New Insights into the Complex Structure and Ontogeny of the Occipito-Vertebral Gap in Barbeled Dragonfishes (Stomiidae, Teleostei)

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ABSTRACT In all stomiid genera there is an occipito-vertebral gap between the skull and the first vertebra bridged only by the flexible notochord. Morphological studies from the early 20th century suggested that some stomiid genera have 1–10 of the anteriormost centra reduced or entire vertebrae missing in this region. Our study reviews this previous hypothesis. Using a new approach, we show that only in *Chauliodus*, *Eustomias* and *Leptostomias gladiator* vertebral centra are actually lost, with their respective neural arches and parapophyses persisting. We present results from a comparative analysis of the number and insertion sites of the anteriormost myosepta in 26 of the 28 stomiid genera. Generally in teleosts the first three myosepta are associated with the occiput, and the fourth is the first vertebral myoseptum. The insertion site of the fourth myoseptum plays an important role in this analysis, because it provides a landmark for the first vertebra. Lack of association of the fourth myoseptum with a vertebra is thus evidence that the first vertebra is reduced or absent. By counting the occipital and vertebral myosepta the number of reduced vertebrae in *Chauliodus*, *Eustomias* and *Leptostomias gladiator* can be inferred. Proper identification of the spino-occipital nerves provides an additional source of information about vertebral reduction. In all other stomiid genera the extensive occipito-vertebral gap is not a consequence of the reduction of vertebrae, but of an elongation of the notochord. The complex structure and ontogeny of the anterior part of the vertebral column of stomiids are discussed comparatively. J. Morphol. 000:000–000, 2010. © 2010 Wiley-Liss, Inc.

KEY WORDS: *Chauliodus*; *Eustomias*; *Leptostomias gladiator*; myosepta; spino-occipital nerves; vertebral reduction; mesopelagic

INTRODUCTION

Several morphological studies in the early 20th century revealed that a number of stomiid genera appear unique among teleosts in having 1–10 of the anteriormost vertebrae reduced or absent (Sell, 1916; Regan and Trewavas, 1930; Beebe, 1934; Tchernavin, 1953; Günther and Deckert, 1955, 1959; Morrow, 1964; Morrow and Gibbs, 1964). Only 14 of the currently valid 28 stomiid genera (Nelson, 2006) have previously been studied with regard to vertebral reduction. Furthermore, this reorganisation of the anterior portion of the vertebral column has never been included as a character in phylogenetic analyses, because it has remained poorly understood. Assumptions about the number of reduced vertebrae are mainly based on Regan and Trewavas (1930). They counted the persisting neural arches, parapophyses, and spinal nerves and so determined the number of reduced vertebral centra, however their conclusions were founded on a critical misinterpretation of the occipital innervation. They identified the nerves anterior to the first neural arch as spinal nerves that have lost their respective vertebrae, whereas these nerves are actually spino-occipital nerves that belong to the occiput and have no associated vertebrae. With a new approach, counting the occipital and vertebral myosepta and spino-occipital nerves, we reinvestigate 26 of 28 stomiid genera, revise previous hypotheses that propose one or more lost vertebrae in stomiids, determine the exact number of reduced vertebral centra in the different taxa and discuss their homology.

1. Occipital myosepta: Myosepta are segmentally arranged sheaths of connective tissue that separate adjacent muscle myomeres. They persist even in the absence of vertebrae, in which case they insert on the notochord. In teleosts there are three myosepta dorsally in the epaxial musculature that are associated with the occipital region (Fig. 1a) as a consequence of an evolutionary incorporation of vertebral segments into the skull
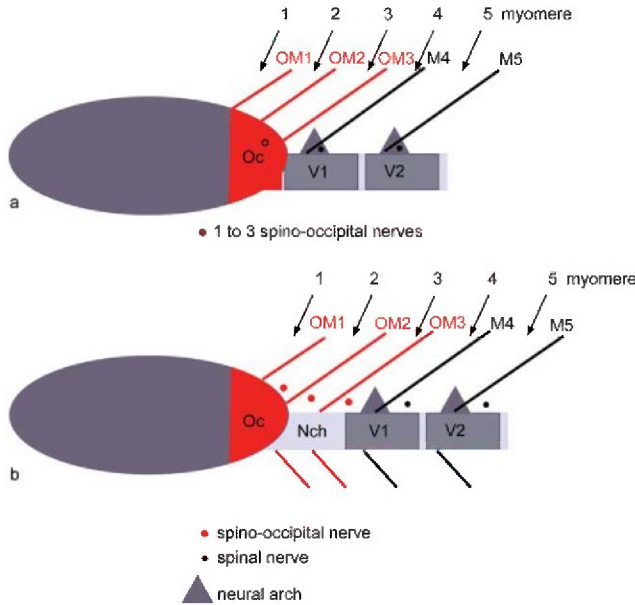
Fig. 1. (a) Generalized scheme of the arrangement of occipital and vertebral myosepta and nerves in relation to the occiput and anterior vertebral column in teleosts. Spino-occipital nerves issue from 1-3 foramina in the skull, while spinal nerves emerge from foramina in the neural arches; (b) Arrangement of occipital and vertebral myosepta and nerves in relation to the occiput and anterior vertebral column in stomiids. The three spino-occipital nerves issue from the neural tube behind the skull and in front of the first neural arch, while spinal nerves emerge behind the associated neural arch. M, myoseptum; Nch, notochord; Oc, occiput; OM, occipital myoseptum; V, vertebra.

at the base of gnathostomes (Allis, 1898; Patterson and Johnson, 1995; Britz and Johnson, 2010; Johnson and Britz, 2010). These occipital myosepta usually insert on the occiput, but in stomiids they may also insert on the notochord between the occiput and the first vertebra (Fig. 1b). The fourth myoseptum attaches to the first vertebra, and the first epineural lies within it. Accordingly, the fourth myoseptum provides a landmark for the first vertebra. Lack of association of the fourth myoseptum with a vertebra is thus evidence that the first vertebra is reduced or absent. The same is valid for the second vertebra, which lies in the fifth myoseptum, the third vertebra within the sixth myoseptum, and so forth.

2. Spino-occipital nerves: The number of spino-occipital nerves varies between one and three among teleosts, with the lower number of one or two due to either fusion or reduction of these nerves (Sagemehl, 1883; Sewertzoff, 1895; Fürbringer, 1897; Allis, 1898, 1903; Herrick, 1899; Parenti and Song, 1996; Nakae and Sasaki, 2007). They are similar to spinal nerves in giving rise to four main branches: an anterior, a dorsal, a lateral, and a ventral branch. Each anterior branch perforates the myoseptum anterior to the myomere it innervates and sends sensory fibers into the antecedent myo-

mere, where it fuses with the dorsal branch of the antecedent nerve (Allis, 1897, 1903). We provide a description of the spino-occipital nerves and a discussion of their significance in determining the first spinal nerve in stomiids.

3. First spinal nerve: The spinal nerve that emerges between the fourth and fifth myoseptum and that innervates the fifth myomere is the first spinal nerve according to Allis (1903). Another definition of the first spinal nerve was given by Parenti and Song (1996) as that one emerging from the first free vertebra, with the second emerging from the second vertebra, and so on. We reinvestigated Parenti and Song's Sudan black stained specimens and concluded that their and Allis' (1903) definitions of the first spinal nerve are congruent. Accordingly, the nerve that emerges from the first vertebra (Parenti and Song, 1996) and that lies within the fifth myomere (Allis, 1903) is the first spinal nerve.

MATERIALS AND METHODS

Specimens of 26 of the 28 stomiid genera were cleared and double stained after Dingerkus and Uhler (1977). *Eupogonesthes* and *Parabathophilus* are not included. To visualize nerve patterns specimens were stained with Sudan Black B after the clearing and double staining process following Song and Parenti (1995). Two *Chauliodus sloani* specimens (USNM uncat.) were overstained with Sudan Black during the clearing and triple staining procedure, which resulted in a staining of the chordacentra within the chordal sheath. The specimens for the histological serial sections were embedded in Paraffin and stained with Azan after Domagk (1933). Radiographs were prepared with a digital radiography system, and pictures were taken with a Zeiss Axiocam attached to a Zeiss SteREO Discovery V12. These pictures are composite images prepared with the Zeiss AxioVision software to increase the depth of field. All radiographs are shown as positive images.

Material Examined

All lengths are given in standard length (SL), unless otherwise noted. Abbreviations of applied methods: C&S, clearing and staining; C&TS, clearing and triple staining; D, dissection; H, histology; R, radiograph.

Gonostomatidae

Gonostoma sp.: USNM 325548, 1 spec. (C&TS: 120 mm)

Stomiidae

Aristostomias xenostoma. USNM 296715, 3 spp. (C&S: 83 mm; R: 123 mm; 140 mm); *Astronesthes niger*: MCZ 133101, 4 spp. (C&S: 26 mm; 37 mm; 48 mm; H: 62 mm); MCZ 147083, 1 sp. (C&S: 29 mm); *Astronesthes indicus*: SIO 92-61, 2 spp. (C&S: 82 mm; D: 98 mm); *Bathophilus filifer*: SIO 76-42, 1 sp. (C&S: TL = 75 mm); SIO 03-189, 2 spp. (H: 80 mm; D: 89 mm); *Bathophilus* sp.: USNM 325530, 1 sp. (C&S: 73 mm); *Bathophilus vaillanti*: USNM 234150, 1 sp. (C&S: 101 mm); *Borostomias panamensis*: SIO 76-54, 2 spp. (C&S: 170 mm; D: 150 mm); SIO 65-188, 1 sp. (H: 125 mm); *Borostomias mononema*: USNM 301093, 1 sp. (R: 239 mm); *Borostomias elucens*: USNM 298939, 1 sp. (alizarin stained: 107 mm); *Chauliodus sloani*: MCZ 129389, 1 sp. (C&S: 26 mm); MCZ 129373, 2 spp. (C&S: 51 mm; H: TL = 50 mm); MCZ 129952, 2 spp. (C&S: 32 mm; 45 mm);

