The larval cephalic morphology of the enigmatic boreid *Caurinus dectes* (Mecoptera) and its phylogenetic significance

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Abstract

The species *Caurinus dectes* was described in 1979 by L. Russell and assigned to the mecopteran family Boreidae. A description of the immature stages published three years later provided important information. In the present study we re-examined larvae which became available through recent collecting efforts. External and internal features of the head are described and documented in detail. The systematic position of *Caurinus* and Boreidae is discussed. The orthognathous head is mainly characterized by plesiomorphic features such as the complete tentorium with well-developed dorsal arms and a broad bridge, the presence of seven well-developed stemmata, the free labrum, the simple mandibles with a basal molar area but without complex mesal appendages, the presence of a tentorio-mandibular muscle, the well-developed set of dorsal and ventral pharyngeal dilators, the placement of the brain and suboesophageal ganglion within the head, and the presence of an occipital furrow. Derived features are deformations of the brain related to size reduction and the greatly reduced labium. The phylogenetic interpretation remains ambiguous. The orthognathous head and some postcephalic features are potential synapomorphies of Boreidae and Pistillifera, whereas the presence of secondary compound eyes is a potential synapomorphy of Pistillifera and Nannochoristidae.

Key words

Caurinus, Boreidae, Mecoptera, larva, head, morphology, phylogeny.

1.   Introduction

Mecoptera are a small group of holometabolous insects with about 550 described species (Beutel et al. 2014). Their placement in a clade Antliophora as sistergroup of Siphonaptera was recently confirmed, both orders forming the sistergroup of the megadiverse Diptera (Misof et al. 2014). The largest monophyletic subgroup of Mecoptera is Pistillifera, comprising the families Meropeidae, Bittacidae, Eomeropidae, Choristidae, Apteropanorpidae, Panorpidae, and Panorpodidae (e.g., Beutel et al. 2014).

Caurinus dectes was discovered in 1976 in forest floor material from the Oregon Coast range (Russell 1979a). The species and genus were formally described in the same year and assigned to the family Boreidae (Russell 1979b), like Nannochoristidae a non-pistilliferan key taxon of Mecoptera (e.g., Kristensen 1989, 1999). Different aspects of *Caurinus* were covered in a comprehensive unpublished PhD thesis, especially the morphology and biology (Russell 1979a). Features of immature stages including eggs, larvae and pupae were treated in Russell

(1982). After a publication gap of more than 20 years the adult head structures were examined in detail (BEUTEL et al. 2008) and this was followed by a description of the sperm ultrastructure (RUSSELL et al. 2013). In 2013, surprisingly a second species of the genus was discovered in Alaska and described by SIKES & STOCKBRIDGE (2013).

Caurinus dectes was included in comprehensive analyses of the relationships within Holometabola (BEUTEL et al. 2011) and Mecoptera (FRIEDRICH et al. 2013). The placement of Boreidae remained ambiguous, either as sistergroup of all other non-nannochoristid families (= Pistillifera; WILLMANN 1987; FRIEDRICH et al. 2013), or as sistergroup of all other mecopterans (BEUTEL et al. 2011). The systematic position of *Caurinus* as sistergroup of the remaining Boreidae (*Hesperoboreus* and *Boreus*) has never been challenged. However, the character evolution remained enigmatic. The adults display seemingly plesiomorphic features of the head, such as for instance the complete lack of a rostrum, the presence of well-developed dorsal tentorial arms, and a large tentorio-mandibular muscle (BEUTEL et al. 2008). The larvae are likely close to the boreid groundplan but formal character analyses are still lacking.

Recently successful collecting activities of the second author yielded rich material of adults and immature stages of *Caurinus*, which was previously considered as extremely rare. This and the serious lack of anatomical data inspired us to carry out a detailed morphological investigation. We focused on the larval head, which is usually rich in phylogenetically relevant features (e.g., BEUTEL et al. 2011) and well-documented in potentially related groups (e.g., BIERBRODT 1942; BEUTEL et al. 2009), in contrast to the postcephalic body, which is comparatively poorly known in Mecoptera and the other antliophoran lineages. Aside from a detailed documentation of structural features, the aims of the present study are a comparative evaluation of larval features (with coded characters), and an informal interpretation of the evolution of larval characters in Mecoptera and Boreidae.

2.   Material and methods

The larvae of *Caurinus dectes* were collected by L. Russell on March 4, 2003 and March 6, 2013 in two different areas in Oregon. The specimens were extracted with a Berlese-Tullgren funnel from forest floor substrate mostly taken at Woods Creek Road (Marys Peak, Benton County) close to *Tsuga heterophylla* (western hemlock). The samples contained liverworts of the genus *Scapania* which is used by *Caurinus* as food source (RUSSELL 1979a). The second sample was taken at Klickitat Mountain (altitude ca. 600 m, Lane County). This material also contained *Scapania*. It was collected close to *Abies procera* (red fir) and yielded 12 larvae.

The larvae were examined with different techniques. Light microscopy was mainly used to visualize the pig-

mentation of the head, the stemmata field, and abdominal structures. SEM-micrographs were used for the documentation of surface structures and also as basis for line drawings. Specimens were dehydrated in a gradual ethanol series and subsequently critical point dried (Balzers CPD 020). To take images in different views, the samples were glued to a metal pin and fixed on a rotatable specimen holder after POHL (2010) and sputtered with platinum (Polaron SC7650 Sputter Coater). Pictures were taken using a LEO 1525 at 10 keV. One specimen was embedded in glycerin and examined with a confocal laser-scanning microscope (Leica TCS-SPE), notably for discriminating sclerotized areas from membranous parts. Autofluorescence of insect tissues at 488 nm laser light was used. The emitted light was recorded in two separate channels (500 – 570 nm, 580 – 690 nm) (see e.g., MICHELS 2007; DEANS et al. 2012).

One specimen was embedded in Araldite® resin for semi-thin cross sectioning (1 µm) with a microtome (Microm HM 360). The sections were stained with toluidine blue and pyronin G. For 3D-reconstruction the sections were digitalized using a Leica DM6000 microscope with slide scanning option (based on MetaMorph software) and subsequently automatically aligned and processed using VSG Amira 5.4.5® software. Skeleton, musculature, nervous system and alimentary system were manually segmented in Amira software. Based on the processed image stack separate surface objects were created using Bitplane Imaris 5.7 software. The raw surfaces were converted and scaled with Transform2 64bit software (freeware, Heiko Stark, FSU Jena, Germany; URL: http://starkrats.de) and finally processed in Autodesk® Maya 2014 software. The surface model assembled in Maya was also used for the creation of the interactive 3D-pdf (Electronic Supplement 1) in Adobe® Acrobat® 9 Pro.

3.   Results

3.1.   Habitus

Figs. 1A, 3A

The entire body has an elongate-ellipsoid shape seen from above, with the largest diameter at the region of the metathorax and abdominal segment I. The posterior abdominal segments are moderately tapering. The average length of stretched larvae is about 2 mm. The cuticle of the head capsule is light brown whereas the coloration of the rest of the body is whitish or light grey. The postcephalic body is characterized by large oblique and nearly vertical folds, an unsclerotized cuticle with a tuberculate or wart-like surface structure, greatly reduced thoracic legs, and missing abdominal appendages. The postcephalic segments are distinctly separated from each other, even though the segmental pattern appears somewhat obscured by the folds.
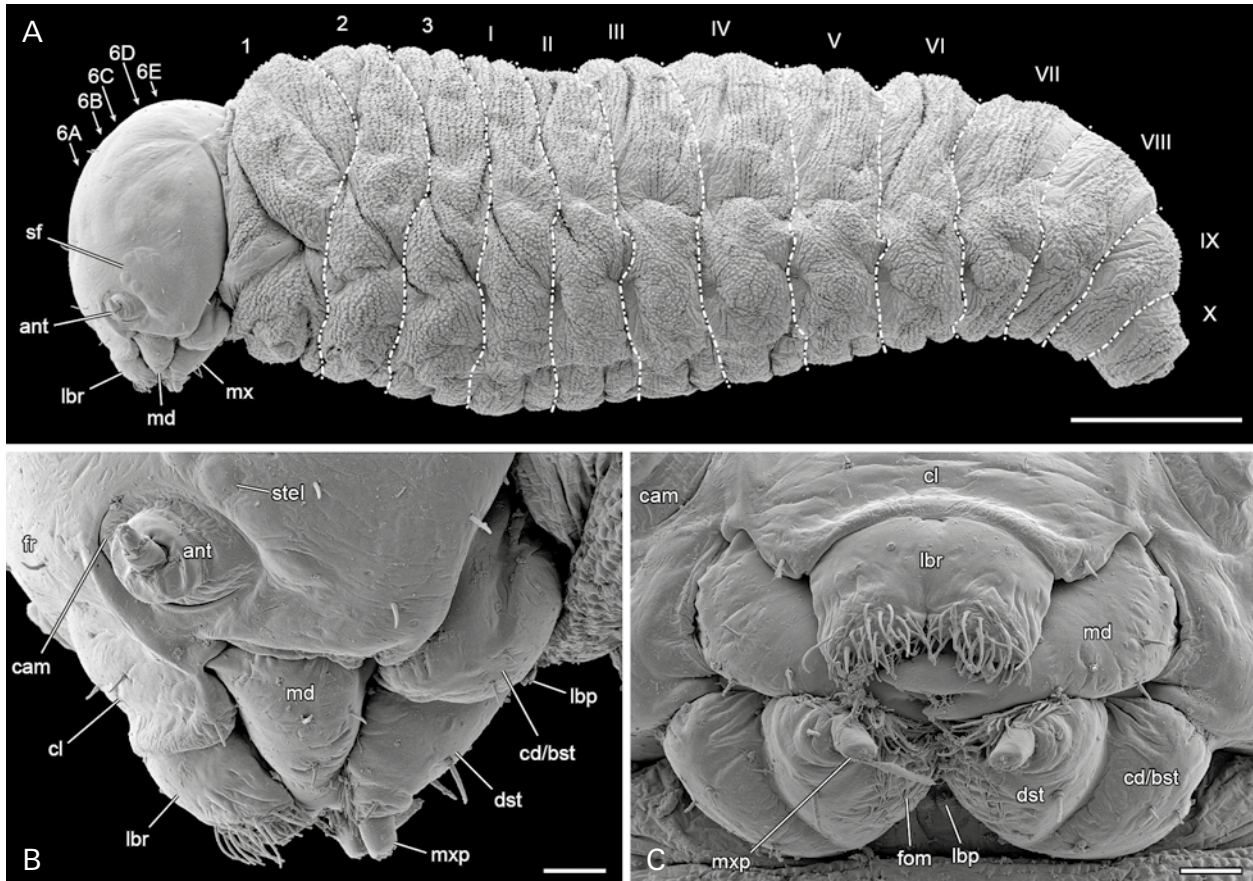
Fig. 1. Larva of *Caurinus dectes*, SEM micrographs. **A**: entire larva, lateral view, postcephalic segmental borders indicated by dotted lines (1−3, thoracic segments; I−X, abdominal segments; 6A−E indicate planes of histological sections in Fig. 6); **B**: detail of mouthparts, lateral view; **C**: detail of mouthparts, ventral view. — *Abbreviations*: ant − antenna; cam − circum-antennal membrane; cd/bst − unseparated cardo and basistipes; cl − clypeus; dst − dististipes; fom − field of microtrichia on dististipes; fr − frons; lbp − labial palp; lbr − labrum; md − mandible; mx − maxilla; mxp − maxillary palp; sf − field of stemmata; steI − stemma I. Scale bars: A, 200 µm; B, C, 20 µm.

