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Structural megadiversity in leaf litter predators - the head anatomy of *Pselaphus heisei* (Pselaphinae, Staphylinidae, Coleoptera)

Rolf Georg Beutel[1], Xiao-Zhu Luo[1], Margarita I. Yavorskaya[2], Paweł Jałoszyński[3]

1 *Institut für Zoologie und Evolutionsforschung, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, 07743 Jena, Germany [rolf.beutel@uni-jena.de]*

2 *Universität Tübingen, Institut für Evolution und Ökologie, Auf der Morgenstelle 28E, 72076 Tübingen, Germany*

3 *Museum of Natural History, University of Wrocław, Wrocław, Poland [scydmaenus@yahoo.com]*

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Corresponding author: Margarita I. Yavorskaya (margarita.yavorskaya@uni-tuebingen.de)

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Abstract

The head anatomy of *Pselaphus heisei* (Pselaphitae) is described and documented. The structural features are evaluated in comparison with findings presented in earlier studies on the subfamily, with a special focus on correlations with predacious habits and the groundplan of Pselaphinae. We found the tentorium, labrum, maxillary palps, shape of head, and a system of dorsal pits and sulci highly variable within the subfamily, reflecting multiple transformations, including many homoplasious changes. The following major characters are identified as groundplan features of Pselaphinae: falciform mandibles; small mola; semiglobular neck; ventrolateral antennal articulation; steep clypeal region; setiform labial palpomere 3; tentorium with nearly vertical main branches and lacking laminatentoria; separation of tentorial bridge from tentorial arms; fusion of dorsal tentorial arms with the head capsule; large brain placed in the posterior third of the head; and a triple cluster of well-developed cephalic glands. The last feature supports a hypothesis that multiple and independent cases of adaptations to myrmecophilous habits observed in various lineages of Pselaphinae were possible by re-programming already existing glands to produce appeasement secretions. The cephalic muscle apparatus of *P. heisei* is similar to what is found in other staphylinoid groups, with some exceptions, whereas it is strongly modified in the myrmecophile *Claviger testaceus*. We propose that the unparalleled structural megadiversity in Pselaphinae is primarily linked with life in the upper soil layers combined with specialized carnivorous habits, with small and agile or mechanically protected arthropods as prey. Within the group, various specialized life habits have evolved, including myrmecophily, termitophily, and also life in deep soil or caves, each with unique morphological adaptations.

Keywords

Glands, micro-CT, musculature, pselaphine beetles, 3D-reconstruction.

1. Introduction

Pselaphinae, also known as short-winged mold beetles or ant beetles, are a group with small brownish adults, often with a cryptic lifestyle (e.g. Park 1947a; Chandler 2001). Nevertheless, they have attracted a lot of attention among coleopterists, also including numerous amateur collectors and taxonomists. Despite their small size and often obscure existence in soil and leaf litter, they are a very successful subgroup of rove beetles, with over 1,200 genera and more than 10,000 described species (Thayer 2016, with later additions). Based on their unusual morphology, they were previously considered as a separate family of Staphylinoidea (e.g. Latreille 1802; Jeannel 1950; De Marzo and Vovlas 1989; see also Newton and Chandler 1989), but are now assigned subfamily rank within Staphylinidae (e.g. Thayer 2016). Pselaphine beetles play an important ecological role in their microhabitats. Park (1947a) stated that they are not a predominant influence in any specific task or in any given community, but that "despite of this lack of drama" they play an essential role in forest floor litter. Aside from rather unspecialized predacious species of upper soil levels, like for instance *Pselaphus heisei* Herbst, 1792 or species of *Bryaxis* Kugelann, 1794 (Schomann et al. 2008), a remarkable spectrum of specialized life styles has evolved within the group, including myrmecophiles, termitophiles and cave dwelling species (e.g. Besuchet 1991; Hlaváč et al. 1999; Chandler 2001; Parker and Grimaldi 2014; Parker 2016a; Jałoszyński et al. 2021; Luo et al. 2021a, 2021b). Aside from the enormous taxonomic and ecological diversity, Pselaphinae are probably unparalleled in Staphylinoidea (if not in Coleoptera) in the extreme variability of structures and shapes of different body regions, with a plethora of specialized structural modifications unknown in other groups of beetles (e.g. De Marzo and Vovlas 1989; Chandler 2001; Parker 2016a, 2016b; Jałoszyński et al. 2020; Luo et al. 2021a, 2021b).

The external aspects of the structural megadiversity were treated in several substantial contributions, for instance Jeannel (1950), De Marzo and Vovlas (1989), Chandler (2001) and Parker (2016). However, as pointed out in Jałoszyński et al. (2021) and Luo et al. (2021a, 2021b), the presently available information on the anatomy is basically restricted to a study on the highly specialized myrmecophile genus *Claviger* Preyssler, 1790 (Clavigeritae) (Jałoszyński et al. 2020; Luo et al. 2021b), and one on a nearly eyeless species of *Bergrothia* Reitter, 1884 (Batrisitae) (Luo et al. 2021a). The already documented structures provided important insight into some aspects of evolution, especially those related to obligatory myrmecophily or the loss of sight, while some unexpectedly discovered features remain puzzling, like for instance the presence of large cephalic glands in non-myrmecophiles (Luo et al. 2021a). It can be expected that studying internal structures of other tribes will substantially increase chances to clarify the currently poorly understood phylogeny, and also factors that triggered a megaradiation within rove beetles. Consequently, the aim of the present contribution is a detailed documentation of external and internal head structures of a less specialized representative of Pselaphinae. For this purpose, we chose the type genus of the subfamily, *Pselaphus* Herbst, 1792 of the supertribe Pselaphitae, represented by its predacious type species, *Pselaphus heisei*. The genus comprises 79 extant species and has a Holarctic, Oriental, Afrotropical (incl. Madagascar), Southern Pacific (New Zealand) and Caribbean (Jamaica) distribution (Newton and Chandler 1989, and later additions). To investigate and document the cephalic anatomy, we used a combination of well-established and modern morphological techniques, notably scanning electron microscopy (SEM), μ-computed tomography (μ-CT), and computer-based 3D reconstruction. The morphological results are compared with observations made in other pselaphines, especially *Claviger testaceus* Preyssler, 1790 (Jałoszyński et al. 2021) and *Bergrothia saulcyi* (Reitter, 1877) (Luo et al. 2021a), but also other members of the subfamily and species of related groups.

2. Material and methods

2.1. Studied species

Pselaphitae: *Pselaphus heisei*; beetles collected from leaf litter in Turze Pole ad Brzozów, SE Poland, by Dariusz Twardy. Specimens were preserved in 75% ethanol.

2.2. Micro-computed tomography (μ-CT) and microtome sections

Specimens were dehydrated with an ascending series of ethanol (70%–80%–90%–95%–100%), stained in iodine solution, transferred to acetone and then dried at the critical point (Emitech K850, Quorum Technologies Ltd., Ashford, UK). One of the dried specimens was scanned at the MPI for the Science of Human History (Jena, Germany) with a SkyScan 2211 X-ray nanotomograph (Bruker, Knotich, Belgium) with an image spatial resolution of 0.30 μm (isotropic voxel size) using the following parameters: 50 kV, 300 μA, 4600 ms exposure time, 0.16° rotation steps, frame averaging on (2), and using Filter (0.5 mm Ti). Projections were reconstructed by NRecon (Bruker, Knotich, Belgium) into TIFF files. AMIRA 6.1.1 (Thermo Fisher Scientific, Waltham, USA) and VG studio Max 2.0.5 (Volume Graphics, Heidelberg, Germany) were used for the three-dimensional reconstruction and volume rendering. The μ-CT-scan is stored in the collection of the Phyletisches Museum Jena (for access, please contact X.-Zh. Luo).

For microtome sectioning, one specimen of *P. heisei* was embedded in araldite CY 212® (Agar Scientific, Stansted/Essex, UK). Sections were cut at 1 μm intervals using a microtome HM 360 (Microm, Walldorf, Germany) equipped with a diamond knife, and stained with tolu-

idine blue and pyronin G (Waldeck GmbH and Co.KG/ Division Chroma, Münster, Germany). The sections are stored in the collection of the Phyletisches Museum.

2.3. Scanning electron microscopy

Specimens were cleared in a warm 10% aqueous solution of KOH for 20–60 min, thoroughly washed in distilled water and dissected; isolated body parts were transferred from 75% to 99% ethanol for 15 min and air-dried, mounted on SEM stubs with carbon tabs and examined uncoated using a Helios Nanolab 450HP scanning electron microscope (FEI, Hillsboro, USA). Images were processed using CorelDraw Graphic Suite 2017; the following adjustments were made: overall brightness and contrast enhanced, and background manually replaced with black.

2.4. Terminology

The nomenclature of v. Kéler (1963) for cephalic muscles was used. Designations introduced by Wipfler et al. (2011) for the entire Neoptera are added in parentheses, for example M7-M. labroepipharyngalis (0lb5).

3. Results

3.1. External head structures

The distinctly prognathous head (Figs 1, 2A, C) is about 0.5 mm long, and the maximum width at the ocular region is ca. 0.3 mm; it is divided into three well-defined regions: (1) a distinctly developed anterior frontal rostrum (fr; Fig. 1A) (ca. 0.13 mm) bearing the antennae and mouthparts (Figs 3A, B, 4A–C); (2) a widened middle area with the laterally placed semiglobular compound eyes (ce; Figs 1A–C, 2A, C, 5A–E, G, 6A, B, 7A–F, 8B–C) and an evenly narrowing postocular region; and (3) a nearly hemispherical neck. The neck region (nr, Figs 1B–C, 2C, 5A, C, E, G) is distinctly retracted into the prothorax, especially on the dorsal side, and demarcated from the anterior portion of the head by a distinct occipital constriction (occ; Fig. 1A). The median region is flattened, with the highest elevation between and behind the compound eyes; the dorsal surface of the anterior region in front of the eyes is distinctly lower than the postocular area. The coloration of the cuticle is brown; it is smooth on most areas of the head capsule, but displays an irregular pattern of meshes separated by narrow, low cuticular ridges on the lateral and ventral areas of the rostrum; a vestiture of long, rather widely spaced setae (ca. 70–100 µm long) is present but mostly confined to the dorsal and lateral areas; median furrows (mf; Figs 1A, 5A) on the anterior and posterior frontal areas, and also the entire neck region are glabrous. No vestiges of dorsal ecdysial sutures are present; the areas of the posterior frons, vertex (vt; Figs 1A, 5A) and genae (ge; Figs 1C, 5E) are completely confluent; an external division between the clypeus (cl; Fig. 5A) and the anterior frontal region is present; this low clypeofrontal ridge (cfr; Fig. 5A) is clearly visible in dorsal view. The well-developed, raspberry-shaped compound eyes are strongly protruding laterally; each is composed of 24 large ommatidia with strongly convex cornea lenses (diameter ca. 20 µm); setae or microtrichia between the lenses are absent; a row of four widely spaced setae is present posteroventrad the slightly emarginated posteroventral margin of the compound eyes; a group of similar setae is inserted in a supraocular groove, and two setae in a smaller concavity above them.

Ocelli are absent. The frontal region is strongly differentiated; widely spaced long and curved setae are inserted on different areas, except for the smooth and glabrous median furrows. The posterior frontal part between the compound eyes is medially divided by a deep furrow, ca. 20 µm wide anteriorly, narrowing posteriorly, and obliterating at the level of the posterior ocular margins; the posterior frontal portion is demarcated from the frontal roof of the rostrum by a deep semicircular emargination, which contains the large openings (diameter ca. 30 µm) of deep frontal pouches (fp; Figs 1A, 5A, 6A) reaching towards the compound eyes; a very dense circle of basally slightly flattened setae secludes the lumen of the pouches, which is filled with very homogenous, unrecognizable substrate, from the outside world. The rostrum formed by the anterior frontal region and the clypeus is dorsomedially divided by a broad furrow (ca. 30 µm), delimited by a very distinctly defined edge, sub-parallel anteriorly, but strongly widening posteriorly towards the lateral margin of the opening of the frontal pouches. Two large frontoclypeal supraantennal lobes (fcl; Figs 1A, 3A, 5A) (ca. 70 µm long and wide) form the anterior part of the frontoclypeal rostrum; they are evenly rounded laterally and anteriorly, and medially separated by a deep (ca. 35 µm), roughly triangular incision; widely spaced long setae are present on the dorsal and ventral side; the dorsal surface is smooth, whereas the lateral and ventral areas display a pattern of roughly pentagonal meshes with raised margins; the large antennal fossae are located on the ventral side of the lobes; a triangular distal clypeal area arises narrowly below the median incision and widens evenly towards the apical clypeal margin; this distinctly delimited flat triangular area and the ventral surface of the supra-antennal lobes have a reticulate surface sculpture; one pair of long setae is inserted on the middle region of the vertical clypeal part and three pairs very close to the apical margin.

