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Description of the larva of *Rhipsideigma raffrayi* (Coleoptera: Archostemata), with phylogenetic and functional implications

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Abstract. Larvae of *Rhipsideigma raffrayi* are described in detail and those of *Distocupes varians* are re-examined. Their morphological structures are evaluated with respect to their functional and phylogenetic significance. Larvae of *Rhipsideigma* are woodborers with a straight body and a wedge-shaped head capsule. Most of their apomorphic features are correlated with their xylobiontic habits. The strong mandibles, the sclerotized ligula and the wedge-shaped head enable the larvae to penetrate rotting wood. The broadened prothorax, prosternal asperities, tergal ampullae, the short legs, and eversible lobes of segment IX play an important role in locomotion in galleries within rotting wood. Leg muscles are weakly developed, whereas the dorsal, pleural and ventral musculature is complex. The larval features allow *Rhipsideigma* to be placed in the clades Archostemata, Cupedidae + Micromalthidae, Cupedidae, Cupedidae excl. *Priacma*, and Cupedidae excl. *Priacma* and *Distocupes*. The monophyly of Cupedidae and Cupedidae, excluding *Priacma*, so far is only supported by apomorphies of the adults. However, the presence of glabrous patches on the prosternum and of a medially divided field of asperities may be larval apomorphies of the family. A clade, which comprises *Rhipsideigma*, *Tenomerga* and probably other genera of Cupedidae with hitherto unknown larvae, is well supported by larval apomorphies such as the broadened prothorax, the presence of coxal asperities and the presence of a distinct lateral longitudinal bulge. Increased numbers of antennomeres and labial palpomeres are apomorphies only found in larvae of *Distocupes*.

INTRODUCTION

The cupedid genus *Rhipsideigma* was designated by Neboiss (1984). It is represented by one species in East Africa, *R. cretaceocincta* (Kolbe, 1897) and four species in Madagascar (Neboiss, 1984, 1989). The distribution of *Rhipsideigma raffrayi* (Fairmaire, 1884) (Fig. 1) is Northern Madagascar according to Neboiss (1984). However, the hitherto undescribed larvae were collected, together with adults, in the central part of the island (21.–22.11.1996, Madagascar, Manankazo env., Ambohitantely Nat. Res., Petr Švácha lgt.), which considerably extends the range of this species. Little is known about the biology of *Rhipsideigma*. However, the fact that the larvae of *R. raffrayi* were collected in dark rotting logs on the ground (Švácha, pers. comm.) strongly suggests that they develop in fungus-infested wood like other species of Cupedidae (Lawrence, 1991).

Little is known about the immature stages of Archostemata. Only the larvae of *Micromalthus debilis* LeConte, 1878 are described in detail (Beutel & Hörnschemeyer, 2002). Descriptions of larvae of *Omma* Newman, 1839 (Ommatidae; Lawrence, 1999), *Priacma serrata* LeConte, 1861 (first instar; Ross & Pothecary, 1970), *Tenomerga* spp. (Böving & Craighead, 1931; Fukuda, 1938) and *Distocupes varians* Lea, 1902 (Neboiss, 1968) only cover external features and some are very short and not well illustrated. Therefore, the main purpose of this study is to provide comprehensive information on the larval morphology of Cupedidae. The larva of the madegassan species *R. raffrayi* Neboiss, 1984 is described in detail and the larva of *Distocupes varians* is re-examined. The morphological data are interpreted with respect to their function, and the phylogenetic position of *Rhipsideigma* is discussed.

MATERIAL AND TECHNIQUES

Larvae of *R. raffrayi* along with adults in the same habitat were collected from rotting logs on the ground. Three specimens, probably one penultimate instar and 2 ultimate instars, were fixed in boiling water and then transferred to ethanol, one slightly damaged larva (probably ultimate instar) was directly transferred to Pampel's fluid. The latter specimen was used for dissection and microtome sections.

For sectioning, selected body parts were embedded in Historesin. Sections were cut at 5 µm with a Microm microtome and stained with methylene blue and acid fuchsin. Drawings were made using an ocular grid or a camera lucida (cross sections).

V. Kéler's (1963) nomenclature is used for muscles of the head and Larsén's (1966) nomenclature for thoracic muscles.

List of larval material compared

Cupedidae: *Distocupes varians* Lea, 1902 (ethanol, one specimen dissected)

Micromalthidae: *Micromalthus debilis* (Bouin, micr.= microtome sections, SEM) (from decaying wood, collected in Madison, Wisconsin by D. K. Young; material deposited in collection of R. G. Beutel).

Ommatidae: *Omma* sp. (ethanol; examined at the Australian National Insect Collection, Canberra)

Lymexylidae, Lymexyloidea: *Hylecoetus dermestoides* (Linnaeus, 1761)

Silvanidae, Cucujoidea: *Oryzaephilus* sp., *Silvanus* sp.

Prostomidae, Tenebrionoidea: *Prostomis* sp. (Bouin, micr., SEM)

Fig. 1. Adult of *Rhipsideigma raffrayi*, dorsal view, fotography courtesy of Ivo Jeniš.

Pyrochroidae: *Pyrochroa* sp. (Bouin, micr., SEM)
Pythidae: *Pytho* spp. (Kahle's, dissected)

RESULTS

The description of internal structures is based on a larva slightly damaged in the posterior thoracic region.

General appearance (Fig. 2)

Length of larvae up to 38 mm. Most parts of elongate body unpigmented or of a light brown colour. Thorax short in relation to rest of body. Prothorax broader and longer than meso- and metathorax. Legs very short. Abdomen elongate, slightly widening posteriorly, very slightly flattened, with tergal ampullae and a longitudinal semi-membranous lateral bulge. Segment IX sclerotized and pointed apically.

Head capsule (Figs 3–5)

Maximum width 3.78 mm. Prognathous, posterior part retracted into voluminous semi-membranous collar region of prothorax (Fig. 3). Most parts cream-coloured or testaceous. Broad anterior margin of frons and lateral area posterior to antennal articulation dark brown. Head almost 2x as broad as long, strongly rounded laterally and

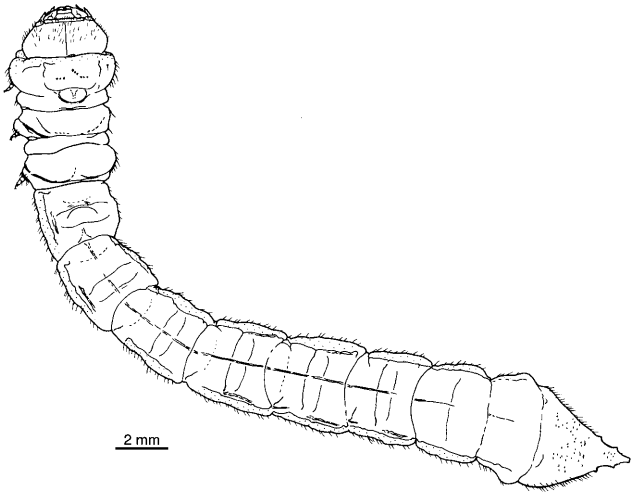


Fig. 2. Larva of *R. raffrayi*, dorsal view.

widened posteriorly. Greatest width posterior to mid-length, distinctly narrowed in occipital region. Well defined neck region absent. Dorsal side longer than ventral side. Hind margin with deep dorsal and ventral triangular emargination. Setae thin, distribution as shown in Figs 3–5. Stemmata absent. Labrum separated from clypeus by a distinct sclerotized fold (Fig. 9). Clypeus large and trapezoid, unpigmented and transparent, separated from dark and strongly sclerotized anterior margin of frons by internal transverse sulcus. Frons completely fused with adjacent parts of head capsule. Frontal suture absent or vestigial, posterior part possibly represented by very faint diverging lines. Coronal suture absent. Median endocarina present, unforked, almost reaching anterior frontal margin. Internally represented by very extensive median apodeme. Maxillary grooves deep, separated from each other by slightly narrowed posterior part of labium. Hypostomal rods distinct, diverging posteriorly. Gula represented by semi-circular, semi-membranous area, posteriorly fused to submento-mentum, covered by unsclerotized, semi-circular fold of anterior prosternal margin.

