

Ontogeny of the Chondrocranium in *Corydoras aeneus* (Gill, 1858) (Callichthyidae, Siluriformes)

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ABSTRACT Callichthyids take a basal position in the loricarioid evolutionary lineage leading up to an algae scraping feeding mechanism in the loricariid family. Therefore, the study of the morphology and development of a callichthyid representative would contribute to a better knowledge on the differences in cranial morphology and their impact on feeding ecology within this superfamily. Therefore, development in the chondrocranium of *Corydoras aeneus* was studied based on 22 cleared and stained specimens and 6 series of serial sections. The latter sections were also digitized and used for 3D reconstructions. Development overall follows the typical siluriform trends in chondrocranial development. Even the low complexity of the chondrocranium at hatching fits the trend observed in other siluriforms, although other studies showed loricarioid hatchlings to generally show more complex chondrocrania. In contrast to other catfish, in *C. aeneus*, the notochord was never found to protrude into the hypophyseal fenestra. In addition, also differing from other siluriforms, a commissura lateralis is present, a state also reported for *Ancistrus* cf. *triradiatus* (Geerinckx et al., [2005] *J Morphol* 266:331–355). The splanchnocranium again has the typical siluriform shape during its ontogeny, with the presence of a compound hyosymplectic-pterygoquadrate plate, although not fused to the neurocranium or interhyal at any time during ontogeny, a state described earlier for *Callichthys callichthys* (Hoedeman, [1960a] *Bull Aquat Biol* 1:73–84; Howes and Teugels, [1989] *J Zool Lond* 219:441–456). The most striking difference found in comparison to other catfishes, however, involves the branchial basket, which arises as a single element with a further differentiation from the middle arches on in both a rostral and caudal direction. *J. Morphol.* 269:522–532, 2008. © 2007 Wiley-Liss, Inc.

KEY WORDS: ontogeny; chondrocranium; cartilage; *Corydoras*; Callichthyidae; catfishes

The highly diverse catfish genus *Corydoras* comprises 152 species ranging in maximal standard length (SL) between 20 mm (*Corydoras habrosus*) and 88 mm (*Corydoras*) (Reis, 2003; Froese and Pauly, 2006; Ferraris, 2007). In studies by Reis (1998) and Britto (2003), morphological data provided a phylogenetic framework for both the family (Callichthyidae), and subfamily (Corydoradinae) to which this genus belongs. In addition, Shimabukuro-Dias et al. (2004) used molecular data to investigate on the phylogenetic affinities within the family, but the phylogeny of the genus itself, however, remains unresolved.

In this study we focus on *Corydoras aeneus*, a species which has already been studied from both a morphological and physiological point of view (e.g., Kramer and McClure, 1980, 1981; Shiba et al., 1982; Kramer and Braun, 1983; Oliveira et al., 1992, 1993; Sire and Huysseune, 1996; Huysseune and Sire, 1997; Huysentruyt and Adriaens, 2005a, b). In contrast to this, however, very little is known about the ontogenesis of the skeleton. Some attention has already been paid to the early skeletal ontogenesis of some aspects of the head in other callichthyids (Hoedeman, 1960a,b), but still a lot of detailed information on, e.g., the development of processes, articulations, and foramina is lacking. Since morphogenesis and differentiation are very intense during early life stages, (Van Snik et al., 1997) a thorough knowledge of anatomical ontogeny is of critical importance in understanding the functional trends during early development, since organisms must be functional at each moment, including the early “temporary” stages (Fukuhara, 1992; Koumoundouros et al., 2001a,b; Geerinckx et al., 2005).

Corydoras aeneus belongs to the family of the Callichthyidae, which itself belongs to the Loricarioidea, a superfamily in which an evolutionary trend has been observed which has led to the presence of a suckermouth in the families Astroblepidae and Loricariidae. In the latter family, the presence of such a suction mouth has ultimately led to the formation of an additional highly specialized feeding mechanism (i.e., algae-scraping). In addition to the presence of this suction disc in Loricariidae, implications of this specialized apparatus involve tilted lower jaws and new muscle configurations, coupled to increased jaw mobility (Geerinckx et al., 2005). Placed within the evolutionary lineage leading up to these adaptations, the Callichthyidae take a basal position with a ventrally

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placed mouth already present but with neither the presence of a sucking disc nor an algae-scraping feeding apparatus. In this context, the study of the morphology and development of *C. aeneus* can contribute to a better knowledge on the differences in cranial morphology and their impact on feeding ecology within this superfamily. This is especially the case for the earliest stages in ontogeny, at which point the yolk sac often becomes depleted and feeding becomes obligatory. Since both hatching as well as yolk depletion in *C. aeneus* occur during chondrocranial development and before neurocranial bone formation, the study was limited to the development of the chondrocranium, whereas the development of the osteocranium will be dealt with in a later stage. In addition, since former studies done on catfish chondrocranial development show no major changes in the chondrocranium after the start of perichondral bone formation, there was no reason to extend our study beyond this point (Adriaens and Verraes, 1997).

Therefore, the aim of this study is to provide a complete description of the ontogeny of the chondrocranium in *Corydoras aeneus*, adding to the wide variety of data on catfish chondrocranial development (Kindred, 1919; Ballantyne, 1930; Bamford, 1948; Srinivasachar, 1957a,b, 1958, 1959; Hoedeman, 1960a; Vandewalle et al., 1985; Surlemont et al., 1989; Surlemont and Vandewalle, 1991; Adriaens and Verraes, 1994, 1997; Geerinckx et al., 2005) and providing a basis for further ongoing ontogenetic research on this species. The data generated this way were compared to the general trends in siluriforms and to similar data published earlier by Geerinckx et al. (2005) on *Ancistrus cf. triradiatus*, a loricariid representative. The comparison of the differences and similarities of both ontogenetic sequences provides additional information on the evolutionary processes leading up to the remarkable niche diversification in the Loricariidae family. This way, we hypothesize that, given the close phylogenetic relationship of the species compared, both ontogenies would exhibit a great amount of similarity, only showing significant differences in the development of those elements associated with the specialized feeding mechanism in *A. cf. triradiatus*.

