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

3

4 **Caio Antunes-Carvalho^{1,2*}, Margarita Yavorskaya², Pedro Gnaspini¹, Ignacio**
5 **Ribera^{2,3}, Jörg Hammel⁴, Rolf Georg Beutel²**

6

7 1: Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua
8 do Matão, Travessa 14, no. 101, 05508-090 São Paulo, SP, Brazil

9 2: Entomology Group, Institut für Spezielle Zoologie und Evolutionsbiologie mit
10 Phyletischem Museum, FSU Jena, Erbertstrasse 1, 07743 Jena, Germany

11 3: Instituto de Biología Evolutiva (CSIC-Universitat Pompeu Fabra), Passeig Maritim
12 de la Barceloneta 37-49, 08003 Barcelona, Spain

13 4: Institute of Materials Research, Helmholtz-Zentrum Geesthacht, Outstation at DESY,
14 Building 66, Notkestr. 85, D-22607 Hamburg, Germany

15

16 * Corresponding author: Caio Antunes-Carvalho, Departamento de Zoologia, Instituto
17 de Biociências, Universidade de São Paulo, Rua do Matão, Travessa 14, no. 101,
18 05508-090 São Paulo, SP, Brazil. E-mail: cantunescarvalho@gmail.com

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21

22 **Abstract** Adult head structures are well known in the coleopteran suborders
23 Archostemata and Adephaga, whereas the available information is very fragmentary in
24 the megadiverse Polyphaga, including the successful superfamily Staphylinoidea. In the
25 present study the cephalic morphology of the cholevine species *Catops ventricosus* is
26 described in detail and documented. The results were compared to conditions occurring
27 in other polyphagan lineages, especially staphylinoid and scarabaeoid representatives.
28 Specific external features documented in *Catops* and potential autapomorphies of
29 Leiodidae include a 5-segmented antennal club with the eighth antennomere smaller than
30 the rest and the presence of periarticular grooves filled with sensilla on antennomeres 7,
31 9 and 10. The firm connection of the head and pronotum is possibly an apomorphy of
32 Cholevinae. The monophyly of Cholevinae excluding Eucatopini and Oritocatopini is
33 supported by the apical maxillary palpomere as long as or shorter than the subapical one,
34 and the presence of cryptic pore plates on the surface of these palpomeres – a feature
35 described and documented here for the first time. The internal cephalic structures of
36 *Catops* are mostly plesiomorphic, as for instance the complete tentorium. The pattern of
37 muscles is similar to what is found in other staphylinoid taxa. The unusual maxillary
38 muscle ‘Mx’ is likely a groundplan apomorphy of the clade Staphyliniformia +
39 Scarabaeoidea. *M. hypopharyngomandibularis* (M13) was identified in *Catops* and is
40 ancestral for Coleoptera, even though it is often missing. The same applies to *M.*
41 *tentoriohypopharyngalis* (M42).

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

44

45 **Introduction**

46 It was shown in previous studies on Archostemata (Beutel et al. 2008) and Adephaga
47 (Dressler and Beutel 2010) that the cephalic anatomy of Coleoptera is a complex and
48 phylogenetically informative character system, which can also reveal important insights
49 in life strategies, especially but not only in the context of feeding. The available
50 information on adult head structures of Coleoptera has considerably increased in the last
51 decade, facilitated by advanced morphological techniques (e.g. Beutel et al. 2008; Anton
52 et al. 2016). Head structures of Archostemata (Hörnschemeyer et al. 2002; Beutel et al.
53 2008), Adephaga (e.g. Dressler and Beutel 2010), and the myxophagan family
54 Lepiceridae (Anton and Beutel 2006) are very well known. In contrast, the available
55 information on the cephalic morphology of the megadiverse Polyphaga is still very
56 fragmentary. Earlier studies are those of Dönges (1954) on the weevil *Cionus* or the study
57 of Schneider (1981) on the Spanish fly *Lytta* (Meloidae), both highly specialized taxa of
58 Cucujiformia. Anatomical data on the presumably basal Scirtoidea (McKenna et al. 2015)
59 became available only recently (Anton et al. 2016) and detailed studies on the extremely
60 species-rich Staphylinoidea are still very sparse. Interestingly, larval head structures are
61 relatively well known (e.g. Beutel and Molenda, 1997; Beutel and Leschen 2005),
62 whereas detailed data on adult cephalic structures are only available for few species of
63 the aquatic Hydraenidae (Beutel et al. 2003), the strongly miniaturized Ptiliidae (Polilov
64 and Beutel 2001), the small family Agyrtidae (Weide and Betz 2009), and few species of
65 the highly diverse Staphylinidae (Weide and Betz 2009; Weide et al. 2010, 2015).

