairly elongate, cone-shaped coxa, a short trochanter, an elongate femur, a tibia which is about half as long as the femur and a slender, elongate tarsus with short double claws. Ventral asperities are absent from the thoracic segments. Musculature (Fig. 10A): Leg muscles are well developed; otherwise similar to cerambycoid larvae.

Abdomen (Fig. 10B). The abdomen is similar to that of the cerambycoid larva (second and third instars). However, the three basal segments combined are not longer than the thorax and the extrusible lobes of the terminal segment are very indistinct or absent. Dorsal and ventral asperities are not recognizable.

Characters and character states

Larvae

1. *Head shape of second and later instars*: (0) parallel-sided, slightly narrowing anteriorly, or evenly rounded; (1) transverse, strongly rounded laterally, greatest width near hind margin; (2) transverse, with distinctly protruding eye region.

The head of the larva of *Omma* Newman is nearly parallel-sided and slightly narrowed anteriorly (Fig. 11; Lawrence, 1999). A similar condition is found in larvae of Sialidae and Trachypachidae and larvae of many other groups of beetles (Beutel, 1993, 1995, 1999a; Beutel & Molenda, 1997). The head of later instars (= post-triungulin) of *M. debilis* and Cupedidae is shortened, distinctly broader than long and strongly rounded laterally, with the greatest width close to the foramen occipitale (Fig. 3; Lawrence, 1991: Fig. 34.67a–c). This presumably derived condition is less distinct in first-instar larvae (Fig. 2; Ross & Pothecary, 1970: *Priacma serrata*).

2. *Posteromedian emarginations of head capsule*: (0) absent; (1) present.

Deep dorsal and ventral posteromedian emarginations are present in all known larvae of Archostemata (Figs 2, 3, 11; Böving & Craighead, 1931; Ross & Pothecary, 1970; Lawrence, 1991, 1999).

3. *Endocarina*: (0) absent; (1) present; (2) present, Y-shaped.

A distinct dorsal endocarina is present in all known larvae of Archostemata (Figs 2, 3, 11A; Böving & Craighead, 1931; Lawrence, 1991, 1999). It is Y-shaped in larvae of *Omma* (Fig. 11A; Lawrence, 1999) and undivided and very extensive in larvae of *Micromalthus*, *Rhipsideigma* Neboiss and *Distocupes* Neboiss. A less extensive median endocarina is present in larvae of Lymexylidae and larvae of some other groups of Coleoptera (e.g. Cerambycidae; Lawrence, 1991).

4. *Frontal suture of second and later instars*: (0) distinct; (1) indistinct or absent.

The frontal suture, which is distinct in larvae of the vast majority of families of Coleoptera, is absent from mature larvae of Archostemata (Figs 2, 3A, 11A; Lawrence, 1999) and from the larvae of Lymexylidae examined. An indistinct V-shaped or lyriform frontal suture may be present in early instars of some species of Cupedidae (Lawrence, 1991).

5. *Stemmata*: (0) more than one pair of stemmata; (1) one pair of distinct stemmata or eyeless.

Five or six stemmata are found in larvae of most families of Coleoptera and four are present in larvae of *Omma* (Lawrence, 1999). Stemmata are usually absent in larvae of Micromalthidae and Cupedidae (Ross & Pothecary, 1970; Lawrence, 1991) and are also absent in later instars of lymexylid larvae (Wheeler, 1991; coded as 1). One pair of stemmata was found in triungulins of *Micromalthus* collected in Hong Kong (Lawrence, 1991).

6. *Endoskeleton*: (0) with well developed tentorial bridge and posterior arms, gular ridge absent; (1) tentorial bridge absent, with elongate gular ridge and unsclerotized posterior arms, posterior arm attached to anatomical mouth (Figs 5–7).

A strong degree of tentorial reduction is found in larvae of *Micromalthus*, *Rhipsideigma* and *Distocupes*. Tentorial bridge, dorsal arms and anterior arms are absent. An unsclerotized posterior arm is continuous with the anterior margin of the elongate gular ridge. Its apex is attached to the anatomical mouth. A similar condition is not described for other beetle larvae. A different type of a partly reduced tentorium occurs in other groups, especially in larvae with a maxillolabial complex mainly moved in vertical direction (Elateriformia in part, Cleroidea, Cucujoidae in part; Beutel, 1995; Beutel & Pollock, 2000; Beutel & Slipinski, 2001). The anterior tentorial parts are also strongly reduced in larvae of *Sialis*. However, the bridge is well developed (Röber, 1942).

7. *Length of antenna*: (0) at least 20% of greatest width of head capsule; (1) less than 20% of greatest width of head capsule.

The antenna is moderately long in larvae of *Omma* (Fig. 11A) but distinctly shortened in larvae of *Micromalthus* and Cupedidae (Figs 2, 3; Böving & Craighead, 1931; Ross & Pothecary, 1970; Lawrence, 1991). The basal antennomere is distinctly broader than long in cupedid larvae and extremely short in larvae of *Micromalthus*. Strongly shortened antennae are also characteristic for larvae of other groups with xylobiontic habits such as Lymexylidae (Wheeler, 1991) or Cerambycidae (Lawrence, 1991).

8. *Antennal muscles*: (0) more than one; (1) one.

Only one longitudinal antennal muscle is present in larvae of *Micromalthus* (Fig. 6). Three muscles are present in larvae of *Rhipsideigma* and *Distocupes*, and in most other coleopteran larvae. At least two thin antennal muscles are present in larvae of *Hylecoetus*.

9. *Shape of distal part of mandible with*: (0) less than 3 apical teeth; (1) 3 apical teeth.

Three well developed apical mandibular teeth are present in all known larvae of Archostemata (Böving & Craighead, 1931; Lawrence, 1991, 1999). The apical part is fairly slender in larvae of *Omma* (Fig. 11A) but distinctly shortened in larvae of Cupedidae (Böving & Craighead, 1931; Ross & Pothecary, 1970; Lawrence, 1991).

10. *Retinaculum*: (0) present; (1) absent.

A distinct, hooklike retinaculum is present in larvae of *Omma* (Fig. 11A) but absent in larvae of *Micromalthus* and Cupedidae (Böving & Craighead, 1931). Probably reduction or loss of the retinaculum has occurred many times independently in Coleoptera.

11. *Shape of mola*: (0) not quadrangular, not delimited by a distinct margin; (1) quadrangular and delimited by a distinct margin.

A characteristic quadrangular mola delimited by a distinct margin is present in larvae of *Micromalthus* and Cupedidae (Böving & Craighead, 1931: Pl. 1, Fig. B, Pl. 2, Fig. D; Lawrence, 1991: Fig. 34.67d). A similar condition is not described for larvae of other groups.

12. *Cardo*: (0) undivided; (1) divided, with separate lateral semi-membranous piece.

A cardo, which is divided into a mesal sclerotized component and a distinct lateral, semi-membranous piece, is characteristic for all archostematan larvae examined (Figs 3B, 11B).

13. *Ligula*: (0) unsclerotized; (1) sclerotized, enlarged and wedge-shaped.

The presence of a very unusual, strongly sclerotized, enlarged and wedge-shaped ligula (Figs 3B, 11B) was interpreted as an archostematan autapomorphy by Lawrence (1999) and Beutel & Haas (2000).