MATERIALS AND METHODS

Thirtyfive *C. aeneus* (Gill, 1858), of which 25 were male, were kept in a separate 1.0 × 0.5 × 0.6 m tank with a water temperature of 24–26°C, pH-level of 8–8.5, and global hardness of 9–12°. Breeding was induced by an artificial rain season. This way, dry season conditions were imitated by lowering the water level to 10 cm and lowering light intensity for a period of 20–30 days. This was followed by an imitation of rain season conditions (daily adding of fresh, colder water and sufficient aeration) (Fuller, 2001). About a week after the start of this artificial rain season, several egg clutches were found on the glass walls of the tank for several consecutive days. Offspring were removed at different ages, killed with an overdose of MS-222 (3-aminoben-

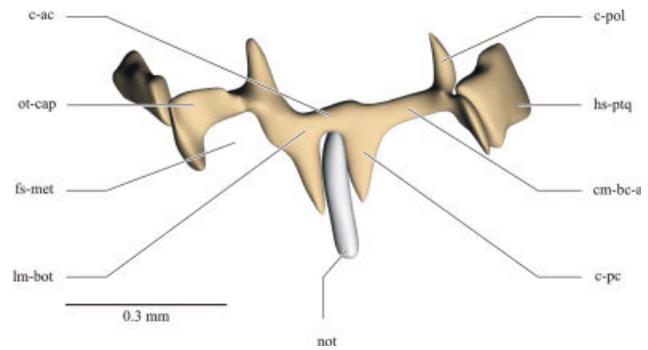


Fig. 1. Dorsal view of a 3D reconstruction of the chondrocranium of *C. aeneus* (3.3 mm SL). c-ac, cartilago acrochordalis; cm-bc-a, commissura basicapsularis anterior; c-pc, cartilago paracordalis; c-pol, cartilago polaris; fs-met, fissura metotica; hs-ptq, hyosymplectic-ptyergoquadrate plate; lm-bot, lamina basiotica; not, notochord; ot-cap, otic capsule.

zoic acid ethyl ester, Sigma), measured and preserved in paraformaldehyde fixative (4%). Twentytwo specimens, ranging in SL from 4.0 to 8.2 mm, were selected for clearing and staining using the method described by Taylor and Van Dyke (1985), in which KOH (0.5–4%) was used as the clearing agent. Staining of cartilage was done using 0.009–0.03% alcian blue in [40 ml glacial acetic acid/60 ml 96–100% alcohol (pH 3–3.5)] and bone staining was done using 0.1% alizarin red + 0.5% KOH. Since the acetic acid used in the cartilage staining step could decalcify bone, for control, this step was omitted in 8 of the 22 specimens, in which, this way, only bone tissue was stained. These specimens were studied using an Olympus SZX7 stereomicroscope. Six additional *C. aeneus* specimens (3.3, 4.0, 4.4, 4.9, 5.3, and 6.3 mm SL) were embedded in Technovit 7100 and 2 µm thick transverse sections were made using a Reichert-Jung Polycut microtome, which were stained with toluidine blue. These serial sections were digitized and used for 3D reconstruction using Amira 3.1.1 (TGS Europe, France) and Rhinoceros (Robert McNeel & Associates, USA) software. In the earliest stages, 3D-reconstructions sometimes yielded some left–right asymmetry, which, however, could very well be an artifact of the digitization, since very low amounts of cartilage are present in these stages. Therefore, which and given the fact that, in no other study done on early catfish chondrocrania, as well as in our cleared and stained specimens a left–right asymmetry was found, this asymmetry was treated as an artifact and not further discussed.

RESULTS

Stage 1: 3.3 mm SL (Hatchling) (see Fig. 1)

Neurocranium. At hatching, the neurocranium is rudimentary and chondrification is concentrated around the notochord tip. Bordering this notochord tip laterally are two parachordal cartilages, which interconnect anterior to the notochord through the acrochordal cartilage. On their lateral margins, both parachordal cartilages connect to the basiotic laminae, making up the primordium of the basal plate. Further laterally this plate contacts the dorsocaudally oriented anterior part of the otic cartilages through the anterior basicapsular commissure. This way, two large posterior metotic fissures appear, through which the nervus glossopharyngeus (IX) and vagus (X) pass. At the rostral margin of this basal cartilaginous skull, two polar cartilages are present.

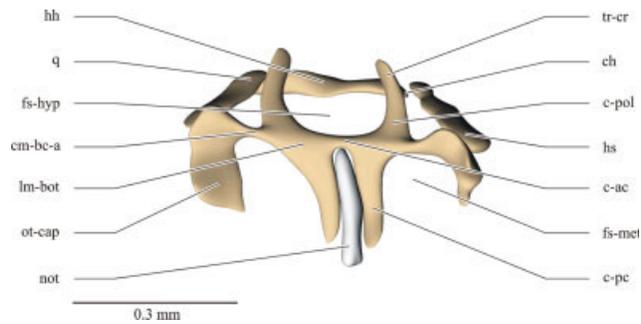


Fig. 2. Dorsal view of a 3D reconstruction of the chondrocranium of *C. aeneus* (4.0 mm SL). c-ac, cartilago acrochordalis; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; c-pc, cartilago parachordalis; c-pol, cartilago polaris; fs-hyp, fissura hypophyseae; fs-met, fissura metotica; hh, hypohyale; hs, hyosymplecticum; lm-bot, lamina basiotica; not, notochord; ot-cap, otic capsule; q, quadratum; tr-cr, trabecula cranii.

Splanchnocranium. At about the time of hatching, the splanchnocranium is confined to the suspensorium, which arises as a single chondrification or hyosymplectic-pterygoquadrate plate (sensu Arratia, 1992) and articulates dorsally with the neurocranium at the level of the otic cartilage. This hyosymplectic-pterygoquadrate plate does not yet bear a process for articulation with the operculare, nor is the foramen truncus hyomandibularis formed at this stage.

Stage 2: 4.0 mm SL (Figs. 2 and 6a,b)

Neurocranium. At 4.0 mm SL, the trabecular bars are formed as rostral expansions of the polar cartilages. As is to be expected in a platybasic teleost skull, these trabecular bars lie well separated from each other and are slightly curved. Not yet touching rostrally, they leave a wide hypophyseal fissure at the anterior margin of the skull. Since the internal carotid artery still passes through this large fissure (and not through a smaller fissure in the cartilaginous trabecular bars themselves), it is impossible to distinguish the trabecular bars from the polar cartilages at this point. Observations on later stages and other siluriform fish, however, lead to the assumption that the posterior part at this point would correspond to the polar cartilage (Adriaens and Verraes, 1997; Geerinckx et al., 2005).

