

The cephalic morphology of the American cockroach *Periplaneta americana* (Blattodea)

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Abstract

The skeleto-muscular system of the head of the American cockroach *Periplaneta americana* is described in detail. The results are compared with previous partial descriptions of the cephalic morphology of this species and other dictyopterans. The head of *Periplaneta* is, as in other cockroaches, mostly characterized by plesiomorphies such as the typical orthopteroid mouthparts, the lateral position of the compound eyes, 5-segmented maxillary palps and 3-segmented labial palps, as well as long antennae. *Periplaneta* shows sexual dimorphism with the compound eyes of the males reaching further ventrally. The epistomal ridge is medially interrupted so that the frons and the clypeus are confluent. The cephalic musculature is typical for a polyneopteran insect and includes 59 muscles. Potential apomorphies for Blattodea in the cephalic area include the absence of the median ocellus, the bipartite condition of *M. verticopharyngealis* (Oph1) and of *M. hypopharyngosalis* (Ohy12), and the presence of oesotendons. The lacinula, a subapical lobelet on the lacinia, is present in almost all studied blattodeans but its potential homology to the dentisetae of Palaeoptera or the lamellae of apterygotes cannot be addressed at the moment. A “perforate” tentorium, a membranous postmola, and a lacinia that fits into the concave mesal wall of the galea are confirmed as autapomorphies of Dictyoptera.

Key words

Anatomy, phylogeny, Dictyoptera, Polyneoptera, head.

1. Introduction

Blattodea includes about 4,000 described species of cockroaches (= paraphyletic “Blattaria”; KLAUSNITZER 2007) as well as about 3,000 species of termites (Isoptera) and is most diverse in the tropics. Most cockroach species are solitary to gregarious and omnivorous but few developed brood care and a subsocial family-based lifestyle, which is often related to wood feeding (e.g. Cryptocercidae or certain Blaberidae such as *Salganea*) and culminated in the states seen in termites. Cockroaches have colonized almost every habitat including forest, grassland, heath,

steppe, salt marshes and deserts (BELL et al. 2007). Some even prefer aquatic habitats. Despite the large species richness and different lifestyles of cockroaches, the few synanthropic species, which are also pests and vectors for diseases (BELL et al. 2007), such as the American cockroach *Periplaneta americana* or the German cockroach *Blattella germanica*, dominate the general and quite negative perception of the group.

Phylogenetic studies of recent years have consistently identified the following principal lineages within Blatto-

dea: Blattidae, Tryonicidae, Lamproblattidae, Nocticolidae, Corydiidae (or Polyphagidae), Cryptocercidae + Isoptera, and Blaberoidea (including Ectobiidae, or Blattellidae, and Blaberidae, the latter being phylogenetically subordinate in the former) (KLASS & MEIER 2006; LO et al. 2007; INWARD et al. 2007; PELLENS et al. 2007; WARE et al. 2008; MURIENNE 2009; ROTH et al. 2009; DJERNÆS et al. 2012, 2015; LEGENDRE et al. 2015; for details on the history of Blattodea systematics see DJERNÆS et al. 2015 and LEGENDRE et al. 2015). DJERNÆS et al. (2015) have tentatively identified Anaplectidae as another major lineage – a group that has been strongly neglected in previous studies and had been considered as representing the basal-most offshoot(s) of the blaberoidean lineage (KLASS & MEIER 2006). LO et al.'s (2007) finding of Nocticolidae being sister to Mantodea is the only recent phylogenetic result that challenged the monophyly of Blattodea, but the more extensive studies of DJERNÆS et al. (2015) and LEGENDRE et al. (2015) found Nocticolidae subordinate in Corydiidae. While there is agreement regarding these principal lineages of Blattodea, recent phylogenetic studies contradict each other regarding the relationships among these lineages. During the last decade nearly all possible combinations between these groups have been proposed (see DJERNÆS et al. 2012, 2015).

Despite the facts that synanthropic cockroaches are common in zoological institutes around the world and that *Periplaneta americana* is a common species for students to dissect (SEIFERT 1995; STORCH & WELSCH 1999), no description of the entire head capsule including the musculature is available for this species or any other cockroach. Nevertheless, several studies focused on specific parts of the head of the American cockroach: CRAMPTON (1917, 1921) and SNODGRASS (1960) provided a treatment of the head capsule. CRAMPTON (1923) described the maxilla, CRAMPTON (1925) the labium, WALKER (1931) the clypeus, labrum and labium, POPHAM (1961) and ZHUZHNIKOV (2007) the mouthparts, WILLEY (1961) the nervous system, BUTLER (1973) the compound eyes, WEBER & RENNER (1976) the ocellus, PASS (1985) the antennal heart, KLASS & EULITZ (2007) the anterior head sulci and the tentorium, and BUDER & KLASS (2013) the hypopharynx. WIPFLER et al. (2011) provided a list with head muscles present in *Periplaneta* but no further information such as the exact origin or insertion. Additionally, *Periplaneta* is used to study the function and biomechanics of the mouthparts, especially the mandible and maxilla (SCHMITT et al. 2014; WEIHMANN et al. 2015a,b). The lack of a complete documentation and the role of *Periplaneta americana* as a model organism in biology (e.g. ROTTE et al. 2009; MATSUI et al. 2013) induced us to present a coherent and well-documented description of the entire cephalic skeleto-muscular system for this species. WILLEY (1961) provided an excellent study of the stomodeal nervous system of *Periplaneta americana*, so we will only describe the parts necessary to understand the skeleto-muscular system.

2. Material and methods

Specimens. This study is based on male and female specimens of *Periplaneta americana* (Linnaeus, 1758). For morphological examination they were fixed in 70% ethanol. Animals were acquired from the breeding of Jörg Bernhardt (www.schaben-spinnen.de) and taken in culture at the Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum of the Friedrich-Schiller-Universität Jena.

Dissection. Specimens were dissected in 70% ethanol under a stereo microscope (Leica MZ 125). To study the interior (epidermis-facing) surface of the head capsule, specimens were macerated with a 10% KOH solution and checked regularly until maceration was completed.

Scanning electron microscopy (SEM). Four animals were transferred from 70% to 100% ethanol, dried with HMDS (Hexamethyldisilazan; BROWN 1993) and subsequently sputter coated with gold (Emitech K500). SEM was performed using a Philips XL30 ESEM with a special sample holder (POHL 2010).

μ-CT and 3-D reconstruction. One female was critical point dried and mounted on a special sample holder for μ-computed tomography (μ-CT). The scan was performed at the Department of Functional Morphology and Biomechanics of the Christian-Albrechts-Universität Kiel on a Skyscan 1172 with a beam strength of 40 kV and 250 μA. The exposure time was 720 ms and a 360° scan with steps of 0.130° was performed. The resulting spatial resolution was 3.07 μm. The μ-CT data was segmented with Visage Imaging Amira 5.2.2 and the individual materials were separated with the algorithm function of Amira. Subsequently they were exported as stacks of tiff-files that were imported in VG Studiomax 2.2. Rendering was done with a combination of volume rendering (Scatter HQ; muscles and internal structures) and isosurface render (used in some images for the skeleton). The CT scan is deposited in the collection of the Phyletisches Museum in Jena, Germany (Polyneoptera/ Blattodea/ *Periplaneta americana* 12). Additionally a binned version can be downloaded from morphDbase (GROBE & VOGT 2009) under the link www.morphdbase.de/?B_Wipfler_20160818-M-3.1. The Electronic Supplement file 1 provides an interactive 3-dimensional PDF of the musculature of *Periplaneta americana*.

Digital microscopy and image processing. For digital microscopy specimens or dissected parts such as mouthparts were critical point dried and subsequently photographed with a Keyence VHX 2000 using the same sample holder as for SEM (POHL 2010). For figure 1 they were imaged without critical point drying in natural coloration. Final images of SEM, digital photography and μ-CT based reconstructions were assembled, edited and labeled with Adobe Photoshop CS6 and Adobe Illustrator CS6.

Terminology. Terminology follows BEUTEL et al. (2014a) for general exoskeletal morphology, WIPFLER et al. (2011) for the cephalic musculature, and BUDER & KLASS (2013) for exoskeletal elements of the hypopharynx (which are

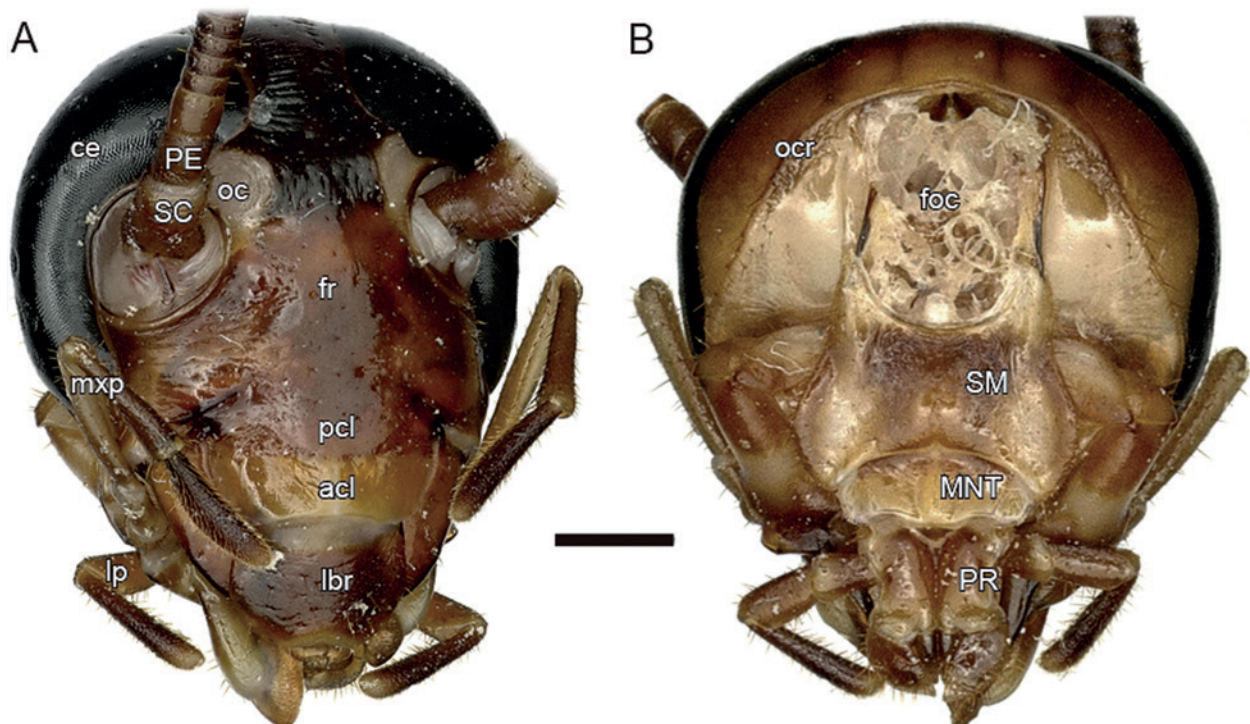


Fig. 1. Digital micrographs of the unmacerated head capsule of ♂ *Periplaneta americana* in natural coloration. **A:** antero-lateral view; **B:** posterior view. Scale bar: 1 mm. — **Abbreviations:** acl: anteclypeus, ce: compound eye, foc: foramen occipitale, fr: frons, lbr: labrum, lp: labial palpus, MNT: mental sclerite, mxp: maxillary palpus, oc: ocellus, ocr: occipital ridge, pcl: postclypeus, PE: pedicellus, PR: prae-mental sclerite, SC: scapus, SM: submental sclerite.

only partly covered in BEUTEL et al. 2014a). We use the term ‘Blattodea’ for the monophyletic group comprising cockroaches and termites and ‘Blattaria’ for the paraphyletic cockroaches (as in e.g. KLASS & EULITZ 2007).

There has been a long discussion concerning the terminology of strengthening and weakening linear structures on the insect head (e.g. DUPORTE 1946, 1957; SNODGRASS 1947; KLASS & EULITZ 2007; WIPFLER et al. 2011). We cannot solve this definition problem but to provide maximum clarity in description, we distinguish between three categories for the structures relevant in this manuscript: (1) Ridges: strengthening ridges on sclerites, which are based on inward folding or thickening of the cuticle, project into the lumen of the body, and are externally either visible as grooves or leveled (termed sulci by KLASS & EULITZ 2007, SNODGRASS 1960: p. 15, WEIDNER 1982: p. 38, and GRIMALDI & ENGEL 2005: p. 121; and costae according to their internal appearance in GRIMALDI & ENGEL 2005: p. 121). (2) Cleavage lines: linear weakenings of the sclerotization or of the entire cuticle in pre-imaginal stages which are predefined breaking lines during ecdysis; they are often still recognizable in the adults (where we did not analyze their detailed structure). (3) Syndeses: narrow stripes of membrane between sclerites which in a more or less hinge-like fashion allow their reciprocal movement (e.g. between the clypeus and the labrum). This terminology is not meant as a set of strict definitions (which would require much research on the cuticular fine structure) but as a categorization convenient for descriptive purposes.

We use the standard terminology of BEUTEL et al. (2014a) to name the various internal ridges of the head. However, we follow GRIMALDI & ENGEL (2005) by subsuming the epistomal and subgenal ridges under the term ‘costa’. In the text we only provide a few references to the illustrations. A complete list of used abbreviations in the morphological description and reference to the respective figures is provided in Electronic Supplement file 2.

Different terminologies for the mandibular incisivi have been proposed (e.g. AHMAD 1950). However, the homology of these teeth is difficult to infer even within one traditional order. We therefore avoid any terminology or homology hypothesis and simply number them.

In the descriptive part, we distinguish between (1) structures or formative elements (abbreviated in small letters) such as the labrum, galea, or tentorial arms and (2) sclerites (abbreviated in capital letters) such as the labral or the stipital sclerite (see e.g. KLASS & MATUSHKINA 2012).

3. Results

3.1. Head capsule

The orthognathous head capsule of the female is overall brownish (Fig. 1 shows it in its original coloration) and

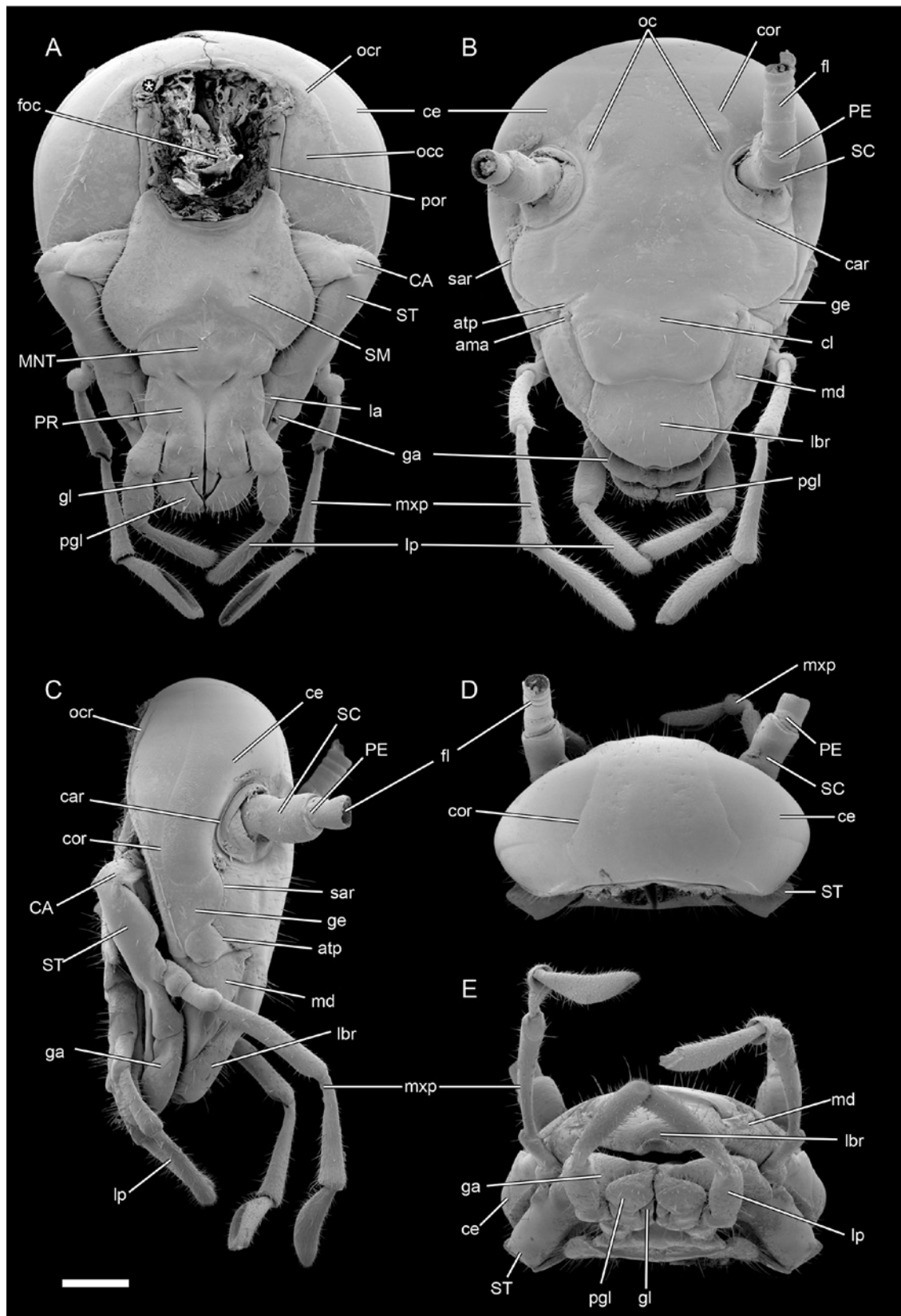


Fig. 2. Scanning electron micrographs of the unmacerated head capsule of ♀ *Periplaneta americana*. **A:** posterior view; **B:** anterior view; **C:** right-lateral view; **D:** dorsal view; **E:** ventral view. Scale bar: 1 mm. — **Abbreviations:** *: postoccipital condyle; ama: anterior mandibular articulation, atp: anterior tentorial pit, CA: cardinal sclerite, car: circumantennal ridge, ce: compound eye, cl: clypeus, cor: circum-ocular ridge, fl: flagellum of antenna, foc: foramen occipitale, ga: galea, ge: gena, gl: glossa, la: lacinia, lbr: labrum, lp: labial palpus, md: mandible, MNT: mental sclerite, mxp: maxillary palpus, oc: ocellus, occ: occipital region of the head capsule; ocr: occipital ridge, PE: pedicellus, pgl: paraglossa, pocr: postoccipital ridge, PR: praemental sclerite, sar: subantennal ridge, SC: scapus, SM: submental sclerite, ST: stipital sclerite.