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

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

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

101

102 **Material and methods**

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

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

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

127 Detailed morphological studies on the head of staphyliniform and scarabaeoid
128 beetles were used for comparison (e.g. Jäch et al. 2000; Beutel et al. 2001, 2003; Anton
129 and Beutel 2004; Polilov and Beutel 2009; Weide and Betz 2009; Weide et al. 2010;
130 Anton and Beutel 2012). Muscles are named following the terminology of von Kéler
131 (1963).

132

133 **Results**

134 **External head capsule**

135 The posterior part of the prognathous head is abruptly narrowed thus forming a distinct
136 neck region, which lies on a lower level dorsally and is retracted into the prothorax (Figs.
137 1 and 2). The posterodorsal border of the exposed part of the head is delimited by an
138 occipital crest, which is firmly connected to the anterior edge of the pronotum (oc, Fig.
139 2a, e). The head capsule is mostly black, but the appendages vary from dark yellowish
140 brown (antennae, maxillary palps and most parts of cardo and stipes) to pale yellow
141 (galea, lacinia and labial palps) (Fig. 1). The dorsal surface of the head except for the
142 neck region is microgranulated and densely covered with regularly distributed, medium
143 length yellowish setae (Fig. 1a, c). The dorsal punctures are enclosed by a distinct rim
144 (Fig. 2b). Setae are also present on most parts of the ventral side of the head, except for
145 the gula (Fig. 2c). The ventral cuticular surface is weakly striated on the mentum and
146 submentum, strongly striated on the genae, and strongly reticulated on the gula (Fig. 2c).

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

162

163 **Cephalic endoskeleton**

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

180

181 **Labrum**

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

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

196

197 **Antenna**

198 The insertion of the 11-segmented (Fig. 2f) antenna is clearly visible from above (Fig.
199 2a). The scapus is composed of a nearly globular articulatory piece and an elongated
200 cylindrical shaft. The cylindrical pedicellus is shorter and also shorter than the elongated
201 antennomere 3. The following segments are distinctly shorter and slightly widening
202 distally. Segment 6 is wider than long. Antennomeres 7-11 form an indistinct club.
203 Antennomere 7 is large and cupola-shaped and its apical part partly covers the small
204 antennomere 8 (Fig. 2f). Segments 9 and 10 are almost as large as 7 and similarly shaped.
205 The terminal antennomere 11 is elongate and subconical on its distal half (Fig. 2f). A
206 distal periarticular gutter bearing sensilla is present on antennomeres 7, 9 and 10, visible
207 through a narrow slit-like opening on the apical surface of these segments (Fig. 2h, i;
208 compare with Fig. 2g). All antennomeres are densely covered with setae. Some longer,
209 curved setae are distributed laterally along the distal face of the antennomeres 7, 9 and
210 10, close to the apical border. On the distal antennomere the setae are laterally inserted at
211 the end of the most expanded part of the segment and also at the apex (Fig. 2f). Numerous
212 short peg-like sensilla are present at the distal margin of antennomeres 7, 9 and 10 (Fig.
213 2i). Some thinner, longer proprioceptive sensilla are also present on these antennomeres,
214 oriented towards the central axis of the antennae (Fig. 2h, i).