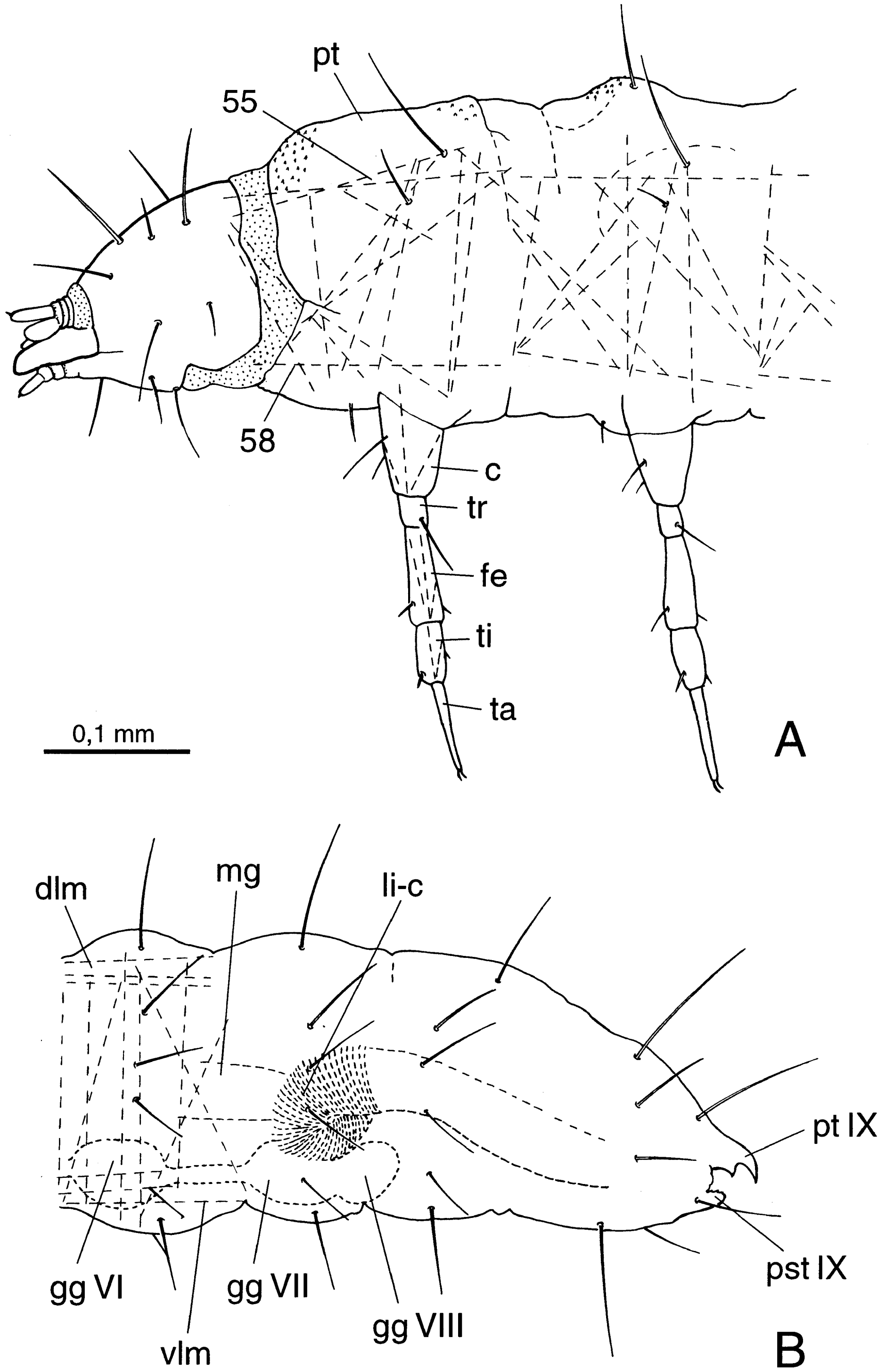

Fig. 10. *Micromalthus debilis*: A, Triungulin larva, head and anterior thorax, lateral view, muscles visible in slide preparation drawn as interrupted lines; B, triungulin larva, posterior abdomen, lateral view, ganglia, hindgut and muscles visible in slide preparation drawn as interrupted lines. c = coxa, dlm = dorsal longitudinal muscles, ggVI–VIII = ganglia VI–VIII, fe = femur, li-c = loop of ileocolon, mg = midgut, pt = protergum, pstIX = sternal process IX, ptIX = tergal process IX, ta = tarsus, ti = tibia, tr = trochanter, vlm = ventral longitudinal muscles, 55 = M. praephragmapostoccipitalis medialis, 58 = M. profurcatentorialis.

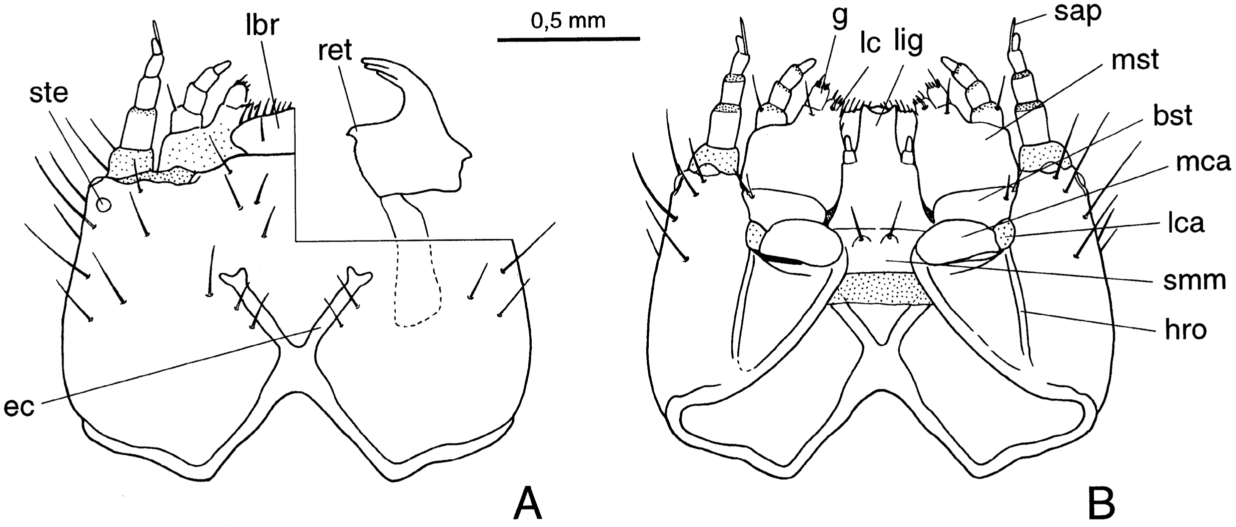

Fig. 11. *Omma* sp. head. A, Dorsal view; B, ventral view. bst = basistipes, ec = endocarina, g = galea, hro = hypostomal rods, lbr = labrum, lc = lacinia, lca = lateral part of cardo, lig = ligula, mca = mesal part of cardo, mst = mediostipes, ret = retinaculum, sap = sensorial appendage, smmt = submento-mentum, ste = stemmata.

14. *Mentum and submentum*: (0) not fused; (1) fused and narrowed between maxillary grooves.

The mentum and submentum are shortened and completely fused to each other in larvae of *Micromalthus* (Figs 3B, 4B), *Rhipsideigma*, *Distocupes*, *Tenomerga* Neboiss and *Omma* (Fig. 11B). The submento-mentum is narrowed between the maxillary grooves.

15. *Labial muscles*: (0) present; (1) absent.

Labial muscles are absent from larvae of *Micromalthus* (Fig. 5), *Rhipsideigma* and *Distocupes*. They are present in larvae of all other groups examined (e.g. *Hylecoetus*).