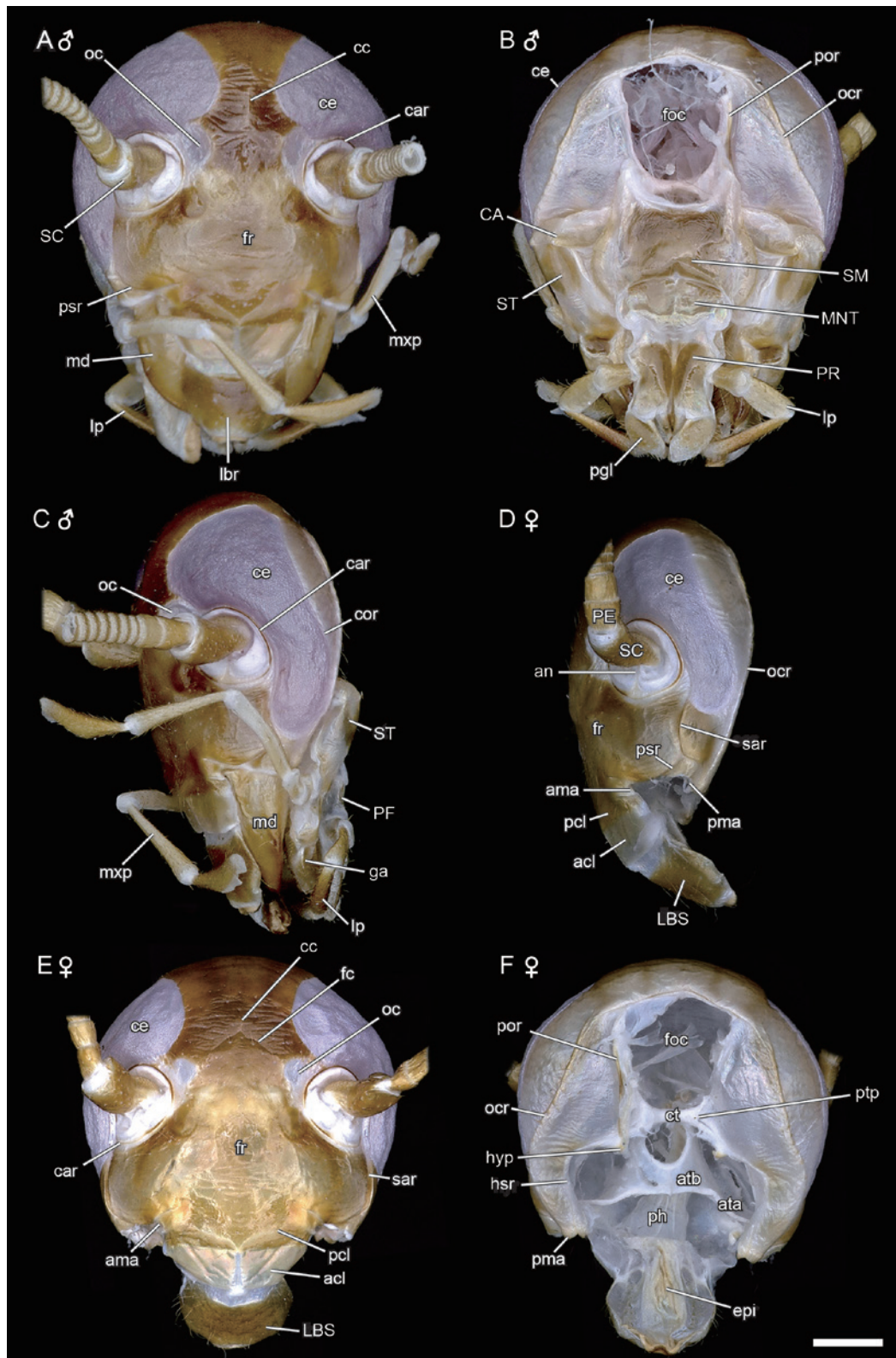


Fig. 3. Comparison between digital micrographs of the macerated head capsule of head capsule of ♂ (A–C; with mouthparts) and ♀ (D–F; mouthparts removed) of *Periplaneta americana*. A+E: anterior view; B+F: posterior view; C+D: left-lateral view. Scale bar: 1 mm. — **Abbreviations:** acl: anteclypeus, ama: anterior mandibular articulation, an: antennifer, ata: anterior tentorial arm, atb: anterior tentorial bridge, CA: cardinal sclerite, car: circumantennal ridge, cc: coronal cleavage line, ce: compound eye, cor: circumocular ridge, ct: corpotentorium, epi: epipharynx, fc: frontal cleavage line, foc: foramen occipitale, fr: frons, ga: galea, hsr: hypostomal ridge, hyp: hypostomal process, lbr: labrum, LBS: labral sclerite, lp: labial palpus, md: mandible, MNT: mental sclerite, mxp: maxillary palpus, oc: ocellus, ocr: occipital ridge, pcl: postclypeus, PE: pedicellus, PF: palpi, pgl: paraglossa, ph: pharynx, pma: posterior mandibular articulation, poc: postoccipital ridge, PR: praemental sclerite, psr: pleurostomal ridge, ptp: posterior tentorial pit, sar: subantennal ridge, SC: scape, SM: submental sclerite, ST: stipital sclerite.

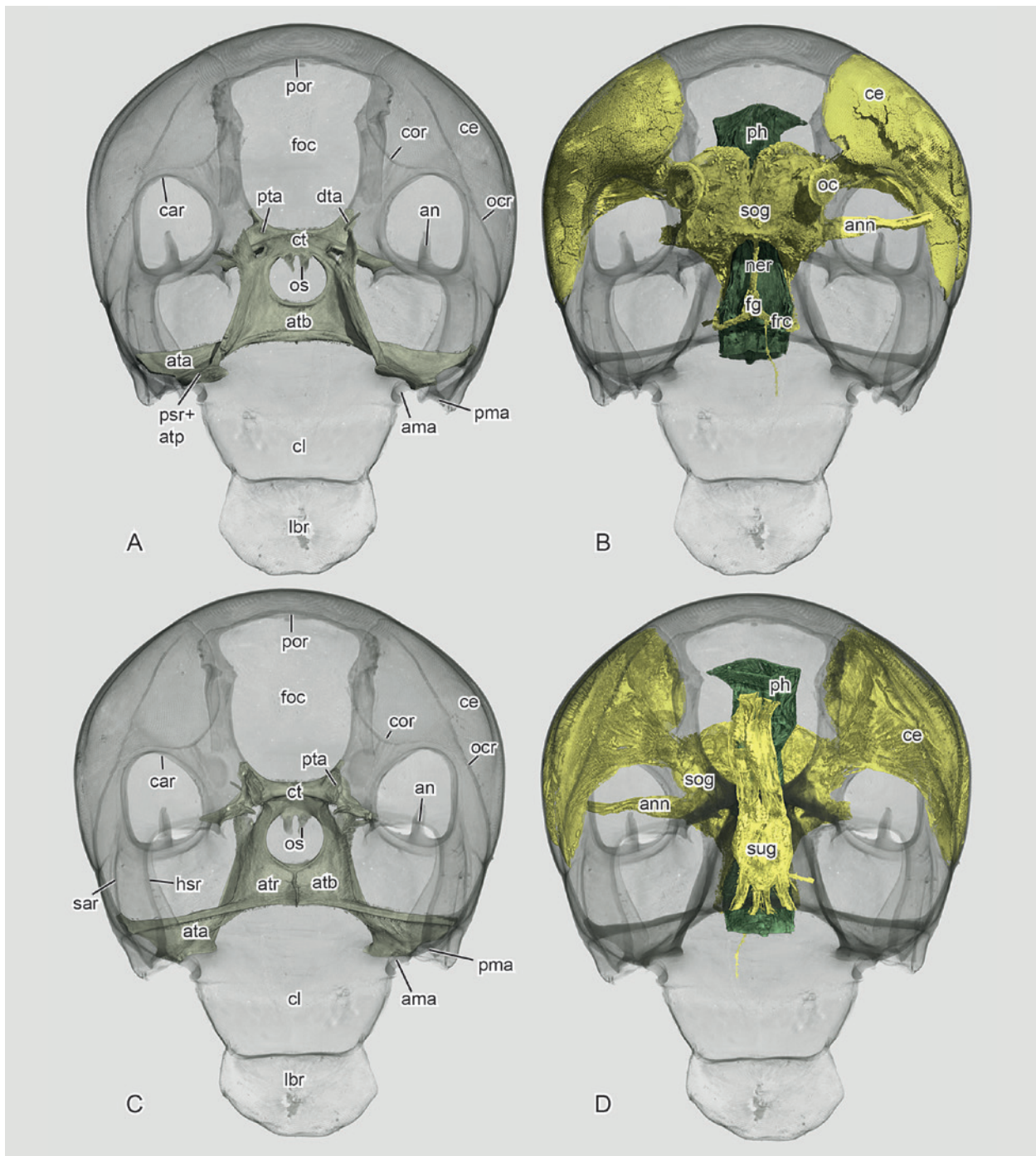


Fig. 4. Three-dimensional reconstructions of the cephalic endoskeleton (A+C) and nervous system in positional relation to the foregut (B+D) of *Periplaneta americana*; cuticle rendered transparent, mouthparts removed. **A+B:** frontal view; **C+D:** posterior view. — **Abbreviations:** ama: anterior mandibular articulation, an: antennifer, ann: antennal nerve, ata: anterior tentorial arm, atb: anterior tentorial bridge, atp: anterior tentorial pit, atr: ridge of anterior tentorial bridge, car: circumantennal ridge, ce: compound eye, cl: clypeus, cor: circumocular ridge, ct: corpotentorium, dta: dorsal tentorial arms, fg: frontal ganglion, foc: foramen occipitale, frc: frontal connective, hsr: hypostomal ridge, lbr: labrum, ner: nervus recurrens, oc: ocellus, ocr: occipital ridge, os: oesotendon, ph: pharynx, pma: posterior mandibular articulation, poc: postoccipital ridge, psr: pleurostomal ridge, pta: posterior tentorial arm, sar: subantennal ridge, sog: supraoesophageal ganglion, sug: suboesophageal ganglion.

flattened in postero-anterior direction. In frontal view it is reversely drop-shaped with the maximum width on the level of the antennal bases. It is sparsely covered with short setae on its frontal surface. Along the occipital ridge there is a row of long setae.

The foramen occipitale (foc, Figs. 2, 3) is nearly square but with its dorsal and ventral boundaries convexly arched. Ventrally it is closed by the posterior base of the labium. The margin of the foramen is surrounded and reinforced by the postoccipital ridge (por, Figs. 2, 3, 4; in

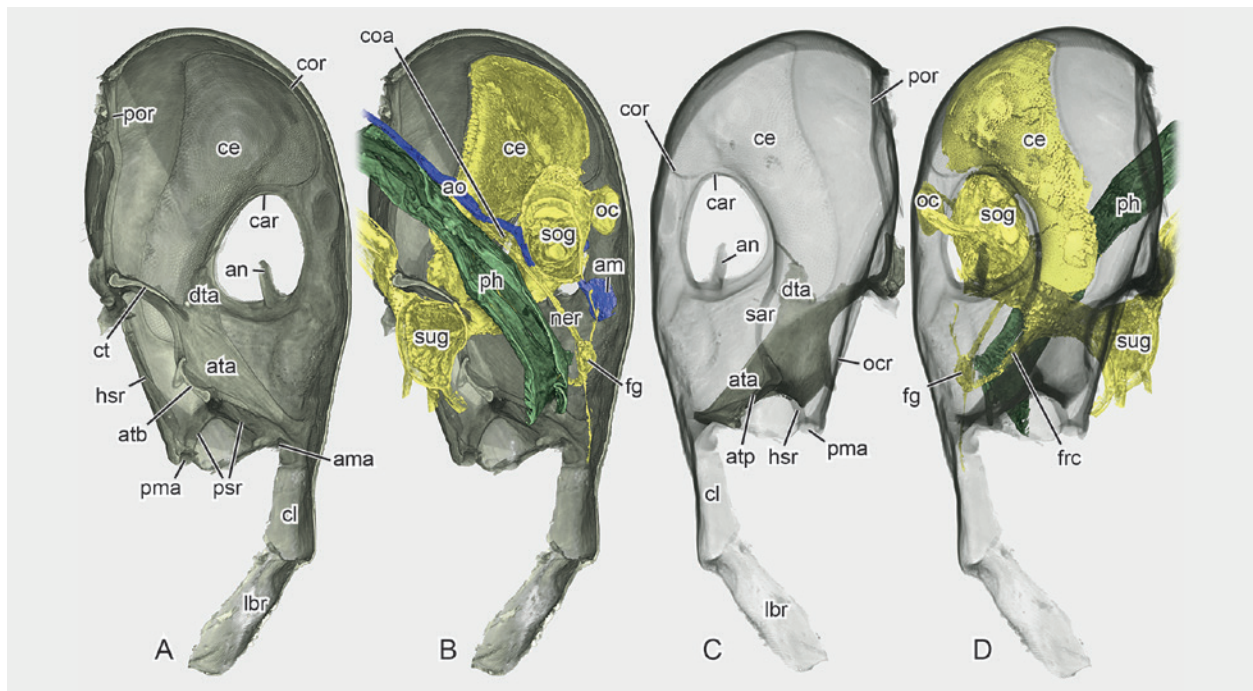


Fig. 5. Three-dimensional reconstructions of the internal cephalic skeleton (A+C), circulatory system (B), and nervous system in positional relation to the foregut (B+D) of *Periplaneta americana*; cuticle rendered transparent, mouthparts removed. **A+B:** midsagittal view (anterior is to the right); **C+D:** lateral view (anterior is to the left). — **Abbreviations:** am: antennal ampulla, ama: anterior mandibular articulation, an: antennifer, ao: aorta, ata: anterior tentorial arm, atb: anterior tentorial bridge, atp: anterior tentorial pit, car: circumantennal ridge, ce: compound eye, cl: clypeus, coa: corpora allata, cor: circumocular ridge, ct: corpotentorium, dta: dorsal tentorial arms, fg: frontal ganglion, frc: frontal connective, hsr: hypostomal ridge, lbr: labrum, ner: nervus recurrens, oc: ocellus, ocr: occipital ridge, ph: pharynx, pma: posterior mandibular articulation, pocr: postoccipital ridge, psr: pleurostomal ridge, sar: subantennal ridge, sog: supraoesophageal ganglion, sug: suboesophageal ganglion.

Fig. 3F partly broken on left side of head), so no postoccipital area is present. Dorso-laterally the postoccipital ridge bears a condyle, which articulates with the lateral cervical sclerite (*, Fig. 2) on each side.

The large kidney-shaped compound eyes (ce, Figs. 2, 3) are positioned laterally on the dorsal part of the head capsule. In the female they end ventrally on the level of the antennal articulations. Each eye is surrounded by a circumocular ridge (cor, Figs. 2, 3, 5). The two lateral ocelli (oc, Figs. 2, 3) are located mesally of the compound eyes and meso-dorsally of the antennal bases. The median ocellus is missing. The antennal bases are positioned in fronto-mesal recesses of the compound eyes. They are facing frontally. Each antennal socket is surrounded by a circumantennal ridge (car, Figs. 2, 3, 4, 5), whose lateral to dorso-lateral part is confluent with the circumocular ridge. From its ventral part a well-developed antennifer (an, Figs. 3, 4, 8) extends to the base of the scapus. The distance between the antennal bases is approximately twice their diameter.

From the fronto-ventral part of the circumocular ridge the laterally arched subantennal ridge (sar, Figs. 2–5) continues ventrally, where it unites with the dorsally arched pleurostomal part of the costa (psr, Figs. 3–5) at its dorsalmost point. From here the costa descends posteriorly towards the posterior mandibular articulation and anteriorly towards the anterior articulation. The lat-

ter branch curves dorso-mesally upon the articulation to continue only for a short distance as an epistomal part of the costa. The entire stretch of the costa anteriorly of the junction with the subantennal ridge represents the anterior tentorial pit (atp, Figs. 2, 4, 5), i.e. these parts are deepened to form the anterior tentorial arms. The pleurostomal and hypostomal parts of the costa delimit the dorsal gena (ge, Fig. 2) from the ventral subgena. Between the anterior and posterior mandibular articulations the subgena is wide due to the arching of the pleurostomal part of the ridge. Posteriorly of the posterior mandibular articulation the hypostomal ridge (hsr, Figs. 3, 4, 5) of the costa runs along the margin of the head capsule. Dorsally, near the beginning of posterior tentorial arms, the hypostomal ridge forms a sclerotized process (hyp, Fig. 3) which articulates with the cardo of the maxilla. The occipital ridge (ocr, Figs. 1–5) starts from the posterior mandibular socket and runs dorso-mesally on the posterior side of the head capsule. This supportive ridge bifurcates near the latero-dorsal edge of the occipital foramen. One branch continues for a short distance dorso-mesally while the other one fuses with the postoccipital ridge.