3.2. Head

3.2.1. Head capsule

The head capsule is well sclerotized and almost completely exposed. Only a very narrow stripe of the posterodorsal region is covered by the dorsal cervical membrane (Figs. 1A, 3A). The head is orthognathous and nearly round in frontal view (Figs. 2A, 3B, 4). It appears oval in lateral, ventral and dorsal view (Figs. 2, 3). A distinct triangular incision of the head capsule is present dorsolaterally. It is anteriorly continuous with a relatively short and indistinct occipital furrow. The cuticle is largely smooth and glabrous. A relatively distinct honeycomb surface pattern with pentagonal and hexagonal fields is present on the genal region above the field of stemmata (Fig. 1A). The pattern is still recognizable in adjacent dorsal and ventral areas but obliterates towards the frontal and occipital regions. The coronal- and frontal sutures are distinctly recognizable (Figs. 2A, 3B). The coronal suture divides the vertex medially and is almost half as long as the dorsal head capsule. It divides into the frontal sutures below the AF2 setae (Fig. 2A). The frontal suture extends laterad from its origin but turns anterad after a relatively

short distance, with an almost right angle between the two sections. The slightly irregular anterior part reaches the level of the dorsal margin of the antennal foramen. The clypeus is distinctly broader than long (Fig. 2A). The anteclypeus is distinctly separated from the broader postclypeus by a transverse furrow. A small bulge is present at its ventral edge. The fronto-clypeal ridge (transverse strengthening ridge) is only weakly developed. A gula and a hypostomal bridge are missing.

3.2.2. Tentorium

The anterior tentorial arms are well sclerotized (Fig. 5A). A distinct lumen is not recognizable on microtome sections (Fig. 6A,B). They are slightly oval in cross section and distally continuous with the mesal rim of antennal foramen. Externally visible anterior tentorial pits are not present (Fig. 1B). Very thin dorsal arms are dorsally attached to the head capsule by connective tissue (Figs. 3B, 4, 5A, 6A,B). The tentorial bridge above the maxillolabial complex is massively developed (Figs. 3C, 5A, 6E). The bases of the anterior tentorial arms form a discrete plate, the corpotentorium (Figs. 5B, 6C,D). The posterior tentorial arms are short.
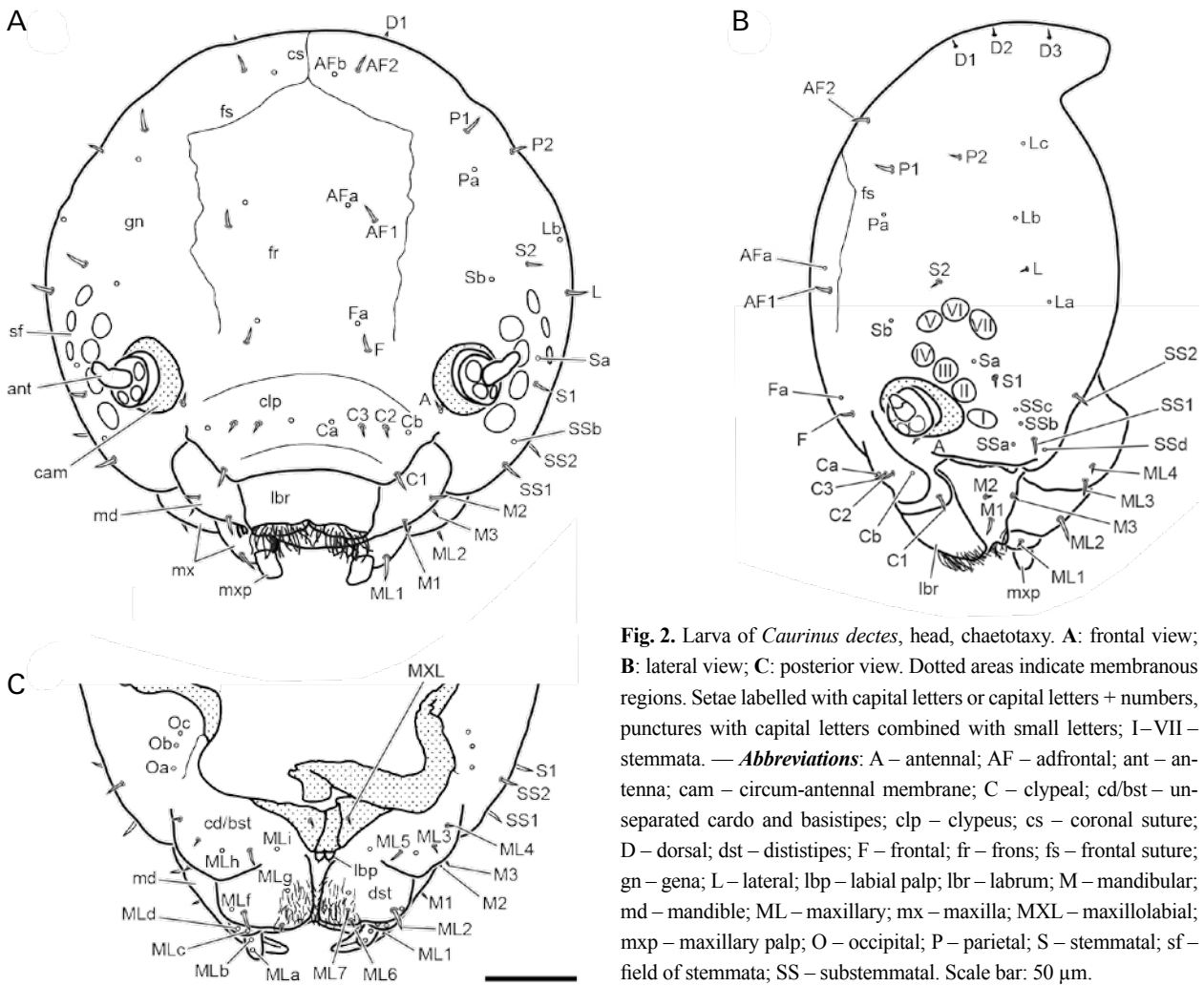
Fig. 2. Larva of *Caurinus dectes*, head, chaetotaxy. **A**: frontal view; **B**: lateral view; **C**: posterior view. Dotted areas indicate membranous regions. Setae labelled with capital letters or capital letters + numbers, punctures with capital letters combined with small letters; I–VII – stemmata. — ***Abbreviations***: A – antennal; AF – adfrontal; ant – antenna; cam – circum-antennal membrane; C – clypeal; cd/bst – unseparated cardo and basistipes; clp – clypeus; cs – coronal suture; D – dorsal; dst – dististipes; F – frontal; fr – frons; fs – frontal suture; gn – gena; L – lateral; lbp – labial palp; lbr – labrum; M – mandibular; md – mandible; ML – maxillary; mx – maxilla; MXL – maxillolabial; mxp – maxillary palp; O – occipital; P – parietal; S – stemmatal; sf – field of stemmata; SS – substemmatal. Scale bar: 50 μm.

