

# Development of the Osteocranium in the Suckermouth Armored Catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes)

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**ABSTRACT** The development of the osteocranium of the suckermouth armored catfish *Ancistrus* cf. *triradiatus* is described based on specimens ranging from prehatching stages to juvenile stages where the osteocranium is more or less fully formed. The first bony elements that arise are the opercle, jaws, and lateralmost branchiostegal rays, as well as the basioccipital and parasphenoid in the skull floor. The supracleithrum and the membranous and perichondral pterotic components form one large, double-layered skull bone during ontogeny, without clear evidence of the involvement of a supratemporal. The Baudelot's ligament ossifies from two sides, i.e., from the basioccipital medially and the supracleithrum laterally. The lower jaw consists of a dentary, mentomeckelian, and angulo-articular, which all soon fuse. The parurohyal, formed by the fusion of a ventral sesamoid bone and a dorsal cartilage element associated with the first basibranchial, is pierced by a vein, unlike in some other siluriforms. The interhyal cartilage disappears during ontogeny; medially of it, a small sesamoid bone appears in a ligament. The largest, canal-bearing cheek plate is not homologous to the interopercle. The results of the present research, with emphasis on bone formations and homologies, are compared with studies on related catfishes. *J. Morphol.* 268:254–274, 2007. © 2007 Wiley-Liss, Inc.

**KEY WORDS:** bone; cartilage; catfishes; ontogeny; ossification; skeleton

Development of structures and the early life history of fishes are closely related. Early life-history stages must also function as organisms, so the study of ontogeny is an obvious necessity, if one wants to understand the integration of, e.g., the feeding apparatus (Lauder et al., 1989). The vital importance of events occurring during early development is easily overlooked (Orton, 1955).

The current study on the loricariid *Ancistrus* cf. *triradiatus* describes and discusses the development of the osteocranium in detail, in continuation of earlier work on the chondrocranium of the species (Geerinckx et al., 2005). Loricariids are well known for their remarkable niche occupation, i.e., the scraping and sucking of algae and other food items off submerged substrates. Of some loricariid species only the adult skeletal morphology has been examined by Alexander (1965), Schaefer (1987, 1988, 1997), Schaefer and Lauder (1986), and others.

Compared with the development of the siluriform chondrocranium, the development of the osteocranium has received remarkably less interest. Relevant publications on the development of the bony skull in catfishes discuss Ariidae (Bamford, 1948; Tilney and Hecht, 1993), Callichthyidae (Hoe-deman, 1960a,b), Clariidae (Surlemont and Vandewalle, 1991; Adriaens et al., 1997; Vandewalle et al., 1997; Adriaens and Verraes, 1998), Claroteidae (Vandewalle et al., 1995), Ictaluridae (Kindred, 1919), Siluridae (Kobayakawa, 1992), and the suspensorium of Diplomystidae, Trichomycteridae, and some other families (Arratia, 1990, 1992). The ontogeny of the Weberian apparatus in *Clarias gariepinus* and *Corydoras paleatus* has been examined by Radermaker et al. (1989) and Coburn and Grubach (1998), respectively. Homology of the anterior vertebrae has been treated by Hoffmann and Britz (2006). The Weberian apparatus and complex vertebra are only briefly discussed in the present paper. Taking into consideration their complexity, a thorough study of these structures would merit a separate paper.

Loricariids are an exceptionally interesting fish taxon, as they are able to respire while attaching to a substrate with their sucker mouth. The added possibility of feeding in their typical manner (aforementioned) is even more unusual. Knowledge of the ontogenetic origin of the osteocranium in loricariids is lacking. The development of many bones (e.g., jaws) is, however, highly interesting, as they are crucially modified key structures in the sucking and scraping device that has evolved in this large and diverse catfish group. Some of these key structures might well have had an influence on the diversity within the large loricariid family.

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TABLE 1. Specimens of *Ancistrus* cf. *triradiatus* used in the present study

No.	UGMD no.	SL (mm)	SkL (mm)	Age (dPF)	Method	Staining	Use
1	—	4.8	—	2	SS	T	Observation
2	—	5.2	—	3	SS	T	Observation
3	175351	5.6	1.24	4	C	AB + AR	Drawing
4	175352	6.0	1.39	4	C	AB + AR	Drawing
5	—	6.1	—	4	SS	T	Observation
6	175353	6.3	1.47	5	C	AB + AR	Observation
7	175354	6.8	1.60	5 <sup>a</sup>	C	AB + AR	Observation
8	—	7.0	—	6	SS	T	Observation
9	175355	7.4	1.82	6	C	AB + AR	Drawing
10	175356	7.7	2.00	6	C	AB + AR	Observation
11	175357	8.0	2.16	7	C	AB + AR	Drawing
12	—	8.0	—	7	SS	T	Observation
13	175358	8.5	2.38	7	C	AB + AR	Observation
14	175359	8.7	2.45	7	C	AB + AR	Observation
15	175360	8.9	2.51	8	C	AB + AR	Observation
16	175361	9.1	2.64	8	C	AR	Drawing
17	175362	9.8	2.98	12	C	AR	Drawing
18	—	10.2	—	14	SS	T	Observation
19	175363	10.8	3.4	18	C	AR	Drawing
20	175364	11.7	3.8	30	C	AB + AR	Drawing
21	—	12.4	—	43	SS	T	Observation
22	175365	14.4	5.0	45	C	AB + AR	Drawing
23	175366	16.4	5.7	67	C	AB + AR	Observation
24	175367	20.7	7.3	96	C	AB + AR	Drawing
25	175368	25.0	10.3	160	C	AB + AR	Observation
26	175369	31.0	12.5	160	C	AB + AR	Observation
27	—	33.5	—	160	SS	T	Observation

AB, alcian blue; AR, alizarin red S; C, clearing; dPF, days postfertilization; SL, standard length; SkL, chondrocranial skull length (from tip of ethmoid plate to end of basis of occipital pilae, thus excluding tectum posterius); SS, serial sections; T, toluidine blue; UGMD, Universiteit Gent Museum voor Dierkunde (Zoology Museum of Ghent University).

<sup>a</sup>Immediately after hatching.

Next to the description of several ontogenetic stages, we discuss our observations in the light of possible homologies or nonhomologies with structures present in related taxa, in order to try to shed some light on the problematic identifications of skeletal elements in loricariids. Finally, some more functional–morphological considerations are made.

## MATERIALS AND METHODS

This study focuses on one loricariid representative *A. cf. triradiatus* (Eigenmann, 1918). Identification up to species level is problematic, as the genus is in need of a thorough revision, and complete determination keys are not available.

Commercially obtained specimens were bred in aquarium tanks of 30–130 cm. Embryos and juveniles (there is no distinct larval stage) were sedated in MS-222 and fixed in a paraformaldehyde–glutaraldehyde solution at different time intervals (Table 1). For prehatching stages, egg membranes were removed prior to fixation. Eight specimens were selected for serial sectioning (Table 1). Toluidine-stained 2- $\mu$ m sections (5  $\mu$ m for 33.5-mm specimen) were prepared (Technovit 7100 embedding, cut with a Reichert-Jung Polycut microtome) and studied using a Reichert-Jung Polyvar light microscope. Other specimens were cleared in toto and stained according to the method of Taylor and Van Dyke (1985). Examination of the specimens was done using an Olympus SZX9 stereoscopic microscope, equipped with a camera lucida for drawing. As an aid to the drawings, dissections (e.g., removal of pectoral girdle or part of the splanchnocranium) were performed in the larger specimens. Drawings figure all cartilaginous and bony elements of the skull, which are visible on the cleared and stained specimens. However, the study of serial sections of specimens demonstrates

that sometimes early ossification is not visible on stained specimens of the same or earlier length or age, a known artifact in in toto staining techniques (Vandewalle et al., 1998). In such cases this is clearly mentioned in the text. All cleared and stained specimens have been deposited in the Zoology Museum of the Ghent University (UGMD 175351–369; see Table 1).

Bone terminology is mostly based on Harrington (1955), Patterson (1975, 1977), Schaefer (1987), and Arratia (2003). We refer to de Beer (1937) and Geerinckx et al. (2005) for terminology of chondrocranial parts.

## RESULTS

No endochondral bone is encountered in *A. cf. triradiatus* up to the 20.7 mm SL stage. The skull is composed of perichondral and membrane bones (including dermal bones), as well as a few sesamoid bones and bones of compound origin.

### 5.6 mm Standard Length (Fig. 1)

Only one pair of bony elements is present in this specimen (in serial sections of the younger 4.8- and 5.2-mm specimens only a cartilaginous skeleton is visible). Near the posterior end of the cartilaginous suspensorium, at the distal tip of the opercular process, the opercles have appeared as small bony splints. No other bony structures are seen. At the future location of each premaxilla, however, four tooth primordia can be recognized.

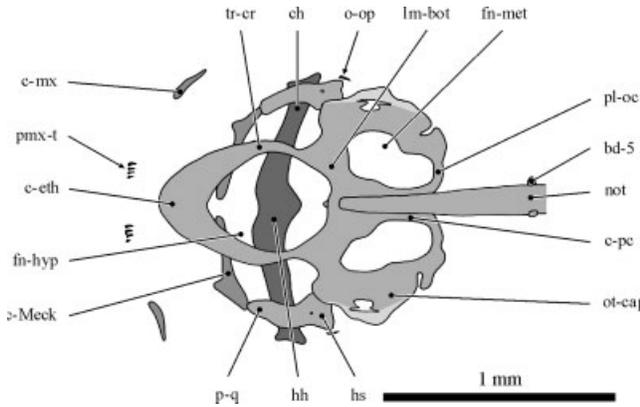


Fig. 1. Dorsal view of the skull of *Ancistrus cf. triradiatus* (5.6 mm SL). bd-5, basiodorsal of fifth vertebra; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pe, cartilago parachordalis; ch, ceratohyale; fn-hyp, fenestra hypophyseae; fn-met, fenestra metotica; hh, hypohyale; hs, hyosymplecticum; lm-bot, lamina basiotica; not, notochord; o-op, os operculare; ot-cap, otic capsule; p-q, pars quadrata of palatoquadratum; pl-oc, pila occipitalis; pmx-t, premaxillary teeth; tr-cr, trabecula cranii.

### 6.0 mm Standard Length (Fig. 2)

**Neurocranium.** The lateralmost protuberances of the otic capsule bear a small odontode, and another small odontode is visible on the right postotic process. Odontodes are extra-oral teeth, part of the body armor of several fish taxa (Bhatti, 1938; Reif, 1982). Serial sections of a 6.1-mm specimen show precursor tissue of the future supporting bones, but no ossification.

**Splanchnocranium.** Thin premaxillae have appeared, supporting four to five teeth. The maxillae arise as thin bony splints supporting the maxillary barbel cartilages, and develop articulation facets for the growing but still short autopalatine (or palatine) cartilages (pars autopalatina of Arratia, 1990). The cleared and stained 6.0-mm specimen has neither dentaries nor dental teeth; however, serial sections of the 6.1-mm specimen show the presence of four short conical teeth at the location where each dentary is to be expected. Both the premaxillary and the dental teeth are still embedded in soft tissue in the 6.1- and 7.0-mm specimens. Two thin branchiostegal rays attach to the paired ventrocaudal process of the hyoid bar. The position of their insertion suggests that they are the lateralmost rays III–IV. The opercles have grown somewhat, and a pair of odontodes is present in the skin covering them.

