

**Cephalic anatomy and three-dimensional reconstruction of the head of  
*Catops ventricosus* (Weise, 1877) (Coleoptera: Leiodidae: Cholevinae)**

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**Abstract** Adult head structures are well known in the coleopteran suborders Archostemata and Adephaga, whereas the available information is very fragmentary in the megadiverse Polyphaga, including the successful superfamily Staphylinoidea. In the present study the cephalic morphology of the cholevine species *Catops ventricosus* is described in detail and documented. The results were compared to conditions occurring in other polyphagan lineages, especially staphylinoid and scarabaeoid representatives. Specific external features documented in *Catops* and potential autapomorphies of Leiodidae include a 5-segmented antennal club with the eighth antennomere smaller than the rest and the presence of periarticular grooves filled with sensilla on antennomeres 7, 9 and 10. The firm connection of the head and pronotum is possibly an apomorphy of Cholevinae. The monophyly of Cholevinae excluding Eucatopini and Oritocatopini is supported by the apical maxillary palpomere as long as or shorter than the subapical one, and the presence of cryptic pore plates on the surface of these palpomeres – a feature described and documented here for the first time. The internal cephalic structures of *Catops* are mostly plesiomorphic, as for instance the complete tentorium. The pattern of muscles is similar to what is found in other staphylinoid taxa. The unusual maxillary muscle ‘Mx’ is likely a groundplan apomorphy of the clade Staphyliniformia + Scarabaeoidea. *M. hypopharyngomandibularis* (M13) was identified in *Catops* and is ancestral for Coleoptera, even though it is often missing. The same applies to *M. tentoriohypopharyngalis* (M42).

**Keywords:** *Catops*, Leiodidae, head morphology, 3d-reconstruction, musculature, Staphyliniformia, Staphylinoidea

## Introduction

It was shown in previous studies on Archostemata (Beutel et al. 2008) and Adephaga (Dressler and Beutel 2010) that the cephalic anatomy of Coleoptera is a complex and phylogenetically informative character system, which can also reveal important insights in life strategies, especially but not only in the context of feeding. The available information on adult head structures of Coleoptera has considerably increased in the last decade, facilitated by advanced morphological techniques (e.g. Beutel et al. 2008; Anton et al. 2016). Head structures of Archostemata (Hörschemeyer et al. 2002; Beutel et al. 2008), Adephaga (e.g. Dressler and Beutel 2010), and the myxophagan family Lepiceridae (Anton and Beutel 2006) are very well known. In contrast, the available information on the cephalic morphology of the megadiverse Polyphaga is still very fragmentary. Earlier studies are those of Dönges (1954) on the weevil *Cionus* or the study of Schneider (1981) on the Spanish fly *Lytta* (Meloidae), both highly specialized taxa of Cucujiformia. Anatomical data on the presumably basal Scirtoidea (McKenna et al. 2015) became available only recently (Anton et al. 2016) and detailed studies on the extremely species-rich Staphylinoidea are still very sparse. Interestingly, larval head structures are relatively well known (e.g. Beutel and Molenda, 1997; Beutel and Leschen 2005), whereas detailed data on adult cephalic structures are only available for few species of the aquatic Hydraenidae (Beutel et al. 2003), the strongly miniaturized Ptiliidae (Polilov and Beutel 2001), the small family Agyrtidae (Weide and Betz 2009), and few species of the highly diverse Staphylinidae (Weide and Betz 2009; Weide et al. 2010, 2015).

With 4135 described species (Newton 2016), Leiodidae are the second largest family of Staphylinoidea. Their distribution is worldwide and they are able to explore an astonishing range of habitats and food resources. In general, leiodid beetles inhabit forested landscapes and are mycophagous relying on various groups of fungi or saprophagous and feeding on different kinds of decaying organic matter involving plant material (e.g. organic matter in the soil, leaf litter), animal matter (e.g. dung, carrion) or the yeasts and bacteria associated with such substrates (Newton 2016). The family is currently organized into six subfamilies and 18 tribes. About half of the total species diversity belongs to Cholevinae, the most species-rich subfamily, encompassing seven tribes and 17 subtribes (Perreau 2000; Bouchard et al. 2011). There is no broad formal cladistic study available focused on Leiodidae or Cholevinae. The only phylogenetic contributions including these groups are broad-scale analyses with insufficient taxonomic sampling regarding subordinate taxa in Leiodidae, or more detailed studies on particular

lineages, thus not providing a well-supported phylogenetic scheme at the family or subfamily level. In this context, Fresneda et al. (2011) is the most complete molecular study with emphasis on Cholevinae. Whereas some studies did not confirm the monophyly of Leiodidae (e.g. Lawrence et al. 2011; McKenna et al. 2015) or Cholevinae (e.g. Fresneda et al. 2011; McKenna et al. 2015), both have been supported as natural groups based on morphological characters evaluated by Newton (1998, 2016). Therefore, the higher-level classification remains an important area of investigation in the systematics of Leiodidae.

The knowledge on the morphology of Cholevinae is predominantly limited to general external features and genitalia, mostly documented and described based on stereomicroscopy and light microscopy, and mainly aiming at taxonomic descriptions. The head morphology of Cholevinae has never been studied in detail, especially the internal soft parts. This contribution aims to explore the cephalic character complex of a representative of Cholevinae by providing a detailed description of the head of *Catops ventricosus* (Weise, 1877). The exo- and endoskeletal structures, musculature, nervous system and digestive tract were studied and documented using scanning electron microscopy, micro-computed tomography and computer based three-dimensional reconstructions. The first 3D model of the head of Leiodidae is provided and the morphological elements are discussed from a phylogenetic point of view. The morphological descriptions and documentation presented here offer the basis for future inferences on the higher-level systematics of Leiodidae using cephalic structures as a source of characters.

## Material and methods

This study is based on adults of *Catops ventricosus* collected inside Arılı Mağarası, a cave in Gümüşhane, Turkey (1777 m, N40°26'50.8" E39°19'19.1). This species lacks sexual dimorphism associated with cephalic characters. Specimens were investigated using scanning electron microscopy (SEM) and synchrotron-radiation micro-computed tomography (SR-μCT). For SEM, the specimen was dried at the critical point (Emitech K850 critical point dryer), sputter-coated with gold (Emitech K500) and fixed on a rotatable specimen holder (Pohl 2010). Images were taken with a FEI (Philips) XL 30 ESEM at 10kv. Specimens used for SR-μCT were dehydrated with ethanol (20–100%) and acetone, dried at the critical point (Emitech K850 critical point dryer) and mounted on a standardized specimen holder. Micro-computed tomography was performed at the

Deutsches Elektronen Synchrotron (DESY, beamline IBL P05 at PETRA III, operated by the Helmholtz-Zentrum Geesthacht, Hamburg, Germany) with a stable beam energy of 8 keV in attenuation contrast mode (Beckmann et al. 2008; Greving et al. 2014). We used an effective magnification of 18x providing a resulting field of view of 2 mm x 2 mm, resulting in an effective pixel size of 1.33 x 1.33  $\mu\text{m}$  in the two times binned reconstructed data set. Radiograms ( $n = 1200$ ) were taken at equal intervals between 0 and  $\pi$  (exposure time of 6.3 s). Stacks of  $\geq 899$  slices were calculated from each set of radiograms using the tomographic reconstruction algorithm 'back projection of filtered projections' (Huesman et al. 1977).