The dorsal frons (fr, Figs. 1, 3) and the ventral clypeus (cl, Figs. 2, 4) are separated from each other only far laterally by the short parts of the costa bearing the anterior tentorial pits; between the pits frons and clypeus are confluent due to the lack of the costa in this area. The

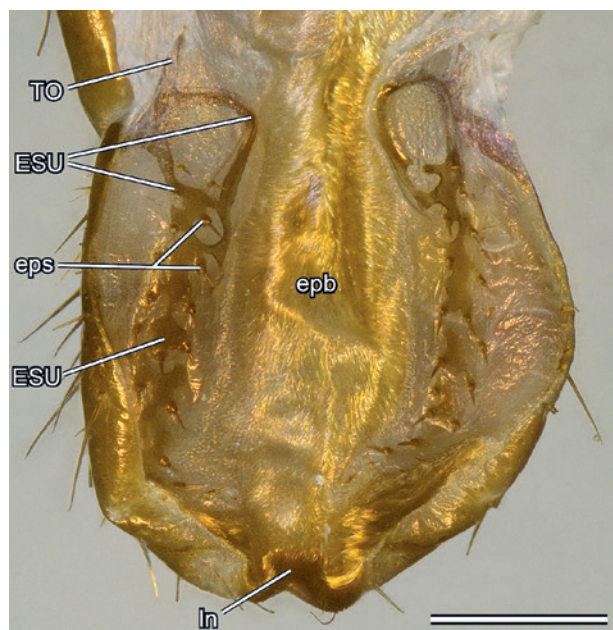


Fig. 6. Digital micrograph of the macerated and critical point dried epipharynx of *Periplaneta americana*, posterior view of clypeolabrum. Scale bar: 500 μ m. — **Abbreviations:** epb: epipharyngeal brush, eps: epipharyngeal setae, ESU: epipharyngeal suspensorium, ln: labral notch, TO: torma.

clypeus is trapezoid and bears a few long setae. It consists of a proximal strongly sclerotized part (postclypeus pcl; Figs. 1, 4) and a distal weakly sclerotized part (anteclypeus acl; Fig. 1, 3); in the latter the median part is especially weakly sclerotized. Distally the clypeus is separated from the labrum by a fairly narrow membranous stripe, which is transversely folded inward (a syndesis in a wider sense, but too wide for a distinctly hinge-like contact). The coronal cleavage line (cc, Fig. 3) runs medially from the foramen over the vertex. In between the compound eyes it branches into the two frontal cleavage lines (fc, Fig. 3), which continue laterally towards the ocelli, where they end.

The head capsule of the male is in almost every respect similar to the female one. Figure 3 compares the head capsules of the two sexes. The only difference refers to the bigger compound eyes. In contrast to the female they reach further ventrally than the antennal articulations. Thus the circumocular ridge is in contact with the hypostomal part of the costa, and there is no discrete subantennal ridge.

3.2. Tentorium

The tentorium is composed of paired anterior (ata, Figs. 3–5), dorsal (dta, Figs. 4, 5), and posterior tentorial arms (pta, Fig. 4) as well as two unpaired connective bridges, the corpotentorium (ct, Figs. 3–5) and the anterior tentorial bridge (atb, Figs. 3–5). The massive and flat anterior tentorial arm (ata, Figs. 3–5) originates from the anterior tentorial pit, which is located on the anterior costa. Each arm is twisted about 120° (left arm clockwise as seen

from the pit) and has reinforced margins on both sides. Left and right anterior tentorial arms are medially interconnected by the anterior tentorial bridge (atb, Figs. 3–5). The epidermis-facing surface of this bridge is smooth on its anterior side but shows a median ridge (atr, Fig. 4) on its posterior side. In their last third the anterior tentorial arms laterally border a round “perforation”, i.e. a medial gap between the anterior tentorial bridge and the corpotentorium, through which the pharynx passes. On the anterior side of this part of the anterior tentorial arm the thin and wing-like dorsal tentorial arm (dta, Figs. 4, 5) has its broad origin. It narrows distally into a slender thread-like part and does not reach the cuticle of the head capsule. On the anterior margin of the corpotentorium paired elongate laminar tendons, the oesotendons (os, Fig. 4), originate. They run ventrally and serve as attachment site for *M. tentoriosuspensorialis* (0hy5). Dorso-posteriorly the anterior tentorial arm continues into the corpotentorium, which is transversely plate-like and laterally receives the short posterior tentorial arms. The posterior tentorial arms (pta, Fig. 4) originate from the posterior tentorial pits (ptp, Fig. 3) at the transition between the hypostomal ridge and the postoccipital ridge. Laterally on the ventral side of the posterior tentorial arms small trabeculae tentorii are located, which serve as attachment site for musculature.

The tentorium bears the origins of antennal, mandibular, maxillary, labial, hypopharyngeal, buccal, and pharyngeal muscles (see Table 1), but not of any suspensory muscles (0te1–6).

3.3. Antenna

The base of the scapus articulates with the head capsule via the antennifer. The scapus (SC, Figs. 2, 3, 8) is a slightly bent sclerite cylinder, half as wide as long and covered with various setae. The pedicellus (PE, Figs. 2, 3, 8) is about 1/3 the length of the scapus. Its setation is less dense than that of the scapus. Along most of the circumference of the antenna the scapus and the pedicellus are separated by a fairly wide membrane, but laterally and mesally there are small areas of close contact. The pedicellus has conspicuous longitudinal grooves on its distal half (Fig. 8A). The flagellum (fl, Figs. 2, 8) has at its base approximately the same diameter as the pedicellus and consists of about 120 flagellomeres. The first is about as long as the pedicellus while the ones in the following third of the antenna are only half as long as wide. In the middle of the flagellum they are as long as wide, while in the distal third they become longer than wide. The distal 15 flagellomeres narrow strongly. The musculature of the antenna is partially illustrated in Fig. 7 and described in Table 1.

3.4. Labrum and epipharynx

The trapezoid labrum (lbr, Figs. 1, 2, 4) and the clypeus together form the clypeolabrum. The labral sclerite (LBS, Fig. 3) is separated from the clypeal sclerotization by a

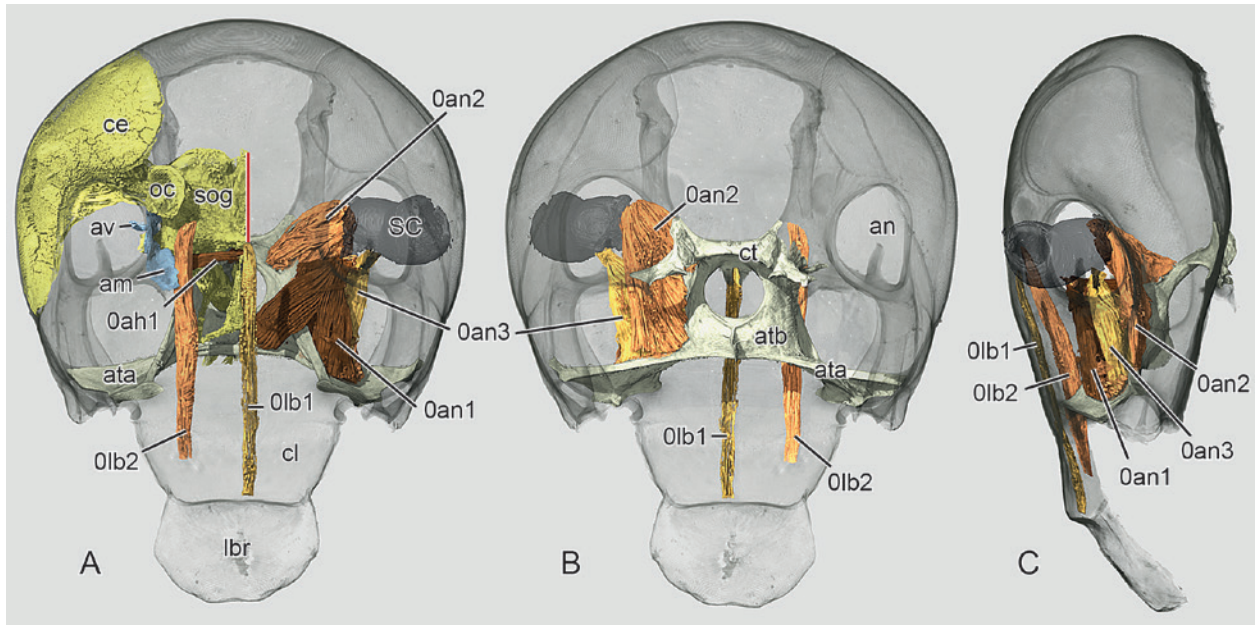


Fig. 7. Three-dimensional reconstructions of the antennal and labral musculature of *Periplaneta americana*, cuticle rendered transparent, mouthparts removed. **A:** anterior view, nervous system and antennal heart added in right hemisphere; **B:** posterior view; **C:** lateral view. — **Abbreviations:** am: antennal ampulla, an: antennifer, ata: anterior tentorial arm, atb: anterior tentorial bridge, av: antennal vessel, ce: compound eye, cl: clypeus, ct: corpotentorium, lbr: labrum, oc: ocellus, SC: scapus, sog: supraoesophageal ganglion.

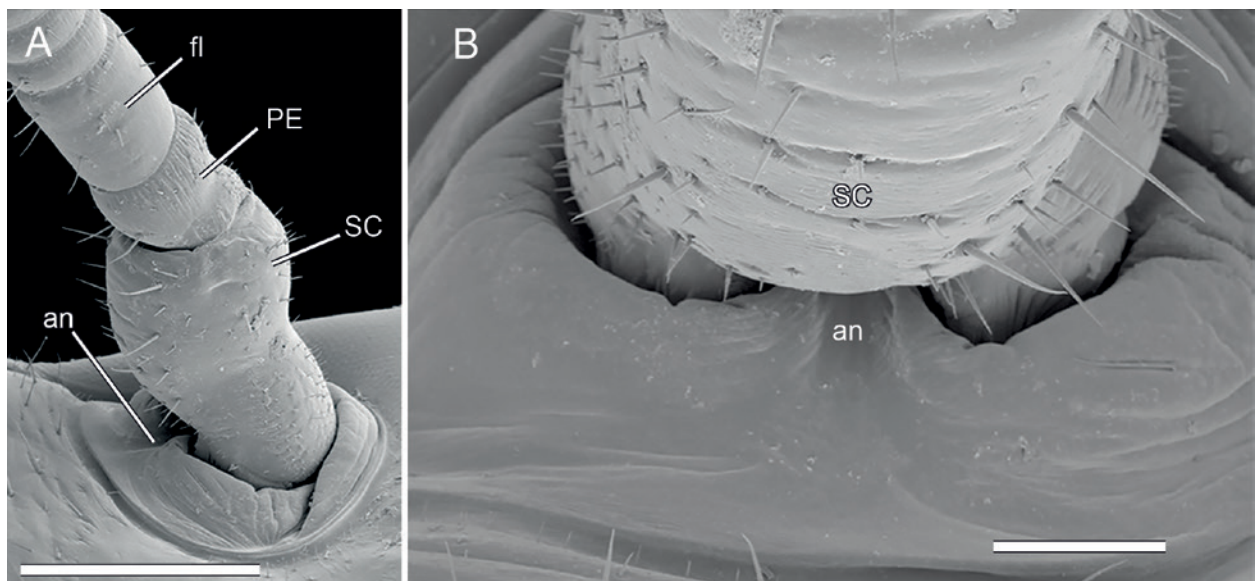


Fig. 8. Scanning electron micrographs of right antennal base and articulation of *Periplaneta americana*. **A:** antennal base and surrounding area, ventral to the left, lateral towards background, scale bar: 500 μ m; **B:** antennifer and surrounding area, scale bar: 200 μ m. — **Abbreviations:** an: antennifer, fl: flagellum of antenna, PE: pedicellus, SC: scapus.

syndesis and takes the entire anterior wall of the labrum. Its distal half and lateral sides bear large setae. The distal edge of the labrum is slightly notched (ln, Fig. 6). This notch is densely setose.

The epipharynx (epi, Figs. 3, 6) is the posterior wall of the clypeolabrum. It forms the roof of the praeoral cavity and ends dorsally in the anatomical mouth opening (opening of foregut). The epipharynx is membranous except for the torma (TO, Fig. 6) and the epipharyngeal suspensorium (ESU, Fig. 6), which are interconnected.

Together they form a central loop-like sclerotization with a long distal extension (main part of suspensorium) and shorter lateral and proximal extensions (parts of the tormae). The lateral tormal extension is firmly connected to the labral sclerite very close to its basal margin. The ribbon-like, irregular, and partly fragmented distal extension serves as attachment for *M. frontoepipharyngealis* (0lb2) and bears several spike-like setae (eps, Fig. 6). Alongside the torma and the proximo-lateral part of the epipharyngeal suspensorium the cuticle is thickened

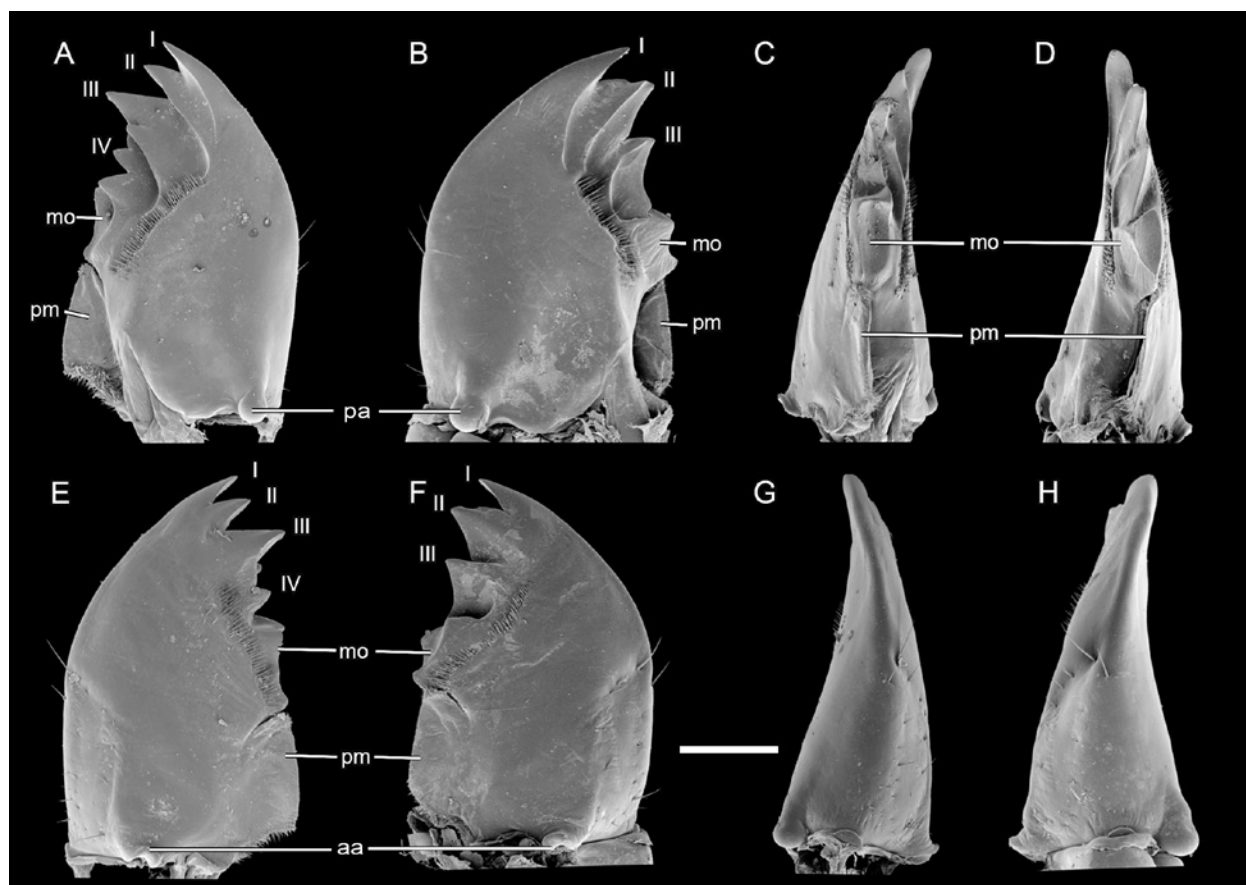


Fig. 9. Scanning electron micrographs of the left (A, C, E, G) and right (B, D, F, H) mandible of *Periplaneta americana*. **A+B:** posterior view; **C+D:** mesal view; **E+F:** anterior view; **G+H:** lateral view. Scale bar: 500 μ m. — **Abbreviations:** I–IV: incisivi, aa: anterior articulation (socket upon elevated area) of mandible, mo: mola, pa: posterior articulation (condyle) of mandible, pm: postmola.

and sclerotized internally, while the surface is soft (thus showing the reverse condition of what is usually found in sclerites, including the remaining suspensorium). The median epipharyngeal area is covered by a brush of microtrichia (epb, Fig. 6). The brush is very strongly developed in the median-most area around the clypeo-labral border. Distally it decreases but the distal margin including the labral notch (ln, Fig. 6) is again densely covered by microtrichia. Proximally of the tormae an unpaired sclerite is embedded in the epipharyngeal membrane. It is laterally more strongly sclerotized and serves as attachment site for *M. clypeopalatalis* (Oci1, Fig. 18).

The musculature of the labrum and epipharynx is partially illustrated in Figs. 7 and 18 and described in Table 1.

3.5. Mandible

Each mandible (md, Figs. 9–11) bears a single and massive sclerite, which articulates with the head capsule via two ball-and-socket joints: the anterior (ama, Figs. 2–5) and posterior (pma, Figs. 3–5) mandibular articulations. The mandible provides the socket for the anterior articulation (aa, Fig. 9) and the ball for the posterior one (pa,

Fig. 9). Both mandibles are slightly bent posteriorly in their distal third.

The mandibles show some left-right asymmetry. The left mandible has four distal incisivi (including the tip; Fig. 9). The distal two (I + II, Fig. 9) are subequal in size, followed by the largest one (III, Fig. 9). On the posterior side a small dent-like tooth is positioned at the base of incisivus III but not counted as an incisivus on its own. The proximal-most incisivus (IV, Fig. 9) is the smallest. The right mandible has three distal incisivi. The proximal one (III) is also the smallest while the second one (II) is slightly longer than the first (I).

Proximally of the incisivi the mola (mo, Fig. 9) follows. In the left mandible, it is a concave area which is approximately twice as high as wide. The mola of the right mandible is convex with a ridge in its middle, thus perfectly fitting into the concave left mola.