16. *Transverse muscles between gular ridges*: (0) absent; (1) present (Figs 5, 7).

A similar muscle is present in larvae of *Orchesia* Latreille (Melandryidae) (Beutel, personal observation), but absent in all other non-archostematan larvae as far as known at present.

17. *Proventriculus*: (0) present; (1) absent (Fig. 5).

A proventriculus is present in larvae of *Micromalthus* (Fig. 5), *Rhipsideigma* and *Distocupes*. It is equipped with distinct cuticular teeth in the cupedid larvae examined. The ingested material is compressed in this compartment of the digestive tract. A compact, cylindrical mass was found in the midgut of the larvae of *Micromalthus* examined.

18. *Width of prothorax of second and later instars*: (0) not broader than following segments; (1) broader than following segments.

The prothorax is broader than the following segments in larvae of *Rhipsideigma* and *Tenomerga* (Böving & Craighead, 1931: Pl. 1, Fig. G; Fukuda, 1938). It is equally broad in larvae of *Distocupes* and also in larvae of *Priacma* (Ross & Pothecary, 1970), *Micromalthus* and *Omma*.

19. *Prosternal glabrous patches of second and later instars*: (0) absent; (1) present.

Glabrous, shiny patches are present anterad the prosternal field of asperities in second and later instar larvae of Cupedidae.

20. *Abdominal segments I–III of second and later instars*: (0) shorter than thorax; (1) longer than thorax.

The abdomen is unusually elongate in later instars of Archostemata (Böving & Craighead, 1931; Fukuda, 1938; Vulcano & Pereira, 1975: Fig. 47; Lawrence, 1991; Lawrence, 1999: Fig. 12). Segments I–III combined are longer than the thorax.

21. *Tergal ampullae of second and later instars*: (0) absent; (1) present.

Tergal ampullae, which probably facilitate boring in fungus-infested wood (Crowson, 1981; Lawrence, 1991) are present in later instars of all archostematan larvae (Fig. 4D).

22. *Sternal asperities of second and later instars*: (0) absent; (1) present.

A prosternal field of asperities is present in larvae of Cupedidae (except for first-instar larvae of *Priacma*; Ross & Pothecary, 1970), whereas asperities are present on all sternites in larvae of *Micromalthus* (Fig. 4C). Sternal asperities are absent in the larva of *Omma* (Lawrence, 1999).

23. *Number of leg segments*: (0) 6; (1) 5.

Six-segmented legs are present in larvae of Archostemata (only first-instar larvae of *Micromalthus*) and Adephaga, whereas they are five-segmented in larvae of Polyphaga and Myxophaga (e.g. Beutel & Haas, 2000).

24. *Legs of second and following instars*: (0) present; (1) absent.

Absence of legs in second and older instars is considered an autapomorphy of Micromalthidae.

25. *Lateral longitudinal bulge of abdominal segments I–VIII*: (0) absent; (1) present.

A semi-membranous longitudinal bulge along the abdominal segments I–VIII is present in larvae of *Tenomerga* (Böving & Craighead, 1931) and *Rhipsideigma*.

26. *Sclerotized process of tergum IX*: (0) absent; (1) present.

A toothed median appendage of tergum IX is present in larvae of *M. debilis* (Figs 2, 4C,D, 10B) and Cupedidae (Lawrence, 1991), but absent in the larva of *Omma* (Lawrence, 1999).

27. *Asperities on segment IX of second and following instars*: (0) absent; (1) present.

Asperities are present on the dorsal and ventral side of the abdominal segment IX of larvae of *Micromalthus* and Cupedidae (except for first-instar larva of *Priacma*; Ross & Pothecary, 1970).

28. *Eversible lobes of segment IX*: (0) absent; (1) present.

Eversible ventral lobes composed of a weakly sclerotized proximal part and a largely membranous distal element are present in larvae of *Micromalthus* (Fig. 4D) and Cupedidae (Beutel, personal observation; Lawrence, 1991: Fig. 34.67e). They may facilitate locomotion in galleries. Similar structures are not described for other larvae of Coleoptera.

29. *Urogomphi*: (0) absent; (1) present.

Urogomphi are absent from tergum IX of all larvae of Archostemata (Figs 2, 4C,D). They are present in most larvae of Adephaga, in Torridincolidae (Beutel, 1999b) and in larvae of many groups of Polyphaga (e.g. Hydrophiloidea, Histeroidea, Staphylinoidea; Frank, 1991; Newton, 1991).

30. *Toothed process of sternum IX*: (0) absent; (1) present.

A sclerotized, toothed process of sternum IX, opposed to the tergal process, is present in larvae of *M. debilis* (Figs 2, 4C,D, 10B), but absent from larvae of other groups of Archostemata or Coleoptera.

31. *Segment X*: (0) exposed; (1) not visible externally.

Segment X is not visible externally in all larvae of Archostemata (Figs 2, 4C,D, 10B). It is exposed in larvae of most other groups of Coleoptera (e.g. Adephaga, Staphyliniformia; Frank, 1991; Newton, 1991).

32. *Distal ends of Malpighian tubules*: (0) not attached to hind gut; (1) attached to hind gut.

The distal ends of the Malpighian tubules are attached to the hindgut and covered by a membrane in larvae of *Micromalthus* (Figs 8D, 9B), whereas free Malpighian tubules are present in larvae of *Rhipsideigma* and *Distocupes*. Cryptonephric Malpighian tubules were considered an autapomorphy of Dermestoidea and Cucujiformia (e.g. Beutel & Haas, 2000). Apparently, a similar condition has evolved independently in Micromalthidae.

33. *Life cycle*: (0) without larviform reproductives, parthenogenesis and vivipary; (1) with 3 different forms of larviform reproductives, parthenogenesis and vivipary.

The complex life cycle of *M. debilis* (see Introduction) is unparalleled in Archostemata and other groups of Coleoptera.

Adults

34. *Exoskeleton*: (0) moderately sclerotized cuticle, with exposed membranes; (1) strongly sclerotized, without exposed membranes.

A strongly sclerotized cuticle and absence of exposed membranes is considered an autapomorphy of Coleoptera (e.g. Beutel & Haas, 2000).

35. *Vestiture*: (0) setae sparse, unmodified; (1) setae scalelike.

Adults of Ommatidae and Cupedidae are characterized by a cuticle densely covered with scalelike or at least broadened setae (*Omma stanleyi*), whereas the cuticle of adults of *Micromalthus* and *Crowsoniella* is smooth (Pace, 1975).

36. *Labrum*: (0) free; (1) partly fused with head capsule; (2) completely fused.

The labrum is completely fused with the head capsule in adults of *Micromalthus* (Hörnschemeyer, personal observation), *Omma* and *Crowsoniella* (Pace, 1975; Lawrence, 1999). It is partly immobilized in adults of *Tetraphalerus* (Lawrence, 1999).

37. *Location of antennal insertion on head capsule*: (0) lateral; (1) dorsal.

The antennae are inserted on the dorsal side of the head in adults of Cupedidae with the exception of *Priacma serrata*.

38. *Mandibular apex*: (0) unmodified, curved; (1) rotated.

A very characteristic tridentate mandible with a rotated apex was considered an autapomorphy of Ommatidae (Lawrence, 1999). A very similar condition with three teeth in a vertical row is present in adults of *Micromalthus* (coded as 1).

39. *Mandibular mola*: (0) absent; (1) present; (2) modified, partly reduced.