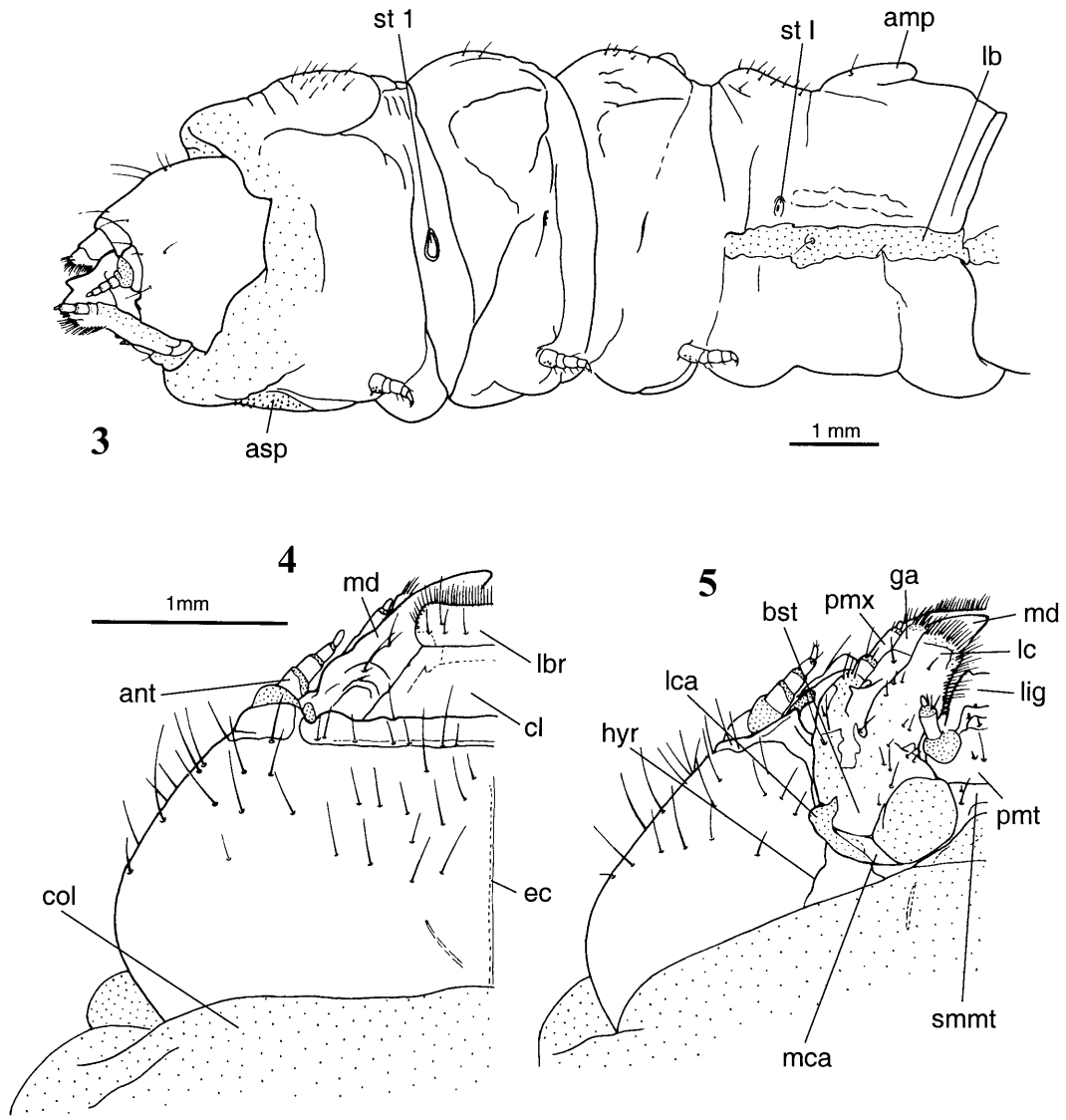
Internal skeletal structures (Figs 6, 7, 9)

Postoccipital ridge very broad laterally. Hypostomal rods internally represented by strong longitudinal sulci. High ridges enclose gula and submentomentum, anteriorly continuous with short and flat posterior tentorial arms. Apical part of posterior arm laterally attached to anatomical mouth. Tentorial bridge, dorsal- and anterior tentorial arms absent.

Labrum (Figs 3, 4, 9, 12)

Transverse, rounded laterally, slightly concave anteriorly. Distribution of setae on dorsal side see Fig. 4. Anterior margin very densely set with hairs.

Musculature (Fig. 9): M 7 (M. labroepipharyngalis): absent; M 9 (M. frontoepipharyngalis): present, strongly developed, composed of 2 subcomponents, O: anterior frontal region, posterior edge of median endocarina and



Figs 3–5. 3 – larva of *R. raffrayi*, head, thorax and abdominal segment I, lateral view. Abbreviations: amp – ampullae, asp – asperities, lb – lateral bulge, st1 – prothoracic spiracle, stI - spiracle of abdominal segment I. 4–5. Larval head of *R. raffrayi*. 4 – dorsal view; 5 – ventral view. Abbreviations: ant – antenna, bst – basistipes, cl – clypeus, col – cervical collar, ec – endocarina, ga – galea, hyr – hypostomal rods, lbr – labrum, lc – lacinia, lca – lateral part of cardo, lig – ligula, mca – mesal part of cardo, md – mandible, pmx – maxillary palp, pmt – prementum, smmt – submento-mentum.

adjacent dorsomesal part of postoccipital ridge, I: epipharynx, anterior to anatomical mouth.

Antenna (Fig. 4)

4-segmented, short, inserted on antennomere-like, membranous structure on dark brown, strongly sclerotized craniolateral margin of head capsule. Antennomere I about as long as broad, antennomeres II-IV slightly longer. Width of antennomeres decreasing towards apex. Sensorial appendage of antennomere III present but small, inserted on ventral side. Apex of distal antennomere with minute sensorial spines.

Musculature (Fig. 8): Mm. tentorioscapalis anterior, posterior, medialis (Mm. 1, 2 and 4): 3 thin muscles, O: anterolateral frontal region, I: base of antennomere I.

Mandibles (Figs 10, 11)

Very strongly sclerotized and pigmented, almost black. Short and compact, roughly triangular, with three strong, shovel-like apical teeth and a distinctly delimited, quadrangular smooth mola. Retinaculum or moveable appendage absent. One thin seta inserted on distinct dorsolateral bulge.

Musculature (Figs 6, 9): M. 11 (M. craniomandibularis internus): largest muscle of head, O: postoccipital ridge, extensive parts of dorsal, dorsolateral, lateral and ventrolateral areas of head capsule, I: adductor tendon; M. 12 (M. craniomandibularis externus): moderately large, O: laterally from posterior part of head capsule, I: abductor tendon.

Maxilla (Figs 5, 6)

Inserted in deep fossa maxillaris, with nearly round, prominent membranous articulatory area lateral to submento-mentum. Separated from mandible by broad transverse bar (Fig. 6). Composed of cardo, stipes, galea, lacinia and 3-segmented palp. Cardo divided into sclerotized mesal part and semi-membranous lateral part. Not clearly separated from stipes mesally, stipito-cardinal hinge reduced. Stipes divided into proximal basistipes and distal mediostipes by very indistinct, interrupted transverse line. Most parts semi-membranous, area proximal to galea sclerotized. Palpifer indistinct. Galea 2-segmented, with semi-membranous proximal part and sclerotized distal part. Apex with a group of elongate spines. Lacinia broad, sclerotized except for anterior and mesal margin, very densely set with mesally directed hairs. Palpomere I about as long as broad, II elongate, III small and subulate.

Maxillary musculature (Figs 6, 7): M. 15 (M. craniocardinalis), absent; M. 17 (M. tentoriocardinalis), 2 short but strong bundles, O: anterior part of gular ridge, I: ventral surface of sclerotized part of cardo; M. 18 (M. tentoriostipitalis): not identified as separate muscle, probably combined with M. 19; M. 19 (M. craniolacinialis), composed of 2 flat, parallel bundles; O: posterior edge of gular ridge and ventrally from posterior head capsule, I: dorsally on transparent area proximal to base of lacinia; M. 21 (M. stipitolacinialis), O: base of basistipes, I: base of lacinia; Mm. 22, 23 (M. stipitopalpalis externus and internus), O: ventrally on basistipes, I: dorsally on base of palpomere I.

Labium (Figs 5, 9, 13)

Submentum and mentum fused, very short, slightly narrowed between maxillary grooves, posteriorly continuous with gular region. Pair of short setae present on anterior mental region and pair of long setae on posterior submental part. Prementum markedly developed, larger than submento-mentum. With one long and one short seta close to the median line and one long seta on large articulatory membrane of palp. Palpomere I about 2 x as long as broad. Palpomere II small, subulate. Ligula large, wedge-shaped, almost black and strongly sclerotized, with transverse subapical edge and slightly emarginate cranial edge.

Musculature: M. 28 (M. submentopraementalis), M. 29 (M. tentoriopraementalis inferior), M. 30 (M. tentoriopraementalis superior), M. 34 (M. praementopalpalis ext.), transverse muscle: absent.

Epipharynx (Figs 9, 12)

Ventral side of labrum sclerotized, densely covered with regularly arranged, mesally directed setae. Posteromedian part semi-membranous, smooth and glabrous. Lateral suspensoria sclerotized, well developed. Ventral side of clypeus lateral to suspensoria glabrous, unpigmented and transparent.