Splanchnocranium. At 4.0 mm SL, the entire hyoid arch is also formed as a single element, incorporating both left and right hypohyals and ceratohyals. In addition, the hyosymplectic-pterygoquadrate plate has broadened and shifted its orientation from oblique to vertical. At this level, the dorsal and ventral parts of the suspensorium can be distinguished as the hyosymplectic and quadrate part respectively. In the branchial basket, which is still very much compressed dorsoventrally, the presence of chondrocytes, as observed on serial sections, already indicates the onset of branchial arch formation, in which all five arches are present and fused together ventrally. In addition, the first

four arches are also fused at the dorsal side of the basket, forming a large dorsal plate.

Stage 3: 4.4 mm SL (Figs. 3 and 6c)

Neurocranium. At this stage, both trabecular bars contact each other rostrally, forming the ethmoid cartilage, and expanding laterally into the solum nasi. Thus, the fissura hypophyseae is closed off, forming the fenestra hypophyseae. At the caudal

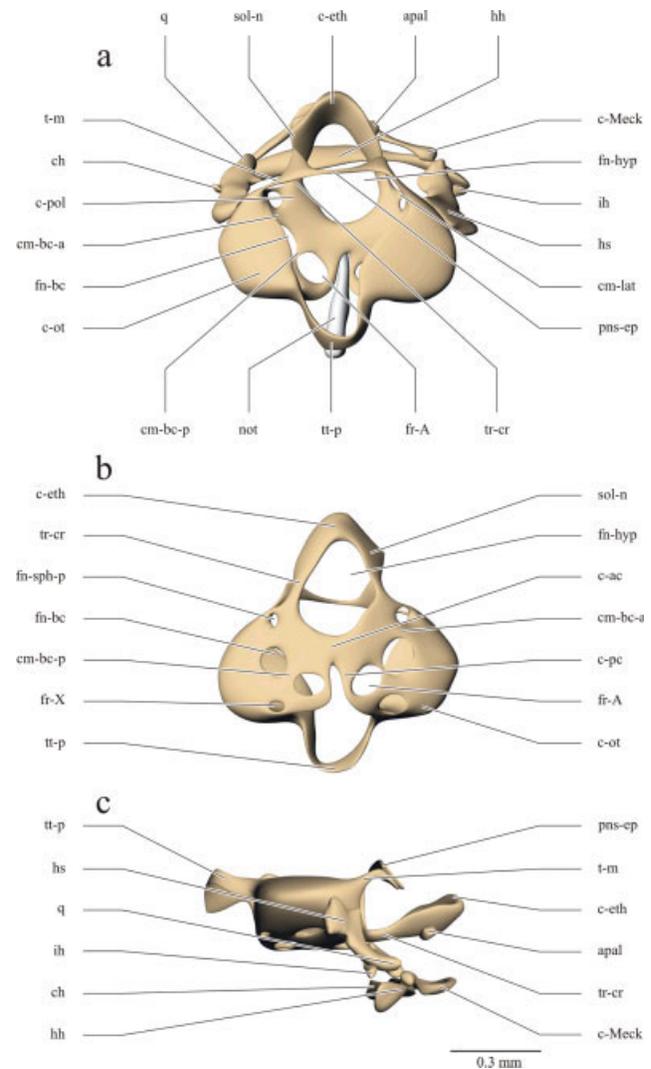


Fig. 3. Three-dimensional reconstruction of the chondrocranium of *C. aeneus* (4.4 mm SL). (a) Dorsal view. (b) Ventral view of the neurocranium. (c) Right lateral view. apal, autopalatium; c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cm-bc-p, commissura basicapsularis posterior; c-Meck, cartilago Meckeli; cm-lat, commissura lateralis; c-ot, otic capsule; c-pc, cartilago parachordalis; c-pol, cartilago polaris; fn-bc, fenestra basicapsularis; fn-hyp, fenestra hypophyseae; fn-sph-p, fenestra sphenoida posterior; fr-A, foramen "A"; fr-X, foramen nervus vagus; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; not, notochord; pns-ep, pons epiphysialis; q, quadratum; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

side of this fenestra, the otic cartilages have expanded ventrolaterally, contacting the polar cartilages through the lateral commissures, splitting up the fenestra sphenoida into anterior and posterior parts. At this stage, serial sections already show the passage of the nervus oculomotorius (III), trochlearis (IV), trigeminus (V), and the mandibular branch of the nervus facialis (VII) through the anterior part and the passage of the ramus hyomandibularis of the nervus facialis (VII) through the posterior part. At the level of the basal plate an additional connection with the otic cartilage is formed through the posterior basicapsular commissure, splitting up the metotic fenestra. Serial sections further indicate that the aperture present between anterior and posterior basicapsular commissure is penetrated by the nervus glossopharyngeus (IX), but not by the nervus vagus (X), which makes this the basicapsular fenestra. The posterior subdivision of the metotic fenestra is not penetrated by any nerves and will here be called foramen "A." Caudally, two occipital pilae have emerged, which fuse at the dorsal side of the neural tube, forming the tectum posterius. At the caudal margin of this chondrocranium, the lamina basiotica has further expanded, rigidifying the neurocranial floor. At the dorsal side of the chondrocranium, both otic capsules have expanded rostrally forming the taeniae marginales, which already interconnect through the epiphyseal bridge but do not yet protrude further rostrally.

Splanchnocranium. At 4.4 mm SL, both the interhyal, Meckel's cartilage and autopalatine first appear, all as separate elements. The hyosymplectic-pterygoquadrate plate has developed a processus opercularis for the later articulation with the opercular bone. In the branchial basket, the central copula has split up into an anterior and a posterior part, with the former part situated near the hypobranchial parts of the first three branchial arches and the latter part with those of arches IV and V. The medial tip of the hypobranchial part of the third arch is situated in between these two copulae. Furthermore, hypobranchials II and III are already present as separate elements. All arches already have ceratobranchial cartilages and arches I-IV bear epibranchials, none of which has detached from the ceratobranchial parts at this point. One large infrapharyngobranchial element is present as a separate element, with the anterior tip articulating with epibranchials one and two, and the posterior part articulating with epibranchials III and IV. Teeth are already present in both the dorsal and ventral part of the basket, but no ossifications supporting these teeth have been formed at this point.