3.2.3. Light sense organs

Compound eyes and ocelli are absent. The field of stemmata is located on the lateral head region above and posterior to the antennal foramen (Figs. 1A, 2B,C, 3A,B, 4). It is distinct, quite extensive, and appears black due to the pigmentation below the cuticle. Seven distinct cornea lenses are recognizable externally (Figs. 2A, 3A,B). Four anterior stemmata (SI–SIV) form a straight oblique line posterior to the antennal articulatory area. The posterior three (SV–SVII) form a shortened semicircle above and posterior to the anterior row. The distances between the stemmata are similar within the two groups (4–5.6 μm). The shape of the cornea lenses varies from almost circular to slightly oval and the diameter varies between 14.4 μm and 19.2 μm.

3.2.4. Chaetotaxy
Fig. 2

The terms for setae are those introduced for lepidopteran caterpillars based on the sensory innervation (Hasenfuss & Kristensen 2003). The homology remains uncertain as no information on the innervation is available for *Caurinus*. The denomination is only based on a similar topo-

logical position. Twenty-eight pairs of cranial setae are present and labelled with capital letters and Roman numbers in Figure 2. All setae are short and not cleft. Three pairs insert in a short row parallel to the coronal suture on the dorsal region of the head capsule (D1–3). D1 and D2 are closer to each other than D2 and D3. On a virtual line continuous with this row three additional pairs are present (AF1, AF2 and F). AF1 is inserted at the level of the dorsal margin of the field of stemmata, AF2 at the ventral end of the coronal suture, and F (frontal seta) at the level of the antennae. The small and strongly curved setae A insert at the ventral margin of antennomere 1. S1 is located within the field of stemmata, between the stemmata I and VII. An additional pair (S2) is present at the dorsal margin of the field of stemmata and two other setae (SS1, SS2) are inserted posterior to it, close to the hind margin of the head capsule. Two pairs of parietal setae (P1, P2) insert posterior to the angle of the frontal suture on the dorsal genal region and a lateral seta (L) on the posterior genal area posterodorsad the posterior stemma of the upper row (VII). Three pairs are present on the postclypeus (C1–3). C1 is laterally placed on the ventrolateral clypeal bulge, C2 and C3 close to the central clypeal region. Three setae on the mandibles (M1–3) are arranged in triangle. Seven pairs are present on the max-

illae (ML1−7). ML3 and ML4 insert ventrolaterally on the basal maxillary sclerite (cardo+basistipes) and ML5 ventrally. ML2 inserts on the posterior part of the dististipes and ML1 on the basal palpomere. ML6 and ML7 are situated within the field of microtrichia on the ventral surface of the dististipes. One pair of setae (MXL) is located ventrally on the membranous area adjacent to the labial palps.

Aside from the setae some small punctured grooves are recognizable on the head capsule and the mouthparts. They probably also have a sensory function (Hasenfuss & Kristensen 2003). They are labelled with small and capital letters, depending on their position.

The punctures Fa and AFa are recognizable dorsomediad the setae F and AF1, respectively. Pa is present ventrad of P1. Sa is located within the field of stemmata and Sb anterior to it. Four punctures (SSa−d) are distributed around the setae SS1. La−c are arranged in a curved row on the posterior genal region, with the seta L inserted between La and Lb. Two punctures Ca and Cb are present on the anteclypeus. Oa−c are arranged in a short line posterodorsad of the SS2 setae. Nine pairs of punctures (MLa−i) are visible on the ventral side of the maxilla. MLa and MLb are located ventrally on the second palpomere, MLc and MLd ventrolaterally on the apical membrane of palpomere 1 and, adjacent to them, MLe on the ventral side of the basal palpomere. MLf is placed laterad of seta ML2, and MLg within the field of microtrichia on the dististipes. MLh and MLi are arranged in an arcuate series with setae ML3 and ML5.

3.2.5. Labrum

The well-developed labrum is movably connected with the ventral anteclypeal margin by an internal membranous fold (Fig. 3B). It is ca. 80 μm wide at its base. The shape is roughly rectangular and it is about half as long as wide (Figs. 1B,C, 2B,C, 3B). The basal margin appears slightly concave and the distal margin is medially incised (Fig. 3B). Paired fields with more than 20 setae are present laterad the incision (Figs. 1C, 2A, 3B). The labral setae are distinctly longer than those of the head capsule (ca. 19 μm).

Musculature (Figs. 3B, 4, 5B): M. labro-epipharyngalis (M.7, nomenclature of v. Kéler 1963): compact, O (= origin): posteromesal region of labrum, I (= insertion): distal epipharynx. M. fronto-labralis (M.8): well-developed, O: centrally on frontal region (ventrad M.46), I: median process of dorsal labral margin.

3.2.6. Antennae

The short, 2-segmented antennae (Figs. 1A,B, 2A,B, 3B) insert in a wide antennal foramen on a nearly round articulatory membrane (Figs. 1B, 2A,B: cam) anterior and below the oblique lower row of stemmata and above the anterior mandibular articulation. The basal antennomere is shaped like an extremely short cylinder and only ca. 6.6 μm long. Three circular to slightly oval disc-shaped sensilla (diameter ca. 7.5 μm) are present on the ventromesal half of its distal surface. Antennomere 2 is also cylindrical but longer and much more slender, with only about 1/3 of the diameter of antennomere 1. It tapers towards its apex and sensilla are present in the distal region (see Russell 1982: peg-like sensilla). Two longitudinal membranous areas described by Russell (1982) are not recognizable in the specimen we examined, possibly due to a fold in this region.

Musculature: One antennal muscle is present (Figs. 4, 5A, 6A), presumably M. tentorio-scapalis anterior (M.1?). It originates laterally at the proximal half of the anterior tentorial arm and is attached ventromesally at the base of antennomere 1.

3.2.7. Mandibles

The mandibles are covered by the labrum in their resting position. The posterior (primary) and anterior (secondary) joints are well-developed (Figs. 1B, 2B, 3A). Distally four teeth are present, with the size increasing towards the apical region. The mandibles are broadest at the base but a typical mola with a grinding surface is missing. A prostheca is also absent. Three setae are inserted on the lateral mandibular surface.

Musculature (Figs. 3A,B, 4, 5B, 6B−E): M. craniomandibularis internus (M.11): largest muscle of head, fills out about 60% of the lumen of the head capsule, O: dorsal and dorsolateral walls of the head capsule, I: mesal rim of mandible with very strong adductor tendon. M. cranio-mandibularis externus (M.12): about 10% of the volume of M.11, O: lateral wall of head capsule, I: lateral mandibular margin by means of a strong abductor tendon. M. tentorio-mandibularis (M.13): extremely thin, composed of few fibers and accompanied by the mandibular nerve, O: anterior tentorial arm, adjacent to the tentorio-antennal muscle, I: posteriorly on the mandibular base.