### 7.4 mm Standard Length (Fig. 3)

**Neurocranium.** On the taenia marginales the dermal frontals have started developing. They are accompanied by two odontodes in the skin. Odontodes can now also be seen on both postotic processes

of the otic capsule. A first indication of the parasphenoid is seen in the posterior half of the hypophyseal fenestra in the serial sections in the 7.0

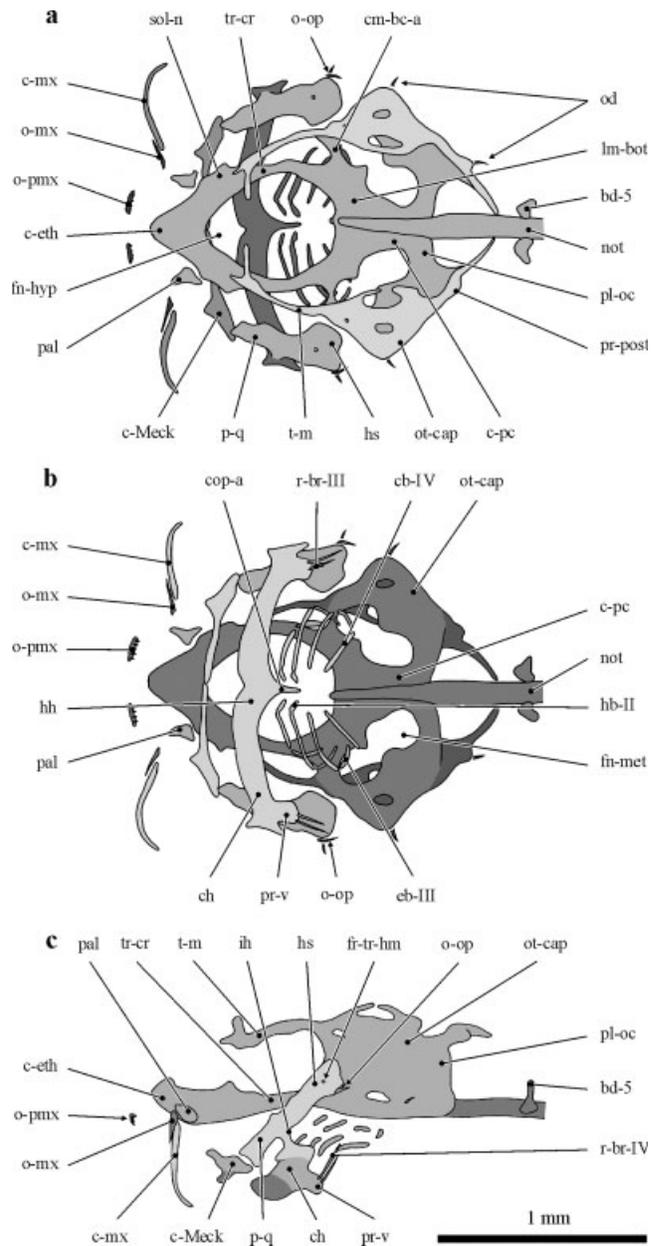


Fig. 2. Skull of *Ancistrus cf. triradiatus* (6.0 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. bd-5, basiodorsal of fifth vertebra; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pe, cartilago parachordalis; cb-IV, fourth ceratobranchiale; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cop-a, anterior copula; eb-III, third epibranchiale; fi-hyp, fenestra hypophyseae; fn-met, fenestra metotica; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; hb-II, second hypobranchiale; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-bot, lamina basiotica; not, notochord; o-mx, os maxillare; o-op, os operculare; o-pmx, os praemaxillare; od, odontode; ot-cap, otic capsule; p-q, pars quadrata of palatoquadratum; pal, palatinum; pl-oc, pila occipitalis; pr-post, processus postoticus of otic capsule; pr-v, ventral process of ceratohyale; r-br-III/IV, third/fourth radius branchiostegalis; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii.

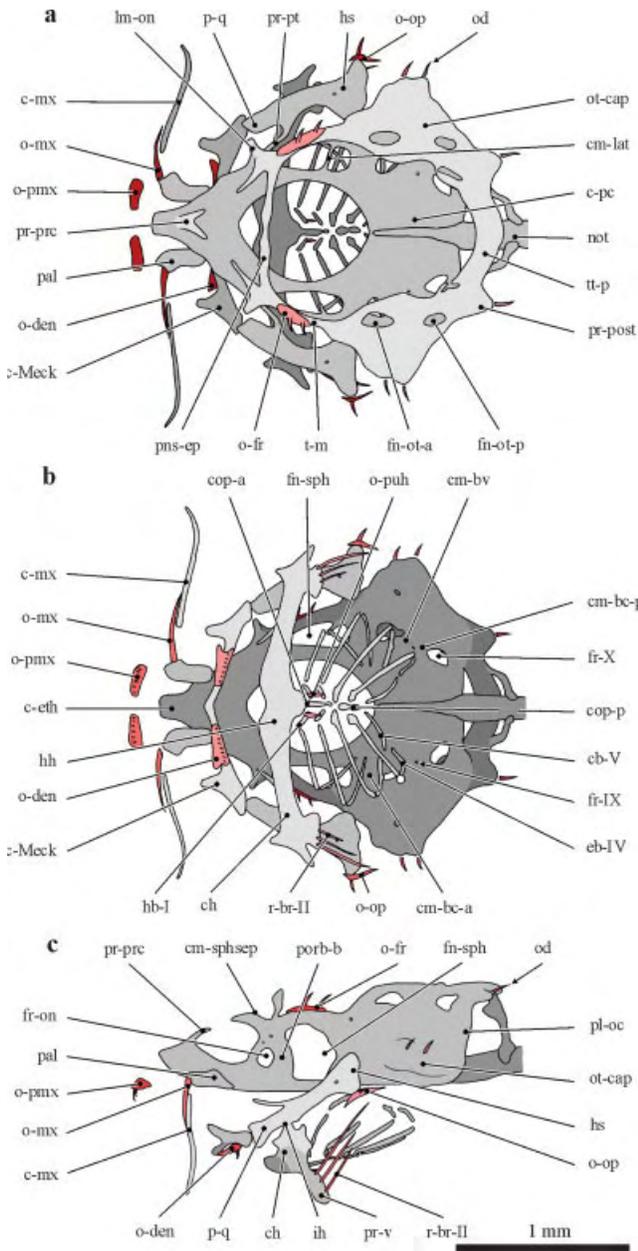


Fig. 3. Skull of *Ancistrus* cf. *triradiatus* (7.4 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; cb-V, ceratobranchiale V; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cm-bc-p, commissura basicapsularis posterior; cm-bv, commissura basivestibularis; cm-lat, commissura lateralis; cm-sphsep, commissura sphenoseptalis; cop-a, anterior copula; cop-p, posterior copula; eb-IV, epibranchiale IV; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fn-sph, fenestra sphenoida; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-on, foramen orbitonasalis; fr-X, foramen nervus vagus; hb-I, hypobranchiale I; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-on, lamina orbitonasalis; not, notochord; o-den, os dentale; o-fr, os frontale; o-mx, os maxillare; o-op, os operculare; o-pmx, os praemaxillare; o-puh, os parurohyale; od, odontode; ot-cap, otic capsule; p-q, pars quadrata of palatoquadratum; pal, palatinum; pl-oc, pila occipitalis; pns-ep, pons epiphysialis; porb-b, preorbital base; pr-post, processus postoticus of otic capsule; pr-pre, processus praecerebralis; pr-pt, processus pterygoideus; pr-v, ventral process of ceratohyale; r-br-II, second radius branchiostegalis; t-m, taenia marginalis; tt-p, tectum posterius.

mm stage, although no bone is visible in the stained 7.4-mm specimen. Also in these sections, the notochordal sheath, where the notochord enters the skull, is slightly ossifying, giving the onset of the basioccipital (also not shown in Fig. 3b). In the 7.4-mm specimen, two odontodes are present on the skin near the lateral protuberance of the cartilaginous otic capsule. Small perichondral ossifications of the otic capsule are seen underneath these last odontodes, representing the first anlage of the autopterotics. Serial sections (7.0-mm specimen) show that initially odontodes are not in direct contact with the dermal frontals or perichondral autopterotics, which are situated deeper in the skin.

**Splanchnocranium.** The premaxillae have grown broader, providing space for about six teeth. The maxillae have also expanded, now touching the cartilaginous autopalatine cartilage bars. The dentaries are visible as curved bony plates. Seven to eight slightly curved conical teeth attach on the posterior half of these, pointing ventrally. In serial sections of a 7.0-mm specimen, thin perichondral ossifications can be recognized on the hyoid bar and suspensorium, representing the onset of the anterior ceratohyals and hyomandibulars; these are not yet visible in the stained 7.4-mm specimen. The first signs of the parurohyal have appeared in the serial sections of the 7.0-mm specimen: a small plate-like sesamoid ossification is present in the tendon of each half of the sternohyoideus muscle (thus only urohyal parts are present at the moment).

The branchiostegal rays III and IV have elongated; branchiostegal rays II have also appeared.

**8.0 mm Standard Length (Fig. 4)**

**Neurocranium.** The frontals are now more substantial, covering most of the taeniae marginales dorsally. Serial sections of an 8.0-mm specimen show that the membranodermal components, covering the taeniae, are already present, while the neurodermal components still have to arise, as well as the supraorbital canals which they will surround. Between the otic fenestrae another pair of odontodes has arisen. A thin sheet of perichondral bone partially covers each half of the otic capsule roof: the supraoccipital thus originates as a paired structure. This remarkable feature is confirmed by the serial sections of the 8.0-mm specimen. At this moment, as well as in later stages, no evidence is seen of separately developing parietal bones. At no moment during ontogeny is there a full separation between the perichondral and membranous parts of the parieto-supraoccipital (we use this name for the bone, but refer to the discussion for a more thorough treatment of this bone). The ossification center of the basioccipital is present as a bony sheath around the cranial part of the notochord, now continuing as a perichondral ossification of the neurocranium floor next to it. The transverse processes of the complex

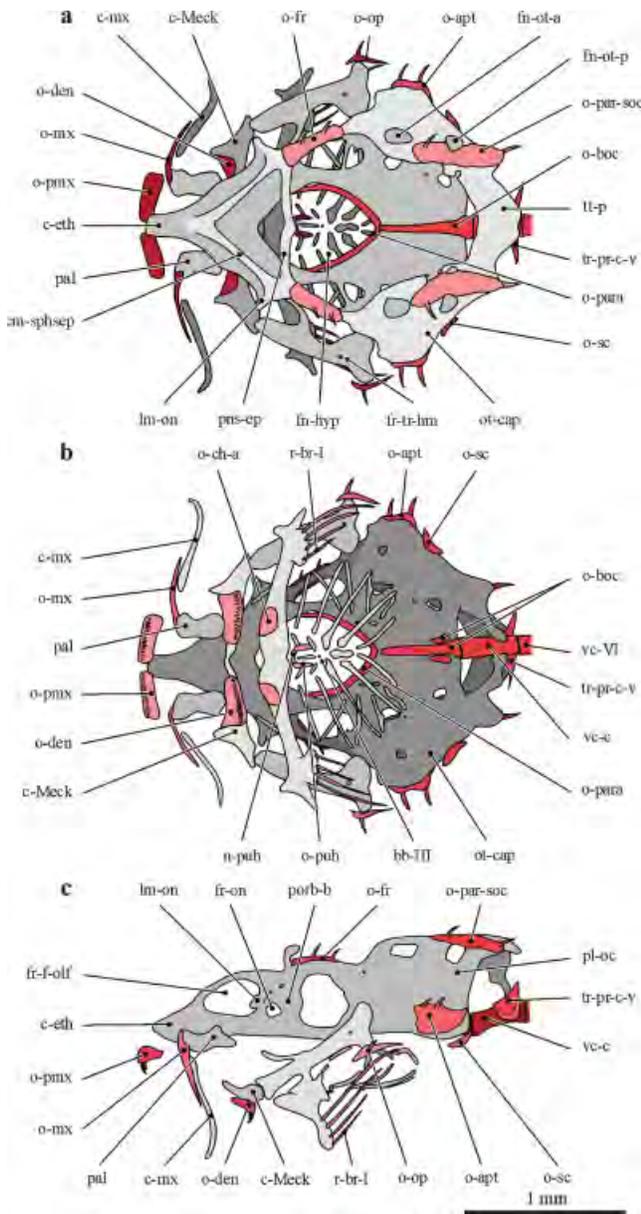


Fig. 4. Skull of *Ancistrus* cf. *triradiatus* (8.0 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. bb-III, third basibranchiale; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; cm-sphsep, commissura sphenoseptalis; fn-hyp, fenestra hypophyseae; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; lm-on, lamina orbitonasalis; n-puh, cartilaginuous nucleus of parurohyale; o-apt, os autopteroticum; o-boc, os basioccipitale; o-ch-a, os ceratohyale anterior; o-den, os dentale; o-fr, os frontale; o-mx, os maxillare; o-op, os operculare; o-para, os parasphenoideum; o-par-soc, os parieto-supraoccipitale; o-pmx, os praemaxillare; o-puh, os parurohyale; o-sc, os supracleithrum; ot-cap, otic capsule; pal, palatinum; pl-oc, pila occipitalis; pns-ep, pons epiphysialis; porb-b, preorbital base; r-br-I, first radius branchiostegalis; tr-pr-c-v, transverse process of complex vertebra; tt-p, tectum posterius; vc-c, vertebral centra of complex vertebrae; vc-VI, sixth vertebral centrum.

vertebra have appeared; they form the ventral floor of the swimbladder capsules.

The parasphenoid is now visible as a narrow band of dermal bone in the lateral and posterior perimeter of the hypophyseal fenestra. Small lateral notches are left in the bone; together with fissures in the trabecular bars they form the foramina for the paired internal carotid arteries (Fig. 4a,b). In the serial sections, but not in the stained 8.0-mm specimen, initiation of perichondral ossification of the prootics is observed.

The lateral protuberances of the otic capsule are now well covered by the paired autopterotics. The supracleithra of the pectoral girdle have appeared just posterior to the otic capsule floor, and are closely associated with the dorsal, articular processes of the cleithra, as could best be seen in serial sections of the 8.0 mm stage. The sections also show that the supracleithra appear separate from the autopterotics. The first, separate ossification of the supracleithra could be recognized in serial sections of the 7.0-mm specimen (Fig. 5a).