A mandibular mola is absent from adults of Archostemata and Adephaga but present in adults of Myxophaga and adults of many groups of Polyphaga (Beutel & Haas, 2000). It is modified and partly reduced in adults of Lymexylidae and Coccinellidae.

40. *Galea*: (0) basal part about as broad as proximal part; (1) divided into a narrow proximal part and a rounded, pubescent distal part (Lawrence, 1999).

A galea with a narrow, stalklike proximal part and a rounded, pubescent distal part is characteristic for adults of Cupedidae (Lawrence, 1999). The distal part is very small but still distinct in adults of *Rhipsideigma*.

41. *Dorsal sensorial patch on apical palpomeres*: (0) absent; (1) small, shallow pit; (2) deep cavity; (3) large flat field; (4) digitiform appendages; (5) distal part broadened and membranous.

A sensorial patch is present on the dorsal surface of the terminal segments of the maxillary palps of most adults of Archostemata (Fig. 12). The patch is very large in *Micromalthus* (Fig. 12D), with a diameter as wide as the diameter of the palpomere. A deep cavity is characteristic for adults of Ommatidae (Fig. 12C; Lawrence, 1999). Six sensilla are present in a flat groove in adults of *Rhipsideigma* (coded as 1).

The maxillary palpomeres of adults of *Crowsoniella* bear several setae and digitiform sensilla (Pace, 1975).

42. *Prementum*: (0) not enlarged, approximately quadrangular; (1) strongly enlarged, platelike; (2) coadapted with mentum, fitting into mental grooves; (3) strongly reduced.

A large and platelike prementum is characteristic for adults of Cupedidae and Ommatidae.

43. *Prosternal grooves for tarsomeres*: (0) absent; (1) present.

Longitudinal prosternal grooves for reception of the forelegs in repose are present in adults of most genera of Cupedidae (Vulcano & Pereira, 1975) and also in adults of *Crowsoniella* (Pace, 1975). They are absent from adults of *Paracupes*, *Priacma* (Vulcano & Pereira, 1975), Ommatidae and *Micromalthus*.

44. *Trochanter and propleura*: (0) separate; (1) fused.

Fusion of the propleura and trochanter is a possible synapomorphy of Myxophaga and Polyphaga (e.g. Beutel & Haas, 2000).

45. *Articulation between prosternal process and mesoventrite*: (0) absent; (1) prosternal process articulates with indistinct concavity of mesoventrite; (2) prosternal process articulates with distinct pit of mesoventrite; (3) prosternal process articulates with hexagonal groove of mesoventrite; (4) broad prosternal process overlaps mesoventrite.

The prosternal process articulates with a shallow concavity of the mesoventrite in adults of *Priacma* and with a distinct pit in adults of other cupedid genera. The process is strongly shortened and does not reach the mesoventrite in adults of *Micromalthus* and Ommatidae.

46. *Elytra*: (0) absent; (1) present.

Presence of elytra with epipleura is an autapomorphy of Coleoptera (Beutel & Haas, 2000). A reticulate pattern is characteristic for larger species of Archostemata (Cupedidae, Ommatidae). It is still recognizable in adults of *Crowsoniella* (Pace, 1975) but probably absent from adults of *Micromalthus*.

47. *Propleura*: (0) largely exposed; (1) invaginated.

An invaginated propleuron is a possible autapomorphy of Polyphaga (Beutel & Haas, 2000).

48. *Shape of penultimate tarsomere*: (0) not distinctly bilobed; (1) distinctly bilobed (Lawrence, 1999).

A distinctly broadened penultimate tarsomere is present in adults of Cupedidae. It is more or less deeply emarginate where the ultimate tarsomere articulates (Neboiss, 1984). The penultimate tarsomere is cylindrical in shape and not broader than the others in adults of *Micromalthus*, Ommatidae and *Crowsoniella*.

49. *Abdominal sterna*: (0) abutting, not overlapping; (1) tegular or overlapping (Lawrence, 1999).

Abutting abdominal sternites are present in adults of Ommatidae and Crowsoniellidae (Lawrence, 1999).

Biology

50. *Habits*: (0) not associated with wood; (1) xylobiontic, wood-boring larval stages.

Results of the phylogenetic analysis (Fig. 13)

The analysis of characters 1–50 resulted in two cladograms with a minimal number of seventy-nine steps (CI = 0.797; RI = 0.203, RC = 0.695). Monophyletic groups and apomorphies are listed in the following paragraphs (CI = 1.000 unless otherwise indicated; Fig. 13).

Archostemata. Dorsal and ventral posteromedian emarginations of head capsule present (2.1); frontal suture absent in later instars (4.1; CI = 0.500); mandible with three apical teeth (9.1); cardo with separate lateral piece (12.1); ligula sclerotized, enlarged and wedge-shaped (13.1); submentum fused with mentum and constricted between maxillary grooves (14.1); abdominal segments I–III combined longer than thorax (20.1; CI = 0.500); tergal ampullae (21.1); segment X not visible externally (31.1); prementum of adults platelike (42.1).

Micromalthidae + *Cupedidae*. Head transverse, strongly rounded laterally, greatest width close to foramen occipitale (1.1); stemmata reduced to one pair or absent (5.1, CI = 0.500); antennal length less than 20% of the head capsule (7.1; CI = 0.500); retinaculum absent (10.1; CI = 0.500); mola quadrangular, with distinct margin (11.1); transverse muscle between gular ridges present (16.1; delayed transformation); sternal asperities (22.1); tergum IX with sclerotized process (26.1); segment IX with ventrolateral eversible lobes (28.1); wood-associated (50.1; CI = 0.500).

Cupedidae. Cuticle of adults densely covered with scale-like setae (35.1; CI = 0.500), galea of adults with narrow stalk and rounded, pubescent distal part (40.1), penultimate tarsomere broadened (48.1; CI = 0.333).

Tenomerga + *Distocupes* + *Rhipsideigma*. Dorsal antennal insertion in adults (37.1; CI = 0.500), antennal grooves on ventral side of prothorax present (43.1; CI = 0.500), prosternal process articulates with distinct pit of mesoventrite (45.2).

Tenomerga + *Rhipsideigma*. Prothorax broader than following segments (18.1), lateral longitudinal bulge of abdominal segments I–VIII present (25.1).

Ommatidae + *Crowsoniella*. Abdominal sternites of adults abutting (49.1).

Ommatidae. Cuticle of adults covered with scales (35.1; CI = 0.500), mandibular apex of adults rotated (38.1; delayed transformation; CI = 0.500), apical palpomeres with deep sensorial pit (41.2; delayed transformation).

Micromalthidae. Only one antennal muscle (8.1), legs present in triungulin larva but absent in following instars (24.1), presence of toothed process on sternum IX (30.1), cryptonephric Malpighian tubules (32.1; CI = 0.500), life cycle with larviform reproductives, parthenogenesis and vivipary (33.1), large sensorial patch on penultimate palpomeres (41.3), prementum of adults strongly reduced (42.3).