Musculature (Fig. 9): M. 43 (M. clypeopalatalis): not identified, probably absent.

Transverse epipharyngeal muscles are absent.

Hypopharynx (Figs 6, 9, 13)

Hypopharynx fused with anterior part of labium, anteriorly continuous with upper surface of prementum. Short, slightly concave, enclosed by distinct lateral edges. Hairs, bristles, or densely pubescent areas absent. Posterior part laterally not fused with posterior part of epipharynx, prepharyngeal tube absent.

Musculature (Fig. 9): M. 41 (M. frontohypopharyngalis): unusually large muscle, represented by 2 subcomponents, M. 41a, O: posterior part of frons and median endocarina, M. 41b, O: dorsomesally from postoccipital ridge, immediately close to posterior component of M 9; I: both subcomponents attached to posterolateral edge of hypopharynx by means of a tendon. M. 42 (M. tentoriohypopharyngalis): thin bundle, O: gular ridge, I: ventrolaterally at anatomical mouth; it cannot be fully excluded that this is a ventral dilator of the anterior pharynx.

Pharynx (Figs 9, 13)

Cylinder shaped, straight and wide.

Musculature (Figs 6, 9, 13): M. 45 (M. frontobuccalis anterior), flat, parallel-sided muscle between M. 9 and M. 41, O: anterior frontal region, lateral to anterior edge of endocarina; I: dorsolaterally on pharynx, immediately posterior to anatomical mouth; M. 46 (M. frontobuccalis posterior): composed of a strong mesal component of seven parallel bundles, O: successively from posterodorsal part of head capsule, mesad to M. 41, I: successively on dorsal folds of pharynx; M. 51 (M. verticopharyngalis): absent; M. 52 (M. tentoriopharyngalis): composed of two strong series of thin bundles, O: gular ridge, I: ventrolaterally and laterally on posterior pharynx; ring musculature: well developed.

Cerebrum and suboesophageal ganglion (Figs 9, 14)

Small in relation to head size. Located in posterior head region.

Cephalic glands (Fig. 9)

Gland-like structures with coiled duct coiled duct present beetwen gular ridges. Orginate in anterior thorax.

Extrinsic head muscles (Fig. 9)

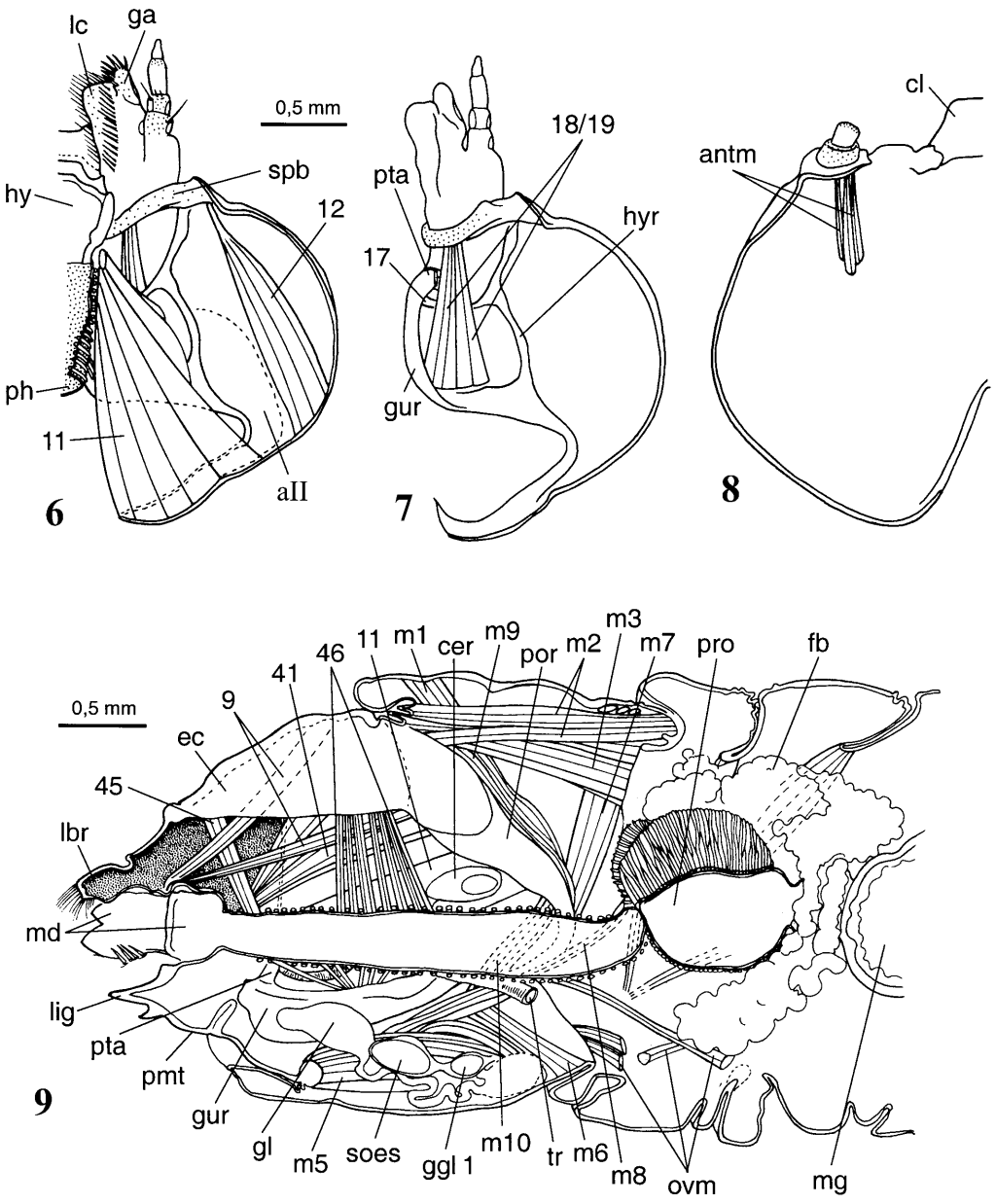
Dorsal muscles: M 1 (M. pronoti primus; MI_2, Speyer, 1922: larva of *Dytiscus marginalis* Linnaeus, 1758), O: medially on anterior protergum, I: dorsolaterally and laterally on postocciput.

M 2 (M. pronoti secundus; MI_1, Speyer, 1922), pair of parallel muscles, O: medially on first phragma, I: medially on dorsal emargination of head.

M 3 (M. pronoti tertius; MI_1, Speyer, 1922), flat and fan-shaped, O: first phragma, laterad to M 2, I: postocciput, laterad to M 2.

M 4 (M. pronoti quartus; $MI_{3a,b}$, Speyer, 1922), not identified, probably absent.

Ventral muscles: M 5 (M. prosterni primus; MI_{4a}, Speyer, 1922), strong bundle composed of several subcomponents, O: on fold separating prosternum from poststernal bulge, below M 6, I: medially, on posteroventral emargination of the head capsule.