Stage 4: 4.9 mm SL (Figs. 4 and 6d)

Neurocranium. At this stage, the taenia marginalis makes contact with the solum nasi, through

the commissura spheno-ethmoidalis, forming the lamina orbitonasalis. Rostrally, the taenia marginalis further expands, forming the onset of the commissura sphenoseptalis. In the skull base, the fenestra basicapsularis is split by the commissura basivestibularis into an anterior and a posterior part, with the latter accommodating the nervus glossopharyngeus (IX).

Splanchnocranium. The hyosymplectic-pterygoquadrate plate further differentiates into a more distinct pars quadratum, which articulates with Meckel's cartilage and a pars hyosymplecticum, articulating with the neurocranium. In the latter, the foramen truncus hyomandibularis is present from this stage on (not visible in Fig. 4). Additionally, the onset of a pterygoid process is present. The hyoid arch has started to split medially and the two lateral halves have begun to differentiate into a more distinct ceratohyal and hypohyal part, with the latter articulating with the interhyal. In the branchial basket, epibranchials II and III have detached from the ceratobranchials but in this specimen, the hypobranchial of the second arch was still loosely connected to the ceratobranchial (even though they were already separated in the specimen used for the previous stage). Cartilage had also disappeared at the level of the articulation between cerato- and epibranchial IV, indicating that both elements probably detach soon after this stage. In addition, the infrapharyngobranchial cartilage has expanded anteriorly and has started to differentiate into a more clear anterior and posterior part, again clearly articulating with, respectively, the first and last two epibranchials.

Stage 5: 5.3 mm SL (Figs. 5 and 6e)

Neurocranium. At this stage, the solum nasi has expanded laterally and the commissura sphenoseptalis now is fused to the ethmoid cartilage at the level of the lamina precerebralis. The preorbital base forms another vertical connection between taeniae marginales and trabeculae cranii slightly behind the lamina orbitonasalis, leaving a small orbitonasal foramen, which disappears later during ontogeny. Therefore a large foramen fila olfactoria appears. The cartilage of the skull floor has expanded further, comprising a caudal expansion of the acrochordal cartilage and closing off both the foramen "A" as well as narrowing the foramen for the passage of the nervus vagus (X).

Splanchnocranium. The pterygoid process of the hyosymplectic-pterygoquadrate has expanded significantly. In the branchial basket the first epibranchial has detached from the rest of the arch but in the fourth arch, this element is still slightly connected to the ceratobranchial. In the fourth and fifth arch, cartilage has disappeared at the level of the infrapharyngobranchial and ceratobranchial, where thin bony tooth plates started to develop.

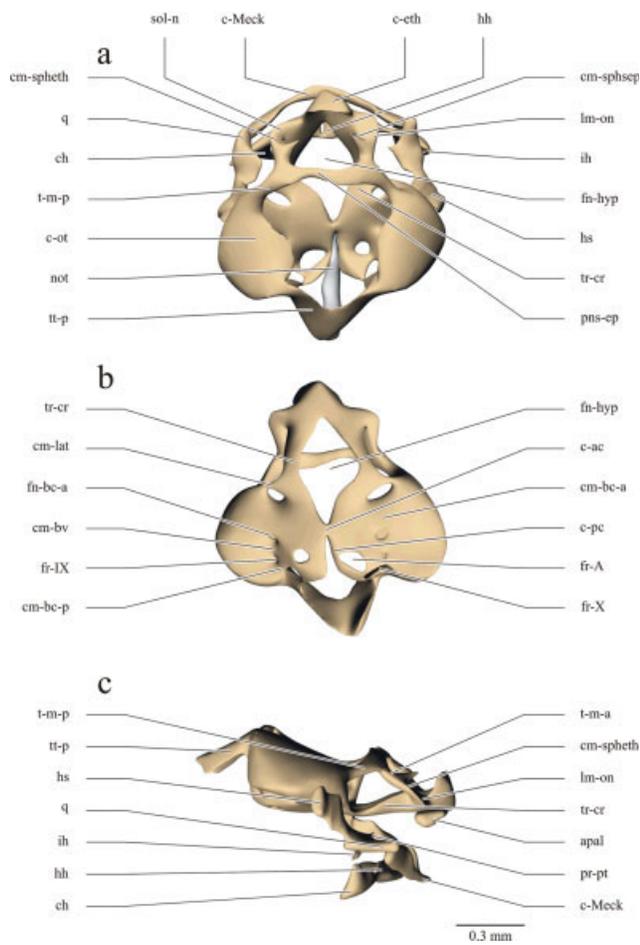


Fig. 4. Three-dimensional reconstruction of the chondrocranium of *C. aeneus* (4.9 mm SL). (a) Dorsal view. (b) Ventral view of the neurocranium. (c) Right lateral view. apal, autopalatinum; c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cm-bc-p, commissura basicapsularis posterior; cm-bv, commissura basivestibularis; c-Meck, cartilago Meckeli; cm-lat, commissura lateralis; cm-spheth, commissura sphenothmoidalis; cm-sphsep, commissura sphenoseptalis; c-ot, otic capsule; c-pc, cartilago parachordalis; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophyseae; fr-A, foramen "A"; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-on, lamina orbitonasalis; not, notochord; pns-ep, pons epiphysialis; pr-pt, processus pterygoideus; q, quadratum; sol-n, solum nasi; t-m-a, taenia marginalis anterior; t-m-p, taenia marginalis posterior; tr-cr, trabecula cranii; tt-p, tectum posterius.

Stage 6: 6.3 mm SL (Fig. 6f)

Neurocranium. No additional changes have occurred in the chondrocranium at this point.

Splanchnocranium. At this point, in the gill arches, all epibranchials have detached from the ceratobranchials and the infrapharyngobranchial part has split up into a posterior and anterior part articulating with the last and first two arches, respectively. In both the fourth and first arch, the

hypobranchial part is still fused to the ceratobranchial part. In the first arch, these elements will separate shortly after this stage, while, in the fourth arch, both elements never detach.