**Splanchnocranium.** The premaxillae have become higher, with the eight erected teeth inserting on the anterior margin. The maxillae have developed complete articular facets for the autopalatine cartilages.

The dentaries now attach firmly to Meckel's cartilages, which have also started to ossify medially, forming the mentomeckelian bones (Fig. 5b; not visible in Fig. 4). The dentaries are best developed posteriorly, and each one supports about ten conical teeth. An angulo-articular bone is not present at this time. Separate from the anterior ceratohyal, the hypohyal and the posterior ceratohyal are visible on the serial sections of the 8.0 mm stage (A. cf. *triradiatus* only develops a ventral hypohyal). The paired sesamoid component of the parurohyal (i.e., the urohyal) is growing, and a dumbbell-shaped cartilage nucleus has separated from the hypohyal region of the hyoid bar. This nucleus contacts the rostral end of the anterior copula, which can be considered the first basibranchial.

The medialmost branchiostegal rays I have appeared, articulating with the medial ends of the broad caudoventral processes of the hyoid bar. The opercles are triangular elements, each composed of a horizontal rod that bears an odontode almost halfway, and a ventral plate extending in the direction of the outer branchiostegal ray.

### 9.1 mm Standard Length (Fig. 6)

**Neurocranium.** At the tip of the snout, the hypethmoid is present as a perichondral ossification of the ventral face of the ethmoid cartilage. The frontals and the now unpaired parieto-supraoccipital have started to cover parts of the postpineal fontanelle. The anterior tips of the frontals have reached the prepineal fontanelle. The autopterotics have

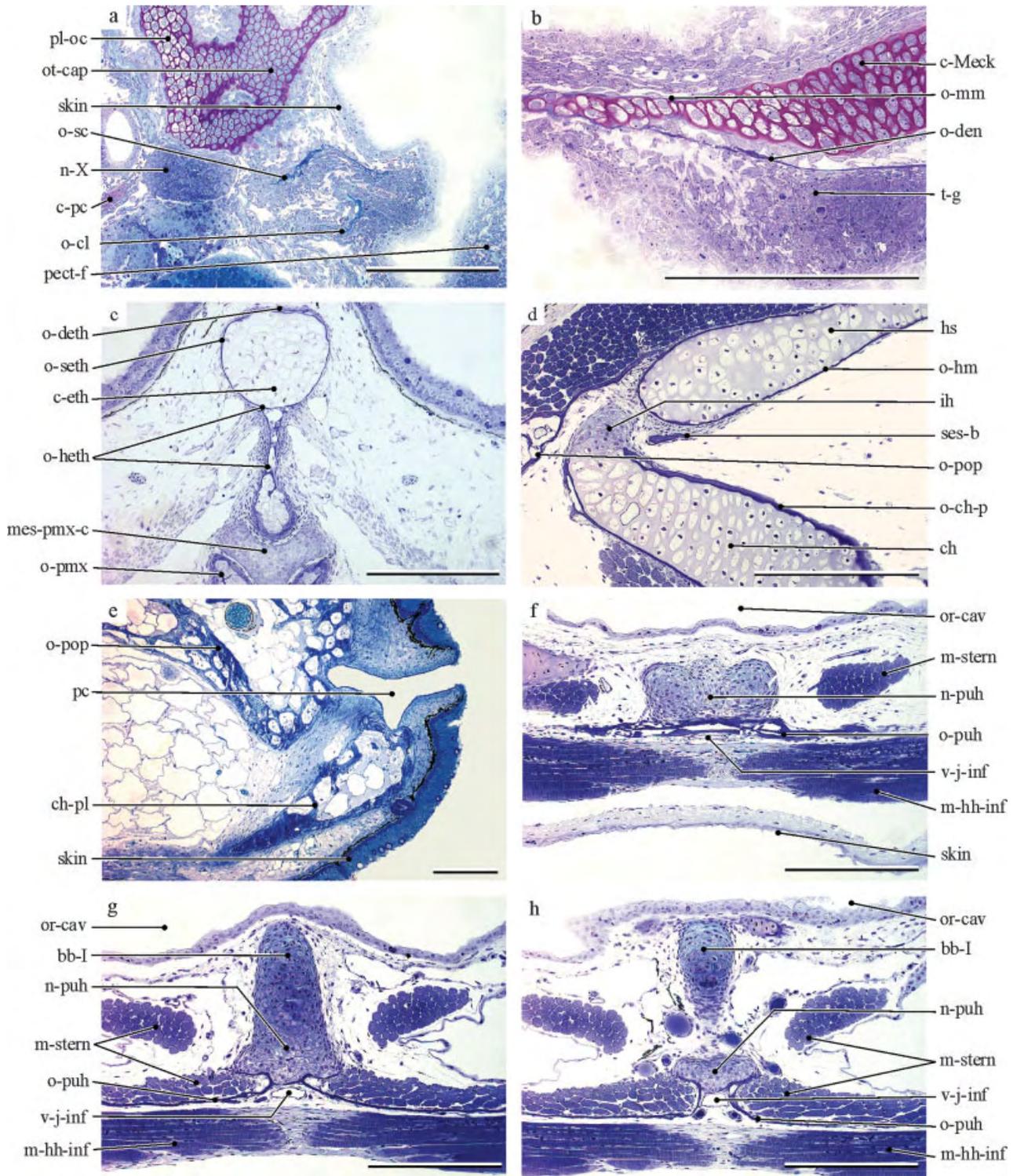


Fig. 5. Histological sections showing details of osteocranium ontogeny. All scale bars represent 200  $\mu\text{m}$ . (a) Section of 7.0 mm stage, at level of supracleithral bone. The autopterotic will form around the otic capsule. (b) Section of 8.0 mm stage, at level of lower jaw, with early jaw bone formation. (c) Rostral tip of ethmoid cartilage of 10.2 mm stage, showing the various components of the mesethmoid bone. (d) Interhyal region of 12.4 mm stage featuring the sesamoid bone and the (reducing) interhyal cartilage. (e) Section of 33.5 mm stage at level of largest cheek plate, where the preopercular canal enters it from the preopercle. (f–h) Sections of 12.4 mm stage, at different levels in the parurohyal bone. bb-I, basibranchiale I; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-pc, cartilago parachordalis; ch, ceratohyale; ch-pl, cheek plate; hs, hyosymplecticum; ih, interhyale; m-hh-inf, musculus hyohyoideus inferior; m-stern, musculus sternohyoideus; mes-pmx-c, mesethmoid-premaxillary cartilage; n-puh, cartilaginous nucleus of parurohyale; n-X, nervus vagus; o-ch-p, os ceratohyale posterior; o-cl, os cleithrum; o-den, os dentale; o-deth, os dermo-ethmoideum; o-heth, os hypo-ethmoideum; o-hm, os hyomandibulare; o-mm, os mentomeckelium; o-pmx, os praemaxillare; o-pop, os praeoperculare; o-puh, os parurohyale; o-sc, os supracleithrum; o-seth, os supra-ethmoideum; or-cav, oral cavity; ot-cap, otic capsule; pect-f, pectoral fin; pl-oc, pila occipitalis; pc, preopercular canal; ses-b, sesamoid bone; t-g, tooth germ; v-j-inf, vena jugularis inferior.

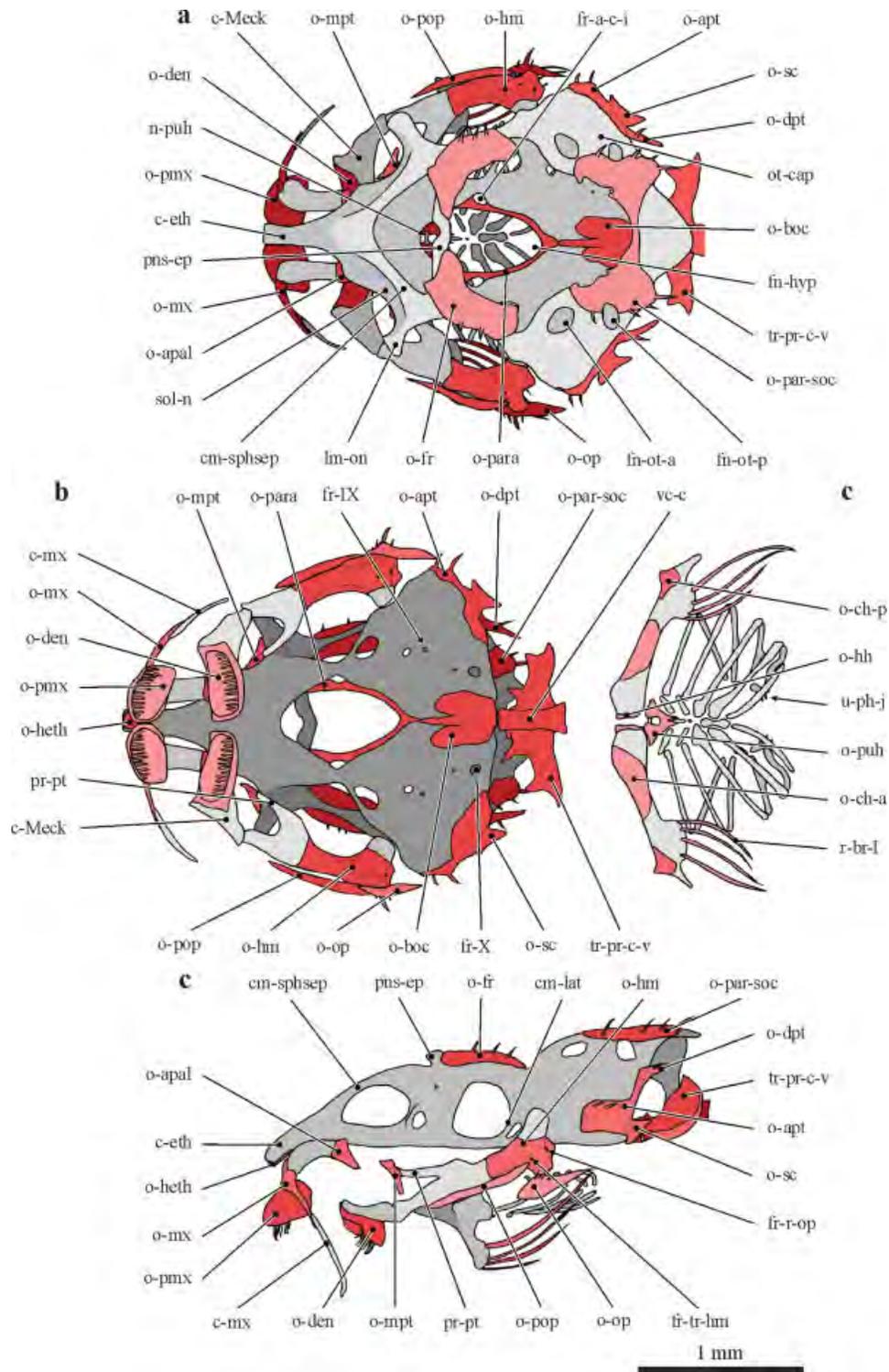


Fig. 6. Skull of *Ancistrus* cf. *triradiatus* (9.1 mm SL). (a) Dorsal view. (b,c) Ventral view of neurocranium and splachnocranium (removed). (d) Lateral view. c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; cm-lat, commissura lateralis; cm-sphsep, commissura sphenoseptalis; fn-hyp, fenestra hypophyseae; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fr-c-int, foramen arteria carotis interna; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-r-op, foramen ramus opercularis nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-X, foramen nervus vagus; lm-on, lamina orbitonasalis; n-puh, cartilaginous nucleus of parurohyale; o-apal, os autopalatatinum; o-apt, os autopteroticum; o-boc, os basioccipitale; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den, os dentale; o-dpt, os dermopteroticum; o-fr, os frontale; o-heth, os hypo-ethmoideum; o-hh, os hypophyale; o-hm, os hyomandibulare; o-mpt, os metapterygoideum; o-mx, os maxillare; o-op, os operculare; fr-r-op, os paraspinoideum; o-par-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-pmx, os praemaxillare; o-puh, os parurohyale; o-sc, os supracleithrum; ot-cap, otic capsule; pns-ep, pons epiphysialis; pr-pt, processus pterygoideus; r-br-I, radius branchiostegalis I; sol-n, solum nasi; tr-pr-c-v, transverse process of complex vertebra; u-ph-j, upper pharyngeal jaw; vc-c, vertebral centra of complex vertebrae.

grown significantly along the lateral and posterior walls of the otic capsule. The dermopterotics appear as posterior projections of the posterior vertical walls of the autopterotics. They form the onset of the roof of the swim bladder capsules. The supracleithra are now fused to the autopterotics and dermopterotics.