Three-dimensional models of head structures are provided. Uncompressed 16bit TIFF image stacks were imported into Amira 5.3.1 (Visage Imaging, Berlin, Germany) where the segmentation of individual structures was conducted. These were subsequently exported to VGStudio MAX 2.0.5 (Volume Graphics, Heidelberg, Germany) for volume rendering.

Detailed morphological studies on the head of staphyliniform and scarabaeoid beetles were used for comparison (e.g. Jäch et al. 2000; Beutel et al. 2001, 2003; Anton and Beutel 2004; Polilov and Beutel 2009; Weide and Betz 2009; Weide et al. 2010; Anton and Beutel 2012). Muscles are named following the terminology of von K  ler (1963).

## Results

### External head capsule

The posterior part of the prognathous head is abruptly narrowed thus forming a distinct neck region, which lies on a lower level dorsally and is retracted into the prothorax (Figs. 1 and 2). The posterodorsal border of the exposed part of the head is delimited by an occipital crest, which is firmly connected to the anterior edge of the pronotum (oc, Fig. 2a, e). The head capsule is mostly black, but the appendages vary from dark yellowish brown (antennae, maxillary palps and most parts of cardo and stipes) to pale yellow (galea, lacinia and labial palps) (Fig. 1). The dorsal surface of the head except for the neck region is microgranulated and densely covered with regularly distributed, medium length yellowish setae (Fig. 1a, c). The dorsal punctures are enclosed by a distinct rim (Fig. 2b). Setae are also present on most parts of the ventral side of the head, except for the gula (Fig. 2c). The ventral cuticular surface is weakly striated on the mentum and submentum, strongly striated on the genae, and strongly reticulated on the gula (Fig. 2c).

The frontoclypeal strengthening ridge is not visible externally (Fig. 2d). The clypeus is moderately sized. Its subparallel lateral margins are approximately one third as long as the straight anterior margin (Fig. 2d). The lateral and anterolateral borders are weakly demarcated by an indistinct ridge which obliterates in the middle region of the anterior border. The lateral surface of the frons anterior to the compound eyes is roundly excavated and the antennal insertion is fully exposed in this region (Fig. 2a). Ocelli are absent. The compound eyes are moderately sized, with a distinctly convex surface and numerous small lenses of the individual ommatidia, and few scattered setae. The anterior edge is evenly rounded whereas the vertical posterior margin is nearly straight. Posteriorly the compound eye is covered by a genal fold (pogf, Fig. 2c) and delimited by a large postocular ridge (por, Fig. 2d). The gula is large and has the shape of an elongated trapezium. It is anteriorly delimited by a smooth transverse depression of its surface and appears convex in lateral view (Fig. 2c). The widely separated anteriorly converging gular sutures are very distinct externally and fissure-shaped. The posterior tentorial pits are not distinctly recognizable externally.

### **Cephalic endoskeleton**

The paired anterior, dorsal, and posterior tentorial arms (ata, dta, pta, Fig. 5a) are well developed. The extensive gular ridges form wall-like structures and are fused with the posterior edge of posterior arms ('PTW' in Weide et al. 2014). They are connected by a thin tentorial bridge or corpotentorium, which is straight in posterior view, with a sinuously curved posterior margin, thus appearing W-shaped in dorsal view (tb, Fig. 5a). The posterior tentorial arms converge anteriorly and merge medially forming a massive median tentorial body or laminatentorium ('lt', Fig. 5a). This structure is composed of a median vertical plate dorsally continuous with a horizontal plate ('hpl' in Anton and Beutel 2004), which is not directly connected with the tentorial arms. The median vertical plate produces a frontally projecting, median vertical lamella (mvl, Fig. 5b). The elongate anterior and dorsal tentorial arms arise from the posterior arms, posterior to the horizontal plate of the laminatentorium. The apically narrow dorsal arms extend toward the dorsal wall of the head capsule at the level of the compound eyes, ending between the longitudinal midline of the head and the dorsal margin of the eyes (Fig. 6b). The anterior arms arise with a relatively robust proximal part at the edge of the frons, close to the antennal foramen (Figs. 4d and 6b). The anterior tentorial pits are not visible externally.

## Labrum

The transverse labrum is connected to the clypeus by an internal membrane. It is ca 2.5 times as wide as long and well visible from above (Fig. 3h). The anterolateral edges are rounded, whereas the median portion of the anterior margin is broadly emarginated and bears a dense fringe of setae (Fig. 3h). The dorsal surface is largely smooth but a sparse vestiture of anteriorly directed setae is present. The dorsal surface is posteriorly delimited by a distinct transverse ridge (trdg, Fig. 3h), which is covered by the apical clypeal margin. The anteromedial region of the ventral side bears a cluster of blunt protuberances and a field of mesally directed microtrichia (Fig. 3i). It is followed posteriorly by a longitudinal epipharyngeal process densely covered with microtrichia (lep, Fig. 3i). Paired paramedian patches of sensilla are present close to the posterior portion of the fields of microtrichia.

Musculature: *Musculus labroepipharyngalis* (M7) – (origin = O) posteriorly on dorsal wall of labrum; (insertion = I) posteriorly on ventral wall of labrum (posterior to area of origin) (Figs. 4a and 6a). *M. frontoepipharyngalis* (M9) – absent.

## Antenna

The insertion of the 11-segmented (Fig. 2f) antenna is clearly visible from above (Fig. 2a). The scapus is composed of a nearly globular articulatory piece and an elongated cylindrical shaft. The cylindrical pedicellus is shorter and also shorter than the elongated antennomere 3. The following segments are distinctly shorter and slightly widening distally. Segment 6 is wider than long. Antennomeres 7-11 form an indistinct club. Antennomere 7 is large and cupola-shaped and its apical part partly covers the small antennomere 8 (Fig. 2f). Segments 9 and 10 are almost as large as 7 and similarly shaped. The terminal antennomere 11 is elongate and subconical on its distal half (Fig. 2f). A distal periarticular gutter bearing sensilla is present on antennomeres 7, 9 and 10, visible through a narrow slit-like opening on the apical surface of these segments (Fig. 2h, i; compare with Fig. 2g). All antennomeres are densely covered with setae. Some longer, curved setae are distributed laterally along the distal face of the antennomeres 7, 9 and 10, close to the apical border. On the distal antennomere the setae are laterally inserted at the end of the most expanded part of the segment and also at the apex (Fig. 2f). Numerous short peg-like sensilla are present at the distal margin of antennomeres 7, 9 and 10 (Fig. 2i). Some thinner, longer proprioceptive sensilla are also present on these antennomeres, oriented towards the central axis of the antennae (Fig. 2h, i).

Musculature: *M. tentorioscapalis anterior* (M1) – (O) dorsal face of horizontal plate of laminatentorium, passing below anterior portion of anterior tentorial arm; (I) ventrally on articulatory piece of scapus (Fig. 4d, e). *M. tentorioscapalis posterior* (M2) – (O) lateral side of posterior tentorial arm; (I) medioposteriorly on articulatory piece of scapus, posterior to insertion of M4 (Fig. 4e). *M. tentorioscapalis medialis* (M4) – (O) lateral face of anterior tentorial arm and basal portion of dorsal tentorial arm; (I) medially on articulatory piece of scapus (Fig. 4e).