After this stage, at around 8 mm SL, cartilage starts to disappear and ossification begins.

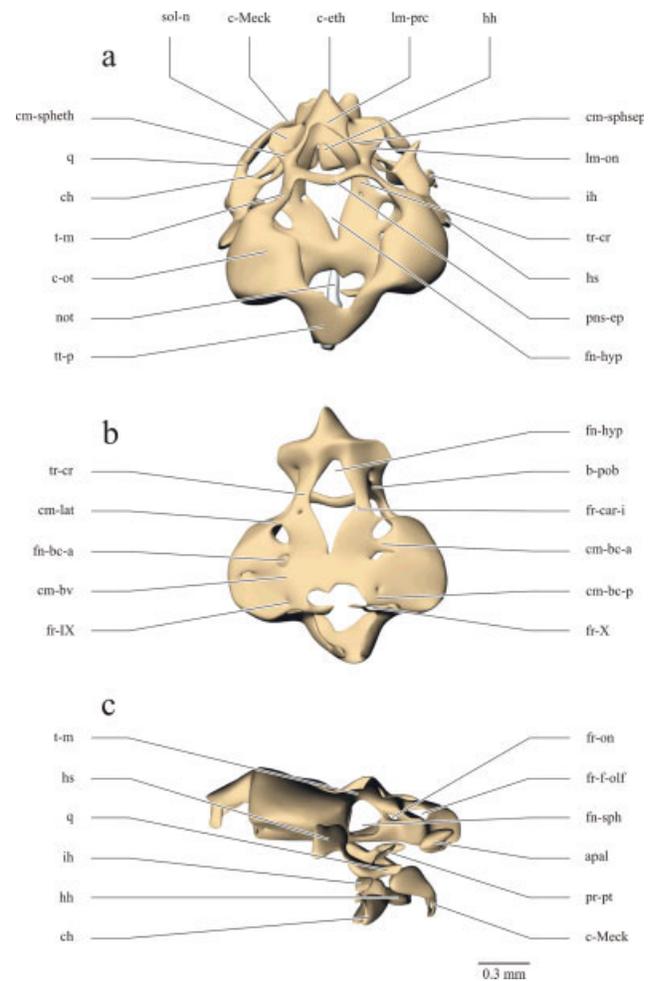


Fig. 5. Three-dimensional reconstruction of the chondrocranium of *C. aeneus* (5.3 mm SL). (a) Dorsal view. (b) Ventral view of the neurocranium. (c) Right lateral view. apal, autopalatinum; b-pob, preorbital base; c-eth, cartilago ethmoideum; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cm-bc-p, commissura basicapsularis posterior; cm-bv, commissura basivestibularis; c-Meck, cartilago Meckeli; cm-lat, commissura lateralis; cm-spheth, commissura sphenothmoidalis; cm-sphsep, commissura sphenoseptalis; c-ot, otic capsule; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophyseae; fr-car-i, foramen arteria carotis interna; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-on, lamina orbitonasalis; lm-prc, lamina precerebralis; not, notochord; pns-ep, pons epiphysialis; q, quadratum; pr-pt, processus pterygoideus; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