MCZ 157964, 2 spp. (C&S: TL = 165 mm; H: TL = 138 mm); SIO 88-178, 3 spp. (C&S: TL = 250 mm; H: TL = 150 mm; D: TL = 130 mm); USNM 201005, 1 sp. (R: TL = 213 mm); USNM 200984, 1 sp. (C&TS: 145 mm); USNM 028467, 2 adult spp. (R); USNM 219960, 1 adult sp. (R); USNM 285137, 1 adult sp. (R); USNM uncat., 2 spp. (C&TS: 230 mm; 260 mm); BMNH 2002.3.1.179, 1 sp. (C&S: TL = 130 mm); *Chauliodus macouni*: SIO 88-22, 3 spp. (C&S: 28 mm; 32 mm; 33 mm); USNM 150561, 1 sp. (R: 162 mm); USNM 270821, 2 spp. (R: 137 mm; 215 mm); *Chauliodus danae*: BMNH 2007.10.31.63, 1 sp. (D: 92 mm); USNM 200998, 2 spp. (R: 150 mm; 155 mm); *Chauliodus barbatus*: USNM 260174-F29, 4 spp. (R: 169 mm; 126 mm; 96 mm; 81 mm); USNM 292506, 1 sp. (R: 175 mm); USNM uncat., 2 spp. (R: 161 mm; 104 mm); USNM 394241, 1 sp. (C&S: 188 mm); *Chauliodus schmidti*: USNM uncat., 2 spp. (R: 126 mm; 122 mm); *Chauliodus pammelas*: USNM 201190, 2 spp. (R: 183 mm; 147 mm); USNM 201193, 2 spp. (R: 218 mm; 184 mm); *Chirostomias pliopterus*: USNM 234059, 1 sp. (R: 118 mm); *Echiostoma barbatum*: BMNH 2007.10.31.9, 1 sp. (C&S: 89 mm); *Eustomias* sp.: USNM 394242, 1 sp. (C&S: 59 mm); MCZ 62637, 4 spp. (C&S: 45 mm; 32 mm; 30 mm; 26 mm); *Eustomias arborifer*: USNM 223956, 1 sp. (R: 259 mm); USNM 223958, 2 spp. (R: 130 mm; 102 mm); *Eustomias bifilis*: SIO 97-89, 2 spp. (C&S: TL = 105 mm; D: TL = 108 mm); *Eustomias bigelowi*: USNM 261306, 1 sp. (R: 153 mm); *Eustomias bimargaritus*: USNM 224105, 1 sp. (R: 142 mm); *Eustomias brevibarbatus*: USNM 260291, 1 sp. (R: 163 mm); *Eustomias curtatus*: USNM 224194, 1 sp. (R: 146 mm); *Eustomias dinema*: USNM 322444, 1 sp. (R: 97 mm); *Eustomias dubius*: USNM 222161, 1 sp. (R: 174 mm); *Eustomias enbarbatus*: USNM 234464, 3 spp. (R: 201 mm; 135 mm; 91 mm); USNM 379968, 1 sp. (R: 111 mm); *Eustomias filifer*: BMNH 2007.10.31.64, 1 sp. (H: TL = 97 mm); *Eustomias fissibarbis*: USNM 270587, 1 sp. (R: 122 mm); *Eustomias furcifer*: USNM 234388, 1 sp. (R: 166 mm); USNM 322866, 1 sp. (R: 149 mm); *Eustomias jimcraddocki*: USNM 323052, 1 sp. (R: 151 mm); *Eustomias macronema*: BMNH 2007.10.31.12, 1 sp. (C&S: TL = 65 mm); *Eustomias macrurus*: USNM 322772, 2 spp. (R: 196 mm; 169 mm); *Eustomias melanostigma*: USNM 223737, 1 sp. (R: 136 mm); *Eustomias obscurus*: USNM 206711, 5 spp. (R: 199 mm (also C&S); 147 mm (also C&TS); 179 mm; 131 mm; 135 mm); USNM 234444, 1 sp. (C&S: 59 mm); USNM 234416, 1 sp. (C&S: SL = 71 mm); *Eustomias satterleei*: USNM 341943, 2 spp. (R: 151 mm; 159 mm); *Eustomias schmidti*: USNM 261301, 1 sp. (R: 195 mm); *Eustomias simplex*: USNM 372020, 1 sp. (R: 205 mm); *Eustomias tomentosis*: USNM 322643, 1 sp. (R: 110 mm); *Flagellostomias boureei*: BMNH 2002.8.5.786, 1 sp. (C&S: 161 mm); *Grammatostomias circularis*: USNM 300011, 1 sp. (R: 90 mm); USNM 270611, 1 sp. (R: 55 mm); *Grammatostomias dentatus*: VIMS 11846, 2 spp. (C&S: 111 mm; 117 mm); USNM 234036, 1 sp. (C&S: 76 mm); *Heterophotus ophistoma*: USNM uncat., 1 sp. (R: 144 mm); *Idiacanthus anstrostomus*: SIO 97-85, 1 sp. (H: 310 mm); SIO 60-459, 2 spp. (C&S: 320 mm; D: 182 mm); SIO 70-237, 3 spp. (C&S: 135 mm; 57 mm; 75 mm); *Leptostomias* sp.: BMNH 2007.10.31.65, 1 sp. (H: 70 mm); BMNH 2007.10.31.66, 1 sp. (C&S: 49 mm); USNM 257245, 3 spp. (R: 69 mm; 74 mm; 93 mm); USNM 257231, 1 sp. (R: 61 mm); USNM 292290, 1 sp. (C&S: 44 mm); USNM 256843, 1 sp. (R: 240 mm); USNM 256844, 1 sp. (R: 177 mm); USNM 301801, 1 sp. (R and C&S: 185 mm); *Leptostomias gladiator*: BMNH 2007.10.31.8, 1 sp. (C&S: 91 mm); BMNH 1929.7.6.13, 1 sp. (R); BMNH 1929.7.6.14, 1 sp. (R); BMNH 1929.7.6.15, 1 sp. (R); BMNH 1929.7.6.16, 1 sp. (R); USNM 234490, 1 sp. (R: 366 mm); *Leptostomias gracilis*: BMNH 1929.7.6.10, 1 sp. (R); *Leptostomias longibarba*: BMNH 1929.7.6.11, 1 sp. (R); *Leptostomias leptobolus*: BMNH 1929.7.6.12, 1 sp. (R); *Leptostomias macropogon*: BMNH 1930.1.12.521, 1 sp. (R); *Leptostomias bermudensis*: USNM 234478, 1 sp. (R: 458 mm); *Leptostomias bilobatus*: USNM 298720, 1 sp. (R: 359 mm); *Leptostomias multifilis*: USNM 300185, 1 sp. (R: 122 mm); *Leptostomias haplocaulus*: USNM 300546, 1 sp. (R: 173 mm); *Leptostomias macronema*: USNM 301803, 1 sp. (R: 64 mm); *Leptostomias*
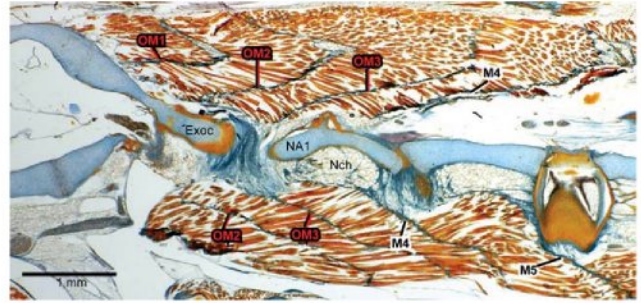

Fig. 2. Sagittal section through the occiput and anterior vertebrae of *Tactostoma macropus* (SIO 89-169, 195 mm), illustrating the attachment site of the three occipital myosepta on the exoccipital and notochord. Ventrally only the second and third occipital myosepta are developed attaching to the notochord. Exoc, exoccipital; M, myoseptum; NA, neural arch; Nch, notochord; OM, occipital myoseptum.

robustus: NSMT-P 63256, 1 sp. (R: 293 mm); *Malacosteus niger*: SIO 73-25, 3 spp. (C&S: 130 mm; H: 100 mm; D: 135 mm); USNM 296813, 1 sp. (C&S: 74 mm); *Malacosteus australis*: USNM 296675, 1 sp. (C&S: 110 mm); *Melanostomias melanops*: BMNH 2007.10.31.10, 1 sp. (C&S: 139 mm); *Melanostomias biseriatus*: USNM 272912, 1 sp. (alizarin stained: 193 mm); *Neonesthes capensis*: USNM uncat., 1 sp. (R: 128 mm); USNM 272906, 1 sp. (C&S: 115 mm); *Odontostomias micropogon*: USNM 343256, 1 sp. (R: 76 mm); *Opostomias mitsuii*: USNM 200816, 1 sp. (R: 113 mm); USNM 320488, 1 sp. (C&S: 170 mm); *Pachystomias microdon*: USNM 296708, 1 sp. (R: 147 mm); USNM 297923, 1 sp. (alizarin stained: 156 mm); USNM 297922, 1 sp. (C&S: 168 mm); *Photonectes parvimanus*: BMNH 1998.8.9.18733, 1 sp. (H: 44 mm); *Photonectes braueri*: BMNH 1998.8.9.18726, 1 sp. (C&S: 62 mm); *Photostomias guernei*: BMNH 2007.10.31.19, 1 sp. (C&S: 112 mm); BMNH 2007.10.31.6, 1 sp. (C&S: 50 mm); *Photostomias* sp.: USNM 296650, 1 sp. (C&S: 92 mm); *Rhadinesthes decimus*: BMNH 2007.10.31.13, 1 sp. (C&S: 138 mm); *Stomias boa ferox*: MCZ 42920, 1 sp. (C&S: 86 mm); MCZ 128612, 1sp. (C&S: 63 mm); MCZ 129017, 1 sp (C&S: TL = 52 mm); MCZ 129070, 6 spp. (C&S: 37 mm; 39 mm; 40 mm; 41 mm; 43 mm; H: 62 mm); USNM 219959, 1 sp. (C&TS: 120 mm); *Stomias atriventer*: SIO uncat., 3 spp. (C&S: 125 mm; H: 185 mm; D: 190 mm); *Stomias boa*: USNM 393605, 1 sp. (C&TS: 240 mm); *Tactostoma macropus*: SIO 89-169, 3 spp. (C&S: 175 mm; H: 195 mm; D: 195 mm); *Thysanactis dentex*: BMNH 1929.7.6.8-9, 2 sp. (R); USNM 365803, 1 sp. (C&S: 76 mm); USNM uncat., 1 sp. (R: 165 mm); *Trigonolampa miriceps*: USNM 219996, 1 sp. (R: 107 mm).

RESULTS
Vertebral Column: Part I: Stomiids With No Vertebral Reduction

Occipital myosepta. In *Neonesthes, Astronesthes, Borostomias, Rhadinesthes, Heterophotus, Stomias, Trigonolampa, Chirostomias, Flagellostomias, Opostomias, Odontostomias, Thysanactis, Photonectes, Melanostomias, Echiostoma, Tactostoma, Idiacanthus, Grammatostomias, Bathophilus, Pachystomias, Photostomias, Malacosteus,* and *Aristostomias* there are three occipital myosepta in the epaxial musculature inserting on the occipital region and the notochord. The first inserts at the anterior margin of the exoccipital bone, the second at the posterior margin of the exoccipital bone, and the third on the notochord (Figs. 1b and 2). In the
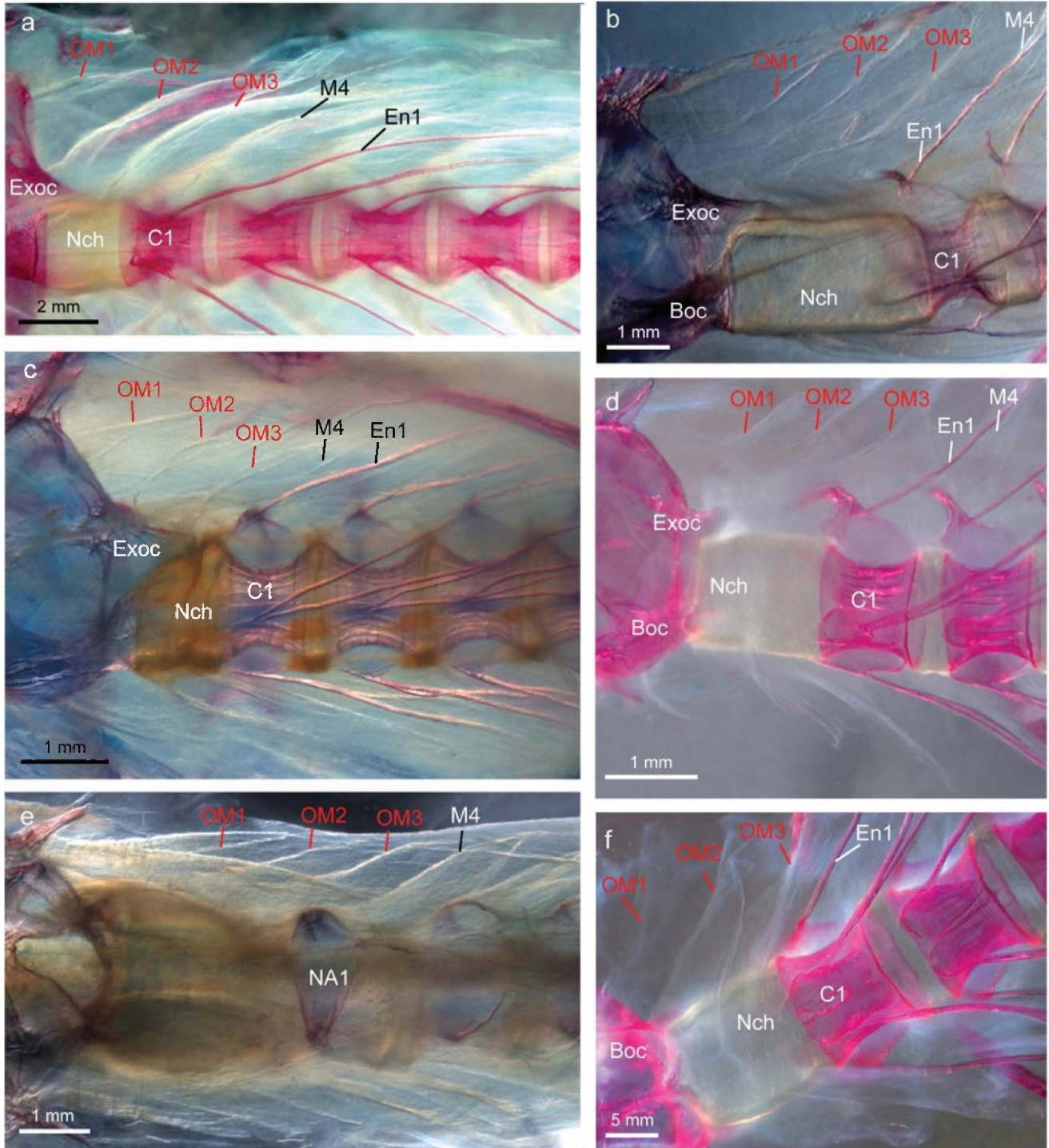
Fig. 3. Arrangement of occipital and vertebral myosepta in relation to the occiput and the vertebral column. Within the first vertebral myoseptum (M4) lies the first vertebra of which just the centrum (C1) is labeled. In (a), (b), (c), and (d) the specimens show a truncation of the basioccipital. (a) lateral view of *Borostomias panamensis* (SIO 76-54, 170 mm); (b) Lateral view of *Flagellostomias bureei* (BMNH 2002.8.5.786, 161 mm); (c) Lateral view of *Echiostoma barbatum* (BMNH 2007.10.31.9, 89 mm); (d) Lateral view of *Bathophilus filifer* (SIO 76-42, TL = 75 mm) (e) Dorsal view of *Photostomias guernei* (BMNH 2007.10.31.19, 112 mm); (f) Ventral view of *Bathophilus filifer* (SIO 76-42, TL = 75 mm). Boc, basioccipital; C, centrum; En, epineural; Exoc, exoccipital; M, myoseptum; NA, neural arch; Nch, notochord; OM, occipital myoseptum.

