Cephalic anatomy of *Zorotypus weidneri* New, 1978: new evidence for a placement of Zoraptera

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Abstract

External and internal head structures of *Zorotypus weidneri* were examined, documented with SEM images and photographs, and reconstructed 3-dimensionally. The results are compared with published results on *Z. hubbardi* and with conditions found in other hemimetabolan lineages, with a main focus on the polyneopteran orders and on Psocoptera and Thysanoptera representing Acercaria. Externally the head of both zorapteran species is very similar but they differ in some internal features such as the presence (*Z. hubbardi*) or absence (*Z. weidneri*) of an ampullo-aortic muscle of the antennal heart and a well-developed cervical gland. Cephalic characters are analysed phylogenetically addressing the controversial issue of the placement of Zoraptera. A position within monophyletic Polyneoptera is confirmed, but weakly supported. The analysis yielded a sister group relationship between Zoraptera and Plecoptera but also with a low support value. The placement of Zoraptera with morphological data is impeded by many preserved plesiomorphies such as the orthognathous head orientation, the complete tentorium, the free labrum or the largely unmodified orthopteroid mouthparts in the winged morphs, and also by modifications apparently caused by miniaturization. Similarly, anomalies in the genome cause problems in the assessment of the phylogenetic affinities of the group.

Key words

Zoraptera, groundlice, head, morphology, phylogeny, Polyneoptera, Acercaria.

1. Introduction

Zoraptera or groundlice are a cryptic and controversial group of small hemimetabolous insects (e.g., Grimaldi & Engel 2005; Mashimo et al. 2014c). The order was introduced by Silvestri (1913) who addressed them as „Insecta terrestria, parva, aptera, agila, praedantia", which means „living in earth, small, apterous, agile and predacious insects". With presently 39 extant and 9 extinct species it belongs to the smallest groups of insects (Engel 2003; Mashimo et al. 2013). The distribution is worldwide, with the exception of the Australian mainland and

Antarctica (MASHIMO et al. 2014c). The group is largely restricted to tropical and subtropical regions. *Zorotypus hubbardi* Caudell, 1918 has expanded its range as far north as Indiana, Iowa and Illinois (RIEGEL 1963; HUBBARD 1990), but this is likely due to transport with woods (MASHIMO et al. 2014c).

Selected aspects of the morphology of Zoraptera were treated in few earlier studies (e.g., CRAMPTON 1920, 1921), but the investigation of the group was neglected for a long time (see e.g., MASHIMO et al. 2014c). Consequently, it was addressed as the least known insect order by KRISTENSEN (1995). In the last two decades the research on Zoraptera has gained remarkable momentum, with studies on the head morphology (BEUTEL & WEIDE 2005; WIPFLER & PASS 2014), thoracic skeletomuscular system (RASNITSYN 1998; FRIEDRICH & BEUTEL 2008), wing base (YOSHIZAWA 2007, 2011), genital structures of different species (HÜNEFELD 2007; DALLAI et al. 2011, 2012a,b, 2014a,b, 2015; MATSUMURA et al. 2014), the egg structure (MASHIMO et al. 2011), the embryonic (MASHIMO et al. 2014a) and postembryonic development (MASHIMO et al. 2014b), and the mating behavior (CHOE 1994, 1995, 1997; DALLAI et al. 2013). The controversial systematic placement of Zoraptera was addressed using morphological characters (e.g., RASNITSYN 1998; BEUTEL & GORB 2001, 2006; BEUTEL & WEIDE 2005; YOSHIZAWA 2007) and molecular data sets (YOSHIZAWA & JOHNSON 2005: 18S rRNA; LETSCH & SIMON 2013; MISOF et al. 2014: transcriptomes). Nevertheless, the "Zoraptera problem" (BEUTEL & WEIDE 2005) is far from being settled. The sister group relationship between Zoraptera and Acercaria (Paraneoptera concept) suggested by HENNIG (1969) and others (e.g., BEUTEL & WEIDE 2005; WILLMANN 2005) has gained little support in recent studies, which favor a placement among polyneopteran lineages (e.g., MINET & BOURGOIN 1986; ENGEL & GRIMALDI 2000; GRIMALDI 2001; WHEELER et al. 2001; YOSHIZAWA 2007; MASHIMO et al. 2014a; MISOF et al. 2014; WIPFLER & PASS 2014; see also TRAUTWEIN et al. 2012 and MASHIMO et al. 2014c). However, the precise position within Polyneoptera, which may or may not be monophyletic (e.g., KRISTENSEN, 1995; KLASS 2009; WIPFLER et al. 2011; LETSCH & SIMON 2013; BEUTEL et al. 2014b) (see MASHIMO et al. 2014c), remains unclear.

The present study has its focus on cephalic structures, a complex character system which has turned out as phylogenetically informative in many studies (e.g., BEUTEL et al. 2011; WIPFLER et al. 2011). The skeletomuscular system of the thorax of winged morphs is almost exclusively characterized by plesiomorphic features (FRIEDRICH & BEUTEL 2008) and the reproductive characters such as male genitalia, spermatogenesis, and spermatozoa are highly variable among species even within the very small order (e.g., GURNEY 1938; DALLAI et al. 2011, 2012a,b, 2014a,b). The head morphology of *Zorotypus hubbardi* was already described (BEUTEL & WEIDE 2005). However, it turned out that some structures have been overlooked or misinterpreted (e.g., WIPFLER & PASS 2014: antennal hearts) and that some features are apparently not conformed with

the groundplan of the order (e.g., blade-like lacinia). In any case, considering the immense problems of placing Zoraptera and the unresolved intraordinal relationships it appeared appropriate to examine other species with an optimized spectrum of morphological techniques (e.g., FRIEDRICH et al. 2014). The morphological results were integrated in a large data matrix for cephalic characters of hemimetabolous insects and analyzed phylogenetically.

2. Material and methods

2.1. Specimens

We used winged and wingless specimens of *Zorotypus weidneri* collected at Manaus (Brazil) in June 2002 preserved in 70 % ethanol mainly for studying external structures. Additional exemplars collected at the same locality in 2014 were fixed in 2.5% glutaraldehyde in phosphate buffer to which 3% of sucrose was added. The specimens were kept in this mixture in a refrigerator for one week. After this they were gradually dehydrated and preserved in 70% ethanol for detailed anatomical investigations. All voucher specimens were deposited in the Phyletischem Museum of the Friedrich-Schiller-Universität Jena.

2.2. Anatomy

We used histological sectioning, scanning electron microscopy (SEM) and confocal laser scanning microscopy (CLSM). Transverse semithin sections were made of the anterior body region of winged and wingless exemplars. The samples were embedded in araldite CY 212® (Agar ScientiWc, Stansted/Essex, England) and cut at 1 µm using a microtome HM 360 (Microm, Walldorf, Germany) equipped with a diamond knife. Sections were stained with toluidine blue and pyronin G (Waldeck GmbH and Co.KG/Division Chroma, Münster, Germany). Successive pictures were taken of every second section using a light microscope (Zeiss Axioplan, Germany) equipped with a camera (PixeLink Capture OEM) (wingless specimen: 360 pictures; winged specimen: 341 pictures). The images were aligned using Amira 5.3.1 software (Visage Imaging, Berlin, Germany). Based on the aligned image stacks we evaluated the arrangement of internal structures and manually traced each element to reconstruct three-dimensional images for the winged specimen. For smoothing, coloring, illumination, and taking pictures we used MAYA 7 (Alias Wavefront, Toronto/Ontario, Canada).

Scanning electron microscopy (SEM, Philips XL 30 ESEM) was used to observe cephalic surface structures. We gradually dehydrated specimens preserved in 70% ethanol with an ethanol-acetone series and dried them at the critical point (Emitech K850 critical point dryer). To

Table 1. Taxon sampling for the cladistic analysis and source of the morphological information.

Taxon	Species	Literature source
Ephemeroptera	*Siphlonurus lacustris* (Eaton, 1870)	BLANKE et al. 2012
Plecoptera	*Perla marginata* (Panzer, 1799)	BLANKE et al. 2012
Plecoptera	*Nemoura cinerea* (Retzius, 1783)	MOULINS 1968
Grylloblattodea	*Grylloblatta campodeiformis* Walker, 1914	WALKER 1931
Grylloblattodea	*Galloisiana yuasai* Asahina, 1959	WIPFLER et al. 2011
Mantophasmatodea	*Karoophasma* sp.	BAUM et al. 2007
Mantophasmatodea	*Austrophasma* sp.	WIPFLER et al. 2011
Blattaria	*Periplaneta americana* Linnaeus, 1758	WIPFLER et al. 2011
Blattaria	*Cryptocercus punctulatus* Scudder, 1862	WIPFLER et al. 2009
Mantodea	*Hymenopus coronatus* (Olivier, 1792)	WIPFLER et al. 2012
Isoptera	*Mastotermes darwiniensis* Frogatt, 1897	WIPFLER et al. 2009
Phasmatodea	*Timema cristinae* Vickery,1993	TILGNER et al. 1999; WIPFLER 2012
Phasmatodea	*Agathemera crassa* (Blanchard, 1851)	WIPFLER et al. 2011
Phasmatodea	*Phyllium siccidifolium* (Linnaeus, 1758)	FRIEDEMANN et al. 2012
Phasmatodea	*Megacrania batesii* Kriby, 1896	FRIEDEMANN et al. 2012
Phasmatodea	*Sipyloidea sipylus* (Westwood, 1859)	FRIEDEMANN et al. 2012
Embioptera	*Embia ramburi* Rimsky-Korsakow, 1906	RÄHLE 1970
Embioptera	*Metoligotoma* sp.	WIPFLER 2012
Dermaptera	*Labidura riparia* (Pallas, 1773)	KADAM 1961
Dermaptera	*Forficula auricularia* Linnaeus, 1758	WIPFLER 2012
Orthoptera / Caelifera	*Xya variegata* (Latreille, 1809)	WIPFLER 2012
Orthoptera / Ensifera	*Troglophilus* sp.	WIPFLER 2012
Orthoptera / Ensifera	*Schizodactylus monstrosus* (Drury, 1773)	KHATAR 1964
Zoraptera	*Zorotypus hubbardi* Caudell, 1918	BEUTEL & WEIDE 2005
Zoraptera	*Zorotypus weidneri* New, 1978	present study
Psocoptera	*Stenopsocus stigmaticus* (Imhoff & Labram, 1846)	BADONNEL 1934
Thysanoptera	*Aeolothrips fasciatus* Linnaeus, 1758	MICKOLEIT 1963
Neuroptera	*Osmylus fulvicephalus* (Scopoli, 1763)	BEUTEL et al. 2010
Hymenoptera	*Macroxyela* sp.	BEUTEL & VILHELMSEN 2007

take pictures of relatively well sclerotized larger parts, we used ethanol-hexamethyldisilazane series in some cases, and dried the samples in a fume hood. Dried samples were mounted on the tip of a fine needle with nail polish and fixed on the rotatable specimen holder developed by POHL (2010) or directly attached on a carbon adhesive sheet. To produce a rotatable SEM movie (El. Suppl. 3) for a wingless specimen, we took SEM images from different angles (every 10 degree) and stacked it using Apple Quicktime (see also CHEUNG et al. 2013). Before spatter coating of a winged specimen, photographs of critical point dried specimens were taken with a Nikon D 90 digital SLR equipped with a 40 mm and with a 63 mm Zeiss Luminar macro lense, plus an adjustable extension bellows. The specimens were illuminated by two flashlights fitted with a transparent cylinder for even and soft light. Helicon Focus Mac Pro X64 was used to combine a stack of partially focused images.