The ventral side of the neck region (nr; Figs 1B, 2C, 5C) has a smooth surface on its lateral and anterior areas; a large median region with a reticulate surface structure represents the posterior gula; it is enclosed by indistinct, curved longitudinal furrows, the vestigial gular sutures (gs; Figs 1B, 2C). An extensive ventral region between the occipital constriction and the posterior tentorial pits, the anterior gular portion, is confluent with the adjacent ventrolateral genal areas; the entire region including the

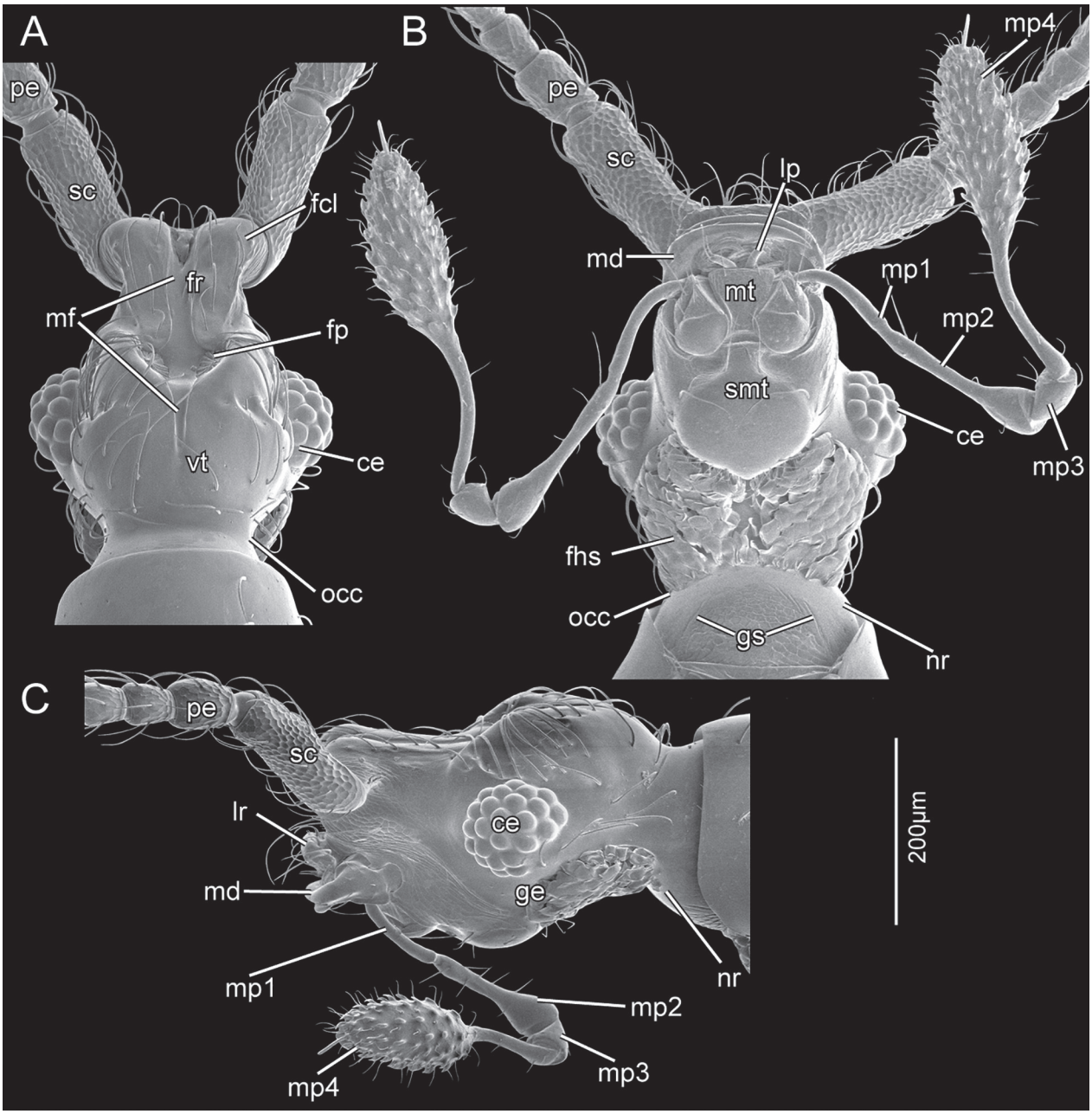

Figure 1. SEM images, head of *Pselaphus heisei*. (**A**) dorsal view; (**B**) ventral view; (**C**) lateral view. Abbreviations: ce, compound eye; fcl, frontoclypeal lobe; fhs, flattened hyaline setae; fp, frontal pouch; fr, frons; ge, gena; gs, gular sutures; lp, labial palp; lr, labrum; md, mandible; mf, median furrow; mp1–4, maxillary palpomere 1–4; mt, mentum; nr, neck region; occ, occipital constriction; pe, pedicellus; sc, scapus; smt, submentum; vt, vertex.

large and medially separated posterior tentorial pits (ptp; Fig. 6B) is covered with flattened hyaline setae (fhs; Fig. 1B), with the socket of each accompanied by a tiny glandular pore (gp; Fig. 2D, hyalinous seta removed, pore shown in close up). A fairly large and roughly circular portion of the ventral wall of the head, anterior to the posterior tentorial pit, is elevated and has a smooth surface (width ca. 0.14 mm); it is of submental origin, but laterally fused with the lateral walls of the rostrum. Two pairs of long setae are inserted on the sides of this bulging region, near the anterior third and on the anterior margin.

3.2. Internal skeletal structures

The main part of the tentorium (t; Figs 5B, I, 6D, 7A, 8D) is a nearly vertically oriented paired structure, comprising the posterior and dorsal arms. Anterior tentorial arms are missing and anterior tentorial pits are not recognizable externally. A tentorial bridge (tb; Fig. 5I) is present as curved sclerotized branches arising at the foramen occipitale, at the border between the gula and the low postoccipital bridge; it is interrupted medially. The large posterior pits (ptp; Fig. 6B) are widely separated from the bridge and also distinctly separated from each other medially. The nearly parallel main tentorial arms are dorsally fused with deep invaginations of the head capsule, externally

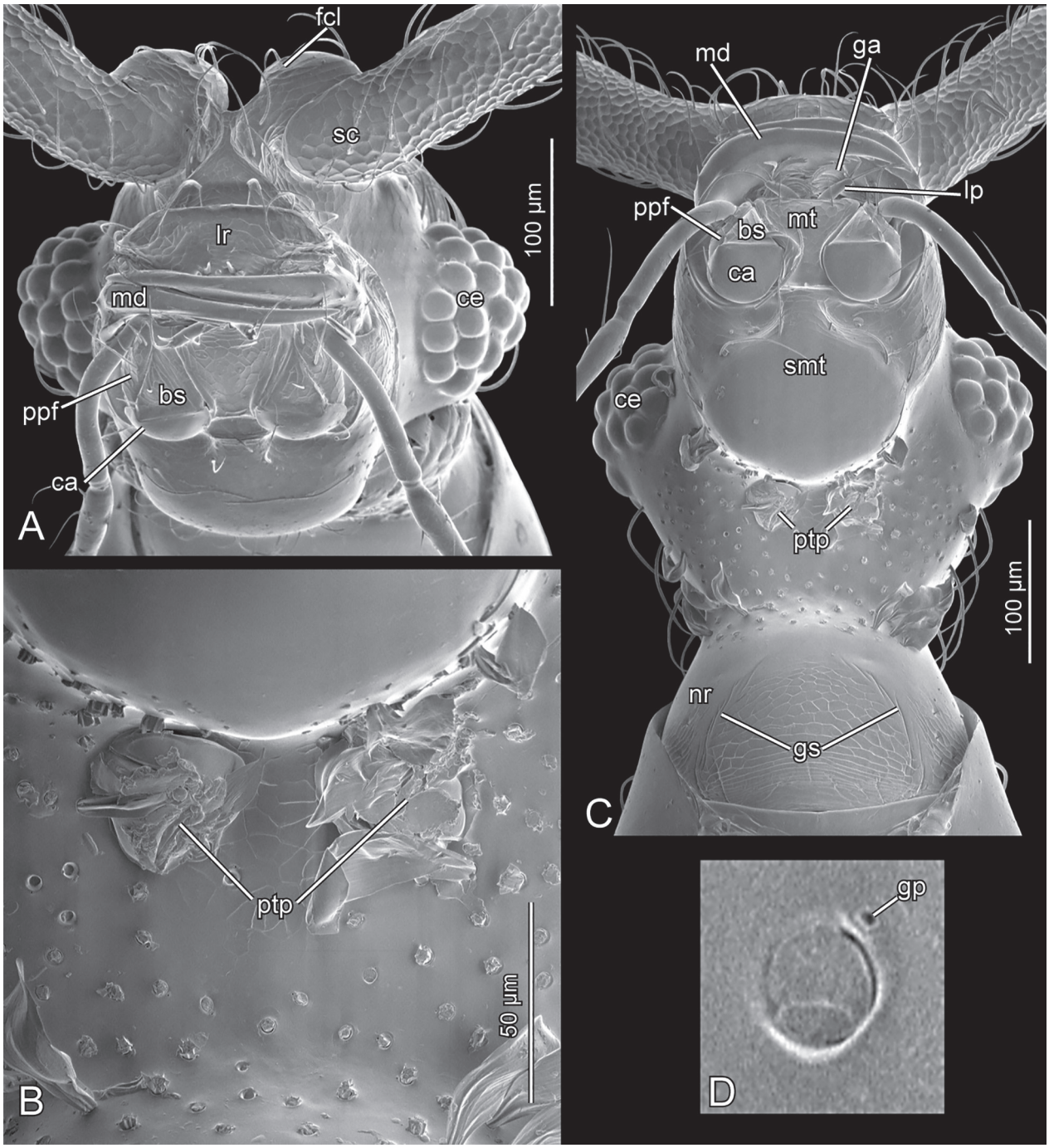

Figure 2. SEM images, head of *P. heisei*, (**A**) frontal view; (**B**–**D**) ventral view, flattened hyaline setae removed. Abbreviations: bs, basistipes; ca, cardo; ce, compound eye; ga, galea; gp, glandular pore; gs, gular suture (vestigial); lp, labial palp; lr, labrum; md, mandible; mt, mentum; nr, neck region; ppf, palpifer; ptp, posterior tentorial pit; sc, scapus; smt, submentum.

visible as frontal pouches (fp; Figs 6A, C–D), resulting in deeply countersunk dorsal tentorial pits (indicated as dorsal attachments of tentorium, dat, in Fig. 6C) (Chandler 1991: vertexal foveae).

3.3. Labrum

The labrum (lr; Figs 1C, 2A, 4C, 5A, E, 8A) is distinctly developed even though unusually shaped, short and only visible in frontal and lateral views. In lateral view the labrum has a rounded and elevated dorsal surface, resembling a broad transverse bead, with several pairs of long and anteriorly curved setae (likely homologous to mediodorsal or anterodorsal transverse row of setae of pselaphines with an unmodified labrum); the strongly sclerotized anterior area in front of these setae appears like an almost vertical ‘battering ram’ and overhangs the distal labral margin; it displays a somewhat irregular reticulate pattern of oblique to transverse cuticular scales, and a pair of short setae (ca. 7 µm) is inserted on the middle region, close to the median line; the thickened distal margin of the labrum bears a fixed, apically rounded median tooth, a pair of more pointed paramedian teeth, and a pair of stout,

curved setae (ca. 20 µm) posterior to the latter. The lateral margin is rounded; a tightly arranged group of three long brachyplumose microtrichia is present in the anterolateral corner, two long curved setae laterally (ca. 80 µm), and an additional pair of long setae posterolaterally. A pair of short (ca. 15 µm) but strongly developed tormae (width ca. 6 µm) is present at the base of the labrum, distinctly separated from the lateral edge, with a bifurcated, laterally directed process at the base.