## **Mandible**

The mandibles are largely symmetrical, with the lateral margins somewhat rounded (Fig. 3a, b). The external side is broad at the base and narrows toward a moderately acute apex, which is proximally adjoined by a sinuous, dorsal cutting edge (Fig. 3a). A retinaculum, in the form of a very weakly developed blunt process, is present at midlength between the mandibular apex and the distal margin of the mola (Fig. 3a). It is slightly more prominent on the right mandible. The well-developed prostheca bears a dense brush of long microtrichia along the mesal border of the ventral mandibular side, from the incisor area to the mola (prst, Fig. 3b). On the ventral face of the mandible, a weak elevation occupies a large area of the mesal region of the surface. A row of hairs arises from the distal and mesal limits of this area (Fig. 3b). A ventral accessory process is present mesally close to the basal mandibular edge (avp, Fig. 3b). Oblique rows of posteriorly directed microtrichia characterize the dorsal surface of the large mola (ml, Fig. 3b). The molar area is delimited by a slight depression of the mandibular surface, and is therefore not firmly united to the rest of the mandible (condition defined as ‘loosely attached’ in Betz et al. 2003). Its mesal grinding surface is densely covered by regularly distributed asperities or small denticles, while the ventral surface bears dense rows of short hairs.

Musculature: *M. craniomandibularis internus* (M11) – (O) posterolateral area of head capsule, slightly posterior to eyes, and from posteriormost cephalic region laterad the occipital foramen; (I) medially on mandibular base, with strong adductor tendon (Figs. 4d–f and 5a). *M. craniomandibularis externus* (M12) – (O) genal region, and from posteriormost part of head capsule, close to occipital foramen and attachment area of M11; (I) laterally on mandibular base with abductor tendon (Figs. 4d–f and 5a). *M. hypopharyngo-mandibularis* (M13), a thin muscle – (O) from region of posterodorsal surface of laminatentorium but exact point of origin not recognizable; (I) medially on mandibular base, relatively close to insertion of M11 (Figs. 4e and 5a).



## Maxillae

The moderately deep maxillary grooves anteromesad the compound eyes have a smooth surface. They are mesally bordered by the anterior third of the lateral edge of the submentum, and posteriorly and laterally by a distinct curved line. A distinct lateral genal edge is present above the lateral maxillary base, with a snap anteriorly directed edge below the ventral mandibular base. The short transverse cardo is rounded posterolaterally and has nearly straight anterior and mesal edges (ca, Figs. 2c and 3d). It is mostly glabrous, with only four setae on its basal part. The basistipes is elongate and triangular, with a single seta at each corner (bs, Fig. 3d). The mediostipes (ms, Fig. 3d) is continuous with the lacinia, which is long and narrow (lc, Fig. 3c). Its mesal edge bears a semimembranous seam densely covered with microtrichia, while the ventral surface is mostly covered with small cuticular protuberances. The apex is strongly sclerotized and hook-shaped. The subapical edge bears a dense set of thorn-like structures (Fig. 3c). The galea is composed of a short proximal segment, subtriangular in ventral view (ga, Fig. 3c). The distal segment is elongate, with a dense apical brush of setae and a fringe of long setae along the mesal edge of the dorsal side. Small finger-like cuticular protuberances are present on the anteromesal edge of the ventral face (Fig. 3c, d). The palpifer is elongate and subtriangular (pf, Fig. 3c). The palp is 4-segmented (mp, Fig. 3c). Palpomere I is very short, whereas the palpomeres II–IV are about twice as long as the maximum width. Palpomeres II and III are distinctly widening distally and slightly curved inwards. Palpomere IV is conical and apically rounded. A parallel arrangement of about 20 digitiform sensilla is present on its dorsal surface (dgts, Fig. 3e, f). Small pore plates are distributed over the surface of palpomeres III and IV (Fig. 3f, g) and a sensorial field is present at the apex of palpomere IV.

Musculature: ***M. craniocardinalis externus* (M15)** – (O) anterolateral genae, level of compound eyes (thin, single bundle), posterior head region, laterally on basal portion of gular ridge; (I) end of dorsally directed process of cardo base (Figs. 4d–f and 5b). ***M. tentoriocardinalis* (M17)** – (O) along lateral surface of posterior tentorial arms; (I) sclerotized process of cardo base (Figs. 4d–f and 5b). ***M. tentoriotipitalis* (M18)** – (O) lateral face of median vertical lamella and median vertical plate of laminatentorium, and from anterior extension of posterior tentorial arm; (I) ventromesally on stipes (Figs. 4c–e and 5b). ***M. craniolacinialis* (M19)** – (O) posterior region of ventral surface of head capsule, immediately posterior to main attachment area of M15; (I) on membranous area

close to basal margin of lacinia (Figs. 4c–f and 5b). *M. stipitolacinialis* (M20), arranged diagonally on base of maxillae – (O) lateral base of basistipes; (I) base of lacinia. *M. stipitogalealis* (M21), arranged longitudinally on maxillary base – (O) lateral base of basistipes, anterior to origin of M20; (I) base of galea (Fig. 4a, b). *M. stipitopalpalis internus* (M23), short muscle arranged vertically in basal part of maxillae between insertions of M20 and M21 – (O) mediostipes; (I) palpifer (Fig. 4b). *M. palpopalpalis maxillae primus* (M24), arranged longitudinally within palpifer – (O) base of palpifer; (I) base of basal maxillary palpomere (Fig. 4a, b).

## Labium

The anteriorly widening submentum is about as large as the mentum and anteriorly delimited by a very slightly convex transverse suture. Its basal margin is not separated from the gula by a suture but the border is clearly indicated by the anterior transverse gular depression and a distinct angle formed by both areas (Fig. 2c). The anterior third of the lateral submental edge forms the mesal margin of the maxillary grove and is adjacent with the cardo. The broad plate-like mentum is trapezoidal and narrowing anteriorly. The converging lateral margins are almost straight (Fig. 2c) and adjacent with the mediostipes. The posterolateral edges of the mentum are levelled with the anterior cardinal margin. The anterior margin is slightly convex. The submental and mental surface are transversely striated and bear a vestiture of short setae, with a slightly higher density on the submentum. In ventral view, the mentum covers part of the base of the prementum. The prementum is completely divided medially (pmt, Fig. 3j). The paired lobes are elongate-ovoid and diverge anteriorly. Longitudinal prominent rows of mesally directed microtrichia are present on the dorsal surface. The mesal edge is densely covered with a row of setae (Fig. 3j). The prementum is laterally connected with a pair of transverse palpigers (Fig. 3j, k). The palps are three-segmented (lp, Fig. 3k). The basal palpomeres are wider than the apical ones. The apical palpomere is longer than the subapical one, and approximately as long as the basal one. All palpomeres are subcylindrical. The laterodistal margin of the basal and subapical palpomere bears a few long setae (two or three). The apical surface of the distal palpomere bears a field of sensilla.

Musculature: *M. submentopraementalis* (M28) – (O) paramedially on anterior part of submentum; (I) medially on membranous fold between prementum and mentum (Figs. 3k, 4a–c and 6a). *M. tentoriopraementalis inferior* (M29) – (O) paramedially on submentum, posterior to origin of M42; (I) posteriorly on sclerotized mesally directed

process of lateral wall of prementum (see origin of M34) (Figs. 3k, 4b, c and 6a). *M. tentoriopraementalis superior* (M30), very thin muscle – (O) medially on submentum, posterior to origin of M28 and close to origin of M42; (I) basal labial palpomere (Figs. 4a–c and 6a). *M. praementopalpalis externus* (M34) – (O) anterior surface of sclerotized, mesally directed process of lateral wall of prementum; (I) basal margin of basal palpomere (Figs. 3k, 4a and 6a).