Confocal laser scanning micrographs (CLSM) of a wingless sample fixed with glutaraldehyde was taken with a Zeiss LSM 700 (Zeiss, Germany), using an excitation wavelength of 405, 488, 555, and 639 nm and a 10 folds objective lens. We applied a long pass emission filter transmitting light with wavelengths of $420-480$, $\geq$ 490, $\geq$ 560, and $\geq$ 640 nm to detect the autofluorescence excited by each laser light. Glycerin was used as medium for scanning.

2.3. Terminology

We used the general morphological terminology of BEUTEL et al. (2014a). Muscles were described according to WIPFLER et al. (2011) (see also BEUTEL et al. 2014a). Muscles not mentioned are absent. We define the space between the functional and anatomical mouth opening, where a closed tube is present as preoral tube. Moreover postoccipital ridge is defined as the ridge around the foramen occipitale which strengthens the posterior head mechanically and serves as attachment area for intrinsic and extrinsic muscles of the head (e.g., BEUTEL et al. 2014a).

2.4. Cladistic analysis

Documented cephalic features of *Zorotypus weidneri* were coded and entered in a data matrix of 128 morphological characters together with data compiled in previous studies (WIPFLER et al. 2011; BLANKE et al. 2012; WIPFLER 2012). Table 1 shows the taxon sampling and the source of information for each species. The data matrix and a character discussion are provided in the electronic supplements 1 and 2. The parsimony analysis was carried out with Winclada/Nona (Ratchet [Island Hopper],
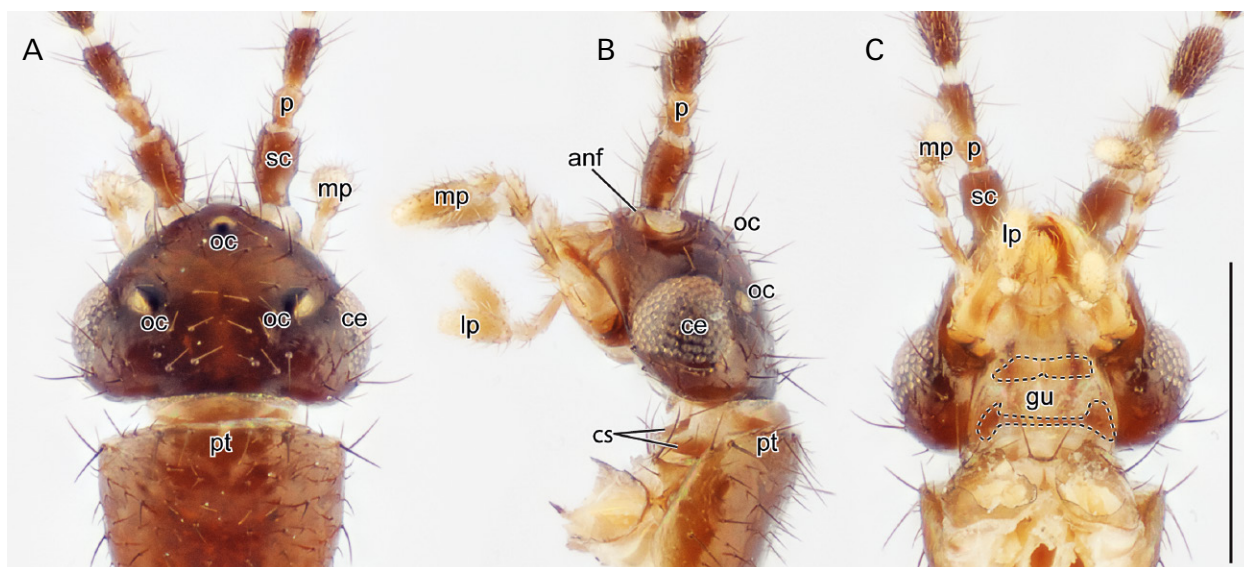
Fig. 1. *Zorotypus weidneri*, head, winged morph. **A**: dorsal view; **B**: lateral view; **C**: ventral view. Scale, 500 μm. The dashed lines in C indicate sclerotized gular areas. — **Abbreviations**: anf, antennifer; ce, compound eyes; cs, cervical sclerites; gu, gula; lp, labial palp; mp, maxillary palp; oc, ocelli; p, pedicellus; pt, prothorax; sc, scapus.

default settings with 1000 iterations) (Goloboff 1999; Nixon 1999, 2000, 2002) and TNT (Wagner trees, 99 999 random seeds, 1000 replications, tree bisection reconnection, 10 trees to save per replicate) (Goloboff et al. 2000). All characters were equally weighted and treated as non-additive. Bremer support values (Bremer 1994) were calculated with TNT. The unambiguous character changes were retrieved from the strict consensus tree in Nona.

3. Morphological results

3.1. External head capsule

(Figs. 1, 2, 3, El. Suppl. 3)

The head capsule is fully exposed, i.e. the posterior parts are not retracted into the prothorax. Ventrolateral cervical sclerites are present as a well-developed pair of protuberances between the posterolateral margin of the head and the anterolateral prothoracic margin (Fig. 1B). The foramen occipitale is distinctly narrowed. The head is orthognathous and about as long as broad, and triangular in dorsal view. The head capsule is dark-brown. Large areas of the ventral mouthparts with thin cuticle are less pigmented. Longer and shorter setae are distributed as shown in Figs. 1 and 3. Compound eyes and three ocelli are present in winged individuals (Fig. 3). The coronal and frontal sutures are absent, but external traces of the postoccipital ridge are recognizable (Fig. 3). The clypeus comprises a less sclerotized anterior anteclypeus and a

posterior postclypeal area (Fig. 3G) which are separated by a shallow external rim corresponding with an internal transverse intraclypeal ridge slightly ventrad the anterior tentorial pits (Fig. 3G). The ridge is moderately sclerotized. The postclypeal region is posteriorly completely fused with the frons. A broad, slightly sclerotized gular area interrupted by a broad, transverse membranous area in its middle region was observed in a winged specimen (Fig. 1C), whereas only a simple short and broad transverse sclerite was recognizable in a wingless one (Fig. 2). A distinct border between the occipital and genal regions is not recognizable (Fig. 3). An epistomal ridge is not present.

3.2. Endoskeleton

(Fig. 3B, 6A,C,E)

The postoccipital ridge is present (Fig. 3B). The tentorium is well developed, and all parts are sclerotized (Fig. 6A,C,E). The flat and straight anterior arms arise from the anterior head capsule close to the lateral mandibular articulation; they are continuous with an internal ridge reaching the clypeus at the area of the anterior tentorial pits (Fig. 6A). The fissure-shaped posterior tentorial grooves are posteriorly continuous with the indistinct hypostomal ridges and the postoccipital ridge (Fig. 3B). The short posterior arms are connected to the anterior arms by the broad and straight tentorial bridge. Accessory mesally directed arms (laminatentorium, "perforated corpotentorium") are absent. The dorsal tentorial arms are the longest and attached to the head capsule dorsolaterad the antennae (Fig. 6A).

Fig. 2. *Zorotypus weidneri*, head, wingless morph, CLSM micrograph, ventral view. Scale, 200 μm. — ***Abbreviations***: ga, galea; la, lacinia; lb, labrum; lp, labial palp; md, mandible; mp, maxillary palp; scl, sclerotized gular area.

3.3. Labrum

(Fig. 3G)

The weakly sclerotized labrum is roughly diamond-shaped and about as long as broad. It is rounded at each corner. The base is distinctly narrowed and connected with the anterior margin of the anteclypeus. The border between both regions is indistinct externally, but clearly recognizable on histological sections. Densely grouped setae are inserted along the anterior labral margin whereas the setation is sparse on the other regions (Fig. 3G). The tormae, which serve as attachment area of M. frontoepipharyngalis (0lb2), are very small.

Musculature (Fig. 7A): M. labroepipharyngalis (0lb5), short – origin (O): central region of external wall of labrum; insertion (I): medially on anterior epipharynx; M. frontolabralis (0lb1) – O: medially on posterior frontal region; I: external wall of labrum, dorsal region of origin of M. labroepipharyngalis (0lb5); M. frontoepipharyngalis (0lb2) – O: posterior frontal region; I: posterolateral edge of labrum, on short tormae.

3.4. Antennae

(Figs. 3C,G, 7A)