hypaxial musculature only the second and third occipital myosepta are present, and they are confluent with their respective epaxial counterparts (see Figs. 3f, 4d–g). The fourth myoseptum attaches to the first centrum (Figs. 3a–f, 4d–g) in all representatives of the above stomiids. The
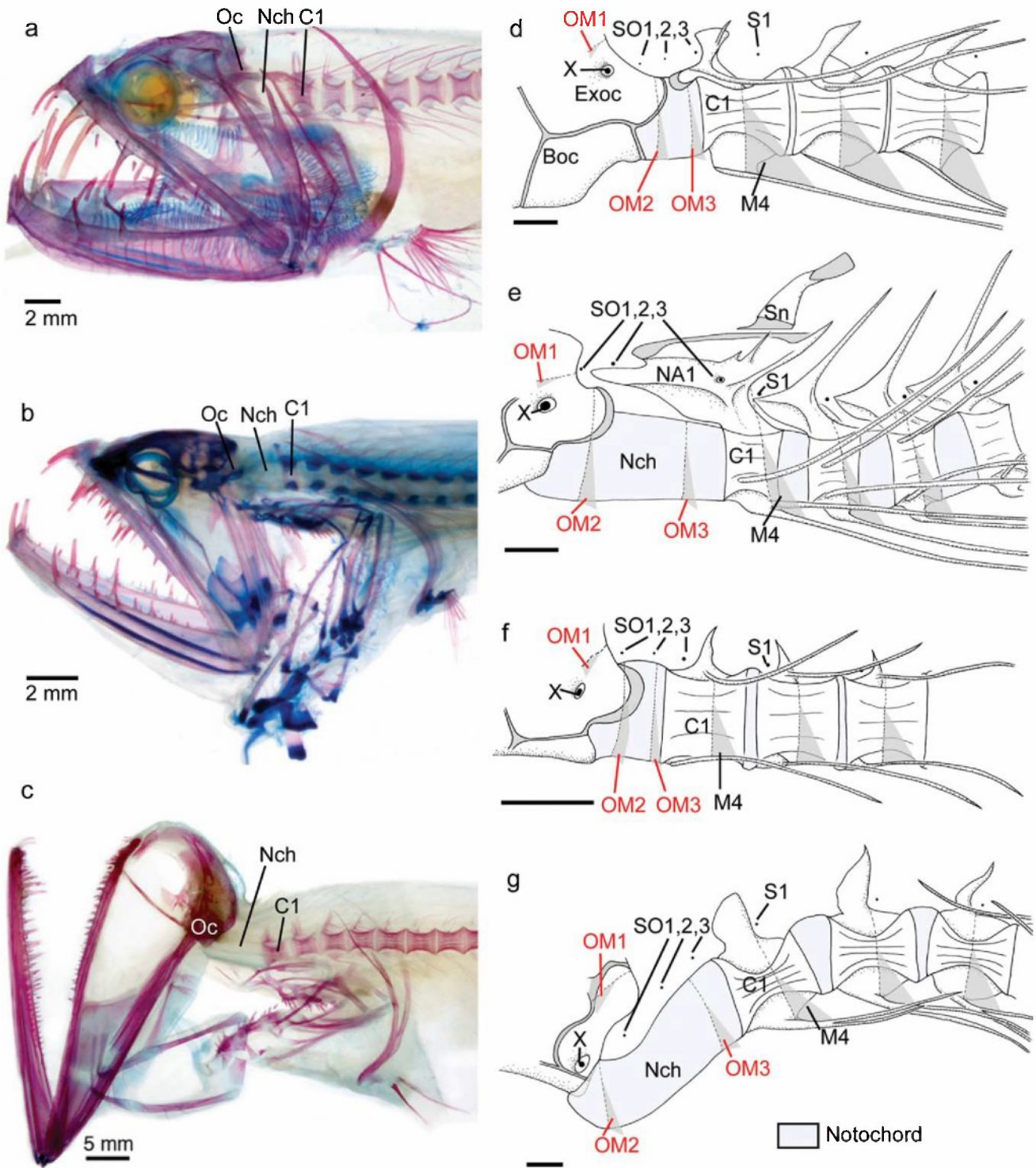
Fig. 4. Occipito-vertebral gap in: (**a**) *Flagellostomias bureei* (BMNH 2002.8.5.786,161 mm); (**b**) *Grammatostomias dentatus* (USNM 234036, 76 mm); (**c**) *Malacosteus niger* (USNM 296813, 74 mm); (**d**) *Borostomias panamensis* (SIO 76-54, 170 mm); (**e**) *Stomias atriventer* (SIO uncat., 125 mm); (**f**) *Idiacanthus anstrostomus* (SIO 70-237, 135 mm); (**g**) *Malacosteus niger* (SIO 73-25, 130 mm). The drawings show where the three spino-occipital nerves (SO1-SO3) exit the spinal cord, the first spinal nerve (S1), the three occipital myosepta (OM1-OM3), and the first vertebral myoseptum (M4). M4 attaches to the first vertebra of which just the centrum (C1) is labeled. Scale bar in drawings: 1 mm. Boc, basioccipital; C, centrum; Exoc, exoccipital; M, myoseptum; NA, neural arch; Nch, notochord; Oc, occiput; OM, occipital myoseptum; S, spinal nerve; Sn, supraneural; SO, spino-occipital nerve; X, vagus nerve.

enlarged occipito-vertebral gap is thus the result of an elongation of the notochord and not of a loss or reduction of vertebrae. The length of the occipito-vertebral gap varies among genera. It is relatively short in basal stomiids like *Astronesthes* and *Borostomias* (Figs. 3a, 4d), but much longer in members of the more derived taxa like *Malacosteus* (Fig. 4c,g). In *Astronesthes, Borostomias* (Figs. 3a, 4d), and *Echiostoma* (Fig. 3c) the exoccipital bone articulates with the first neural arch; the basioccipital bone does not reach as far posteriorly as the exoccipital bone and is excluded from this articulation due to its truncated condition. In most other stomiids, which show no such articulation between the exoccipital bones and the first neural arch, the truncation of the basioccipital bone is associated with an enlargement of the notochord (Fig. 3b, 4e).

Spino-Occipital and Spinal Nerves

There are four myomeres anterior to the first vertebra and fourth myoseptum. The fifth myomere lies between the fourth and fifth myosepta and the first and second vertebra (see Fig. 1). The spinal nerve that innervates this fifth myomere is the first spinal nerve. Three spino-occipital nerves leave the spinal cord between the vagus nerve and the first spinal nerve (Fig. 5b). In stomiids all three spino-occipital nerves remain separate along their entire course. The first spino-occipital nerve is thin (particularly its ventral branch), and the second and third are similar in size to spinal nerves. All four branches of each nerve mentioned above can be seen in Figure 5a of the gonostomatid stomiiform *Gonostoma sp.*, which shows an identical condition to that in stomiids. Only in *Stomias* and *Astronesthes* the third spino-occipital nerve emerges through the first enlarged neural arch and was therefore misidentified in *Stomias* as the first spinal nerve in Schnell et al. (2008). In stomiids, the spinal nerves do not emerge through foramina within the neural arches, but instead leave the spinal canal posterior to the corresponding neural arches. Thus, Allis' (1903) landmark that the first spinal nerve emerges between the fourth and fifth myoseptum, or in other words between the first and second vertebra, is critical for identifying the first spinal nerve in stomiids.

Vertebral Column: Part II: Stomiids With Vertebral Reduction

Chauliodus (Figs. 6–11). We investigated six of the nine *Chauliodus* species (*C. sloani, C. barbatus, C. danae, C. macouni, C. pammelas, C. schmidti*). *Chauliodus dentatus, C. minimus, C. vasnetzoui* were not included in this study.
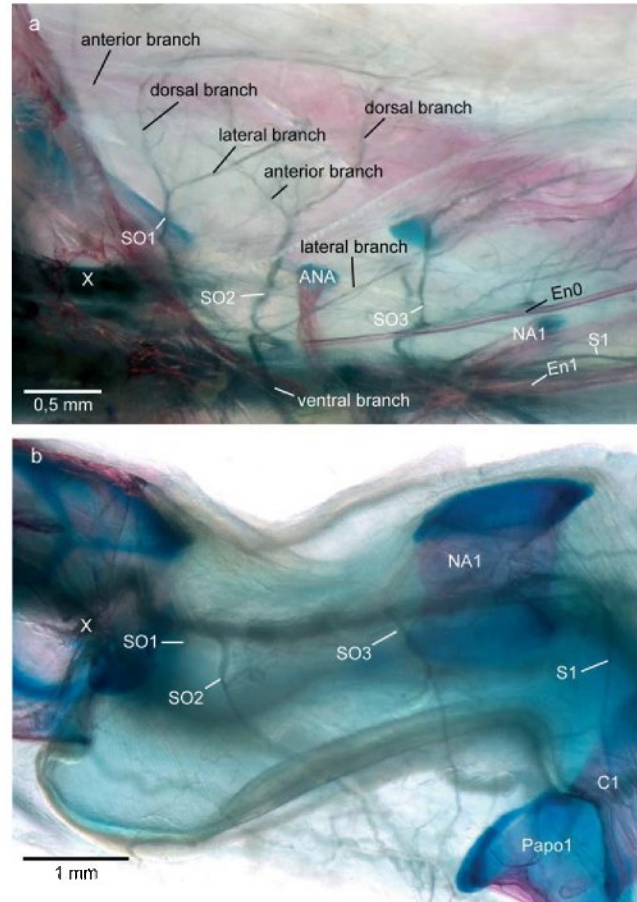
Fig. 5. (a) Lateral view of a cleared and triple stained *Gonostoma* sp. (USNM 325548, 120 mm), note the four branches of each spino-occipital nerve (anterior, dorsal, lateral and ventral branch); (b) Lateral view of the occiput and the first vertebra of *Eustomias obscurus* (USNM 206711, 147 mm), note the ventral branches of the three spino-occipital nerves (SO1-SO3). The vagus nerve (X) was cut at the vagus foramen in both specimens. ANA, accessory neural arch; C, centrum; En, epineural; NA, neural arch; Papo, parapophysis; S, spinal nerve; SO, spino-occipital nerve; X, vagus nerve.