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

222

223 **Mandible**

224 The mandibles are largely symmetrical, with the lateral margins somewhat rounded (Fig.
225 3a, b). The external side is broad at the base and narrows toward a moderately acute apex,
226 which is proximally adjoined by a sinuous, dorsal cutting edge (Fig. 3a). A retinaculum,
227 in the form of a very weakly developed blunt process, is present at midlength between the
228 mandibular apex and the distal margin of the mola (Fig. 3a). It is slightly more prominent
229 on the right mandible. The well-developed prosthema bears a dense brush of long
230 microtrichia along the mesal border of the ventral mandibular side, from the incisor area
231 to the mola (prst, Fig. 3b). On the ventral face of the mandible, a weak elevation occupies
232 a large area of the mesal region of the surface. A row of hairs arises from the distal and
233 mesal limits of this area (Fig. 3b). A ventral accessory process is present mesally close to
234 the basal mandibular edge (avp, Fig. 3b). Oblique rows of posteriorly directed
235 microtrichia characterize the dorsal surface of the large mola (ml, Fig. 3b). The molar
236 area is delimited by a slight depression of the mandibular surface, and is therefore not
237 firmly united to the rest of the mandible (condition defined as ‘loosely attached’ in Betz
238 et al. 2003). Its mesal grinding surface is densely covered by regularly distributed
239 asperities or small denticles, while the ventral surface bears dense rows of short hairs.

240 Musculature: *M. craniomandibularis internus* (M11) – (O) posterolateral area of
241 head capsule, slightly posterior to eyes, and from posteriormost cephalic region laterad
242 the occipital foramen; (I) medially on mandibular base, with strong adductor tendon (Figs.
243 4d–f and 5a). *M. craniomandibularis externus* (M12) – (O) genal region, and from
244 posteriormost part of head capsule, close to occipital foramen and attachment area of
245 M11; (I) laterally on mandibular base with abductor tendon (Figs. 4d–f and 5a). *M.*
246 *hypopharyngo-mandibularis* (M13), a thin muscle – (O) from region of posterodorsal
247 surface of laminatentorium but exact point of origin not recognizable; (I) medially on
248 mandibular base, relatively close to insertion of M11 (Figs. 4e and 5a).

249

250 **Maxillae**

251 The moderately deep maxillary grooves anteromesad the compound eyes have a smooth
252 surface. They are mesally bordered by the anterior third of the lateral edge of the
253 submentum, and posteriorly and laterally by a distinct curved line. A distinct lateral genal
254 edge is present above the lateral maxillary base, with a snap anteriorly directed edge
255 below the ventral mandibular base. The short transverse cardo is rounded posterolaterally
256 and has nearly straight anterior and mesal edges (ca, Figs. 2c and 3d). It is mostly
257 glabrous, with only four setae on its basal part. The basistipes is elongate and triangular,
258 with a single seta at each corner (bs, Fig. 3d). The mediostipes (ms, Fig. 3d) is continuous
259 with the lacinia, which is long and narrow (lc, Fig. 3c). Its mesal edge bears a
260 semimembranous seam densely covered with microtrichia, while the ventral surface is
261 mostly covered with small cuticular protuberances. The apex is strongly sclerotized and
262 hook-shaped. The subapical edge bears a dense set of thorn-like structures (Fig. 3c). The
263 galea is composed of a short proximal segment, subtriangular in ventral view (ga, Fig.
264 3c). The distal segment is elongate, with a dense apical brush of setae and a fringe of long
265 setae along the mesal edge of the dorsal side. Small finger-like cuticular protuberances
266 are present on the anteromesal edge of the ventral face (Fig. 3c, d). The palpifer is
267 elongate and subtriangular (pf, Fig. 3c). The palp is 4-segmented (mp, Fig. 3c). Palpomere
268 I is very short, whereas the palpomeres II–IV are about twice as long as the maximum
269 width. Palpomeres II and III are distinctly widening distally and slightly curved inwards.
270 Palpomere IV is conical and apically rounded. A parallel arrangement of about 20
271 digitiform sensilla is present on its dorsal surface (dgts, Fig. 3e, f). Small pore plates are
272 distributed over the surface of palpomeres III and IV (Fig. 3f, g) and a sensorial field is
273 present at the apex of palpomere IV.