3.2.8. Maxillolabial complex

The large transverse basal sclerite of the maxilla is formed by the fused cardo and basistipes (see e.g., Hinton 1958; Beutel et al. 2009). It articulates laterally with the postgenal area (Fig. 3C). Cardinal and basistipital portions are indistinguishably fused. The dorsal margin is strengthened, whereas the anterolateral areas are rather thin. The dorsal margin continues ventromesally and forms an anteriorly directed rod-like extension (Figs. 3C, 6C−E), which runs along the inner rim of the maxilla into the endite lobe (Fig. 6B: mxl). The cardo+basistipes is in contact with the posteriormost part of the dististipes. The dististipes is connected with the lateral region of distal maxillary element, whose mesal part is very weakly sclerotized and covered with dense fields of microtrichia (Figs. 1C, 3C: fom). The dististipes also bears the short 2-segmented maxillary palp. The proximal palpomere is relatively broad and short compared to the distal one. Distally it bears a round sensorium, laterad of palpo-
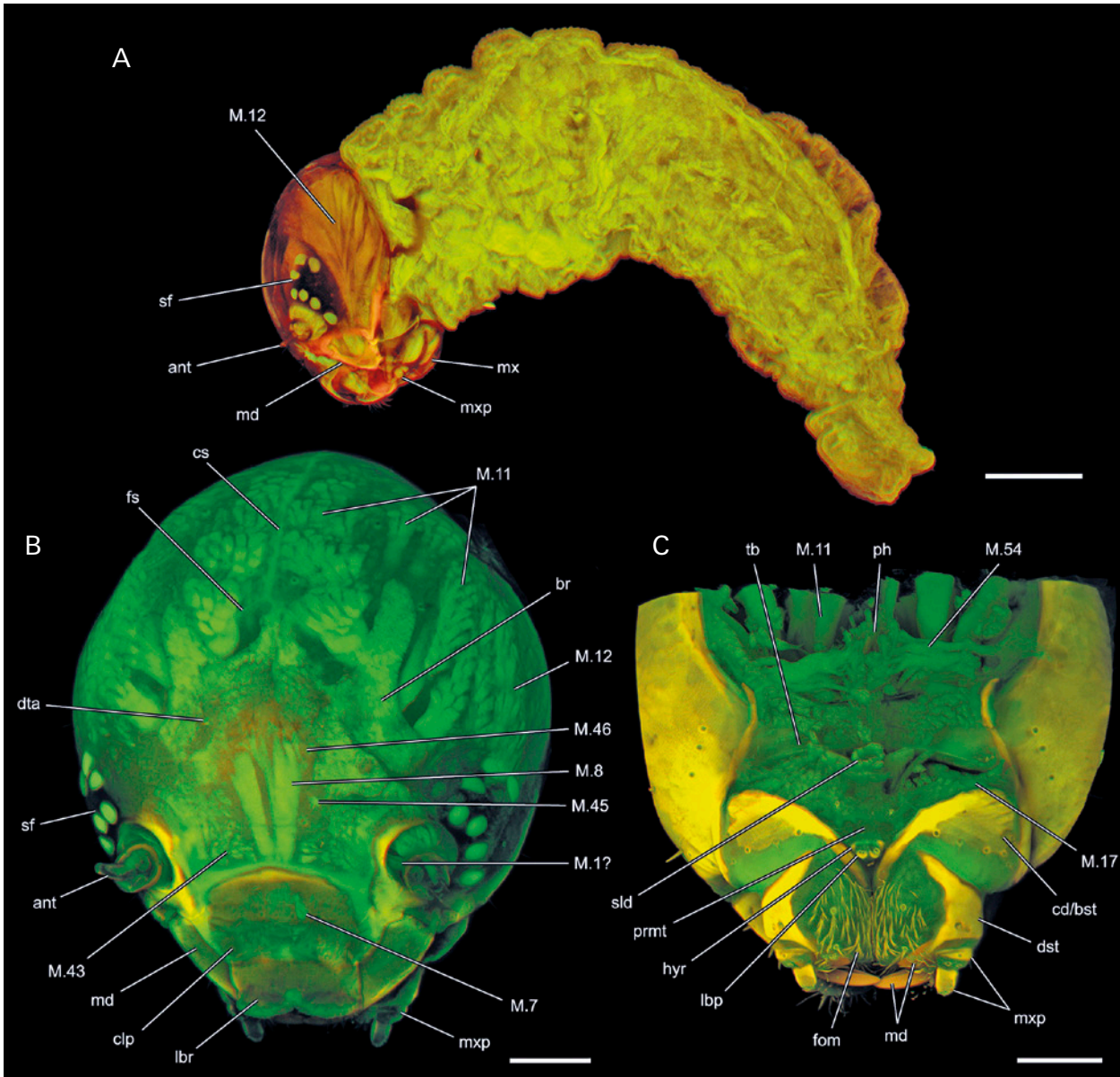
Fig. 3. Larva of *Caurinus dectes*, CLSM images. **A**: entire larva, lateral view; **B**: head, anterior view; **C**: ventral half of the head, posterior view. — ***Abbreviations***: ant – antenna; br – brain; cd/bst – unseparated cardo and basistipes; clp – clypeus; cs – coronal suture; dst – dististipes; dta – dorsal tentorial arm; fom – field of microtrichia; fs – frontal suture; hyr – posterior rods of hypopharynx; lbp – labial palp; lbr – labrum; M.1? – M. tentorio-scapalis; M.7 – M. labro-epipharyngalis; M.8 – M. fronto-labralis; M.11 – M. cranio-mandibularis internus; M.12 – M. cranio-mandibularis externus; M.17 – M. tentorio-cardinalis; M.43 – M. clypeo-epipharyngalis; M.45 – M. fronto-pharyngalis anterior; M.46 – M. fronto-pharyngalis posterior; M.54 – M. cranio-pharyngalis ventralis; md – mandible; mx – maxilla; mxp – maxillary palp; ph – pharynx; prmt – prementum; sf – field of stemmata; sld – salivary duct; tb – tentorial bridge. Scale bars: A, 100 μm; B, C, 50 μm.

mere 2 (Fig. 3C), which is slightly longer and more slender. The apical area of palpomere 2 also bears a round sensorium on its lateral side. Ten small sensilla on the mesal side resemble the apical sensilla of antennomere 2 in size and shape. A well-defined lacinia and galea are not developed. However, a pair of small endite lobes located between the mandibles and hypopharyngeal lobe is recognizable on histological sections (Fig. 6B: mxl). The homology of these lobes is uncertain as no muscles are attached.

The labial part of the complex is distinctly reduced and difficult to interpret. It is mainly formed by a trian-

gular area mesad the maxillary bases, which is undivided and unsclerotized (Figs. 2C, 3C, 6D,E). It is posteriorly not distinctly delimited from the neck membrane. The anterior region of the labial area is apparently the prementum as it bears the labial palps. The rudimentary palps are the only well-sclerotized parts of the labium and composed of an indistinct basal part and a small rounded single palpomere with sensilla of different shapes and sizes (Figs. 2C, 3C). In front of the palps, the premental area is continuous as a narrow stripe between the maxillae, largely covered by them and only recognizable on histological sections (Fig. 6D). This membranous region
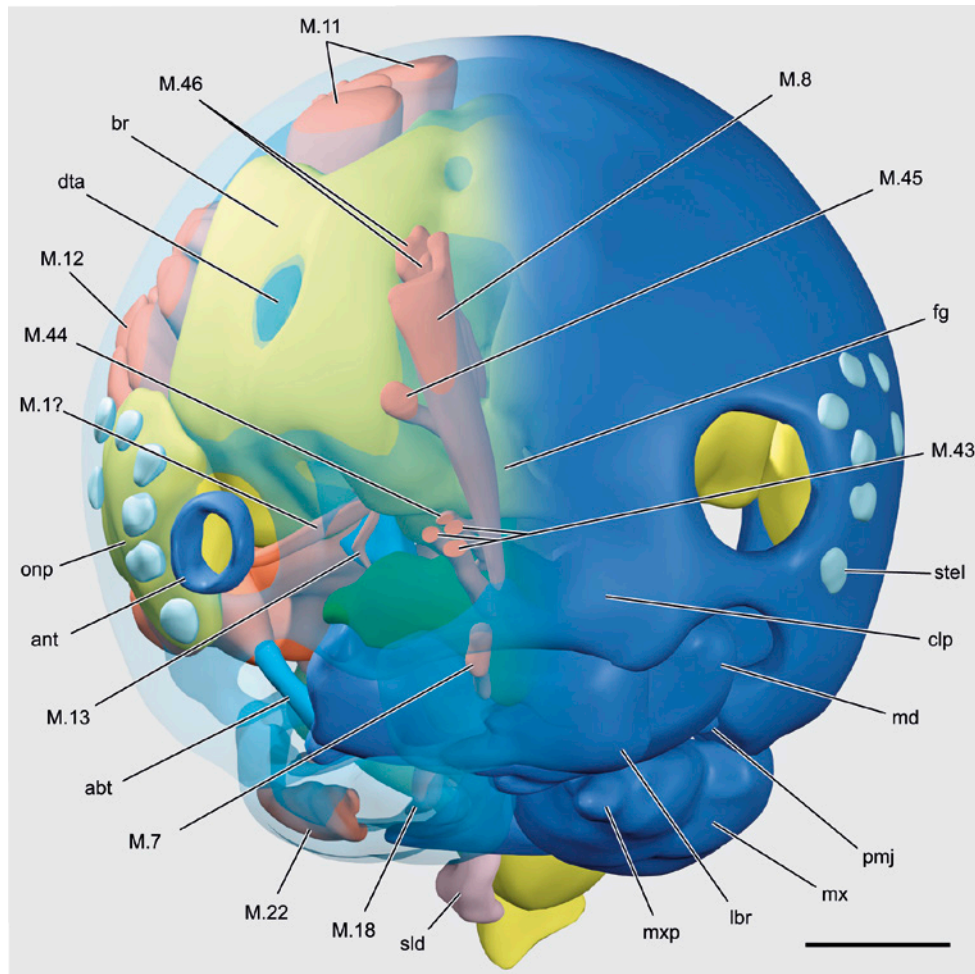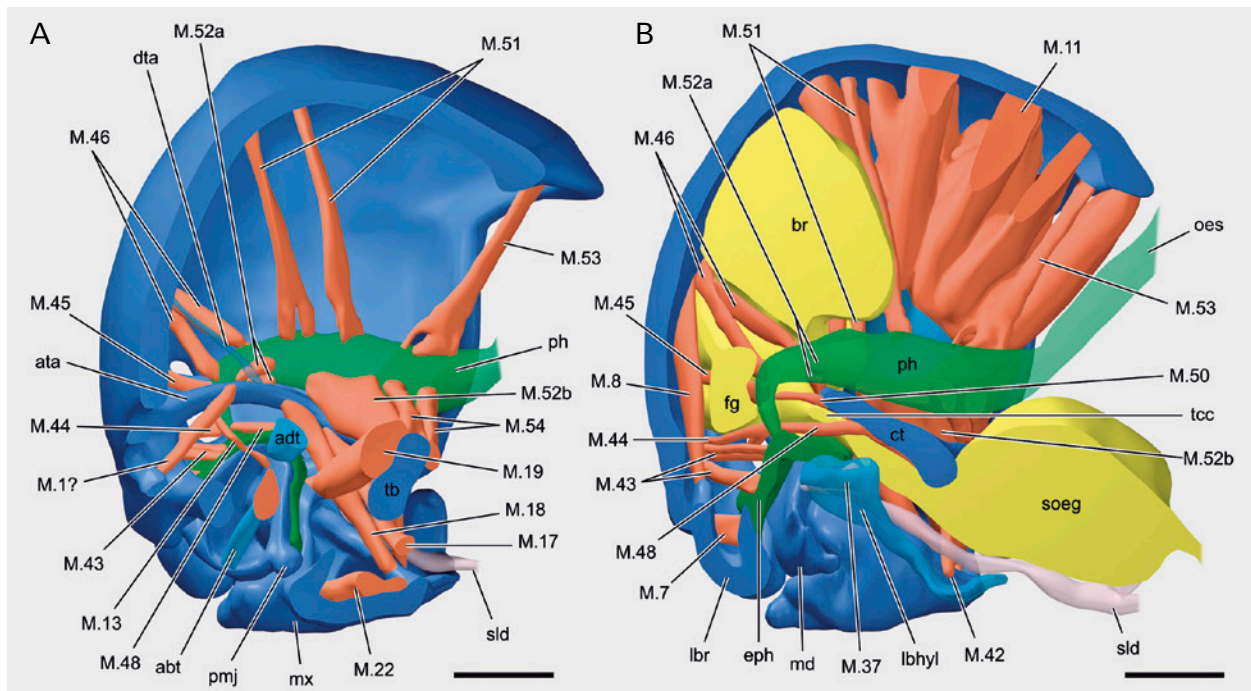
Fig. 4. Larva of *Caurinus dectes*, head, 3D reconstruction, frontal view, skeleton of left half semi-transparent. — ***Abbreviations***: abt – abductor tendon of mandible; ant – antenna; br – brain; clp – clypeus; dta – dorsal tentorial arm; fg – frontal ganglion; lbr – labrum; M.1? – M. tentorio-scapalis; M.7 – M. labro-epipharyngalis; M.8 – M. fronto-labralis; M.11 – M. cranio-mandibularis internus; M.12 – M. cranio-mandibularis externus; M.13 – M. tentorio-mandibularis; M.18 – M. tentorio-stipitalis; M.22 – M. basistipito-dististipitalis lateralis; M.43 – M. clypeo-epipharyngalis; M.44 – M. clypeo-cibarialis; M.45 – M. fronto-pharyngalis anterior; M.46 – M. fronto-pharyngalis posterior; md – mandible; mx – maxilla; mxp – maxillary palp; onp – optic neuropile; pmj – posterior mandibular joint; sld – salivary duct; steI – stemma I. Scale bar: 50 μm.