Musculature (Fig. 7G): M7, M. labroepipharyngalis, O: posterior area of the dorsal wall of the labrum, close to the median line, I: anterior area of the epipharynx; M9, M. frontoepipharyngalis, O: anterior clypeofrontal area, close to the midline, anterior to the origin of M45, I: tormae at the posterolateral labral corner.

3.4. Antennae

The antennae are inserted on the ventral side of the rounded frontoclypeal supraantennal lobes (fcl; Figs 1A, 3A, 5A). They are ca. 1 mm long, eleven-segmented, and bear a three-segmented distal club. The roughly cylindrical scapus (sc; Figs 1A–C, 2A, 3A, 5A) is strongly elongate and subequal in length to antennomere 11 (both nearly 0.2 mm); it has a strongly curved short proximal region, and the visible basal edge has an approximately parallel orientation to the longitudinal antennal axis; the antennal articulation with the head capsule is not visible externally; the distal articulatory scapal portion is countersunk in a proximal concavity of the main part of the segment, whereas the proximal part lies within the lumen of the supra-antennal lobe; the remaining exposed surface of the scapus displays a pattern of deep pentagonal cells resembling hammered metal; about two dozens of long setae are evenly distributed over the surface. The pedicellus (pe; Figs 1A–C, 3A) is ca. 75 µm long and subcylindrical; a short, smooth basal pedestal is delimited from the distal portion of the segment by a slightly raised ring; the surface pattern of the distal cylindrical part is similar to that of the scapus; less than ten setae are inserted on the pedicellar surface in its middle region. Flagellomere 1 (fl1; Fig. 3A) is slightly shorter than the pedicellus and slightly longer than each of the three following segments; it slightly widens towards its apex after a short, smooth basal part; the cuticular microsculpture is less distinct than that on the scapus and pedicellus; five or six setae are inserted on the surface in the middle region. Flagellomeres 2-6 (fl2-6; Fig. 3A) are very similar, only 5 is slightly longer. The apical three segments (fl7-9, Fig. 3A) are slightly asymmetrical and form a loose but distinct club; the proximal club segment is slightly longer and broader than the pedicellus; it is distinctly widened distally, but the apical articulatory area is not wider than those of the other flagellomeres; like on the following two antennomeres, the density of the setae is distinctly increased; the surface microsculpture is largely obliterated on all three club segments, but still distinct on the basal areas; the penultimate antennomere is similar to the preceding one but shorter and stout; the apical segment is by far the largest, slightly longer than the scapus, fusiform, and strongly widened in its middle region; the setation is also dense, and strongly concentrated on the apical region.

Musculature (Figs 7A–B): M1, M. tentorioscapalis anterior, O: ventral half of the dorsal tentorial arm; I: anteroventral margin of the scapal base; M2, M. tentorioscapalis posterior, O: dorsalmost region of the dorsal tentorial arm, I: posterodorsal margin of the scapal base; M4, M. tentorioscapalis medialis, O: upper half of the dorsal tentorial arm, between the areas of origin of M1 and M2, I: medioventral area of the scapal base; M5, M. scapopedicellaris anterior, O: laterodorsal wall of the scapus, I: dorsolaterally on the basal margin of the pedicellus; M6, M. scapopedicellaris posterior, O: dorsolateral wall of the scapus, I: ventromedially on the basal margin of the pedicellus.

3.5. Mandibles

The slightly asymmetrical, broadly falciform mandibles are largely concealed below the labrum in their resting position, but well-developed and prominent when extended. They are mostly flat but a large, conspicuous protuberance (mpb; Fig. 4A) is present on the dorsal side of the basal portion. The surface is smooth; only few setae are present on the proximal region, close to the lateral margin. The articulation is dicondylic, with a very large dorsal condyle articulating with the head capsule, thus forming the secondary (dorsal) joint (smdj; Fig. 4A). The basal mandibular half is roughly parallel-sided and ca. 80 µm wide; a flat lamella (lml; Fig. 4A) is present proximolaterally. The distal mandibular part is strongly curved inwards, with a rounded outer edge; a curved longitudinal concavity (clc; Fig. 4B) is present on the ventral side of the bending area. The sharp mandibular apical tooth (at; Fig. 4 A–B) is followed by two or three medium sized subapical teeth (sat; Fig. 4 A) and two small teeth; the latter are continuous with the straight mesal edge of the proximal mandibular portion. The number and shape of preapical teeth were found to vary among individuals (two different beetles are shown in Figs 3A and 3B), and between the left and right mandible. A prostheca and mola are missing.

Musculature (Figs 7C–D): M11, M. craniomandibularis internus, largest cephalic muscle, O: large area of the lateral wall of the head capsule but posteriorly not reaching the neck region; I: with a tendon on the mesal mandibular base; M12, M. craniomandibularis externus, distinctly smaller than M11, consisting of two separate bundles with a shared a tendon, O: ventrolateral area of the capsule, M12a in front of the ventral base of the tentorium, M12b posterolaterad the ventral tentorial base, between bundles of M11; I: with a tendon on the lateral mandibular base.

3.6. Maxillae

The maxillary groove is very shallow; a smooth peristomal concavity is present laterad the basal half of the maxilla, delimited by a distinct, rounded ridge. The cardo

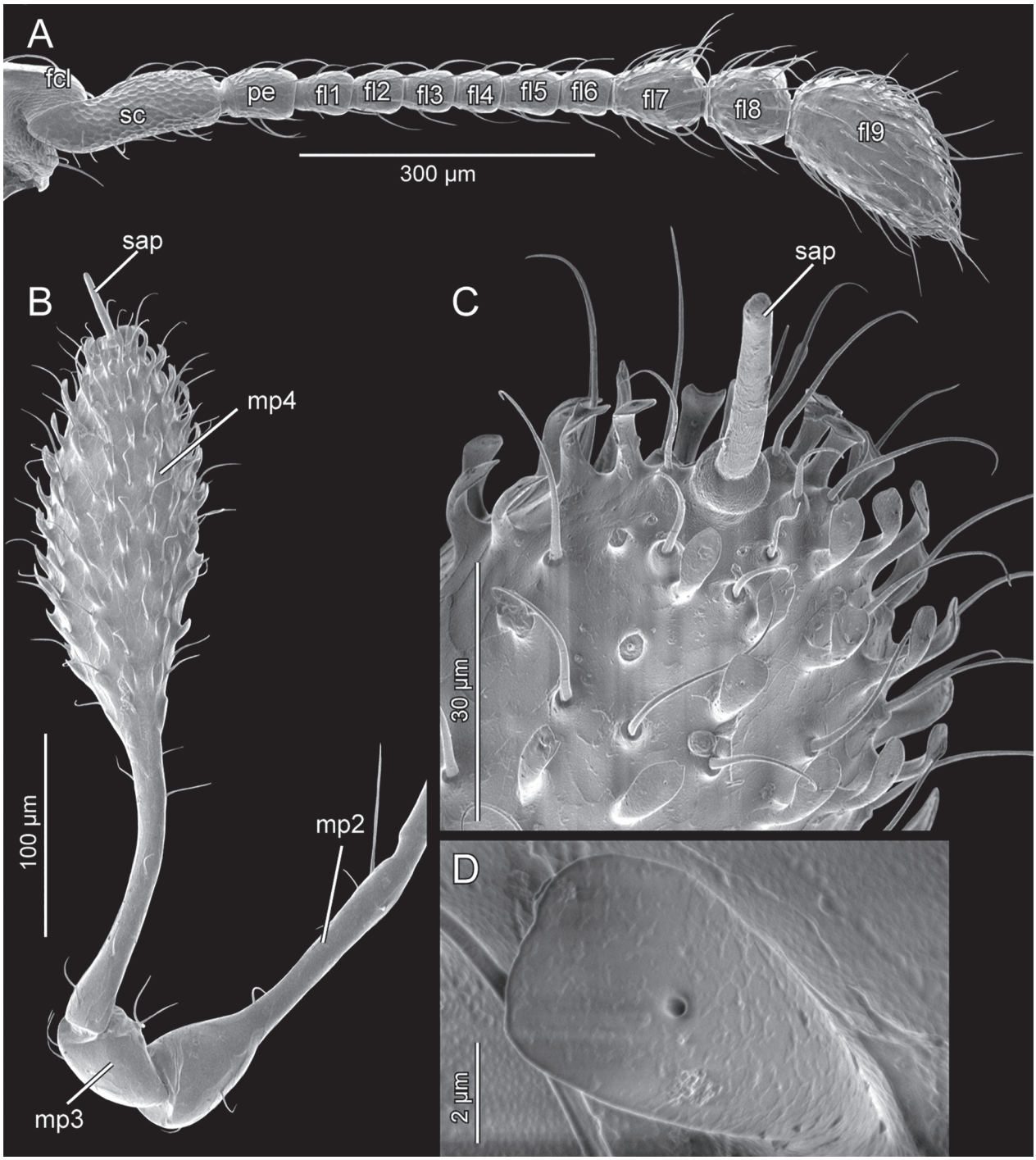

Figure 3. SEM images, antenna (**A**), maxillary palp (**B**), apical region of palpomere 4 (**C**), and spatulate projection on apical region of palpomere 4 (**D**) of *P. heisei.* Abbreviations: fcl, frontoclypeal lobe; fl1–9, flagellomeres 1–9; mp2–4, maxillary palpomeres 2–4; pe, pedicellus; sap, sensory appendage; sc, scapus.

(ca; Fig. 2A, C, 4B, 5G) is large in comparison to the remaining maxillary body, hemispherical, largely smooth and glabrous, except for one long seta inserted on the outer basilateral region. The largely glabrous stipes forms an angle of ca. 45° relative to the horizontal longitudinal axis of the head; the triangular basistipes (bs; Fig. 2A, C, 4B, 5G) is broadly connected with the distal margin of the cardo; a pattern of meshes with raised borders is present but faint; two short setae are inserted on the outer lateral margin; the narrow mediostipes (Fig. 4B) is laterally connected with the mesal basistipital edge; it bears a pattern of longitudinal furrows and its mesal apex is strongly pointed; its oblique apical edge and the apical part of the palpifer enclose the base of the galea (ga; Fig. 2C); mesally it is fused with the lacinia. The galea is composed of a short, sclerotized basigaleomere with a lateral concavity, and a very dense tuft of long and curved bristles. A sharply pointed hook-shaped structure is present on the apex of the lacinia, and bristles similar to those on the galea are inserted along the mesal edge. The large palpifer (ppf; Fig. 2A, C, 4B, 5G) is broadly connected with the lateral basistipital edge and proximally also with

Figure 4. SEM images, mouthparts of *P. heisei.* (**A**) mandibles, dorsal view; (**B**) right mandible, mentum and part of maxilla, ventral view; (**C**–**D**) labrum-epipharynx, ventral view. Abbreviations: at, apical tooth; bs, basistipes, ca, cardo; clc, curved longitudinal concavity; lml, lamella; lp, labial palp; lr, labrum; mpb, mandibular protuberance; mt, mentum; pll, plate-like lobe; ppf, palpifer; sat, subapical tooth; smdj, secondary mandibular joint.

the oblique lateral part of the distal cardinal margin; its surface bears a distinct pattern of meshes and a long seta in the middle region (ca. 50 µm) and a short seta (ca. 15 µm) distally. The long and four-segmented maxillary palp is inserted on the oblique apical articulatory area of the palpifer; the extremely elongate basal palpomere (mp1; Fig. 1C) is cylindrical, over six times as long as broad and slightly curved; the articulation with palpomere 2 is only vaguely recognizable on the surface as an indistinct and broad constriction (clearly visible in transparent slides); palpomere 2 (mp2; Figs 1C, 3B) is nearly 1.3 times as long as 1 and its proximal 2/3 are subcylindrical, indistinctly broader than palpomere 1 and straight, and its distal part is distinctly widening distally, almost club-shaped, with distal articulating surface oblique in relation to the long axis of the palpomere; few thin setae are inserted on its smooth surface, by far the longest of them close to the base (ca. 70 µm); a short (ca. 60 µm) palpomere 3 (mp3; Figs 1 B, C, 3B) is obliquely attached to the apical articulatory area of the preceding segment; it has an evenly rounded outer margin and a much shorter, nearly straight mesal edge, and a slightly oblique distal articulatory area; four thin setae are inserted on the distal half, two on the outer and two on the mesal surface; its apical articulatory area is distinctly widened; palpomere 4 (mp4; Figs 1B–C, 3B) is ca. 0.37 mm long and by far the largest segment; the basal half is slender, cylindrical, slightly curved and smooth, with only few thin setae inserted on its surface; the distal half is conspicuously widened, fusiform, with a maximum width of ca. 80 µm; it bears a rich array of various surface structures, including many unmodified setae of ca. 25 µm length, sensilla campaniformia of different size, and specifically shaped cuticular projections (ca. 15 µm), curved, distally broadened and flattened, with a spatulate distal part which bears a single pore; the very slender, smooth and glabrous sensory appendage on apex of palpomere 4 (length ca. 40 µm, basal width ca. 4 µm) is inserted on a globular papilla; it is slightly narrowing distally and rounded apically.