Vertebral Reduction

In most of the investigated specimens of *Chauliodus sloani, C. danae, C. pammelas,* and *C. schmidti* centra of the first six vertebrae are absent, however there is some intraspecific variation. The respective neural arches and parapophyses persist and are associated with a myoseptum in which the epineural of each neural arch is situated (see Fig. 6). One specimen of *C. sloani* lacks the first seven centra (Fig. 7e), and in others the sixth centrum is developed as a small ventral or dorsal ossification (Fig. 7c,d). Such a ventral ossification was also seen in some specimens of *C. schmidti*. In one specimen of *C. danae* the seventh centrum is represented by only a small partial ossification dorsally. In *C. macouni* and *C. barbatus* only the first two centra are reduced (Fig.
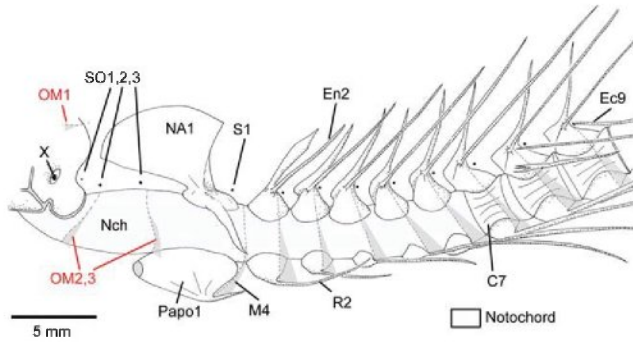
Fig. 6. *Chauliodus sloani* (SIO 88-178, TL = 250 mm), this drawing shows the arrangement of occipital and vertebral myosepta and nerves in relation to the occiput and the vertebral column. The anterior six centra are absent. C, centrum; Ec, epicentral; En, epineural; M, myoseptum; NA, neural arch; Nch, notochord; OM, occipital myoseptum; Papo, parapophysis; R, rib; S, spinal nerve; SO, spino-occipital nerve; X, vagus nerve.

7a,b), and in all three *C. barbatus* specimens examined a small ventral ossification of the second centrum is developed (Fig. 7b). Such an ossification was not identified in any of the adult specimens of *C. macouni* we examined.

Ontogeny

In stomiids, ossification of the skeleton takes place relatively late in development, during the phase of transformation. In all stomiids we examined, the vertebral column ossifies caudorostrally, so that the anteriormost vertebrae are the last to ossify (Fig. 8a–d). We did not have appropriate stages to determine which vertebra ossifies first, but in a 26-mm specimen of *C. sloani* there are no centra ossified yet (Fig. 8b). Completely mineralized rings (chordacentra), that develop from dorsal and ventral centers of ossification, are found in a 32-mm specimen (Fig. 8c), wherein the 18th vertebral centrum is about to ossify; thus, three quarters of the total number of centra are ossified posteriorly. The 13th centrum is ossified dorsally in a 45-mm specimen (Fig. 8d), and in a 51-mm specimen the 9th centrum is ossified (Fig. 8e). Both chordacentra and autocentra can be identified in the posterior part of the vertebral column of a 45-mm specimen (Fig. 8d) and are illustrated for an adult specimen in Figure 9a,b.

The first neural arch and parapophyses are greatly enlarged in all *Chauliodus* species examined, and in adults the first neural arch has a ventrally projecting ossification (Fig. 10d). In *C. macouni*, the tip of this projection is directed dorsally in larval and adult specimens. In a 28-mm specimen of *C. macouni* this ossification can be identified as an epineural (Fig. 10a) as it lies within the fourth myoseptum. In a 32-mm specimen of *C. sloani* this epineural curves caudally and then slightly dorsally (Fig. 10c), but in

an adult specimen (Fig. 10d) it is directed ventrally. In all species examined this epineural lies within the fourth myoseptum, thus establishing that the first neural arch and parapophyses belong to the first vertebral segment.

Occipital Myosepta and Nerves

In the epaxial musculature, an anterior muscle mass that attaches to the first enlarged neural arch is separated from the rest of the epaxial musculature by a sheath of connective tissue (see Fig. 11). Tchernavin (1953) called this muscle *musculus dorsalis 8*, and considered it a separation of the epaxial musculature. We identify the connective tissue sheath that separates the *musculus dorsalis* 8 from the rest of the epaxial musculature as the first occipital myoseptum and the *musculus dorsalis* 8 most likely as part of the first myomere.

There are three spino-occipital nerves in front of the first neural arch. The first spino-occipital nerve is very thin in the specimen examined and thus could not be traced further distally. The second spino-occipital nerve pierces the second myoseptum to enter and thus innervate the third myomere, and the third pierces the third myoseptum to enter and innervate the fourth myomere. The fifth myomere between the first and second neural arch and parapophysis is innervated by the first spinal nerve.

There is dense connective tissue around and posterior to the enlarged exoccipitals (Fig. 10b). Several cartilaginous elements (Fig. 10b) are developed within this connective tissue in larger specimens, but are not present in larval specimens (Fig. 10a,c). During further development these cartilages eventually fuse into a single element, which is situated anterior to the third occipital myoseptum.

Leptostomias with a Comparison to *Thysanactis, Opostomias,* and *Odontostomias* (Figs. 12–14)

We investigated 11 of the 12 *Leptostomias* species (*L. gladiator, L. gracilis, L. longibarba, L. macropogon, L. leptolobus, L. bermudensis, L. bilobatus, L. haplocaulus, L. macronema, L. multifilis, L. robustus*). *Leptostomias analis* was not included in this study.