Discussion

The monophyly of Archostemata, as proposed by Crowson (1955), Lawrence (1982), Lawrence & Newton (1982),

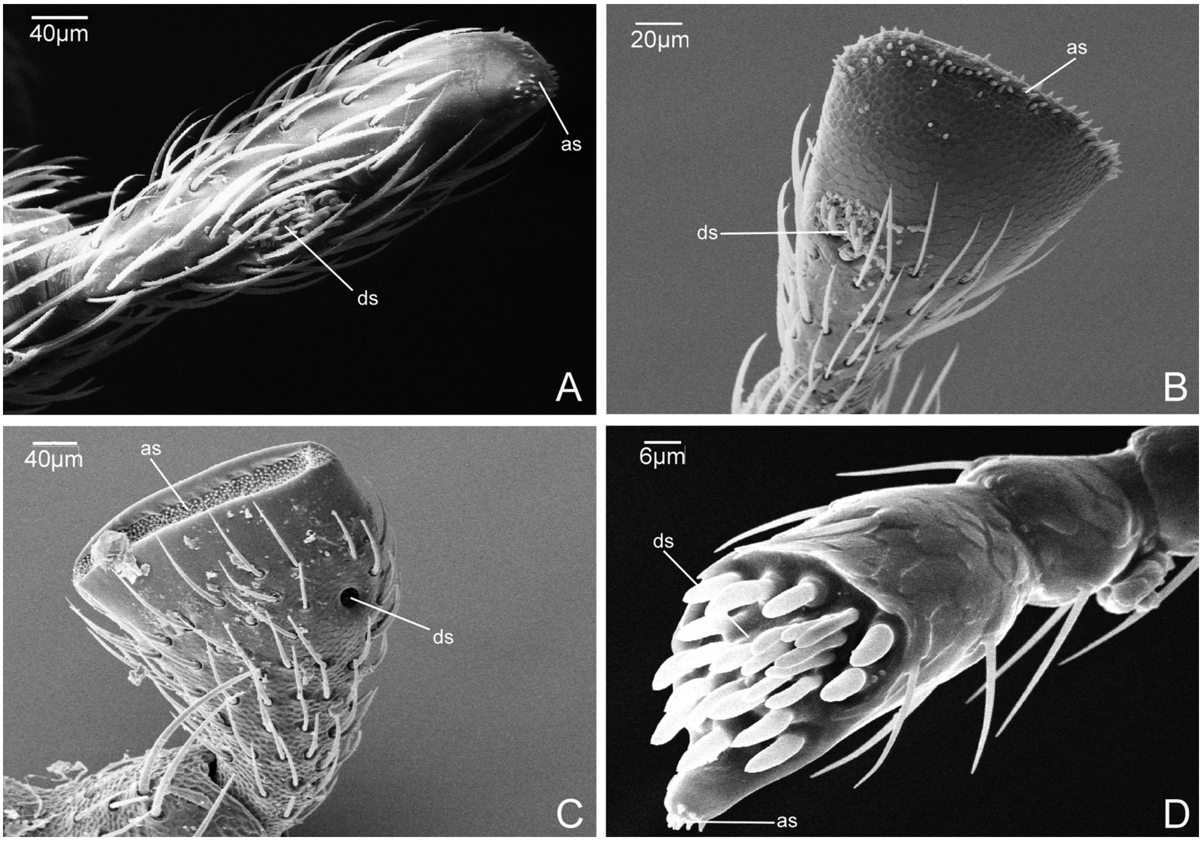

Fig. 12. Terminal segments of maxillary palps of adults. A, *Priacma serrata*; B, *Distocupes varians*; C, *Omma stanleyi*; D, *Micromalthus debilis*. as = apical sensilla, ds = dorsal sensilla.

Beutel (1997) and Beutel & Haas (2000), is supported by ten unambiguous autapomorphies. The relatively low branch support value of 2 is largely due to missing data. It was increased to 7 when the archostematan taxa with unknown larvae, *Tetraphalerus* and *Crowsoniella*, were excluded from the analysis. A close relationship between Micromalthidae and Lymexylidae (Barlet, 1996) would require sixteen additional steps, and is therefore very unlikely. Barlet's hypothesis was based on a noncladistic interpretation of structural similarities, which were not presented as well defined character states: '... même silhouette, mêmes proportions relatives des trois segments et surtout l'exceptionel allongement du metathorax.' (Barlet, 1996). Contrary to Barlet (1996), the metendosternite of adults of *M. debilis* is very similar to that of Cupedidae (Barlet, 1996: Fig. 1; Crowson, 1938; Baehr, 1975). Besides that, Barlet (1996) emphasizes structural features shared by *Micromalthus* and representatives of Lymexylidae, which are in fact common to all adults of Coleoptera ('... les coxae sont situées tout à l'arrière dans les trois segments thoraciques.').

Adults of most archostematan subgroups display a considerable number of character states, which probably belong to the groundplan of Coleoptera, e.g. incompletely sclerotized elytra, presence of mesothoracic sterno-coxal articulation, mesoventrite with discrimen and transverse suture, exposed metatrochantinus, apical part of alae rolled in resting position and comparatively complete pterothoracic muscle system (see Beutel & Haas, 2000). Some plesiomorphic features are also preserved in the larvae, e.g. clypeofrontal suture distinct, labrum not fused with clypeus, antenna with four antennomeres and sensorial appendage, maxillary groove deep, galea and lacinia separate, tibia and tarsus separate, and presence of two claws (see Beutel & Haas, 2000). However, the immature stages are mainly characterized by derived characters, which distinguish them very clearly from an hypothesized larval groundplan of Coleoptera (Lawrence & Newton, 1982; Beutel, 1997).

Ommatidae + Crowsoniella is the sister group of a clade comprising Micromalthidae and Cupedidae. The monophyletic origin of the latter two families is well supported by a considerable number of synapomorphies, which are probably correlated with wood-boring habits. Extrusible lobes at segment IX probably support locomotion in galleries. A head capsule, which is distinctly widened posteriorly, is also found in the wood-associated larvae of

Rhysodidae (Beutel, 1992), Buprestidae, Pythidae (Lawrence, 1991) and Prostomidae (Beutel, personal observation). Stemmata are also absent from most larvae of Buprestidae (Lawrence, 1991) and later instars of Lymexylidae (Wheeler, 1991), and they are indistinct or absent in larvae of Cerambycidae (Lawrence, 1991). Shortened antennae occur in larvae of Buprestidae, Callirhipidae, Eucnemidae, Lymexylidae and Cerambycidae (Beutel, personal observation; Lawrence, 1991), but also occur in some larvae with burrowing habits, e.g. Heteroceridae and Throscidae (Becker, 1991; Beutel, 1995). A proventriculus and a loop or fold of the hindgut are also described for some representatives of Cerambycidae (Švácha *et al.*, 1997: Fig. 53). Another feature commonly found in families with xylobiontic or plant-mining larvae is the shortening or complete loss of legs (Buprestidae, Cerambycidae, Curculionidae) (Anderson, 1991; Lawrence, 1991). Ventral asperities are also present on the prosternum of some larvae of Buprestidae (Lawrence, 1991) and dorsal and ventral rugose, sclerotized areas are present in some larvae of Eucnemidae. The assumption that all these derived features are adaptations to xylobiontic habits is strongly supported by their presence in larvae of non-related wood-associated families of several lineages of Coleoptera (Adephaga, Elateriformia, Cucujiformia) (see also Crowson, 1981). Larvae of Cupedidae and Micromalthidae clearly belong to the straight wood-boring type as defined by Crowson (1981).

The proposed placement of *Micromalthus* is in contrast to Crowson's argument in favour of a closer affinity with Ommatidae (Crowson, 1975). However, the similarities he pointed out were partly due to symplesiomorphy (form and insertion of antennae) or based on inaccurate data (lack of overlapping ventrites) (see Lawrence, 1999). The orientation of the mandibular teeth in adults of both families is indeed a shared, derived feature. However, the present analysis implies that this condition has evolved independently in both groups. Reversal in Cupedidae appears very unlikely.