### Epipharynx

An epipharyngeal process projects medially from the posterior margin of the ventral side of the labrum (lep, Fig. 3i). This structure is subtriangular, relatively broad at its base and narrowing towards its apex. It is densely covered with posteriorly directed microtrichia (Fig. 3i). The posterior part of the epipharynx (not shown in Fig. 3i) is laterally fused with the corresponding edges of posterior hypopharynx forming a short, closed prepharyngeal tube (Fig. 6a).

Musculature: *M. clypeopalatalis* (M43), multiple short bundles – (O) along clypeal area; (I) dorsal wall of cibarium (Figs. 4d and 6). *M. clypeobuccalis* (M44) – (O) frons, anterior to M45; (I) dorsolateral wall of posterior epipharynx.

### Hypopharynx

The hypopharynx is firmly connected with the posterior part of the prementum (hpp, Fig. 3j). It is composed of a pair of elongated, posteriorly divergent lobes. The dorsal surface of each of them is densely covered with multiple oblique parallel rows of microtrichia. A conspicuous tuft of erect microtrichia is present medially on the posterior part of the dorsal surface (ht, Fig. 3j). The concave lateral walls of the hypopharynx are sclerotized and medially fused (Fig. 3k).

Musculature: *M. frontohypopharyngalis* (M41) – (O) large area on posterior frons; (I) large attachment area on posterolateral hypopharyngeal apodeme (Figs. 3k, 4e, f and 6). *M. tentorihypopharyngalis* (M42) – (O) paramedially on submentum, between origin of M28 and M29; (I) medially on ventral premental strut (Figs. 3k, 4c and 6a). Additionally, an extrinsic muscle ('Mx' in Jäch 2000; see details in the discussion) of unclear homology (not covered by v. Kéler, 1963) originates from the gena, approximately at the level of the hind edge of the compound eyes (Mx, Fig. 4d, e). It is laterally attached to the membranous area linked to the ventral hyopharyngeal surface.

## Pharynx

The pharynx displays a typical pattern with longitudinal folds for muscle attachment in cross section (phr, Fig. 4f), with a circular to ovoid lumen gradually narrowing towards the posterior cephalic region, before it abruptly expands into a large oesophagus. The pharyngeal wall is very thin.

*M. frontobuccalis anterior* (M45) – (O) frons, anterior to M46; (I) dorsolaterally on precerebral pharynx, anterior to M46 (Figs. 4e and 6). *M. frontobuccalis posterior* (M46), several bundles – (O) posterior frons; (I) dorsolaterally on precerebral part of pharynx (Figs. 4f and 6). *M. tentoriobuccalis anterior* (M48), long, thin paired muscle stretching between tritocerebral commissure and suboesophageal ganglion – (O) anteromedially on tentorial bridge; (I) medially on ventral margin of posterior hypopharynx (Figs. 3k, 4e, f and 6). *M. tentoriobuccalis posterior* (M50) – (O) tentorial bridge; (I) ventromedially on anterior pharynx. *M. verticopharyngalis* (M51) – absent. *M. tentoriopharyngalis* (M52), three bundles – (O) mesally on gular ridges; (I) ventrolaterally on posterior pharynx.

## Brain and suboesophageal ganglion

The medium-sized brain in the posterodorsal head region does not reach the occipital foramen posteriorly (cer, Figs. 4f and 6). It lies below the vertex dorsally and is enclosed by M11 laterally, the pharynx ventrally, and M46 anteriorly. The frontal ganglion is well developed (gfr, Figs. 4f and 6a) and also the frontal connectives and tritocerebral commissure. The suboesophageal ganglion fills the entire space between the gula, posterior tentorial arms and tentorial bridge. Anteriorly it reaches the laminatentorium (soe, Fig. 6a).

## Discussion

### Head capsule, appendages and labiohypopharyngeal complex

A series of apparent plesiomorphies documented in *Catops* had already been identified as typical for microphagous Staphylinoidea, and possible as groundplan features of the entire superfamily (Betz et al. 2003). This includes a cibarial roof with parallel rows of microtrichia corresponding to similar elements on the dorsal molar surface (Fig. 3a), brush-, comb- or rake-like maxillary structures (Fig. 3c), mandibles with a subapical hyalinous or hairy prosthema and a well-developed mola with grinding surfaces (Fig. 3b),

and epipharyngeal and hypopharyngeal median tufts of posteriorly directed hairs (Fig. 3i, j). Most of these characteristics were also observed in Myxophaga (Anton and Beutel 2006) and polyphagan groups outside Staphylinodea (Beutel et al. 2001; Anton and Beutel 2004, 2012; Anton et al. 2016). The basal coleopteran interrelationships revealed in a comprehensive recent study (McKenna et al. 2015) suggest that a similar configuration may be a groundplan feature of the entire Coleoptera, with independent losses in Adephaga and Archostemata, as previously hypothesized by Beutel et al. (2001). In contrast to the apparently conservative entire complex, some components of the mandibles and maxillae (e.g. prostheca, mandibular apex, retinaculum, galea, lacinia) are very diverse, even between less inclusive taxa such as for instance Leiodidae (e.g. Betz et al. 2003; Moldovan et al. 2004). This variability probably reflects the strong selective pressures involving the paired mouthparts in the context of preferred food material (Betz et al. 2003). The high variability impedes the groundplan reconstruction of these structures for Leiodidae or Cholevinae. Nevertheless, unlike other leiodids, the species studied here is not specialized on a particular food substrate or habitat, which likely represents the plesiomorphic way of life among Cholevinae.

Another noteworthy character confirmed for *Catops* is the strong constriction of the labiohypopharyngeal complex (Fig. 3k), which occurs at the level of the basal maxillary portion. As a result, the labiohypopharyngeal complex appears hourglass-shaped in cross-section. This feature has been found in many other staphyliniform beetles (e.g. Jäch et al. 2000; Beutel et al. 2001; Beutel et al. 2003; Anton and Beutel 2004; Weide and Betz 2009), and more recently in the scarabaeoid *Glaresis* (Anton and Beutel 2012). The absence in some subordinate taxa such as the leiodine genus *Agathidium* (Weide and Betz 2009) is apparently due to secondary modification. The presence of this derived condition has been postulated as autapomorphy of a clade Staphyliniformia including Scarabaeodea (Beutel and Leschen 2005), which is equivalent with Staphyliniformia in a narrower sense + Scarabaeodea as recovered by McKenna et al. (2015).

Based on molecular data, McKenna et al. (2015) recovered Leiodidae as monophyletic except for the unexpected position of *Colon* as sister to Hydraenidae + Ptiliidae. Likewise, Cholevinae was recovered as monophyletic with the exclusion of *Afrocatops* (Oritocatopini) (McKenna et al. 2015), and with the exclusion of *Eucatops* (Eucatopini) in Fresneda et al. (2011). Specific external features documented here for the head of *Catops* have been considered as potential autapomorphies of Leiodidae (Newton 2016). This includes a moderately compact 5-segmented antennal club with the eighth

antennomere smaller than the rest (Fig. 2f), and the presence of periarticular grooves filled with sensilla (Fig. 2h, i) on antennomeres 7, 9 and 10. An unusual derived feature of Cholevinae is the head shape firmly connected to the pronotum with the margin of contact delimited by a transverse carina (Fig. 2e; absent medially in Eucatopini and Oritocatopini). In many species of Leptodirini, however, this characteristic is secondarily modified, presumably as a result of the morphological changes associated to subterranean habits. As described here for *Catops* (Fig. 2c), a conspicuous genal fold covers the posterior face of the compound eyes in cholevines as a whole, although it has been lost in several eyeless Leptodirini. This trait differentiates Cholevinae from most other leiodids, but a similar condition is found in the head of the few members of Platypsyllinae even though the eyes are missing. The presence of the postocular genal fold in the mentioned groups as well as its occurrence in Hydraenidae (Jäch et al. 2000; Beutel et al. 2003) and within Hydrophiloidea (Beutel 1994; Beutel et al. 2001; Anton and Beutel 2004) probably reflects independent gains.