The antenna is composed of nine segments (Fig. 3C). The large scapus is two times longer than wide, with a distinct proximal constriction; its base is inserted on an articulatory membrane, and a projection is formed by the
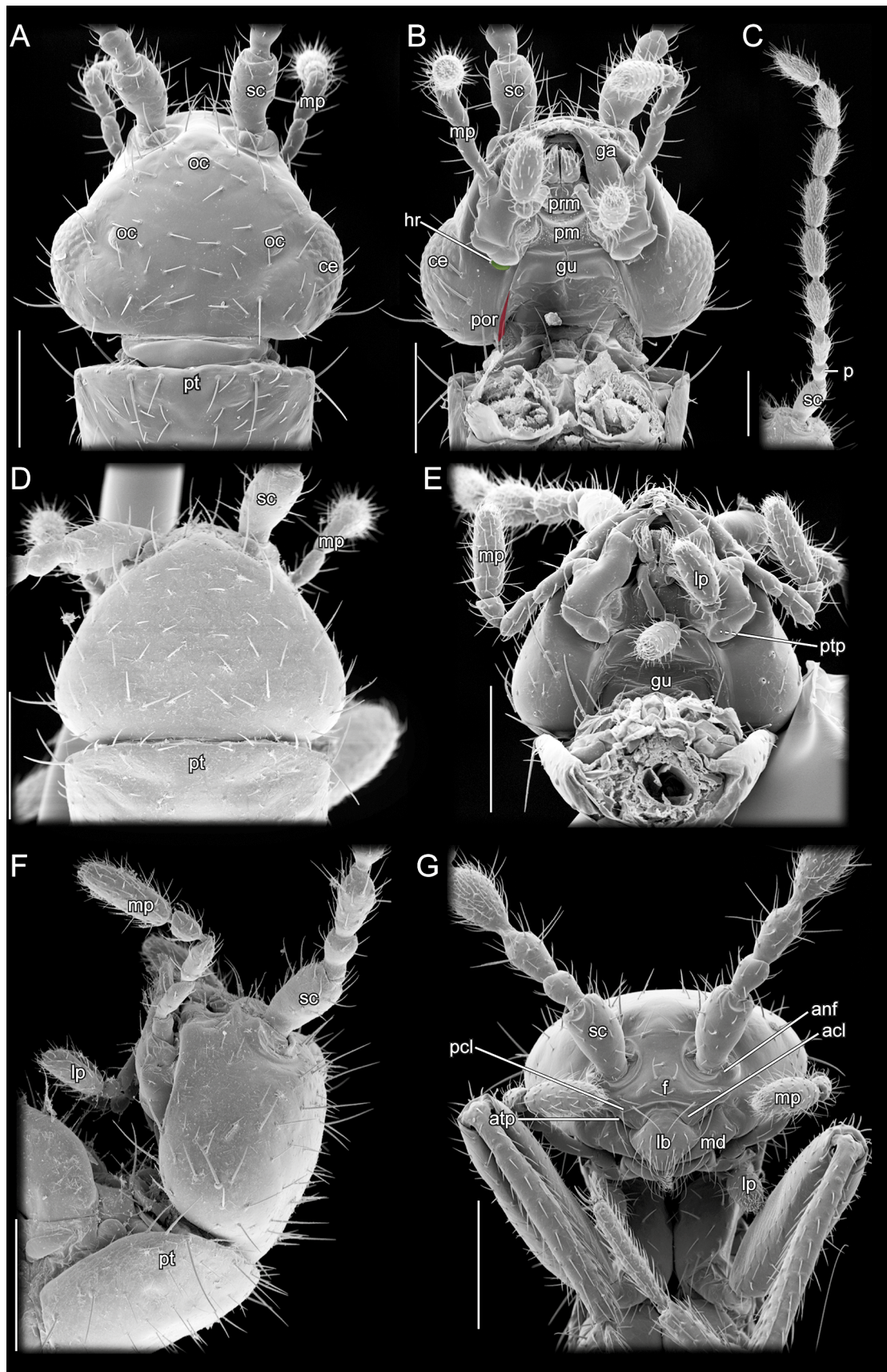
Fig. 3. *Zorotypus weidneri*, head, winged (A,B) and wingless (C–G) morphs, SEM micrographs. **A,D**: dorsal view; **B,E**: ventral view; **C,F**: lateral view; **G**: frontal view. Scale, A,B,D–G: 100 μm; C: 200 μm. — *Abbreviations*: acl, anteclypeus; anf, antennifer; atp, anterior tentorial pit; ce, compound eyes; ga, galea; gu, gula; hr, hypostomal ridge; lb, labrum; lp, labial palp; md, mandible; mp, maxillary palp; oc, ocelli; p, pedicellus; pcl, postclypeus; pm, postmentum; por, postoccipital ridge; prm, praementum; pt, prothorax; ptp, posterior tentorial pit; sc, scapus.

sclerotized cuticle enclosing it (Fig. 1B, 3G); this anten-nifer is not in direct contact with the sclerotized base of the scapus. The pedicellus is the shortest antennomere, with a relatively narrow basal part and distinctly widen-ing apically, almost appearing club-shaped. The base of the pedicellus is surrounded by a relatively wide articu-latory membranous area (Fig. 1), and the outline of the socket on the scapula is sinuate. The Johnston's organ is present but poorly developed. Flagellomere 1 is small and tapering towards its base. Flagellomeres 2–7 are dis-tinctly longer and broader than antennomeres 2 and 3. All flagellomeres are covered with setae (sensilla) of differ-ent length. The distribution of the setae is shown in Fig. 3C,G. The lens-shaped ampullae of the antennal hearts are largely membranous and located above the antennal insertion areas (Figs. 7A).

Musculature (Fig. 7A): a transverse muscle connecting the antennal hearts is homologous to M. interampullaris or ampullo-ampullaris (0ah1) and muscle Mxy in Beutel & Weide (2005). The muscles linking the antennal hearts and the aorta (M. ampulloaortica, 0ah2) in *Z. hubbardi* (Wipfler & Pass 2014) are missing in *Z. weidneri*. M. tentorioscapalis anterior (0an1) – O: antero-mesal and antero-lateral part of basal region of anterior and dorsal tentorial arms; I: ventrally on scapal base; M. tentorio-scapalis posterior (0an2) – O: postero-mesal region of dorsal tentorial arm; I: dorsally on scapal base; M. tento-rioscapalis lateralis (0an3) – O: lateral surface of basal part of anterior tentorial arm, posterior to origin of dorsal arm; I: anterolaterally on scapal base; M. scapopedicel-laris lateralis (0an6) – O: posterior wall of scapus; I: pos-teriorly on pedicellar base; M. scapopedicellaris medialis (0an7), distinctly larger than 0an6 – O: large parts of ba-sal scapus; I: large part of pedicellar base.

3.5. Mandibles

(Figs. 4A – D, 5, 7B)

The asymmetric mandibles are strongly sclerotized and roughly triangular with a rounded lateral margin (Fig. 4A–D). They are largely covered by the labrum in their resting position (Fig. 3G). The ventral side is adjacent to the anterior surface of the maxillae. Five teeth are pre-sent on the distal half of both mandibles. The two apical teeth of the right mandible are equally sized and lie above each other; the relatively large subapical tooth is sepa-rated from the smaller following intermediate tooth by a deep incision; the triangular proximal tooth is posteri-orly adjacent with the molar area, which is equipped with dentes molares (Figs. 4D, 5C,D; arrowhead); a prostheca is absent on the right mandible; the dorsal apical tooth is longer than its ventral counterpart; the triangular and pointed subapical tooth is the largest; a small intermedi-ate tooth is followed by the proximal tooth. On the left mandible, dentes molares are almost completely lacking, but some weakly developed projections are present on

the distal molar area and an area with a granular surface and fine brush-like structures on the proximal region (Fig. 5A,B); an apically branched stick-like prostheca is inserted on the ventral surface of the subapical tooth of the left mandible (Fig. 4B). Two cuticular tendons arise from the base of each mandible, the strongly developed adductor tendon on the mesal edge and the narrow ab-ductor tendon laterally.

Musculature (Fig. 7B): M. craniomandibularis inter-nus (0md1), by far the largest muscle of the head, with three subunits – O: dorso-laterally from the posterior head capsule; I: laterally, mesally, and posteriorly on the strongly developed adductor tendon; M. craniomandibu-laris externus posterior (0md3) – O: posterolaterally from the head capsule; I: narrow abductor tendon; M. tento-riomandibularis medialis inferior (0md8) – O: ventral side of anterior tentorial arm; I: mesal inner surface of the mandible; M. tentoriomandibularis lateralis inferior (0md6) – O: ventral side of anterior tentorial arm; I: ven-trally on the basal margin of the mandible.

3.6. Maxillae

(Figs. 2, 3B,E, 4E–I, 7C)

The maxillae are well developed and symmetrical (Figs. 2, 3B,E). The base of the cardo is almost completely sur-rounded by an extensive articulatory membrane and also forms a distinctly defined articulation with the head cap-sule; the distribution of setae is shown in Fig. 4E–I; its shape is more or less cylindrical and it is subdivided into a mesal proxicardo and a lateral disticardo by an indis-tinct line resulting from a stronger sclerotization; at its distal edge it appears broadly fused with the stipes on the external side but an articulation membrane is present; the stipital and the cardinal margins connected to this mem-brane are reinforced by a distinct ridge. A slender and cuticular tendon for attachment of M. craniocardinalis (0mx1) arises from the basal edge of the disticardo. The stipes bears a thin internal ridge; it is fused with the laci-nia on the dorsal side (Fig. 4E–F). The sickle-shaped la-cinia is larger than the galea; the surface of its mesal side is smooth with only few setae (Fig. 4E,F); the tip bears two small distal teeth (Fig. 4I, arrowhead). The apical part of the small galea bears a group of mesally directed strong spines (Fig. 4F,H), and a few rows of claw-like projections are present on its surface. The palp is 5-seg-mented; a palpifer is not recognizable; the short proximal palpomere is slightly wider than long; palpomeres 2 and 3 are narrowed at their base and almost 3–5 × as long as palpomere 1; palpomere 4 is slightly longer than 1; the apical palpomere is by far the largest and basally dis-tinctly narrowed. The setation is shown in Fig. 4E–H.