The proximal end of the mesal surface of the mandible is formed by the membranous postmola (pm, Fig. 9). Seen from anterior, it is a rhomb-shaped structure with a slightly convex mesal edge. It is densely covered with microtrichia (Fig. 10C), which are longer in the lateral areas. The proximal edge of the postmola bears a dense cluster of thin hair-like setae (Fig. 10D). The anterior and posterior surfaces of the gnathal armature each bear a row of short, more robust setae (Fig. 10A). Both rows

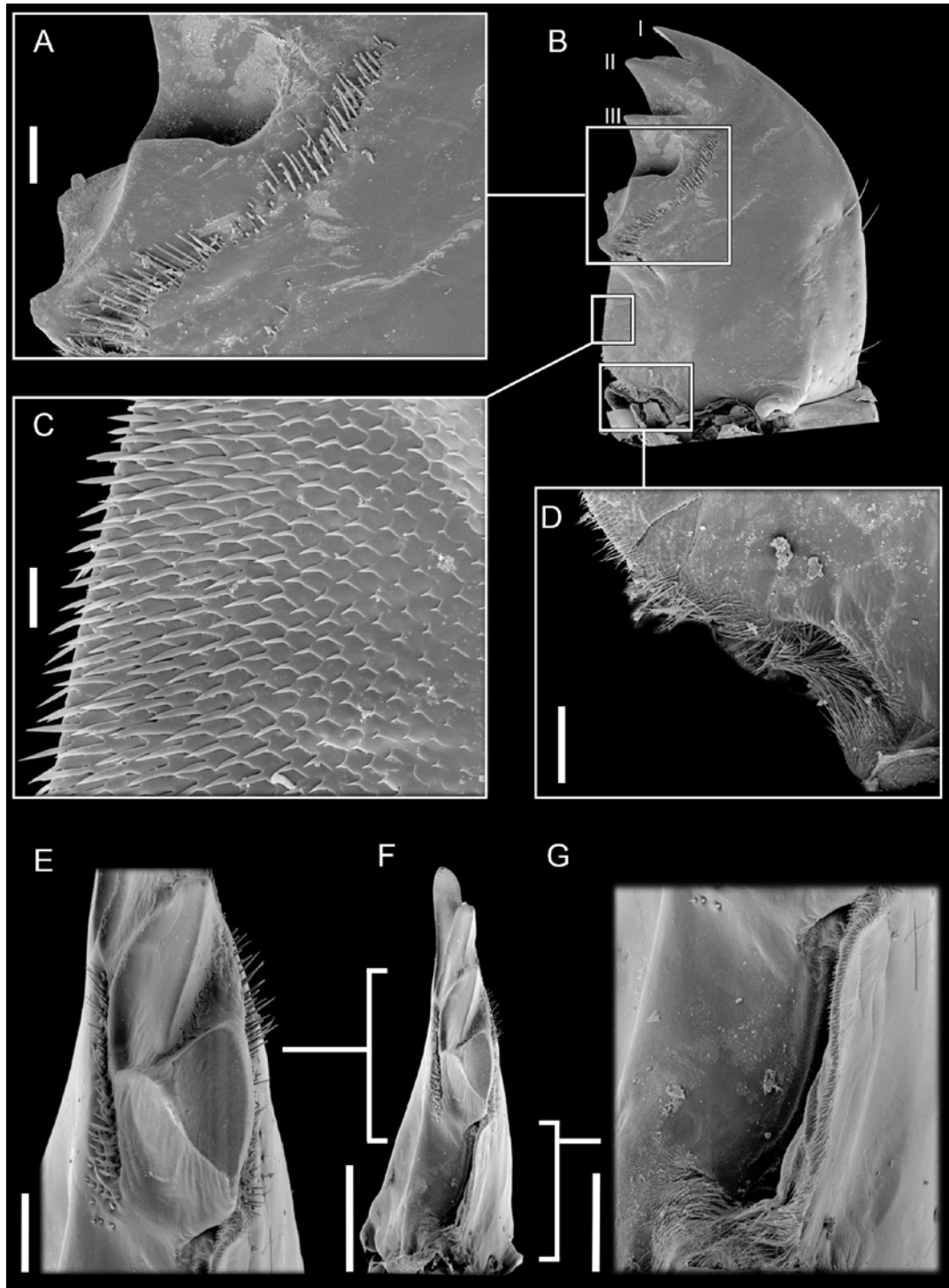


Fig. 10. Scanning electron micrographs of details of the right mandible of *Periplaneta americana*. **A:** setation at mola and proximal incisus III on anterior side of mandible, scale bar: 20 μ m; **B:** overview of anterior side of mandible; **C:** surface of postmola in anterior view, scale bar: 20 μ m; **D:** setation on proximal part of edge of postmola in anterior view, scale bar: 100 μ m; **E:** mola in mesal view, scale bar: 200 μ m; **F:** overview of mesal side of mandible, scale bar: 500 μ m; **G:** postmola in mesal view, scale bar: 200 μ m.

extend from the base of incisus II to the basal edge of the mola. The lateral surface of the mandible bears a few scattered setae of varied length.

The strong mandibular adductor tendon originates mesally from the basal margin of the mandibular sclerite and reaches deeply into the lumen of the head capsule. Internally the tendon gradually widens and then divides

into three wing-like branches: Quite close to the mandible a sail-like basal wing of the tendon (bwt, Fig. 11) protrudes laterally; on the distalmost point of the basal wing the tendon forks into a narrow lateral wing (lwt, Fig. 11) and a fairly wide mesal wing (mwt, Fig. 11). The mesal wing reaches further mesally than the attachment of the tendon on the mandible. All wings serve as

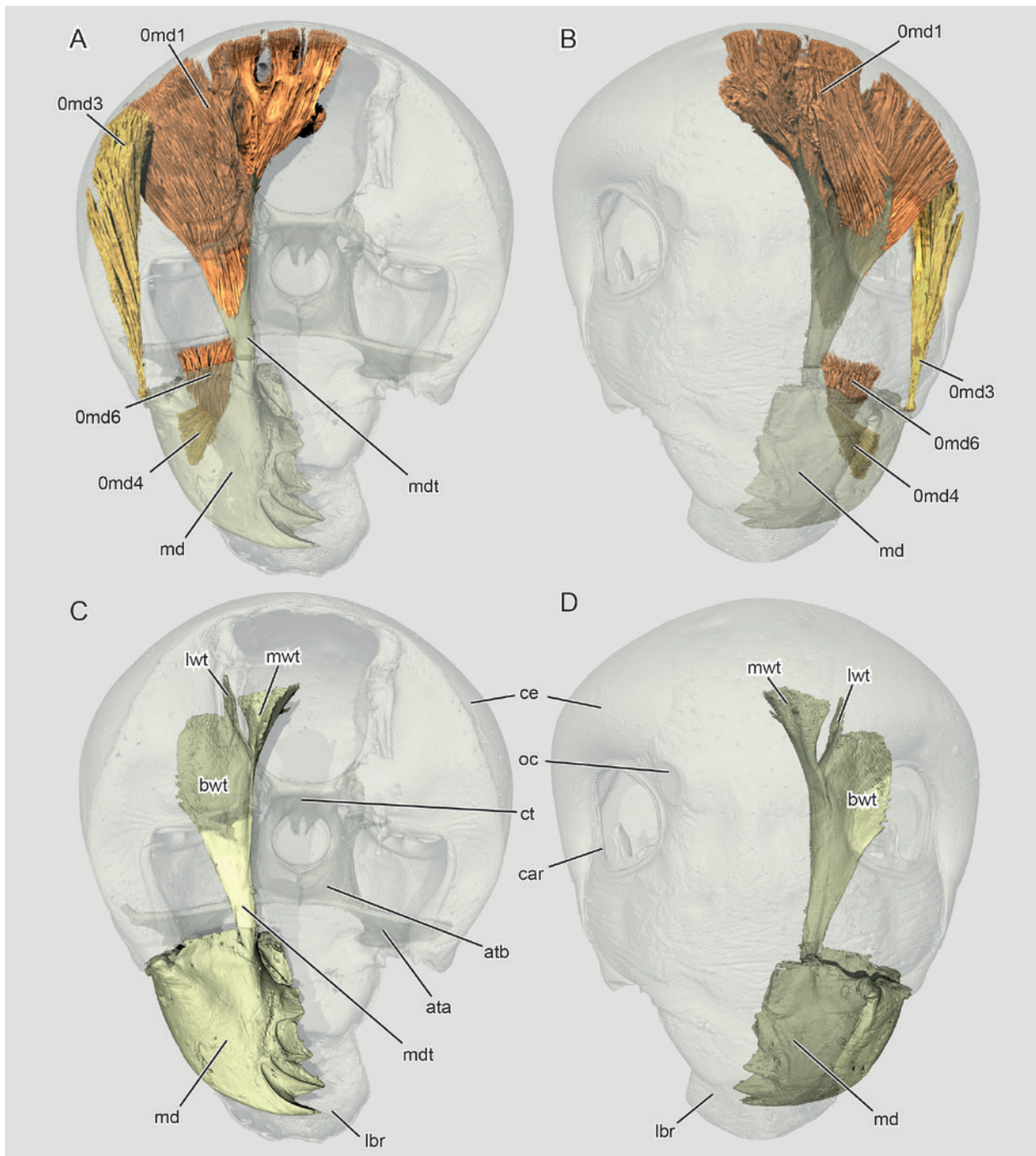


Fig. 11. Three-dimensional reconstructions of mandibular musculature and tendon of adductor muscle of *Periplaneta americana*, head capsule rendered transparent, all mouthparts except left mandible removed. **A:** posterior view of mandibular musculature; **B:** anterior view of mandibular musculature; **C:** posterior view of adductor tendon; **D:** anterior view of adductor tendon. — **Abbreviations:** ata: anterior tentorial arm, atb: anterior tentorial bridge, bwt: basal wing of the adductor tendon, car: circumantennal ridge, ce: compound eye, ct: corpotentorium, lbr: labrum, lwt: lateral wing of adductor tendon, md: mandible, mdt: mandibular adductor tendon, mwt: mesal wing of adductor tendon, oc: ocellus.

attachment for *M. craniomandibularis internus* (0md1). The mandibular abductor (0md3) inserts on a slim and unbranched tendon arising laterally from the basal mandibular margin.

The musculature of the mandible is illustrated in Fig. 11 and described in Table 1.

3.6. Maxilla

The maxilla articulates with the hypostomal ridge. On its postero-lateral side the maxilla is well sclerotized while the antero-mesal side, which faces the head capsule, is membranous.

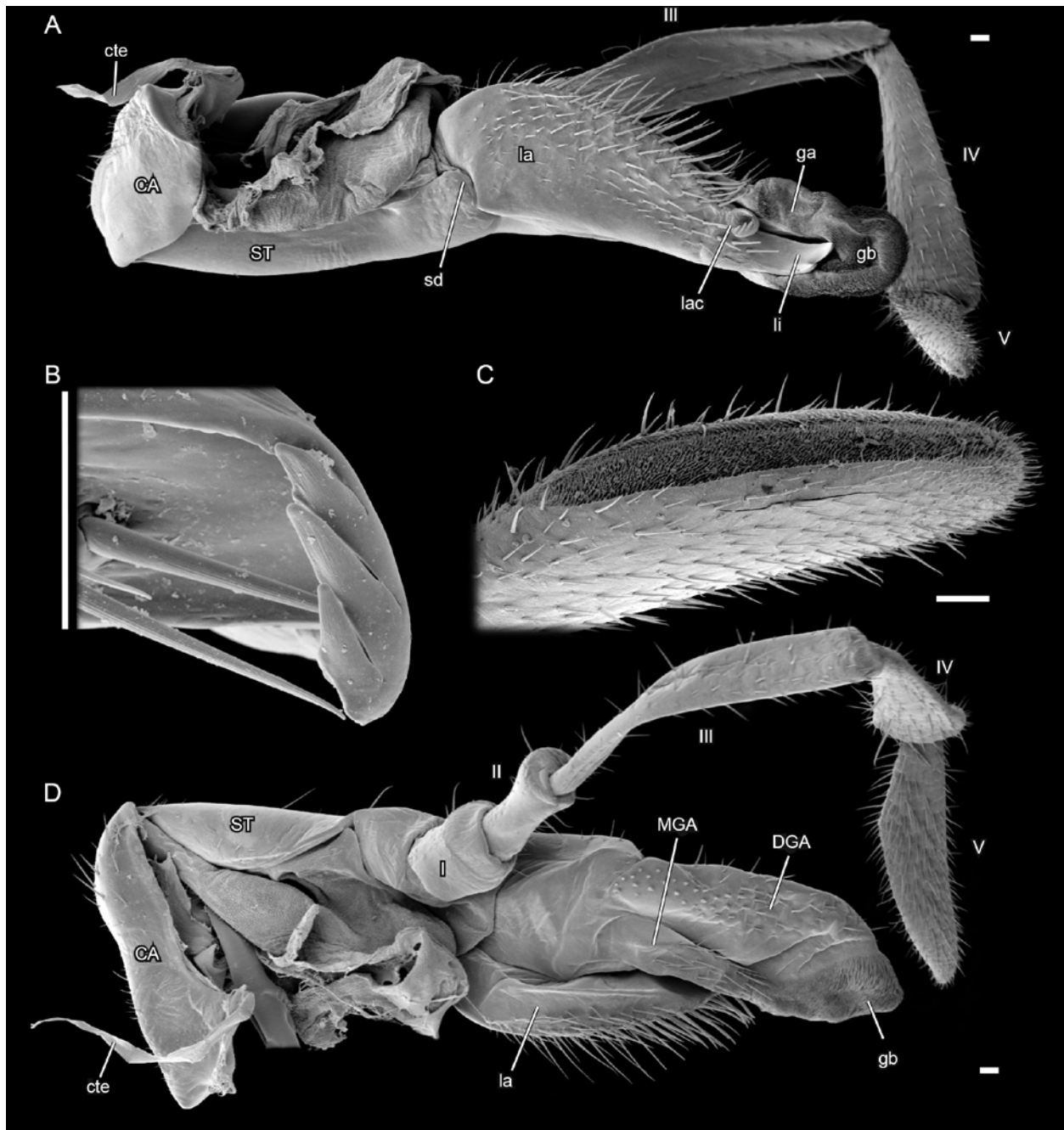


Fig. 12. Scanning electron micrographs of left maxilla of *Periplaneta americana*. **A:** maxilla in postero-mesal view; **B:** detail of lacinula in antero-proximal view; **C:** sensory field on distal palpomere in posterior view; **D:** maxilla in anterior view. All scale bars: 100 μm . — **Abbreviations:** CA: cardinal sclerite, cte: cardinal tendon, DGA: distogaleal sclerite, ga: galea, gb: galeal brush, I–V: maxillary palpomeres, la: lacinia, lac: lacinula, li: teeth or incisivi of lacinia, MGA: mesogaleal sclerite, sd: stipital disc, ST: stipital sclerite.

The cardo (CA, Figs. 12–14) is a sparsely setose boat-shaped, transversely oriented sclerite. It bears a strong cardinal ridge (cr, Figs. 13, 14) which delimits the mesal from the lateral part. At the anterior end of the cardinal ridge the long tendon (cte, Fig. 12) of *M. craniocardinalis* (0mx1) originates. The mesal margin of the cardo articulates with the process on the hypostomal ridge.

The stipital sclerite (ST, Figs. 12–14) articulates with the cardinal sclerite mesally on its posterior side; the articulation is supported by the posterior end of the

cardinal ridge. Apart from this articulation the sclerites are separated by a wide membrane anteriorly and by a narrow membrane posteriorly, the latter forming a cardino-stipital syndesis (css, Figs. 13). Proximally, near the syndesis, the stipital sclerite is sparsely setose. On the posterior side of the maxilla, the stipital sclerite has a distal semi-circular extension, the stipital disk (sd, Figs. 12, 13). It is synsclerotic with the lacinial and basigaleal sclerites. On the posterior surface of the stipes, the stipital ridge (sr, Fig. 13) runs from the cardino-stipital articulation distally and ends shortly proximally of the lacinial

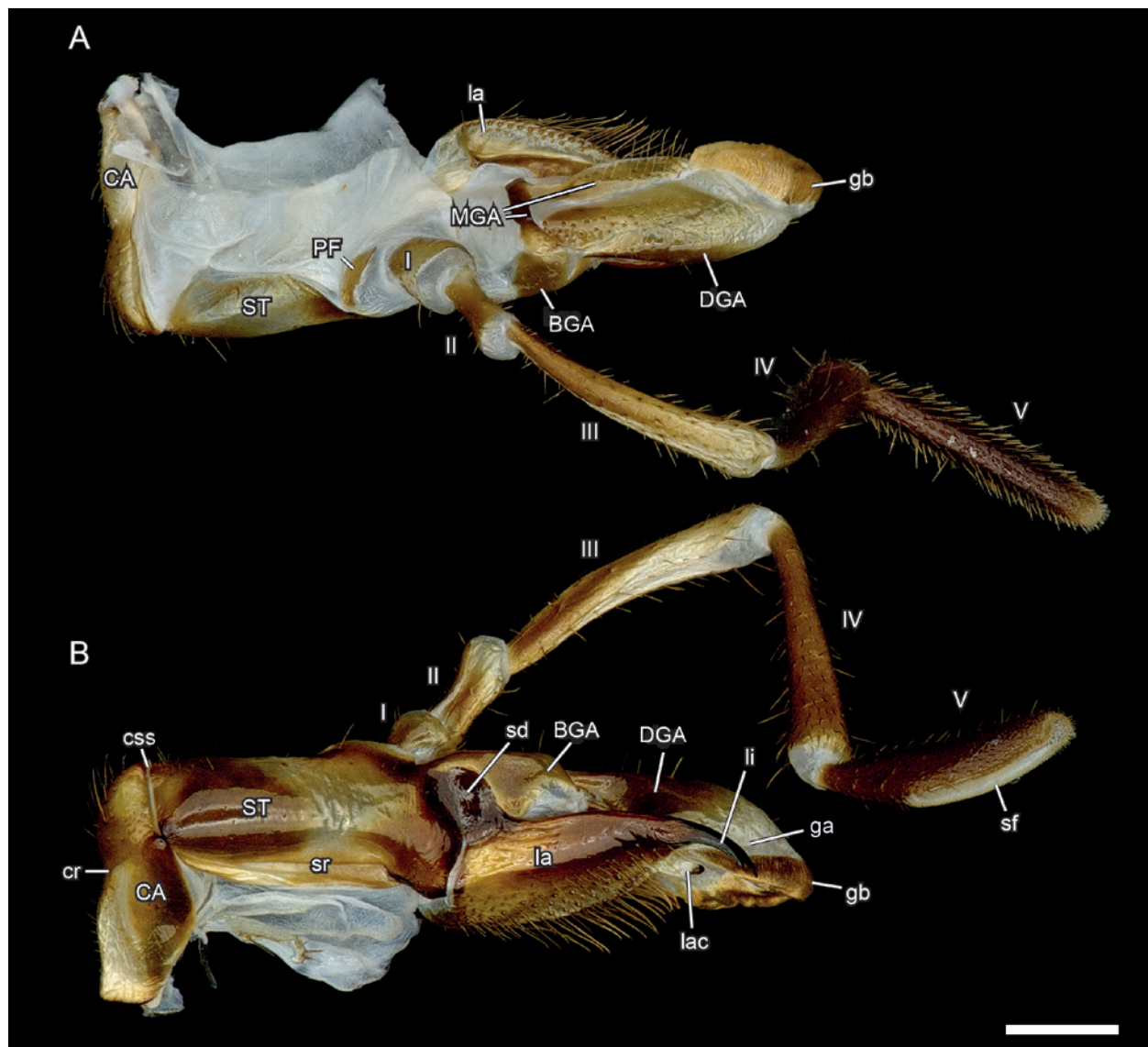


Fig. 13. Digital micrographs of right maxilla of *Periplaneta americana*. **A:** maxilla in anterior view; **B:** maxilla in posterior view. Scale bar: 500 µm. — **Abbreviations:** BGA: basigaleal sclerite, CA: cardinal sclerite, cr: cardinal ridge, css: cardino-stipital syndesis, DGA: distigaleal sclerite, ga: galea, gb: galeal brush, I–V: maxillary palpomeres, la: lacinia, lac: lacinula, li: teeth or incisivi of lacinia, MGA: mesogaleal sclerite, PF: palpifer, sd: stipital disc, sf: sensory field on the maxillary palp, sr: stipital ridge, ST: stipital sclerite.

base. It is a prominent internal ridge which serves for muscle attachment.