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

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

291

292 **Labium**

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

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

317 process of lateral wall of prementum (see origin of M34) (Figs. 3k, 4b, c and 6a). *M.*
318 *tentoriopraementalis superior* (M30), very thin muscle – (O) medially on submentum,
319 posterior to origin of M28 and close to origin of M42; (I) basal labial palpomere (Figs.
320 4a–c and 6a). *M. praementopalpalis externus* (M34) – (O) anterior surface of sclerotized,
321 mesally directed process of lateral wall of prementum; (I) basal margin of basal
322 palpomere (Figs. 3k, 4a and 6a).

323

324 **Epipharynx**

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

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

334

335 **Hypopharynx**

336 The hypopharynx is firmly connected with the posterior part of the prementum (hpp, Fig.
337 3j). It is composed of a pair of elongated, posteriorly divergent lobes. The dorsal surface
338 of each of them is densely covered with multiple oblique parallel rows of microtrichia. A
339 conspicuous tuft of erect microtrichia is present medially on the posterior part of the
340 dorsal surface (ht, Fig. 3j). The concave lateral walls of the hypopharynx are sclerotized
341 and medially fused (Fig. 3k).

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

350

351 **Pharynx**

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

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

366

367 **Brain and suboesophageal ganglion**

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

375

376 **Discussion**

377

378 **Head capsule, appendages and labiohypopharyngeal complex**

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

385 and epipharyngeal and hypopharyngeal median tufts of posteriorly directed hairs (Fig. 3i,
386 j). Most of these characteristics were also observed in Myxophaga (Anton and Beutel
387 2006) and polyphagan groups outside Staphylinoidea (Beutel et al. 2001; Anton and
388 Beutel 2004, 2012; Anton et al. 2016). The basal coleopteran interrelationships revealed
389 in a comprehensive recent study (McKenna et al. 2015) suggest that a similar
390 configuration may be a groundplan feature of the entire Coleoptera, with independent
391 losses in Adephaga and Archostemata, as previously hypothesized by Beutel et al. (2001).
392 In contrast to the apparently conservative entire complex, some components of the
393 mandibles and maxillae (e.g. prostheca, mandibular apex, retinaculum, galea, lacinia) are
394 very diverse, even between less inclusive taxa such as for instance Leiodidae (e.g. Betz
395 et al. 2003; Moldovan et al. 2004). This variability probably reflects the strong selective
396 pressures involving the paired mouthparts in the context of preferred food material (Betz
397 et al. 2003). The high variability impedes the groundplan reconstruction of these
398 structures for Leiodidae or Cholevinae. Nevertheless, unlike other leiodids, the species
399 studied here is not specialized on a particular food substrate or habitat, which likely
400 represents the plesiomorphic way of life among Cholevinae.

401 Another noteworthy character confirmed for *Catops* is the strong constriction of the
402 labiohypopharyngeal complex (Fig. 3k), which occurs at the level of the basal maxillary
403 portion. As a result, the labiohypopharyngeal complex appears hourglass-shaped in cross-
404 section. This feature has been found in many other staphyliniform beetles (e.g. Jäch et al.
405 2000; Beutel et al. 2001; Beutel et al. 2003; Anton and Beutel 2004; Weide and Betz
406 2009), and more recently in the scarabaeoid *Glaresis* (Anton and Beutel 2012). The
407 absence in some subordinate taxa such as the leiodine genus *Agathidium* (Weide and Betz
408 2009) is apparently due to secondary modification. The presence of this derived condition
409 has been postulated as autapomorphy of a clade Staphyliniformia including
410 Scarabaeoidea (Beutel and Leschen 2005), which is equivalent with Staphyliniformia in
411 a narrower sense + Scarabaeoidea as recovered by McKenna et al. (2015).