Musculature (Figs 7E–F): M15, M. craniocardinalis, a moderately sized muscle, O: anterolateral area of the ventral wall of the head capsule, I: lateral branch of the cardinal process; M17, M. tentoriocardinalis, two separate bundles, O: both from the anterolateral area of the ventral wall

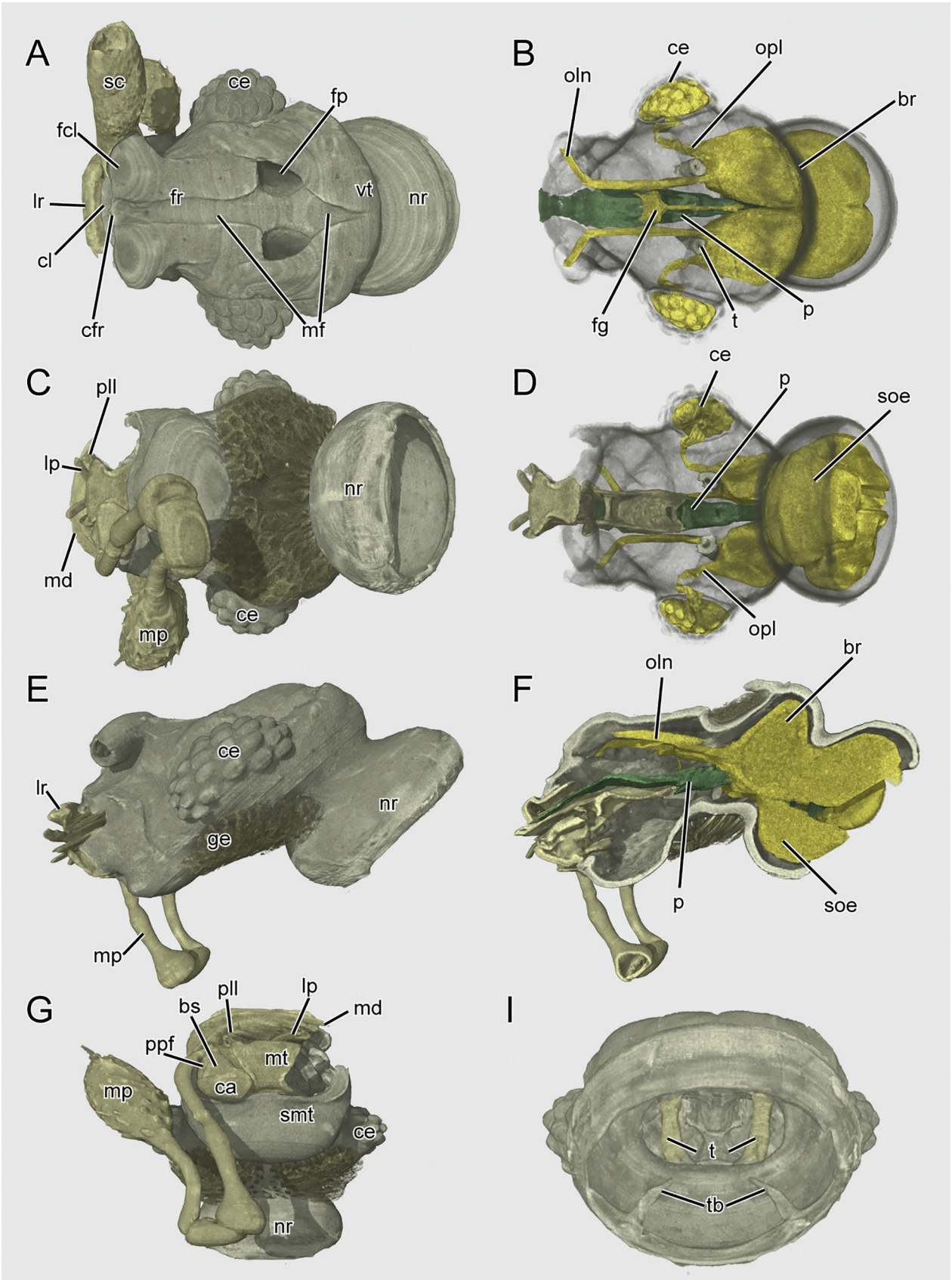

Figure 5. 3D reconstruction, head of *P. heisei*. (**A**) head, dorsal view; (**B**) nervous and digestive system, head capsule rendered transparent, dorsal view; (**C**) head, ventral view; (**D**) nervous and digestive system, head capsule rendered transparent, ventral view; (**E**) head, lateral view; (**F**) nervous and digestive system, head capsule rendered transparent, sagittal view; (**G**) head with right maxillary palp, ventral view; (**I**) head, posterior view. Abbreviations: br, brain; bs, basistipes; ca, cardo; ce, compound eye; cfr, clypeofrontal ridge; cl, clypeus; fcl, frontoclypeal lobe; fg, frontal ganglion; fp, frontal pouch; fr, frons; ge, gena; lp, labial palp; lr, labrum; md, mandible; mf, median furrow; mp, maxillary palp; mt, mentum; nr, neck region; oln, olfactory nerve; opl, optic lobe; p, pharynx; pll, plate-like lobe; ppf, palpifer; sc, scapus; smt, submentum; soe, suboesophageal ganglion; t, tentorium; tb, tentorial bridge; vt, vertex.

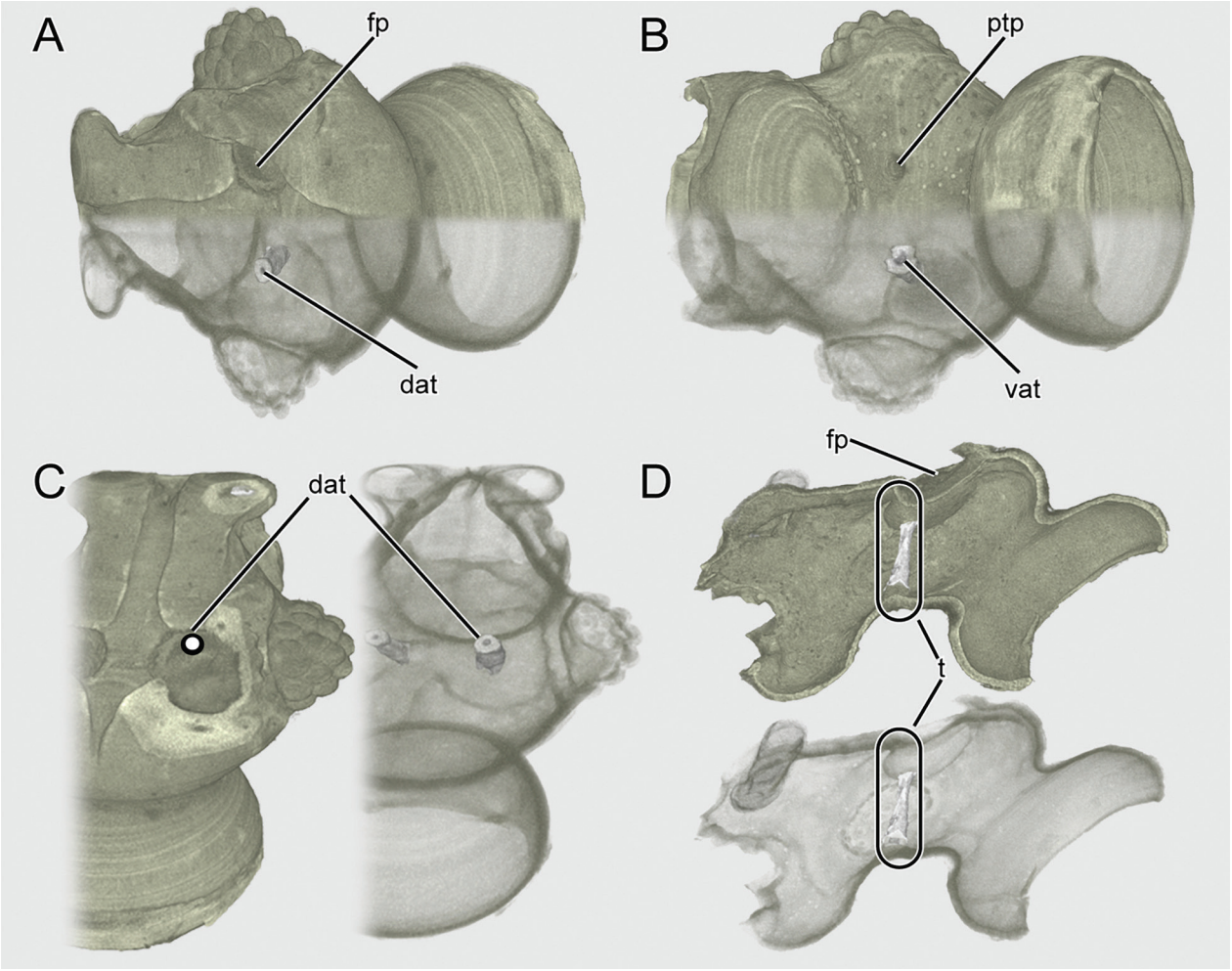

Figure 6. 3D reconstruction, head of *P. heisei*, tentorium. (**A**) dorsal view; (**B**) ventral view, flattened hyalinous setae removed, (**A**–**B**) upper half with intransparent cuticle, lower half with transparent cuticle; (**C**) dorsal view, uppermost part of frontal pouch cut off, cuticle intransparent on left side, transparent on right side; (**D**) sagittal view, upper half with cuticle intransparent, lower half with transparent cuticle. Abbreviations: dat, dorsal attachment of tentorium; fp, frontal pouch; ptp, posterior tentorial pouch; t, tentorium; vat, ventral attachment of the tentorium.

of the head capsule, I: separately on the mesal branch of the cardinal process, M17a on the typical attachment area on the mesal margin of the cardinal process, and M17b laterad this insertion site; M18, M. tentoriostipitalis, O: in front of the ventral base of the tentorium, I: with a tendon on the mediostipital base; M19, M. craniolacinialis, O: in front of the ventral tentorial base, I: with a thin tendon on the lacinial base; M21, M. stipitogalealis, O: base of the basistipes, I: basal area of the galea; M22, M. stipitopalpalis externus, O: base of the dorsal plate of the palpifer, I: laterally on the base of palpomere 1; M23, M. stipitopalpalis internus, O: base of the basistipes, I: basal margin of the palpifer; M26, M. palpopalpalis tertius, O: anteriormost wall of palpomere 2, I: basal margin of palpomere 3; M27, M. palpopalpalis quartus, O: along the ventral wall of palpomere 3, I: basal margin of palpomere 4.