The maxillary palp is 5-segmented (mxp, Figs. 1, 2, 3). The base of the 1st palpomere articulates disto-laterally with the stipital sclerite and proximo-mesally with the well-developed palpifer (PF, Figs. 3, 13), a small half-moon-shaped sclerite located antero-mesally of the stipital sclerite in the anterior wall of the maxilla. Palpomeres I and II are sparsely setose (Figs. 12, 13). Palpomeres III and IV are about twice as densely setose as I and II, while the setation of the distal one (V) is even denser. Palpomeres are separated by membranes of varied width and show no articulations between each other. Palpomere I is nearly as broad as long. Palpomere II widens strongly in its distal half and is approximately twice as long as its base is wide. Palpomeres III, IV and V are elongate. On the mesal surface of the distal palpomere a membranous

sensory field (sf, Fig. 13) is located. It is an elongate oval groove, approximately half the length of the palpomere and densely covered with sensilla.

The galea (ga, Figs. 12–14) bears 3 sclerites, the basi- (BGA, Fig. 13), disti- (DGA, Figs. 12, 13) and mesogaleal sclerites (MGA, Figs. 12, 13). On the posterior maxillary surface the basigaleal sclerite is synsclerotic with the lateral and distal margins of the stipital disk (sd). Distally of the basigalea the distigaleal sclerite extends over the disto-lateral half of the galea except for the apex. Basally it is well sclerotized while distally the sclerotization gradually decreases and obliterates. Disto-mesally of the distigaleal sclerite, well separated by a membranous area, the galeal brush (gb, Figs. 12, 13) is located on the meso-apical part of the galea. The mesogalea is an L-shaped sclerite on the antero-mesal side of the galea. Its transverse basal part is widely separated from the stipes;

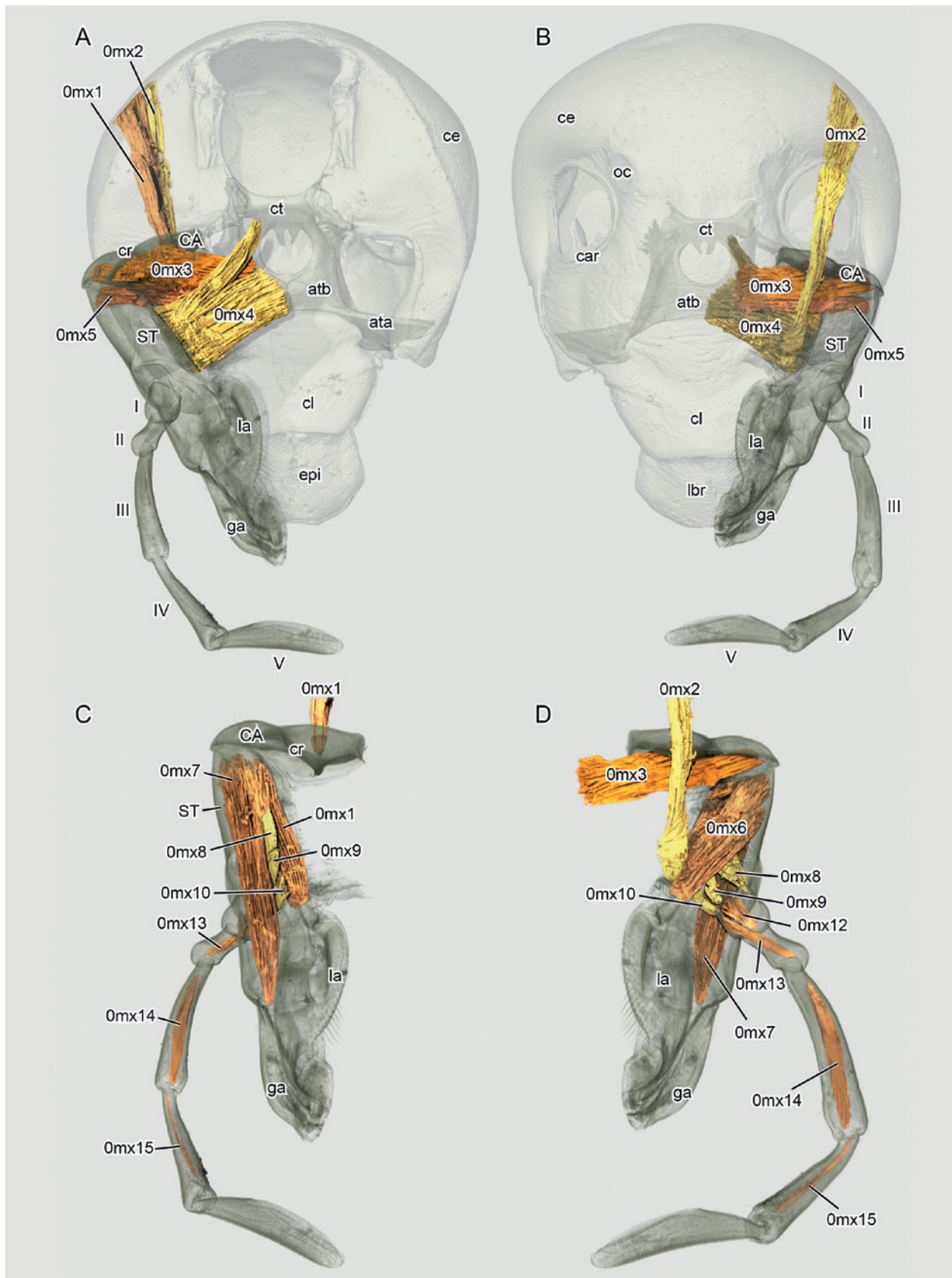


Fig. 14. Three-dimensional reconstructions of maxillary musculature of *Periplaneta americana*. **A:** left maxilla and head capsule in posterior view, cuticle rendered transparent and other mouthparts removed; **B:** left maxilla and head capsule in anterior view, cuticle rendered transparent and other mouthparts removed; **C:** left maxilla in posterior view, cuticle rendered transparent; **D:** left maxilla in anterior view, cuticle rendered transparent. — **Abbreviations:** ata: anterior tentorial arm, atb: anterior tentorial bridge, CA: cardinal sclerite, car: circumantennal ridge, ce: compound eye, cl: clypeus, cr: cardinal ridge, ct: corpotentorium, epi: epipharynx, ga: galea, I–V: maxillary palpomeres, la: lacinia, lbr: labrum, oc: ocellus, ST: stipital sclerite.

laterally it is interjacent between the bases of the distal and basigaleal sclerites (and somewhat synsclerotic with both), while mesally it shows a 90° bend to continue in its elongate distal part. This part reaches the meso-proximal end of the galeal brush; the distal two thirds of the mesogalea bear long mesally directed setae.

The lacinia (la, Figs. 12–14) has its base postero-mesally of the galea. It bears a single sclerite, whose posterior surface is heavier than the anterior one. It is narrowly synsclerotic with the stipes along the mesal margin of the stipital disk, while further mesally the stipes and lacinia are separated by a membranous syndesis, which allows for meso-lateral movements of the lacinia. The entire mesal surface of the lacinial sclerite bears rows of setae on both the anterior and posterior sides; the setae increase in length distally. Distally the lacinia narrows strongly and ends in two strongly sclerotized lacinial teeth (or incisi) (li, Figs. 12, 13). At the distal end of the mesal setation and at the base of the lacinial teeth, the lacinula (lac, Figs. 12, 13) is located. It is a membranous lobe slightly longer than the setae. Only its tip is strongly sclerotized and bears three small teeth. In resting position the distal part of the lacinia fits into the concave mesal wall of the galea, being buried in the galeal brush.

The musculature of the maxilla is illustrated in Fig. 14 and described in Table 1.

3.7. Labium

The labium bears a submental sclerite (SM), a mental sclerite (MNT), a praemental sclerite (PR) and the paired 3-segmented palps (lp), palpiger sclerites (PG), glossae (gl), and paraglossae (pgl) (Figs. 1–3, 15, 16).

The submental sclerite is a strongly sclerotized plate. Its lateral margins are densely setose, contrasting the sparse setation of its remaining parts. The basal margin is concave and connected with the cervical membrane. Baso-laterally it articulates with the head capsule at the ventral end of the postoccipital ridge (Fig. 3F). In the distal half, the lateral margins are strongly convex. Distally it is separated from the mental sclerite via a narrow proximally arched membranous stripe, which is shaped as a pair of syndeses in the larger lateral parts but is distinctly wider in the median part.

The mental sclerite is also a strongly sclerotized plate and nearly oval. It is approximately half as long as the submental sclerite at midline and bears two pairs of setae, a mesal and a lateral one. The mental and the praemental sclerites are separated by a broad membranous area.

The praemental sclerite is an almost square plate with a slightly convex basal margin. Laterally it has concave emarginations embracing the base of the labial palps. Its surface is sparsely setose. In the distal half, a median praemental cleft divides the sclerite. From the base of the cleft a midline ridge runs proximally; it soon forks, the branches enclosing a near-triangular area upon the base of the praemental sclerite. The main body of the palpiger sclerite (PG, Fig. 15) is located in the lateral labial wall

proximally of the palpal base. From there it extends distally in the anterior labial wall towards the base of the labial palp, where it forms an articulation (not shown). The second articulation of palpomere I is located at the lateral margin of the praementum (art 0-I, Fig. 15). The palpal vestiture with setae strongly increases along the three palpomeres, with palpomere III being densely covered. Palpomere I is club-shaped and approximately as long as wide. II is slightly longer than I but has the same width. Palpomere III is three times as long as wide. Its apical surface is flat and extremely densely covered with setae (Fig. 16F). Palpomeres I and II articulate upon each other on the anterior (not shown) and posterior surfaces (art I-II, Fig. 15). Palpomeres II and III articulate via a lateral joint (art II-III, Fig. 15). Distally on the praementum, two lobes originate on each side. The mesal glossa bears a single sclerite and is narrowed distally. It bears a field of tapering microtrichia distally. The lateral paraglossa is longer than the glossa. Its lateral margin is concave while its mesal margin follows the shape of the glossa. Its basal two thirds bear a sclerite and several long setae. Distally the paraglossa is membranous with a disto-mesal field of tapering microtrichia. Disto-mesally the right and left paraglossae are in contact with each other.

The musculature of the labium is illustrated in Fig. 15 and described in Table 1.

3.8. Hypopharynx

The hypopharynx (hph, Figs. 16–18) is a tongue-like, largely membranous structure with several sclerites in its wall. It forms a slope towards the anatomical mouth opening and is divided in a distal lingual and a proximal suspensorial part. On the distal tip there is a small notch or low recess. The tip and the anterior and antero-lateral surface of the lingual part are densely covered with long tapering microtrichia (fch, Fig. 17). The suspensorial part is bare of such vestiture, except for a small field of microtrichia located disto-medially shortly behind the border to the lingual part.

The sclerites, many of which are interconnected, are classified into lingual and suspensorial ones. In the lateral area of the distal hypopharynx the lateral lingual sclerite (LLS, Fig. 17) is embedded. Its weakly sclerotized anterior part is triangular and in touch with the field of microtrichia. Proximally it is synsclerotic with the plate-like distal part of the suspensorial sclerotization (SDP, Figs. 16, 17). Postero-distally it continues into the second, more strongly sclerotized part of the lateral lingual sclerite, which is also triangular. This part does not reach the field of microtrichia anteriorly. Proximally it reaches underneath the suspensorial plate but is well separated from it by membrane. At its proximal-most point it continues, via a near-180° bend, into the ventral lingual sclerite (VLS, Figs. 16, 17). The latter continues disto-mesally, where the sclerites from both sides nearly unite in the posterior wall of the hypopharynx. The base of each ventral lingual sclerite additionally forms a postero-mesally directed arm

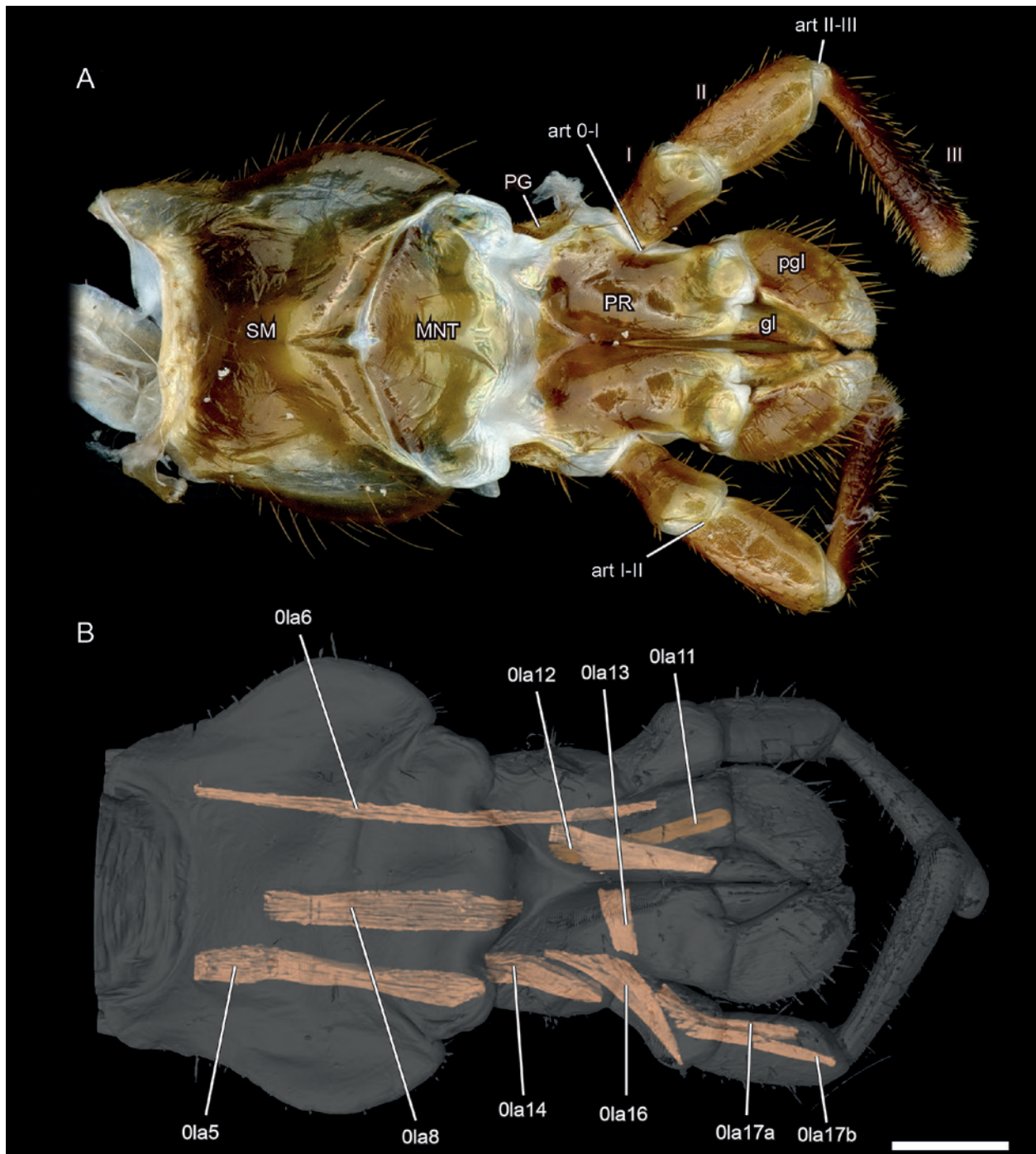


Fig. 15. Labium of *Periplaneta americana* in posterior view. **A:** digital micrograph; **B:** three-dimensional reconstruction, cuticle rendered transparent. Scale bar: 500 μm . — **Abbreviations:** art 0-I: lateral articulation between praemental sclerite and palpomere I; art I-II: posterior articulation between palpomeres I and II; art II-III: lateral articulation between palpomeres II and III; gl: glossa, MNT: mental sclerite, PG: palpiger, pgl: paraglossa, PR: praemental sclerite, SM: submental sclerite.

(SBH, Figs. 17) located at the very base of the hypopharynx; the left and right postero-mesally directed arms are only narrowly separated at midline, each ends at the flanks of the opening of the unpaired salivary duct (sad, Fig. 18) into the salivarium. The postero-mesally directed arms span the largely membranous posterior wall of the hypopharynx, which immediately distally of the arms forms on each side a dome-shaped invagination (see *ilg* of BUDER & KLASS 2013).

The suspensorial sclerites are composed of the plate-like distal part (SDP), a wide loral arm (SLA), and a slender oral arm (SOA) (Figs. 17, 18). All three parts are synsclerotic in the lateral wall of the hypopharynx. The sclerotization of the plate-like distal part consists of a more strongly sclerotized distal portion and a more weakly sclerotized, somewhat domed proximal portion bearing a row of long setae. The plate-like distal part is distally synsclerotic with the lateral lingual sclerite.