**Splanchnocranium.** Premaxillae and dentaries now form basket-like structures. Their ventral edges are complete at the tooth-bearing side, but not yet at the other, mouthward side (posterior in premaxillae, anterior in dentaries). The posterior ends of the autopalatine bones have appeared. The tip of the pterygoid process of each suspensorium has started to ossify perichondrally, and a small membranous bony sheet forms around it. These perichondral and membranous elements constitute the anlage of each metapterygoid. From the rostral end of this bone, a ligament stretches toward the ventralmost aspect of the posterior autopalatine ossification. A partial perichondral ossification of each hyomandibular is faintly visible, with membranous extensions caudally (leaving an opening for the path of the opercular branch of the facial nerve) and lateroventrally, in the direction of the preopercle. The long and slender membranodermal preopercles have appeared along the central part of the suspensoria (the neurodermal gutter-like part is not yet present in this stage). Posterior to the path of the inferior jugular vein the paired urohyal ossifications of the sternohyoideus tendon have fused. The dumbbell-shaped cartilage nucleus is in contact with the tendon anterior to the path of the vein. In this stage the parurohyal bone thus still consists only of a sesamoid (“urohyal”) component. In the branchial basket paired bony plates have developed, lying against each fourth infrapharyngobranchial. These upper pharyngeal toothplates (or “jaws”) already bear two pointed teeth each at this stage (Fig. 6c). Serial sections of a 10.2-mm specimen demonstrate, however, that these rudimentary teeth are still covered by the epidermal pharyngeal tissue, so they cannot yet be functional.

**9.8 mm Standard Length (Fig. 7)**

**Neurocranium.** Some additional bony structures have appeared, while the skull bones already present have become enlarged so as to form a more rigid support of the braincase. The frontals have elongated and now connect the otic capsules and the sphenoseptal commissures, and have overgrown a large part of the epiphysial bridge as well. The parieto-supraoccipital consists of a large plate, membranous as well as perichondral, and makes up a bony tectum between both otic capsules. Four bones provide support of the skull floor in the midline. As the notochord is relatively smaller, when compared with the 9.1-mm specimen, the basioccipital becomes the most important supporting element in

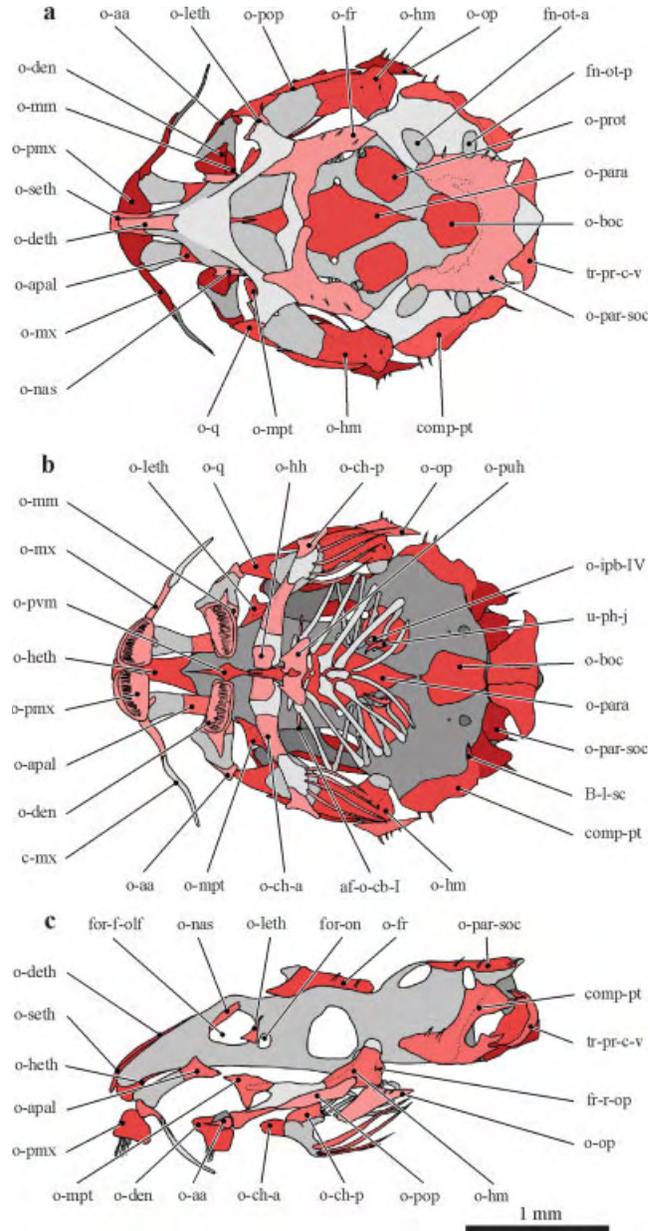


Fig. 7. Skull of *Ancistrus* cf. *triradiatus* (9.8 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. ap-o-cb-I, anterior process of os ceratobranchiale I; B-l-sc, ossified Baudelot's ligament pars supracleithralis; c-mx, cartilago maxillaris; comp-pt, compound pterotic bone; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-r-op, foramen ramus opercularis nervus facialis; o-aa, os angulo-articulare; o-apal, os autopalatinum; o-boc, os basioccipitale; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den, os dentale; o-deth, os dermo-ethmoideum; o-fr, os frontale; o-heth, os hypoethmoideum; o-hh, os hypohyale; o-hm, os hyomandibulare; o-ipb-IV, os infrapharyngobranchiale IV; o-leth, os latero-ethmoideum; o-mm, os mentomeckelium; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-para, os parasphenoidium; o-par-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-pmx, os praemaxillare; o-prot, os prooticum; o-puh, os parurohyale; o-q, os quadratum; o-seth, os supra-ethmoideum; o-vm, os vomerale; tr-pr-c-v, transverse process of complex vertebra; u-ph-j, upper pharyngeal jaw.

the posterior skull floor. It can be discerned from the notochordal ossification of the complex vertebra. The parasphenoid now fills the whole hypophyseal fenestra, and has become rhomboid-shaped, as the medial cartilage in front of the fenestra has reduced. Only the two foramina for the internal carotid arteries remain. More anteriorly, cartilage reduction has freed space for the membranous vomeral bone, suturing with the parasphenoid. Around the ethmoid cartilage the various elements of the mesethmoid are seen. The supraethmoid and the hypoethmoid are dorsal and ventral perichondral bones, respectively, connected only at the tip. The hypoethmoid has a medioventral process, which is the onset of the typical loriciid mesethmoid disc (Fig. 7c). Most of this process lacks a cartilaginous precursor (Fig. 5c). On the dorsal side of the ethmoid cartilage, a dermal sheet, the dermethmoid, develops. It covers the posterior part of the supraethmoid. Serial sections of a 10.2-mm specimen show that these three bony elements later fuse to form a tube-like mesethmoid bone around the ethmoid cartilage.

The lateral ends of the orbitonasal laminae have ossified perichondrally. Small membranous extensions bear one odontode each. Thus the lateral ethmoids are composed of perichondral and membranous elements. The nasal bones, containing the rostral part of the supraorbital canals, have arisen on top of the nasal sacs. In serial sections of the 10.2-mm specimen only the canal-supporting neurodermal element is already present. The neurodermal parts of the frontals have also developed, being well visible in the anterior halves of these bones. It is not certain whether the neurodermal parts of the frontals have arisen separately, or from ossification centra of the membranodermal parts. Only serial sections of a specimen between 8.0- and 10.2-mm SL could show this.

The perichondral prootics are seen in the skull floor. In the serial sections of the 10.2-mm specimen most of the perichondral orbitosphenoids, pterosphenoids, and autosphenotics are present and relatively well-developed, but they are not seen on the stained 9.8-mm specimen.

The compound pterotic bone complex has grown extensively; it consists of three main spatial elements: a largely perichondral casing covering the lateral and posterior walls of the cartilaginous otic capsule, a dorsal dermal extension forming the roof of the swim-bladder capsule, and a ventral membranous extension forming part of this capsule's floor. The original components of this compound bone cannot be clearly distinguished anymore. From the ventral extension, at the location where the supracleithrum could be identified in the 9.1-mm specimen, Baudelot's ligament runs medially toward the posterior ventral surface of the basioccipital. It starts to ossify laterally, from the compound pterotic.

**Splanchnocranium.** The ventrocaudal processes of the autopalatine bones, on which the extensor tentaculi muscles and the autopalatine-meta-

pterygoid ligaments insert, are well developed. Both the upper and lower jaws have fully developed their tooth-bearing baskets. Thus the premaxillae are complete, while the coronoid processes of the dentaries are not yet completely developed. The latter bones have formed ventrolateral flanges toward the angulo-articulars. The ossification of the latter bones has started at the articulation facets for the suspensoria, and extend rostrally. All three elements of both suspensoria are now present. The membranous sheets of the metapterygoids have grown extensively dorsally and ventrally, giving the bones a triangular outline. The quadrates and hyomandibulars are now both present, and the canal-bearing preopercles have broadened. The preopercles surround the preopercular canals.

The largely perichondral anterior ceratohyals have developed membranous sheets growing dorsally from the anterior edge of the bones, while the posterior ceratohyals still lack any membranous extension. The interhyals have partly reduced (not visible on Fig. 7), separating the suspensoria and the hyoid bar. Various ligaments have developed along the suspensorial-hyoid connection. In a ligament at the inner side of the rudimentary interhyal cartilages, sesamoid bones appear (Fig. 5d).

The urohyal has developed further. The paired sesamoid bones in the sternohyoideus tendon are now fused anterior and posterior to the inferior jugular vein. Anteriorly both tips of the sesamoid bone almost touch the developing hypohyals posteroventrally; posteriorly the bone reaches up to a quarter of the sternohyoideus length. The cartilage nucleus still shows no sign of ossification. As seen in the serial sections of the 10.2-mm specimen, the remainder of the partly reduced first basibranchial is still continuous with this cartilage nucleus.

The branchial basket is still completely cartilaginous, except for the upper pharyngeal jaws and newly formed anterior processes originating from the first ceratobranchials.

### 10.8 mm Standard Length (Fig. 8)

**Neurocranium.** Between the 9.8 and 10.8 mm stages, extensive ossification of the skull has taken place. All neurocranial bones are now present. In the skull roof the various bones have grown closer and often already touch each other. The frontals have completely overgrown the epiphysial bridge and now separate the anterior from the posterior fontanelle (in the chondrocranium these two fenestrae are referred to as the prepineal and postpineal fontanelles). From this stage on, the supraorbital canals and the anterior part of the otic canals are quite visible in the stained specimens, running through the nasals, frontals, and dermosphenotics.

The orbitosphenoids are now well developed, and cover the preorbital bases and the anterior halves of the trabecular bars. In rostral view they are L-