3.7. Labium

The submentum (smt; Figs 1B, 2B) is completely fused with the adjacent areas of the ventral wall of the head capsule; its large and smooth, nearly circular posterior region is distinctly elevated and convex; several long setae are inserted close to its posterior margin, a very long pair laterad the lateral margin, and one pair anteriorly; the raised anteromedian submental region is anteriorly connected with the mentum by an internalized membranous fold; the very indistinctly convex anterior margin is slightly thickened; the anterolateral submental region is slightly concave and forms a part of the shallow fossa maxillaris with its anterior margin. The large mentum (mt; Fig. 1B, 2C, 4B, 5G) (length ca. 70 µm) is inserted between the maxillae; a short and steep proximal portion is demarcated from the much larger anterior region by a transverse bulge; the anterior part is distinctly widening anteriorly, with a straight anterior margin (ca. 70 µm); a somewhat irregular bulge is present along the lateral edge; the anterolateral corners are rounded; the anterior portion completely covers the prementum; an indistinct pattern of meshes is present and a pair of setae is inserted close to the anterior margin. In contrast to the main body of the prementum, the labial palps are externally visible (lp; Figs 1B, 2C, 4B, 5G); the small palpomere 1 is al-

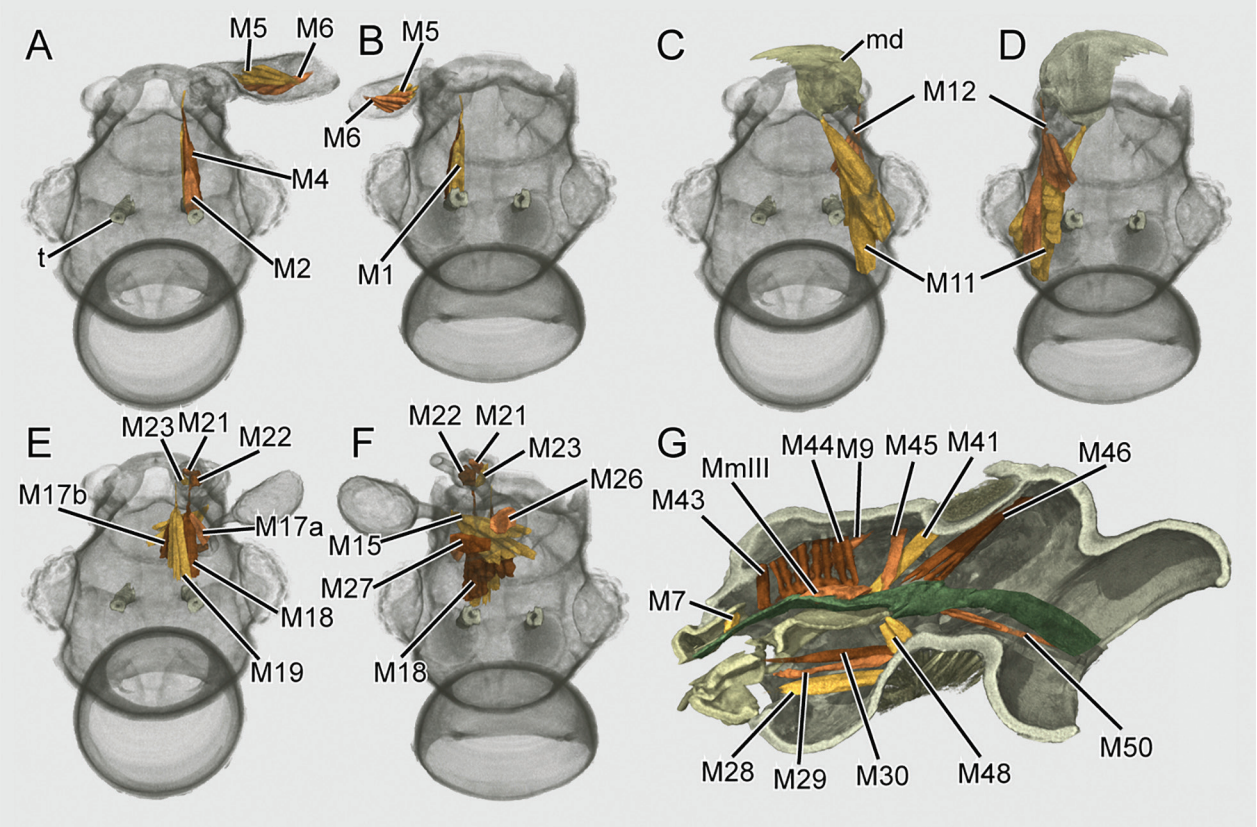

Figure 7. 3D reconstruction, head of *P. heisei*. (**A**–**B**) antennal muscles; (**C**–**D**) mandibular muscles; (**E**–**F**) maxillary muscles; (**G**) labral-epipharyngeal, pharyngeal and labio-hypopharyngeal muscles; (**A**), (**C**) and (**E**) dorsal view, (**B**), (**D**) and (**F**) ventral view, (G) sagittal view. Abbreviations: M1 – M. tentorioscapalis anterior (0an1); M2 – M. tentorioscapalis posterior (0an2); M4 – M. tentorioscapalis medialis (0an4); M5 – M. scapopedicellaris lateralis (0an6); M6 – M. scapopedicellaris medialis (0an7); M7 – M. labroepipharyngalis (0lb5); M9 – M. frontoepipharyngalis (0lb2); M11 – M. craniomandibularis internus (0md1); M12 – M. craniomandibularis externus (0md3); M15 – M. craniocardinalis externus (0mx1); M17a, M17b - M. tentoriocardinalis (0mx3); M18 – M. tentoriostipitalis (0mx4/0mx5); M19 – M. craniolacinialis (0mx2); M21 – M. stipitogalealis (0mx7); M22 – M. stipitopalpalis externus (0mx8); M23 – M. stipitopalpalis internus (0mx10); M26 – M. palpopalpalis tertius (0mx14); M27 – M. palpopalpalis quartus (0mx15); M28 – M. submentopraementalis (0la8); M29 – M. tentoriopraementalis (0la5); M30 – M. tentoriopraementalis superior (0la6); M41 – M. frontohypopharyngalis (0hy1); M43 – M. clypeopalatalis (0ci1); M44 – M. clypeobuccalis (0bu1); M45 – M. frontobuccalis anterior (0bu2); M46 – M. frontobuccalis posterior (0bu3); M48 – M. tentoriobuccalis anterior (0bu5); M50 – M. tentoriobuccalis posterior (0bu6); MmIII – Mm. compressores epipharyngis; md, mandible; t, tentorium.

most completely concealed; the slender palpomere 2 is spindle-shaped and ca. 30 µm long; a very long seta (ca. 40 µm) longer than palpomere 2 is inserted on its apex; a very slender, setiform palpomere 3 (ca. 15 µm) is inserted subapically on palpomere 2; it is more than 8 times as long as wide and has a smooth surface. Setiferous plate-like lobes (pll; Figs 4B, 5G) resembling paraglossae (Jeannel 1950: fig. 4, "languette") are visible externally, laterad the palps, but inconspicuous (pll; Fig. 4B). It is likely that these structures are extensions of the anterior hypopharynx rather than true labial structures (see Luo et al. 2021a: figs 2c, 3b, 7c).

Musculature (Fig. 7G): M28, M. submentopraementalis, a seemingly unpaired median muscle, O: ventral wall of the head capsule, anterior to the tentorial base, I: ventromedially on the hind margin of the prementum; M29, M. tentoriopraementalis inferior, O: ventral wall of the head capsule, directly posterad M28, I: posterolaterally on the prementum; M30, M. tentoriopraementalis superior, O: ventral wall of the head capsule, posterolaterad M29, I: dorsally on the posterior margin of the prementum; M34, not visible, probably absent.

3.8. Epipharynx and hypopharynx

The anteriormost epipharynx, i.e. the ventral side of the labrum (Fig. 4C–D), is sclerotized, smooth and glabrous; it lacks any microtrichia but two short, curved rows of three round pores with a distinctly elevated margin are present on the posterior portion. The posterior epipharynx, which forms the roof of a closed prepharyngeal tube, has a smooth surface and is distinctly sclerotized (Figs 8B–C). The anterior hypopharynx, which forms a structural unit with the anterior labium, is not visible externally (Figs 4B, 7G), with the possible exception of the plate-like lobes (pll; Fig. 4B). The posterior hypopharynx is laterally fused with the posterior epipharynx, thus forming the weakly sclerotized floor of the prepharynx (pph; Fig. 8B–C). Suspensorial sclero-

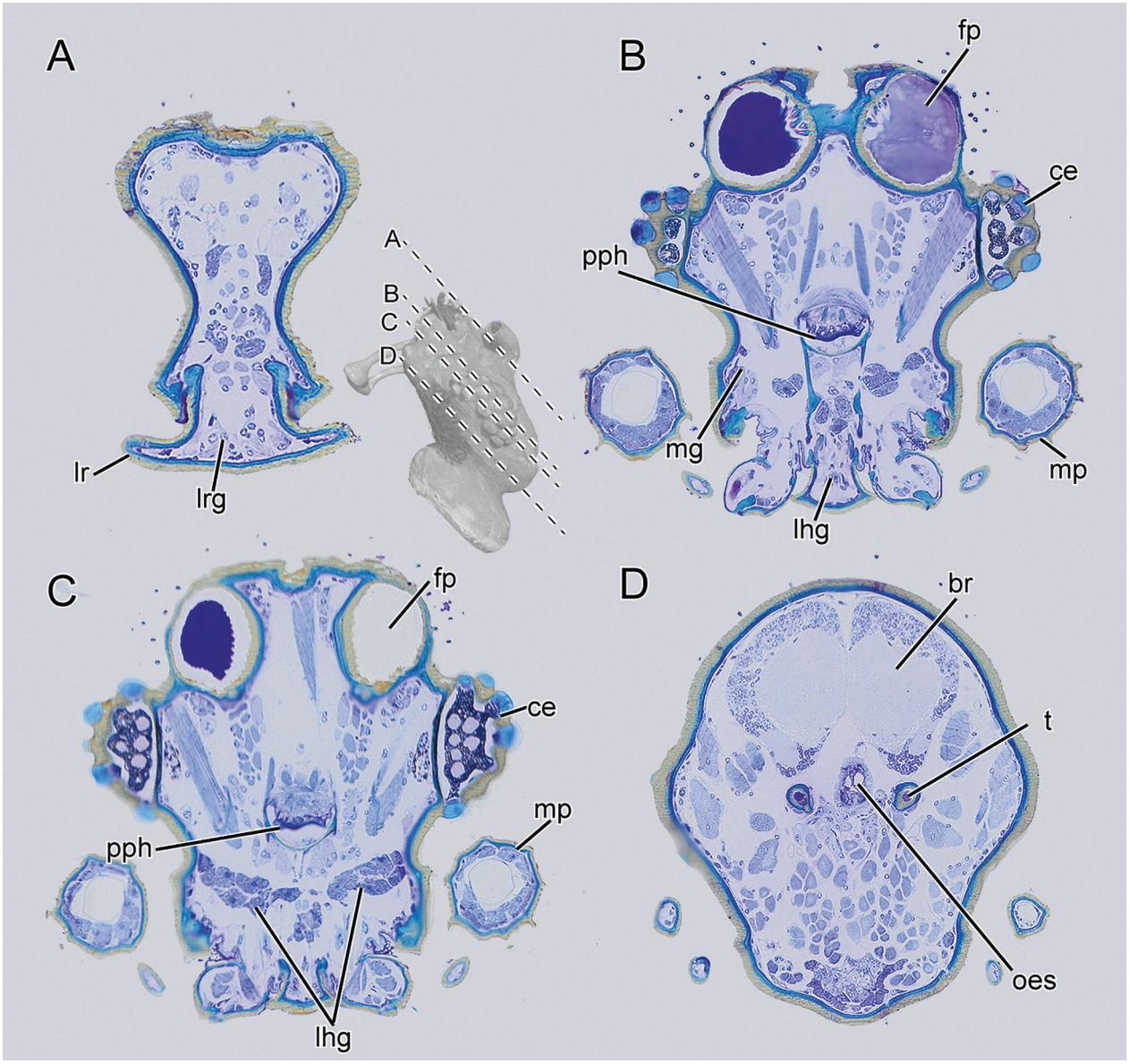

Figure 8. Histological sections of *P. heisei*. (**A**) labral region; (**B**–**C**) middle frontal region; (**D**) posterior frontal region (see inserted figure with dotted lines indicating position and orientation of sections). Abbreviations: br, brain; ce, compound eye; fp, frontal pouch; lhg, labiohypopharyngeal gland; lr, labrum; lrg, labral gland; mg, mandibular gland; mp, maxillary palp; oes, oesophagus; pph, prepharynx; t, tentorium.

tizations are not recognizable (microtome sections and µ-CT data).

Musculature (Fig. 7G): M41, M. frontohypopharyngalis, well-developed, moderately flattened muscle, O: central frontal region, posterolaterad M45 (see below), I: posterior edge of prepharyngeal tube, laterad the functional mouth and below the frontal ganglion; M43, M. clypeopalatalis, bipartite muscle complex formed by a single anterior pair and a series bundles, O: clypeofrontal region close to the median line; I: anterior bundle to the middle region of the epipharynx, the series of bundles on the epipharyngeal wall of the prepharyngeal tube; M44, M. clypeopalatalis, a single pair between the last bundle of the posterior subunit of M43 and M45; O: I: dorsal wall of the prepharyngeal tube, directly anterior to the anatomical mouth opening; MmIII, M. buccalis transversalis, a strong transverse bundle anterior to the anatomical mouth; additionally thin transverse muscles are present between bundles of M43 and M44.