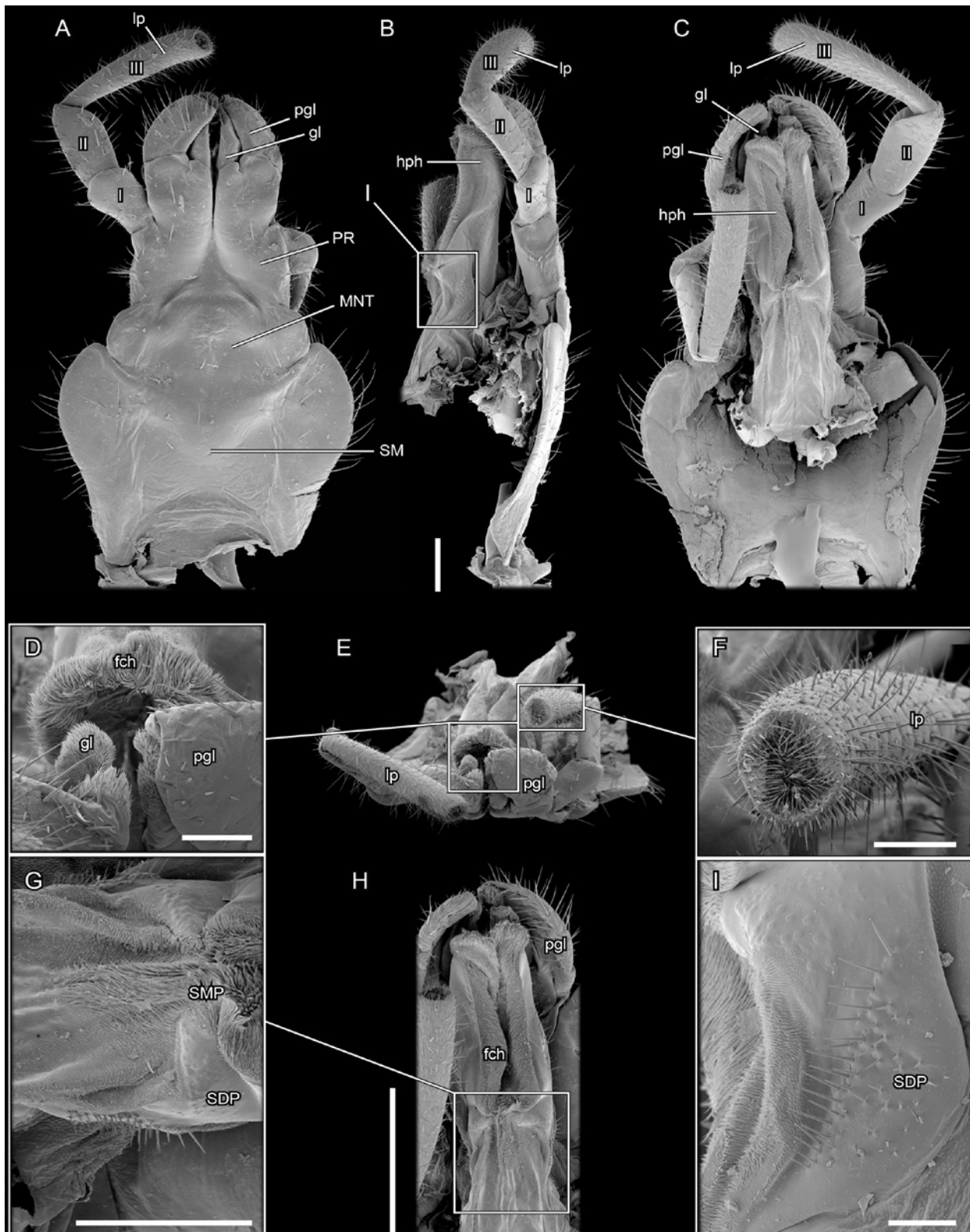


Fig. 16. Scanning electron micrographs of details of labium and hypopharynx of *Periplaneta americana*. **A:** labium in posterior view; **B:** labium and hypopharynx in lateral view; **C:** labium and hypopharynx in anterior view; scale bar for A–C: 500 µm; **D:** detail of ventral view of labium and hypopharynx, scale bar: 200 µm; **E:** ventral view of labium and hypopharynx, scale bar: 500 µm; **F:** tip of labial palp in ventral view, scale bar: 200 µm; **G:** hypopharyngeal field of microtrichia in border region between lingual and suspensorial parts in anterior view (distal is to the left), scale bar: 500 µm; **H:** hypopharynx in anterior view, scale bar: 1 mm; **I:** Setation of hypopharyngeal sclerite SDP and microtrichia anteromesally of it in lateral view (distal is towards the bottom, anterior to the right), scale bar: 100 µm. — **Abbreviations:** fch: field of microtrichia on dorsal and distal surface of hypopharynx, gl: glossa, hph: hypopharynx, lp: labial palp, MNT: mental sclerite, pgl: paraglossa, PR: praemental sclerite, SDP: plate-like distal part of hypopharyngeal suspensorium, SM: submental sclerite, SMP: arm-like disto-mesal part of suspensorium.

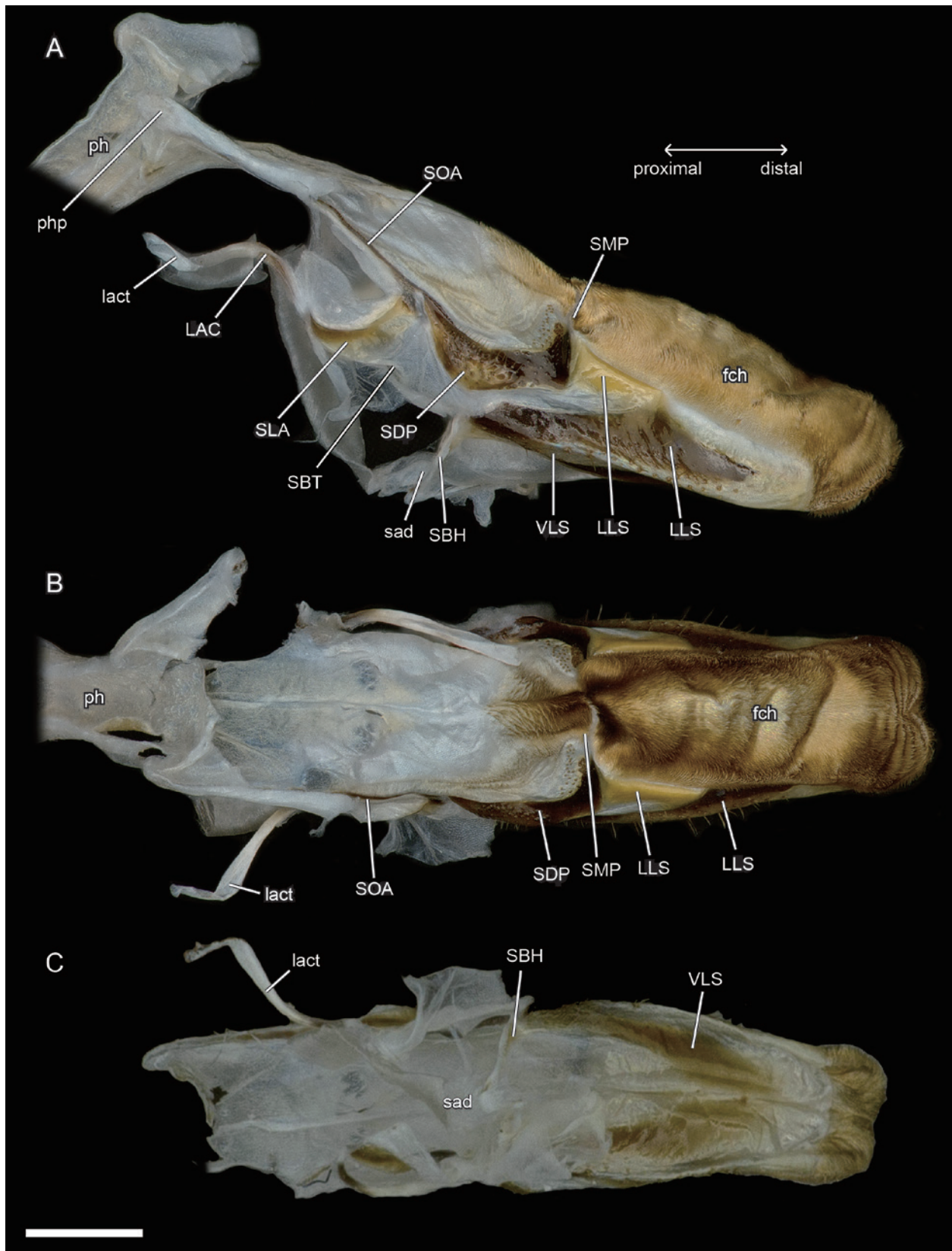


Fig. 17. Digital micrographs of hypopharynx of *Periplaneta americana*. **A:** lateral view; **B:** frontal view; **C:** posterior view. Scale bar: 500 μ m. — **Abbreviations:** fch: field of microtrichia on dorsal and distal surface, LAC: linguactual sclerite, lact: linguactual tendon / apodeme, LLS: lateral lingual sclerite of hypopharynx, ph: pharynx, php: pharyngeal pouch, sad: salivary duct, SBH: arm at base of ventral lingual sclerite, SBT: basitendinal sclerite of hypopharynx, SDP: plate-like distal part of hypopharyngeal suspensorium, SLA: loral arm of hypopharyngeal suspensorium, SMP: arm-like disto-mesal part of hypopharyngeal suspensorium, SOA: oral arm of hypopharyngeal suspensorium, VLS: ventral lingual sclerite of hypopharynx.

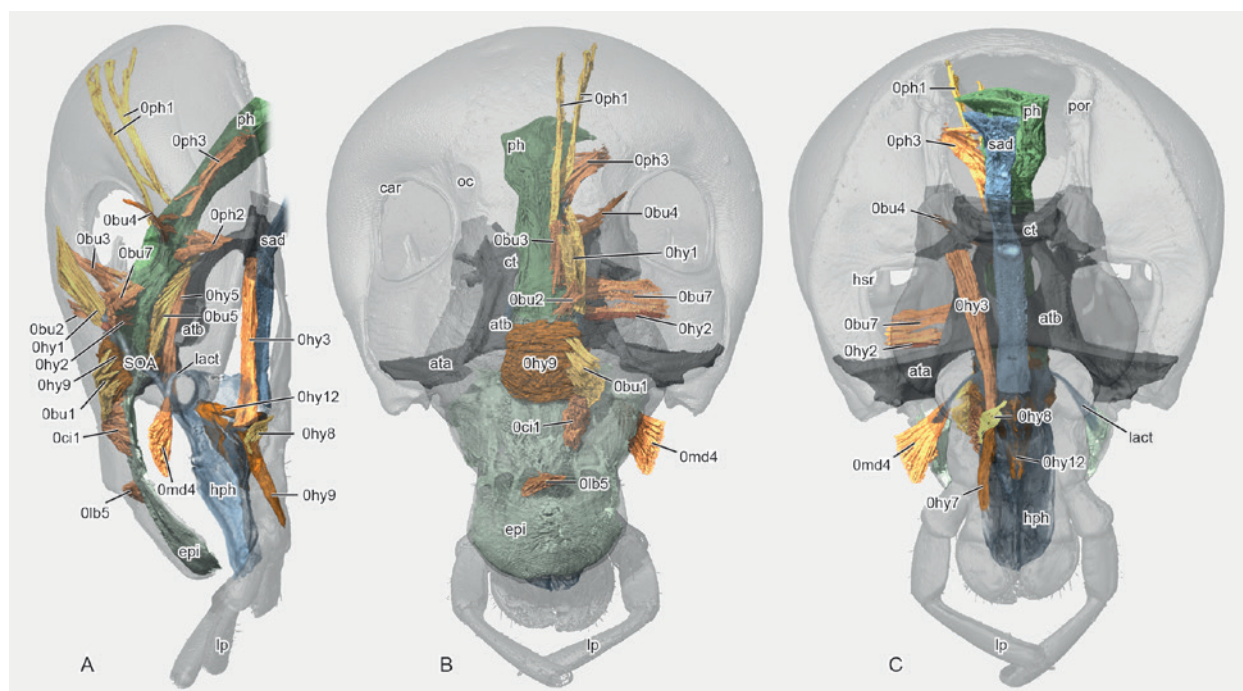


Fig. 18. Three-dimensional reconstruction of musculature of hypopharynx, buccal cavity and foregut of *Periplaneta americana*, cuticle rendered transparent, all mouthparts except hypopharynx and labium removed. **A:** left-lateral view; **B:** anterior view; **C:** posterior view. — **Abbreviations:** ata: anterior tentorial arm, atb: anterior tentorial bridge, car: circumantennal ridge, ct: corpotentorium, epi: epipharynx, hph: hypopharynx, hsr: hypostomal ridge, lact: linguactual tendon, lp: labial palp, oc: ocellus, ph: pharynx, pocr: postoccipital ridge, sad: salivary duct, SOA: oral arm of hypopharyngeal suspensorium.

From the junction between the lateral lingual sclerite and the plate-like distal part an arm-like sclerotization (SMP, Fig. 17) extends antero-mesally. It is shaped as a deep, thick-walled groove. Left and right arm-like sclerotizations abut upon each other in the dorsal midline of the hypopharynx (but are not connected). These arms are largely hidden due to their groove-like condition and a slight overfolding by the microtrichia-bearing area (fch) that immediately joins the arm-like sclerotization distally. The oral arm (SOA) is a long and slender bar which runs far dorsally in the lateral wall of the pharynx (ph, Figs. 3–5) where it ends in a pharyngeal pouch (php, Fig. 17). Several hypopharyngeal muscles are attached to the oral arm, which span the opening of the pharynx. The loral arm (SLA) is a sickle-shaped sclerite located in the postero-lateral hypopharyngeal wall. The anterior border of the loral arm is very sharp while on its postero-distal side it continuously fades out into membrane. The linguacutal sclerite (LAC, Figs. 17, 18) is positioned proximally of the loral arm, narrowly separated from it by membrane. The proximal part of the sclerite forms a strongly curved apodeme (lact, Figs. 17, 18), which extends ventrally into the lumen of the mandible (in Fig. 17 it is twisted backwards due to the preparation of the hypopharynx, while Fig. 18 shows its natural orientation).

In the membranous proximal lateral wall of the hypopharynx a weak, isolated lateral sclerite ("basitendinal" sclerite, SBT) is embedded on each side. Mesally the sclerites of both sides approach each other (by invagination of the hypopharyngeal wall) and are linked by M. lorolateralis.

The musculature of the hypopharynx is partially illustrated in Fig. 18 and described in Table 1.

3.9. Pharynx

The pharynx (ph, Figs. 3–5) is a tube with a transversely oval cross section slightly wider than high. Its opening (the functional mouth) is located slightly ventrally of the frontal ganglion and is held in position by the oral arms of the hypopharyngeal suspensorium and *M. oralis transversalis* (0hy9). The posterior wall of the pharynx continues into the hypopharynx while the anterior wall continues into the epipharynx. At rest the pharyngeal wall is folded in a longitudinal direction, which likely allows for considerable expansion when food is taken up. The pharynx is equipped with an inner layer of ring muscle fibers (*M. anularis stomodaei*; closer to the pharyngeal wall) followed by a layer of longitudinal muscle fibers (*M. longitudinalis stomodaei*).

The musculature of the pharynx is illustrated in Fig. 18 and described in Table 1.

3.10. Central nervous system

The supraoesophageal ganglion (sog, Figs. 4, 5) is well developed; an external distinction between proto-, deuto- and tritocerebrum was not possible based on our data. Frontally a pair of ocellar nerves (oc, Figs. 4, 5)

Table 1. Head musculature of *Periplaneta americana*. Abb. = Abbreviation.

Muscle name	Abb.	Origin	Insertion	Presumed function
M. tentorioscapalis anterior	0an1	meso-frontal area of the anterior tentorial bridge, anterior and dorsal tentorial arm	ventro-mesal scapal edge	depressor of antenna
M. tentorioscapalis posterior	0an2	lateral corpotentorium, anterior tentorial bridge and dorsal tentorial arms	dorsal scapal edge	levator of antenna
M. tentorioscapalis lateralis	0an3	anterior tentorial arm and lateral anterior tentorial bridge	ventro-lateral scapal edge	depressor and rotator of antenna
M. tentorioscapalis medialis	0an4	absent		
M. frontopedicellaris	0an5	absent		
M. scapopedicellaris lateralis	0an6	dorsal interior wall of scapus	lateral edge of pedicellus	extensor of flagellum
M. scapopedicellaris medialis	0an7	ventral interior wall of scapus	mesal edge of pedicellus	flexor of flagellum
M. intraflagellaris	0an8	absent		
M. interampullaris	0ah1	antennal ampulla	antennal ampulla of opposite side	dilator of ampulla
M. ampulloaortica	0ah2	antennal ampulla, together with 0ah1	cephalic aorta, posteriorly of the supraoesophageal ganglion	dilator of ampulla
M. ampulloparyngealis	0ah3	absent		
M. ampullofrontalis	0ah4	absent		
M. frontoparyngealis	0ah5	absent		
M. frontolabralis	0lb1	mesally on frons, on the level of the tips of the antennifers	mesally on the baso-frontal wall of the labral sclerite, near the insertion mesally merged	levator of labrum
M. frontoepipharyngealis	0lb2	mesally on the frons, laterally and slightly posteriorly of 0lb1	tormae	depressor of labrum
M. epistoepipharyngealis	0lb3	absent		
M. labralis transversalis	0lb4	ventral labral wall	ventral labral wall of opposite side	compressor of labrum
M. labroepipharyngealis	0lb5	inner labral wall, directly ventrally of the insertion of 0lb1	inner epipharyngeal wall, laterally and slightly ventrally of the origin	dilator of cibarium
M. labrolabralis	0lb6	absent		
M. craniomandibularis internus	0md1	in several bundles along the dorsal and dorso-lateral head capsule; some bundles reaching across the midline on the opposite site; one bundle on the postgena, laterally of the foramen occipitale	tendon arising mesally from the basal margin of the mandible	adductor of mandible, antagonist of 0md3
M. craniomandibularis externus anterior	0md2	absent		
M. craniomandibularis externus posterior	0md3	lateral head capsule, posteriorly of the compound eye	tendon arising laterally from the basal margin of the mandible	abductor of mandible, antagonist of 0md1
M. hypopharyngomandibularis	0md4	distal tip of the linguacutal apodeme of the hypopharynx	antero-lateral inner mandibular wall	protractor of anatomical mouth opening, antagonist of 0hy1
M. tentoriomandibularis lateralis superior	0md5	absent		
M. tentoriomandibularis lateralis inferior	0md6	posterior side of anterior tentorial arm, directly before the anterior tentorial bridge	proximo-mesally on the posterior inner mandibular wall	supporting 0md1 in adduction of mandible, might also act as proprioceptor for opening of mandible
M. tentoriomandibularis medialis superior	0md7	absent		
M. tentoriomandibularis medialis inferior	0md8	absent		
M. craniocardinalis	0mx1	in two bundles: bundle 1 on lateral postgena, directly laterally of postgenal bundle of 0md1, bundle 2 on lateral vertex, directly laterally of bundles of 0md1 and posteriorly of compound eye	with a long tendon on distal tip of cardinal tendon	promotor of maxilla, adductor of cardo, thus promoting stipes
M. craniolacinalis	0mx2	lateral vertex, in between bundles of 0md1, directly antero-mesally of origin of bundle 2 of 0mx1	anterior lacinal margin, together with 0mx6	adductor of lacinia
M. tentoriocardinalis	0mx3	lateral areas of anterior tentorial bridge	along entire posterior inner wall of cardo, on both sides of cardinal ridge	adductor of cardo and protractor of maxilla
M. tentoriostipitalis anterior	0mx4	mesal areas of anterior tentorial bridge including mesal ridge, one bundle on lateral side of corpotentorium	along entire mesostipes and mesal wall of inner stipital ridge	adductor of maxilla

Table 1 continued.