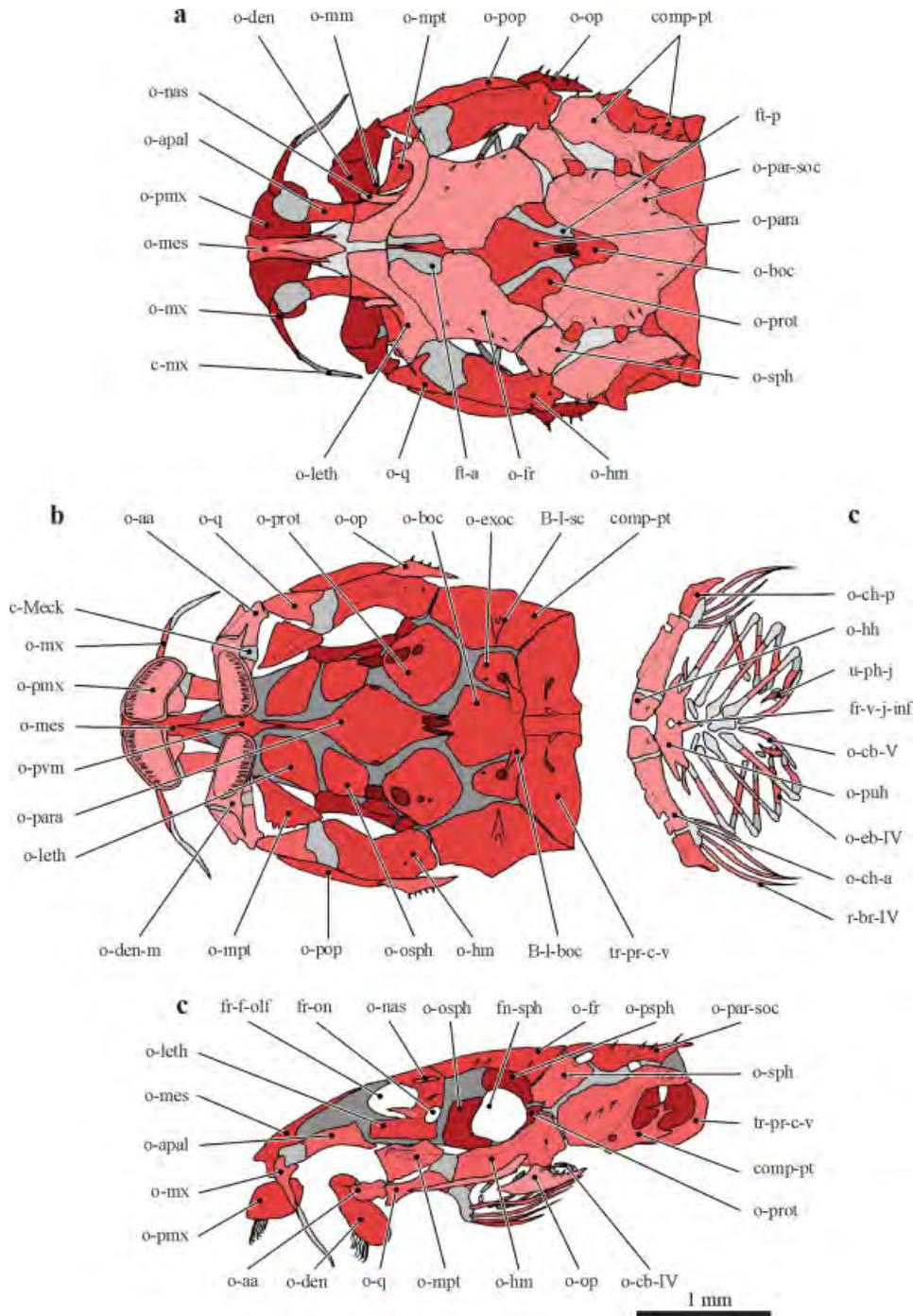


Fig. 8. Skull of *Ancistrus* cf. *triradiatus* (10.8 mm SL). (a) Dorsal view. (b,c) Ventral view of neurocranium and splachnocranium (removed). (d) Lateral view. B-l-boc, ossified Baudelot's ligament pars basioccipitalis; B-l-sc, ossified Baudelot's ligament pars supraclithralis; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; comp-pt, compound pterotic bone; fn-sph, fenestra sphenoida; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-v-j-inf, foramen vena jugularis inferior; ft-a, fontanella anterior; ft-p, fontanella posterior; o-aa, os angulo-articulare; o-apal, os autopalatinum; o-boc, os basioccipitale; o-cb-IV/V, os ceratobranchiale IV/V; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den-m, os dento-mentomeckelium; o-den, os dentomeckelium; o-eb-III, os epibranchiale III; o-exoc, os exoccipitale; o-fr, os frontale; o-hh, os hypohyale; o-hm, os hyomandibulare; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-osph, os orbitosphenoidum; o-para, os parasphenoidum; o-par-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-pmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoidum; o-puh, os parurohyale; o-q, os quadratum; o-sph, os sphenoticum; o-vm, os vomerale; r-br-IV, radius branchiostegalis IV; tr-pr-c-v, transverse process of complex vertebra; u-ph-j, upper pharyngeal jaw.

shaped, with broad horizontal parts, reaching toward the parasphenoid, and narrower vertical parts forming the anterior margins of the orbits, and covering the anterior parts of the taeniae marginales. The foramina for the ophthalmic branches of the trigeminal nerves are enclosed by them. The pterosphenoids have covered the main parts of the taeniae marginales. The sphenotic fenestrae are surrounded by the orbitosphenoids, pterosphenoids, and prootics. The prootics have now covered the basiotic laminae, the posterior parts of the trabecular bars, and a part of the anterior basicapsular commissures. The lateral commissures of the chondrocranium are ossified as well, providing the prootics with an anterior foramen. The parieto-supraoccipital has grown to a massive, U-shaped compound bone, including a small posterior process. This bone, as well as the sphenotics and pterotics, take part in the closing of the two otic fenestrae that characterize the chondrocranial skull of *A. cf. triradiatus* (Geerinckx et al., 2005). The lateral ethmoids, grown extensively since the 9.8 mm stage, touch the frontals, but not yet the mesethmoid. Only posteriorly are the hypoethmoid and supraethmoid parts of the mesethmoid still unconnected. The ventral mesethmoid disc has grown to the level of the premaxillae, where a mesethmoid-premaxillary cartilage is present, as already shown by serial sections of the 10.2-mm specimen.

In the skull floor the basioccipital has started to form deep sutures with the parasphenoid. The exoccipitals have appeared, and have foramina for the glossopharyngeal and vagal nerves. All paired skull floor bones are still separated by broad cartilage zones; only the unpaired medial bones interdigitate with each other, forming the main axial supportive structure of the skull. The epioccipitals, developing as perichondral ossifications of the posterior skull wall, can be recognized in the 10.2-mm serial sections. Two ventral processes project laterally from the posterior half of the basioccipital. These are the medial ossifications of Baudelot's ligaments (analogous to the lateral, supracleithral parts of the ligaments, the medial ossifications spread from the basioccipital bone). From the ventral layer of the compound pterotics, lateral trabecles have begun to grow dorsally. Thus, the lateral walls of the airbladder capsules start to form.

Some neuromasts of the infraorbital canals have appeared and invaginated; the first bony encapsulation of these canals occurs by the fifth infraorbitals, as shown by serial sections of the 10.2-mm specimen.

**Splanchnocranium.** The upper and lower jaws now bear 12–15 teeth each. The posterior attachment facets for the retractor premaxillae muscles on the premaxillae are now well developed. The dermal dentaries and perichondral mentomeckelia have fused. This is already the case in the (serially sectioned) 10.2-mm specimen. The angulo-articular bones have covered the lateral halves of Meckel's

cartilages, leaving only small posterior regions unossified, which will remain as such to the adult stage. The angulo-articulars acquire rostradorsal membranous sheets that provide space for the developing adductor mandibulae muscles (which also insert on the coronoid processes of the dentaries). More than half of the autopalatine cartilages are now enclosed by the autopalatine bones. The metapterygoids have developed lateral ridges.

The cartilaginous hyoid bar is now almost completely replaced by bone. Both the anterior and posterior ceratohyals have developed anterior membranous extensions. These extensions are orientated slightly dorsally, so that the hyoid bar actually consists of a horizontal perichondral plane and an almost vertical membranous plane. In the anterior ceratohyals, large notches are left for the passage of the arteries supplying the lateral parts of the musculus hyohyoideus inferior, originating from the hypobranchial artery (Fig. 8c).

The central regions of all epibranchials and ceratobranchials have begun to ossify perichondrally. First signs of these ossifications are visible in serial sections of the 10.2-mm specimen. The second basibranchial and the first hypobranchials are also starting to ossify. Strips of membrane bone have developed against the fifth ceratobranchials. These lower pharyngeal tooth plates are not (yet) continuous to the ceratobranchials, and already bear two teeth each. Three to four teeth can be counted on the upper pharyngeal toothplates (or jaws).

### 11.7 mm Standard Length (Fig. 9)

**Neurocranium.** The outline of the original chondrocranium is not easy to make out anymore, as most of it has now been covered by perichondral bone (Fig. 9). Also, the dermal bony elements have overlain or hidden the cartilaginous skeleton. The otic fenestrae of the otic capsule roof are fully closed by the parieto-supraoccipital, sphenotics and pterotics, and the anterior and posterior fontanelles have severely shrunk as the parieto-supraoccipital and the frontals have expanded. The mesethmoid is now completely tube-like, with the hypoethmoid and supraethmoid parts fully connected at both left and right sides. The mesethmoid now reaches the frontals, but does not yet cover them. The lateral ethmoids now enclose the nasal sacs on three sides, and touch each other below the dermethmoid roof. They have contacted the vomer ventrally. The medial floor of the ethmoid cartilage reduces where the vomer covers it ventrally. The three bones bordering the sphenoid fenestrae, i.e., the orbitosphenoids, pterosphenoids, and prootics, restrict the fenestrae by the formation of membranous bony sheets at the perimeter. The compound pterotics have developed spectacularly, expanding the dorsal and ventral layers, as well as connecting them laterally by means of trabecles carrying numerous odontodes

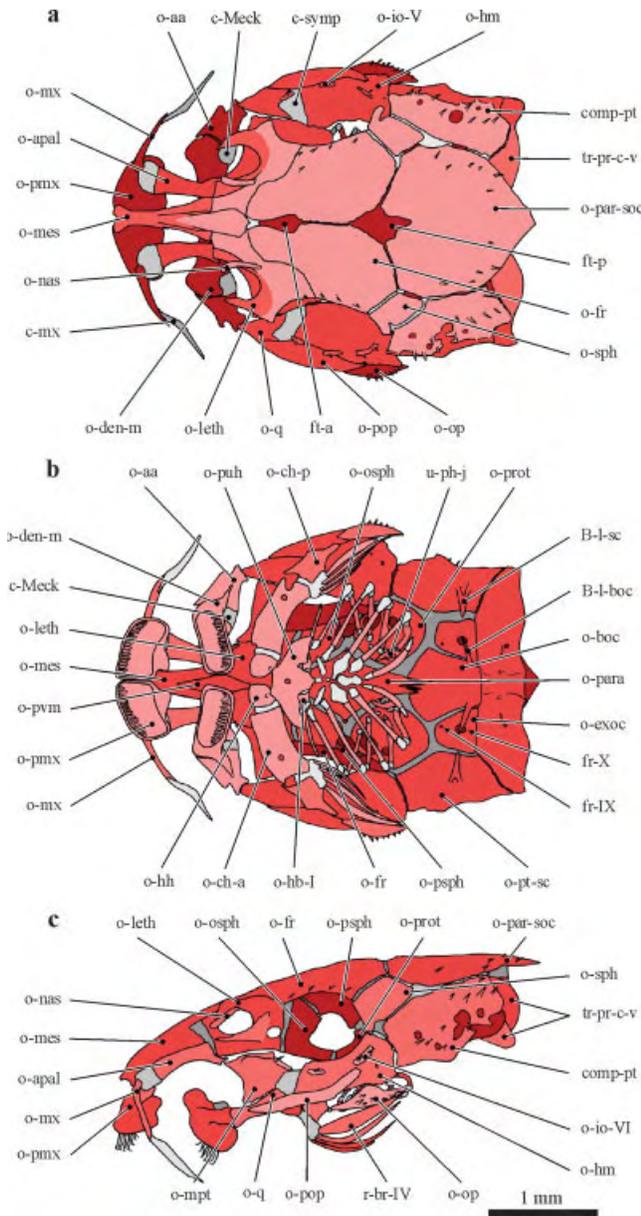


Fig. 9. Skull of *Ancistrus* cf. *triradiatus* (11.7 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. B-l-boc, ossified Baudelot's ligament pars basioccipitalis; B-l-sc, ossified Baudelot's ligament pars supracleithralis; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-symp, cartilago symplecticum; comp-pt, compound pterotic bone; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; ft-a, fontanella anterior; ft-p, fontanella posterior; o-aa, os angulo-articulare; o-apal, os autopalatatinum; o-boc, os basioccipitale; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den-m, os dento-mentomeckelium; o-exoc, os exoccipitale; o-fr, os frontale; o-hb-I, os hypobranchiale I; o-hh, os hypohyale; o-hm, os hyomandibulare; o-io-V/VI, os infraorbitale V/VI; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-par-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-pmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-puh, os parurohyale; o-q, os quadratum; o-sph, os sphenoticum; o-vm, os vomerale; r-br-IV, radius branchiostegalis IV; tr-pr-c-v, transverse process of complex vertebra; u-ph-j, upper pharyngeal jaw.

(the only connection between the dorsal and ventral layers thus far was rostrally, at the level of the otic pilae). These trabecles leave various small foramina. The connections with the transverse processes of the complex vertebra are reinforced by means of fine sutures dorsally and ventrally. The basioccipital, exoccipitals, epioccipitals, and medial parts of the pterotics are tightly connected to these transverse processes. The basioccipital and the parasphenoideum are deeply sutured. In the skin below the eye, three small canal bones are now present: infraorbitals IV to VI.

**Splanchnocranium.** As the jaw bones had already attained their more or less final shape in the 10.8-mm specimen, the only significant difference now is an increase in size, and a closer contact including suturing between dento-mentomeckelia and angulo-articulars. The autopalatine bones are now completely formed; the cartilaginous rostral articular heads for the maxillae remain cartilaginous during further ontogeny. The original outline of the cartilaginous suspensoria is not visible anymore, as the proportion of membrane bone has increased and the cartilage has become reduced, except for the symplectic cartilages and the articular heads for the neurocranium and the opercle (the articular cartilage at the facet for the lower jaw is minute). The hyomandibulars have started suturing weakly with the pterotics dorsocaudally. The lateral ridges of the metapterygoids have expanded into large sheets. As the cartilaginous interhyal connections between the suspensoria and the hyoid bar have been lost, the ligamentous connections grow stronger. The final shape of the sesamoid bones medial to the former interhyal locations is cylindrical.