Vertebral Reduction and Occipital Myosepta

Three epaxial occipital myosepta are present in front of the fourth myoseptum, which attaches to the first neural arch and parapophysis and in which the first epineural lies. *Leptostomias gladiator* is the only species of the genus in which the anterior six vertebral centra are not ossified in adult
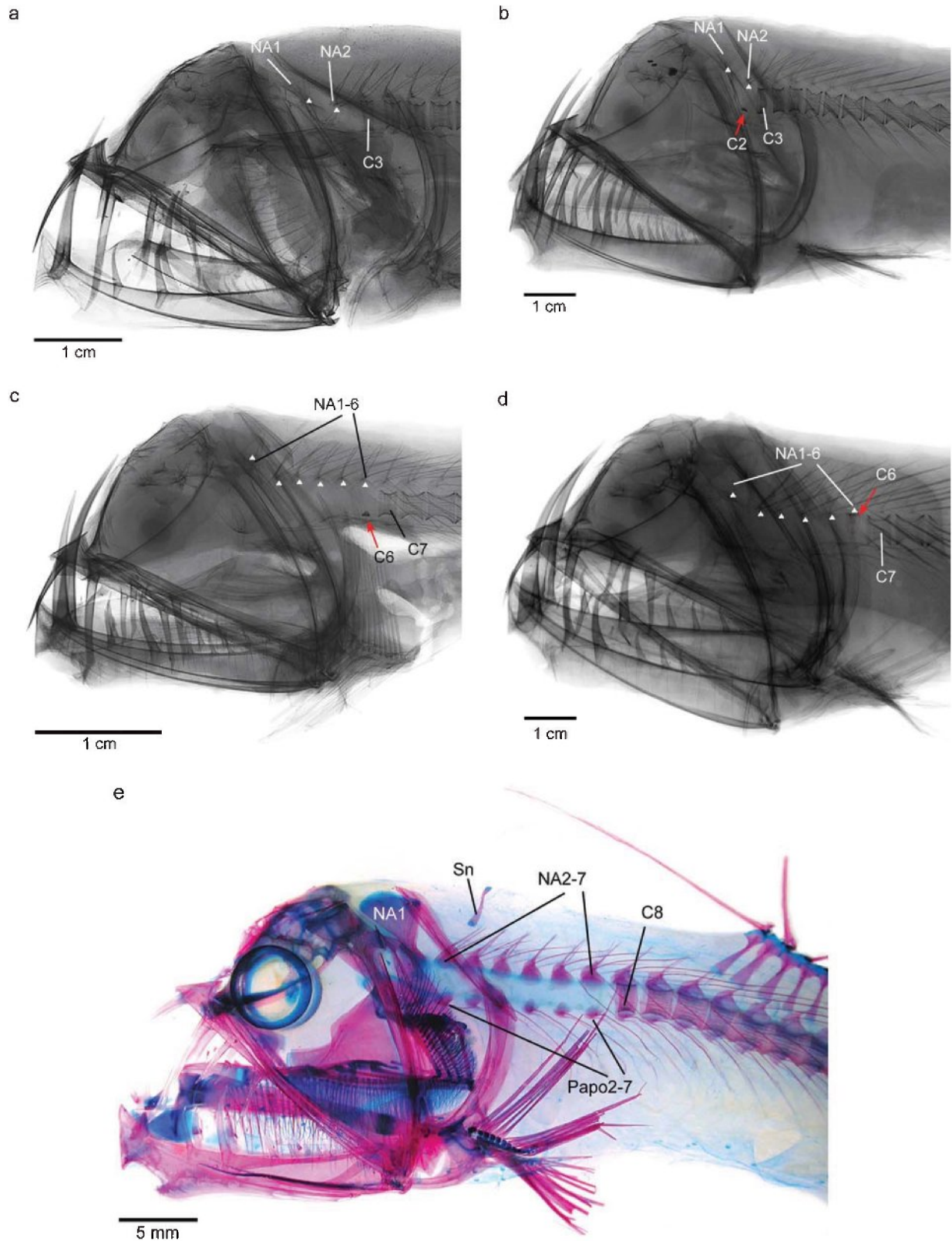
Fig. 7. Variation of centra formation among species of the genus *Chauliodus*. (**a**) *C. macouni* (USNM 150561, 162 mm), the first two centra are absent; (**b**) *C. barbatus* (USNM uncat.,104 mm), the first vertebral centrum is absent and a ventral ossification of the second centrum is present (marked by arrow); (**c**) C. sloani (USNM 285137, adult), the sixth centrum has a small ventral ossification (marked by arrow). (**d, e**) Intraspecific variation of centra formation in *Chauliodus sloani*. (d) (USNM 201005, TL = 213 mm), the sixth centrum has a partial ossification dorsally; (**e**) (BMNH 2002.3.1.179, TL = 130 mm), seven centra are absent in this specimen. C, centrum; NA, neural arch; Papo, parapophysis; Sn, supraneural.
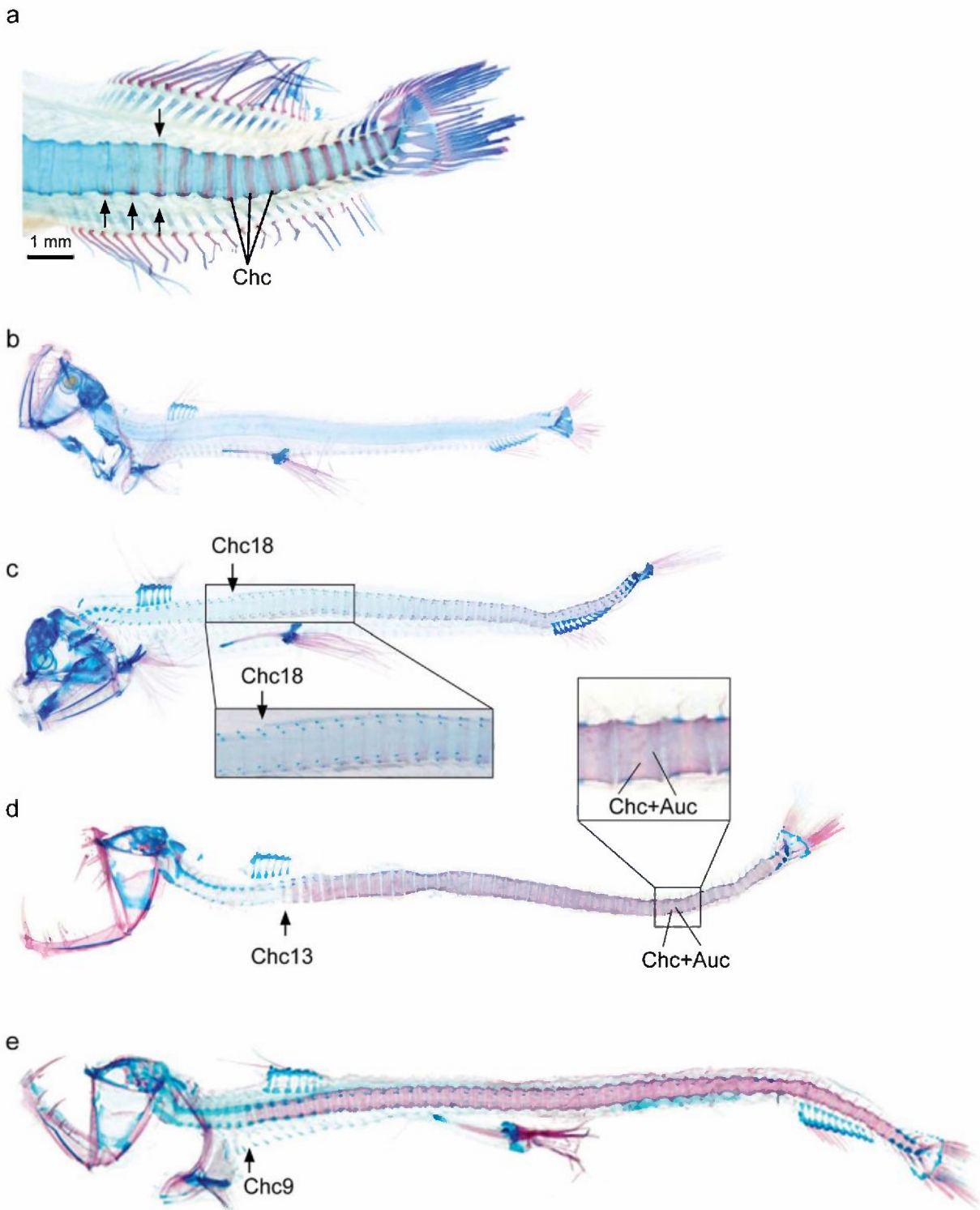
Fig. 8. Centra formation in the development of stomiids. (**a**) *Leptostomias* sp. (USNM 292290, 44 mm), caudorostral development of the vertebral centra; (**b**) *Chauliodus sloani* (MCZ 129389, 26 mm), no vertebral centra are ossified yet; (**c**) *C. sloani* (MCZ 129952, 32 mm), the 18th vertebral centrum is about to ossify. All vertebral centra posteriorly are already ossified, but none anteriorly; (**d**) *C. sloani* (MCZ 129952, 45 mm), the 13th vertebral centrum is about to ossify; (**e**) *C. sloani* (MCZ 129373, 51 mm), the 9th vertebral centrum is about to ossify. Auc, autocentrum; Chc, chordacentrum.
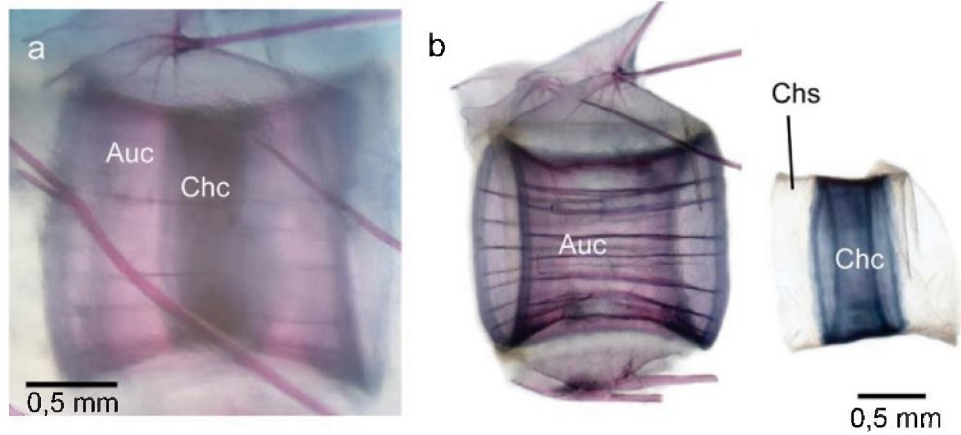
Fig. 9. Centra formation through chorda- and autocentra in *Chauliodus sloani* (USNM uncat., 230 mm). (**a**) Chordacentrum within the autocentrum; (**b**) Chordacentrum within the chordal sheath and autocentrum separated. Auc, autocentrum; Chc, Chordacentrum; Chs, chordal sheath.

specimens; their respective neural arches and parapophyses, however, are present (see Fig. 12). In members of the remaining 10 species we examined the first six vertebral centra are present as slender bony rings around the notochord (Fig. 13a). In adults of *Thysanactis* (see Fig. 13), *Odontostomias*
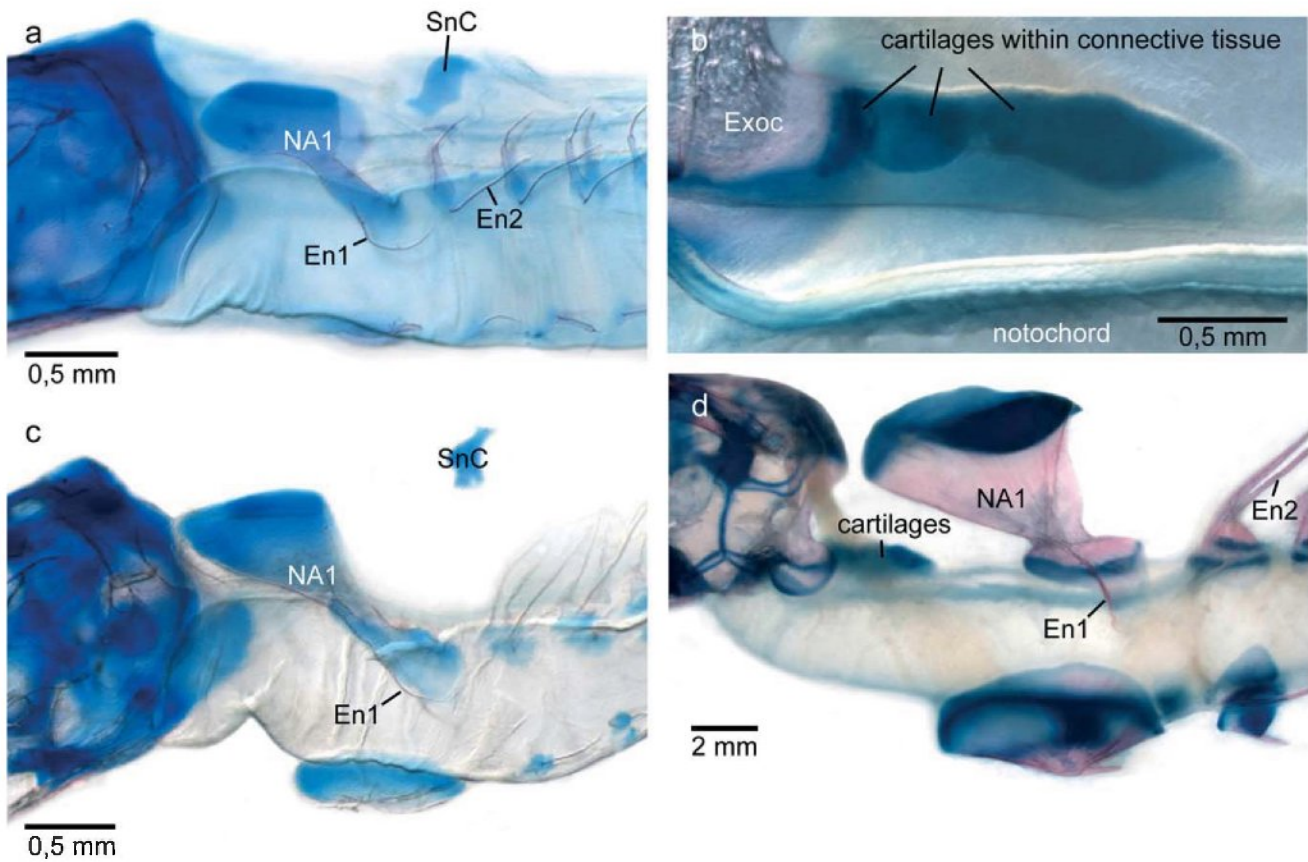

Fig. 10. Development of the first epineural and cartilages within connective tissue in *Chauliodus* spp. (**a**) *C. macouni* (SIO 88-22, 28 mm), first epineural is directed dorsally at its tip; (**b**) *C. sloani* (USNM uncat., 260 mm), cartilages within the dense connective tissue; (**c**) *C. sloani* (MCZ 129952, 32 mm), the first epineural curves caudally and then slightly dorsally; (**d**) *C. sloani* (USNM uncat., 260 mm), The first epineural is directed ventrally. En, epineural; Exoc, exoccipital; NA, neural arch; SnC, supraneural cartilage.
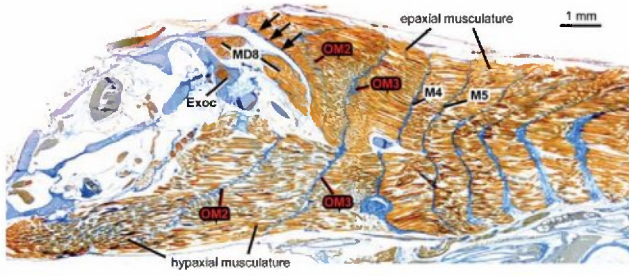
Fig. 11. Parasagittal section of the head and anterior body of *Chauliodus sloani* (MCZ 157964, TL = 138 mm), connective tissue sheath (marked by arrows) separates the *musculus dorsalis 8* portion from the rest of the epaxial muscles. Exoc, exoccipital; M, myoseptum; MD8, *musculus dorsalis 8* (see Tchernavin, 1953); OM, occipital myoseptum.
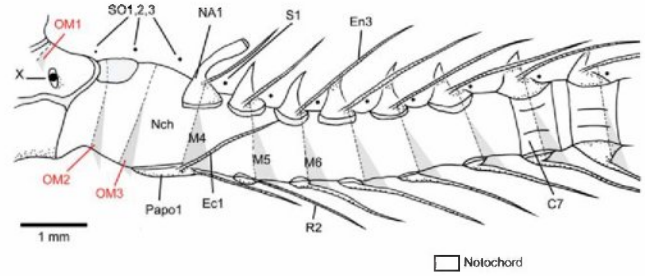
Fig. 12. Occiput and anterior vertebral column of *Leptostomias gladiator* (BMNH 2007.10.31.8, 91 mm), the first six vertebral centra are absent and three spino-occipital nerves and three occipital myosepta (dorsally) anterior to first neural arch and parapophysis are present. C, centrum; Ec, epicentral; En, epineural; M, myoseptum; NA, neural arch; Nch, notochord; OM, occipital myoseptum; Papo, parapophysis; R, rib; S, spinal nerve; SO, spino-occipital nerve; X, vagus nerve.

and *Opostomias* the first six vertebral centra are also developed as small bony rings.