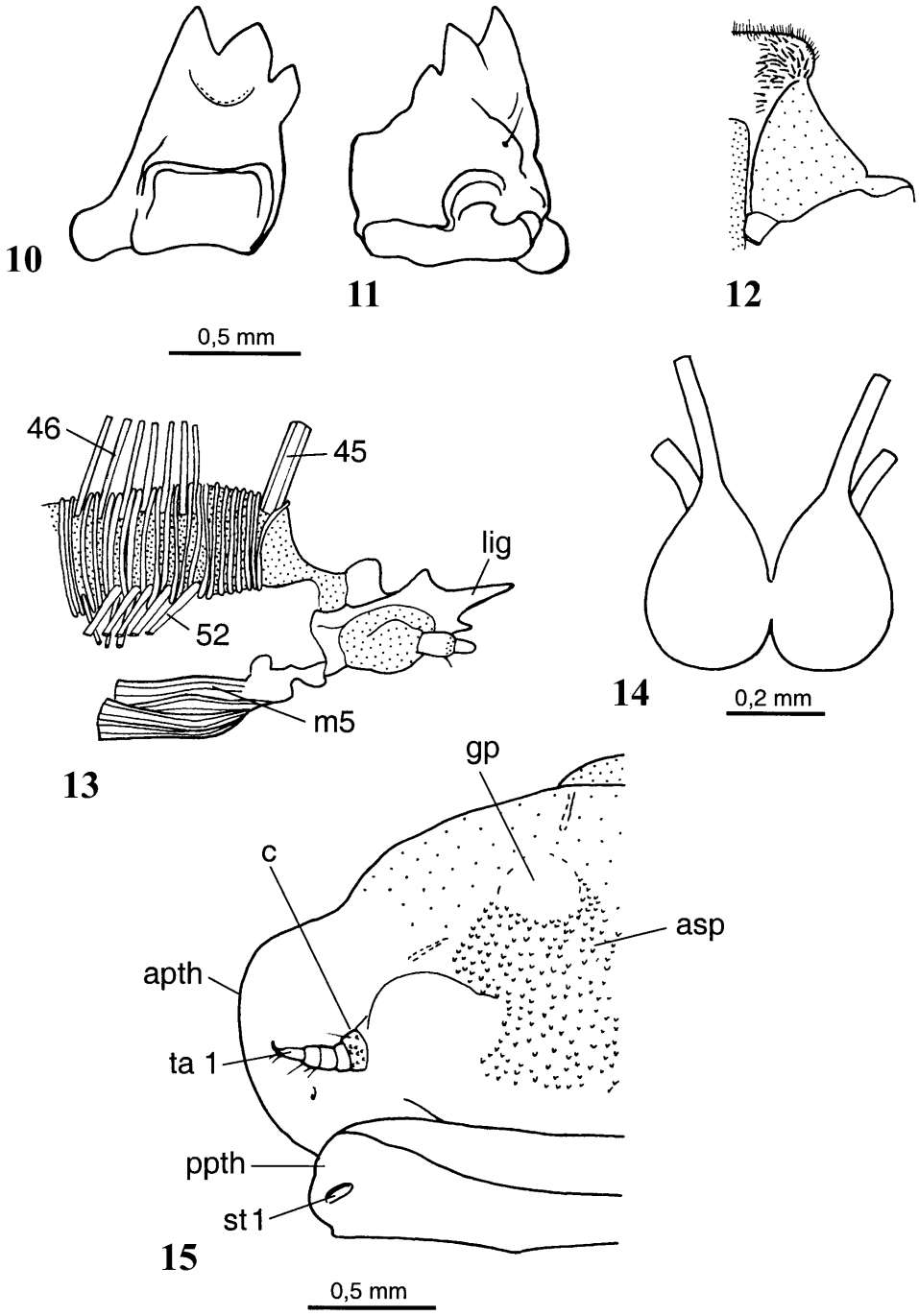
Figs 6–9. 6–8. Larval head of *R. raffrayi*, horizontal sections. 6 – ventral part; 7 – ventral part, labium, hypopharynx, pharynx, mandible muscle removed; 8 – dorsal part. Abbreviations: antm – antennal muscles, aII – attachment area of M. craniomandibularis internus, cl – clypeus, ga – galea, gur – gular ridge, hy – hypopharynx, hyr – hypostomal rods, lc – lacinia, ph – pharynx, pta – posterior tentorial arm, spb – mandibular-maxillary separating bar, 11 – M. craniomandibularis internus, 12 – M. craniomand. ext., 17 – M. tentoriocardinalis, 18 – M. tent.-stipitalis, 19 – M. craniolacinialis. 9. Larva of *R. raffrayi*, head and prothorax, sagittal section. Abbreviations: cer – cerebrum, ec – endocarina, fb – fat body, ggI1 – prothoracic ganglion, gl – gland, gur – gular ridge, lbr – labrum, lig – ligula, md – mandible, mg – midgut, ovm – oblique ventral muscles, pmt – prementum, por – postoccipital ridge, pro – proventriculus, pta - posterior tentorial arm, soes – suboesophageal gangion, tr – trachea, 9 – M. frontoepipharyngalis, 11 – M. craniomandibularis internus, 41 – M. frontohypopharyngalis, 45 – M. frontobuccalis anterior, 46 – M. frontobucc. posterior, m1 – M. pronoti primus, m2 – M. pronoti secundus, m3 – M. pronoti tertius, m5 – M. prosterni primus, m6 – M. prosterni secundus, m7 – M. dorsoventralis primus, m8 – M. dorsoventralis secundus, m9 – M. dorsoventralis tertius, m10 – M. dorsoventralis quartus.

M 6 (M. prosterni secundus; MI_{4b}, Speyer, 1922), flat and broad muscle, O: mesally on ventral fold separating anterior from posterior prothorax, I: laterally on cervical membrane.

Dorsoventral muscles: M 7 (M. dorsoventralis primus; MI_{7a}, Speyer, 1922), O: posterior margin of anterior part of protergum, I: laterally on postoccipital ridge.

M 8 (M. dorsoventralis secundus; MI_{7b}, Speyer, 1922), one slender muscle, O: anterolateral corner of mesotergum, I: ventrolaterally on postoccipital ridge.

M 9 (M. dorsoventralis tertius; absent in *D. marginalis*; Speyer, 1922), probably represented by one slender muscle, O: anterior protergum, laterad to M 1, I: laterally on postocciput.



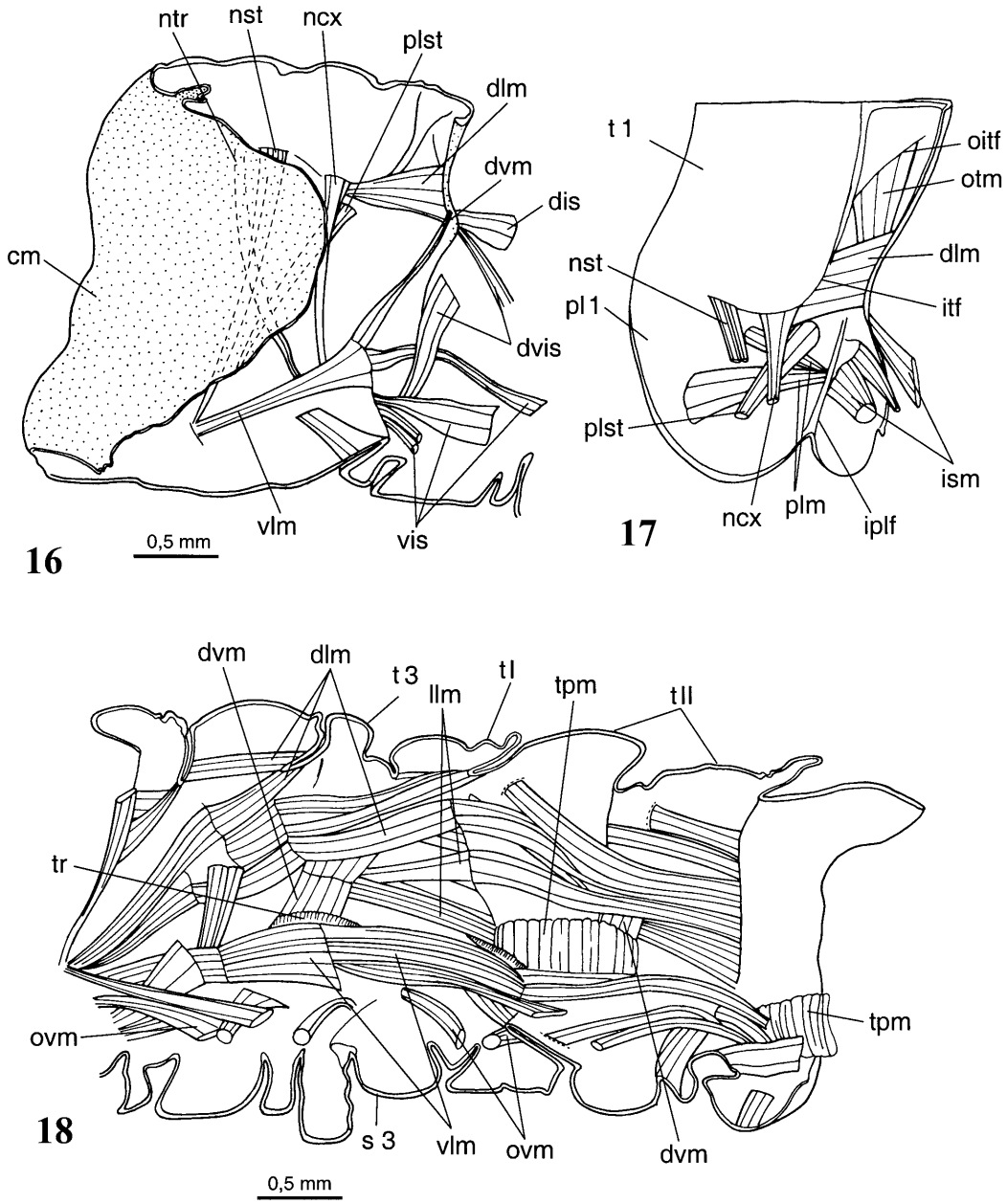
Figs 10–15. Larva of *R. raffrayi*. 10–11. Mandibles. 10 – mesal view; 11 – dorsal view; 12 – labrum and epipharynx, ventral view; 13 – labium and pharynx, lateral view; 14 – cerebrum, dorsal view. Abbreviations: lig – ligula, m5 – M. prosterni primus, 45 – M. frontobuccalis anterior, 46 – M. frontobucc. posterior, 52 – M. tentoriopharyngalis posterior; 15 – prothorax, ventral view. Abbreviations: apth – anterior part of prothorax, asp – asperities, c – coxa, gp – glabrous patches, ppth – posterior part of prothorax, st1 – prothoracic spiracle, ta1 – tarsus.