Lateral to the quadrates, at the rostral tip of the preopercles, the preopercular canals now turn ventrally. Thin neurodermal ossification is present around them. These are the first signs of the larger of two cheek plates that will develop in this region (Fig. 5e). Membranodermal elements are not yet visible in this specimen.

The branchiostegal rays have grown and are now all flattened (the lateral ones more than the medial ones). Both anterior tips of the sesamoid urohyal bone almost touch the developing hypohyals posteroventrally; posteriorly the bone reaches up to a third of the length of the sternohyoideus muscle. The hypohyals acquire a depression near the anterior (par)urohyal tips. The middle shaft region of the ceratobranchials and epibranchials have further ossified, leaving the heads (and growth regions) still cartilaginous. The fifth ceratobranchials and lower pharyngeal jaws have fused.

**14.4 mm Standard Length (Fig. 10)**

**Neurocranium.** Both fontanelles are now completely closed. The posterior growth of the parieto-

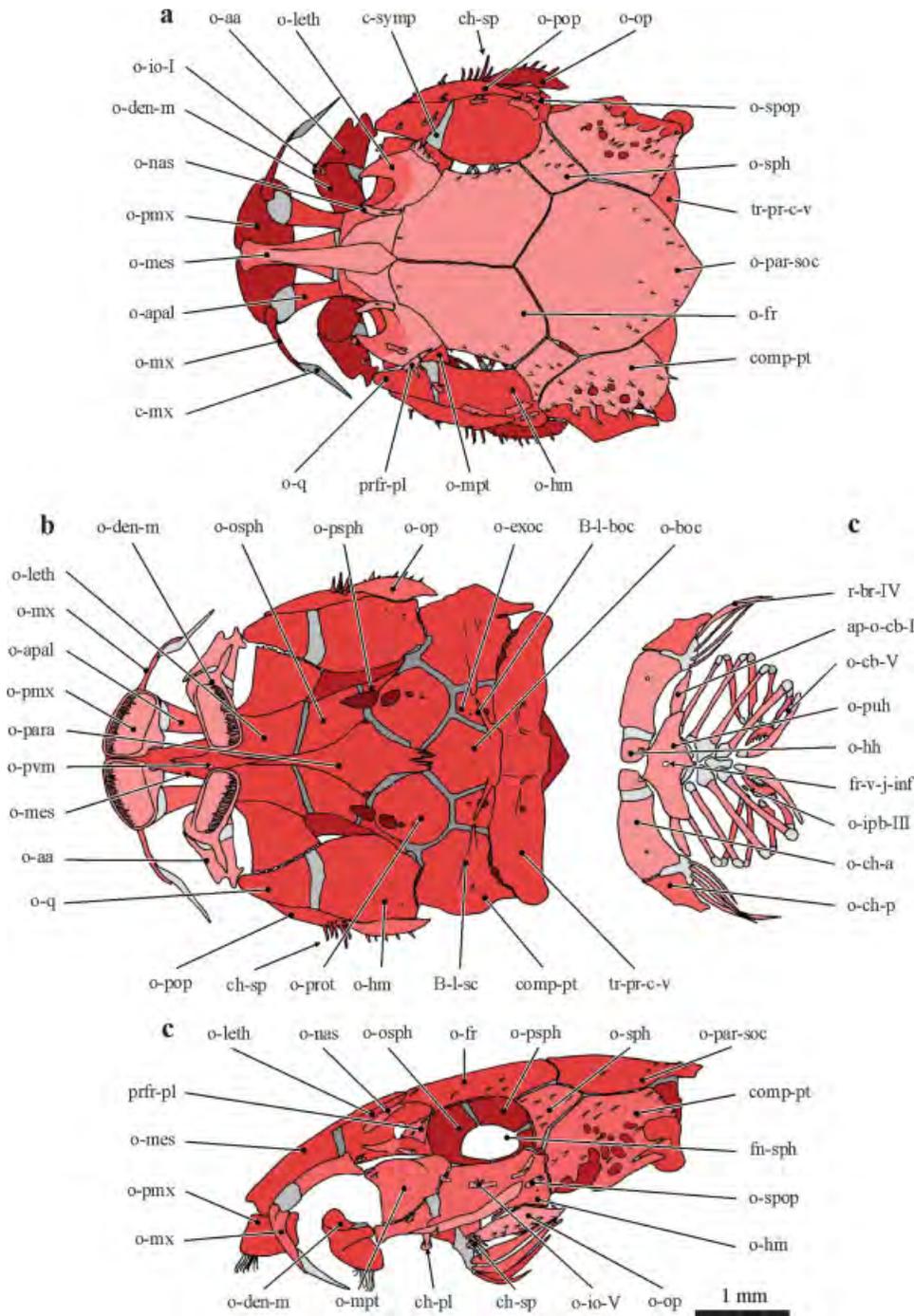


Fig. 10. Skull of *Ancistrus cf. triradiatus* (14.4 mm SL). (a) Dorsal view. (b,c) Ventral view of neurocranium and splachnocranium (removed). (d) Lateral view. ap-o-cb-I, anterior process of os ceratobranchiale I; B-l-boc, ossified Baudelot's ligament pars basioccipitalis; B-l-sc, ossified Baudelot's ligament pars supracleithralis; c-mx, cartilago maxillaris; c-symp, cartilago symplecticum; ch-pl, cheek plates; ch-sp, cheek spines; comp-pt, compound pterotic bone; fn-sph, fenestra sphenoida; fr-v-j-inf, foramen vena jugularis inferior; o-aa, os angulo-articulare; o-apal, os autopalatium; o-boc, os basioccipitale; o-cb-V, os ceratobranchiale V; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den-m, os dento-mentomeckelium; o-exoc, os exoccipitale; o-fr, os frontale; o-hh, os hypohyale; o-hm, os hyomandibulare; o-io-V, os infraorbitale V; o-ipb-III, os infrapharyngobranchiale III; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-par-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-pmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-puh, os parurohyale; o-q, os quadratum; o-sph, os sphenoticum; o-spop, os suprapraeoperculare; o-vm, os vomerale; prfr-pl, prefrontal plate; r-br-IV, radius branchiostegalis IV; tr-pr-c-v, transverse process of complex vertebra.

supraoccipital also has elongated the skull (in the earliest stages the posterior end of the skull was demarcated by the tectum posterius). The major skull roof bones have also started suturing. The dermal lateral processes of the sphenotics, enclosing the posterior portions of the infraorbital canals, have grown. On top of the lateral connections of the lateral ethmoids and the frontals, thin odontode-bearing dermal layers, the prefrontal plates, have appeared. Beneath the skull floor, Baudelot's ligaments are almost completely ossified: only a thin region of each ligament between the medial ossification from the basioccipital and the lateral ossification from the ventral ridge of the supracleithrum (compound pterotic) remains ligamentous at this moment. Most infraorbital bones (usually six on each side in *A. cf. triradiatus*, but sometimes only five) are present, or at least an odontode can be seen indicating the future location of the bone (the supporting bone underneath is often more difficult to see than the odontode itself). Minute dermal platelets carrying odontodes now appear in the cheek region and behind the skull as well.

**Splanchnocranium.** The suspensoria have attained their approximate final shape by now: the metapterygoids have made contact with the collateral quadrate and hyomandibular, suturing with both. They are ligamentously connected to the lateral ethmoids (dorsally) and the autopalatine bones (rostrally). The membranous dorsal parts of the hyomandibulars have become completed and form rounded, thin sheets, supporting the eyes. The hyomandibulars articulate with the neurocranium at the level of the contact between the collateral prootic, pterotic, and sphenotic. Just anterior to this articulation, the membranous parts of the hyomandibulars form two processes fitting into the serrate lateral edges of the prootics. These serrations have developed together with these hyomandibular processes. The hyomandibular-pterotic sutures have expanded to most of the contact zone between both bones, which is the final adult configuration, though the sutures will become stronger during further development. The preopercles approach the quadrates and the hyomandibulars, though are not yet fused to any of these bones. Between the preopercles and the most rostral margin of the pterotics the preopercular canals are now enclosed by the paired supra-preopercles, dermal canal-bones bearing odontodes just like the infraorbitals. Anterior processes are formed on both opercles and point ventromedially. Near these processes, sturdy bony elements are developing, bearing large spiny odontodes, the so-called cheek spines. The dermal cheek plates lateral to the quadrates bearing the end of the preopercular canals have expanded a little, as membranodermal bony sheets supporting a few odontodes are added to the neurodermal gutter-like components.

The adult shape of the parurohyal is more or less reached. The cartilage nucleus dorsal to the sesa-

moid urohyal bone has condensed, and on its ventral side, bone formation connects it to this sesamoid part (Fig. 5f-h). The bone now has a compound nature. Both parurohyal tips fit in holes of the hypohyal bones. It appears that the centers of the hypohyal cartilages have reduced so that the depressions, mentioned in the previous stage, now pierce the bones and have become holes. The bony first ceratobranchials and their spongy anterior processes have fused; in earlier stages the processes were only loosely connected to the first ceratobranchial bones via the cartilage at the medial ends of the bones. The uncinat processes of the epibranchials that have arisen since the bones started to develop are now well visible; the largest are borne by the third epibranchials. The infrapharyngobranchials III and IV show the first signs of perichondral ossification.

### 20.7-mm Standard Length Specimen (Fig. 11) and Further Development

**Neurocranium.** As all neurocranial elements had already attained their approximate final shape at the 14.4 mm stage; this and later stages are mainly characterized by growth and reinforcement of the skull by means of further suturing of dermal bones, closer synchondral contacts between the perichondral bones, and heavier ossification of the various elements. As the skull floor bones have also thickened, the bony recesses for the paired maculae can be easily seen: the utriculus is borne by a recess in the prootic, while the more posteriorly situated sacculus is enclosed by the basioccipital, and the lagena by both the basioccipital and exoccipital. Baudelot's ligaments are completely ossified, providing a direct bony connection between the basioccipitals and compound pterotics. The ligaments form continuous transverse ridges, though sutures can be seen in the positions where the sesamoid ossifications from the basioccipital and supracleithral sides touch each other. No teeth develop on the ventral surface of the vomer. The prefrontal plates have grown, and will become almost rectangular when specimens reach maturity. Of the major skull bones, the compound pterotics expand most during further growth, broadening the posterior part of the skull. As seen in the 20.7-mm specimen, the lateral ethmoids have not yet closed completely anteriorly, leaving the anterior part of the nasal sacs less supported. In the 33.5-mm specimen the closure is established.

The infraorbital bones have grown and almost touch each other. The supra-preopercles and the preopercles have almost touched as well. So now the infraorbital and preopercular canals are more or less completely enclosed in bone. The number of platelets in the snout region has increased. They can be divided into prenasal plates (on top of the mesethmoid) and lateral plates (between the preopercular