Muscle name	Abb.	Origin	Insertion	Presumed function
M. tentoriostipitalis posterior	0mx5	anterior area of anterior tentorial bridge, in between 0mx3 and 0mx4	dorsal inner stipital wall, close to stipito-cardinal ridge, in between distal parts of 0mx6	adductor of stipes and protractor of maxilla
M. stipitoclacialis	0mx6	with two bundles on lateral inner wall of stipes and one bundle on postero-mesal inner wall	anterior lacinial margin, together with 0mx2	adductor of lacinia, supports 0mx2
M. stipitogalealis	0mx7	dorsal inner stipital wall, directly ventrally of insertion of 0mx5	baso-lateral distogalea	abductor of galea
M. stipitopalpalis externus	0mx8	dorsally on lateral wall of inner stipital ridge	dorsally on maxillary palpomere I	abductor of maxillary palp
M. stipitopalpalis medialis	0mx9	lateral wall of inner stipital ridge, ventrally of 0mx8	anteriorly on maxillary palpomere I	adductor or flexor of maxillary palp
M. stipitopalpalis internus	0mx10	ventral lateral wall of inner stipital ridge, ventrally of 0mx9	ventrally on maxillary palpomere I	adductor of maxillary palp
M. stipitalis transversalis	0mx11	outer stipital wall, close to stipitocardinal border	stipital ridge	a very delicate structure
M. palpopalpalis maxillae primus	0mx12	basally on anterior wall of maxillary palpomere I	meso-basally on maxillary palpomere II	adductor of maxillary palpomere II
M. palpopalpalis maxillae secundus	0mx13	basally on anterior wall of maxillary palpomere I, ventrally of 0mx12	latero-basally on maxillary palpomere III	abductor of maxillary palpomere III
M. palpopalpalis maxillae tertius	0mx14	basally on anterior wall of maxillary palpomere III	meso-basally on maxillary palpomere IV	adductor of maxillary palpomere IV
M. palpopalpalis maxillae quartus	0mx15	basally on anterior wall of maxillary palpomere IV	internal apodeme of maxillary palpomere V	adductor of maxillary palpomere V
M. postoccipitoglossalis medialis	0la1	absent		
M. postoccipitoglossalis lateralis	0la2	absent		
M. postoccipitoparaglossalis	0la3	absent		
M. postoccipitopraementalis	0la4	absent		
M. tentoriopraementalis	0la5	mesally on anterior part of trabeculae tentorii	laterally on basal praementum	retractor of praementum
M. tentorioparaglossalis	0la6	anterior part of trabeculae tentorii, directly laterally of 0la5	anteriorly on praementum, in between labial palp and paraglossa	retractor of praementum
M. tentorioglandularis	0la7	absent		
M. submentopraementalis	0la8	mesally on submentum	meso-basally on praementum	retractor of praementum
M. postmentomembranus	0la9	absent		
M. submentomentalis	0la10	absent		
M. praementoparaglossalis	0la11	on inner praemental wall, dorso-laterally of end of praemental cleft, directly dorsally of 0la12	on baso-mesal edge of paraglossa	adductor of paraglossa
M. praementoglossalis	0la12	on inner praemental wall, slightly laterally of end of praemental cleft, directly ventrally of 0la11	on baso-mesal edge of glossa	adductor of glossa
M. praementopalpalis internus	0la13	inner wall of praemental cleft, near end of cleft	ventral basal margin of labial palpomere I	adductor of labial palpomere I
M. praementopalpalis externus	0la14	antero-lateral part of base of praementum	dorsal basal margin of labial palpomere I	adductor of labial palpomere I
M. praementomembranus	0la15	absent		
M. palpopalpalis labii primus	0la16	antero-lateral part of base of praementum, directly ventrally of 0la14	lateral basal margin of labial palpomere II	adductor of labial palpomere II
M. palpopalpalis labii secundus	0la17	meso-basal wall of labial palpomere II	in 2 bundles, the one mesally and the other laterally on basal edge of labial palpomere III	adductor of labial palpomere III
M. frontooralis	0hy1	frons, directly laterally of 0lb1	distal tip of oral arm of hypopharynx	retractor of anatomical mouth opening, antagonist of 0md4
M. tentoriooralis	0hy2	subgena, in middle between antennal base and anterior mandibular articulation	laterally on oral arm of hypopharynx, slightly proximally of insertion of 0hy1	dilator of anatomical mouth opening, antagonist of 0hy9
M. tentoriohypopharyngealis	0hy3	anterior part of trabeculae tentorii, directly laterally of 0la6	dorsal side of basal hypopharyngeal apodeme	retractor of opening of salivary duct, antagonist of 0hy7
M. postoccipitalohypopharyngealis	0hy4	absent		
M. tentoriosuspensorialis	0hy5	oesotendons, together with 0bu5 and 0bu6	mesally on hypopharyngeal membrane, slightly ventrally of anatomical mouth opening	dilator of cibarium

Table 1 continued.

Muscle name	Abb.	Origin	Insertion	Presumed function
M. postmentoloralis	Ohy6	absent		
M. prementosalvarialis anterior	Ohy7	posterior wall of prementum, mesally of articulation of labial palpus	proximally on ventral side of basal hypopharyngeal apodeme	protractor of opening of salivary duct, antagonist of Ohy3
M. prementosalvarialis posterior	Ohy8	antero-lateral wall of base of prementum, slightly mesally of O1a 14	distally on ventral side of basal hypopharyngeal apodeme	dilator of opening of salivary duct
M. oralis transversalis	Ohy9	oral arm	oral arm of opposite side, fibres running on both sides of pharynx	contractor of anatomical mouth opening, antagonist of Ohy2 and Obu 1
M. loroloralis	Ohy10	mesal wall of lateral („basitendinal“) hypopharyngeal sclerite	mesal wall of lateral hypopharyngeal sclerite of opposite side	unclear
M. lorosalvarialis	Ohy11	absent		
M. hypopharyngosalvarialis	Ohy12	anteriorly on oral sclerite of hypopharyngeal suspensorium	with several bundles across entire membranous posterior wall of hypopharynx	dilator of salivarium
M. anularis salivarii	Ohy13	absent		
M. tentoriofrontalis posterior	Ote1	absent		
M. tentoriofrontalis anterior	Ote2	absent		
M. tentoriofrontalis dorsalis	Ote3	absent		
M. posterotentorialis	Ote4	absent		
M. tentorientoralis longis	Ote5	absent		
M. tentorientoralis brevis	Ote6	absent		
M. clypeopalatalis	Oci1	slightly laterally of midline of clypeus	on epipharynx, immediately in front of anatomical mouth opening	dilator of cibarium
M. clypeobuccalis	Obu 1	on clypeus, directly dorsally of Oci1	on anterior pharynx, behind anatomical mouth opening, in between bundles of Ohy9	dilator of anterior pharynx, antagonist of Ohy9
M. frontobuccalis anterior	Obu2	mesally on frons	anterior surface of pharynx, directly dorsally of frontal connective	dilator of pharynx, antagonist of Ost1
M. frontobuccalis posterior	Obu3	mesally on frons, directly dorsally of origin of Ob1	anterior surface of pharynx, dorsally of insertion of Obu2, ventrally of brain	dilator of pharynx, antagonist of Ost1
M. tentoriobuccalis lateralis posterior	Obu4	dorsal tentorial arm	lateral pharyngeal wall, directly dorsally of circum-oesophageal connective	dilator of pharynx, antagonist of Ost1
M. tentoriobuccalis anterior	Obu5			
M. tentoriobuccalis posterior	Obu6	oesotendons, together with Ohy5	along posterior wall of pharynx, slightly ventrally of insertion of Obu2	dilator of pharynx, antagonist of Ost1
M. tentoriobuccalis lateralis anterior	Obu7	subgena, in middle between antennal base and anterior mandibular articulation, directly dorsally of Ohy2	lateral pharyngeal wall, directly dorsally of insertion of Ohy2	dilator of pharynx, antagonist of Ost1
M. verticopharyngealis	Oph1	in two bundles on vertex, in between bundles of Omd1	two bundles on anterior surface of pharynx, first bundle on same level as insertion of Obu4, directly dorsally of brain, second bundle further dorsally	dilator of pharynx, antagonist of Ost1
M. tentoriopharyngealis	Oph2	ventro-anterior margin of posterior tentorial arms and corporotentorium	posterior wall of pharynx, same level of insertion of Oph1	dilator of pharynx, antagonist of Ost1
M. postoccipitopharyngealis	Oph3	on postoccipital ridge on lateral side of occipital foramen	broadly along lateral pharyngeal wall, from the insertion of the dorsal bundle of Oph1 to the point where the pharynx leaves the head capsule	dilator of pharynx, antagonist of Ost1
M. annularis stomodaei	Ost1	ring muscle layer around pharynx, ends where the pharynx leaves the head capsule		constrictor of pharynx, antagonist to pharyngeal dilators
M. longitudinalis stomodaei	Ost2	longitudinal muscles along pharynx, ends where the pharynx leaves the head capsule		contractor of pharynx

arises from it; no vestige of a median ocellar nerve was found. The antennal nerves (ann, Fig. 4) and the optical lobes are strongly developed. The frontal connectives (frc, Figs. 4, 5) originate from the anterior side of the circumoesophageal connectives and turn ventro-anteriorly around the pharynx to join the frontal ganglion placed on the anterior side of the pharynx (fg, Figs. 4, 5). The unpaired nervus recurrens (ner, Figs. 4, 5) runs from the frontal ganglion dorsally along the anterior side of the pharynx. It passes beneath the supraoesophageal ganglion and joins the corpora allata (coa, Fig. 5). The supraoesophageal ganglion is connected with the suboesophageal ganglion (sug, Figs. 4, 5) via massive circumoesophageal connectives. The tritocerebral commissure (not illustrated) runs ventrally around the pharynx. The suboesophageal ganglion is much smaller than the supraoesophageal ganglion.

3.11. Circulatory organs

The aorta (ao, Fig. 5) is a thin tube located on the dorsal side of the pharynx. It ends below the supraoesophageal ganglion. At its end, M. ampulloaortica (0ah2, not illustrated) inserts. The paired antennal ampullae (am, Figs. 5, 7) are attached to the frontal head wall mesally of the antennal base, approximately on the same level as the antennifer. The antennal vessels (av, Fig. 7) extend from the ampulla into the antenna. Along their course in the head capsule they are strongly curled.

4. Discussion

4.1. Comparison with previous studies

In general, our description provided herein is in most points congruent with previous studies. The main differences will be discussed in the following.

Head posture. In several articles the head position of *Periplaneta* and other cockroaches is described as being hypognathous (POPHAM 1961; WIPFLER et al. 2011). Cockroaches have a highly moveable head which can be bent under the prothorax. Living individuals of *Periplaneta* hold their heads most of the time in a position where the mouthparts point directly downward (orthognathy) (SNODGRASS 1944; pers. obs.) and the antennae forward. We thus consider this as the typical head orientation. The overall proportions of the head also agree with the orthognathous condition rather than with the hypognathous one. However, after their death, the head often takes a backward position, which might have caused most previous authors to consider the head posture in this species as being hypognathous.

Cephalic ridges. *Periplaneta americana* shows sexual dimorphism in its head morphology. In females the com-

pound eyes end on the level of the ventral end of the antennal base; the circumocular and subgenal ridges are thus far apart from each other, and the subantennal ridge connecting them is long and distinct. In males, the compound eyes are bigger and reach far ventrally, whereby the circumocular ridge is in close contact with the subgenal ridge and a subantennal ridge is absent (likely fused with the circumocular ridge, see KLASS & EULITZ 2007). KLASS & EULITZ (2007) based their study on dictyopteran head ridges (“sulci” therein) mostly on male specimens and also illustrated their state in male *Periplaneta americana*. Regarding other Blattidae studied therein, *Shelfordella lateralis* (only a female examined) shows a similar condition as females of *Periplaneta americana*, though with the eyes somewhat smaller, whereas *Eurycotis floridana* males show much smaller eyes than female *Periplaneta americana* and *Shelfordella lateralis*. The differences in the Blattidae are thus related to both interspecific variation and sexual dimorphism. The complex morphological correlations between compound eye size and the outline of the circumantennal ridge and the circumocular, subantennal, and subgenal ridges are discussed in KLASS & EULITZ (2007). SNODGRASS (1960) apparently studied a female of *Periplaneta americana*.

Several authors including KLASS & EULITZ (2007) described short lateral vestiges of the epistomal ridge in *Periplaneta*. However, statements on whether lateral parts of the epistomal ridge are absent or present depend on the definition of the border between the epistomal and subgenal ridges. KLASS & EULITZ (2007) define this border as being directly above the anterior mandibular articulation. On this basis, *Periplaneta* has short lateral parts of the epistomal ridge. SEIFERT (1995) and WIPFLER et al. (2012) define the mesal end of the anterior tentorial pit as the border. According to this definition, *Periplaneta* has no epistomal ridge. Both definitions are obviously problematic in some respect and cannot be reasonably applied to all insects. In the present contribution, we thus follow GRIMALDI & ENGEL (2005) by subsuming the epistomal ridge and subgenal ridge as costa. On this basis, the part of the costa in between the anterior tentorial pits is absent – with consensus across the literature. *Periplaneta* has lower mandibular biting strength and a comparatively smaller M. craniomandibularis internus (Omd1) than other studied insects (WEIHMANN et al. 2015a). It is likely that it thus requires less structural integrity between the anterior mandibular articulations, which led to the loss of this part of the ridge. Another reason could be the far anteriorly located transverse stabilization of the left and right halves of the head by the additional anterior tentorial bridge; however, this is also present in Mantodea, which have a well-developed epistomal part of the costa (KLASS & EULITZ 2007).

Mandibles. A slight asymmetry in the structure of the left and right mandibles is confirmed for *Periplaneta americana*. However, for the left mandible ZHUZHNIKOV (2007) describes a second small tooth, which was not found in the present study. Possibly some specimens have two small teeth while others have only one.

Hypopharynx. The hypopharynx of *Periplaneta americana* was described in detail by BUDER & KLASS (2013). Both descriptions are mostly congruent. However, herein we describe short sclerite ribbons extending ventromesally along the posterior base of the hypopharynx (SBH, Fig. 17), which are synsclerotic with the lateral and ventral lingual sclerite. BUDER & KLASS (2013) found only a pair of tiny isolated sclerites near the opening of the salivary duct, representing vestiges of median parts of the SBH clips. However, we cannot exclude that there is intraspecific variability in this character. For several other Blattodea they reported similar conditions as observed here in *Periplaneta*, with a connection to the lingual sclerites and a gap at midline.

Head muscles. Some differences to previous descriptions were also found in the musculature (see Table 2). DORSEY (1943) only addresses selected muscle systems but information for the antenna, the mandible and the maxilla is missing. Additionally some muscles of the foregut such as *M. verticopharyngealis* (Oph1) were not described. WIPFLER et al. (2011) provided a list with muscles present in *Periplaneta* but no details on their origin and insertion. The present findings contradict that study in several points: *M. tentoriomandibularis medialis inferior* (Omd8) and *M. tentoriofrontalis anterior* (Ote2) were reported as present by WIPFLER et al. (2011) but are found absent in the present study, while for *M. loroloralis* (Ohy10), *M. tentoriobuccalis lateralis anterior* (Obu4) and *M. stipitopalpalis medianus* (Omx9) the situation is contrariwise. Our re-evaluation of the CT-scan studied by WIPFLER et al. (2011) revealed that *M. tentoriomandibularis medialis inferior* (Omd8) and *M. tentoriofrontalis anterior* (Ote2) are indeed absent, whereas *M. tentoriobuccalis lateralis anterior* (Obu4) is present. *M. loroloralis* (Ohy10) is an extremely small muscle which is hard to find. It is therefore possible that previous authors overlooked it. *M. stipitopalpalis medianus* (Omx9) is absent in both the left and the right maxilla of the specimen studied by WIPFLER et al. (2011) but present in the specimen studied here. Apparently there are individuals which have three extrinsic muscles of the maxillary palp while others have only two.

4.2. Phylogenetic implications

In the context of our current insights for *Periplaneta americana*, the following studies on other blattodean species permit consideration of some phylogenetic implications: YUASA (1920), SNODGRASS (1935), STRENGER (1942) and PRADL (1971) studied the head capsule of *Blatta orientalis* (Linnaeus, 1758); SNODGRASS (1943, 1944) and PRADL (1971) the one of *Blattella germanica* (Linnaeus, 1758); and PRADL (1971) the one of *Blaberus giganteus* (Linnaeus, 1758). VISHNOI (1956, 1962) gave a detailed description of the head of the termite *Odontotermes obesus*. WALKER (1933) studied the exterior head capsule of *Termopsis angusticollis*. Additionally HUDSON (1945), KLASS & EULITZ (2007), BUDER & KLASS (2013), and ZHU-

ZHIKOV (2007) provided information about the anterior head ridges, tentorium, hypopharynx, and mouthparts of various blattodean species.