The question of the ancestral life style of archostematan larvae cannot be definitely settled with the scarce available information on the life history of Ommatidae and Crowsoniellidae. The only known larva of *Omma* was collected in soil (Lawrence, personal communication). Adults of *Crowsoniella relicta* were found in calcareous substrate around the base of a chestnut tree (Pace, 1975), and adults of *Tetraphalerus* species occur in open scrubby country far from forests or large trees (Monros & Monros, 1952). However, the larvae of these taxa are unknown. In the

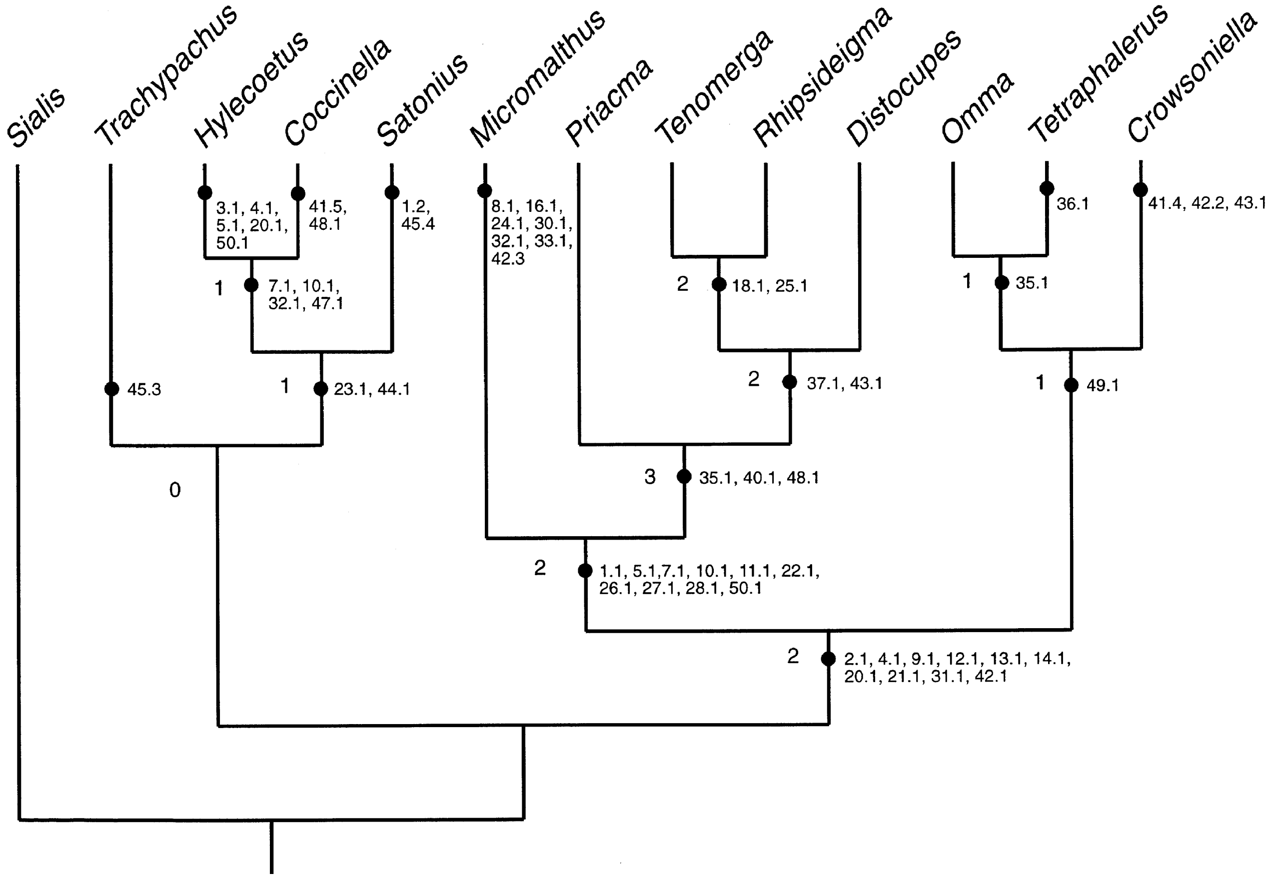

Fig. 13. Minimal length cladogram showing the position of Micromalthidae. Unambiguous apomorphies are mapped on the cladogram, numbers to the left of the branches are branch support values (Bremer, 1988, 1994).

analysis presented above, wood-boring habits were unequivocally placed as a synapomorphy of Micromalthidae and Cupedidae and not as a groundplan feature of Archostemata. Nevertheless, if all available data are examined, the latter possibility appears more plausible. Several autapomorphies of archostematan larvae have almost certainly evolved in correlation with xylobiontic habits. The dorsal endocarina strengthens the head capsule and provides an additional muscle attachment area. An undivided, median endocarina is also found in larvae of Buprestidae, Cerambycidae (Lawrence, 1991) and Lymexylidae (Beutel, personal observation) and paired or forked endocarinae are present in larvae of Colydiidae (in part) and Monommidae (Lawrence, 1991). Posteromedian emarginations of the head capsule are also present in larvae of Cerambycidae (in part; Švácha *et al.*, 1997) and Buprestidae (in part; Lawrence, 1991). Short mandibles with a tridentate apex are a typical feature in larvae of Buprestidae, Zopheridae (Lawrence, 1991) and Chrysomelidae (Lawson, 1991). Tergal ampullae, which facilitate locomotion in galleries (Crowson, 1981), occur in larvae of Histeridae, Cleridae (Crowson, 1981) and Cerambycidae (Lawrence, 1991). An abdomen elongated in relation to the thorax is found in some larvae of Buprestidae, Eucnemidae (Becker, 1991) and Cerambycidae (Lawrence, 1991). The wedge-shaped, strongly sclerotized ligula appears much better suited for the penetration of rotting wood than for burrowing in loose soil or sand. It is possible that endogeous habits of larvae and feeding on roots of shrubs (Lawrence, 1991) will be confirmed as a general feature of Ommatidae. However, in this case, it would still appear plausible to interpret this as a secondarily modified life style, which has evolved as an adaptation to xeric conditions. *Omma* and *Tetraphalerus* occur in dry regions of Australia and South America, respectively, and species of the latter genus are often found in areas with little or no tree cover (see above).

In addition to the features discussed above, the monophyly of Archostemata and of the clade comprising Micromalthidae and Cupedidae is also supported by some larval characteristics, which are probably not correlated with xylobiontic habits, e.g. presence of a lateral piece of the cardo, presence of a transverse muscle connecting the gular ridges, and partly reduced tentorium with unsclerotized posterior arms attached to the anatomical mouth. The latter condition enables M. tentoriostipitalis to function not only as a flexor of the maxilla, but also as a ventral dilator of the prepharynx and anterior pharynx, together with the unusually strong M. frontohypopharyngalis.

Cupedidae is supported by several unambiguous derived features of adults, a specifically modified galea, broadened penultimate tarsomeres and cuticle densely covered with scalelike setae. The latter condition may be a groundplan feature of Archostemata. This interpretation implies secondary loss in Micromalthidae and Crowsoniellidae, which may have resulted from size reduction. The presence of glabrous spots on the prosternum is a possible larval apomorphy of the family. A basal position of *Priacma* is strongly suggested by the widely separated antennal bases of adults, which are inserted laterally as in adults of Micromalthidae and Ommatidae. Another possible plesiomorphy of *Priacma* is the absence of a distinct anteromedian pit of the mesoventrite (Beutel, personal observation; Baehr, 1975: Fig. 3), which articulates with the apex of the prosternal process in other cupedids (Lawrence, 1999). A plesiomorphic feature shared with adults of *Paracupes* is the absence of longitudinal grooves on the prosternum (Vulcano & Pereira, 1975).