A set of cryptic pore plates on the preapical and apical maxillary palpomeres of *Catops* (see detail in Fig. 3f, g) has not been reported before in the literature. These structures are present in many species of Cholevinae, including representatives of the most diverse tribes, such as Anemadini, Cholevini, Ptomaphagini and Leptodirini (CAC pers. obs.). Similar structures were not found in Eucatopini and Oritocatopini. They are also lacking in outgroup taxa such as in Camiarinae (*Agyrtodes*), Leiodinae (*Colenisia*, *Decuria*, *Zeadolopus*), Platypsyllinae (*Leptinus*), and in Agyrtidae (*Zeanecrophilus*) (CAC pers. obs.). It is uncertain if the pore plates are associated to maxillary glands, since we could not detect any evidence based on the  $\mu$ CT scans. Due to its very small size, the pore plate may have been overlooked in some groups, but based on the available data, it seems to be apomorphic for a group inside the subfamily – i.e. Cholevinae minus Eucatopini and Oritocatopini. The presence of an apical maxillary palpomere shorter than or at most as long as the subapical one, as documented in *Catops* (Fig. 2c, d), is a derived condition also shared by Cholevinae with the exception of Eucatopini and Oritocatopini, whose apical maxillary palpomere is elongate. As mentioned above, Oritocatopini and Eucatopini have been phylogenetically isolated from the remaining Cholevinae in recent molecular analyses (Fresneda et al. 2011; McKenna et al. 2015). More data are required to understand their phylogenetic position within Leiodidae.

## **Tentorium and cephalic musculature**

The internal cephalic structures of *Catops* are mainly plesiomorphic. The tentorium agrees with the configuration suggested for the groundplan of Staphyloidea (Weide et al. 2014), formed by paired anterior, dorsal and posterior arms, a fused laminatentorium, and an uninterrupted tentorial bridge. In contrast, in the related leiodid *Agathidium* and Agyrtidae, the dorsal tentorial arms are missing in the former and the laminatentorium is unfused in the latter (Weide et al. 2014). A laminatentorium is lacking in the highly miniaturized Ptiliidae (Polilov and Beutel 2009).

The pattern of muscles is similar to what is found in other staphylinoid taxa (e.g. Jäch et al. 2000; Beutel et al. 2003) and is close to the hypothesized groundplan of Staphyloidea, which according to Weide et al. (2010) is composed by the following muscles: 1, 2, 4, 7, 9, 11, 12, 15, 17-19, Mx, 28-30, 34, 41, 43-46, 48, 50. The muscle 'Mx' was first described in Hydraenidae (Jäch et al. 2000) and later reported in other staphylinoid groups such as Agyrtidae and Staphylinidae (Oxytelinae and Omaliinae: Weide and Betz 2009; Proteininae: Anton and Beutel 2012). It originates on the genal region and inserts on the membranous area between the maxilla and hypopharynx. Whereas it is present in *Catops*, the muscle was not found in the leiodid *Agathidium* (Leiodinae, Agathidini), and is apparently also missing in Ptiliidae (Polilov and Beutel 2009) and in the staphylinids Tachyporinae and Aleocharinae (Weide and Betz 2009). The occurrence of 'Mx' in Hydrophilidae ('M19a' in Spercheinae: Beutel et al. 2001; 'Mx2' in Helophorinae: Anton and Beutel 2004; Hydrochinae: Anton and Beutel 2012) and Sphaeritidae (Anton and Beutel 2012) suggests its presence in the groundplan of Staphyliniformia. However, the recent discovery of a likely homologue in Geotrupidae and Scarabaeidae (named as '*M. craniobasimaxillaris*' by Anton and Beutel 2012) suggests that this unusual muscle has appeared even earlier in the evolution of beetles, with independent loss in several groups. The presence of 'Mx' in the groundplan of Coleoptera can be ruled out as it was not found in Adephaga (Dressler and Beutel 2010), Archostemata (Hörschemeyer et al. 2002, 2006; Beutel et al. 2008), and Myxophaga (Anton and Beutel 2006), and is also absent in Dascillidae (Anton and Beutel 2012) and cucujiform taxa (Schneider 1981; Ge et al. 2015). Like the hypopharynx strongly narrowed between the maxillary bases this is likely a groundplan apomorphy of a clade comprising Staphyliniformia and Scarabaeoidea.

The presence of *M. frontoepipharyngalis* (M9) is ancestral for Coleoptera (e.g. Weide and Betz 2009) and is preserved in the groundplan of Staphyloidea. However, it is missing in *Catops* and also in *Agathidium* (Weide and Betz 2009), in the agyrtid

*Necrophilus* (Weide and Betz 2009), and in the ptiliid *Mikado* (Polilov and Beutel 2009). A lineage formed by Leiodidae + Agyrtidae together with Hydraenidae + Ptiliidae has been placed as the sister group of the remaining Staphylinoidea (Beutel and Leschen 2005; McKenna et al. 2015). The presence of *M. frontoepipharyngalis* in Hydraenidae (Jäch et al. 2000; Beutel et al. 2003) shows that it is present in the groundplan of this clade and was apparently reduced two or more times independently.

The presence of *M. hypopharyngomandibularis* (M13) in Cholevinae is apparently a plesiomorphic feature. Its exact point of origin could not be clarified in *Catops*, but it is inserted medially on the dorsal internal surface of the mandible (Fig. 5a). The muscle was not identified in detailed studies on the head of Adephaga (Dressler and Beutel 2010), Archostemata (Hörschemeyer et al. 2002, 2006; Beutel et al. 2008), Myxophaga (Anton and Beutel 2006) and of various lineages of Polyphaga (e.g. Beutel et al. 2003; Weide and Betz 2009; Anton and Beutel 2012; Anton et al. 2016). However, it is documented for *Gyrinus* and *Dermestes* (Honomichl 1975, 1976: as *M. tentoriomandibularis*) and also in *Lytta* (Schneider 1981) and is therefore very likely ancestral for Coleoptera. It also occurs in many other groups of insects, for instance in the primarily wingless Archaeognatha and Zygentoma (Blanke et al. 2012), in Odonata and Ephemeroptera (Blanke et al. 2012), in polyneopteran orders (Wipfler et al. 2011), and in different groups of Holometabola including the basal Hymenoptera (Beutel and Vilhelmsen 2007; Beutel et al. 2008). It is usually extremely thin and may have been overlooked in some studies. Nevertheless, it was apparently reduced several or many times independently in Coleoptera.