Musculature (Fig. 7C): M. craniocardinalis (0mx1) – O: dorsolaterally on posterior head capsule, between M. cra-nimandibularis externus posterior (0md3) and M. cranio-lacinialis (0mx2); I: narrow abductor tendon of cardo;
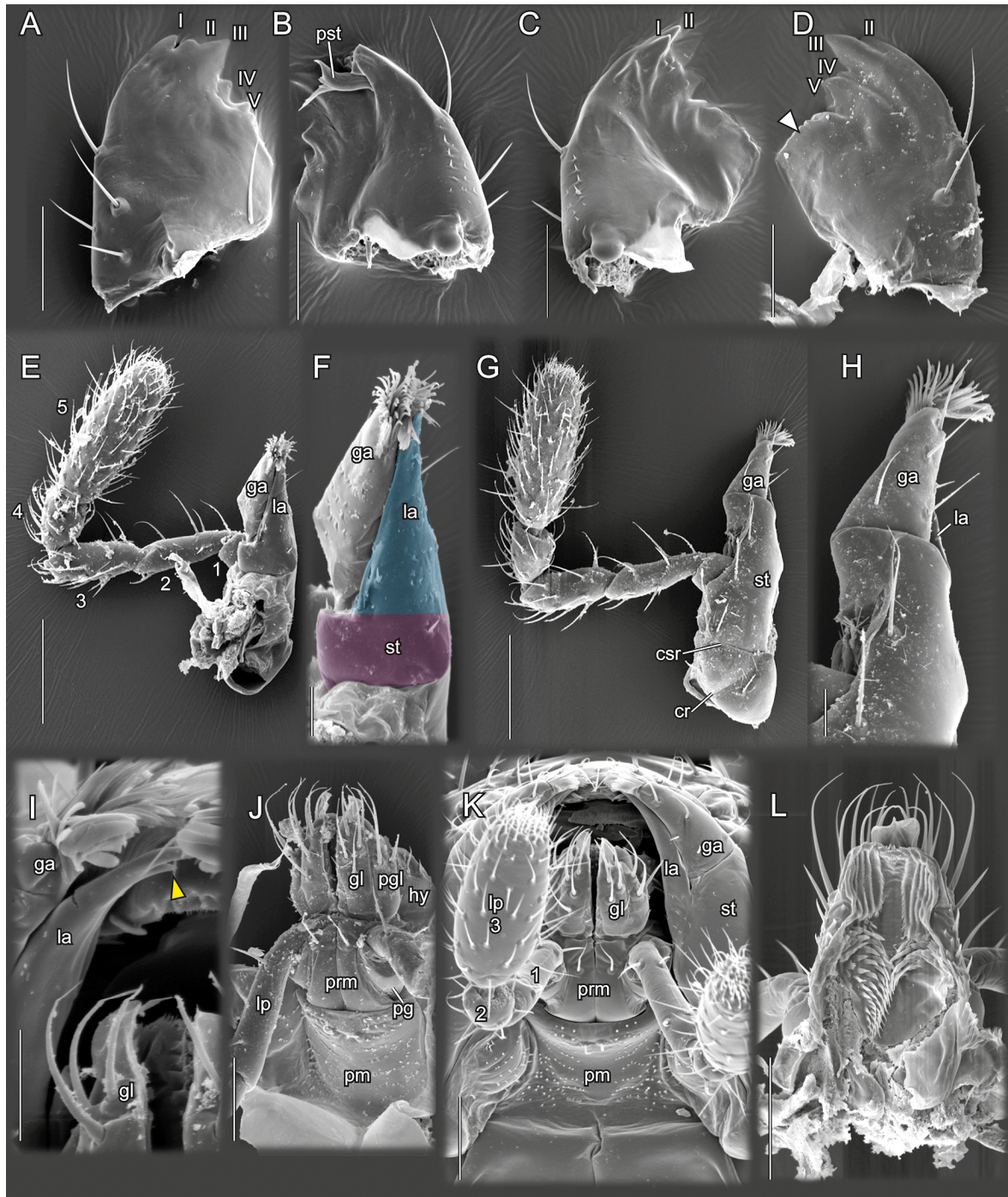
Fig. 4. *Zorotypus weidneri*, mouthparts, SEM micrographs. **A**: left mandible, dorsal view; **B**: left mandible, ventral view; **C**: right mandible, ventral view; **D**: right mandible, dorsal view, white arrowhead indicates the position equipped with dentes molares; **E**: left maxilla, dorsal view; **F**: lacinia and galea (enlarged), the practical border between the lacinia and stipes are shown in the different colors; **G**: right maxilla, ventral view; **H**: lacinia of G enlarged; **I**: galea (enlarged), yellow arrowhead indicates two small distal teeth; **J**: labium except for palpi, ventro-lateral view; **K**: labium, ventral view; **L**: hypopharynx, dorsal view. Scale bars, A–D, J–L: 50 μm; E,G: 100 μm; F,H: 20 μm; I: 25 μm. — ***Abbreviations***: I–V in A–D, mandibular teeth; 1–5 in E, maxillary palpomeres; 1–3 in K, labial palpomeres; cr, cardinal ridge; csr, cardostipital suture; ga, galea; gl, glossa; hy, hypopharynx; la, lacinia; lp, labial palp; pg, palpiger; pgl, paraglossa; pm, postmentum; prm, praementum; pst, prostheca; st, stipes.

M. tentoriocardinalis (0mx3) – O: anterior tentorial arm, close to origin of M. tentoriostipitalis (0mx5); I: laterally on the inner surface of the cardo; M. tentoriostipitalis anterior (0mx4) – O: ventral side of anterior and dorsal tentorial arm; I: ventrally on mesal stipital edge, proximad to attachment of M. craniolacinialis (0mx2); M. tentoriostipitalis posterior (0mx5), narrow muscle – O: ventral side of anterior tentorial arm; I: basally on stipes;
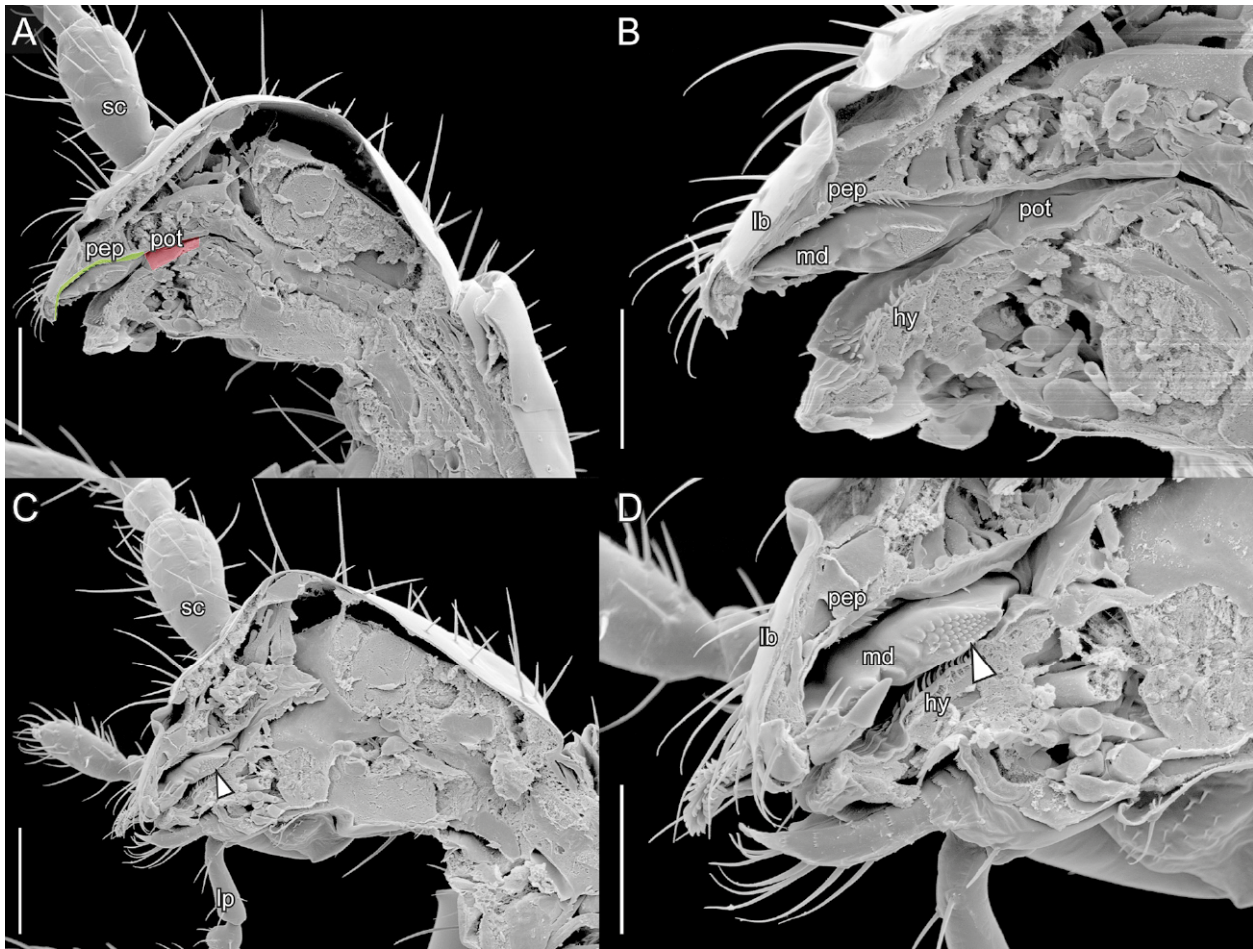
Fig. 5. *Zorotypus weidneri*, head, wingless morph, sagittal section. **A**: left half; **B**: mouth parts (A, enlarged); **C**: right half; **D**: mouth parts (C, enlarged). White arrowhead indicates molares on right mandible. Scale bars, A,C: 100 μm; B,D: 50 μm. — **Abbreviations**: hy, hypopharynx; lb, labrum; lp, labial palp; md, mandible; pep, preepipharynx; pot, preoral tube; sc, scapus.

M. craniolacinialis (0mx2) – O: head capsule between M. craniocardionalis (0mx1) and dorsal component of M. craniomandibularis internus (0md1); I: basal edge of lacinia by means of a short tendon; M. stipitolacinialis (0mx6) – O: laterally on stipital base; I: base of lacinia, close to insertion of 0mx2; M. stipitogalealis (0mx7) two subunits – O: ventral edge of mediostipes; I: base of galea; M. stipitogalealis dorsalis (0mx16) – O: dorsal edge of mediostipes; I: base of galea; M. stipitopalpalis externus (0mx8) – O: ventrally from stipes, close to mesal edge; I: posteriorly on base of palpomere 1; M. stipitopalpalis medialis (0mx9) – O: ventrally from stipes, close to mesal edge; I: posteriorly on the base of palpomere 1; M. stipitopalpalis internus (0mx10) – O: anterior to M. stipitopalpalis externus (0mx8); I: anteriorly on the base of palpomere 1; M. palpopalpalis maxillae primus (0mx12) – O: anteriorly from the basal part of palpomere 1; I: base of palpomere 2; M. palpopalpalis secundus (0mx13) – O: basal part of palpomere 2; I: base of palpomere 3; M. palpopalpalis tertius (0mx14) – O: basal part of palpomere 3; I: base of palpomere 4; M. palpopalpalis quatrus (0mx15) – O: posteriorly on the basal part of palpomere 4; I: anteriorly on the base of palpomere 5.