A close relationship between *Tenomerga* and *Rhipsideigma* is suggested by the broadened prothorax of larvae and by the presence of a lateral longitudinal bulge of abdominal segments I–VIII. At least the former apomorphy is probably correlated with xylobiontic habits. A similar condition is found in larvae of Lymexylidae, Buprestidae (in part; Lawrence, 1991), Eucnemidae (in part; Becker, 1991) and Cerambycidae (in part; Lawrence, 1991).

Micromalthidae is the archostematan group with the greatest number of derived character states. An obviously autapomorphic feature is the complete reduction of legs in the cerambycoid, curculionoid and reproductive larvae. The legs of the first instars are distinctly longer in relation to body size compared to other archostematan larvae (Fig. 10A). The triungulins are agile and ensure at least a limited dispersal, especially when no adults develop. Another potential autapomorphy is the presence of cryptonephric Malpighian tubules. The improved water re-absorption may enable the larvae to survive when the wood they inhabit desiccates. The most complex and unusual autapomorphy of Micromalthidae is the reproductive system with paedogenesis, haplodiploidy, thelytoky and extremely rare adult males. This highly specialized condition evokes the idea of an 'evolutionary dead end street'. Yet, *Micromalthus debilis* is widespread, inhabits different host trees (*Quercus*, *Castanea*), is able to infest timber of different woods (*Ptinus*, *Pseudotsuga*, *Acacia*, *Eucalyptus*) (Lawrence, 1991), and is obviously successful (D. A. Pollock, personal communication).

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References

Anderson, D.M. (1991) Curculionidae (broad sense) (Curculionoidea). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 594–612. Kendall/Hunt Publishing Co, Dubuque, Iowa.

Arnett, R.H. (1968) *The Beetles of the United States*. American Entomological Institute, Ann Arbor, Michigan.

Baehr, M. (1975) Skelett und Muskulatur des Thorax von *Priacma serrata* LeConte (Coleoptera, Cupedidae). *Zeitschrift für Morphologie der Tiere*, **81**, 55–101.

Barber, H.S. (1913a) Observations on the life history of *Micromalthus debilis* Lec. *Proceedings of the Entomological Society of Washington*, **15**, 31–45.

Barber, H.S. (1913b) The remarkable life history of a new family (Micromalthidae) of beetles. *Proceedings of the Biological Society of Washington*, **26**, 185–190.

Barlet, J. (1996) Quelques précisions au sujet de *Micromalthus* (Insecta Coleoptera). *Bulletin de la Société Royale des Sciences de Liège*, **65**, 373–378.

Becker, E.C. (1991) Throscidae (Elateroidea) (= Trixagidae). Eucnemidae (Elateroidea) (= Melasidae, including Perothopidae, Phylloceridae). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 418–421. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Beutel, R.G. (1992) On the morphology of the head of the larva of *Omoglymmius hamatus* (LeConte) and the systematic position of Rhysodidae (Coleoptera, Adephaga). *Entomologica scandinavica*, **23**, 169–184.

Beutel, R.G. (1993) Phylogenetic analysis of Adephaga (Coleoptera) based on characters of the larval head. *Systematic Entomology*, **18**, 127–147.

Beutel, R.G. (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research*, **33**, 145–171.

Beutel, R. (1997) Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Verhandlungen des Naturwissenschaftlichen Vereins Hamburg NF*, **31**, 1–164.

Beutel, R.G. (1999a) Morphology and evolution of the larval head structures of Hydrophiloidea and Histeroidea (Coleoptera: Staphyliniformia). *Tijdschrift voor Entomologie*, **142**, 9–30.

Beutel, R.G. (1999b) Description of the larva of *Satonius kurosawai* (Satô, 1982) (Coleoptera: Torridincolidae). *Water Beetles of China*, **2**, 53–59.

Beutel, R.G. & Haas, F. (2000) Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, **16**, 1–39.

Beutel, R.G. & Molenda, R. (1997) Comparative morphological study of larvae of Staphylinoidea (Coleoptera, Polyphaga) with phylogenetic implications. *Zoologischer Anzeiger*, **236**, 37–67.

Beutel, R.G. & Slipinski, S.A. (2001) Comparative study of larval head structures of Sphindidae and Protocucujidae (Cucujoidea, Coleoptera). *European Journal of Entomology*, **98**, 219–232.

Beutel, R.G. & Pollock, D.A. (2000) Larval head morphology of *Phycosecis litoralis* (Pascoe) (Coleoptera, Phycosecidae) with phylogenetic implications. *Invertebrate Taxonomy*, **14**, 825–835.

Böving, A.G. (1929) On the classification of beetles according to larval characters. *Bulletin of the Brooklyn Entomological Society*, **24**, 55–80.

Böving, A.G. & Craighead, F.C. (1931) An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana*, **11**, 1–351, pls 1–125.

Bremer, K. (1988) The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, **42**, 795–803.

Bremer, K. (1994) Branch support and tree stability. *Cladistics*, **10**, 295–304.

Costa, C., Vanin, S.A. & Casari-Chen, S.A. (1988) *Larvas de Coleoptera do Brasil*. Museo de Zoologia, Universidade de São Paulo, São Paulo.

Crowson, R.A. (1938) The metendosternite in Coleoptera: a comparative study. *Transactions of the Royal Entomological Society of London*, **87**, 397–416.

Crowson, R.A. (1955) *The Natural Classification of the Families of Coleoptera*. Nathaniel Lloyd Ltd, London.

Crowson, R.A. (1975) The systematic position and implications of *Crowsoniella*. *Bolletino del Museo Civico di Storia Naturale Verona*, **2**, 459–463.

Crowson, R.A. (1981) *The Biology of Coleoptera*. John Murray, London.

van Emden, F. (1932) Über die Adephagen-Verwandtschaft von *Micromalthus*. *Zoologischer Anzeiger*, **98**, 255–258.

Forbes, W.T.M. (1926) The wing-folding patterns of the Coleoptera. *Journal of the New York Entomological Society*, **34**, 42–115, pls 7–18.

Frank, J.H. (1991) Staphylinidae (Staphylinoidea) (including Brathinidae, Empelidae). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 341–352. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Fukuda, A. (1938) Descriptions of the larva and pupa of *Cupes clathratus* Solsky. *Transactions of the Natural History Society of Formosa*, **28**, 390–393.

Hennig, W. (1969) *Die Stammesgeschichte der Insekten*. Waldemar Kramer, Frankfurt am Main.

Hubbard, H.G. (1878) Description of the larva of *Micromalthus debilis* Lec. *Proceedings of the American Philosophical Society*, **17**, 666–668.

Jäch, M. & Komarek, A. (2000) Bemerkenswerte Käferfunde aus Österreich (IX) (Coleoptera: Micromalthidae et Dytiscidae). *Koleopterologische Rundschau*, **70**, 223–224.

Jeannel, R. & Paulian, R. (1949) Les coleóptères. *Traité de Zoologie* (ed. by P.-P. Grassé), pp. 771–1077. Masson, Paris.

von Kéler, S. (1963) *Entomologisches Wörterbuch*. Akademie Verlag, Berlin.