Posterior to and around the enlarged exoccipitals of *Leptostomias*, *Thysanactis* and *Opostomias* there is dense connective tissue, within which three cartilaginous elements develop (see Fig. 14) as in *Chauliodus*. These cartilages also fuse eventually into a single cartilage on each side of the notochord and are not yet developed in larval specimens. They are situated between the first and

the third occipital myosepta with the second occipital myoseptum inserting on them.

Eustomias (Figs. 15 and 16)

In all species of *Eustomias*, the highly derived anterior part of the vertebral column exhibits a unique curvature of the notochord. This extreme curvature involves absence of several centra and
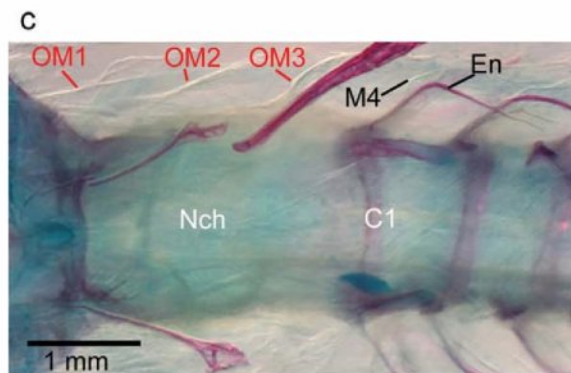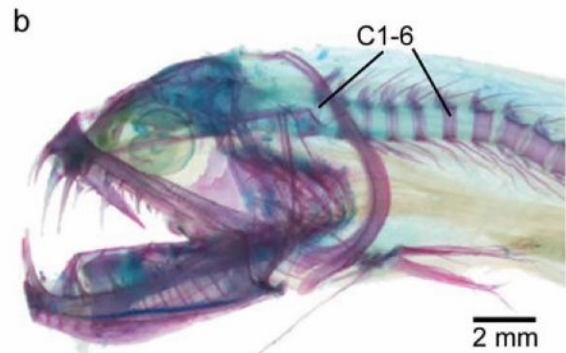

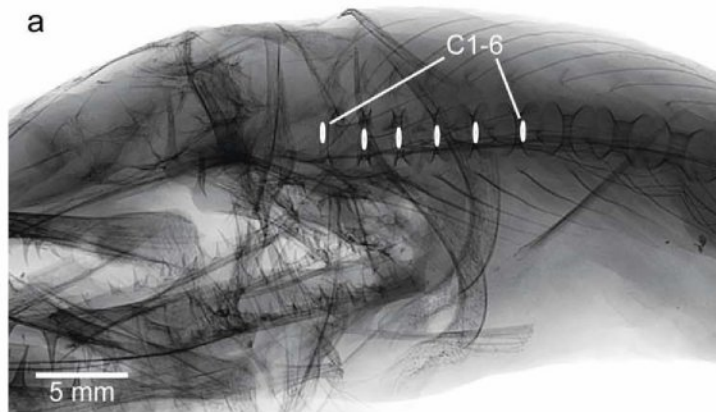Fig. 13. First six vertebrae in Leptostomias (except L. gladiator) and Thysanactis. (a) *Leptostomias* sp. (USNM 256844, 177 mm); (b) *Thysanactis dentex* (USNM 365803, 76 mm), the first six vertebral centra are ossified as small rings; (c) *T. dentex* (USNM 365803, 76 mm), arrangement of the occipital and vertebral myosepta. C, centrum; En, epineural; M, myoseptum; Nch, notochord; OM, occipital myoseptum.
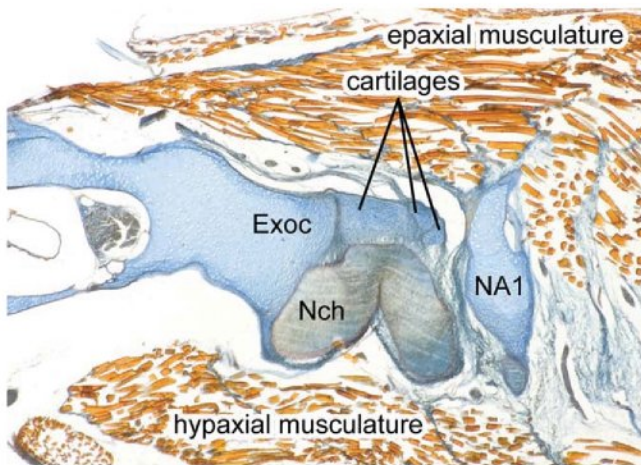
Fig. 14. Parasagittal section of the occiput and the anterior vertebral column of *Leptostomias* sp. (BMNH 2007.10.31.65, 70 mm) to illustrate the presence of three cartilages within connective tissue behind the exoccipital. Exoc, exoccipital; NA, neural arch; Nch, notochord.

neural arches. Nineteen of the ~116 species of *Eustomias* were examined in this study, covering all five subgenera of *Eustomias*.

Vertebral Reduction and Occipital Myosepta

The first vertebra, identified by its association with the first vertebral myoseptum, bears a spineless neural arch, a centrum and a parapophysis. The latter supports a branched rib (see Fig. 15). The neural arch is dislocated from its respective centrum, which lies posterior to it within the downward bend of the notochord (Figs. 15, 16a). Several of the succeeding centra or entire vertebrae are absent. The next complete vertebra is the 8th in *Eustomias macronema*, *E. satterleei*, *E. tomentosis*, *E. schmidti*, *E. bigelowi*, *E. jimcraddocki*, *E. dinema* and the 9th in *E. bifilis*, *E. obscurus*, *E. enbarbatus*, *E. fissibarbis*, *E. brevibarbatus*, *E. macrurus*, *E. bimargaritus*, *E. melanostigma*, *E. simplex*, *E. dubius*, *E. curtatus*, and *E. arborifer* (Figs. 15, 16a). A partial ventral ossification of the 8th centrum is present in several specimens of *E. bifilis*, *E. obscurus*, *E. enbarbatus* and *E. fissibarbis*, but the first completely ossified vertebra is the 9th (see Fig. 15). In one adult specimen of *E. arborifer* the 9th centrum is represented by only a ventral ossification, and thus the first complete vertebra is the 10th.

The fourth myoseptum attaches to the first neural arch and parapophysis, and the first rib lies within this myoseptum (see Fig. 15). Posterior to the first vertebra two parapophyses represent the second and third vertebral segments. Their respective centra and neural arches are absent in all investigated *Eustomias* species, except *E. obscurus* (see below). The fifth myoseptum attaches to the second parapophysis and the sixth myoseptum to the third. The rib of each parapophysis lies within

its respective myoseptum (see Fig. 15). At the level of the sixth myoseptum, the notochord bends upward and then gradually straightens out posteriorly; in this region four or five vertebral centra are absent, but their neural arches and parapophyses remain.

Variation in *Eustomias obscurus*

Uniquely within the genus, *E. obscurus* has an additional centrum within the upward bend of the notochord belonging to the fourth neural arch and its ribless parapophysis (Fig. 16a). The fifth and sixth parapophyses are represented as minute basiventrals (Fig. 16c). The fifth parapophysis lacks a rib, and the rib of the sixth vertebra lies free within its corresponding myoseptum, which is the 9th (Fig. 16c). Small ossifications of the fifth, sixth, and seventh vertebral centra lie dorsally between their respective neural arches (Fig. 16b). Both chordacentra and autocentra can be identified. *E. obscurus* is the only species in which a cartilaginous accessory neural arch was found within the third myoseptum anterior to the first neural arch (Fig. 16a).

DISCUSSION
Part I: Stomiids With No Vertebral Reduction

The extensive occipito-vertebral gap of stomiids is a rare feature among teleosts, and it is not surprising that previous authors (Sell, 1916; Regan and Trewavas, 1930; Beebe, 1934; Tchernavin, 1953; Günther and Deckert, 1955, 1959; Morrow, 1964; Morrow and Gibbs, 1964) suggested that this gap involved loss of anterior vertebrae. Contra Regan and Trewavas (1930), there are no missing vertebral centra in any stomiids other than *Chauliodus*, *Eustomias*, and *Leptostomias*
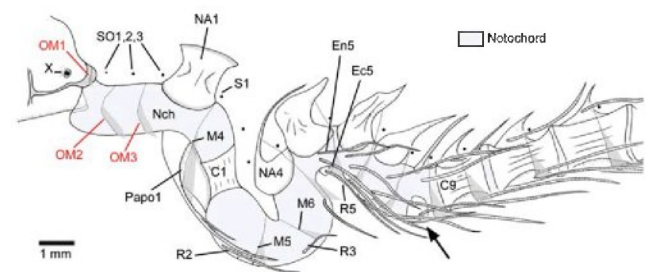
Fig. 15. Occiput and anterior vertebral column of *Eustomias bifilis* (SIO 97-89, TL = 105 mm) in lateral view. Illustrated are the three spino-occipital nerves and occipital myosepta in front of the dislocated first vertebra; the arrow indicates the ventral ossification of the 8th centrum. The first complete vertebra is the 9th. C, centrum; Ec, epicentral; En, epineural; M, myoseptum; NA, neural arch; Nch, notochord; OM, occipital myoseptum; Papo, parapophysis; R, rib; S, spinal nerve; SO, spino-occipital nerve; X, vagus nerve.

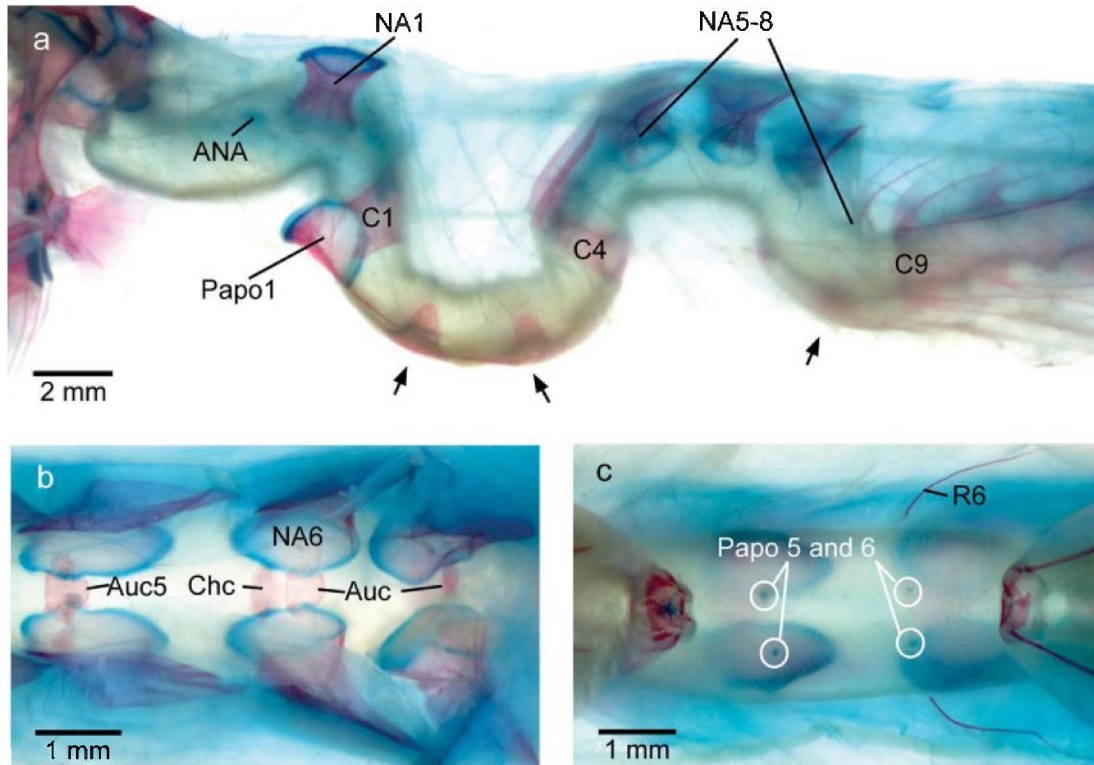Fig. 16. Anterior vertebral column in *Eustomias obscurus* (USNM 206711, 199 mm). (**a**) Lateral view, arrows indicate the ventral ossifications of centra 2, 3, and 8. The first complete vertebra is the 9th; (**b**) Dorsal view of the neural arches 5–7 and dorsal ossification of the chorda- and autocentra; (**c**) Ventral view of the minute basiventrals 5 and 6. ANA, accessory neural arch; Auc, autocentrum; C, centrum; Chc, chordacentrum; NA, neural arch; Papo, parapophysis; R, rib.