M 10 (M. dorsoventralis quartus; MI_6, Speyer, 1922), O: anterior prosternum, I: laterally on postoccipital ridge.

M 11 (M. dorsoventralis quintus; MI_{11}, Speyer, 1922?), absent

Prothorax (Figs 2, 3, 15–17)

Connected with head by voluminous, semimembranous cervical collar, with separate, semimembranous ventromedian extension (Figs 3, 5). Longer and broader than following thoracic segments (Fig. 2). Divided into a longer anterior part and a shorter, ring-like posterior section (Figs 3, 15). Both parts separated by distinct fold (Fig. 3). Protergum sclerotized and shiny, but with same pigmentation as other parts of prothorax. With distinct posteromedian extension resembling a scutellum. Broad anterior part with moderately distinct shoulder region. Pleura of anterior and posterior part rounded and unsclerotized, with dense groups of very fine setae. Cen-

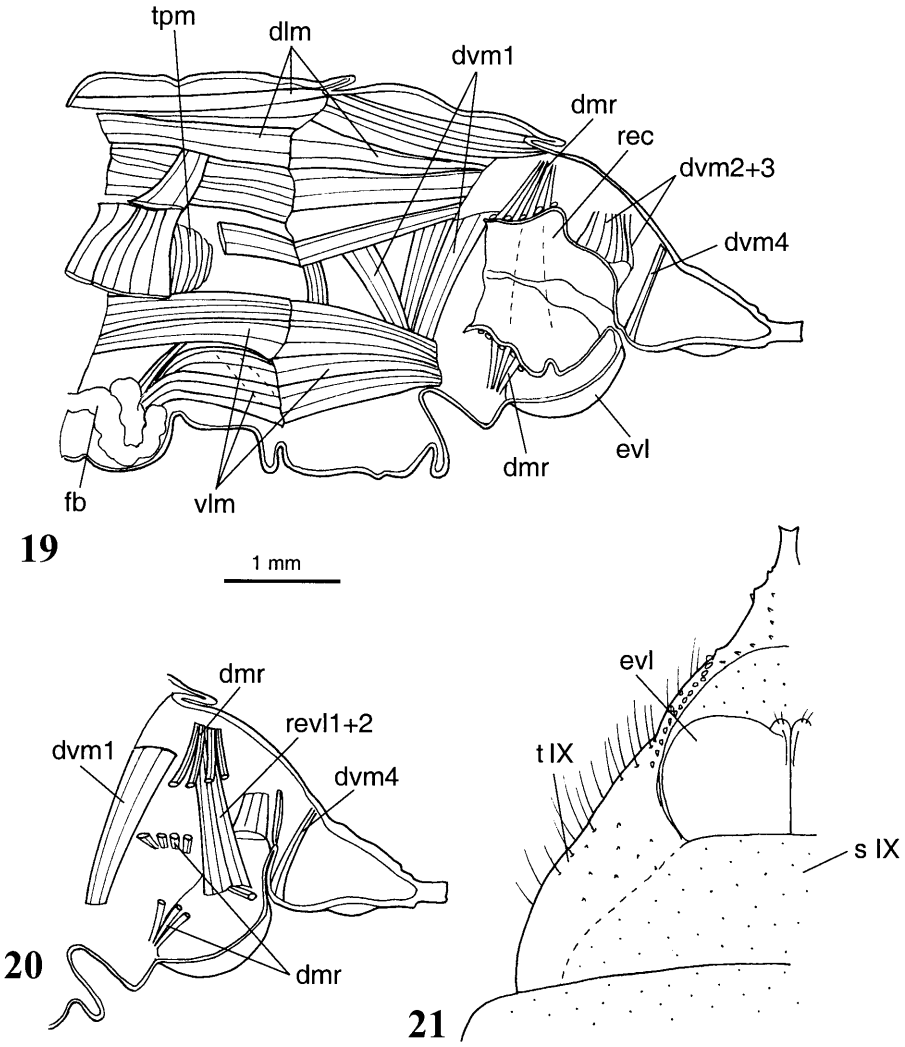


Figs 16–18. 16–17. Larva of *R. raffrayi*, prothorax. 16 – sagittal section, cervical muscles partly removed; 17 – sternum and pleura. Abbreviations: cm – cervical membrane, dis – dorsal intersegmental muscle, dlm – dorsal longitudinal muscles, dvis – dorsoventral intersegmental muscle, dvm – dorsoventral muscle, iplf – intrapleural fold, ism – intersegmental muscle, itf – intratergal fold, ncx – notocoxal muscle, nst – notosternal muscle, ntr – nototrochantinal muscle, oitf – oblique intratergal fold, otm – oblique tergal muscle, pl1 – propleura, plm – intrapleural muscles, plst – pleurosternal muscle, t1 – protergum, vis – ventral intersegmental muscle, vlm – ventral longitudinal muscles. 18. Larva of *R. raffray*i, mesothorax, metathorax and anterior abdominal segments, sagittal section. Abbreviations: dlm – dorsal longitudinal muscles, dvm – dorsoventral muscles, llm – lateral longitudinal muscle, ovm – oblique ventral muscle, s 3 – metasternum, tpm – tergopleural muscles, tr – trachea, t 3 – metatergum, t I, II – abdominal terga I, II, vlm – ventral longitudinal muscles.

tral area of sternum slightly sclerotized, with paired smooth and pigmented patches, and larger medially divided field of posteriorly directed, dark brown spines (= paired patches of asperities; Lawrence, 1991; Fig. 15). Legs 6-segmented, very short. Inserted ventrolaterally on an elevation anteriorly delimited by a precoxal rim. Composed of coxa with ventral spines, trochanter, moderately elongate femur, short tibia and moderately elongate, cone-shaped tarsus (Fig. 15). Tarsal apex with two setae. Pretarsus formed by single claw. Spiracle located laterally in pleura of posterior section of prothorax (Fig. 3).

Musculature (Figs 9, 16, 17; cervical muscles see above):

With complex system of dorsal, ventral and dorsoventral muscles (dis, vis, dvis). Flat and broad longitudinal- (dlm) and oblique (otm) muscles arise from intratergal



Figs 19–21. Larva of *R. raffrayi*, posterior abdominal segments. 19 – sagittal section, segments VIII and IX; 20 – sagittal section, segment IX, hind gut removed; 21 – VII, VIII and IX, ventral view. Abbreviations: dlm – dorsal longitudinal muscles, dmr – dilators of rectum, dvm – dorsoventral muscles, evl – eversible lobes, fb – fat body, rec – rectum, revl – retractors of eversible lobes, s IX – sternum IX, tpm – tergopleural muscle series, t IX – tergum IX, vlm – ventral longitudinal muscles.

folds and insert on posterior tergal margin. Two slender bundles originate from lateral tergal margin (nst) and insert on precoxal rim. Broad and flat muscle with same insertion originates from the ventral fold separating the anterior and posterior part of the prothorax (vlm). Pleurosternal muscle (plst) originates from posterodorsal pleural area. Two muscles with origin on anterior and dorsal pleura insert laterally on intrapleural fold (plm). Two thin extrinsic leg muscles, probably M. nototrochantinalis (ntr) and M. notocoxalis (ncx), originate from lateral tergal area. One short muscle, probably M. furcacoxalis, originates from small apodeme attached to precoxal rim.