3.9. Prepharynx and pharynx

The closed prepharyngeal tube (pph; Fig. 8C) is fairly broad anteriorly, but narrower and higher posteriorly, almost heart-shaped in cross section where it connects with the anatomical mouth below the frontal ganglion. The pharynx (p, Figs 5B, D, F) is fairly wide anteriorly but distinctly narrowed between the brain and suboesophageal complex; the folds for attachment of dilator muscles are indistinct.

Musculature (Fig. 7G): M45, M. frontobuccalis anterior, O: central region of the frontal area, I: dorsally on the anteriormost pharynx, directly behind the anatomical

mouth opening; M46, M. frontobuccalis posterior, two long oblique bundles, O: frontal region, posterior to M41 and M45, I: dorsal pharyngeal wall, anterior to the brain; M48, M. tentoriobuccalis anterior, two short, stout bundles, almost vertically oriented, O: between the tentorial bases, I: ventrally on the anteriormost pharynx, directly posterior to the anatomical mouth, opposed to M45; M50, M. tentoriobuccalis posterior, O: from the apical part of the medially interrupted tentorial bride, I: ventrally on the precerebral pharynx, below the insertion of M46.

3.10. Nervous system

The brain (br; Figs 5B, F) and suboesophageal ganglion (soe; Figs 5D, F) are large in relation to the head size, occupying a large proportion of the lumen of the posterior half of the head, and almost completely filling out the narrowed neck region. The upper portion of the two protocerebral hemispheres is strongly inclined posterad, thus reaching the foramen occipitale; the lower protocerebral region and the deutocerebrum are slightly broader than the protocerebral portion in the neck region, and separated from it by a distinct constriction, corresponding with the occipital constriction of the head capsule. The optic lobes (opl; Fig. 5B) originate from the protocerebrum anterolaterally; they are distinctly developed but fairly thin and elongated, forming a conspicuous loop around M. craniomandibularis (M11) internus; the optic neuropils are indistinct; the thick olfactory nerves (oln; Figs 5B, F) are similar in diameter to the optic lobes and separated from them by the dorsal tentorial arms; they originate from the anterolateral deutocerebral region and enter the antennal lobes and scapus. The compact suboesophageal ganglion lies in the ventral half of the neck region. The unusually long, almost quadrangular frontal ganglion above the anatomical mouth releases an indistinct, short nervus procurrens anteromedially and a distinct nervus recurrens posteromedially; the frontal connectives originate anterolaterally.

3.11. Glands

Three well-developed glandular clusters are present in the head, unpaired labral and labiohypopharyngeal glands, and paired mandibular glands. The relatively small labral glands (lrg; Fig. 8A) are located within and posterad the labrum, the mandibular glands (mg; Fig. 8B) within the mandibular lumen and posterior to the mandibles. The labiohypopharyngeal cluster (lhg; Fig. 8B–C) is the largest; it extends from the tentorial base to the prementum and reaches its greatest width in the postocular region, where it almost reaches the lateral walls of the head capsule.

A rather diffuse tissue is present in the apical antennomere. However, an unambiguous interpretation as gland is not possible with the material at hand.

4. Discussion

Even though the present contribution on the unspecialized predacious *Pselaphus heisei* adds information on external and internal head structures, the available morphological data for Pselaphinae are still too limited for a formal character evaluation. Internal soft parts of crucial taxa are completely unknown, notably of *Protopselaphus* Newton and Thayer, 1995, the sister taxon of Pselaphinae, and also of Faronitae, probably the sister group of all remaining pselaphine supertribes (Newton and Thayer 1995; Parker 2016b). In the following we discuss different head structures with respect to their functional or phylogenetic significance (or both). The first part is focused on features likely linked with predaceous habits, the second part on characters where such a functional background is lacking or not apparent.

4.1. Predacious habits as ancestral condition

It was pointed out by Park (1947a) that the leaf mold carpet of forest floor, the typical pselaphine habitat, is inhabited by "imponderable numbers" of small animals, including for instance earthworms, millipedes, isopods, springtails (Collembola), insect larvae and mites. He suggested that the small predacious pselaphines feed on a variety of prey they can overpower with their forelegs and mandibles, and that mites may play a special role as food source. The predacious habits of pselaphine species of several supertribes were investigated by Engelmann (1956), and later Schomann et al. (2008) using springtails as prey. The authors observed the role of different appendages in the process, notably the antennae in detection and the fore legs and mandibles in capture, but also the maxillary palps supporting detection and seizure. Park (1947b) described that certain species of *Batrisodes* Reitter, 1882 feed on armoured mites (Oribatida) under natural conditions, confirmed also by laboratory experiments. Alternative feeding on earthworms by species of the same genus was reported by the same author. Feeding on living springtails was observed many times under laboratory conditions by the senior author (PJ) for members of Euplectini, Brachyglutini, Iniocyphini, Bythinini, and Pselaphini.

That predaceous habits belong to the groundplan of Pselaphinae is clearly indicated by one feature found in *P. heisei* and many other species (e.g. Schomann et al. 2008: fig. 19A; Luo et al. 2021a), falcate mandibles with several sharp subapical teeth. As this condition is also found in Faronitae (Park and Carlton 2014, 2015a: fig. 2d), it is likely a groundplan apomorphy of the subfamily. In contrast, the mandibles of *Protopselaphus* display only an apical tooth, are rather triangular than falcate, and bear a dense elongate brush of microtrichia along their mesal edge (Newton and Thayer 1995: figs 8, 9). The loss of the brush is arguably another autapomorphy of Pselaphinae, although it is developed in Clavigeritae (Jałoszyński et al.

2020), as a part of an elaborate capillary apparatus to feed on a liquid regurgitate of ant workers. The presence of a small mola is probably part of the groundplan of the subfamily, like for instance in Faronitae (Park and Carlton 2014, 2015a: fig. 2d) or in *Bergrothia* (Luo et al. 2021a), and the complete absence like in *P. heisei* (Figs 4A–B) is a derived condition. The atrophied condition of the mandibles of *Claviger* (Jałoszyński et al. 2020) is obviously correlated with myrmecophilous habits, with adults being fed by the host ants. That a mandibular mola belongs to the groundplan of Staphylinoidea and Staphylinidae is clearly indicated by the presence in some rove beetle subfamilies and in Leiodidae and related groups (e.g. Betz et al. 2003; Antunes-Carvalho et al. 2017).

Schomann et al. (2008: fig. 3) observed a distinct rise of the anterior body and a downward movement of the head during the predatory strike. The semiglobular neck, likely another autapomorphy of Pselaphinae, probably functions like a ball-and-socket joint with the anterior prothoracic foramen, thus facilitating the orientation of the mouthparts towards the prey. The strongly pronounced neck region is present in *P. heisei* and all other groups of pselaphines including the myrmecophilous Clavigeritae (Chandler 2001; Jałoszyński et al. 2020). In contrast, it is indistinct in *Protopselaphus* (Newton and Thayer 1995: fig. 2) and also indistinct or absent in many other groups of Staphylinidae (e.g. Blackwelder 1936).

The role of the antennae in prey detection and capture in different pselaphine species was described by Engelmann (1956) and Schomann et al. (2008). Specific antennal features are shared by Pselaphinae and *Protopselaphus* (Newton and Thayer 1995), including a moderately distinct three-segmented club, an enlarged apical segment, pedunculate antennomeres, and a rich array of sensilla. The proximal antennomeres of many pselaphines appear disproportionally thick in relation to the size of the anterior portion of the head (Fig. 2A; Jałoszyński et al. 2020; Luo et al. 2021a). However, this is a gradual modification and depends on the width of the anterior frontal region. The articulation of the antenna is highly unusual in *P. heisei* as compared to other beetles (e.g. Anton and Beutel 2004; Antunes-Carvalho et al. 2017), on the ventral side of distinctly developed supraantennal frontal lobes of the frontal rostrum (Fig. 1A). A shifted antennal insertion is apparently a gradual modification in Pselaphinae, with various intermediate stages. A ventrolateral articulation as it is found in *Bergrothia* (Luo et al. 2021a: figs 2a, b) and the extinct Cretaceous †*Burmagluta* Yin and Cai, 2021 (Yin et al. 2019) is possibly a groundplan apomorphy of Pselaphinae. The functional significance of this feature is rather unclear. The modified articulation possibly facilitates screening the underground with the antenna, movements relevant in the context of prey detection. Glands in the apical antennomere were identified in different species of Batrisini by De Marzo and Vít (1983). However, the secretions likely play no role in prey capture, but rather function as female attractants, as such glands are known only in males (De Marzo and Vít 1983).

The German common name "Palpenkäfer" (palp beetles) refers to another complex autapomorphy of Pselaphinae, the greatly modified (and extremely diverse) maxillary palps. This appendage is usually characterized by a short and often triangular palpomere 3, a large, terminal club-shaped palpomere 4, and a peg-like sensorial apical 'pseudosegment' (e.g. Schomann et al. 2008: fig. 24; Luo et al. 2021a). The palp with its well-developed muscles can be involved in prey detection and capture as described in detail in Schomann et al. (2008), even involving secretion of viscous substances in species of *Bryaxis*. The maxillary palps of *P. heisei* are enormously elongate, which is a typical feature of Pselaphini (e.g. Chandler 2001). Not only palpomeres 2 and 4 are remarkably long, but also palpomere 1. This is in very clear contrast to other groups of Pselaphinae, were the basal segment is very short and inconspicuous, very likely a groundplan feature of the subfamily, and also of the entire Staphylinidae.

The long range of the palps is certainly important for the small predacious species of Pselaphinae. Palpomere 4 of *Pselaphus* displays an unusually dense array of various sensilla and hair-like structures, including curved and apically spatulate cuticular projections, presumably with glandular openings (Figs 3B–C). It was suggested by Schomann et al. (2008) that elusive prey like springtails is entangled between various cuticular surface structures of the palps of *P. heisei*. Similar structures are known in other Pselaphini, with various modifications. Additionally, plumose and erect setae with glandular openings at their insertion sites can be found on palpomeres of many species of Goniaceritae (Jałoszyński, unpublished obs.). Consequently, the "entangling mechanism" of prey capture may be common in this group, and realized by different morphological modifications. The elaborate, conspicuous, and variously modified maxillary palps have been extensively used for taxonomic purposes, as their unique structure offers unambiguous diagnostic features for genera and tribes. No other subfamily among the megadiverse Staphylinidae shows a comparable degree of diversity in the structure and shape of these appendages.

The documentation of the labrum of Pselaphinae is sparse, as this structure is usually partly concealed (e.g. Luo et al. 2021a: fig. 1). However, it is likely that it plays a role in prey capture in various group. The known broad morphological diversity of labrum may reflect particular prey preferences or feeding techniques. A group of four stout labral setae (peg-like sensilla) has been identified as an autapomorphy of Batrisitae by Kurbatov (2007). It is conceivable that these large structures, apart from providing sensorial information, help to fix prey in the preoral space, combined with prominent lateral labral regions often projecting anterolaterad (Kurbatov 2007: figs 26-51). It is likely that three non-articulated spines at the apical margin of the labrum of *P. heisei* (Figs 4C-D) fulfil a similar function, as this is also known from predacious beetle larvae of different groups (e.g. Beutel 1993, 1999). The labral structure of *Pselaphus* supports the close relationship between Pselaphitae and Clavigeritae (Parker 2016b): the anterior surface of the labrum is nearly vertical in both supertribes, forming a bulldozer-like structure, and distinctly microreticulate. As this large vertical labral surface is obviously not unique for myrmecophilous Clav-

igeritae, it very likely represents a feature inherited from a common ancestor. The labrum of the distantly related *Bergrothia* (Luo et al. 2021a: fig. 6b) gradually and weakly declines anterad, and lacks a microsculpture. As its shape and orientation resemble a condition found in many unspecialized Staphylinoidea (e.g. Weide and Betz 2009), it is likely plesiomorphic and part of the groundplan of Pselaphinae. In other large groups within Staphylinidae (or Staphylinoidea), the labrum is relatively uniform, and not as diverse as in Pselaphinae (e.g. Blackwelder 1936; Antunes-Carvalho et al. 2017). An example is Scydmaeninae, a subfamily of rove beetles of over 5,500 described species with exoskeletal structures very well studied at the genus level (data in more than 200 studies by Jałoszyński). Their mandibles display a remarkable morphological diversity, reflecting various specialized prey-capture techniques. In contrast, the labrum is typically a transverse, weakly declining and slightly convex structure, with rounded sides and a straight, convex or dentate anterior margin, and a setose dorsal surface. In contrast to Pselaphinae, deviations from this general scheme are relatively minor in Scydmaeninae.