is laterally flanked by a pair of long, well-sclerotized rods (Fig. 6D,E: hyr), which originate from the posterior end of the main hypopharyngeal element, which bears the opening of the salivary duct, and reaches behind the level of the labial palps (Fig. 3C: hyr).

Musculature (Figs. 3C, 4, 6D,E): M. tentorio-cardinalis(-basistipitalis) (M.17): two parallel, closely adjacent bundles, O: posterior tentorial arm, I: posterolaterally on cardo+basistipes. M. tentorio-stipitalis (M.18): two parallel, closely adjacent bundles, O: corpotentorium and base of anterior tentorial arm, I: posteriorly on mesal edge of cardo+basistipes. M. cranio- lacinialis (M.19): well-developed, I: head capsule below M. cranio-mandibularis internus and close to the posterior tentorial grooves, I: mesal endite lobe by thin tendon. M. basistipito-dististipitalis lateralis (M.22): O: lateral half of cardo+basistipes, I: laterally on dististipes. Mm. tentorio-praementales inferior/superior (M.29/30): probably absent (see. M.42). Intrinsic labial muscles absent.

3.2.9. Preoral cavity and mouth opening

The preoral cavity is dorso-ventrally compressed. It is laterally bordered by the mandibular bases. The semimembranous epipharynx forms the roof. Only the insertion sites of the frontal and labral muscles are slightly sclerotized. The inner surface of the epipharynx is smooth without any microtrichia. The hypopharyngeal sclerite is ventrally fused with the anterior labial region forming a slender prelabio-hypopharyngeal lobe which appears triangular in cross section (Figs. 5B, 6B,C: lbhyl). The proximal epi- and hypopharynx fuse along their lateral edges thus forming a short prepharyngeal tube (Fig. 5B). It has a very narrow lumen and is posteriorly continuous with the precerebral pharynx. The border, i.e. the anatomical mouth opening, is indistinct but marked by the position of the frontal ganglion. A sclerotized hypopharyngeal suspensorium (oral arms) could not be observed in histological sections.

Fig. 5. Larva of *Caurinus dectes*, head, 3D reconstruction. **A**: parasagittal section, mesal view (nervous system removed); **B**: sagittal section, mesal view. — ***Abbreviations***: abt – abductor tendon of mandible; adt – adductor tendon of mandible; ata – anterior tentorial arm; br – brain; ct – corpotentorium; dta – dorsal tentorial arm; eph – epipharynx; fg – frontal ganglion; lbhyl – prelabio-hypopharyngeal lobe; lbr – labrum; M.1? – M. tentorio-scapalis; M.7 – M. labro-epipharyngalis; M.8 – M. fronto-labralis; M.11 – M. cranio-mandibularis internus; M.13 – M. tentorio-mandibularis; M.17 – M. tentorio-cardinalis; M.18 – M. tentorio-stipitalis; M.19 – M. cranio-lacinialis; M.22 – M. basistipito-dististipitalis lateralis; M.37 – M. hypopharyngo-salivarialis; M.42 – M. tentorio-hypopharyngalis; M.43 – M. clypeo-epipharyngalis; M.44 – M. clypeo-cibarialis; M.45 – M. fronto-pharyngalis anterior; M.46 – M. fronto-pharyngalis posterior; M.48 – M. tentorio-cibarialis; M.50 – M. tentorio-pharyngalis anterior; M.51 – M. cranio-pharyngalis anterior; M.52a/b – M. tentorio-pharyngalis posterior; M.53 – M. cranio-pharyngalis posterior; M.54 – M. cranio-pharyngalis ventralis; md – mandible; mx – maxilla; oes – oesophagus; ph – pharynx; pmj – posterior mandibular joint; sld – salivary duct; soeg – suboesophageal ganglion; tb – tentorial bridge; tcc – tritocerebral commissure. Scale bars: 50 μm.

Musculature (Figs. 3B, 4, 5, 6A,C,E): M. tentorio-hypo-pharyngalis (M.42): slender, O: posterior tentorial arm, I: posterior end of prelabio-hypopharyngeal lobe, close to the base of the labial palp. M. clypeo-epipharynygalis (M.43): three slender, closely adjacent bundles O: posterior half of clypeus, below the clypeo-frontal ridge, I: mesally on the epipharynx. M. clypeo-cibarialis (M.44): slender, O: ventral (clypeal) face of clypeo-frontal ridge (dorsad M.43), I: anatomical mouth opening (below frontal ganglion, opposite to the insertion of M.48). M. tentorio-cibarialis (M.48): slender, O: centrally on ventral side of corpotentorium (between paired attachment sites of M.18), I: ventral side of cibarium (opposite to M.44).

3.2.10. Pharynx

The lumen of the precerebral pharynx is narrow but it widens posteriorly below the central part of the brain (Fig. 5B). Folds for attachment of dilators are distinctly developed in this area (Fig. 6B–E).
Musculature of precerebral pharynx (Figs. 3B, 4, 5, 6A): M. fronto-pharyngalis anterior (M.45): moderately sized, O: frons above clypeo-frontal ridge, I: dorsally on precerebral pharynx (directly above frontal ganglion). M. fronto-pharyngalis posterior (M.46): subdivided into two main sections, O: frons (dorsolaterad of M.8), I: dorsally on precerebral pharynx (anterior part close to M.47, posterior part between circumoesophageal connectives). M. tentorio-pharyngalis lateralis (M.47?): slender, O: anterior tentorial arm (close to anterior tentorial pit), I: laterally on precerebral pharynx (laterad M.45). M. tentorio-pharyngalis anterior (M.50): O: mesally on anterior margin of corpotentorium and base of anterior tentorial arms, I: ventrally on precerebral pharynx (opposite to M.45).
Musculature of postcerebral pharynx (Figs. 3C, 5, 6B–E): M. cranio-pharyngalis anterior (M.51): two subcomponents, O: wall of head capsule, between antero-mesal bundles of M.11, I: dorsolaterally on anterior postcerebral pharynx (opposite M.52). M. cranio-pharyngalis posterior (M.53): O: cranium, between posteriormost bundles of M.11, I: dorsolaterally on posterior region of postcerebral pharynx (opposite M.52). M. tentorio-pharyngalis posterior (M.52): composed of two main portions, M.52a: two very short, parallel bundles, O: anterior tentorial arm and base of dorsal tentorial arm (Fig. 6B), I: laterally on pharynx (between posterior bundle of M.46 and anterior bundle of M.51), M.52b: strongly developed, O: posterior