Mesothorax (Figs 2, 3, 18)

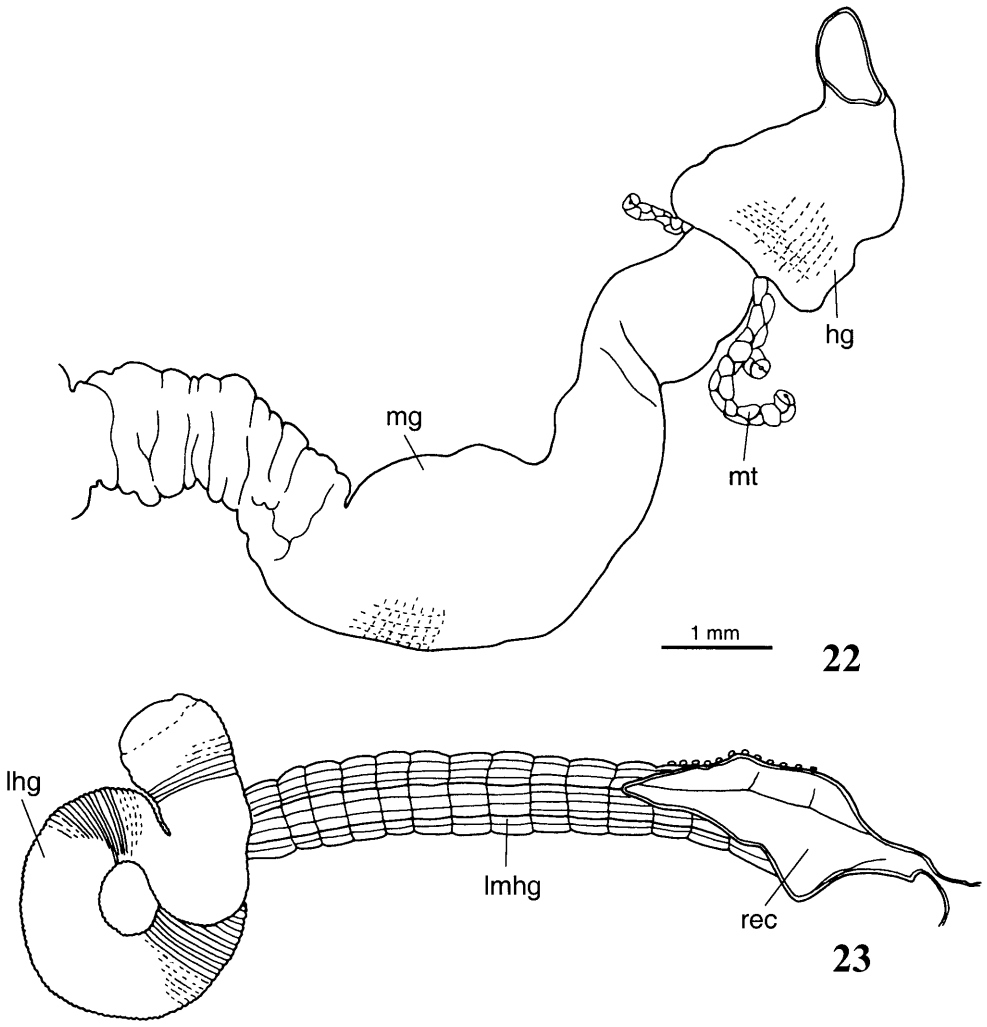
Shorter and narrower than prothorax, but also divided into longer anterior- and shorter, ring-like posterior section. Tergum with distinct shoulder region, but less strongly sclerotized than pronotum and without posterior pseudo-scutellar region. Anterior part of pleura with slit-like depression superficially resembling a compressed, longitudinal spiracle. Postpleura distinctly bulging. Sternal field of asperities absent. Legs like those on prothorax.

Musculature (Fig. 18): longitudinal and oblique dorsal muscles (dlm), dorsolateral and lateral muscles well developed, attached to hind margin of prothorax. Large ventral longitudinal muscles (vlm) and several oblique, ventral muscles (ovm) attached to hind margin of anterior prosternal section. Leg muscles similar to those of prothorax.

Metathorax (Figs 2, 3, 18)

Similar to mesothorax in shape and extension, but posterior section less distinct (Fig. 3).

Musculature (Fig. 18): with strong dorsal (dlm), dorsolateral, lateral and ventral (vlm) musculature. Dorsoventral muscle broad and flat (dvm). Leg muscles similar to those of prothorax.



Figs 22–23. Larva of *R. raffrayi*, digestive tract. 22 – mid gut and anterior hind gut; 23 – posterior hind gut. Abbreviations: hg – hind gut, lhg – loop of hind gut, lmhg – longitudinal muscles of the hind gut, mg – mid gut, mt – malpighian tubules, rec – rectum.

Abdominal segments I-VII (Figs 2, 18)

Distinctly longer than thoracic segments, I slightly shorter than segments II-VI. Terga with indistinct anterior transverse ampulla and distinct posterior ampulla. Pleural membranes form a distinct lateral longitudinal bulge. Longitudinal impressions on the lateral area of the tergites indicate attachment of strong tergopleural muscles (tpm). Sternites with anterior-, intermediate- and posterior transverse line and posterior transverse bulge. Sternal asperities absent.

Musculature: with complex system of dorsal, lateral and ventral muscles (Fig. 18: dlm, llm, vlm). Dorsoventral muscles (dvm) less strongly developed. Compact, regular series of muscles extend between the lateral tergal impressions and the ventral side of the lateral longitudinal bulges (see above; tpm). Oblique, thin muscles, with origin on mesal and lateral parts of sternites, insert immediately close to the ventral attachment area of the tergopleural muscles.

Abdominal segment VIII (Figs 2, 19)

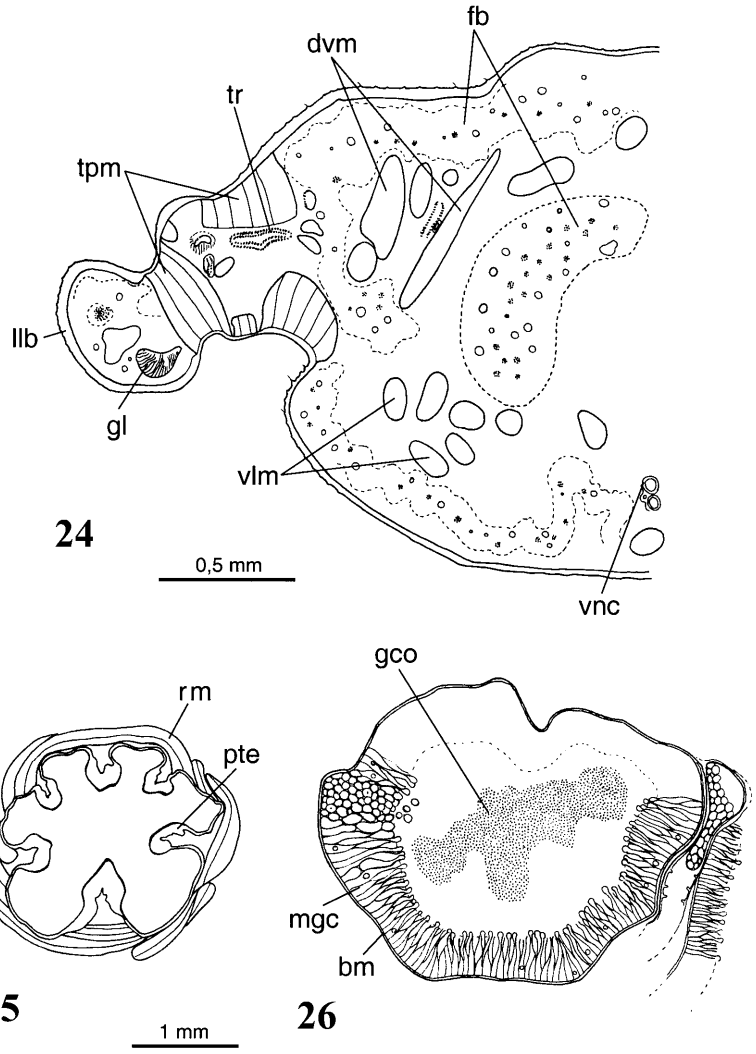
Shorter than anterior abdominal segments, with indistinct ampullae.

Musculature: with several dorsoventral muscle bands and very strong dorsal, lateral and ventral muscles. Tergo-pleural muscle series absent.

Abdominal segment IX (Figs 19–21)

Tergite sclerotized, extends to ventral side of segment. With apically truncate, narrow sclerotized apex with several subapical teeth. Dorsal side with minute spines, more distinct pointed tubercles present posterolaterally. Lateral margin with a row of thin hairs. Sternum well developed anteriorly, unsclerotized, indistinctly separated from tergum. Urogomphi absent. Large eversible lobes present posterior to sternum.

Musculature (Figs 19, 20): Large dorsoventral muscle originates from anterior tergal margin and inserts on hind margin of sternite VIII (dvm1). A broad and a narrow dorsoventral muscle insert immediately lateral to the eversible lobes (dvm2+3) and an additional dorsoventral muscle connects the posterior part of tergite IX with the posteroventral wall of the segment (dvm4). Two dorsolateral muscles insert on the eversible lobe (revl1+2) and an additional thin muscle arises between them. Rectum



Figs 24–26. Larva of *R. raffrayi*, cross sections. 24 – anterior part of segment III, gut removed; 25 – proventriculus; 26 – anterior mid gut. Abbreviations: bm – basement membrane, dvm – dorsoventral muscles, fb – fat body, gco – gut contents, gl – glands, llb – lateral longitudinal bulge, mgc – mid gut cells, pte – proventricular teeth, rm – ring muscles, tpm – tergopleural muscles series, tr – trachea, vlm – ventral longitudinal muscles, vnc – ventral nerve cord.

suspended by series of thin dorsal, ventral and lateral dilators (dmr).