Among the staphyliniform beetles hitherto investigated, *M. tentoriohypopharyngalis* (M42) is uniquely present in *Catops*. It was also identified in Hydraenidae (*Hydraena*: Jäch et al. 2000; *Ochthebius* and *Limnebius*: Beutel et al. 2003) with a submental origin, even though in this case the homology remains disputable. In any case, the presence in *Catops* is in contrast to the suggested absence in the groundplan of Staphylinoidea (Weide et al. 2010). Moreover, the muscle was also found in *Glareis* (Anton and Beutel 2012), a basal representative of Scarabaeoidea (see McKenna et al. 2015), suggesting its presence in the groundplan of Staphyliniformia + Scarabaeoidea. *M. tentoriobuccalis anterior* (M48) was misidentified in many studies as M42 (e.g. Beutel et al. 2001; Anton and Beutel 2004, 2006; Weide and Betz 2009), until this issue was clarified in Beutel et al. (2009) and Weide and Betz (2010).



## Functional interpretation of the feeding apparatus

*Catops ventricosus* is frequently found in caves or under leaf litter of forested landscapes. They forage on debris derived from different kinds of decaying organic matter such as carrion, dung or plant material (Salgado 1985; Salgado-Costas and Vázquez-Blanco 1993; Salgado and Fernández 1998). However, facultative feeding on fungal spores does also occur. The functional configuration of the feeding apparatus is similar to the condition encountered in most other staphylinoids feeding on small particles (see Betz et al. 2003). The robust brush of hairs on the apex of the galea plays a major role in food acquisition, although the distal portion of the lacinia is probably also involved in this function. The interactions between the maxillary endite lobes of both sides transport food substrate towards the upper side of the labiohypopharyngeal complex and the preoral cavity. The mandibles likely support this process, sweeping food particles towards the galeae and laciniae with the dense prosthecal brushes, and presumably also onto the dorsal labiohypopharyngeal surface. In the median region of the transition zone of the dorsal prementum and anterior hypopharynx, an area surrounded by a dense field of microtrichia probably concentrates the collected food particles, which are subsequently transported into the preoral cavity. This process is supported by retraction of the prementum, induced by contractions of *M. submentopraementalis* (M28), *M. tentoriopraementalis inferior* (M29) and *M. tentorihypopharyngalis* (M42). Grinding takes place between the molar surface of the mandibles. The epi- and hypopharyngeal tufts of microtrichia along with the prostheca keep the food particles within the preoral space while the material is processed. Parallel rows of microtrichia on the ventral and dorsal molar surfaces interact with similar elements on the cibarial roof and hypopharynx, respectively, transporting the fine particles towards the anatomical mouth. *M. frontohypopharyngalis* probably supports this process by elevating the hypopharynx, thereby narrowing the preoral space and bringing mandibles and hypopharynx in closer contact. In some staphylinids, this process probably results in a trituration of the food substrate by interaction of grinding structures on the ventral molar surface with correspondent structures of the hypopharynx (Weide et al. 2010). This is unlikely in the case of *Catops* as grinding structures are lacking on the hypopharynx. *M. tentoriobuccalis anterior* (M.48) is also involved in the transport by retracting the hypopharynx, which supports the shifting of substrate towards the anatomical mouth (Weide et al. 2014).

## Conclusions

The muscle equipment of the head of *Catops* is largely plesiomorphic, probably close to the groundplan of Staphyliniformia. Our study shows that most cephalic muscles reported here are shared with other staphylinoid lineages. This suggests that the head anatomy is a rather conserved character system in the evolution of this highly diverse superfamily. The same applies to the general traits of the mouthparts and epi- and hypopharynx, mainly characterized by plesiomorphic traits correlated to feeding on small particles. However, *Catops* also displays typical apomorphic features that define the head of Leiodidae and Cholevinae, such as the interrupted five segmented antennal club and the occipital carina abutting with the anterior pronotal edge, respectively. *Catops* has been used as an outgroup representative in higher-level phylogenetic inferences focused on head characters (e.g. Polilov and Beutel 2009; Beutel et al. 2010; Dressler and Beutel 2010; Randolph et al. 2014), although its cephalic morphology has not yet been documented or described in detail. The present contribution is the first to provide a complete characterization of the head structures of a representative of Cholevinae, offering a broad repertoire of characters potentially useful for future phylogenetic studies. When detailed information on cephalic structures of a broader spectrum of staphylinoid beetles become available, the recent molecular phylogeny of McKenna et al. (2015) will be an excellent framework for tracing the character transformations and reaching a deeper understanding of the evolution of the head in this highly successful superfamily.

## Acknowledgments

We are grateful to many members of the Entomology Group (Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena, Germany) for their assistance in different stages of this work. The  $\mu$ CT data acquisition was arranged by Lars Möckel and Katharina Schneeberg. Benjamin Fabian and David Neubert kindly supported CAC with the use of Amira and VGStudio software. Special thanks go to Dr. Hans Pohl, who kindly provided training and advice on scanning electron microscopy and made available a rotatable specimen holder. We are also very grateful to Arnaud Faille and Javier Fresneda for kindly providing valuable specimens. The  $\mu$ CT scans were taken at DESY (Hamburg, Germany), which is gratefully acknowledged. The PhD study of CAC as well as his research internship at the Friedrich-Schiller-Universität was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (2012/19002-0 and 2014/22088-0). PG was also supported by FAPESP (2013/06314-7) and MY by the DAAD, which is

589 also gratefully acknowledged. The stay of IR in the Phyletisches Museum in Jena was  
590 funded by a Salvador de Madariaga grant (PRX14/00583). The helpful comments of two  
591 reviewers are greatly appreciated.

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## References

- Anton, E. & Beutel, R. G. (2004). On the head morphology and systematic position of *Helophorus* (Coleoptera: Hydrophiloidea: Helophoridae). *Zoologischer Anzeiger*, 242, 313–346.
- Anton, E. & Beutel, R. G. (2006). On the head morphology of Lepiceridae (Coleoptera: Myxophaga) and the systematic position of the family and suborder. *European Journal of Entomology*, 103, 85–95.
- Anton, E. & Beutel, R. G. (2012). The adult head morphology of *Dascillus* (L.) (Dascilloidea: Dascillidae) and *Glaresis* Erichson (Scarabaeoidea: Glaresidae) and its phylogenetic implications. *Arthropod Systematics and Phylogeny*, 70(1), 3–42.
- Anton, E., Yavorskaya, M. I. & Beutel, R. G. (2016). The head morphology of Clambidae and its implications for the phylogeny of Scirtoidea (Coleoptera: Polyphaga). *Journal of Morphology*, 277(5), 615–633.
- Beckmann, F., Herzen, J., Haibel, A., Müller, B. & Schreyer, A. (2008). High density resolution in synchrotron-radiation-based attenuation-contrast microtomography. *Proceedings of SPIE*, 7078, 70781D–70781D-13. doi: 10.1117/12.794617
- Betz, O., Thayer, M. K. & Newton, A. F. (2003). Comparative morphology and evolutionary pathways of the mouthparts in spore-feeding Staphylinioidea (Coleoptera). *Acta Zoologica*, 84, 179–238.
- Beutel, R. G. (1994). Phylogenetic analysis of Hydrophiloidea (Coleoptera: Polyphaga: Staphyliniformia) based on characters of the head of adults and larvae. *Koleopterologische Rundschau*, 64, 103–131.
- Beutel, R. G., Anton, E. & Bernhard, D. (2001). Head structures of adults of *Spercheus* (Coleoptera: Spercheidae): their function and possible significance to staphyliniform phylogeny. *Annales Zoologici*, 51(4), 473–484.
- Beutel, R. G., Anton, E. & Jäch, M. A. (2003). On the evolution of the adult head structures and the phylogeny of Hydraenidae (Coleoptera, Staphyliniformia). *Journal of Zoological Systematics and Evolutionary Research*, 41, 256–275.
- Beutel, R. G., Friedrich, F. & Whiting, M. (2008). Head morphology of *Caurinus* (Boreidae, Mecoptera) and its phylogenetic implications. *Arthropod Structure and Development*, 37, 418–433. doi: 10.1016/j.asd.2008.02.002