Klausnitzer, B. (1975) Probleme der Abgrenzung von Unterordnungen bei den Coleoptera. *Entomologische Abhandlungen des Staatlichen Museums für Tierkunde Dresden*, **40**, 269–275.

Kukalová-Peck, J. & Lawrence, J.F. (1993) Evolution of the hind wing in Coleoptera. *Canadian Entomologist*, **125**, 181–258.

Lawrence, J.F. (1982) Coleoptera. *Synopsis and Classification of Living Organisms* (ed. by S. Parker), pp. 482–553. McGraw-Hill, New York.

Lawrence, J.F. (1991) Ommatidae (Archostemata) (= Ommadidae, including Tetraphaleridae), Cupedidae (Archostemata) (= Cupesidae), Micromalthidae (Archostemata), Buprestidae (Buprestoidea) (incl. Schizopodidae), Zopheridae (Tenebrionoidea) (including Merycidae). Cerambycidae (Chrysomeloidea) (including Disteniidae, Hypocephalidae, Oxypeltidae, Parandridae, Spondylidae, Vesperiidae). *Immature Insects*, Vol. 2 (ed. by

F. W. Stehr), pp. 298–302, 386–388, 518–519, 556–561. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Lawrence, J.F. (1999) The Australian Ommatidae (Coleoptera), with a new species, a putative larva and comments on the suborder Archostemata. *Invertebrate Taxonomy*, **13**, 369–390.

Lawrence, J.F. & Newton, A.F., Jr (1982) Evolution and classification of beetles. *Annual Review of Ecology and Systematics*, **13**, 261–290.

Lawrence, J.F. & Newton, A.F. Jr (1995) Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson* (ed. by J. Pakaluk & S. A. Slipinski), pp. 634–797. Muzeum i Instytut Zoologii PAN, Warszawa.

Lawson, F.A. (1991) Chrysomelidae (Chrysomeloidea) (= Cassididae, Cryptocephalidae, Megalopodidae, Sagridae, etc.). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 568–585. Kendall/Hunt Publishing Co., Dubuque, Iowa.

LeConte, J.L. (1878) The Coleoptera of Michigan. *Proceedings of the American Philosophical Society*, **17**, 613.

Machatschke, J.W. (1962) Bemerkungen zum System der Coleoptera. *Bericht der 9. Wanderversammlung der Deutschen Entomologischen Gesellschaft*, **1961**, 121–137.

Maddison, W.P. & Maddison, D.R. (1992) *MacClade, Version 3: Analysis of Phylogeny and Character Evolution.* Sinauer, Sunderland, Massachusetts.

Marshall, A.T. & Thornton, I.W.B. (1963) *Micromalthus* (Coleoptera: Micromalthidae) in Hong Kong. *Pacific Insects*, **5**, 715–720.

Monros, F. & de Monros, M.M. (1952) Las expecies Argentinas de Cupedidae (Coleoptera). *Annales de la Sociedad Cientifica Argentina*, **104**, 19–41.

Neboiss, A. (1968) Larva and pupa of *Cupes varians* Lea, and some observations on its biology (Coleoptera; Cupedidae). *Memoirs of the National Museum of Victoria*, **28**, 17–19.

Neboiss, A. (1984) Reclassification of *Cupes* Fabricius (s.lat.), with descriptions of new genera and species (Cupedidae: Coleoptera). *Systematic Entomology*, **9**, 443–447.

Newton, A.F. Jr (1991) Agyrtidae (Staphylinoidea). Leiodidae (Staphylinoidea) (= Anisotomidae, Liodidae, including Camiaridae, Catopidae, Cholevidae, Colonidae, Leptodiridae). Sphaeritidae (Hydrophiloidea). Leptinidae (Staphylinoidea) (including Platypsyllidae). Scydmaenidae (Staphylinoidea). Micropeplidae (Staphylinoidea). Dasyceridae (Staphylinoidea). Scaphidiidae (Staphylinoidea). Silphidae (Staphylinoidea). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 324–341, 353–355. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Nixon, K.C. & Carpenter, J.M. (1993) On outgroups. *Cladistics*, **9**, 413–426.

Pace, R. (1975) An exceptional endogeous beetle: *Crowsoniella relicta* n. gen. n. sp. of Archostemata Tetraphaleridae from Central Italy. *Bolletino del Museo Civico di Storia Naturale, Verona*, **2**, 445–458.

Patterson, N.F. (1938) Note on the external morphology of South African specimens of *Micromalthus* (Coleoptera). *Transactions of the Royal Entomological Society of London*, **87**, 287–290.

Pringle, J.A. (1938) A contribution to the knowledge of *Micromalthus debilis* LeC. (Coleoptera). *Transactions of the Royal Entomological Society of London*, **87**, 271–286, 1 pl.

Röber, H. (1942) Morphologie des Kopfes und des Vorderdarmes der Larve und Imago von *Sialis flavilatera. Zoologische Jahrbücher für Anatomie*, **67**, 61–118.

Ross, D.A. & Pothecary, D.D. (1970) Notes on the adults, eggs, and first-instar larvae of *Priacma serrata* (Coleoptera: Cupedidae). *Canadian Entomologist*, **102**, 346–348.

Švácha, P., Wang, J.-J. & Chen, Sh.-Ch. (1997) Larval morphology and biology of *Philus antennatus* and *Heterophilus punctulatus*, and systematic position of the Philinae (Coleoptera: Cerambycidae and Vesperidae). *Annales de la Société Entomologique de France (N.S.)*, **33**, 323–369.

Swofford, D.L. (1991) *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.* Illinois Natural History Survey, Champaign, Illinois.

Vulcano, M.A. & Pereira, F.S. (1975) Cupesidae (Coleoptera). *Arquivos do Instituto Biológico, São Paulo*, **42**, 31–68.

Wheeler, Q. (1991) Lymexylidae (Lymexyloidea). *Immature Insects*, Vol. 2 (ed. by F. W. Stehr), pp. 446–447. Kendall/Hunt Publishing Co., Dubuque, Iowa.

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Appendix 1. Data matrix. Question marks refer to missing data, hyphens to inapplicable characters.

	Characters																																																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Sialis	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Trachypachus	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0
Micromalthus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	1	0	2	0	1	0	0	3	3	0	0	0	1	0	0	0	1
Priacma	?	1	1	?	1	?	1	?	1	1	1	1	?	?	?	?	?	0	?	?	?	?	0	?	0	?	?	?	0	0	1	?	0	1	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1
Tenomerga	1	1	1	1	1	?	1	?	1	1	1	1	1	1	?	?	?	1	1	1	1	1	0	0	1	1	1	1	0	0	1	?	0	1	1	0	1	0	0	1	1	1	1	0	2	1	0	1	0	1
Distocupes	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1	1	1	0	2	1	0	1	0	1
Rhipsideigma	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	0	0	1	1	1	1	0	2	1	0	1	0	1
Omma	0	1	2	1	0	?	0	?	1	0	0	1	1	1	?	?	?	0	0	1	1	0	0	0	0	0	0	0	0	0	1	?	0	1	1	2	0	1	0	0	2	1	0	0	0	1	0	0	1	0
Tetraphalerus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	0	2	1	0	0	0	1	0	0	1	?
Crowsoniella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	2	0	–	0	0	4	2	1	0	0	1	0	0	1	0
Hylecoetus	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	?	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0	0	0	0	1	0	1	1	0	0	1
Coccinella	0	0	0	0	0	0	1	0	0	1	–	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0	5	0	0	1	0	1	1	1	0	0
Satonius	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	4	1	0	0	0	0