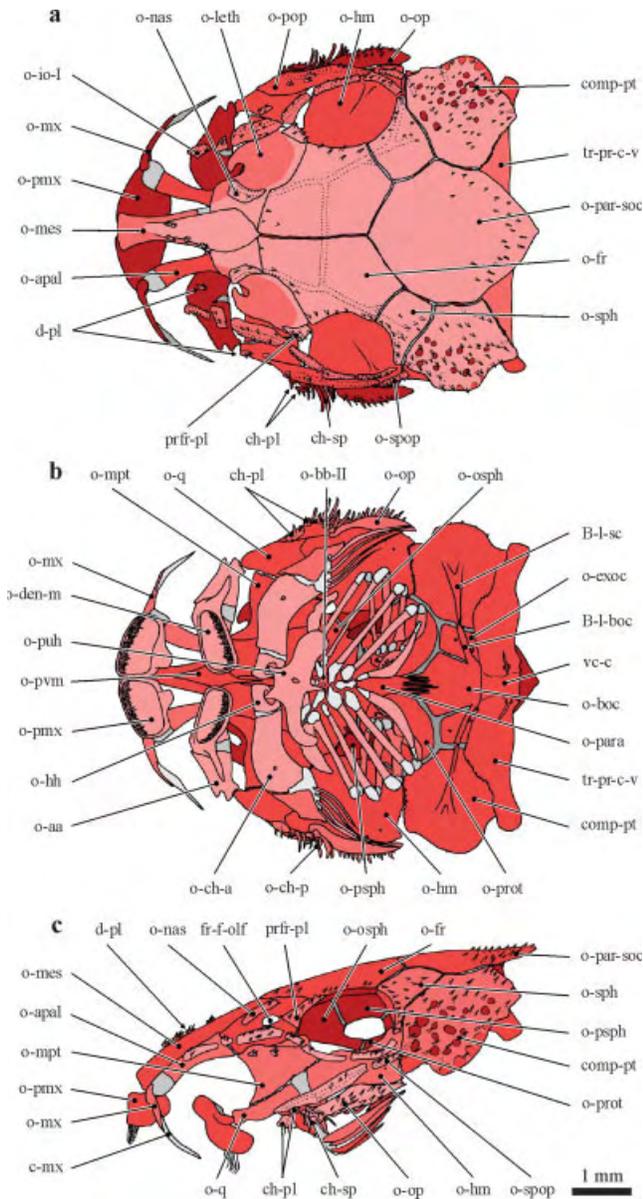


Fig. 11. Skull of *Ancistrus cf. triradiatus* (20.7 mm SL). (a) Dorsal view. (b) Ventral view. (c) Lateral view. B-l-boc, Baudelot's ligament pars basioccipitalis; B-l-sc, Baudelot's ligament pars supracleithralis; c-mx, cartilago maxillaris; ch-pl, cheek plates; ch-sp, cheek spines; comp-pt, compound pterotic bone; d-pl, dermal plate; fr-f-olf, foramen fila olfactoria; o-aa, os angulo-articulare; o-apal, os autopalatinum; o-bb-III, os basibranchiale III; o-boc, os basioccipitale; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den-m, os dento-mentomeckelium; o-exoc, os exoccipitale; o-fr, os frontale; o-hh, os hypohyale; o-hm, os hyomandibulare; o-io-I, os infraorbitale I; o-leth, os latero-ethmoideum; o-mes, os mesethmoideum; o-mpt, os metapterygoideum; o-mx, os maxillare; o-nas, os nasale; o-op, os operculare; o-osp, os orbitosphenoideum; o-para, os parasphenoideum; o-par-soc, os parieto-supraoccipitale; o-pop, os praepopulare; o-pmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-puh, os parurohyale; o-q, os quadratum; o-sph, os sphenoticum; o-spop, os suprapraepopulare; o-vm, os vomerale; prfr-pl, prefrontal plate; tr-pr-c-v, transverse process of complex vertebra complex vertebra; vc-c, vertebral centra of complex vertebrae.

and infraorbital canals). Lateral to the hyomandibular and the pterotic bones, platelets will also soon appear (the first are observed in the 25.0 mm stage; most are present at 31.0 mm SL). A complete coverage of similar, overlapping plates appears under the skin of the rest of the body, leaving only the belly unprotected. In the 31.0-mm specimen thin sclerotic bones have appeared, which support the eyeballs anteriorly and posteriorly.

**Splanchnocranium.** The upper and lower jaws now carry about 30 teeth each, a number that will have doubled when the animals reach adulthood. The preopercles and the suspensoria have started to fuse. In later stages it is very difficult to differentiate between these bones. A short stretch of the preopercles lies directly under the skin, and now carries a few odontodes. During further development, the preopercles broaden somewhat, further overgrowing the quadrates and hyomandibulars. The anterior processes of each opercle have grown, and the articulation of the bone with the hyomandibular is reinforced by the presence of a serration on the opercle posterior to the articulation. A second, paired cheek plate has developed dorsal to the first one. It consists of an odontode-supporting plate only, thus not bearing a canal. The cheek spines are now well visible. The rostral processes of the parurohyal pierce the hypohyals; the horizontal sesamoid sheet continues to grow until the posterior margin is more or less rounded in the 25.0 mm stage, and reaches to almost half of the sternohyoideus length. The dorsal region of the parurohyal cartilage nucleus degenerates, and the ventral region further ossifies, although part of it stays cartilaginous even in adults. The very small third basibranchial is ossified in specimens of over 50 mm SL, while the posterior copula, consisting of the fourth and fifth fused basibranchials, remains cartilaginous. The second hypobranchials remain cartilaginous as well, while the third to fifth hypobranchials stay fused to the cartilage heads of the corresponding ceratobranchials. The anterior processes of the first ceratobranchials have broadened and grown to the same length as the ceratobranchials. The tips of the cerato- and epibranchials do not ossify. Also, the infrapharyngobranchials maintain their cartilaginous articular caps.

## DISCUSSION

Ossification in *A. cf. triradiatus* starts as early as the fourth day after fertilization. At 5.6 mm SL the first dermal bone can be recognized, i.e., the opercle. This is only 1 day after the formation of the first chondrocranial elements (Geerinckx et al., 2005), or 1 day before hatching occurs. The early appearance of the opercle, followed by the formation of the first branchiostegal rays and most dentulous bones, is a general trend in siluriforms and other teleosts (Weisel, 1967; McElman and Balon, 1980; Tilney

and Hecht, 1993; Vandewalle et al., 1995, 1997; Adriaens and Verraes, 1998). Generally, the onset of splanchnocranial ossification is earlier than the first appearance of neurocranial elements (e.g., de Beer, 1937; Bamford, 1948; Surlemont and Vandewalle, 1991; Tilney and Hecht, 1993; Vandewalle et al., 1994, 1995; Adriaens and Verraes, 1998). Within the neurocranium, dorsal and ventral elements appear more or less simultaneously in *A. cf. triradiatus*. The ontogeny of some skull bones of both neurocranium and splanchnocranium of *A. cf. triradiatus* is briefly treated, while a few merit a more thorough discussion.

### Neurocranium

The most important bone in the ethmoid region of *A. cf. triradiatus*, the mesethmoid, has a complex development. The dorsal and ventral perichondral components can be identified as the supra- and hypoethmoid bones. They are connected over the rostral tip of the ethmoid cartilage. A dermal element, called dermethmoid or rostral by Patterson (1975), soon overgrows the supraethmoid and stretches further posteriorly. Although these parts can be discerned based on their perichondral or dermal nature, as well as their location, they are actually connected more or less from the moment they arise. The ethmoid cartilage shows a small ventral protrusion, but most of the ventral disc of the mesethmoid does not form perichondrally around the ethmoid cartilage, but is an extension of the hypoethmoid. It is mostly membranous, although cartilage can be seen in serial sections (Fig. 5c). Its development is related to the formation of ligaments to the maxillae, premaxillae, and mesethmoid-premaxillary cartilage (Geerinckx et al., 2005).

The nasal sac is bordered on all sides only by the lateral ethmoid, as in the loricariids *Hypostomus plecostomus* (Schaefer, 1987) and *Pterygoplichthys* (Howes, 1983), but unlike in *Hypoptopoma*, where the nasal sac is free anteriorly (Howes, 1983).

The membranodermal component of the frontal appears first, with the neurodermal (canal-bearing) component ossifying from it (or perhaps separately) somewhat later in ontogeny. First both parts can be well distinguished, but later they fuse more intimately. This is often seen in other teleostean canal bones as well (Daget, 1964). Exceptions in *A. cf. triradiatus* are the infraorbital bones, nasal and canal-bearing cheek plates (see later), where the first ossification occurs around the canal. The anterior part of the adult frontal is relatively narrow, while the posterior part is broad enough to reach the orbit (as in *Otocinclus* [Schaefer, 1997] and *Farlowella* [Retzer and Page, 1996] but unlike the situation in *Hypostomus plecostomus* [Schaefer, 1987]).

In many siluriforms and other teleosts, the skull floor bones appear earlier than the roof bones; usually the parasphenoid is the first bone to arise, more

or less together with the basioccipital ossification around the notochord (Kobayakawa, 1992; Vandewalle et al., 1995, 1997; Adriaens and Verraes, 1998). Hoedeman (1960b) noted a slightly earlier development of some roof bones, i.e., the frontals and pterotics. When the parasphenoid ossifies, it is a U-shaped dermal sheet in the perimeter of the hypophyseal fenestra, also seen in *Chrysichthys auratus* (Vandewalle et al., 1995) and *Clarias gariepinus* (Adriaens and Verraes, 1998). In various teleosts, the early appearance of the parasphenoid has been linked to the necessity of protecting the braincase from the physical particularities of food passing in the buccal cavity, from the moment of the transition from endogenous to exogenous feeding (Verraes, 1974; Vandewalle et al., 1997, 1999; Adriaens and Verraes, 1998; Wagemans et al., 1998; Gluckmann et al., 1999). In *A. cf. triradiatus* though, the bone appears at 7.4 mm SL or 6 days after fertilization. Exogenous feeding starts around 9 mm or 8–9 days after fertilization. It could be hypothesized that parasphenoid ossification is related to the respiration movements and buccal pressure differences during respiration. Mechanical loading might be an important factor in inducing ossification (Mabee and Trendle, 1996; Adriaens and Verraes, 1998).

In siluriforms the posterior skull roof is composed of one large bone, known as the compound parieto-supraoccipital in siluriforms. Argumentation for the developmental fusion of paired parietal and supraoccipital ossification centra is given by Bamford (1948), Arratia and Menu-Marque (1981, 1984), and Fink and Fink (1996). In some cases (Callichthyidae, Clariidae) no developmental evidence was found (Hoedeman, 1960b; Adriaens and Verraes, 1998). In the ontogeny of *A. cf. triradiatus* separate parietals are never present. The parieto-supraoccipital arises as a paired, mostly perichondral bone. The development of the bone is somewhat complicated by the early presence of odontodes on the postotic processes, and posterior to the location where the possible parietals could be expected. There, membranous bone is soon added to the perichondral layer. The fact that a cleared and stained 8.0-mm SL specimen as well as serial sections of another 8.0-mm SL specimen show one paired ossification anlage for the parieto-supraoccipital, is unusual. This might be correlated to the presence of odontodes on the skull roof, possibly hastening ossification in the region of the bone that will support it. We can, however, only speculate on the exact cause of this ossification pattern. We apply the name parieto-supraoccipital, not supraoccipital alone, but whether the parietals are fused to the supraoccipitals, or missing, can, however, not be concluded unambiguously from our data. The ossification centra might be close to each other, masking a possible double origin. The ending of the parietal branch of the supraorbital canal between the frontal and the sphenotic could be interpreted as an argument that

the parietal is absent, but the branch might just have been reduced as well. It is absent in various catfishes (Arratia and Huaquín, 1995). Arratia and Huaquín (1995) regarded the absence of a parietal branch of the supraorbital canal as a synapomorphic condition for loricarioids. According to their definition, this branch commonly runs from the frontal into (or above) the parieto-supraoccipital bone in catfishes, or does not reach it (thus might have been reduced). Schaefer (1987) reported this branch in the sphenotic in *Hypostomus plecostomus*, and in the frontal in *Otocinclus* (Schaefer, 1997), where he rather confusingly called it “posterior” branch, posterior to a “parietal” (= epiphysial) branch. Whether this branch has disappeared in all loricarioid taxa except loricariids, or has secondarily reappeared in this family, remains to be verified.

According to Arratia (2003), a separate epioccipital is missing in *Nematogenys* and most trichomycterids, and also in *Hypostomus* and in scoloplacids. It has, however, been noted in other loricariids and in trichomycterids (Schaefer, 1987, 1997; Schaefer and Aquino, 2000). In *A. cf. triradiatus* it appears as a perichondral ossification of the middle part of the occipital pila. We favor the name epioccipital, and not epiotic (Schaefer, 1997; Arratia, 2003), following the argumentation of Patterson (1975).

In siluriforms the identification of the bone usually termed posttemporo-supracleithrum, in the posterolateral corner of the skull, is not easy. Arratia and Gayet (1995) stated that there is no developmental evidence that the bone termed posttemporo-supracleithrum in siluriforms is a compound element. It could be the posttemporal or supraclithrum alone, or the result of the early fusion of both elements during the earliest moments of ossification. Adriaens et al. (1997) suggested that in *Clarias gariepinus* the cleithral notch and the attachment of the Baudelot’s or transscapular ligament on it indicate it is at least composed of the supraclithrum, while the presence of an anteroventral process connecting the posterior element to the pterotic and a dorsal oblique process attaching it to the epioccipital might indicate that the posttemporal is also part of it (Adriaens and Verraes, 1998).

In Callichthyidae, Scoloplacidae, Astroblepidae, and Loricariidae, the (posttemporo)-supracleithrum is fused to the pterotic (Regan, 1911; Arratia, 2003). The detection of the separate bones in this “compound pterotic” in loricariids has been further complicated. Analogous to the argumentation of Adriaens et al. (1997), Aquino and Schaefer (2002) considered the cleithral articular notch and Baudelot’s ligament on the compound pterotic as indirect evidence of the incorporation of the supraclithrum into the ventral aspect of the pterotic. As Lundberg (1975) did, they concluded that there is no real evidence indicating the incorporation of the posttemporal as well, but that does not mean this component is absent in (all) loricariids. Aquino and Schaefer

(2002) also referred to Coburn and Grubich (1998), who suggested that loss or fusion of these elements may correlate to the loss of the first two occipital vertebral segments which they observed in the development of *Corydoras paleatus* (Callichthyidae) (see later for an account on the anterior vertebrae of *A. cf. triradiatus*). In *A. cf. triradiatus* the supraclithrum could be observed as a separate ossification, before fusing to the ventral layer of the pterotic (Fig. 5a). The cleithral dorsal process is closely associated to the supraclithrum, and the articular notch will form on this part of the “compound pterotic” bone. Baudelot’s ligament attaches and ossifies from this point as well (in case the posttemporal also would be incorporated, it would lie between the pterotic and the supraclithrum). To us, the name “compound pterotic” seems most appropriate for the complex. The posttemporal is most probably never present in *A. cf. triradiatus*.