A typical pselaphine feature is a very steep clypeus, strongly declining from the anterior region of the frontal rostrum. This condition is present in *P. heisei* (Fig. 2A) and *Claviger* (Jałoszyński et al. 2020), and many other pselaphines including species of Faronitae (Chandler 2001; Park and Carlton 2015b: figs 2, 3L–M; Park and Chandler 2017: figs 2G–L, 3a), but not in *Bergrothia* (Luo et al. 2021a: fig. 1a) and many other Batrisitae. The condition in basal Faronitae suggests that a steep clypeal region is a groundplan apomorphy of Pselaphinae, with reversal in some groups including *Bergrothia*. It is likely that the derived configuration helps to fix agile prey like springtails between the mandibles, labrum and wide antennal bases.

The cephalic digestive tract of *P. heisei* is similar to what is found in other beetles in its general configuration (e.g. Anton and Beutel 2004; Dressler and Beutel 2010; Antunes-Carvalho et al. 2017). A feature of the preoral space distinguishing the hitherto examined species of Pselaphinae from other staphyliniform groups (e.g. Beutel et al. 2003; Anton and Beutel 2004; Antunes-Carvalho et al. 2017) is the absence of longitudinal epipharyngeal and hypopharyngeal lobes with dense arrays of microtrichia. The presence of these structures is likely linked with feeding on small particles such as fungal spores (Yavorskaya et al. 2017). Their absence in Pselaphinae may be an additional adaptation to secondarily acquired predacious habits.

4.2. Evolution of cephalic features within the group

An intriguing and characteristic but puzzling character system of Pselaphinae is the presence of furrows, foveae, non-foveal pits, and other cephalic (and also thoracic and abdominal) surface structures, and also various modes of ‘deformation’ of the head capsule (e.g. Chandler 2001). These structural modifications are clearly absent in the groundplan of Staphylinoidea and Staphylinidae (e.g. Blackwelder 1936; Beutel et al. 2003; Thayer 2016; Antunes-Carvalho et al. 2017; Yavorskaya et al. 2017). A more or less elongate frontal rostrum with anterolateral supraantennal lobes is present in *P. heisei* and many other groups, including some representatives of Faronitae (Chandler 2001: fig. 32). However, this feature is extremely variable in most supertribes and often indistinct or not recognizable (e.g. *Bergrothia*; Luo et al. 2021a: fig. 1b), rendering it problematic on a higher taxonomic level. Similarly, a V- or U-shaped frontal fovea or groove (Chandler 2001: vertexal sulcus) is very widespread among the supertribes. This structural modification is very characteristic for the subfamily and unknown in other groups of Staphylinidae. Nevertheless, its extreme variability and frequent absence renders it highly problematic for phylogenetic reconstructions. Moreover, the function of this dorsal modification of the head capsule is completely unclear, although it is conceivable that at least various sulci or grooves increase the rigidity of the head capsule. Interestingly, this system of pits and grooves is lacking or vestigial in Clavigeritae (Jałoszyński et al. 2020).

The presence of a very distinct longitudinal median frontal furrow is arguably a derived groundplan feature of Pselaphinae. This structure is absent in Protopselaphinae (Newton and Thayer 1995) but present in Faronitae (e.g. Chandler 2001; Park and Carlton 2015b: fig. 3l-m; Park and Chandler 2015b, 2017) and many other pselaphines (e.g. Chandler 2001) including *P. heisei* (Fig. 1A). The furrow may be a result of narrowing the anterior region of the head, with supraantennal tubercles becoming approximate, and a large and weakly concave anteromedian frontal area becoming squeezed to form a longitudinal groove. Consequently, a primary narrowing and secondary widening of the anterior head region may cause the median furrow to develop and become obliterated. Both processes might have occurred independently in various lineages, as the shape of the head varies greatly within some supertribes. Therefore, this feature is another problematic character system for phylogenetic reconstruction.

A conspicuous feature observed in *P. heisei* (Fig. 1) is the presence of very deep foveae situated anteromesally to the compound eyes, secluded from the outside world by a very dense rosette of flattened setae and filled with very homogenous material. These unusual structural modifications are missing in *Bergrothia* (Luo et al. 2021a) and *Claviger* (Jałoszyński et al. 2020), and also in *Protopselaphus* (Newton and Thayer 1995). However, densely setose pits combined with pouches occur in different groups of Pselaphinae (e.g. Chandler 2001: classified as ‘non-foveate pits’ [p. 26]). For instance, pouches of some species of *Euplectops* Reitter, 1882 (Euplectitae) are extending back as far as the cervical region, or taking up half of the cephalic lumen in some male *Bunoderus* Raffray, 1904 (Goniaceritae) (Chandler 1983, 2001). The distinct enlargement in males of the latter genus suggests a role in a sexual context. However, the function is still elusive, and also the phylogenetic significance. Various shapes, placements, and setal arrangements of these pits

and pouches, and their unknown contents and function(s) make it almost impossible to assess the homology between tribes and genera. Remarkably, similar pouches do not only occur in various subgroups of Pselaphinae, but also on other body regions in non-related staphylinid subfamilies, Scydmaeninae and Dasycerinae (Jałoszyński, pers. obs.), or even in certain species of Coccinellidae (e.g. Jałoszyński and Ślipiński 2014).

A potential synapomorphy of *Protopselaphus* and Pselaphinae is the V- or U-shaped tentorium, with nearly vertical main branches, each comprising the posterior and dorsal arm, and lacking laminatentoria completely. This is in clear contrast to the presumably ancestral condition found in other staphylinoid beetles (Weide et al. 2014: fig. 3; Antunes-Carvalho et al. 2017). Another potential synapomorphy is the separation of the tentorial bridge from these structures. It is placed right in front of the foramen occipitale, a condition also found in Scydmaeninae, another group of Staphylinidae with well-developed and demarcated neck region (e.g. Jałoszyński 2020). The bridge is complete in *Protopselaphus* (Newton and Thayer 1995) like in other staphylinid and staphylinoid beetles (e.g. Blackwelder 1936; Antunes-Caravalho et al. 2017), clearly an ancestral condition. It is present but medially interrupted in *P. heisei* (Fig. 5I), and absent in *Bergrothia* (Luo et al. 2021a) and *Claviger* (Jałoszyński et al. 2020). The hypopharyngeal retractor, M. tentoriopharyngalis anterior (M50), arises from the tentorial bridge in *P. heisei* (Fig. 7G) and many other beetles (e.g. Anton and Beutel 2004; Weide et al. 2010; Antunes-Carvalho et al. 2017), but from the ventral head capsule in *Bergrothia* (Luo et al. 2021a) and *Claviger* (Jałoszyński et al. 2020). The dorsal tentorial pits are another potential synapomorphy of *Protopselaphus* and Pselaphinae, indicating a firm fusion of the dorsal arms with the head capsule. This is usually not the case in beetles (e.g. Antunes-Carvalho et al. 2017), although a fusion not marked externally by pits occurs in some species of Scydmaeninae (Jałoszyński, unpublished obs.). Anterior arms, usually an important attachment site for antennal muscles, are present in *Protopselaphus* (Newton and Thayer 1995: fig. 2) and *Bergrothia* (Luo et al. 2021a: fig. 5f). In contrast, they are completely reduced in *Pselaphus* and *Claviger* (Jałoszyński et al. 2020), and probably in many other pselaphines (e.g. Nomura 1991), being a part of the remarkable morphological diversity of head structures in Pselaphinae.

An unusual feature of *P. heisei*, possibly an autapomorphy of the genus, is a dense vestiture of broadened and flattened hyaline setae on the anterior gular region. The arrangement of these structures is so dense that they form a continuous mass covering a large ventral area of the head. Mechanical removal of the setae revealed small pores, presumably glandular openings, at each setal insertion. Similar setae densely cover the ventral precoxal region of the prothorax, a large anterior area of the mesoventrite, and the first exposed abdominal sternite. The massive, bulging submental region of the head seen in anterior view (Figs 1B–C) may have a protective function for this setal cover that otherwise would be prone to abrasion during moving forward among soil particles, or during feeding. The setae could function as an evaporation apparatus for glandular secretions. However, their ventral and rather hidden placement does not support this explanation; neither the simple shape and dense, overlapping coverage appear well-suited to increase evaporation. It seems more likely that these specialized setal patches are rendered hydrophobic by glandular secretions deposited on the scaly setae, and help surviving periodical flooding of habitats where *P. heisei* can be found. This species inhabits *Sphagnum* cushions and other mosses on water edges, marshes and moist meadows, and leaf litter in such places (Jałoszyński, pers. obs.). The ventral cephalic, pro- and mesothoracic, and abdominal hydrophobic surfaces may help surviving flooding, when the beetles are trapped inside moss cushions. Behavioural observations are needed to verify this hypothesis. Patches of similar hyaline setae are not known among Batrisitae and Clavigeritae.

A very unusual, apparently derived antennal feature observed in *P. heisei* and other pselaphine genera (e.g. Jeannel 1950; Luo et al. 2021a: fig. 3c) is a basal articulatory piece of the scapus countersunk in the cylindrical distal part of the antennomere. This is clearly absent in the groundplan of Staphylinoidea and Staphylinidae (Blackwelder 1936; Beutel et al. 2003; Thayer 2016; Antunes-Carvalho et al. 2017). Interestingly, a plesiomorphic condition is found in *Faronus lafertei* Aubé, 1844 (Jeannel 1950: fig. 2b), like in *Protopselaphus* (Newton and Thayer, 1995: fig. 6) and other staphylinoid beetles (e.g. Antunes-Carvalho et al. 2017). Consequently, this is a potential synapomorphy of Pselaphinae excluding Faronitae ("higher Pselaphinae" of Parker 2016b). The functional significance of this feature in free-living pselaphines is unclear. It is possibly related with the unusual articulation with the supraantennal lobes. In myrmecophile pselaphines this modification likely increases the protection of the short and very compact antennae (Jałoszyński et al. 2020). However, it is evident that this was rather a pre-adaptation, and not a specialized transformation unique for inquilines.

In contrast to the maxillae and especially the maxillary palps, the prementum of pselaphine beetles is inconspicuous, more or less retracted, and not visible externally at all in *P. heisei* (Fig. 2) and *Claviger* (Jałoszyński et al. 2020). This is clearly a derived condition compared to a distinctly exposed prementum in other groups of Staphylinoidea (Blackwelder 1936; Antunes-Carvalho et al. 2017). A setose appendage of the prementum or anterior hypopharynx (Jeannel 1950: "languette") is inconspicuous in *P. heisei* (pll, Fig. 4B) but prominent in *Bergrothia* (Luo et al. 2021a: fig. 4e, h, pll) and *Claviger* (Jałoszyński et al. 2020: figs 3c, 4h). The labial palps in Pselaphinae (and Protopselaphinae) are modified in a very different manner than those of the maxillae. Newton and Thayer (1995) coded palpomere 3 for *Protopselaphus* and all pselaphine terminal taxa as "represented only by elongate hyaline process" in their matrix. Indeed, the terminal palpomere in these groups is slender, strongly elongate, rod-like and asetose. However, in Protopselaphinae, this structure is easily recognizable as a palpomere, about as thick as its

Table 1. Musculature of Pselaphinae, some other Staphyliniformia and Elateriformia (Clambidae) (partly based on Anton et. al 2016; Antunes-Carvalho et al. 2017; Beutel & Haas 1998, 2000; Betz et al. 2003; Polilov & Beutel 2009; Weide & Betz 2009; Weide et al. 2010; Yavorskaya et al. 2017). The numbering of head muscles generally follows v. Keler (1963). — Abbreviations: + – muscle present, - – muscle absent, ? – unknown condition, the number of bundles is given in some cases (instead of +).