3.7. Labium

(Figs. 1C, 2, 3B,E, 4J,K, 7D)

Large parts of the labium are weakly sclerotized and all parts are of a yellowish or creamy-white coloration (Fig. 1C). Postmentum, prementum and endite lobes are laterally bordered by the maxillae (Figs. 2, 3B,E). The prementum is about as large as the postmentum and medially divided by a median internal cleavage (Fig. 4J,K). The postmentum bears many small, nipple-like projections on the surface (Fig. 4K); it is composed of a small mentum and a much larger submentum. The well-developed glossae and slightly smaller paraglossae are basally fused; the paraglossae are not visible in ventral view. Both endite lobes are ventrally attached to the prementum. The laterodistal part of the paraglossae is closely adjacent with the lateral hypopharyngeal margin. The glossae are densely set with setae, especially on their anterior region. The palp is 3-segemented. A distinct palpiger is present (Fig. 4J). The proximal palpomere is elongate, about 4−5 × as long as wide; palpomere 2 is small,
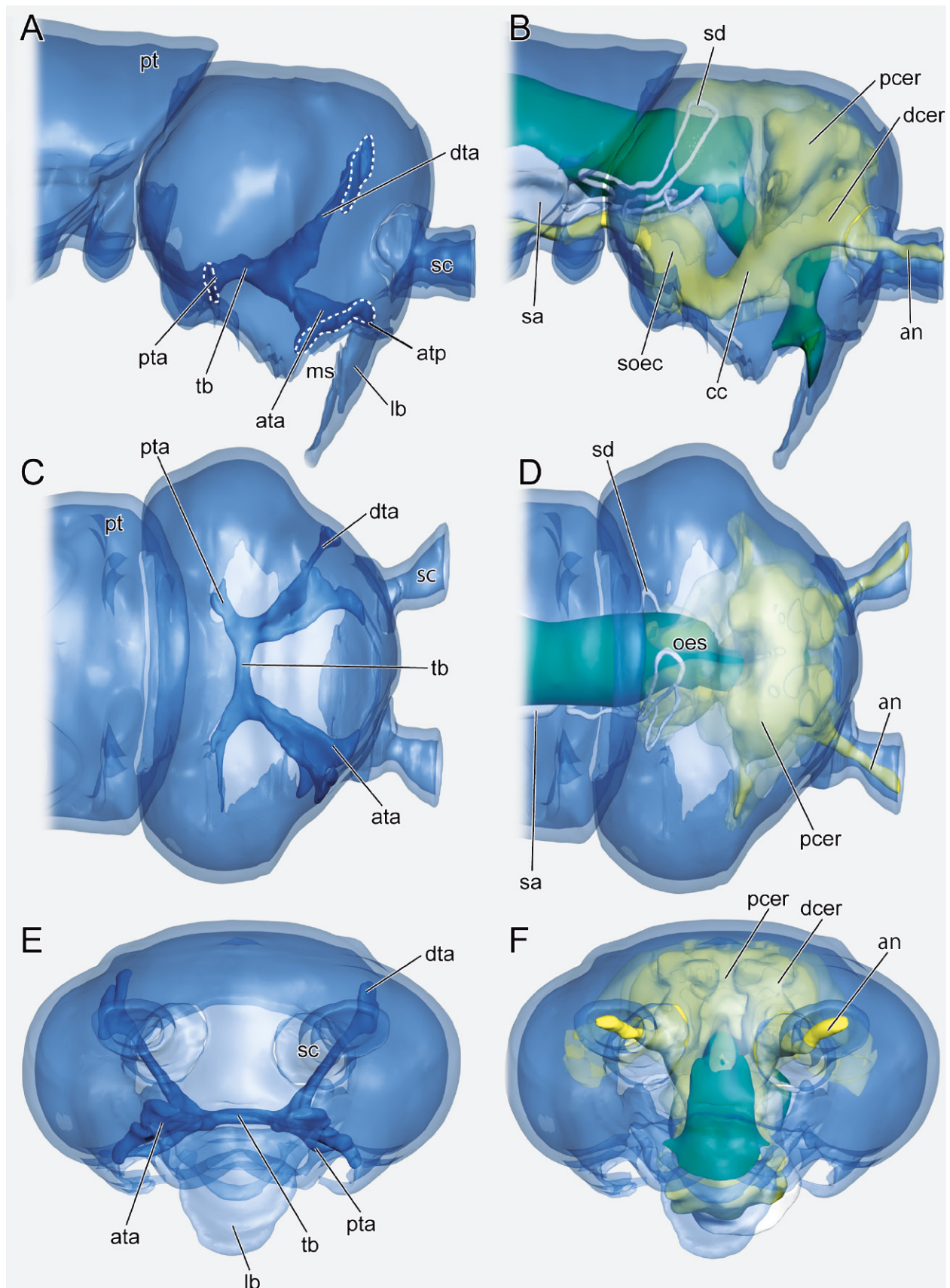
Fig. 6. *Zorotypus weidneri*, head, winged morph, 3D reconstructions of internal structures. **A**,**B**: lateral view; **C**,**D**: dorso-fronal view; **E**,**F**: frontal view. The dashed lines in A indicate attachment areas of tendon arms to the cranium. — ***Abbreviations***: an, antennal nerve; ata, anterior tentorial arm; atp, anterior tentorial pit; cc, circumoesophageal connective; dcer, deutocerebrum; dta, dorsal tentorial arm; lb, labrum; ms, mandible socket; oes, oesophagus; pcer, protocerebrum; pt, prothorax; pta, posterior tentorial arm; sc, scapus; sa, salivary acinuous structure; sd, salivary duct; soec, suboesophageal complex; tb, tentorial bridge.

about as long as wide; its base is distinctly narrowed; the apical palpomere is the largest, with a strongly narrowed basal part, and an apex densely set with short setae (Fig. 4K).

Musculature (Fig. 7D): M. submentopraementalis (0la8) – O: mediobasal part of gula, I: dorsally on median internal ridge; M. tentoriopraementalis (0la5) – O: posterior tentorial arm and base of tentorial bridge, I: laterobasal edge of prementum; M. praementoparaglossalis (0la11) – O: median internal ridge of prementum, I: basal edge of paraglossa; M. praementoglossalis (0la12) – O: base of median internal ridge of prementum; I: posterior margin of glossa; M. praementopalpalis internus (0la13) – O: median internal ridge of prementum; I: base of palpomere 1; M. praementopalpalis externus (0la14), bipartite muscle, with a large main subcomponent and slender lateral subcomponent – O: on the lateral wall of the prementum and a large premental apodeme, which reaches the anterior mental region posteriorly (main subcomponent); I: laterally on the base of palpomere 1; M. palpopalpalis labii primus (0la16) – O: mesal wall of palpomere 1; I: laterally on the base of palpomere 2; M. palpopalpalis labii secundus (0la17), uncertain – 0: palpomere 2; I: basally on palpomere 3.

3.8. Epipharynx

(Figs. 5, 7F)

The epipharynx is semimembranous and divided into a flat anterior part (preepipharynx) which forms the roof of the open preoral cavity, and a posterior part forming the roof of the short preoral tube (Fig. 5). The posthypopharynx forms the floor of this tube and the mesal mandibular bases the lateral walls of its anterior part.

Musculature (Fig. 7F): M. clypeopalatalis (0ci1), well developed and composed of several muscles – O: anterolateral part of postclypeus; I: medially on the preepipharynx and the roof of the preoral tube. The bundles of 0ci1 are separated by well-developed transverse muscles (= M. annularis stomodaei, 0st1).

3.9. Salivarium and salivary glands

(Figs. 6B,D, 7E)

The salivarium is present as a flat and very narrow pocket between the hypopharynx and the labium. Its dorso-ventral wall and the anterolateral edges are sclerotized. The salivarium is connected to the salivary glands by very slender ducts; they coalesce shortly before reaching the salivarium. The appearance of the paired salivary gland differs distinctly between the wingless and winged specimens. In the winged form it is very long and convoluted in the posterior head region; it extends into the thorax

where it reaches the posterior prothoracic margin posteriorly (Fig. 6B,D); the prothoracic part is surrounded by acinuous structures, which are intensively stained with toluidine blue in histological sections. The salivary duct also reaches the thorax in the wingless specimen we examined but is shorter; the acinuous structure is poorly developed.

Musculature (Fig. 7E): M. praementosalivarialis anterior (0hy7) – O: lateral wall of the prementum, I: medially on the salivary sclerite; M. praementosalivarialis posterior (0hy8) – O: posterolateral wall of prementum, I: laterally on the salivary sclerite; M. annularis salivarii (0hy13), probably represented by a small transverse muscle connecting the anterolateral edges of the salivary sclerite; M. craniohypopharyngealis (0hy3) – O: ventrally on postoccipital phragma, I: salivarium.

3.10. Hypopharynx

(Figs. 4L, 5, 7E)

The prehypopharynx lies above the prementum and distinctly reaches beyond the anterior margin of the paraglossae. The dorsal surface is semimembranous; it is covered with longitudinal rows of ridges fringed with wedge-shaped surface structures anteriorly and with posteriorly directed projections posteriorly (Fig. 4L). The posthypopharynx forms the floor of the preoral tube (Fig. 5). The lateral edge of the posterior preoral tube, which is a prolongation of the postero-lateral margin of the prehypopharynx, is reinforced by distinctly sclerotized and narrow suspensoria (Fig. 7E).

Musculature (Fig. 7E): M. frontooralis (0hy1) – O: posterior frontal area, laterad the origin of M. frontoepipharyngalis (0lb2); I: apex of the suspensorium at the anatomical mouth; M. tentoriosuspensorialis (0hy5) – O: tentorial bridge; I: ventromedially on the posterior hypopharynx; M. tentoriooralis (0hy2) – O: distal end of the anterior tentorial arm; I: middle region of the suspensorium.

3.11. Pharynx and oesophagus

(Figs. 6B,D,F, 7F)

The lumen of the pharynx is rather narrow. Distinct folds for attachment of dilators surround the tube. It is posteriorly continuous with the wide oesophagus, which is characterized by strongly developed internal folds (oesophageal folds).