Abdominal segment X (Fig. 21)

Not visible externally as a distinct segment or proleg-like structure. Possibly represented by eversible lobes on ventral side of segment IX.

Spiracles (Fig. 3)

All spiracles of longitudinal-annular type. Prothoracic spiracle larger than those of abdominal segments I-VIII.

Postcephalic gut (Figs 9, 22, 23, 25, 26)

Oesophagus similar to pharynx, wide, with well developed layer of ring muscles (Fig. 9). Posterior part of foregut widened, forming a proventriculus with internal cuticular teeth and well developed ring musculature. Midgut elongate, with very high cylindrical cells and a basement membrane (Figs 22, 26). Anterior part with folds, middle part moderately widened. Midgut separated from hindgut by distinct valvula pylorica (Fig. 22). Anterior hindgut widened, with thin muscle layer. Middle part forms loop with strongly developed ring musculature (Fig. 23). Posterior part straight, with well developed longitudinal muscles arranged in regular sections. Rectum widened, with ring muscles and dorsal-, lateral- and ventral dilators (Figs 19, 20). Anus opens between eversible lobes.

Malpighian tubules (Fig. 22)

Four free malpighian tubules originate at midgut-hindgut border.

Postcephalic glands (Fig. 24)

Glands covered by the strong intrinsic muscle bundles of the lateral longitudinal bulge present in abdominal segments I-VII.

DISCUSSION

Most apomorphic features found in larvae of *Rhipsideigma raffrayi* are probably associated with its xylobi-

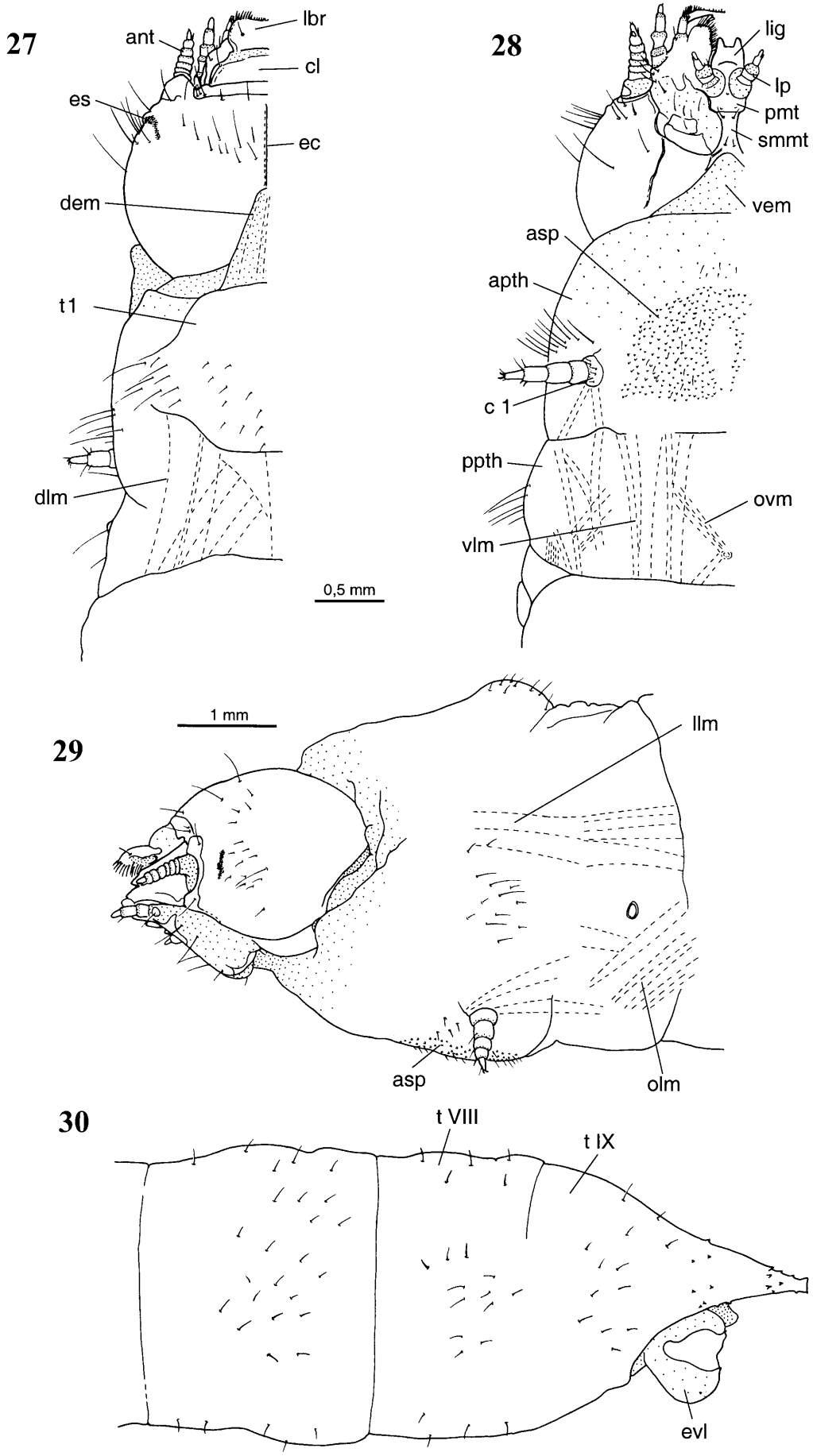
ontic habits. The functional interpretations that follow should be treated tentatively as they are not based on experiments or direct observation. The mandibles of larvae of *R. raffrayi* (Figs 10, 11) are stout and tridentate like in other cupedid and micromalthid larvae and some of the larvae of other groups with wood-boring habits, such as Callirhipidae or Cerambycidae (Lawrence, 1991). The shovel-like apices remove material, thus enabling the larvae to bore into rotting wood. The sclerotized, wedge-shaped ligula (Figs 5, 9) may have an additional role. Contraction and relaxation of M. frontohypopharyngalis (M. 41) results in retraction and protraction of the labio-hypopharyngeal complex, and therefore in forward-backward movements of the ligula. This may facilitate the penetration of the substrate. The labium as a whole is shortened, the mentum and submentum are fused and retractor muscles are absent (Figs 5, 9). Other modifications of head structures probably correlated with wood-boring are short antennae, the absence of stemmata and the presence of an extensive median endocarina (Figs 3, 4). Similar derived features are also characteristic of the xylobiontic larvae of other groups of Coleoptera not closely related to Cupedidae (e.g. Buprestidae, Callirhipidae, Cerambycidae). The endocarina of cupedid larvae strengthens the head capsule and provides an additional area of attachment for the unusually large M. frontohypopharyngalis (Fig. 9). The head capsule of archostematan larvae is wedge-shaped as in larvae of Rhysodidae (Beutel, 1992), Buprestidae (Lawrence, 1991) and Cerambycidae (Lawrence, 1991; Švácha et al., 1997). In contrast, a globular head capsule is found in other larvae associated with wood such as Lymexylidae and Melandryidae (part.) (Wheeler, 1991; pers. obs. Beutel), and a strongly flattened head in larvae of Cucujidae, Pythidae (part.), Pyrochroidae and Prostomidae (pers. obs. Beutel). Larvae with the latter type of head seem to be restricted to subcortical habitats, whereas a globular head is at least present in some wood-boring forms.

External structures and the musculature of the body segments of larvae of *R. raffrayi* are also clearly modified compared to those features of larvae of other groups, e.g. *Dytiscus marginalis* Linnaeus, 1758 (Speyer, 1922) or *Tenebrio molitor* Linnaeus, 1758 (Jösting, 1942; Doyen, 1966). Larvae of *R. raffrayi* clearly belong to the straight wood-boring type as defined by Crowson (1981) and most derived features of their thorax and abdomen are probably adaptations for locomotion in galleries. The leg muscles are only feebly developed (Fig. 16). In contrast, the intersegmental muscles are unusually complex. It is plausible to assume, that they play an important role in locomotion together with tergal and sternal modifications and hemolymph pressure. The prothorax of larvae of *R. raffrayi* is broadened (Fig. 2) as in some buprestid and cerambycid larvae. Its broad shoulders and ventral asperities are used to anchor the anterior part of their body in a gallery. Then, the following segments are drawn forwards by contraction of the intersegmental muscles. It is likely that the tergal ampullae (Figs 2, 3) are used to hold the body segments in a fixed position for short intervals during the forward movement. The ventral eversible lobes, together with asperities of segment IX (Fig. 21) may then be used to fix the abdominal apex. The following anterior movement of the head and prothorax is achieved by the combined activity of the mandibles, sclerotized ligula, the short legs, and possibly hemolymph pressure.