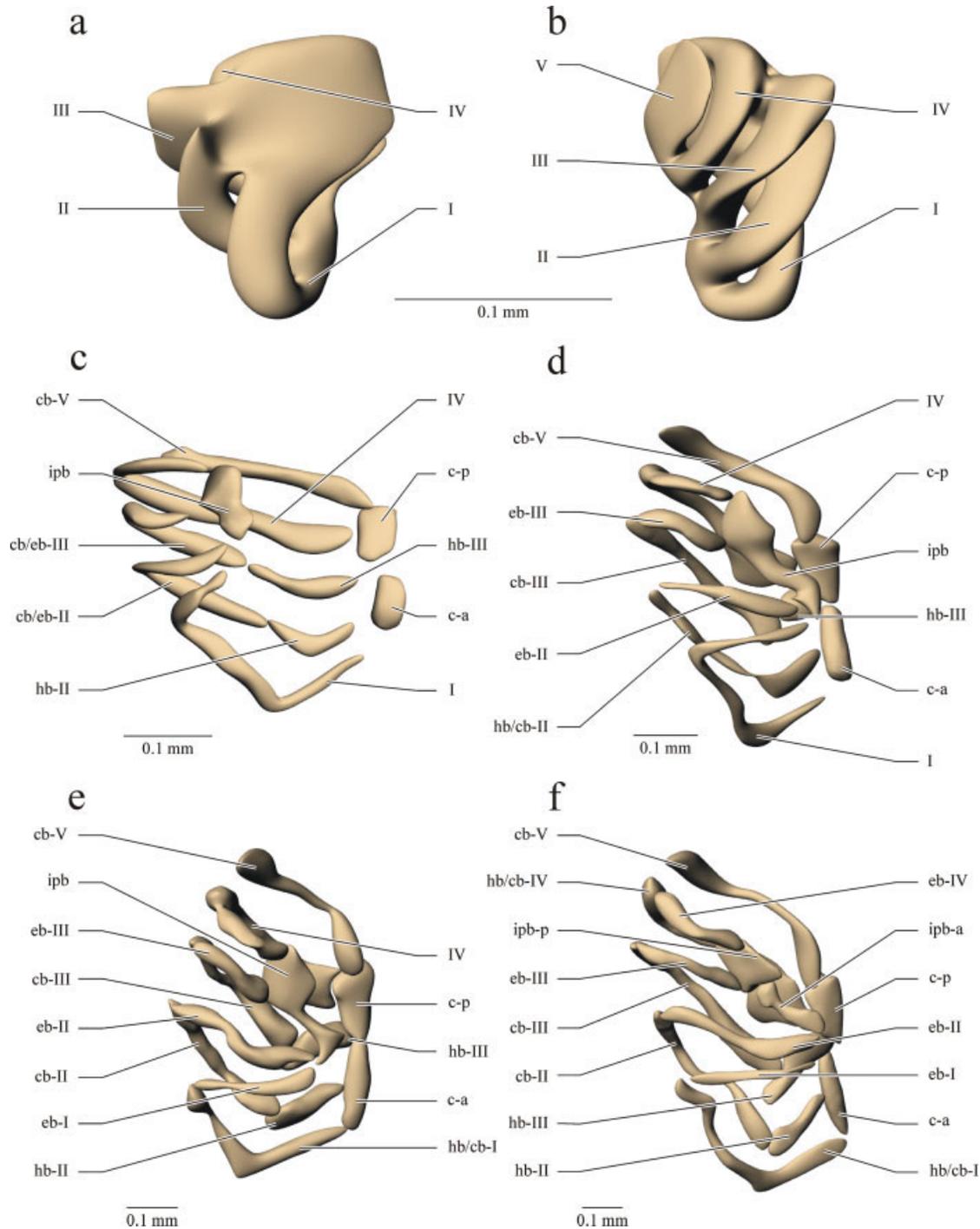


Fig. 6. Three-dimensional reconstruction of right half of the branchial basket of *C. aeneus*. (a) Stage 2, Dorsal view; (b) Stage 2, Ventral view; (c) Stage 3, Dorsal view; (d) Stage 4, Dorsal view; (e) Stage 5, Dorsal view; (f) Stage 6, Dorsal view. c-a, copula anterior; cb, ceratobranchial; c-p, copula posterior; eb, epibranchial; hb, hypobranchial; ipb, infrapharyngobranchial; ipb-a, infrapharyngobranchial anterior; ipb-p, infrapharyngobranchial posterior. Roman numerals indicate arch number./-symbol indicates fusion of elements.

DISCUSSION

At hatching the chondrocranium is rudimentary and concentrated around the notochord tip, a situation common in catfishes (Adriaens and Verraes, 1997). The fact that chondrification has started in

both the neurocranium and splanchnocranium at this stage is a state also described in most studies dealing with teleost ontogeny (e.g., de Beer, 1937; Adriaens and Verraes, 1997; Geerinckx et al., 2005). In contrast, however, the complexity of the

chondrocranium at hatching is highly variable in teleosts. Species like *Salmo letnica*, *S. trutta fario* (Salmoniformes), and *Oryzias latipes* (Belontiiformes) already exhibit a fairly high level of neurocranial chondrification at hatching, while in other teleost species such as *Mastacembelus armatus* (Synbranchiiformes), *Solea solea* (Pleuronectiiformes) and *Hepsetus odoe* (Characiformes) no chondrification is present at that time (de Beer, 1927; Bhargava, 1958; Bertmar, 1959; Langille and Hall, 1987; Wagemans and Vandewalle, 1999; Ristovska et al., 2006). However, several studies indicate that siluriform chondrocrania are generally limited in complexity at the time of hatching. Species like *Chrysichthys auratus* (Claroteidae) and *Heterobranchus longifilis* and *Clarias gariepinus* (Clariidae) show little to no chondrification at hatching while the chondrocranium in hatchlings from other species like *Heteropneustes fossilis* (Heteropneustidae) is only slightly developed (Srinivasachar, 1959; Adriaens and Verraes, 1997; Vandewalle et al., 1997, 1999). Studies on species of the Loricarioidea superfamily, like *Ancistrus* cf. *triradiatus* (Loricariidae) and *Callichthys callichthys* (Callichthyidae), however, show hatchlings of this group to have a more developed chondrocranium (Hoedeman, 1960a; Geerinckx et al., 2005). As an exception, *Hoplosternum littorale* (Callichthyidae), only showed localized patches of connective tissue where chondrification was taking place, but without actual cartilage being formed at the time of hatching (Ballantyne, 1930). This way, the complexity of the chondrocranium at hatching in *C. aeneus* seems to fit the general trend found in Siluriformes, rather than that found in the Loricarioidea. In this context, egg size has often been suggested as a key factor influencing larval development and chondrocranium complexity at hatching since this implies an increase in yolk material, frequently related with the duration of the prehatching development (Araujo-Lima, 1994; Adriaens and Vandewalle, 2003). For example, in *Galeichthys feliceps* (egg size: 15.6 mm) (Ariidae) hatchlings already possess complete bony skulls, whereas in the loricariid *Ancistrus* cf. *triradiatus* (egg size: 3.1 mm) a highly developed chondrocranium is present at that point (Tilney and Hecht, 1993; Geerinckx et al., 2005). In comparison, the egg size of 1.5 mm in *C. aeneus* is rather small, indeed resulting in a less developed chondrocranium at hatching (Huysentruyt and Adriaens, 2005b). Next to body size and clutch size, egg size is often suggested to be related to parental care (Kolm and Ahnesjö, 2005). Such parental care, observed in many loricariid species (Suzuki et al., 2000), is unreported in Callichthyidae, which could explain the smaller egg size in members of this group. As a result, yolk sac amount is also limited, which speeds up the time of hatching during development. Indeed, *C. aeneus* hatches 3 days after fertilization at a SL of

3.5 mm, at which stage the chondrocranium is still primordial, shortening the period between onset of chondrification (hatching) and yolk sac depletion (4.4 mm) to 3 days. For comparison, the larger egg size in *A. cf. triradiatus* indeed leads to a prolonged prehatching period of 5 days, yielding a much more complex neurocranium at hatching. After this, development takes another 5 days until the yolk sac becomes depleted, this way prolonging the entire period of chondrocranial formation up to the level of yolk sac depletion (and thus functional complexity) up to 10 days. Therefore, although the pathways of chondrocranial development seem to be more or less rigid within large taxa, the time available for this development could very well play an important role in creating the necessary opportunities for the evolution of innovative structures from the earliest stages on.