gladiator. As in other teleosts, the first three myosepta are occipital myosepta and the first vertebra is associated with the fourth myoseptum in *Neonesthes, Astronesthes, Borostomias, Rhadinesthes, Heterophotus, Stomias, Trigonolampa, Chirostomias, Flagellostomias, Opostomias, Odontostomias, Thysanactis, Photonectes, Melanostomias, Echiostoma, Tactostoma, Idiacanthus, Grammatostomias, Bathophilus, Pachystomias, Photostomias, Malacosteus,* and *Aristostomias*. In the hypaxial musculature there are only two occipital myosepta, which are continuous with the second and the third dorsally, and only these two ventral, not the three dorsal, occipital myosepta were mentioned in *Stomias* in Schnell et al. (2008).

Rosen (1985) argued that neoteleosts are characterized primitively by a cervical gap (here called the occipito-vertebral gap). Stiassny (1996) believed that among neoteleosts an extensive elaborated cervical gap characterized by exoccipital facets is unique for the myctophiform Neoscopelidae and a synapomorphy of this group. However, as demonstrated here, the length of the occipito-vertebral gap of some stomiids, e.g., *Malacosteus*, the result of notochordal elongation, greatly exceeds that of any other known fish species. In addition, the posterior extension of the exoccipitals relative to that of the basioccipital differs from the condition found in other teleosts; the exoccipitals reach further posteriorly, and due to the posterior truncation of the basioccipital, the gap between the occiput and the first vertebra appears much wider.

Part II: Stomiids With Vertebral Reduction

The only stomiids lacking vertebral centra are *Chauliodus, Eustomias,* and *Leptostomias gladiator*. The number of missing centra, however, varies inter- and intragenerically in these taxa, as does the configuration of the anterior part of the vertebral column. In *Chauliodus*, the number of lost centra ranges from two in *C. macouni* and *C. barbatus* to six in *C. sloani, C. danae, C. pammelas, C. schmidti,* and seven in one adult specimen of *C. sloani*. Tchernavin (1953:98) suggested that seven centra are reduced anteriorly, arguing that a "rudimentary first neural arch" was fused with the enlarged neural arch. This neural arch, which is actually the first, is associated with the fourth myoseptum and we consider that Tchernavin (1953) misidentified an anterior extension of this arch as his rudimentary first neural arch. Crane (1966), in a study of the late Tertiary radiation of viperfishes, started his count of anterior vertebrae with the second vertebra specifically excluding the most anterior one. Allowing for that his counts of reduced

vertebral centra are congruent with the counts presented here.

Leptostomias gladiator, like some *Chauliodus* species, lacks six centra, but has a first neural arch and parapophysis that are only slightly enlarged compared to the succeeding ones. *Chauliodus*, in contrast, has the first neural arch and parapophysis greatly enlarged, serving as an insertion point for muscles of the highly derived first anterior part of the epaxial musculature (Tchernavin, 1953). All other *Leptostomias* species investigated have no missing centra, and the first six centra are ossified as small rings. Regan and Trewavas (1930) suggested that the first fully developed centrum of *L. gladiator* is the eighth, but they were misled by the number of neural arches identified. They correctly identified six pairs of parapophyses, but misleadingly reported "seven paired neurapophyses," noting that "the first neural arch is represented by a pair of small bones that articulate with the exoccipital" (p. 41). These "bones" are actually cartilages that develop within the dense connective tissue posterior to the exoccipitals. Regan and Trewavas (1930) stated that the same condition also characterizes the anterior vertebral column of *Thysanactis dentex*. We are able to show that the monotypic genus *Thysanactis* and the genera *Opostomias* and *Odontostomias* are characterized by the development of six slender anteriormost vertebral centra, which are also found in all investigated *Leptostomias* species except *L. gladiator*.

In *Eustomias*, the anterior part of the vertebral column is unique in showing an extensive curvature. Two groups can be distinguished based on the position of the first complete vertebra: the eighth in one group and the ninth in the other. Regan and Trewavas (1930) distinguished a third type exemplified by *E. obscurus* only. This species differs clearly from all other *Eustomias* species in having the fourth centrum also developed and in possessing small dorsal or ventral ossifications of those centra that are absent in the other species of the genus. Furthermore *E. obscurus* is the only species examined that has an accessory neural arch and lacks the fourth and fifth rib. Regan and Trewavas (1930) assumed that the first fully ossified vertebra is either the 10th or the 11th depending on the group. Here again, they were misled by the three spinooccipital nerves that they mistook for spinal nerves that had lost their respective vertebrae. Accordingly, they assumed that the first two (spino-occipital) nerves belong to two unossified vertebrae and the third to the following vertebral segment. Regan and Trewavas (1930) had no clear landmarks for the first spinal nerve, which is critical since there are no foramina in the neural arches in stomiids through which the spinal nerves emerge. As a result they erroneously presumed that the nerve in front of the neural arch belonged to the following neural arch. However, as we establish in the introduction,

the nerve that emerges from the first vertebra (Parenti and Song, 1996) and that lies within the fifth myomere (Allis, 1903), is the first spinal nerve. Accordingly, in stomiids, the first spinal nerve is the one that lies posterior to its neural arch.

A summary of the number of reduced vertebral centra in the genera *Chauliodus*, *Eustomias*, and *Leptostomias* with possible variation is presented in Table 1.

Ossification of the Vertebral Centra in Early Ontogeny

The sequence of ossification of the vertebral centra in stomiids provides a possible explanation for the variation in the number of reduced anteriormost centra. Ossification sequence of vertebral centra is highly variable among teleosts, most commonly proceeding in a rostrocaudal direction (Potthoff et al., 1988; Potthoff and Tellock, 1993). Weisel (1967) reported the first ossified vertebra to appear in about the middle of the vertebral column in poeciliids and the ossification of the centra to proceed bidirectionally. This pattern has also been observed in the clupeiform *Opisthonema oglinum* (Richards et al., 1974). A similar ossification sequence was reported for the stomiiform *Vinciguerria lucetia* by Ahlstrom and Counts (1958), where ossification of the centra starts in the precaudal region and proceeds anteriorly and posteriorly. In the Myctophidae the centra ossify in a rostrocaudal direction; only *Hygophum atratum* and *H. reinhardti* are exceptional in showing a caudorostral direction of ossification of their centra (Moser and Ahlstrom, 1970). In stomiids, ossification of vertebral centra also proceeds caudorostrally, so that the anteriormost centra are the last to ossify (Crane, 1966), and in some taxa like *Chauliodus*, *Leptostomias gladiator*, and *Eustomias* apparently never ossify.

Accessory Neural Arch and Cartilages Within Connective Tissue

Between the exoccipitals and the first neural arch a condensation of dense connective tissue is found in *Chauliodus*, *Leptostomias, Thysanactis*, and *Opostomias*, within which three paired cartilages develop and eventually fuse in late development [(Benjamin, 1990) regarding formation of cartilage within connective tissue]. In *Stomias,* a pad of dense connective tissue lies on both sides of the elongated notochord and embraces the enlarged exoccipitals (Schnell et al., 2008). In contrast, the connective tissue in *Chauliodus, Leptostomias, Thysanactis*, and *Opostomias* is of no such defined pad-like structure. Because the cartilages develop anterior to the third occipital myoseptum they are not homologous with the accessory neural arch (ANA) as suggested by Fink (1985) or even

TABLE 1. *Summary of the number of reduced vertebral centra in the genera* Chauliodus, Leptostomias, *and* Eustomias *with possible variations*

Genera	Species	Completely reduced vertebral centra (C)	Variations
Chauliodus	*C. macouni*	C1,C2	
	C. barbatus	C1,C2	Partial ventral ossification of C2 possible.
	C. pammelas	C1-C6	
	C. sloani	C1-C6	Partial ventral or dorsal ossification of C6 possible. In one adult specimen examined, also C7 was reduced.
	C. danae	C1-C6	In one adult specimen examined, also C7 was reduced, but with a partial ventral ossification of C7.
	C. schmidti	C1-C6	Partial ossification of C6 possible.
Leptostomias	*L. gladiator*	C1-C6	
	All other 11 species of *Leptostomias*[a]	0	
Eustomias	Group 1[b]	C2-C7	Partial ventral ossification of C2 in *E. macronema*.
	Group 2[c]	C2-C8	Partial ventral ossification of C2 and C8 in *E. bifilis, E. enbarbatus* and *E. fissibarbis*. In one specimen of *E. arborifer* C9 was reduced, but showed a partial ventral ossification in C9.
	E. obscurus	C2,C3, C5-C8	Partial ventral ossification of C2, C3 and C8; partial dorsal ossification of C5, C6 and C7.

[a]*Leptostomias gracilis, L. longibarba, L. macropogon, L. leptolobus, L. bermudensis, L. bilobatus, L. haplocaulus, L. macronema, L. multifilis, L. robustus, L. analis.*
[b]*Eustomias macronema, E. satterleei, E. tomentosis, E. schmidti, E. bigelowi, E. jimcraddocki, E. dinema.*
[c]*Eustomias bifilis, E. enbarbatus, E. fissibarbis, E. brevibarbatus, E. macrurus, E. bimargaritus, E. melanostigma, E. simplex, E. dubius, E. curtatus, E. arborifer.*

with the first basidorsal or neural arch as suggested by Regan and Trewavas (1930) for *Leptostomias*. Supportive evidence that these homology propositions are erroneous can be found in early ontogeny. The three cartilages appear much later in development than all following basidorsals. Furthermore, an important criterion for the homology of ANA is its association with the third occipital myoseptum (Johnson and Britz, 2010). The only stomiid we examined that develops a cartilaginous ANA within the third occipital myoseptum is *Eustomias obscurus*, whereas Fink (1985) also reported such an ANA for *E. macrurus*.

Chorda- and Autocentra

Vertebral centra may originate in development from different sources; Arratia and Schultze (1992) distinguished between arco-, chorda-, and autocentra based on their origin. The presence of chordacentra throughout the vertebral column is a feature of basal teleosts according to Laerm (1982:198). He argued that "evolution from a basically chordacentrous structure at the pholidophorid level, through a chordacentrous-autocentrous structure at the primitive teleost level to a predominantly autocentrous stage [is] characteristic of modern teleosts". In stomiids two sources are involved in centra formation, a chordacentrum formed by mineralisation of the chordal sheath and an autocentrum formed by direct ossification surrounding the notochord and chordacentrum (Mookerjee, 1936; Laerm, 1976; Arratia et al.,

2001). François (1966, 1967) described this condition for several euteleosts like *Clupea, Esox,* and *Salmo* [for the condition in *Salmo* see also (Arratia and Schultze, 1992; Nordvik et al., 2005)]. In addition to stomiids, the only other neoteleost for which chordacentra and autocentra have been reported is the poeciliid *Gambusia affinis* (Kamel, 1953).