Fig. 6. Larva of *Caurinus dectes*, head, histological sections (for location of section planes see arrows in Fig. 1A). — ***Abbreviations***: abt – abductor tendon of mandible; adt – adductor tendon of mandible; ata – anterior tentorial arm, bst – basistipes; cam – circum-antennal membrane; ccc – crystalline cone cells; coc – circumoesophageal commissure; col – corneal lens; ct – corpotentorium; dst – dististipes; dta – dorsal tentorial arm; fg – frontal ganglion; hyr – hypopharyngeal rods; lbhyl – prelabio-hypopharyngeal lobe; lbr – labrum; M.1? – M. tentorio-scapalis; M.7 – M. labro-epipharyngalis; M.11 – M. cranio-mandibularis internus; M.12 – M. cranio-mandibularis externus; M.17 – M. tentorio-cardinalis; M.18 – M. tentorio-stipitalis; M.19 – M. cranio-lacinialis; M.22 – M. basistipito-dististipitalis lateralis; M.37 – M. hypopharyngo-salivarialis; M.42 – M. tentorio-hypopharyngalis; M.43 – M. clypeo-epipharyngalis; M.44 – M. clypeo-cibarialis; M.45 – M. fronto-pharyngalis anterior; M.46 – M. fronto-pharyngalis posterior; M.47? – M. tentorio-pharyngalis lateralis; M.48 – M. tentorio-cibarialis; M.51 – M. cranio-pharyngalis anterior; M.52a/b – M. tentorio-pharyngalis posterior; M.54 – M. cranio-pharyngalis ventralis; md – mandible; mxl – maxillary endite lobe; mxp – maxillary palp; nel – neurilemma; nep – neuropil (brain); nmx – nervus maxillaris; onp – optic neuropile; pek – perikarya (brain); ph – pharynx; pic – pigment cells; sld – salivary duct; soeg – suboesophageal ganglion; tb – tentorial bridge. Scale bars: 50 μm.

tentorial arms, I: ventrolaterally on postcerebral pharynx (opposite to the bundles of M.51). M. cranio-pharyngalis ventralis (M.54): two strong branches, O: cranial regions close to the base of the posterior tentorial arms, I: ventrolaterally on postcerebral pharynx (behind M.52b, opposite to M.53).

3.2.11. Salivary system

The large salivary glands are located in the thorax. Paired salivary ducts unite below the suboesophageal ganglion (Fig. 5B). The thin-walled unpaired duct runs towards the tip of the hypopharyngo-labial lobe (Figs. 3C, 5B, 6B–E: sld). Close to the salivary orifice the U-shaped floor of the duct is well sclerotized, whereas the roof is mostly membranous (Fig. 6C). Only the posteriormost part of the roof is slightly sclerotized, forming a defined muscle attachment site (Fig. 6B).
Musculature (Fig. 6C): M. hypopharyngo-salivarialis (M.37): compact, O: hypopharynx, I: roof of distal part of salivary duct.

3.2.12. Brain and suboesophageal ganglion

The brain is moderately enlarged in relation to the head size. It is mainly restricted to the anterior half of the head capsule and fills out about 30% of the volume (Fig. 5B). Proto- and deutocerebrum form a unit without externally recognizable borders. The posterior face of the brain forms one median and two lateral lobes, which fill in the gaps between the bundles of M. cranio-mandibularis internus (Figs. 3B, 4, 5B, 6B). The anterior face is curved around the anterior tentorial arms and the fronto-pharyngeal muscles. Two large anterior lobes are folded around the dorsal tentorial arm and are in tight contact with each other anterior to this structure, creating the impression that it passes through the brain (Figs. 4, 6A). Large ellipsoid optic lobes are present laterally. The compact frontal ganglion is closely associated with the brain, with thick and very short frontal connectives (Figs. 5B, 6A). The nervus recurrens is very thin. The circumoesophageal connectives are very thick dorsally (Fig. 6A–C: coc). Below the pharynx the connectives taper distinctly before they reach the suboesophageal ganglion below the tentorial bridge (Figs. 5B, 6D). A short tritocerebral commissure is present between the tentorio-cibarial and the tentorio-pharyngeal muscles (Mm. 48, 50). The suboesophageal ganglion is completely shifted to the prothorax (Fig. 5B). The first thoracic ganglion is connected to it by very short connectives.

4. Phylogenetically relevant larval characters

The following cephalic characters are mainly adopted from Beutel et al. (2009). As the focus of the present study lies on the evolution of larval head structures in Mecoptera the following descriptions are restricted to ingroup and closely related outgroup taxa (i.e. Diptera and Siphonaptera). For characters of the postcephalic body see also Friedrich et al. (2013).

Characters of head

1. Orientation of mouthparts: (0) orthognathous; (1) prognathous or slightly inclined. Orthognathous in Boreidae and Pistillifera (Applegarth 1939; Setty 1939; Byers 1987; Beutel et al. 2009). Distinctly prognathous in Nannochoristidae (Pilgrim 1972).
2. Lateral eyes: (0) compound eyes; (1) isolated stemmata. Typical stemmata are present in Boreidae, seven in *Caurinus* and three in Boreinae. Compound eyes are present in Nannochoristidae (simplified; Melzer et al. 1994) and in Pistillifera with the exception of *Panorpodes* (Jiang et al. 2014).
3. Shape of anterior clypeus: (0) anteriorly wider than long; (1) longer than wide anteriorly. Distinctly broader than long in *Caurinus* (Figs. 2A, 3B) and *Nannochorista* (Beutel et al. 2009), but longer than wide in *Boreus* and Pistillifera (Currie 1932; Applegarth 1939; Bierbrodt 1942; Jiang et al. 2014).
4. Narrow ventromedian zone of weakness behind/ above mouthparts: (0) absent; (1) present. Absent in *Caurinus* and *Boreus*. Present in *Nannochorista* and the known larvae of Pistillifera (Currie 1932; Applegarth 1939; Bierbrodt 1942; Byers 1987; Beutel et al. 2009).
5. Dorsal tentorial arm: (0) present; (1) absent. Present, but thin in *Caurinus* (Figs. 5A, 6A), *Panorpa* (Bierbrodt 1942; Beutel et al. 2009) and *Nannochorista* (Beutel et al. 2009). Absent in *Boreus*, and *Apterobittacus* (Applegarth 1939).
6. M. fronto-epipharyngalis (M.9): (0) present; (1) absent. Absent in *Caurinus* and other mecopteran groups (Table 1; Beutel et al. 2009) with the exception of *Nannochorista* (Beutel et al. 2009).
7. Insertion site of M. fronto-epipharyngalis (M.9): (0) tormae; (1) epipharynx, close to the median line. This muscle is inserted close to the mid-line and separated from the tormae in *Nannochorista* (Beutel et al. 2009). It is usually attached on the tormae in other insects.
8. Number of antennal segments: (0) 3; (1) 2. Two in Boreidae (Fig. 1B; Russell 1982; Byers 1987) like in Siphonaptera (Sharif 1937; Widhalm-Finke 1974), but three in Nannochoristidae (Beutel et al. 2009), Panorpodidae (Jiang et al. 2014), Panorpidae (Bierbrodt 1942) and Bittacidae (Pilgrim 1972; Byers 1987).
9. Length of antenna: (0) more than 20% of maximum width of head capsule; (1) less than 20% of maximum width of head capsule. Strongly shortened in *Caurinus* and *Boreus* (Fig. 1B; Russell 1982). Moderately long in larvae of Nannochoristidae and the known larvae of Pistillifera (Currie 1932; Applegarth 1939; Bierbrodt 1942; Jiang et al. 2014).
10. Number of extrinsic antennal muscles: (0) 2; (1) 1. One in *Caurinus* (Fig. 4), *Nannochorista* and *Panorpa* (Bierbrodt 1942), but two in *Boreus* (Beutel et al. 2009).
11. Origin of extrinsic antennal muscles: (0) dorsal tentorial arms; (1) anterior tentorial arms; (2) hypo-

pharyngeal suspensorium. In *Boreus*, one muscle originates from a sclerotization reinforcing the prepharynx laterally (suspensorium) and another one from the anterior tentorial arm (BEUTEL et al. 2009). A single muscle originates from the anterior tentorial arm in *Caurinus* (Fig. 5A) and *Nannochorista* (BEUTEL et al. 2009). The antennal muscle arises from the ligamentous dorsal tentorial arm in *Panorpa* (BIERBRODT 1942; BEUTEL et al. 2009). Two muscles originate from the hypopharyngeal suspensorium in *Nosopsyllus* (SHARIF 1937).

12.   Lacinia mobilis: (0) absent; (1) present. Present in Nannochoristidae (PILGRIM 1972; BEUTEL et al. 2009) but absent in Boreidae and all known larvae of Pistillifera (CURRIE 1932; APPLEGARTH 1939; BIERBRODT 1942; BYERS 1987).

13.   Mandibular acanthae (prosthecal brush): (0) absent; (1) present. Present in Nannochoristidae (PILGRIM 1972; BEUTEL et al. 2009). Absent in Boreidae and all known larvae of Pistillifera (CURRIE 1932; APPLEGARTH 1939; BIERBRODT 1942; BYERS 1987).

14.   Position of maxillary base: (0) distant from mandible; (1) close to mandible. In a posterior position and widely separated from the mandibular articulation in larvae of *Caurinus* (Fig. 1B), *Boreus* (BEUTEL et al. 2009: fig. 10A) and Nannochoristidae (BEUTEL et al. 2009). Shifted anteriorly and placed at a level with the posterior mandibular joint in larvae of *Apterobittacus* (APPLEGARTH 1939), *Panorpa* (BIERBRODT 1942: fig. 2), and *Panorpodes* (JIANG et al. 2014).

15.   Shape of proximal maxillary element: (0) not distinctly broadened; (1) distinctly transverse. The proximal maxillary sclerite formed by the cardo and dististipes is not distinctly widened and pronouncedly transverse in Boreidae and *Nannochorista* (BEUTEL et al. 2009). This is the case in all examined pistilliferan larvae (CURRIE 1932; APPLEGARTH 1939; BIERBRODT 1942; BYERS 1987).