- Beutel, R. G., Ge, S.-Q. & Hörnschemeyer, T. (2008). On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. *Cladistics*, 23, 1–29.
- Beutel, R. G. & Leschen, R. A. B. (2005). Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. *Systematic Entomology*, 30(4), 510–548. doi: 10.1111/j.1365-3113.2005.00293.x
- Beutel, R. G. & Molenda, R. (1997). Comparative morphological study of larvae of Staphylininoidea (Coleoptera, Polyphaga) with phylogenetic implications. *Zoologischer Anzeiger*, 236, 37–67.
- Beutel, R. G. & Vilhelmsen, L. (2007). Head anatomy of Xyelidae (Hexapoda: Hymenoptera) and phylogenetic implications. *Organisms Diversity and Evolution*, 7, 207–230. doi: 10.1016/j.ode.2006.06.003
- Beutel, R. G., Zimmermann, D., Krauß, M., Randolph, S., & Wipfler, B. (2010). Head morphology of *Osmylus fulvicephalus* (Osmylidae, Neuroptera) and its phylogenetic implications. *Organisms Diversity and Evolution*, 10, 311–329. doi: 10.1007/s13127-010-0024-0
- Blanke, A., Wipfler, B., Letsch, H., Koch, M., Beckmann, F., Beutel, R. & Misof, B. (2012). Revival of Palaeoptera—head characters support a monophyletic origin of Odonata and Ephemeroptera (Insecta). *Cladistics*, 28(6), 560–581. doi: 10.1111/j.1096-0031.2012.00405.x
- Bouchard, P., Bousquet, Y., Davies, A. E., Alonso-Zarazaga, M. A., Lawrence, J. F., Lyal, C. H. C., Newton, A. F., Reid, C. A. M., Schmitt, M., Ślipiński, S. A. & Smith, A. B. T. (2011). Family-group names in Coleoptera (Insecta). *ZooKeys*, 88, 1–972. doi: 10.3897/zookeys.88.807
- Dönges, J. (1954). Der Kopf von *Cionus scrophulariae* L. (Curculionidae). *Zoologische Jahrbuch (Anat)*, 74, 1–76.
- Dressler, C. & Beutel, R. G. (2010). The morphology and evolution of the adult head of Adephaga (Insecta: Coleoptera). *Arthropod Systematics and Phylogeny*, 68(2), 239–287. doi: 10.1111/j.1096-0031.2012.00405.x
- Fresneda, J., Grebennikov, V. V. & Ribera, I. (2011). The phylogenetic and geographic limits of Leptodirini (Insecta: Coleoptera: Leiodidae: Cholevinae), with a description of *Sciaphyes shestakovi* sp. n. from the Russian Far East. *Arthropod Systematics & Phylogeny*, 69(2), 99–123.

- Ge, S.-Q., Hua, Y., Ren, J., Ślipiński, A., Heming, B., Beutel, R. G., Yang, X.-K., & Wipfler, B. (2015). Transformation of head structures during the metamorphosis of *Chrysomela populi* (Coleoptera, Chrysomelidae). *Arthropod Systematics and Phylogeny*, 73 (1), 129–152.
- Greving, I., Wilde, F., Ogurreck, M., Herzen, J., Hammel, J. U., Hipp, A., Friedrich, F., Lottermoser, L., Dose, T., Burmester, H., et al. (2014). P05 imaging beamline at PETRA III: first results. *Proceedings of SPIE* 9212, Developments in X-Ray Tomography IX, 92120O, ed Stuart RS, pp 92120O-92120O-92128.
- Honomichl, K. (1975). Beitrag zur Morphologie des Kopfes der Imago von *Gyrinus substriatus* Stephens, 1829 (Coleoptera, Insecta). *Zoologische Jahrbücher für Anatomie*, 94, 218–295.
- Honomichl, K. (1976). Feinstruktur eines Muskelrezeptors im Kopf von *Dermestes maculatus* De Geer (Insecta, Coleoptera). *Zoomorphology* 85, 59–71.
- Hörschemeyer, T., Beutel, R. G. & Pasop, F. (2002). Head structures of *Priacma serrata* Leconte (Coleoptera, Archostemata) inferred from X-ray tomography. *Journal of Morphology*, 252, 298–314.
- Hörschemeyer, T., Goebels, J., Weidemann, G., Faber, C. & Haase, A. (2006). The head morphology of *Ascioplaga mimeta* (Coleoptera: Archostemata) and the phylogeny of Archostemata. *European Journal of Entomology*, 103, 409–423.
- Huesman, R., Gullberg, G., Greenberg, W. & TF, B. (1977). RECLBL Library users manual: Donner algorithms for reconstruction tomography. Lawrence Berkeley Laboratory, University of California, Livermore.
- Jäch, M. A., Beutel, R. G., Díaz, J. A. & Kodada, J. (2000). Subgeneric classification, description of head structures, and world check list of *Hydraena* Kugelann (Insecta: Coleoptera: Hydraenidae). *Annalen des Naturhistorischen Museums Wien*, 102B, 177–258.
- von Kéler, S. (1963). *Entomologisches Wörterbuch*. Berlin: Akademie Verlag.
- Lawrence, J. F., Ślipiński, A., Seago, A. E., Thayer, M. K., Newton, A. F. & Marvaldi, A. E. (2011). Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici*, 61(1), 1–217. doi: 10.3161/000345411X576725
- McKenna, D. D., Farrell, B. D., Caterino, M. S., Farnum, C. W., Hawks, D. C., Maddison, D. R., Seago, A. E., Short, E. Z., Newton, A. F. & Thayer, M. K. (2015). Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as