Vertebral Modifications and Trophic Ecology in Stomiids

The occipito-vertebral gap plus an additional reduction of anterior vertebral centra in *Chauliodus, Eustomias,* and *Leptostomias gladiator,* allows a considerable degree of head bending. Together with characters like the elongated jaws studded with daggerlike teeth, and the loss of gill rakers (Morrow and Gibbs, 1964; Morrow, 1964), the external and internal morphology of stomiids has led to the assumption that these fishes are predators of large prey items (Tchernavin, 1953; Günther and Deckert, 1955, 1959). Sutton and Hopkins (1996) analyzed the stomach contents of stomiids of the eastern Gulf of Mexico and calculated that 80% of the investigated species (e.g., *Idiacanthus, Thysanactis, Melanostomias, Bathophilus, Eustomias, Leptostomias, Aristostomias, Stomias* and *Chauliodus*) feed mainly on myctophids. They found fish and crustaceans in the stomachs of *Stomias* and *Chauliodus*, and fish and copepods in *Thysanactis*. All other taxa they studied were strictly piscivorous. Marshall (1960) hypothesized that "in such surroundings it is an

advantage to be able to take the largest possible meal that comes along, and at the same time, not to turn aside from a copepod" (p. 108). The fact that *Malacosteus* was found to feed almost solely on copepods (Sutton, 2005) is surprising as we found in this genus the largest occipito-vertebral gap among all stomiids with no vertebral reduction. *Malacosteus* also lacks a mouth floor (Morrow, 1964) and possesses one of the largest jaws relative to body length (Sutton, 2005). Such adaptations would be expected to correlate with the ingestion of large prey items rather than a copepod diet. Sutton (2005) saw a correlation between the diet of *Malacosteus* and the ability to emit red bioluminescence from their suborbital photophore and their photo-sensitivity for such a long-wave light, the latter depending on bacteriochlorophyll derivatives, that cannot be synthesized by vertebrates and thus may be derived from its copepod diet. The diet of repre-sentatives of those genera with loss of centra or incomplete vertebrae in the anterior part of the ver-tebral column, does not differ significantly from the diet of most other stomiids.

CONCLUSIONS

The reorganization of the anterior part of the vertebral column was never included in phyloge-netic studies, because it has remained poorly understood. The purpose of this study was to investigate in all stomiid taxa the character of lost or reduced vertebrae, to test its homology and hopefully to use the resulting insight to elucidate stomiid phylogeny. However, as we have shown, the occipito-vertebral gap of most stomiid genera does not result from loss or reduction of vertebrae. The evolutionary loss of vertebrae in *Chauliodus, Leptostomias gladiator* and *Eustomias* might have been facilitated by the caudorostral ossification sequence of the vertebral centra typical of stomiids, with the anteriormost centra failing to ossify. According to the most recent cladogram (Fink, 1985), which was based on 323 morphologi-cal characters, these three taxa do not form a monophyletic group. This conclusion is supported by the high inter- and intrageneric variability in the number of lost vertebral centra and the differ-ing configurations of the anterior part of the verte-bral column described herein. We suggest that ver-tebral reduction has evolved independently in the three taxa and is not a synapomorphy for them. Such a specialization of the anterior vertebral col-umn appears to be unique within teleosts, but obviously not within the family Stomiidae.

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LITERATURE CITED

Ahlstrom EH, Counts RC. 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pa-cific. Fish Bull Fish Wildl Serv US 58:363–416.

Allis EP. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. J Morphol 12:487–770.

Allis EP. 1898. The homologies of the occipital and first spinal nerves of *Amia* and teleosts. Zool Bull 2:83–97.

Allis EP. 1903. The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. J Morphol 18: 45–308.

Arratia G, Schultze H-P. 1992. Reevaluation of the caudal skele-ton of certain actinopterygian fishes: III. Salmonidae. Homo-logization of caudal skeletal structures. J Morphol 214: 187–249.

Arratia G, Schultze H-P, Casciotta J. 2001. Vertebral column and associated elements in dipnoans and comparison with other fishes: Development and homology. J Morphol 250: 101–172.

Beebe W. 1934. Deep-sea fishes of the Bermuda oceanographic expeditions. Family Idiacanthidae. Zoologica 16:149–241.

Benjamin M. 1990. The cranial cartilages of teleosts and their classification. J Anat 169:153–172.

Britz R, Johnson GD. 2010. Occipito-vertebral fusion in actino-pterygians: Conjecture, myth and reality. Part 1: Nonteleosts. In: Nelson JS, Schultze H-P, Wilson MVH, editors. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Dr. Friedrich Pfeil. pp 77–93.

Crane JM. 1966. Late Tertiary radiation of viperfish (Chaulio-dontidae) based on a comparison of Recent and Miocene species. Bull Los Angeles County Mus Nat Hist Sci 115:1–37.

Dingerkus G, Uhler LD. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of carti-lage. Stain Technol 52:229–232.

Domagk G. 1933. Neuerungen auf dem Gebiet der histologi-schen Technik. Medizin und Technik 1:126–136.

Fink WL. 1985. Phylogenetic interrelationships of the stomiid fishes (Teleostei: Stomiiformes). Misc Publ Mus Zool Univ Michigan 171:1–127.

François Y. 1966. Structure et développment de la vertèbre de *Salmo* et des téléostéens. Arch Zool Exp Gén 107:287–328.

François Y. 1967. Structure vertèbrales des actinopterygiens. Coll Int du Cent nat de la Rech Sci 163:155–172.

Fürbringer M. 1897. Über die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morpho-logie. Festschrift zum 70. Geburtstage von Carl Gegenbaur. Bd.III: pp 349–788.

Günther K, Deckert K. 1955. Zweiter Versuch einer morpholo-gisch-anatomischen Funktionsanalyse der Nahrungserwerbs-und Atmungsapparate von Tiefseefischen. Zoologische Bei-träge (NF) 1:241–365.

Günther K, Deckert K. 1959. Morphologie und Funktion des Kiefer- und Kiemenapparates von Tiefseefischen der Gattungen *Malacosteus* und *Photostomias* (Teleostei. Isospondyli, Stomiatoidea, Malacosteidae). Dana Rep 49:1–54.

Herrick CJ. 1899. The cranial and first spinal nerves of *Menidia*: a contribution upon the nerve components of the bony fishes. J Comp Neurol 9:153–455.

Johnson GD, Britz R. 2010. Occipito-vertebral fusion in actinopterygians: Conjecture, myth and reality. Part 2: Teleosts. In: Nelson JS, Schultze H-P, Wilson MVH, editors. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Dr. Friedrich Pfeil. pp 95–110.

Kamel A. 1953. On the development of the vertebral column in *Gambusia affinis*. Bull Fac Sci Egypt Univ 32:95–116.

Laerm J. 1976. The development, function, and design of amphicoelous vertebrae in teleost fishes. Zool J Linn Soc 58:237–254.

Laerm J. 1982. The origin and homology of the neopterygian vertebral column. J Paleontol 56:191–202.

Marshall NB. 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Disc Rep 31:1–122.

Mookerjee HK. 1936. The development of the vertebral column and its bearing on the study of organic evolution. Proc Indian Sci Congr 23:307–343.

Morrow JE Jr. 1964. Family Malacosteidae. In: Bigelow HB, Breder CM, Cohen DM, Mead GW, Merriman D, Olsen YH, Schroeder WC, Schultz LP, Tee-Van J, editors. Fishes of the Western North Atlantic. New Haven: Mem Sears Found Mar Res No. 1(Part 4), pp 523–549.

Morrow JE Jr, Gibbs RH Jr. 1964. Family Melanostomiatidae. In: Bigelow HB, Breder CM, Cohen DM, Mead GW, Merriman D, Olsen YH, Schroeder WC, Schultz LP, Tee-Van J, editors. Fishes of the Western North Atlantic. New Haven: Mem Sears Found Mar Res No. 1(Part 4), p 351–510.

Moser HG, Ahlstrom EH. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. species with narrow-eyed larvae. Bull Los Angeles County Mus Nat Hist Sci 7:1–145.

Nakae M, Sasaki K. 2007. Review of spino-occipital and spinal nerves in Tetraodontiformes, with special reference to pectoral and pelvic fin muscle innervation. Ichthyol Res 54:333–349.

Nelson JS. 2006. Fishes of the World, 4th ed. New York: John Wiley & Sons. 601 p.

Nordvik K, Kryvi H, Totland GK, Grotmol S. 2005. The salmon vertebral body develops through mineralization of two preformed tissues that are encompassed by two layers of bone. J Anat 206:103–114.

Parenti LR, Song J. 1996. Phylogenetic significance of the pectoral-pelvic fin association in acantomorph fishes: A reassessment using comparative neuroanatomy. In: Stiassny MLJ, Parenti L, Johnson GD, editors. Interrelationships of Fishes. San Diego: Academic Press. pp 427–444.

Patterson C, Johnson GD. 1995. The intermuscular bones and ligaments of teleostean fishes. Smith Contr Zool 559:1–83.

Potthoff T, Tellock JA. 1993. Osteological development of the snook. *Centropomus undecimalis* (Teleostei, Centropomidae). Bull Mar Sci 52:669–716.

Potthoff T, Kelley S, Collins LA. 1988. Osteological development of the red snapper. *Lutjanus campechanus* (Lutjanidae). Bull Mar Sci 43:1–40.

Regan CT, Trewavas E. 1930. The fishes of the families Stomiatidae and Malacosteidae. Dana Rep 6:1–143.

Richards WJR, Miller RV, Houde E. 1974. Egg and larval development of the Atlantic thread herring, *Opisthonema oglinum*. Fish Bull US 72:1123–1136.

Rosen DE. 1985. An essay on euteleostean classification. Am Mus Novit 2827:1–57.

Sagemehl M. 1883. Beiträge zur Vergleichenden Anatomie der Fische. I. Das Cranium von *Amia calva* L. Morphol Jahrb 9:73–94.

Schnell NK, Bernstein P, Maier W. 2008. The "pseudo-craniovertebral articulation" in the deep-sea fish *Stomias boa (Teleostei: Stomiidae)*. J Morphol 269:513–521.

Sell J. 1916. Zur Kenntnis der Morphologie und Histologie der Wirbelsäule von *Chauliodus sloani* (Bloch und Schneider) [Phd dissertation]. Leipzig: University of Leipzig. 41 p.

Sewertzoff AN. 1895. Die Entwicklung der Occipitalregion der niederen Vertebraten im Zusammenhang mit der Frage über die Metamerie des Kopfes. Bull Soc Imp Natural Moscou 9:186–284.

Song J, Parenti LR. 1995. Clearing and staining whole fish specimens for simultaneous demonstration of bone, cartilage, and nerves. Copeia 1:114–118.

Stiassny MLJ. 1996. Basal ctenosquamate relationships and the interrelationships of the myctophiform (scopelomorph) fishes. In: Stiassny MLJ, Parenti L, Johnson GD, editors. Interrelationships of Fishes. San Diego: Academic Press. pp 405–426.

Sutton TT. 2005. Trophic ecology of the deep-sea fish *Malacosteus niger* (Pisces: Stomiidae): An enigmatic feeding ecology to facilitate a unique visual system? Deep-Sea Res I 52:2065–2076.

Sutton TT, Hopkins TL. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: Strategies, selectivity and impact of a top mesopelagic predator group. Mar Biol 127:179–192.

Tchernavin VV. 1953. The feeding mechanism of a deep sea fish, *Chauliodus sloani* Schneider. London: British Museum (Natural History). 101 p.

Weisel GF. 1967. Early ossification in the skeleton of the sucker (*Catostomus macrocheilus*) and the guppy (*Poecilia reticulata*). J Morphol 121:1–18.