16.   Posteromesal process of the proximal maxillary element: (0) absent; (1) present. A distinct process resembling a condyle is present on the proximal maxillary sclerite of pistilliferan larvae (APPLEGARTH 1939; BIERBRODT 1942). It is missing in Boreidae and *Nannochorista* (BEUTEL et al. 2009).

17.   Galea and lacinia: (0) extensively united, but separate origins clearly discernible; (1) completely united, composite formation without clear indication of double origin. A recognizable border between the components of the inner maxillary lobe is absent in Boreidae (POTTER 1938; RUSSELL 1982; BEUTEL et al. 2009). A distinct furrow demarcating the galea from the lacinia is present in *Nannochorista* (BEUTEL et al. 2009) and also in *Panorpa* (BIERBRODT 1942) and *Apterobittacus* (APPLEGARTH 1939), and *Panorpodes* (JIANG et al. 2014).

18.   M. tentoriocardinalis (M.17): (0) well developed; (1) absent. Present and well developed in *Caurinus* and *Boreus*, and also in *Nannochorista* (Table 1; BEUTEL et al. 2009). Absent in *Panorpa* (BIERBRODT 1942) and other pistilliferan larvae (HINTON 1958).

19.   Distance between labial palps and salivary orifice: (0) palps sessile, on non-produced prelabial area, distant from salivary orifice; (1) borne on elongate, palpomere-like prelabial processes, adjacent to salivary orifice. The palps are not placed on produced prelabial areas and widely separated from the salivary orifice in *Caurinus*, *Boreus* and *Nannochorista*. In Pistillifera they are inserted on prominent premental lobes. These structures resembling palpomeres arise immediately adjacent to the salivary orifice (see BEUTEL et al. 2009).

20.   Mm. cranio-/tentoriopraementalis: (0) single bundle; (1) absent. All labial muscles are absent in *Caurinus*, *Boreus* and *Nannochorista* (BEUTEL et al. 2009). One premental muscle is present in *Panorpa* (BIERBRODT 1942: part of M.p.lb).

21.   Anterior part of epipharynx: (0) not exposed; (1) slightly or distinctly exposed. Completely concealed in *Caurinus*, *Boreus* and Pistillifera, but exposed in *Nannochorista* (BEUTEL et al. 2009).

22.   M. verticopharyngalis (M.51): (0) one bundle; (1) two or three separate subcomponents. Composed of at least two separate subunits in *Caurinus* and *Boreus*, and also in Siphonaptera (SHARIF 1937; BEUTEL et al. 2009). Three subunits are present in *Panorpa* and *Nannochorista* (BEUTEL et al. 2009).

23.   M. tentoriopharyngalis (M.52): (0) one or several bundle arranged as one unit; (1) two or three distinct subcomponents. Composed of several distinctly separated subcomponents with different areas of origin in *Nannochorista* (BEUTEL et al. 2009) and *Caurinus* (Fig. 5). Several bundles forming one unit in *Boreus* and *Panorpa* (BIERBRODT 1942).

Characters of postcephalic body

24.   Number of leg segments: (0) more than 4; (1) 3. The larval legs are three-segmented in larvae of Mecoptera excluding Nannochoristidae (BYERS 1987; KLUGE 2003).

25.   Shape of abdomen: (0) elongate and slender (campodeiform); (1) eruciform or scarabaeiform. Slender, with thin, smooth cuticle in larvae of Nannochoristidae (PILGRIM 1972; FRAULOB et al. 2012). Eruciform in the known larvae of Boreidae and Pistillifera (e.g., BYERS 1987; JIANG et al. 2014).

26.   Conical ventral protuberances on segments I–VIII: (0) absent; (1) present. Conical fleshy protuberances are absent in Boreidae and Nannochoristidae (PILGRIM 1972; BYERS 1987), but present on the ventral side of abdominal segments I–VIII of Panorpidae and Bittacidae (BYERS 1987). The atypical unpaired median processes of Panorpodidae (JIANG et al. 2014) are very likely homologous to the protuberances of the other pistilliferan larvae.

27.   Segment XI: (0) absent; (1) present. Segment XI is present in Boreidae (RUSSELL 1982), but absent in Nannochoristidae and Pistillifera (BYERS 1987; FRAULOB et al. 2012).

28.   Four adhesive terminal lobes: (0) absent; (1) present. Absent in *Nannochorista* and *Boreus* but present in the larvae of *Caurinus* and in most described larvae of Pistillifera (BYERS 1987). The terminal "abdominal sucker" described by JIANG et al. (2014) for *Panorpodes* differs distinctly from the typical condition.

29.   Habitat: (0) terrestrial; (1) semiaquatic; (2) aquatic. Larvae of Boreidae and Pistillifera are terrestrial whereas those of Nannochoristidae are aquatic (PILGRIM 1972; BYERS 1987).

30.   Association with bryophytes: (0) absent; (1) present. Larvae of Boreidae are associated with bryophytes (RUSSELL 1982).

5.   Discussion

The monophyletic origin of Boreidae is well supported by molecular data (WHITING 2002), and also features of the life habits and larval and adult morphology (RUSSELL 1979a, 1982; PENNY 1977; BEUTEL et al. 2008; FRIEDRICH et al. 2013). Previously suggested larval apomorphies of the family are the two-segmented very short antennae (RUSSELL 1982; PENNY 1977) and two-segmented maxillary palps (KALTENBACH, 1978; RUSSELL 1982). PENNY (1977) noted the occurrence of three-segmented palps within Boreidae, but COOPER (1974) described maxillary palps with two palpomeres in *Boreus notoperates*, and this is also conform with our own observations in larvae of *Boreus westwoodi*. Another typical feature of Boreidae is the presence of typical stemmata. Seven as they are present in *Caurinus* are probably a groundplan character state of the family, and probably of the order Mecoptera, whereas the presence of only three is an apomorphy of Boreinae (BYERS 1987; COOPER 1974). The one-segmented labial palps of *Caurinus* are likely an autapomorphy of the genus. The loss of the sensilla placodea on the penultimate antennomere is another apomorphy of Boreinae (RUSSELL 1982).

The monophyletic origin of Mecoptera was challenged in several recent studies with respect to Boreidae and Nannochoristidae (WHITING 2002; WHITING et al. 2003; BEUTEL & BAUM 2008). However, considering the robust support for the monophyly of the order in recent analyses of comprehensive molecular and morphological data sets (WIEGMANN et al. 2009; FRIEDRICH & BEUTEL 2010; BEUTEL et al. 2011), we interpret the paraphyly as an artefact, mainly due to the specialized aquatic habits of the immatures of Nannochoristidae, which differ strikingly from the terrestrial life style of the other mecopteran larvae. Consequently, no convincing larval apomorphies support the monophyly of Mecoptera (see e.g., BEUTEL et al. 2011).

The phylogenetic interpretation of larval features investigated in the present study remains ambivalent, suggesting a sistergroup relationship Boreidae + Pistillifera or alternatively a sistergroup relationship between Bo-

reidae and the entire remaining Mecoptera (see MISOF et al. 2014), i.e. a clade Nannochoristidae + Pistillifera. A potential synapomorphy of Boreidae and Pistillifera is the orthognathous head, implying prognathism in the groundplan of Antliophora and Mecoptera. A prognathous head does not only occur in Nannochoristidae, but also in Siphonaptera and the vast majority of dipteran lineages (e.g., NEUGART et al. 2009). Other arguments would be the concealed epipharynx, the absence of the lacinia mobilis, and unbranched cephalic setae (BIERBRODT 1942; COOPER 1974; BEUTEL et al. 2009; TAN & HUA 2008). However, in these cases the polarity of the characters is quite unclear. Postcephalic potential synapomorphies of Pistillifera and Boreidae are the strongly sculptured thoracic and abdominal surface (KALTENBACH 1978; BYERS 1987), and the thoracic pleural folds (RUSSELL 1982). Both features are absent in Nannochoristidae and also in Siphonaptera and Diptera. The presence of four terminal adhesive lobes in *Caurinus* and Pistillifera is another strong argument, as this is a unique structure in holometabolan larvae (e.g., BEUTEL et al. 2011). This implies that the secondary loss is an additional autapomorphy of Boreinae (Boreidae excl. *Caurinus*).

Alternatively, a placement of Boreidae as sistergroup of a clade Nannochoristidae + Pistillifera is suggested by several features. A strong argument is the absence of stemmata and the presence of secondary compound eyes in non-boreid Mecoptera (SUZUKI & NAGASHIMA 1989; MELZER et al. 1994). Stemmata are probably a derived groundplan feature of Aparaglossata (Holometabola excl. Hymenoptera; BEUTEL et al. 2011; PETERS et al. 2014). However, it is conceivable that the more or less well-developed compound eyes of most larvae of Pistillifera (e.g., BIERBRODT 1942; BYERS 1987; TAN & HUA 2008) and the aberrant larval light sense organs of *Nannochorista* (MELZER et al. 1994) have evolved independently. The complete absence of eyes in larvae of *Panorpodes kuandianensis* (JIANG et al. 2014) is apparently due to secondary reduction. Additional arguments for a clade Nannochoristidae + Pistillifera are the presence of a ventral hypostomal bridge and a ventral ecdysial line (BEUTEL et al. 2009), and arguably also an antennal base completely encircled by the sclerotized wall of the head capsule. A potential synapomorphy of adult males of Nannochoristidae and Pistillifera is the closed genital capsule (WILLMANN 1981a,b; see also FRIEDRICH et al. 2013). However, it cannot be excluded that the condition found in Boreidae is due to reversal.