412 Based on molecular data, McKenna et al. (2015) recovered Leiodidae as
413 monophyletic except for the unexpected position of *Colon* as sister to Hydraenidae +
414 Ptiliidae. Likewise, Cholevinae was recovered as monophyletic with the exclusion of
415 *Afrocatops* (Oritocatopini) (McKenna et al. 2015), and with the exclusion of *Eucatops*
416 (Eucatopini) in Fresneda et al. (2011). Specific external features documented here for the
417 head of *Catops* have been considered as potential autapomorphies of Leiodidae (Newton
418 2016). This includes a moderately compact 5-segmented antennal club with the eighth

419 antennomere smaller than the rest (Fig. 2f), and the presence of periarticular grooves filled
420 with sensilla (Fig. 2h, i) on antennomeres 7, 9 and 10. An unusual derived feature of
421 Cholevinae is the head shape firmly connected to the pronotum with the margin of contact
422 delimited by a transverse carina (Fig. 2e; absent medially in Eucatopini and
423 Oritocatopini). In many species of Leptodirini, however, this characteristic is secondarily
424 modified, presumably as a result of the morphological changes associated to subterranean
425 habits. As described here for *Catops* (Fig. 2c), a conspicuous genal fold covers the
426 posterior face of the compound eyes in cholevines as a whole, although it has been lost
427 in several eyeless Leptodirini. This trait differentiates Cholevinae from most other
428 leiodids, but a similar condition is found in the head of the few members of Platypsyllinae
429 even though the eyes are missing. The presence of the postocular genal fold in the
430 mentioned groups as well as its occurrence in Hydraenidae (Jäch et al. 2000; Beutel et al.
431 2003) and within Hydrophiloidea (Beutel 1994; Beutel et al. 2001; Anton and Beutel
432 2004) probably reflects independent gains.

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

451

452 **Tentorium and cephalic musculature**

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

460 The pattern of muscles is similar to what is found in other staphylinoid taxa (e.g.
461 Jäch et al. 2000; Beutel et al. 2003) and is close to the hypothesized groundplan of
462 Staphyloidea, which according to Weide et al. (2010) is composed by the following
463 muscles: 1, 2, 4, 7, 9, 11, 12, 15, 17-19, Mx, 28-30, 34, 41, 43-46, 48, 50. The muscle
464 'Mx' was first described in Hydraenidae (Jäch et al. 2000) and later reported in other
465 staphylinoid groups such as Agyrtidae and Staphylinidae (Oxytelinae and Omaliinae:
466 Weide and Betz 2009; Proteininae: Anton and Beutel 2012). It originates on the genal
467 region and inserts on the membranous area between the maxilla and hypopharynx.
468 Whereas it is present in *Catops*, the muscle was not found in the leiodid *Agathidium*
469 (Leiodinae, Agathidini), and is apparently also missing in Ptiliidae (Polilov and Beutel
470 2009) and in the staphylinids Tachyporinae and Aleocharinae (Weide and Betz 2009).
471 The occurrence of 'Mx' in Hydrophilidae ('M19a' in Spercheinae: Beutel et al. 2001;
472 'Mx2' in Helophorinae: Anton and Beutel 2004; Hydrochinae: Anton and Beutel 2012)
473 and Sphaeritidae (Anton and Beutel 2012) suggests its presence in the groundplan of
474 Staphyliniformia. However, the recent discovery of a likely homologue in Geotrupidae
475 and Scarabaeidae (named as '*M. craniobasimaxillaris*' by Anton and Beutel 2012)
476 suggests that this unusual muscle has appeared even earlier in the evolution of beetles,
477 with independent loss in several groups. The presence of 'Mx' in the groundplan of
478 Coleoptera can be ruled out as it was not found in Adepaga (Dressler and Beutel 2010),
479 Archostemata (Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008), and Myxophaga
480 (Anton and Beutel 2006), and is also absent in Dascillidae (Anton and Beutel 2012) and
481 cucujiform taxa (Schneider 1981; Ge et al. 2015). Like the hypopharynx strongly
482 narrowed between the maxillary bases this is likely a groundplan apomorphy of a clade
483 comprising Staphyliniformia and Scarabaeoidea.