- a stepping stone for diversification of nonphytophagous beetles. *Systematic Entomology*, 40(1), 35–60. doi: 10.1111/syen.12093
- McKenna, D. D., Wild, A. L., Kanda, K., Bellamy, C. L., Beutel, R. G., Caterino, M. S., Farnum, C. W., Hawks, D. C., Ivie, M. A., Jameson, M. L., Leschen, R. A. B., Marvaldi, A. E., Mchugh, J. V., Newton, A. F., Robertson, J. A., Thayer, M. K., Whiting, M. F., Lawrence, J. F., Ślipiński, A., Maddison, D. R., & Farrell, B. D. (2015). The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, 40(4), 835–880. doi: 10.1111/syen.12132
- Moldovan, O. T., Jalžić, B., & Erichsen, E. (2004). Adaptation of the mouthparts in some subterranean Cholevinae (Coleoptera, Leiodidae). *Natura Croatica*, 13(1), 1–18.
- Newton, A. F. (1998). Phylogenetic problems, current classification and generic catalog of World Leiodidae (including Cholevidae). *Museo Regionale di Scienze Naturali di Torino Atti*, 8, 41–177.
- Newton, A. F. (2016). Leiodidae Fleming, 1821. *Handbook of Zoology, Vol. IV, Arthropoda: Insecta; Coleoptera, Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), Vol. 1, 2<sup>nd</sup> ed.* (ed. by R. G. Beutel and R. A. B. Leschen), pp. 364–376. Walter De Gruyter, Berlin and New York.
- Perreau, M. (2000) Catalogue des Coléoptères Leiodidae Cholevinae et Platypsyllinae. *Memoires de la Societ  Entomologique de France*, 4, 1–460.
- Pohl, H. (2010). A scanning electron microscopy specimen holder for viewing different angles of a single specimen. *Microscopy Research and Technique*, 73(12), 1073–1076. doi:10.1002/jemt.20835
- Polilov, A. A., & Beutel, R. G. (2009). Miniaturisation effects in larvae and adults of *Mikado* sp. (Coleoptera: Ptiliidae), one of the smallest free-living insects. *Arthropod Structure and Development*, 38, 247–270. doi: 10.1016/j.asd.2008.11.003
- Randolf, S., Zimmermann, D., & Aspöck, U. (2014). Head anatomy of adult *Nevrorthus apatelios* and basal splitting events in Neuroptera (Neuroptera:Nevrorthidae). *Arthropod Systematics & Phylogeny*, 72(2), 111–136.
- Salgado, J. M. (1985). Nuevos datos sobre Catopidae (Col.) capturados en cuevas. *Bolet n de la Asociaci n espa ola de Entomolog a*, 9, 271–277.

- 725 Salgado, J. M., & Fernández, M. (1998). Estudio de los Leiodidae: Cholevinae  
726 (Coleoptera) en las cuencas de los ríos Bernesga, Torío y Porma (León, España).  
727 *Boletín de la Asociación española de Entomología*, 22(1-2), 81–97.
- 728 Salgado-Costas, J. M., & Vázquez-Blanco, M. G. (1993). Estudio de los Carábidos y  
729 Colévidos (Coleoptera) de Cueva Rosa (Asturias, España). *Boletín de la*  
730 *Asociación española de Entomología*, 17(1), 131–142.
- 731 Schneider, W. (1981). Zur Kopfmorphologie der Imago des Ölkäfers *Lytta vesicatora*  
732 (Coleoptera: Meloidea). *Entomologica Generalis*, 7(1), 69–87.
- 733 Weide, D. & Betz, O. (2009). Head morphology of selected Staphylinioidea (Coleoptera:  
734 Staphyliniformia) with an evaluation of possible groundplan features in  
735 Staphylinidae. *Journal of Morphology*, 270, 1503–1523. doi: 10.1002/jmor.10773
- 736 Weide, D., Thayer, M. K., & Betz, O. (2014). Comparative morphology of the tentorium  
737 and hypopharyngeal–premental sclerites in sporophagous and non-sporophagous  
738 adult Aleocharinae (Coleoptera: Staphylinidae). *Acta Zoologica*, 95, 84–110. doi:  
739 10.1111/azo.12011
- 740 Weide, D., Thayer, M., Newton, A. F., & Betz, O. (2010). Comparative morphology of  
741 the head of selected sporophagous and non-sporophagous Aleocharinae  
742 (Coleoptera: Staphylinidae): musculature and hypopharynx-prementum complex.  
743 *Journal of Morphology*, 271, 910–931.
- 744 Wipfler, B., Machida, R., Müller, B. & Beutel, R. (2011). On the head morphology of  
745 Grylloblattodea (Insecta) and the systematic position of the order, with a new  
746 nomenclature for the head muscles of Dicondylia. *Systematic Entomology*, 36,  
747 241–266. doi: 10.1111/j.1365-3113.2010.00556.x



## Figure legends

**Fig. 1** *Catops ventricosus*, head, habitus, photomicrographs. **a** Dorsal view; **b** Ventral view; **c** Frontal view. Images produced by focus stacking.

**Fig. 2** SEM micrographs of the head of *Catops ventricosus*. **a** Dorsal view; **b** Dorsal surface of vertex; **c** Ventral view; **d** Frontal view; **e** Lateral view; **f** Antenna; **g** Eighth antennomere; **h** Ninth antennomere; **i** Detail of the narrow slit opening on the distal surface of the ninth antennomere. Abbreviations: *bs* basistipes, *ce* compound eye, *cl* clypeus, *ca* cardo, *ga* galea, *ge* gena, *gu* gula, *lc* lacinia, *lp* labial palp, *lr* labrum, *md* mandible, *mp* maxillary palp, *ms* mediotypes, *mt* mentum, *oc* occipital crest, *pf* palpifer, *pmt* prementum, *pogf* postocular genal fold, *por* postocular ridge, *smt* submentum, *sc* scapus.

**Fig. 3** SEM micrographs of the mouthparts of *Catops ventricosus*. **a** Dorsal view of left mandible; **b** Ventral view of left mandible; **c** Dorsal view of left maxilla; **d** Ventral view of left maxilla; **e** Dorsal view of apical maxillary palpomere; **f** Lateral view of apical maxillary palpomere; **g** Lateral view of subapical maxillary palpomere; **h** Dorsal surface of labrum; **i** Ventral surface of labrum; **j** Dorsal surface of hypopharynx-prementum complex; **k** Ventral surface of hypopharynx-prementum complex, with arrows indicating areas of origin of selected cephalic muscles. The details in **f** and **g** show pore plates on the surface of the apical and subapical maxillary palpomere, respectively. Abbreviations: *avp* mandibular accessory ventral process, *bs* basistipes, *ca* cardo, *dgts* digitiform sensilla, *ga* galea, *hpp* hypopharynx, *ht* tuft of hairs of the hypopharynx (or longitudinal hypopharyngeal process), *lep* longitudinal epipharyngeal process, *lc* lacinia, *lp* labial palp, *mcnd* mandibular condyle, *ml* mola, *mp* maxillary palp, *ms* mediotypes, *pf* palpifer, *pmt* prementum, *prst* prostheca, *trdg* transversal dorsal ridge. For muscle determination, see the main text.

**Fig. 4** Transverse  $\mu$ CT sections through the head of *Catops ventricosus*. **a–f** Sections in anterior-posterior sequence. Abbreviations: *ata* anterior tentorial arm, *gfr* frontal ganglion, *phr* pharynx. See the main text for muscle identifications.

**Fig. 5** 3D reconstructions of the head capsule, tentorium and muscles associated to mandible and maxilla of *Catops ventricosus*. **a** Dorsal view of the mandibular muscle system; **b** Dorsal view of the maxillar muscle system. *ata* anterior tentorial arm; *dta* dorsal tentorial arm, *hpl* horizontal plate of the laminatentorium, *lt* laminatentorium, *md* mandible, *mp* maxillary palp, *mvl* median vertical lamella of the laminatentorium, *mxl* maxilla, *pta* posterior tentorial arm, *tb* tentorial bridge.

**Fig. 6** 3D reconstructions of the head of *Catops ventricosus*. **a** Sagittal view; **b** Frontal view, transparent cuticle. Muscles associated with mandible, maxilla and antenna not included. Antennae and mouthparts on right side removed in **b**. Abbreviations: *ata* anterior tentorial arm, *cer* cerebrum, *dta* dorsal tentorial arm, *epp* epipharynx, *gfr* frontal ganglion, *hpp* hypopharynx, *lr* labrum, *md* mandible, *mp* maxillary palp, *mt* mentum, *phr* pharynx, *pta* posterior tentorial arm, *soe* suboesophageal ganglion, *tb* tentorial bridge.