The diet of larvae of *R. raffrayi* is unknown, but it is likely they feed on rotting wood infested with fungus and micro-organisms as do other larvae of Cupedidae and larvae of Micromalthidae (Lawrence, 1991). The preoral chamber, pharynx and the pharyngeal musculature is very similar to that found in larvae of *Micromalthus*. The dense brush of hairs on the lacinia is used to sweep material removed by the mandibular apices into the preoral chamber. The smooth mandibular mola (Figs 10, 11) is not suited for grinding, but rather for compacting material. No openings of glands in the anteroventral head region (Fig. 9) were found, but it is likely that the food is mixed with secretions in the preoral chamber. Transport to the posterior region of the digestive tract is achieved by alternating contractions of the muscles of the wide and straight pharynx (Fig. 9). A pumping apparatus is formed by the pharyngeal ring musculature and 2 corresponding sets of dorsal and ventral dilators, M. tentoriohypopharyngalis (M 42) and M. frontobuccalis anterior (M 45), and M. frontobuccalis posterior (M 46) and M. tentoriopharyngalis (M 52), respectively. The latter 2 muscles are composed of corresponding series of bundles (Fig. 9).

The postcephalic digestive tract is also similar to that of *Micromalthus debilis*. A proventriculus with cuticular teeth and well developed ring muscles is present (Fig. 25). It is likely that a compact cylindrical food mass is formed here. The mid gut (Figs 22, 26) is devoid of caeca and regenerative crypts and unusually long. Another feature shared by larvae of both taxa is the presence of a loop in the hind gut (Fig. 26), with well developed ring muscles. A similar condition is described for some wood-boring larvae of Cerambycidae (Švácha et al., 1997: fig. 53). The posterior hind gut of larvae of *R. raffrayi* is characterised by a regular and unusually strong longitudinal musculature (Fig. 26). Another characteristic feature is the presence of ventral, lateral and dorsal dilators of the rectum (Figs 19, 20).

The larval features examined allow *Rhipsideigma* to be placed in the clades Archostemata, Cupedidae + Micromalthidae, Cupedidae, Cupedidae excl. *Priacma*, and Cupedidae excl. *Priacma* and *Distocupes* (Fig. 31; Beutel & Hörnschemeyer, 2002). Dorsal and ventral posteromedian emarginations of the head capsule, a strongly reduced or absent frontal suture, a shortened postlabium with fused submentomentum, a sclerotized, enlarged and wedge-shaped ligula and tergal ampullae are presumptive autapomorphies of Archostemata. A posteriorly widened head capsule, presence of only one pair of stemmata or complete reduction, a distinctly delimited, quadrangular mola, sternal asperities and asperities on segment IX, the presence of a pointed, sclerotized process on tergite IX and the presence of eversible lobes on the terminal seg-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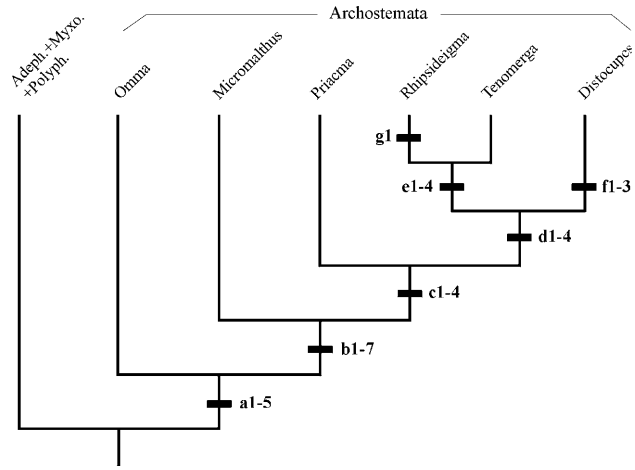

Fig. 31. Phylogenetic position of *Rhipsideigma raffrayi* and *Distocupes varians* within the Archostemata (modified from Beutel & Hörnschemeyer, 2002). Characters apply to larvae if not otherwise stated: a – Archostemata: 1 – head capsule with dorsal and ventral emarginations, 2 – frontal suture vestigial or absent, 3 – posterior labium shortened, submentum fused with mentum, 4 – ligula sclerotized, enlarged and wedge-shaped, 5 – tergal ampullae present. b – Micromalthidae + Cupedidae: 1 – head more than 1.7 times wider than long, 2 – stemmata reduced, 3 – mola of mandible quadrangular, with distinct margin, 4 – segment IX with ventrolateral eversible lobes, 5 – tergum IX with sclerotized posteromedian process, 6 – tergum IX with asperities, 7 – abdominal sternites of adults overlapping. c – Cupedidae (adults): 1 – cone-shaped protuberances on dorsal side of head, 2 – galea with narrow stalk and rounded, pubescent distal part, 3 – prosternal process reaching beyond hind margin of procoxae, 4 – propleuro-mesepisternal locking mechanism with propleural condyle and mesepisternal socket. d – Cupedidae excl. *Priacma* (adults): 1 – antennal insertion shifted dorsally, 2 – ligula with divided lobes, 3 – prosternal groove for protarsomeres, 4 – anteromedian pit of mesoventrite for reception of prosternal process present. e – Cupedidae excl. *Priacma* and *Distocupes*: 1 – prothorax broader than following segments, 2 – coxal asperities, 3 – lateral longitudinal bulge of abdominal segments present, 4 – strong tergopleural muscle series present. f – *Distocupes*: 1 – antenna composed of 7 antennomeres, 2 – labial palp composed of 3 palpomeres, 3 – subapical labial palpomere with sensorial appendages. g – *Rhipsideigma* (adults): 1 – apices of elytra extended into an acute point.

ment are presumptive synapomorphies of larvae of Cupedidae and Micromalthidae. The monophyly of Cupedidae and of Cupedidae excluding *Priacma* is presently only supported by apomorphies of adults (Beutel & Hörnschemeyer, 2002). However, the glabrous patches on the prosternum and the medially divided prosternal field of asperities may turn out to be larval apomorphies of the family. A clade that consists of *Rhipsideigma*, *Tenomerga* and probably other genera of Cupedidae, of which the larvae are unknown, is well supported by larval apomorphies such as the broadened prothorax, the presence of coxal asperities and the presence of a distinct lateral longitudinal bulge (Figs 2, 3, 15; Böving & Craighead, 1931; pers. obs. Beutel). These presumably apomorphic character states are absent in first instar larvae of *Priacma serrata* (Ross & Pothecary, 1970), but their presence in the undescribed later instars cannot be excluded.

Several internal features of the head are either autapomorphies of Archostemata or synapomorphies of Micromalthidae and Cupedidae. The internal structures of larvae of Ommatidae are unknown. Elongate gular ridges and a strongly reduced tentorium, the posterior arms of which are attached to the anatomical mouth (Figs 7, 9) have not been described for larvae of other groups of Coleoptera. The gular ridges are the attachment area of a series of ventral pharyngeal dilators (Fig. 9). The unusual connection between the tentorium and the anterior pharynx indicates a double function for the M. tentoriocardinalis (M 17). It functions as a levator of the maxilla and a dilator of the anatomical mouth, together with M. frontopharyngalis anterior (M 45). Another unusual feature is the strongly enlarged M. frontohypopharyngalis (M 41), which has an extensive area of attachment on the median endocarina. Complete absence of labial muscles is another feature that has not been described for other beetle larvae.

Archostemata is the earliest group of Coleoptera represented in the fossil record and the sister group of the other 3 suborders (Beutel, 1997; Lawrence, 1999; Beutel & Haas, 2000). Nevertheless, comparatively few groundplan features are preserved in the larvae. The large number of derived features found in larvae of Cupedidae and other archostematan families is apparently due to their highly specialised wood-boring habits, which may have been acquired in the early Mesozoic. The earliest traces of insect-created galleries in wood date back to the Triassic (Crowson, 1975) and it is plausible to assume that they were made by cupedid larvae.

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Figs 27–30. 27–28. Larva of *Distocupes varians*, head and prothorax. 27 – dorsal view; 28 – ventral view. Abbreviations: ant – antenna, apth – anterior prothorax, asp – asperities, cl – clypeus, c1 – procoxa, dem – dorsal emargination, dlm – dorsal longitudinal muscles, ec – endocarina, es – eyespot, lbr – labrum, lig – ligula, lp – labial palp, ovm – oblique ventral muscles, pmt – prementum, ppth – posterior prothorax, t1 – protergum, smmt – submento-mentum, vem –ventral emargination, vlm – ventral longitudinal muscles. 29–30. Larva of *Distocupes varians*. 29 – head and prothorax, lateral view; 30 – posterior abdominal segments, lateral view. Abbreviations: asp – asperities, evl – eversible lobes, llm –lateral longitudinal muscles, olm – oblique longitudinal muscle, tVIII/IX – tergum VIII/IX.

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