Family	Subfamily	Genus	No. of muscle																									
			1	2	4	7	9	11	12	15	17	18	19	28	29	30	41	42	43	44	45	46	48	50	51	52	67	68	69
Ptiliidae	Ptiliinae	*Mikado*	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-	+	+	+	+	-	-	+	+	+	-
Ptiliidae		*Ptenidium*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	-	-	+	+	+	-
Leiodidae	Cholevinae	*Catops*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+
Hydraenidae	Ochtebiinae	*Ochtebius*	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	+	?	+	+	?	-	-	+	?	?	?
Staphylinidae	Aleocharinae	*Aleochara*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Autalia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Oligota	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Oxypoda	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Eumicrota	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Gyrophaena	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
		Homalota	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	-	+	?	?	?	?	?
	Pselaphinae	*Claviger*	+	+	+	+	-	+	+	+	+	+	+?	+	-	+	+	-	+	+	+	+	+	-	-	-	+	+	+
		Bergrothia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+	+	+	-	-	-	+	+	+
		Pselaphus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	-	-	+	+	+
Hydrophilidae		*Helophorus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+	+	-	+	+	+	+	+	+
Clambidae		*Clambus*	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+	+	+	+	-	+	-	+	+	+	+

equivalent in Scydmaeninae, Euaesthetinae or Solieriinae (e.g. Jałoszyński 2020; Clarke and Grebennikov 2009; also, Jałoszyński, unpublished obs.). In contrast, it is setiform in Pselaphinae, barely recognizable as a segment, often obscured by a much longer and thicker seta inserted more apically on palpomere 2, while the modified palpomere 3 is inserted subapically. We were unable to find any illustrations of labial palps of Faronitae, but in the remaining supertribes palpomere 3 is invariantly setiform, except for taxa with reduced palps. It should be noted that labial palpomere 3 is coded equally for all Pselaphinae in Newton and Thayer (1995), including Clavigeritae. However, it was recently shown that the labial palps are entirely lacking in *Claviger* (Jałoszyński et al. 2020). The setiform palpomere 3 is likely a groundplan apomorphy of Pselaphinae, or alternatively an apomorphy of the subfamily excluding Faronitae.

Compound eyes are present and functional in the groundplan of Pselaphinae (e.g. Jeannel 1950; De Marzo and Vovlas 1989; Chandler 2001), but generally with a relatively small number of ommatidia, up to 60 according to Chandler (2001). Sexual dimorphism occurs, for instance with 23 cornea lenses in males of *Bryaxis puncticollis* (Denny, 1825) and only 14 in females of the same species (Schomann et al. 2008). With their acone apposition ommatidia and fused rhabdomeres (Meyer-Rochow 1999), they are adapted to low light intensity, and it is unclear whether some species with comparatively well-developed eyes use them for visual hunting. Functional compound eyes with a limited number of ommatidia is likely a groundplan feature of Pselaphinae, but far-reaching reduction is common. The vestigial eyes are non-functional in *Bergrothia* (Luo et al. 2021a), and light sense organs are missing completely in *Claviger* (Jałoszyński et al. 2020).

The very large relative size of the brain and its placement in the posterior third of the head is likely an autapomorphy of Pselaphinae, or a possible synapomorphy shared with *Protopselaphus*. The increase in size and posterior shift are obviously a result of small body size, an effect of miniaturization as observed in many beetles with very small body size (e.g. Grebennikov and Beutel 2002; Polilov and Beutel 2009; Yavorskaya et al. 2017). Another feature is linked with the formation of the neck region, a constriction separating the anterior protocerebral part from the posterior portion (Fig. 2C; Luo et al. 2021a: fig. 8). This corresponds directly with the cephalic constriction separating the anterior cephalic region from the semiglobular neck. The protocerebral optic lobes are preserved in *P. heisei*, even though relatively thin and curved around the mandibular flexor due to the posterior shift of the brain. In contrast, the optic lobes and neuropils are absent in *Bergrothia saulcyi*, a species with strongly reduced compound eyes, and also in the eyeless *Claviger testaceus* (Jałoszyński et al. 2020; Luo et al. 2021a). The antennal nerves are thick in all three pselaphine taxa with available anatomical data (Fig. 5; Jałoszyński et al. 2020: fig. 6b; Luo et al. 2021a: fig. 6b). This underlines the functional importance of these appendages, regardless of predatory or myrmecophilous habits.

The cephalic musculature of *P. heisei* (Figs 7, 8) largely conforms with conditions observed in other staphylinoid beetles (e.g. Evans 1965; Beutel et al. 2003; Weide and Betz 2009; Antunes-Carvalho et al. 2017; Yavorskaya et al. 2017) (Table 1). An intrinsic (M7) and an extrinsic (M9) labral muscle are present, normally developed extrinsic and intrinsic antennal muscles (M1, 2, 4-6), a strongly developed mandibular flexor (M11) and a smaller extensor (M12), a well-developed set of extrinsic and

intrinsic maxillary muscles, three premental retractors, and a standard set of hypopharyngeal, prepharyngeal and pharyngeal muscles. Derived features are the absence of the hypopharyngeal mandibular muscle (M13), which occurs as a very thin bundle in various groups of beetles (e.g. Dressler and Beutel 2010; Antunes-Carvalho et al. 2017; Yavorskaya et al. 2017), the obsolete condition or absence of the muscle of the labial palp, and the absence of M. verticopharyngalis. The latter muscle is missing in many groups of Coleoptera (e.g. Weide and Betz 2009), notably in all examined small species with the brain shifted posteriorly (Yavorskaya et al. 2017). Interestingly, the dorsal prepharyngeal dilators (M43, M44) are strongly developed in *Claviger*, moderately in *Pselaphus*, and rather weakly in *Bergrothia* (Fig. S1).

The extrinsic and intrinsic antennal muscles are also well-developed in *Bergrothia saulcyi* (Luo et al. 2021a: fig. 7a), and the former even unusually large in the obligatory myrmecophile *Claviger* (Jałoszyński et al. 2020). The extrinsic bundles originate on the dorsal arms of the tentorium in *Pselaphus* and *Bergrothia*, instead of the anterior arms as in most adult beetles (e.g. Beutel et al. 2001, 2003; Anton and Beutel 2004, Antunes-Carvalho et al. 2017). In contrast, the areas of origin are partly shifted to the head capsule in *Claviger* (Jałoszyński et al. 2020: fig. 5b–c), demonstrating a considerable variability, even within such a limited sample of Pselaphinae. The sites of origin of extrinsic antennal muscles differ in *Claviger* and *Pselaphus*, genera recovered as closely related in a recent combined morphological and molecular analysis, while they are similar in *Pselaphus* and *Bergrothia*, the latter genus belonging to Batrisitae, found to be phylogenetically distant from Pselaphitae and Clavigeritae (Parker 2016a: fig. 6b). It is very likely that the latter condition, i.e. exclusive origin on the tentorium, is plesiomorphic within the subfamily.

In contrast to other staphyliniform beetles (e.g. Anton and Beutel 2004; Antunes-Carvalho et al. 2017; Yavorskaya et al. 2017), M. craniobasimaxillaris (Mx) is absent in all hitherto examined pselaphines. A plesiomorphic feature of *P. heisei* compared to *Bergrothia* and *Claviger* is the origin of M. tentoriopharyngalis (M50) on the interrupted tentorial bridge, instead of the ventral wall of the head capsule. Derived features of the highly specialized species of *Claviger* include the loss of the extrinsic labral muscle (M9), the origin of parts of the extrinsic antennal muscles on the head capsule, the modest size of the mandibular flexor (M11), the reduction of intrinsic maxillary muscles, notably of the muscles of the palp, and the loss of two out of three premental retractors (Jałoszyński et al. 2020).

An intriguing character system documented in *P. heisei*, *Claviger* (Jałoszyński et al. 2020) and *Bergrothia* (Luo et al. 2021a) is a triple cluster of well-developed cephalic glands. This configuration is not present in other groups of Staphylinoidea (e.g. Beutel et al. 2003; Antunes-Carvalho et al. 2017; Yavorskaya et al. 2017). It was demonstrated that these organs, or at least a part of them, are involved in appeasing ants in *Claviger* (Cammaerts 1974, 1992; see also Luo et al. 2021a). Even though this likely applies to myrmecophilous taxa like Clavigeritae, this is obviously not the case in the less specialized predacious *P. heisei* and *Bergrothia* (Luo et al. 2021a). It is conceivable that these glands are associated with digestion in some way as they open in the preoral region (Luo et al. 2021a). However, the precise function of each of the differentiated subunits is yet unknown, and also the evolutionary transformation leading to the appeasement function in myrmecophilous species. The tripartite cluster of labral, mandibular and labiohypopharyngeal glands are possibly a groundplan apomorphy of Pselaphinae. However, it is unknown whether they are present in Faronitae, and data are also lacking for Protopselaphinae and other groups of the omaliine lineage. It is possible that these glands were a part of a set of pre-adaptations to myrmecophily (other than those recognized by Parker 2016a). Re-programming of their secretions to function as appeasement compounds for ants may explain why specialized myrmecophilous habits evolved independently so many times in each large lineage of Pselaphinae.

The presently available morphological information of Pselaphinae is not even remotely sufficient for a formal character analysis. However, an overwhelming morphological diversity of head structures is obvious, by far surpassing what is found in related groups of staphylinid beetles (e.g. Blackwelder 1936; Naomi 1987; Weide and Betz 2009; Weide et al. 2014; Thayer 1978, 1987, 2016). It is an intriguing question, which circumstances in the life history or microhabitats of Pselaphinae resulted in an enormously increased phenotypic plasticity, with an extreme structural diversity including rampant homoplasy. It is likely that life in soil combined with predatory habits, often specialized on small agile or armoured arthropods like springtails or mites, has played an important role. Even though the connection of some features with predatory behaviour is not obvious or non-existent, this is still quite clear in many other cases. It is noteworthy that the ecologically similar but phylogenetically distant staphylinid subfamily Scydmaeninae also comprises small-sized soil predators with diverse feeding adaptations (Jałoszyński 2012a, b, 2018; Jałoszyński and Olszanowski 2013, 2015, 2016), yet showing far less morphological diversity.

5. Conclusions

The study of cephalic structures of the free-living and predacious *P. heisei* made it possible to compare presumably unspecialized conditions with features previously described for the extreme myrmecophile *Claviger testaceus* and the blind *Bergrothia saulcyi*, the latter presumably adopted to periodic shifts into deep soil layers. These species belong in three different supertribes of Pselaphinae, and although such a small sample out of over 10,000 known species is insufficient to draw general conclusions, we identify possible groundplan features of the subfamily: falciform mandibles with several sharp subapical teeth and a vestigial mola but lacking a mesal microtrichial

brush (secondarily developed in specialized, liquid-feeding Clavigeritae); a semiglobular neck; a ventrolateral articulation of the antennae below supraantennal frontal lobes; a steep clypeal region; a setiform labial palpomere 3; V- or U-shaped tentorium, with nearly vertical main branches, each comprising the posterior and dorsal arm, and lacking laminatentoria; separation of the tentorial bridge from the tentorial arms; a firm fusion of dorsal tentorial arms with the head capsule, with fusion sites usually visible externally as dorsal tentorial pits; functional compound eyes with a limited number of ommatidia; a very large brain placed in the posterior third of the head; a constriction separating the anterior protocerebral part from the posterior portion (linked with the development of the occipital constriction); a triple cluster of well-developed cephalic glands. A strongly modified, largely vertical labrum is a possible synapomorphy of Pselaphitae and Clavigeritae. The shape of the head capsule, especially of its preocular region, the dorsal system of foveae and sulci, the shape and orientation of the labrum, and especially the maxillary palps were all found very variable within only three examined pselaphine species, documenting an enormously high morphological diversity, likely including frequent homoplasious transformations. To explore the genetic background of the structural megadiversity in Pselaphinae will be an intriguing target of future investigations, screening genomes or transcriptomes of pselaphines and other staphylinid beetles to detect changes enabling accelerated evolution of morphological structures.

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Supplementary material

File 1

Authors: Beutel RG, Luo X-Z, Yavorskaya M, Jałoszyński P (2021)

Data type: .pdf

Explanation note: Figure S1. Comparison of pharyngeal, labral-epipharygeal and labial-hypopharygeal muscles of *Claviger testaceus*, *Begrothia saulcyi*, *Pselaphus heisei*, in sagittal view.

Link: https://doi.org/10.3897/asp.79.e68352.suppl1