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

487 *Necrophilus* (Weide and Betz 2009), and in the ptiliid *Mikado* (Polilov and Beutel 2009).
488 A lineage formed by Leiodidae + Agyrtidae together with Hydraenidae + Ptiliidae has
489 been placed as the sister group of the remaining Staphylinoidea (Beutel and Leschen
490 2005; McKenna et al. 2015). The presence of *M. frontoepipharyngalis* in Hydraenidae
491 (Jäch et al. 2000; Beutel et al. 2003) shows that it is present in the groundplan of this
492 clade and was apparently reduced two or more times independently.

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

509 Among the staphyliniform beetles hitherto investigated, *M.*
510 *tentoriohypopharyngalis* (M42) is uniquely present in *Catops*. It was also identified in
511 Hydraenidae (*Hydraena*: Jäch et al. 2000; *Ochthebius* and *Limnebius*: Beutel et al. 2003)
512 with a submental origin, even though in this case the homology remains disputable. In
513 any case, the presence in *Catops* is in contrast to the suggested absence in the groundplan
514 of Staphylinoidea (Weide et al. 2010). Moreover, the muscle was also found in *Glaresis*
515 (Anton and Beutel 2012), a basal representative of Scarabaeoidea (see McKenna et al.
516 2015), suggesting its presence in the groundplan of Staphyliniformia + Scarabaeoidea. *M.*
517 *tentoriobuccalis anterior* (M48) was misidentified in many studies as M42 (e.g. Beutel et
518 al. 2001; Anton and Beutel 2004, 2006; Weide and Betz 2009), until this issue was
519 clarified in Beutel et al. (2009) and Weide and Betz (2010).

520

521 **Functional interpretation of the feeding apparatus**

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

553

554 **Conclusions**

555 The muscle equipment of the head of *Catops* is largely plesiomorphic, probably
556 close to the groundplan of Staphyliniformia. Our study shows that most cephalic muscles
557 reported here are shared with other staphylinoid lineages. This suggests that the head
558 anatomy is a rather conserved character system in the evolution of this highly diverse
559 superfamily. The same applies to the general traits of the mouthparts and epi- and
560 hypopharynx, mainly characterized by plesiomorphic traits correlated to feeding on small
561 particles. However, *Catops* also displays typical apomorphic features that define the head
562 of Leiodidae and Cholevinae, such as the interrupted five segmented antennal club and
563 the occipital carina abutting with the anterior pronotal edge, respectively. *Catops* has been
564 used as an outgroup representative in higher-level phylogenetic inferences focused on
565 head characters (e.g. Polilov and Beutel 2009; Beutel et al. 2010; Dressler and Beutel
566 2010; Randolph et al. 2014), although its cephalic morphology has not yet been
567 documented or described in detail. The present contribution is the first to provide a
568 complete characterization of the head structures of a representative of Cholevinae,
569 offering a broad repertoire of characters potentially useful for future phylogenetic studies.
570 When detailed information on cephalic structures of a broader spectrum of staphylinoid
571 beetles become available, the recent molecular phylogeny of McKenna et al. (2015) will
572 be an excellent framework for tracing the character transformations and reaching a deeper
573 understanding of the evolution of the head in this highly successful superfamily.

574

575

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592

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748 **Figure legends**

749

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

752

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

761

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

776

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

780

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

787

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

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