Musculature (Fig. 7F): M. clypeobuccalis (0bu1) – absent; M. frontobuccalis anterior (0bu2) – O: anterior part of the frontal area; I: dorsally on the anatomical mouth; M. frontobuccalis posterior (0bu3), a series of bundles – O: posterior frontal area, close to the anterior margin of
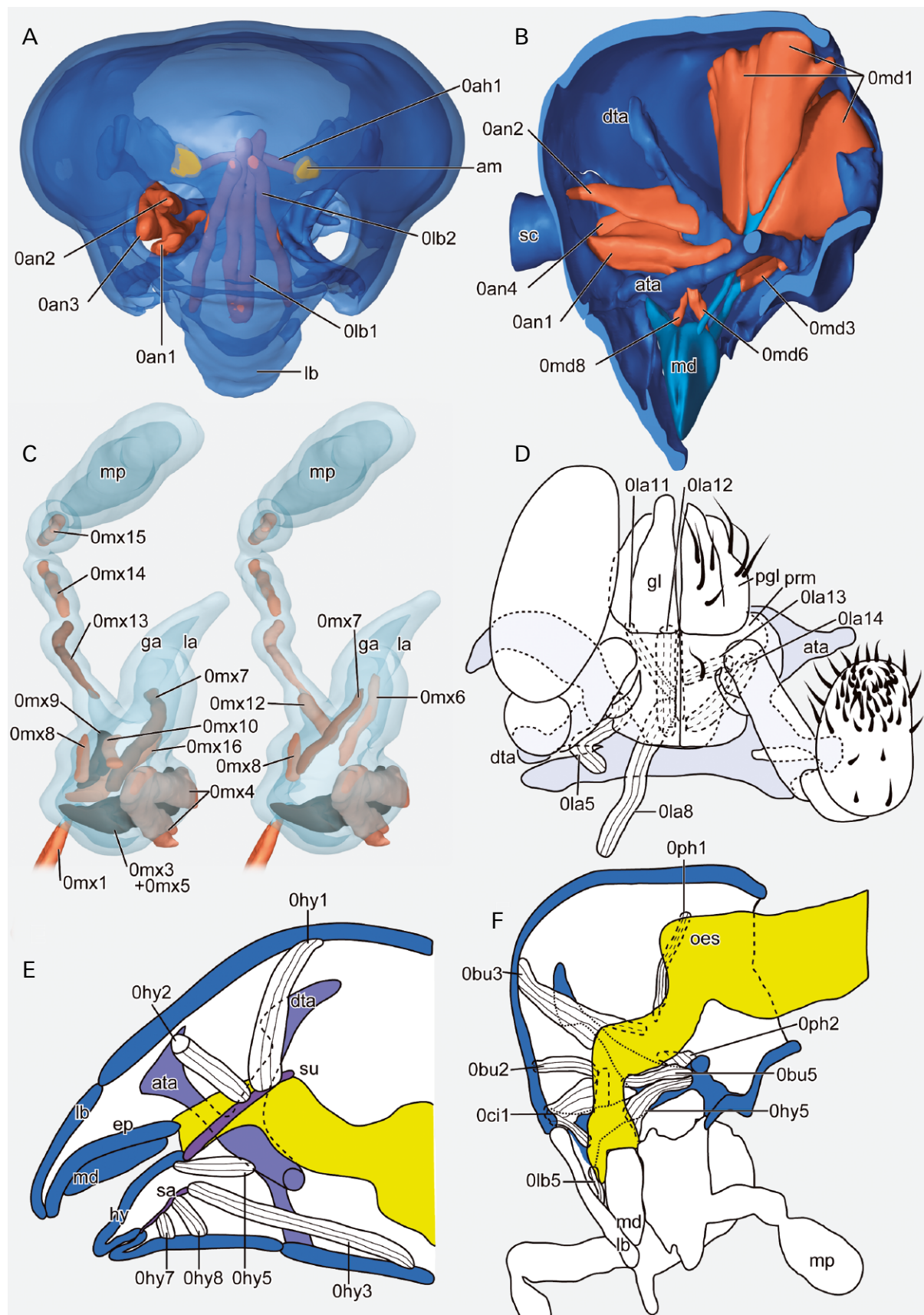
Fig. 7. *Zorotypus weidneri,* head, winged morph, 3D reconstructions of internal structures. **A**: head, frontal view; **B**: sagittal plane of head; **C**: maxillae, ventral view; **D**: labium, ventral view; **E**: sagittal plane, hypopharyngal muscles; **F**: sagittal plane, pharyngeal muscles. — *Abbreviations*: am, antennal heart ampulla; ata, anterior tentorial arm; dta, dorsal tentorial arm; ep, epipharynx; ga, galea; gl, glossa; hy, hypopharynx; la, lacinia; lb, labrum; md, mandible; mp, maxillary palp; oes, oesophagus; pgl, paraglossa; prm, praementum; sa, salivarium; sc, scapus; su, suspensorium. Muscles are explained in section 3 (text).

the brain; I: dorsal side of the precerebral pharynx; M. tentoriobuccalis lateralis (0bu4) – O: laterally from the head capsule, close to the origin of the anterior tentorial arm; I: laterally on the anatomical mouth; M. tentoriobuccalis anterior (0bu5) – O: middle of tentorial bridge; I: ventral wall of the pharynx; M. tentoriobuccalis posterior (0bu6) – unclear; M. verticopharyngalis (0ph1) – O: posterior head capsule between the posterior part of the brain and the dorsal bundles of M. craniomandibularis internus (0md1); I: dorsally on the posterior pharynx; M. tentoriopharyngalis (0ph2) – O: basally on the dorsal tentorial arm; I: ventrally on the pharynx, below the attachment of M. verticopharyngalis (0ph1); M. oralis transversalis (0hy9) connects the upper edges of the anatomical mouth on the ventral side, attached to the suspensorium on both sides; M. annularis stomodaei (0st1) – a ring muscle layer is present over the whole length of the cephalic foregut; it is less regularly arranged at the oesophageal folds which are posteriorly adjacent with the pharynx; M. longitudinalis stomodaei (0st2) – longitudinal muscles are present on the dorsal and ventral sides of the pharynx; they are covered by 0st1.

3.12. Cervical glands

Absent.

3.13. Brain and suboesophageal complex

(Figs. 6B,D,F, 8)

The brain and suboesophageal complex are very large in relation to the total size of the head (Fig. 6B,D,F). The shape is distinctly modified to make it fit closely between muscles and endoskeletal structures. Distinct recesses are present at the position of the anterior parts of M. craniomandibularis internus (0md1) and the posterior part of the dorsal tentorial arms. The brain is strongly inclined posteriorly. Two symmetric protocerebral lobes extend to the foramen occipitale posteriorly. The optic neuropils and ocellar nerves were only recognizable in the winged specimen, but the general shape and size of the brain apparently does not differ distinctly between the morphs (Fig. 8). The antennal nerves arising from the deutocerebrum are distinct (Fig. 6F). The tritocerebral commissure is not recognizable as a separate structure. The circumoesophageal connective is very broadly connected with the suboesophageal complex, which reaches the anatomical mouth region anteriorly and the ventral neck region posteriorly. The connectives linking it with the prothoracic ganglion are long and moderately thick. The frontal ganglion is distinctly developed.

4. Results of the cladistics analyses

The cladistics analysis of 128 morphological characters resulted in 20 (NONA) or 10 (TNT) trees of equal length with 257 steps (Ci: 55 / Ri: 68). Fig. 9 shows the strict consensus tree. Electronic supplements 1 and 2 contain the matrix and a character list, respectively. The retrieved apomorphies of selected clades (unambiguous character states in bold) are presented below:

Eumetabola (Bremer support [BS] 1): 48(1) posterior tentorial arms without trabeculae tentoria, 61(1) undivided stipes, **67(1)** lacinia without incisivi, 107(0) M. tentoriobuccalis lateralis absent.

Acercaria (BS 2): 22(2) scapus and pedicellus equally long, **79(1)** labium with median longitudinal channel, **113(1)** insertion of lacinia detached from stipes, **115(1)** strongly enlarged cibarial dilators.

Holometabola (BS 2): 73(1) anteriorly or dorsally orientated maxillary palps, 81(1) reduced glossae, **126(1)** presence of larval stemmata, **127(1)** immature stages with different body shape than adults.

Polyneoptera (BS 3): 2(0) ocelli reduced, **20(0)** insertion of antenna close to mandibular articulation, 21(0) antennifer present, 76(1) postmentum with submentum and mentum, **80(1)** median cleft of prementum present, **89(0)** origin of M. tentoriopraementalis inferior on ventral apodeme (trabeculae tentorii).

Eukinolabia (BS 2): 1(1) head capsule prognathous or slightly inclined, 16(1) tormae without mesal extension, 28(0) presence of M. tentorioscapalis medialis (0an4), 80(0) prementum without median cleft, 83(1) paraglossae twice as long or longer than glossae, **91(1)** origin of M. tentorioparaglossalis on basal edge of prementum.

Xenonomia + [Dictyoptera + (Zoraptera + Plecoptera)] (BS 1): 27(0) presence of M. tentorioscapalis lateralis, 73(1) anteriorly or dorsally orientated maxillary palps, 82(0) paraglossa cylindrical, as wide as thick.

Xenonomia (BS 5): 33(0) non-pulsatile antennal ampullae, 38(1) antennal ampulla connected to supraesophageal ganglion, **39(1)** tissue between antennal ampulla and supraesophageal ganglion with oval nuclei, **77(1)** angle between submentum and mentum more than 60°, **84(1)** ventrally orientated labial palps, 90(1) absence of M. tentorioparaglossalis, 99(1) distinctly flattened hypopharynx.

Dictyoptera + (Plecoptera + Zoraptera) (BS 1): 2(2) 3 ocelli, 107(0) absence of M. tentoriobuccalis lateralis.

Dictyoptera (BS 5): 26(0) origin of antennal muscles on anterior tentorial arms only; 32(1) bipartite antennal vessel wall; **45(1)** secondary anterior tentorial bridge ("perforation of the corpotentorium"); **52(1)** presence of mandibular postmola; **66(1)** lacinia enclosed in galeal cavity; 76(0) postmentum uniformly sclerotized.

Blattodea (BS 1): **2(1)** 2 ocelli, **117(1)** M. verticopharyngealis with two components, **119(1)** M. hypopharyngosalivarialis with two components.

Zoraptera + Plecoptera (BS 3): 16(1) tormae without mesal extensions, **49(2)** 5 incisivi on the left mandible,
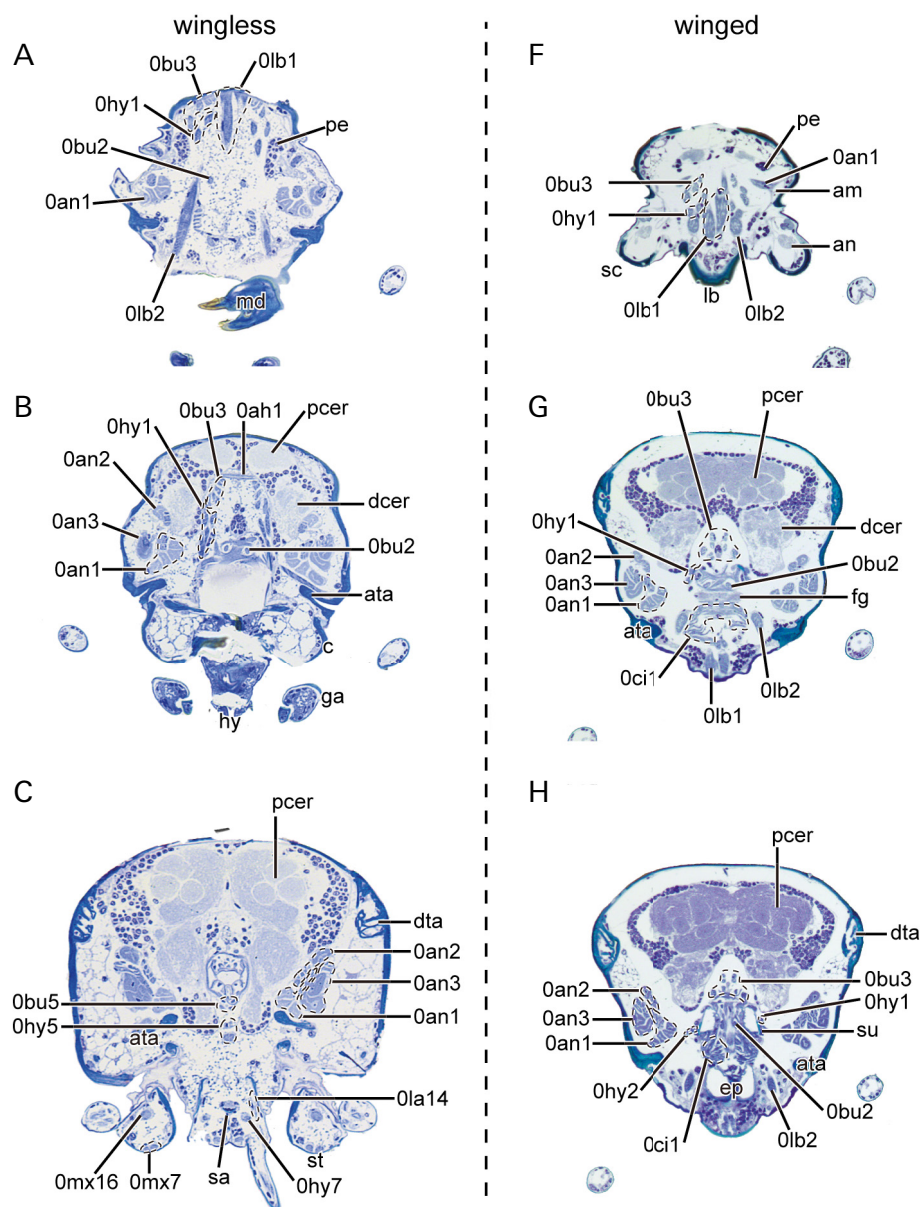
**50(3)** 5 incisivi on right mandible, 57(1) absence of M. hypopharyngomandibularis.