Neurocranium

Skull floor. As in other siluriform fish, the *C. aeneus* skull is of the platybasic type, often related to the reduction in eye size, as is typical for this group (Daget, 1964; Adriaens and Verraes, 1997). At hatching, the rostral cartilages of the chondrocranial floor do not yet expand beyond the polar cartilages, as could be observed by examination of serial sections revealing that the path of the arteria carotis interna commonly accepted to mark the border between the trabeculae cranii s.s. and the polar cartilages (Goodrich, 1958; Bertmar, 1959; Adriaens and Verraes, 1997) passes in front of them. Examination of sections of later ontogenetic stages showed the trabeculae cranii s.s. to be present only from 4.0 mm SL on, with the arteria carotis interna running medial to this cartilage through the hypophyseal fenestra. Finally, from 4.9 mm SL on, these cartilages expand medially, forming a fissura through which this artery runs. At 5.3 mm SL this fissura closes medially, incorporating the artery in the trabecular bars. Since, however, like in *Ancistrus* cf. *triradiatus*, no evidence of cartilage resorption is seen, the mechanism suggested for the appearance of this fissure is that of allometric growth of the trabecular bars (Geerinckx et al., 2005). The notochord never protrudes into the hypophyseal fenestra in *C. aeneus*, a situation different from other catfish like *Ariopsis felis* and *Arius jella* (Ariidae), other loricarioids like *A. cf. triradiatus* and even other callichthyids like *Callichthys callichthys* (Bamford, 1948; Srinivasachar, 1958; Hoedeman, 1960a; Geerinckx et al., 2005). Further, at 4.4 mm SL, the trabecular bars fuse with the ethmoid cartilage closing the hypophyseal fenestra. This fusion occurs at the caudal border of the ethmoid plate, as is generally the case, although this fusion has been reported to occur at the dorsal face of the ethmoid plate in *Callichthys callichthys* and *Hoplosternum littorale* (Ballantyne,

1930; Hoedeman, 1960a). The ethmoid cartilage then expands further in both a dorsal and lateral direction, forming the precerebral lamina and solum nasi respectively. Also at 4.4 mm SL the metotic fenestra is split into an anterior and posterior part, with the first accommodating the passage of the nervus glossopharyngeus (IX). Since in teleosts no nerves pass through the basicapsular fenestra, the anterior fenestra found here is homologous to the basicapsular fenestra and the commissure dividing both the anterior and posterior fenestra can be designated the commissura basicapsularis posterior (Daget, 1964). As a consequence, the posterior fenestra cannot be homologized to any of the described fenestrae in teleost chondrocrania and is therefore here called foramen "A." At 4.8 mm SL the basicapsular fenestra is again split, this time providing passage for the glossopharyngeus (IX) nerve in the posterior part, making these openings, the fenestra basicapsularis anterior and posterior, split up by the commissura basivestibularis. From a SL of 5.3 mm SL on, the foramen "A" disappears and caudally, the lamina basiotica has further expanded, filling up the neurocranium floor, leaving the fenestra of the vagus (X) nerve.

Skull roof. An actual skull roof in *C. aeneus* is formed from a SL of 4.4 mm SL on. At this point, at the rostral skull roof margin, the otic capsules have formed taeniae marginales that interconnect through the epiphyseal bridge. At its caudal side both halves of the neurocranium also interconnect, forming the tectum posterius as a skull roof element. In other catfish, loricarioids and even callichthyids, the tectum posterius generally closes at a much higher SL. This occurs at a SL of about 7 mm in *Clarias gariepinus* (7.1 mm), *Ancistrus cf. triradiatus* (6.8 mm) and *Callichthys callichthys* (6–7 mm), while in *Heteropneustes fossilis* (12 mm) and *Arius jella* (29 mm), this state is first reported at even greater body lengths (Srinivasachar, 1958, 1959; Hoedeman, 1960a; Adriaens and Verraes, 1997; Geerinckx et al., 2005). Rostrally, the taeniae marginalis anteriores (in front of the epiphyseal bridge) are significantly reduced in *C. aeneus* and the bifurcation into an anteriorly directed commissura sphenoseptalis and a laterally directed commissura sphenothmoidalis is situated almost at the level of the epiphyseal bridge itself. A reduction of these anterior parts is indeed common in siluriforms (Adriaens and Verraes, 1997; Geerinckx et al., 2005), but such a significant reduction or a complete absence of these structures is a condition commonly found in loricarioids like the loricariid *A. cf. triradiatus* and the callichthyids *Callichthys callichthys* and *Hoplosternum littorale* (Ballantyne, 1930; Hoedeman, 1960a; Geerinckx et al., 2005).

Skull wall. As in other catfish, the lamina orbitonasalis is the first preotic vertical commissure to develop in *Corydoras aeneus*, separating the fenestra sphenoida from what is later to be the foramen

fila olfactoria (Geerinckx et al., 2005). Shortly after this, the preorbital base and commissura sphenoseptalis are formed as additional vertical connections between the taeniae marginales and the trabeculae cranii. At the caudal margin of the orbital region, a commissure splits the fenestra sphenoida into an anterior and posterior part. Formerly, the absence of a lateral commissure was believed to be a typical siluriform feature, but recently, Geerinckx et al. (2005) showed a true lateral commissure to be present in *Ancistrus cf. triradiatus*. Given this, and given the fact that, as in *A. cf. triradiatus*, the nervus oculomotorius (III), trochlearis (IV), trigeminus (V) and the mandibular branch of the nervus facialis (VII) pass through the anterior part of the sphenoid fenestra and that the ramus hyomandibularis of the nervus facialis (VII) passes through the posterior part, we also designated this commissure to be a true lateral commissure.

Splanchnocranium. In the splanchnocranium, no fusion of the "hyosymplectic-ptyergoquadrate plate" with the interhyal or neurocranium is observed. Such a fusion has been suggested by Hoedeman (1960a) for *Callichthys callichthys* and has since been confirmed by Howes and Teugels (1989) for *Corydoras paleatus*, at least for the earliest stages. Observations on cleared and stained specimens and serial sections, however, clearly indicate that in *Corydoras aeneus*, the interhyal is formed as a separate element from the earliest stages on and that the "hyosymplectic-ptyergoquadrate plate" never fuses to the neurocranium.

The palatine also arises as a single element, a state that is indeed typical for siluriform fish (Adriaens and Verraes, 1997). Hoedeman (1960a) also mentions the fact that both halves of Meckel's cartilage in *Callichthys callichthys* are "anteriorly connected by ligamentous tissue, but do not fuse." In all *C. aeneus* specimens examined here, both halves of Meckel's cartilage remain fused during almost the entire chondrocranial development, only separating near the start of ossification. In *Ancistrus cf. triradiatus*, this situation is remarkably different with both halves of Meckel's cartilage arising separately, after which they fuse and later separate again at the onset of ossification in the lower jaw. This increase in lower jaw mobility has been argued to be an important structural innovation in the families Astroblepidae and Loricariidae and thus seems to have its basis early in ontogeny. The situation of the early Meckel's cartilage in *A. triradiatus* also differs structurally from that found in *C. aeneus*, since both these cartilages are directed medially in the former species and rostrally in the latter and in siluriform species in general.