In general the blattodean head is characterized by several plesiomorphies such as the lateral position of the compound eyes, biting mouthparts, 5-segmented maxillary palps, 3-segmented labial palps, and long antennae. However, the blattodean head also shows several apomorphies. The most striking is the loss of the median ocellus. This loss under retention of only the lateral ocelli has, for example, also occurred in some species of the dipteran group Mycetophilidae (SÖLI 1996) but not in any other lower neopteran group (e.g. YUASA 1920). We found the loss of this ocellus to be accompanied by the loss of the associated ocellar nerve, showing that the plesiomorphic pathway of light perception has been lost (which would not necessarily be the case with the absence of the cuticular differentiation of an ocellus). Other potential apomorphies of Blattodea corroborated by the present study are the bipartite state of *M. verticopharyngealis* (Oph1) and of *M. hypopharyngosalivaris* (Ohy12) (WIPFLER 2012). Another potentially derived character is the presence of oesotendons. They are cuticular tendons of the corpotentorium which serve as attachment structures for *M. tentoriosuspensorialis* (Ohy5) and *M. tentoriobuccalis* (Obu5+6). KLASS & EULITZ (2007) report oesotendons for all studied cockroaches with the exception of *Cryptocercus* and *Mastotermes*. In these two taxa the “perforation” of the tentorium is comparatively small, which might correlate with a reduction of the tendons. LO et al. (2007) provided the only study which places these two taxa jointly as sister group to the remaining dictyopterans, thus challenging the monophyly of Blattodea. All other studies on blattodean phylogeny consider *Cryptocercus* and *Mastotermes* as nested deeply within monophyletic Blattodea. Structures similar to oesotendons also seem to occur in the silverfish *Thermobia* (CHAUDONNET 1950) and the caeliferan *Acridella* (HUDSON 1945), which caused KLASS & EULITZ (2007) to assume that their presence in Blattodea might be plesiomorphic and their absence in Mantodea apomorphic. However, oesotendons are neither described in most polyneopteran groups (e.g. Phasmatodea: FRIEDEMANN et al. 2012; Plecoptera: HOKE 1924), nor in Palaeoptera (BLANKE et al. 2012, 2013) or the relic silverfish *Tricholepidion* (BLANKE et al. 2014). It may appear more likely that they evolved independently several times and are apomorphic for Blattodea. Twisted anterior tentorial arms are likewise observed in all studied cockroaches (KLASS & EULITZ 2007) but also in various other polyneopteran groups such as Dermaptera (KAMP 1973; GILES 1963) or Plecoptera (HOKE 1924; MOULINS 1968). In the latter this character is highly variable (HOKE 1924). Even though twisted arms are not reported in Mantodea (LEVEREAULT 1936; KLASS & EULITZ 2007; WIPFLER et al. 2012) it is difficult to polarize this character for Blattodea due to the unclear relationships among the lower neopteran insects (see BEUTEL et al. 2014b for a review). WIPFLER et al. (2012) proposed the absence of *M. tentoriobuccalis lateralis anterior* (Obu4)

Table 2. Presumed homologies of the cephalic muscles of *Periplaneta americana* with muscles reported in other studies. — **Abbreviations:** +: muscle present, -: muscle absent, /: muscle not studied, ?: unclear homology, *: apparently present in some individuals while absent in others (see Discussion).

Muscle name	Abbreviation	<i>Periplaneta americana</i> (present study)	<i>Periplaneta americana</i> (WIPFLER et al. 2011)	<i>Periplaneta americana</i> (DORSEY 1943)	<i>Blattella germanica</i> (SNODGRASS 1943, 1944)	<i>Odontotermes obesus</i> (VISHNOI 1956, 1962)	<i>Hymenopus coronatus</i> (WIPFLER et al. 2012)	<i>Stagmomantis carolina</i> (LEVEREAULT 1938)	<i>Mantis religiosa</i> (CARBONARO 1949)
M. tentorioscapalis anterior	0an1	+	+	/	–	3	1	5	35
M. tentorioscapalis posterior	0an2	+	+	/	–	4	2	4	36
M. tentorioscapalis lateralis	0an3	+	+	/	–	–	3	6	37
M. tentorioscapalis medialis	0an4	–	–	/	–	3	–	–	–
M. frontopedicellaris	0an5	–	–	/	–	–	–	–	–
M. scapopedicellaris lateralis	0an6	+	+	/	–	5	5	7	38+39
M. scapopedicellaris medialis	0an7	+	+	/	–	6	6	8	40
M. intraflagellaris	0an8	–	–	–	–	–	–	–	–
M. interampullaris	0ah1	+	+	/	/	/	–	/	/
M. ampulloaortica	0ah2	+	+	/	/	/	–	/	/
M. ampulloparyngealis	0ah3	–	–	/	/	/	–	/	/
M. ampullofrontalis	0ah4	–	–	/	/	/	–	/	/
M. frontoparyngealis	0ah5	–	–	/	/	/	–	/	/
M. frontolabralis	0lb1	+	+	4	3	1	8	2	1
M. frontoepipharyngealis	0lb2	+	+	3	4	2	9	3	2
M. epistoeipharyngealis	0lb3	–	–	–	–	–	–	–	–
M. labralis transversalis	0lb4	+	+	2	–	–	?	–	–
M. labroepipharyngealis	0lb5	+	+	1	+	–	7	1	3
M. labrolabralis	0lb6	–	–	–	–	–	–	–	–
M. craniomandibularis internus	0md1	+	+	/	28	8	11	19	4
M. craniomandibularis externus anterior	0md2	–	–	/	–	–	–	–	–
M. craniomandibularis externus posterior	0md3	+	+	/	27	7	12	20	5
M. hypopharyngomandibularis	0md4	+	+	14	29	9	13	22	6
M. tentoriomandibularis lateralis superior	0md5	–	–	/	–	–	–	–	–
M. tentoriomandibularis lateralis inferior	0md6	+	+	/	30	10	14a	21	7
M. tentoriomandibularis medialis superior	0md7	–	–	/	–	–	–	–	–
M. tentoriomandibularis medialis inferior	0md8	–	+	/	–	–	14b	–	–
M. craniocardinalis	0mx1	+	+	/	31	11	15	23	8
M. craniolacinalis	0mx2	+	+	/	32	14	19	26c	12
M. tentoriocardinalis	0mx3	+	+	/	33	12	17	24+25	9+10
M. tentoriostipitalis anterior	0mx4	+	+	/	34	13a–c	18	27+28	11
M. tentoriostipitalis posterior	0mx5	+	+	/	33?	13d	18	25	?
M. stipitolacinalis	0mx6	+	+	/	41	15	20	26a,b	13
M. stipitogalealis	0mx7	+	+	/	42	16	21	37	14
M. stipitopalpalis externus	0mx8	+	+	/	–	18	22a	30	16
M. stipitopalpalis medialis	0mx9	+	–*	/	–	–	22b	31	16
M. stipitopalpalis internus	0mx10	+	+	/	–	17	23	29	15
M. stipitalis transversalis	0mx11	–	+	/	–	–	+	–	–
M. palpopalpalis maxillae primus	0mx12	+	+	/	–	19	24	32+33	17
M. palpopalpalis maxillae secundus	0mx13	+	+	/	–	20	25	34	18
M. palpopalpalis maxillae tertius	0mx14	+	+	/	–	21	26	35	19
M. palpopalpalis maxillae quartus	0mx15	+	+	/	–	22	27	36	20
M. postoccipitoglossalis medialis	0la1	–	–	–	–	–	–	–	–
M. postoccipitoglossalis lateralis	0la2	–	–	–	–	–	–	–	–
M. postoccipitoparaglossalis	0la3	–	–	–	–	–	–	–	–
M. postoccipitopraementalis	0la4	–	–	–	–	–	–	–	–
M. tentoriopraementalis	0la5	+	+	21	44	23	29	39	23
M. tentorioparaglossalis	0la6	+	+	20	43	–	30	38	22
M. tentorioglandularis	0la7	–	–	–	–	–	–	–	–
M. submentopraementalis	0la8	+	+	22	45	24	28	44	21
M. postmentomembranus	0la9	–	–	–	–	–	–	–	–

Table 2 continued.

Muscle name	Abbreviation	<i>Periplaneta americana</i> (present study)	<i>Periplaneta americana</i> (WIPELER et al. 2011)	<i>Periplaneta americana</i> (DORSEY 1943)	<i>Blattella germanica</i> (SNODGRASS 1943, 1944)	<i>Odontotermes obesus</i> (VISHNOI 1956, 1962)	<i>Hymenopus coronatus</i> (WIPELER et al. 2012)	<i>Stagmomantis carolina</i> (LEVERAULT 1938)	<i>Mantis religiosa</i> (CARONARO 1949)
M. submentomentalis	Ola10	–	–	–	–	–	–	–	–
M. praementoparaglossalis	Ola11	+	+	29	+	26	31	49	28
M. praementoglossalis	Ola12	+	+	28	+	25	32	50	29
M. praementopalpalis internus	Ola13	+	+	23	+	28	33	46	30
M. praementopalpalis externus	Ola14	+	+	24	+	27	34	45	31
M. praementomembranus	Ola15	–	–	–	–	–	–	–	–
M. palpopalpalis labii primus	Ola16	+	+	25	+	29	35	47	32
M. palpopalpalis labii secundus	Ola17	+	+	26+27	+	30	36	48	33+34
M. frontooralis	Ohy1	+	+	10	13	45	41	11	45
M. tentoriooralis	Ohy2	+	+	31	14	46	47	12	47
M. tentoriohypopharyngealis	Ohy3	+	+	19	16	31	42	43	24
M. postoccipitalohypopharyngealis	Ohy4	–	–	–	–	–	–	–	–
M. tentoriosuspensorialis	Ohy5	+	+	–	+	–	M c.	15?	49
M. postmentoloralis	Ohy6	–	–	–	–	–	–	–	–
M. praementosalivialis anterior	Ohy7	+	+	17	19	34	38	41	26
M. praementosalivialis posterior	Ohy8	+	+	18	20	35	39	40	25
M. oralis transversalis	Ohy9	+	+	12+13?	–	40	67	–	–
M. loroloralis	Ohy10	+	–	–	–	–	M b.	–	–
M. lorosalivialis	Ohy11	–	–	–	–	–	–	–	–
M. hypopharyngosalivialis	Ohy12	+	+	15+16	17+18	32+33	37	42	27
M. anularis salivarii	Ohy13	–	–	–	–	–	?	–	–
M. tentoriofrontalis posterior	Ote1	–	–	–	–	–	–	–	–
M. tentoriofrontalis anterior	Ote2	–	+	–	–	–	–	–	–
M. tentoriofrontalis dorsalis	Ote3	–	–	–	–	–	–	–	–
M. posterotentorialis	Ote4	–	–	–	–	–	–	–	–
M. tentoritentorialis longis	Ote5	–	–	–	–	–	–	–	–
M. tentoritentorialis brevis	Ote6	–	–	–	–	–	–	–	–
M. clypeopalatalis	Oci1	+	+	5–8	5a	36+37	43	9	42+43
M. clypeobuccalis	Obu1	+	+	–	5b?	41	–	–	–
M. frontobuccalis anterior	Obu2	+	+	9	6	42	45	10	44
M. frontobuccalis posterior	Obu3	+	+	11	7	43	46	13	46
M. tentoriobuccalis lateralis posterior	Obu4	+	–	–	–	–	–	–	–
M. tentoriobuccalis anterior	Obu5	+	+	30	+	38	48	16	50
M. tentoriobuccalis posterior	Obu6	+	+	30	+	48+49	50	17	51
M. tentoriobuccalis lateralis anterior	Obu7	+	–	–	–	–	–	–	–
M. verticopharyngealis	Oph1	+	+	–	8	44+47	51	14	48
M. tentoriopharyngealis	Oph2	+	+	–	+	50+51	52a	18	52
M. postoccipitopharyngealis	Oph3	+	+	–	11	–	52b	–	–
M. annularis stomodaei	Ost1	+	+	12+13	–	–	68	–	41
M. longitudinalis stomodaei	Ost2	+	+	–	–	–	69	–	–

as a potential apomorphy for Blattodea as it was not described in any previous work about cockroaches or termites. The present study clearly rejects this argument as this muscle is present in *Periplaneta americana* (Table 2 provides an attempt to homologize the musculature described for Dictyoptera). Whether its absence is an apomorphy of termites or any other blattodean lineage has to be clarified by future studies.

We report the presence of a M. loroloralis (Ohy10) which contains fibers. It is also described for the embio-

pteran *Embia* (RÄHLE 1970), the zygentomans *Thermobia* (CHAUDONNET 1950) and *Tricholepidion* (BLANKE et al. 2014), Phasmatodea (MARQUARDT 1940; FRIEDEMANN et al. 2012), and Ephemeroptera (STANICZEK 2001). However, in Phasmatodea, *Embia* and *Thermobia* this muscle interconnects the loral arms of the hypopharynx rather than the lateral hypopharyngeal sclerites and lacks transverse striation and innervation. In *Thermobia* it is described as having a large portion of tendinous fibers (CHAUDONNET 1950). MOULINS (1971) reports a similar structure in the

cockroach *Blaberus*, which connects a sclerite very close to but separate from the loral arm. This sclerite is most likely homologous to the lateral hypopharyngeal sclerite (SBT) described here in *Periplaneta*. Whether this distinct sclerite is only present in cockroaches but absent in other groups cannot be answered since detailed studies of the hypopharynx are missing for most lower neopteran groups. If absent in other groups, the lateral hypopharyngeal sclerite (SBT) found in Blattodea may well be a detached part of the loral arm, as indeed suggested by the attachment of *M. loroloralis* (see also discussion of “M14” = *M. loroloralis* in BUDER & KLASS 2013). Another intriguing question is whether or not this muscle has in all groups a high proportion of tendinous fibers or is even a collagenous structure devoid of fibers in some species. Our CT-scans do not allow a more detailed description of its composition in *Periplaneta americana*.

One of the most interesting structures observed in the head of *Periplaneta* is the lacinula, the subapical lobelet(s) on the lacinia. Similar structures have been reported for various cockroaches (ZHUKHIV 2007). The only studied cockroach without a lacinula is *Polyphaga aegyptica* (Polyphagidae) (ZHUKHIV 2007). ZHUKHIV (2007) described various forms of this structure ranging from a “rigid pigmented process resembling the apical claw” to highly complex ones as observed in *Periplaneta americana*. He divided them into 4 categories which correlate to the clades Cryptocercidae (type I: a rigid process resembling the lacinial teeth), Ectobiidae (type II: 2–3 soft processes in a row), Blattidae (type III: a soft process with distal sclerotized processes) and Blaberidae (type IV: conical bases with sclerotized apical setae). EIDMANN (1923) and CRAMPTON (1923) reported structures similar to those of *Cryptocercus* in Orthoptera and Plecoptera. Additionally CRAMPTON homologized them with a distinct lamella (“midappendix, or modified lacinula”) on the lacinia of apterygote hexapods such as Collembola, Archaeognatha and Zygentoma. BLANKE et al. (2012, 2013, 2014) distinguished between sclerotized dentisetae, which are present in Odonata and Ephemeroptera, and hyaline lamellae in similar position, which are found in Zygentoma (including *Tricholepidion*) and most other apterygote hexapods as well as in Ephemeroptera (in the latter next to sclerotized dentisetae). They thus concluded that the presence of dentisetae is a potential autapomorphy of Palaeoptera. The presence of structurally similar elements in polyneopteran insects requires a reconsideration of this discussion. However, little and preliminary information is currently available and a homology between the dentisetae in Palaeoptera, the hyaline lamellae in apterygotes, and the lacinula in Blattodea cannot be clearly addressed at the moment. Nevertheless it is highly interesting that the lacinula in Blattodea shows a high degree of variability within the group including sclerotized and non-sclerotized forms.

Termites (Isoptera) are the morphologically most derived group within Blattodea. One major difference to the remaining Blattodea is the prognathous head in this group (VISHNOI 1956, 1962; WALKER 1933). Other parts of the

head also differ from cockroaches, such as the labium, which is only bipartite (post- and praementum) compared to the tripartite state in cockroaches (submentum, mentum, praementum). However, as for most cockroaches, little information is available on the termite head and important species for the understanding of the cockroach-termite transition such as *Mastotermes* or *Cryptocercus* have not been studied so far. Thus no precise conclusions can be made at the moment.

A sister group relationship between Blattodea and Mantodea (together: Dictyoptera) is very well supported by various morphological and molecular studies (KLASS 1995, 2003; KJER et al. 2006; ISHIWATA et al. 2011; DJERNÆS et al. 2012, 2015; MISOF et al. 2014; WIPFLER et al. 2015; LEGENDRE et al. 2015). The mantodean head was studied by YUASA (1920), DUPORTE (1946), SNODGRASS (1947), BEIER (1968), LOMBARDO (1984), WALKER (1933), LEVEREAULT (1936) and WIPFLER et al. (2012). In the head area, the present study supports the proposed dictyopteran apomorphies, including a “perforate” tentorium (HUDSON 1945; KLASS & EULITZ 2007), a membranous postmola (WEIDNER 1970), and a lacinia that lies in a cavity of the galea (CRAMPTON 1923). However, the relationships among the polyneopteran lineages, including the question concerning the sister group of Dictyoptera, still remain largely unsolved (see BEUTEL et al. 2014b for a review).

In general the head is far too sporadically studied across Blattodea to derive detailed phylogenetic information from this character system. The present study shows clearly that even for specimens where information is already present, a detailed re-evaluation might be necessary. In the past, characters of the polyneopteran head provided ambivalent phylogenetic signal: the hypopharynx (BUDER & KLASS 2013) and the anterior head ridges (KLASS & EULITZ 2007) contributed little or conflicting phylogenetic signal for Dictyoptera, whereas the antennal heart (WIPFLER & PASS 2014) and analysis of the entire head morphology (e.g. BLANKE et al. 2012, 2013; WIPFLER 2012; MATSUMURA et al. 2015) provided valuable evolutionary and phylogenetic information for our understanding of polyneopteran interrelationships. The present contribution forms a sound basis for further investigations on the blattodean head.

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Electronic Supplement Files

at <http://www.senckenberg.de/arthropod-systematics>
 (“Contents”)

File 1: wipfler&al-periplanetahead-asp2016-electronicsupplement1.pdf — Interactive PDF of the head of *Periplaneta americana*. Click on the image to activate it.

File 2: wipfler&al-periplanetahead-asp2016-electronicsupplement2.pdf — List of used abbreviations in the morphological description and reference to the respective figures.