Zoraptera (BS 6): 5(1) absence of coronal and frontal (epicranial) sutures, 48(1) absence of trabeculae tentorii on posterior tentorial arms, 89(1) origin of M. tentorio-praementalis inferior on posterior tentorial arms, **123(1)** galea with distal spines, **124(1)** moveable prostheca on left mandible, **125(1)** adults with winged and wingless morphs, **128(1)** presence of prominent intraclypeal ridge.

5. Discussion

The monophyly of the small order Zoraptera was never disputed. The contrast between the great uniformity of general body features and a conspicuous variability of genitalia was pointed out in several studies (e.g., Gurney 1938; Dallai et al. 2011, 2012a,b, 2014a,b; Mashimo et al. 2013). The flightless morphs display a number of apomorphies apparently linked with the loss of wings, whereas the winged morphs are apparently close to the groundplan of Neoptera in their general body morphology including the head.

Zorotypus weidneri displays the same set of plesiomorphic cephalic features which was already described for the North American *Z. hubbardi* (Beutel & Weide 2005). This includes the orthognathous orientation of the head, the complete tentorium (without accessory anterior bridge = "unperforated corpotentorium"], the free labrum, the largely unmodified orthopteroid mouthparts, the unmodified anterior digestive tract, and the complex cephalic muscle system (Beutel & Weide 2005). Despite of the overall external similarity, the heads of the two species differ in several noteworthy internal characters. An ampullo-aortic muscle of the antennal heart (character
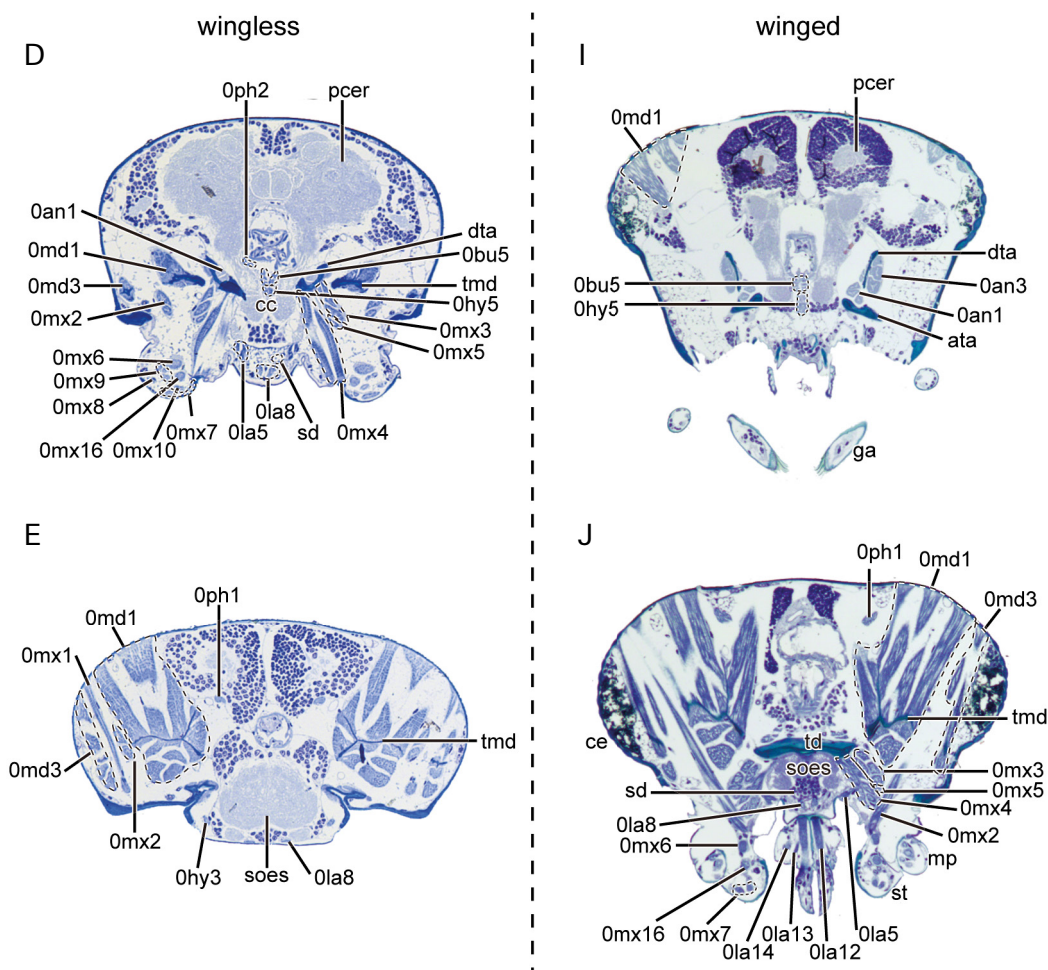
← ↑ **Fig. 8.** *Zorotypus weidneri*, head, wingless (A–E) and winged (F–J) morphs, histological sections. Images from upper to lower lines are shown from frontal part to neck regions. Scale bars 250 μm. — ***Abbreviations***: an, antennal nerve; am, antennal heart ampulla; ata, anterior tentorial arm; c, cardo; cc, circumoesophageal connective; ce, compound eyes; dcer, deutocerebrum; dta, dorsal tentorial arm; ep, epipharynx; fg, frontal ganglion; ga, galea; hy, hypopharynx; lb, labrum; md, mandible; mp, maxillary palp; pcer, protocerebrum; pe, perikaryon; sa, salivarium; sc, scapus; sd, salivary duct; soes, suboesophageal complex; st, stipes; su, suspensorium; tb, tentorial bridge; tmd, tendon of mandible.

35) (WIPFLER & PASS 2014), M. hypopharyngosalivaris (0hy12, character 105) and a well-developed cervical gland (due to unclear outgroup homology not in the matrix) are present in *Z. hubbardi* (BEUTEL & WEIDE 2005) but are lacking in *Z. weidneri*. M. submentopraementalis (0la8) is divided into two subcomponents in *Z. hubbardi* (character 92) and two tentoriopraemental retractors are present. The former muscle is formed by an undivided bundle in *Z. weidneri* and only one tentoriopraemental muscle is present in this species. A unique feature in *Z. weidneri* is the presence of an additional dorsal stipitogaleal muscle (M. stipitogalealis dorsalis: 0mx16). This muscle is neither present in *Z. hubbardi* (which also lacks the first stipitogaleal muscle) nor in any other studied insect (WIPFLER et al. 2011; WIPFLER 2012). It is very likely that this muscle is derived from a muscle with a very similar position, M. stipitogalealis (0mx7).

The most conspicuous complex of zorapteran autapomorphies is the distinct wing dimorphism, linked with the presence or absence of compound eyes and ocelli, and distinct differences in the brain, notably the presence or absence of optic neuropils. Two additional potential cephalic autapomorphies were suggested by BEUTEL & WEIDE (2005), a reduced number of nine antennomeres and the presence of a movable prostheca on the left mandible (e.g., SILVESTRI 1913) (character 124). Our cladistic analysis characters revealed the following additional autapomorphies: a galea with distal spines (character 123), the absence of the frontal and coronal (epicranial) sutures (character 5, also absent in some other taxa, e.g., *Mastotermes*, *Metoligotoma*), the dimorphism with secondarily eyeless (and wingless) morphs with reduced optic lobes (see above, character 125), and finally the presence of a prominent intraclypeal ridge (character 128), which is confirmed for *Z. weidneri* and also *Z. hubbardi* (BEUTEL & WEIDE 2005). This structure is not the epistomal ridge since M. clypeopalatis (0ci1), which is very conservative in its clypeal origin, attaches dorsad of it. The identity of
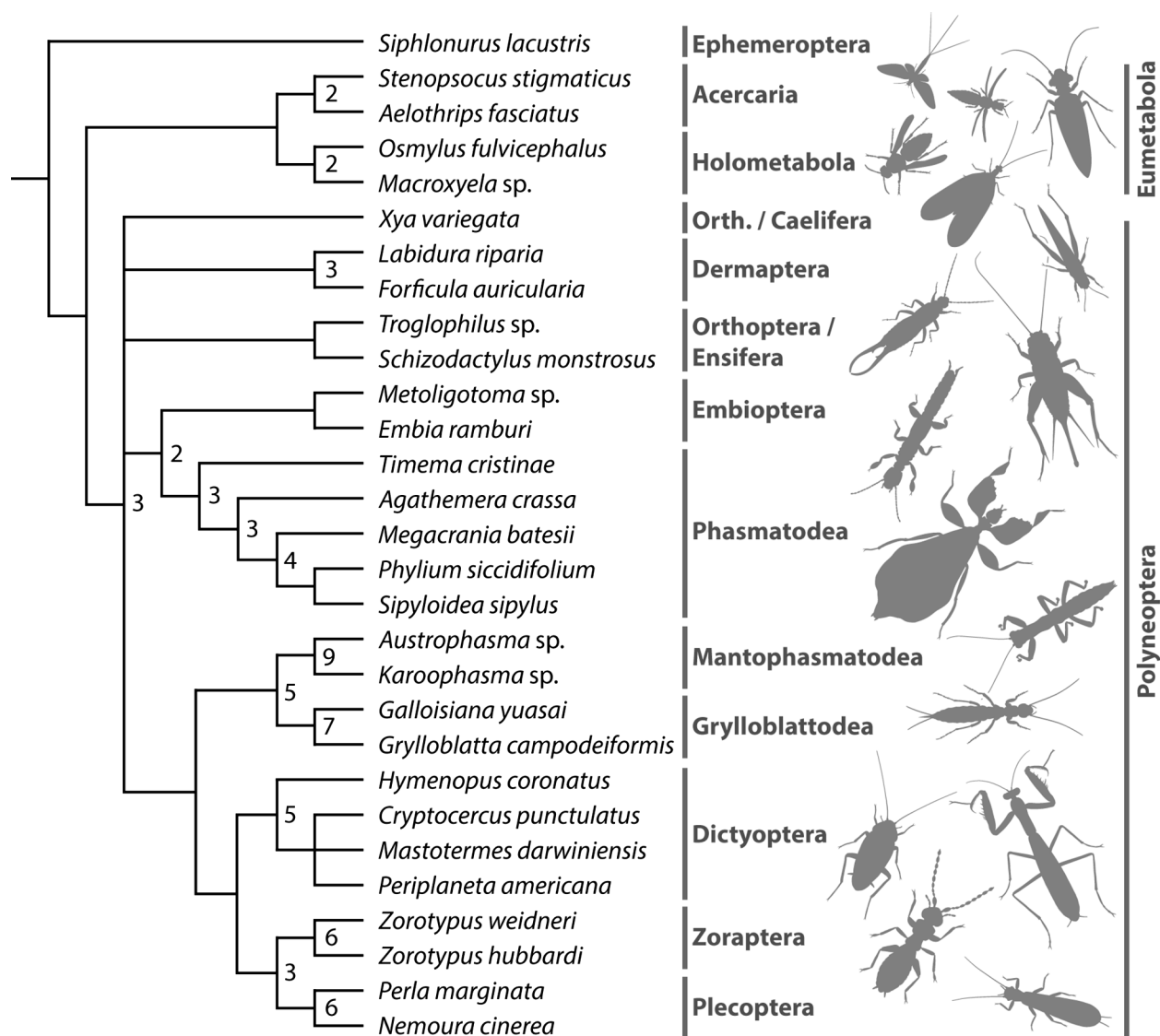
Fig. 9. Strict consensus tree of 20 (NONA) or 10 (TNT) equally parsimonious trees with 257 steps (Ci: 55 / Ri: 68) based on 128 morphological characters of the head. Relationships of neopteran groups, with a main focus on Polyneoptera and Zoraptera. Bremer support higher than 1 indicated at nodes.