Due to the phylogenetic ambiguities, the interpretation of character evolution and the larval groundplan of the order remain uncertain. The polarity of several important characters is ambivalent. A main unclear issue is whether the head of ancestral immature mecopterans was orthognathous or prognathous. Other ambivalent characters are the absence (Boreidae) or presence (Nannochoristidae and Pistillifera) of a hypostomal bridge and ventral ecdysial line, and the exposed (Nannochoristidae) or concealed (Boreidae and Pistillifera) anterior epipharynx.

Table 1. Proposed homology of the larval head muscles of *Caurinus*, *Panorpa* (Bierbrodt 1942) and *Nannochorista* (Beutel et al. 2009) and their assignment to the standard head nomenclatures of v. Kéler (1963) and Wipfler et al. (2011). Abbreviations: 'X' = present, 'O' = absent, '?' = uncertain homology.

	Caurinus	*Panorpa*	*Nannochorista*		
Name	**present study**	**Bierbrodt 1942**	**Beutel et al. 2009**	**Kelér 1963**	**Wipfler et al. 2011**
M. fronto-labralis	X	M. retr. labr.	M. 8	8	0lb1
M. labro-epipharyngalis	X	M. labr. ep.	M. 7	7	0lb5
M. fronto-epipharyngalis	0	M. prot. ep.	M. 9	9	0lb2
M. clypeo-epipharyngalis	X	M. dil. d. or.	M. 43	43	0ci1
M. clypeo-cibarialis	X	M. dil. d. or.	M. 44	44	0bu1
M. fronto-pharyngalis anterior	X	M. dil. d. ant. phar.	M. 45	45	0bu2
M. fronto-pharyngalis posterior	X	M. dil. d. post. phar.	M. 46	46	0bu3
M. tentorio-pharyngalis lateralis	X	M. dil. d. lat. phar.?	M. 47	47?	0hy2? 0bu4?
M. fronto-hypopharyngalis	0?	0	M. 41	41	0hy1
M. tentorio-hypopharyngalis	X?	M. p. lb.	M. 42	42	0hy3
M. tentorio-cibarialis	X	M. tent. phar. inf.	M. 48	48	0bu5
M. tentorio-pharyngalis anterior	X	M. tent. phar. sup.	M. 50	50	0bu6
M. tentorio-pharyngalis posterior	X	0	M. 52	52	0ph2
M. cranio-pharyngalis ventralis	X	M. gul. phar.	M. 54	54?	0ph2?
M. cranio-pharyngalis anterior	X	M. par. phar. ant. & post.	M. 51	51	0ph1
M. cranio-pharyngalis posterior	X	M. occ. phar	M. 53	53?	0ph3
M. tentorio-scapalis	X	M. d. sc.	MM 1/2/3/4	1?	0an1?
M. cranio-mandibularis internus	X	M. add. mand.	M. 11	11	0md1
M. cranio-mandibularis externus	X	M. abd. mand.	M. 12	12	0md3
M. tentorio-mandibularis	X	0	M. 13	13	0md4
M. tentorio-cardinalis	X	0	M. 17	17	0mx3
M. tentorio-stipitalis	X	M. add. sti.1	M. 18	18	0mx4
M. cranio-lacinialis	X	M. add. sti.2	M. 19	19	0mx2
M. cranio-dististipitalis	0	M. prom. lac	M. 19a	0	?
M. stipito-palpalis externus	X	M. ext. p .mx.	M. 22	22	0mx8
M. stipito-palpalis internus	0	0	M. 23	23	0mx10
M. hypopharyngo-salivarialis	X	M. dil. spp.	M. 37	37	0hy12

Several characters found in *Caurinus* are apparently plesiomorphic. This includes the complete tentorium with relatively thin but distinct dorsal arms and a broad bridge, the presence of more than three well-developed stemmata (groundplan of Aparaglossata; Peters et al. 2014), the free labrum, the simple mandibles with a basal molar area but without complex mesal appendages, the presence of a tentorio-mandibular muscle, the well-developed set of dorsal and ventral pharyngeal dilators, and the placement of the brain within the head. The presence of an occipital furrow is arguably also plesiomorphic as this structure also occurs in hymenopteran larvae (e.g., Beutel et al. 2008; but see Beutel et al. 2011). Within Boreidae most of these features remain stable. However, the loss of several stemmata is very likely a synapomorphy of *Boreus* and *Hesperoboreus* (Boreinae) as pointed out above, whereas the vestigial labium and the strongly shortened antennae are probably autapomorphies of *Caurinus*. The interpretation of the broad clypeus in *Caurinus* is ambiguous. This could be due to reversal as a narrowed clypeus is arguably a synapomorphy of Boreidae (groundplan) and Pistillifera (Beutel et al. 2009).

A character complex typical for Mecopterida is the set of modifications of the maxillae and its musculature, as for instance the formation of a maxillolabial complex, a basal maxillary element comprising the cardo and stipes, and the presence of a cranio-dististipital muscle (Hinton 1958; Beutel et al. 2009; Table 1). A separation of the maxillary endite lobes is still recognizable in *Nannochorista* and Pistillifera (Beutel et al. 2009), whereas they are indistinguishably fused in Boreidae, another potential autapomorphy of this family.

Miniaturization has apparently also played a certain role in *Caurinus*, even though the size is not extremely small and the modifications moderate. The internal structures appear densely packed and the brain moderately enlarged in relation to the entire head, even though it is not shifted to the thorax as it is often the case in very small larvae (e.g., Grebennikov & Beutel 2002; Beutel et al. 2005; Polilov & Beutel 2009). Other characters possibly related to size reduction is the extremely short and 2-segmented antenna, the presence of only one antennal muscle, and the greatly reduced labium with one-segmented palps.

Apparently the placement of Boreidae and the character evolution cannot be unambiguously clarified with the presently available data. In a recent study on insect phylogeny using transcriptomes the relationships of the three main mecopteran lineages also remained unresolved (Misof et al. 2014). Analyses of transcriptomic data with a broader taxon sampling of Antliophora (Antliophora

subproject of 1KITE; www.1KITE.org) may help to clarify this difficult issue and help to understand the evolution of larval characters in Mecoptera.

6.   Acknowledgements

7.   References

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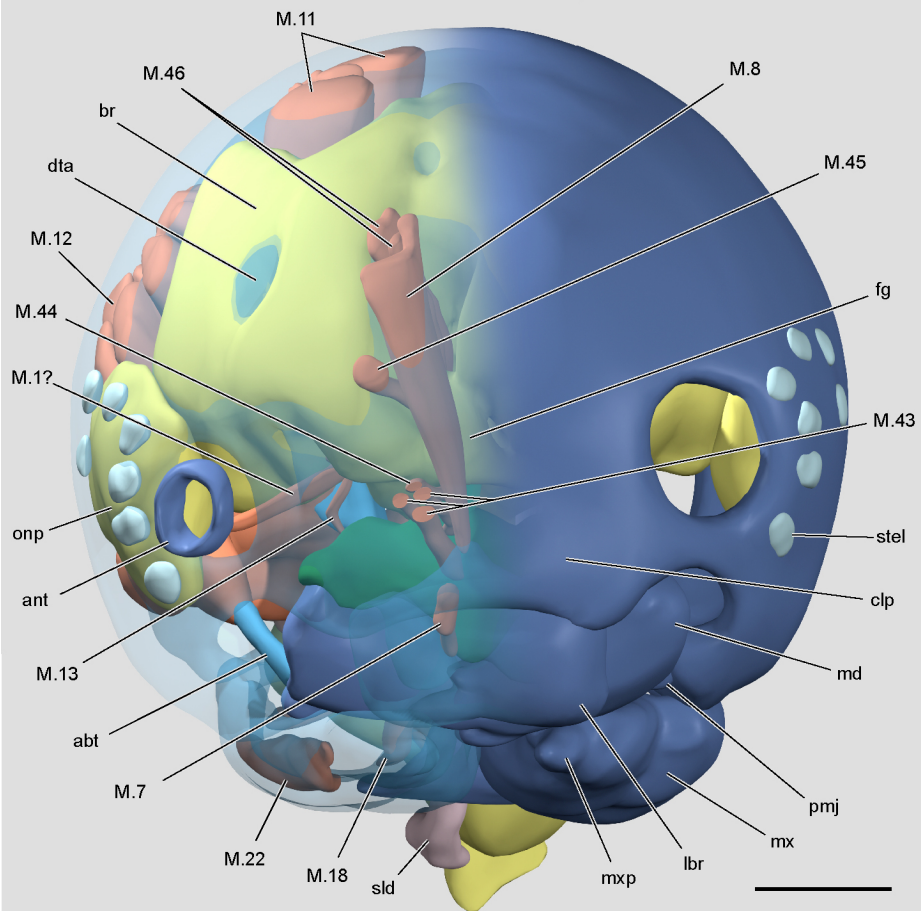
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Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2015

Band/Volume: 73

Autor(en)/Author(s): Fabian Benjamin, Russel Loren, Friedrich Frank, Beutel Rolf Georg

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