All elements of the splanchnocranium in *C. aeneus* are present from a SL of 4.4 mm on, corresponds to the point of yolk sac depletion. Since at that point starvation becomes a major threat for larval survival (Bailey and Houde, 1989), this point

is critical during larval development (Pedersen et al., 1990; Jardine and Litvak, 2003). From this stage on, exogenous feeding becomes obligatory and the presence of a functional feeding apparatus is required (van Snik et al., 1997; Jardine and Litvak, 2003). It has also been suggested that a fusion between lower jaw and hyosymplectic-ptyergoquadrate plate is crucial in the passive mouth opening mechanisms acting during early ontogeny of fishes, but again, such a fusion was not present in any of the stages examined here (Surlemont et al., 1989; Adriaens et al., 2001).

Branchial arches. The development of the branchial arches in *C. aeneus* differs from the situation described in siluriform fish up to this point. Generally, in siluriformes, chondrification in each arch starts with the ceratobranchials, followed by the hypobranchials and basibranchials, and eventually the epi- and pharyngobranchials (Srinivasachar, 1959; Adriaens and Verraes, 1997; Vandewalle et al., 1997). In *C. aeneus*, however, we found that all different elements arose simultaneously and continuously with each other. Since we did not notice this initial single formation of the branchial basket in our cleared and stained specimens, these observations are probably the result of the detailed observation method used in this study. In this study, serial sections for 3D reconstructions of these early branchial baskets were also used, in contrast to only the cleared in stained specimens used in former studies on branchial arch ontogeny of fish. However, Adriaens and Verraes (1997), also mention that the general ontogenetic sequence in siluriform branchial arches involves a differentiation in an antero-posterior direction. In *C. aeneus*, differentiation started with the separation of an infrapharyngobranchial plate, which, based on its position and articulation with the epibranchials, probably resembles a continuous infrapharyngobranchial I–IV. At the same moment of this differentiation, the central copula detaches from all arches and splits into the typical anterior and posterior copula. Several authors have argued that the anterior part is the fusion of the first three basibranchials, with the posterior copula being a fused basibranchial IV and V (Srinivasachar, 1959; Adriaens and Verraes, 1997; Vandewalle et al., 1997). At the same time of the formation of both copulae, the hypobranchials of arches II and III separate as well. However, in the specimen of Stage 3 (4.4 mm SL) examined here, we found the basibranchial of arches II and III to be separate, while in the Stage 4 specimen (4.9 mm SL), the basibranchial was still loosely connected to the ceratobranchial part. At this point, however, the epibranchials of arches II and III have also separated, indicating that both arches differentiate rapidly and almost simultaneously, before arches I and IV. After this, the epibranchial of arch I first detaches at Stage 5 (5.3 mm SL), shortly after which the epibranchial

of arch IV also separates from the ceratobranchial part. At this point, the infrapharyngobranchial plate has also split into an anterior and posterior part. The last element to detach is the first hypobranchial, which separates at around 8 mm SL. The configuration of the gill arch basket at the end of chondrocranial differentiation does resemble the typical siluriform state. The basket has five arches with an anterior and posterior copula, separate hypobranchials in the first three arches and separate epibranchials in the first four (Adriaens and Verraes, 1997). Adriaens and Verraes (1997), however, also suggested the presence of a remnant cartilaginous infrapharyngobranchial I and II, articulating with the epibranchials of these two arches in adult *Clarias gariepinus*. Huysentruyt and Adriaens (2005a) also observed the presence of such a small cartilaginous mass in adult *Corydoras aeneus*, which was also placed in homology with a fused infrapharyngobranchial I and II. The ontogenetic sequence observed here, however, suggests otherwise. In Stage 4, an anterior projection of the cartilaginous infrapharyngobranchial plate is indeed observed, articulating with the epibranchial parts of these first two arches. In the later stages, however, this projection degenerates, with even a loss of contact between the epibranchial of the first arch and the infrapharyngobranchial plate in Stage 6. Therefore, the cartilaginous mass seen in adult *C. aeneus* cannot be homologous to these infrapharyngobranchials and probably resembles the cartilaginous tips of epibranchials I and II, which have come in close contact to each other or have fused.

CONCLUSIONS

In general, the chondrocranium in *C. aeneus* follows the typical siluriform trends in chondrocranial development as described by Adriaens and Verraes (1997). The skull is of the platybasic type, as described for all Siluriformes and the notochord does not protrude into the hypophyseal fenestra because of the presence of the acrochordal cartilage (Adriaens and Verraes, 1997; Vandewalle et al., 1999). In contrast to the general situation found in catfishes, but similar to the situation described for *Ancistrus cf. triradiatus* by Geerinckx et al. (2005), a commissura lateralis was found. The splanchnocranium again has the typical siluriform shape during its ontogeny, with the presence of a compound hyosymplectic-ptyergoquadrate plate present, although not fused to the neurocranium or interhyal as described for *Callichthys callichthys* by Hoedeman (1960a) and Howes and Teugels (1989). In general, as hypothesized, development of the chondrocranium was very similar to that of *A. cf. triradiatus*, with one of the main differences found in the development of the lower jaw. This resulted in an increase in jaw mobility in the loriciid species, used for algae scraping. In comparison

to all siluriforms, including *A. cf. triradiatus*, however, the most striking differences found involved the ontogeny of the branchial basket. Whereas, generally, chondrification occurs in a ventrodorsal and antero-posterior direction, in *C. aeneus*, the branchial basket arises as a single element and differentiation first starts dorsally, followed by arches II and III and then proceeds in both an anterior and posterior direction. Since we did not notice this initial single formation of the branchial basket in our cleared and stained specimens, these observations are probably the result of the detailed observation method used in this study. To find out whether or not this pattern is indeed more common in siluriforms, further histological comparative research on branchial basket development is needed.

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