the muscle is confirmed by its insertion below the frontal ganglion. The assumption that the border between clypeus and frons runs on the level of the anterior tentorial pits would imply that the postclypeus would be a very thin stripe with slightly broadens laterally to serve as origin for M. clypeopalatis (0ci1). This appears unlikely. The area between the antennal sockets definitely belongs to the frons as M. frontobuccalis anterior (0bu2) originates there. Additional potential autapomorphies with a high degree of homoplasy are the absence of trabeculae tentorii on the posterior tentorial arms (character 48, also absent in *Hymenopus*, *Embia* and Eumetabola) and the origin of M. tentoriopraementalis inferior on the posterior tentorial arms (character 89, also present in *Siphlonurus*, Mantophasmatodea, *Hymenopus*, *Embia* and Eumetabola). In fact it is conceivable that the latter condition is a plesiomorphic condition with parallel modification in most non-eumetabolan pterygote groups.

The position of Zoraptera is one of the most disputed issues in systematic entomology (see Mashimo et al. 2014c for a detailed review). The sister group relationship with Acercaria suggested by Hennig (1969) was also tentatively supported in the first detailed study on the cephalic morphology of a zorapteran species (Beutel & Weide 2005). In other studies with a main focus on head morphology (Wipfler et al. 2011; Blanke et al. 2012, 2013; Friedemann et al. 2012; Wipfler 2012) or attachment structures (Beutel & Gorb 2001) Zoraptera were placed as sister group of Eumetabola, and an alternative placement as sister group of Holometabola was suggested by Rasnitsyn (1998) based on an informal evaluation of thoracic features. Analyses of molecular data sets (e.g. Ishiwata et al. 2011; Letsch & Simon 2013; Wang et al. 2013) and characters of the wing articulation (Yoshizawa 2011), antennal heart (Wipfler & Pass 2014) or thorax (Wipfler et al. 2015) suggest a position among the polyneopteran

orders, and this is also clearly supported by embryological features (MASHIMO et al. 2014a). This systematic placement is also confirmed by the results of the present study. Monophyletic Polyneoptera including *Zoraptera* are seemingly well supported (Bremer support 3), even though all potential apomorphies (e.g., antenna inserted close to mandibular articulation: character 20, antennifer present: character 21) are highly homoplastic (e.g. antennifer also present in Zygentoma) and the polarity is questionable in some cases (e.g., postmentum divided into submentum and mentum: character 76). Additionally the deeper nodes of Polyneoptera and thus the potential apomorphies of the group are affected by the non-monophyly of Orthoptera, which are apparently well supported by characters of the thorax such as the saddle-shaped pronotum and hindlegs modified for jumping (e.g., KRISTENSEN 1975), but not by a single shared apomorphic feature of the head. Within Polyneoptera, our analysis suggests a placement of Zoraptera as sister group of Plecoptera with a relatively high branch support value of 3. Nevertheless, the potential synapomorphies yielded by the analyses are less than convincing, for instance tormae without mesal extensions (character 16) and the presence of five incisivi on the right and left mandible (characters 49–50). The absence of M. hypopharyngomandibularis (character 57) is a simple reduction which also occurs in Thysanoptera (MICKOLEIT 1963) and Holometabola (BEUTEL & VILHELMSEN 2007; BEUTEL et al. 2010). In Polyneoptera it is not only reduced in Plecoptera (MOULINS 1968; BLANKE et al. 2012) and Zoraptera, but also in Dermaptera (STRENGER 1952; KADAM 1961). The presence is plesiomorphic as it is also well-developed in Odonata (BLANKE et al. 2012), Ephemeroptera (STANICZEK 2001) and apterygote insects (CHAUDONNERET 1950; BLANKE et al. 2014). It is likely that the muscle was reduced several times independently. Considering the lack of any convincing synapomorphy and the alternative placements in studies based on different character sets, a zorapteran-plecopteran clade should be clearly considered as a working hypothesis. This result is even more weakened by the fact that the plecopteran head is only very insufficiently studied and a detailed treatment of an antarctoperlarian species is completely lacking. Zoraptera were alternatively placed as sister taxon of Embioptera (GRIMALDI & ENGEL 2005; YOSHIZAWA 2011), Dictyoptera (YOSHIZAWA & JOHNSON 2005; ISHIWATA et al. 2011), Dermaptera (TERRY & WHITING 2005; MISOF et al. 2014), Plecoptera + Dermaptera (MISOF et al. 2007), or as sistergroup of larger subunits of Polyneoptera (SIMON et al. 2012; LETSCH & SIMON 2013). An enforced clade Zoraptera + Dermaptera would require three additional steps in our data set and the only retrieved potential apomorphy would be the absence of M. hypopharyngomandibularis (0md4) which is also missing in Plecoptera. Embioptera + Zoraptera (274 steps) and Dictyoptera + Zoraptera (267 steps) are not supported by any cephalic apomorphies.

It is apparent that the "Zoraptera problem" cannot be solved with cephalic features alone and the identified autapomorphies of Polyneoptera are also not fully convincing. The placement of the very small order is apparently impeded by several factors. One of them is the large number of preserved plesiomorphic features of all body parts except for the genitalia (BEUTEL & WEIDE 2005; FRIEDRICH & BEUTEL 2008; DALLAI et al. 2012a,b). Despite conspicuous apomorphic features in the genital apparatus this character system does not help in the context of interordinal phylogenetic relationships in the case of Zoraptera. It was pointed out in DALLAI et al. (2011, 2012a,b, 2013, 2014a,b, 2015) and MATSUMURA et al. (2014) that the evolution of genital structures was greatly accelerated within the order and at present the groundplan is unclear as an intraordinal phylogeny is lacking. Another set of problems may be related to miniaturization. Within Polyneoptera, zorapteran species are unusually small, with a body size of ca. 2 mm or less. Most features suggesting phylogenetic affinities with Acercaria are likely linked with size reduction, such as the reduced number of tarsomeres and Malpighian tubules, and the far-reaching condensation of the abdominal ganglionic chain (see e.g., KRISTENSEN 1991; BEUTEL & WEIDE 2005). Another character complex affected by the reduced body size is the wing structure and venation, which differs profoundly from the typical polyneopteran pattern that includes leathery forewings, a rich venation including many cross veins, and an enlarged and fan-shaped hind wing vannus. Apparently, Zoraptera are a relict group of the southern hemisphere with a considerable number of preserved plesiomorphies on one hand, and a specialization of different body regions related to miniaturization on the other. Moreover, the group is affected by the conspicuous dimorphism and the gregarious habits, which are likely correlated.

Zoraptera are not only a highly unusual group on the phenotypic level but genetic peculiarities were also revealed in several investigations. The 18S rDNA, which was used in many studies, shows different unusual characteristics, a drastically high substitution rate resulting in strongly elongated branches, long insertions at helix E23, and modifications of the secondary structure at helices 12 and 18 (YOSHIZAWA & JOHNSON 2005). The 18S rDNA sequence is differing so strongly that KJER (2004) assumed an acarine contamination. The high substitution rate apparently also applies to the 28S rRNA (WANG et al. 2013). In transcriptome analyses the placement of Zoraptera is also highly unstable (SIMON et al. 2012; LETSCH & SIMON 2013). Analyses of 1478 orthologous genes (MISOF et al. 2014) yielded a sistergroup relationship between Zoraptera and Dermaptera, but with a low support value. Clearly the precise position of the order remains an open question.

Like in the case of Zoraptera, Strepsiptera were a long lasting and challenging problem in systematic entomology (e.g., POHL & BEUTEL 2013). Unlike Zoraptera, the highly specialized endoparasitic Strepsiptera are almost exclusively characterized by apomorphies in all life stages including the extremely small primary larvae. Recently, analyses of entire genomes and transcriptomes unambiguously placed Strepsiptera as sistergroup of

monophyletic Coleoptera (Niehuis et al. 2012). It remains open whether full genome analyses will also solve the Zoraptera problem.

6. Acknowledgements

7. References

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Electronic Supplement Files

at http://www.senckenberg.de/arthropod-systematics ("Contents")

File 1: matsumura&al-zorapterahead-asp2014-electronicsupplement-1.pdf. – Morphological data matrix based on Wipfler et al. (2011), Blanke et al. (2012) and Wipfler (2012).

File 2: matsumura&al-zorapterahead-asp2014-electronicsupplement-2.docx. – Character discussion. Additional information about the characters were provided in Wipfler et al. (2011), Blanke et al. (2012) and Wipfler (2012).

File 3: matsumura&al-zorapterahead-asp2014-electronicsupplement-3.mov. – Rotatable SEM movie of the head in *Zorotypus weidneri*.