The double-layered nature of the compound pterotic is considered a derived characteristic for loricariids by Aquino and Schaefer (2002), who added that the dorsal layer of the bone in loricariids is not homologous to that in other catfishes, as it does not bear the postotic canal. Also, this dorsal layer would appear prior to the ventral layer, which includes the neurodermal component enclosing the canal. This ossification sequence of the dermopterotic is not seen as such in *A. cf. triradiatus*. The ventral layer develops slightly earlier, and is grown to almost its full extent when the dorsal, strictly membranodermal layer starts to reach over the swimbladder capsule. Both are continuous with each other and the autopterotic at the occipital pila from the beginning, but only late in development they are connected by trabecles laterally.

The absence of a pterotic branch of the postotic canal was considered a synapomorphy of loricarioids by Arratia and Huaquín (1995), who noted its absence in trichomycterids and nematogenyids. In a paper discussing the pterotic branch homology, however, Schaefer and Aquino (2000) could identify this branch in all loricarioids except scoloplacids and astroblepids. It is present in *A. cf. triradiatus* as well.

The ossification pattern of Baudelot’s ligament in *A. cf. triradiatus* is interesting. As in other catfishes, it stretches from the ventral face of the supraclithrum toward the basioccipital, thereby forming a transverse ridge on the posteroventral skull floor. Two ossification centers are present in *A. cf. triradiatus*, one from the attachment point on the basioccipital, and one from the supraclithrum. In adults the boundary between both parts can still be seen, at the level of the basioccipital-pterotic contact. The boundary is also seen in *Hypostomus plecostomus* and *Otocinclus vittatus* (Schaefer, 1987, 1997). Not much is known about the ossification sequence of the ligament in other siluriforms (Fink and Fink, 1996), but in the ictalurid *Trogloglanis*

*pattersoni* only one large ossification seems to arise from the supracleithrum (Lundberg, 1982).

The identification of the complex vertebra in loricariids is problematic, as a reduction in number of the anterior vertebral centra appears to have occurred. In literature on loricariid morphology, there appears to be a general consensus on the identification of the sixth vertebra, which carries a pair of large ribs connecting the vertebral column with the lateral dermal plates posterior to the head (Alexander, 1964; Chardon, 1968; Schaefer, 1987, 1997). The earlier assumption of Bridge and Haddon (1893) that it might be the fifth was based on an unclear account of Reissner (1859). The sixth centrum is immovably sutured to the fifth, and its neural spine sutures to the posterior process of the parieto-supraoccipital. Chardon (1968) distinguished the fifth centrum from the first four, the centra of which must have become reduced significantly. In a developmental study of the Weberian apparatus in the callichthyid *Corydoras paleatus*, Coburn and Grubich (1998) concluded that the first two vertebrae are missing, and the third and fourth lack basidorsals and basiventrals. The situation in *A. cf. triradiatus* might be similar. The fourth and fifth centra originate as one long vertebral centrum. Their parapophyses form the bony encapsulation of the swimbladder. The basidorsals of the fifth vertebra reach toward the cartilaginous tectum posterius. The resulting complex of vertebrae (up to the fifth) has a length of twice that of vertebra six or seven. A recent paper by Hoffmann and Britz (2006) discusses the homology of the anterior vertebral centra among otophysans. Contrary to the previous view, it hypothesizes that it is the fourth (not the fifth) basidorsal which contacts the tectum synoticum, and thus the fifth (not the sixth) which bears the large ribs and touches the parieto-supraoccipital process. It is the fourth vertebra that forms the os suspensorium, a feature of the fourth vertebra in otophysans (Hoffmann and Britz, 2006).

Six, or rarely five infraorbital bones are present in *A. cf. triradiatus*. Usually six are found in hypostomine loricariids, though only five are found in Hypopomatinae (Schaefer, 1997). In one specimen of *A. cf. triradiatus*, there is no canal in the second infraorbital. Such a disjunct canal is slightly reminiscent to the situation in certain Trichomycteridae, where most of the infraorbital canal is lost, except for the part in the first infraorbital (Arratia and Huaquín, 1995). The shape and late ossification of the first bone of the infraorbital series, as well as the absence of an antorbital branch of the infraorbital canal, suggest the bone corresponds to infraorbital I and not to the antorbital. It does not match the criteria Arratia and Huaquín (1995) used for the identification of this bone in Diplomystidae.

The prefrontal plate might be homologous to the supraorbital-like tendon bone Arratia (1987) described in Diplomystidae. Howes (1983) noticed

the resemblance in position between the loricariid prefrontal plate with the supraorbital bone of some nonsiluriform taxa, but they are most probably not homologous (Fink and Fink, 1981; Howes, 1983).

The ossification of the infraorbital, nasal and suprapreopercle and the canal-bearing cheek plate differs from the situation in other canal bones. First, a neurodermal tube of bone arises around the sensory canal; only later the membranodermal component is formed against and on top of it. Adriaens and Verreaes (1998) describe the same phenomenon in the infraorbital, nasal, and suprapreopercular bones in *Clarias gariepinus*.

The number of prenasal and lateral plates or scutes varies in different specimens, particularly, the prenasal plates are variable in both number and shape. Schaefer (1997) mentioned a more rigid pattern of these plates in *Otocinclus*.

Sclerotic bones are present in larger specimens, although Fink and Fink (1996) regarded their absence as synapomorphic for Siluriphysi. Similar bones were also found in young *Callichthys* sp. by Arratia (1987).

### Splanchnocranium

During ontogeny, the tooth-bearing dentary of the lower jaw in *A. cf. triradiatus* fuses to the mentomeckelian (Fig. 5b) and angulo-articular bones. In the adult stage only a rudiment of Meckel's cartilage persists. As in other loricariids, as well as astroblepids, callichthyids, and most trichomycterids, a coronomeckelian bone is absent (Mo, 1991; de Pinna, 1993).

The double posterior process of the autopalatine bone acts as a double insertion point for the extensor tentaculi muscle subdivisions. In the basal siluriform *Diplomystes* and *Hypsidoris* a similar, but even larger, single posterior extension is present, posterior to the articulatory facet with the lateral ethmoid (Arratia, 1987; Grande, 1987). During early ontogeny, no sign is found of a palatine splint bone as is seen in *Otocinclus* (Schaefer, 1997); it can, however, be seen in adult *A. cf. triradiatus* (Geerinckx, personal observation). Schaefer (1997) considered it a dermal or sesamoid ossification, variably present in loricariids.

The view of Howes and Teugels (1989), suggesting the presence of dermal ento- and ectopterygoids next to the perichondral metapterygoid in some catfishes, is opposed to the hypothesis supported by Alexander (1965), Gosline (1975), Arratia (1990, 1992), Fink and Fink (1996), and Adriaens and Verreaes (1998), who reported only the metapterygoid to be present, as a perichondral ossification of the chondrocranial pterygoid process, and having membranous outgrowths. The latter interpretation is followed in this paper. The interpretation of Hoedeman (1960a), with the metapterygoid being part of the hyomandibular ossification, is incorrect. Ectoptery-

goids are only found in some individuals within the Diplomystidae (Arratia, 1992). Sesamoid ento- or ectopterygoids are also lacking in *A. cf. triradiatus* (they are present in several catfish families; Arratia, 1992; Kobayakawa, 1992; Diogo et al., 2001).

The hyomandibular articulation with the sphenotic, prootic and pterotic bones has also been observed in some trichomycterids (Arratia, 2003), but is uncommon in siluriforms (where usually only one or two of these bones are involved). In adult individuals of *A. cf. triradiatus* the hyomandibular trunk enters the hyomandibular bone at the medial side and leaves it at its lateroventral margin, medial to the preopercle, whereas it leaves the bone at the lateral side in *Hypostomus* and *Otocinclus* (Schaefer, 1987, 1997).

Schaefer (1988) elaborated on the identity of the largest, canal-bearing cheek plate, present in many loricariids. He concluded that it is not homologous with the interopercle of most other catfishes, as no other teleosts possess a canal in the interopercle, and this canal communicates directly with the preopercular canal terminus (his exit 5) in primitive siluriforms. In the loricariid genus *Delturus* a true interopercle might be present, although the homology issue remains problematic (Armbruster, 2004). No ontogenetic stage of *A. cf. triradiatus* shows any sign of the interoperculo-mandibular ligament, which is assumed to be lacking in most loricariids as well as in astroblepids (Schaefer, 1988; Armbruster, 2004). Development of the cheek plate in *A. cf. triradiatus* starts with a neurodermal gutter-like bone surrounding the canal at 11.7 mm SL, followed by the addition of a small odontode-bearing membranodermal component at 14.4 mm SL. Schaefer (1988) observed an opposite sequence in *Sturisoma* sp.: the odontode-bearing part arises before a canal is observed in the bone.

In adults of *A. cf. triradiatus* the suprapreopercle is fused to the sixth infraorbital bone (Geerinckx, personal observation). This could not (yet) be observed in any of the examined embryonic and juvenile specimens. The infraorbital and preopercular canals, however, remain separated. In *Otocinclus* both canals sometimes share a pore between the sphenotic, pterotic, and posterior (fifth) infraorbital bone (Schaefer, 1997; personal observation).

The cartilaginous interhyal connects the chondrocranial hyoid arch with the hyosymplectic cartilage (Geerinckx et al., 2005). In *A. cf. triradiatus* it is lost during ontogeny. The final articulation between the hyoid bar and the suspensorium is assisted by a series of ligaments. The loss of the interhyal is also seen in *Clarias gariepinus* (Nawar, 1954; Adriaens and Verraes, 1994). A cylinder-shaped sesamoid bone arising in a ligament at the medial side of the original interhyal location (Fig. 5d) might well be unique for loricariids. It is present in *Hypostomus plecostomus* and *Otocinclus vittatus* (though interpreted as an interhyal by Schaefer,

1987, 1997). It is hypothesized to act as a support, strengthening the articulation, which may well be needed to resist the strong forces exerted by the suction used by loricariids to keep the body attached to substrates, often in fast flowing water. The absence of the interhyal is shared by loricariids and scoloplacids (Bailey and Baskin, 1976).

The branchiostegal rays articulate with the ventrocaudal process of the hyoid bar, which is a large and cartilaginous extension of the hyoid bar at the level of the joint between the anterior and posterior ceratohyal. Arratia (1987) saw a similar situation in *Loricarichthys* sp., and a different situation in *Callichthys callichthys*, where three separate cartilage elements connect the four branchiostegal rays with the hyoid arch, while the rays articulate with the ceratohyals directly in other catfishes including diplomystids.

The minuscule cartilage nucleus present in front of the infrapharyngobranchial III in adult specimens (Geerinckx, personal observation) has not been found in any of the studied developmental stages, and must, therefore, develop later than the 12.4 mm stage (its apparent absence in the older in toto-stained specimens [14.4–25.0 mm] might be due to very weak alcian staining). Alexander (1965) stated that the loricariid *Hypostomus plecostomus* has no pharyngeal teeth, as “it does not require them.” This stands against the observation by Schaefer (1987), who counted numerous teeth on both the upper and lower pharyngeal jaw in the same species, exactly as in *A. cf. triradiatus*. The lower pharyngeal jaws arise independently as supporting plates for the pharyngeal teeth, and coalesce secondarily with the fifth ceratobranchials that appear at the same moment, as in other siluriforms (McMurrich, 1884; Vandewalle et al., 1999). The development of the upper pharyngeal jaws has started much earlier than that of the lower, a sequence also observed in other siluriforms (Adriaens and Verraes, 1998).

In *A. cf. triradiatus* the parurohyal is pierced by one blood vessel, the inferior jugular vein (Fig. 5h). This vein receives blood from vessels draining the hyohyoideus inferior, protractor hyoidei and intermandibularis muscles, before ascending through the center of the parurohyal. It then receives several more veins from the sternohyoideus, before running to the sinus venosus, crossing the ventral aorta at the right side. This vein has also been reported by Nawar (1955) in *Clarias gariepinus*, though not piercing the parurohyal. Instead, in *C. gariepinus* a direct branch of the ventral aorta descends through it, before sending branches into the hyohyoideus inferior (Adriaens and Verraes, 1998; personal observation). In *A. cf. triradiatus*, the arteries irrigating the hyohyoideus inferior branch off from the aorta ventralis and run above the parurohyal, entering the muscle more laterally. These strikingly different configurations also differ from the situation in *Nem-*

*atogenys*, *Trichomycterus*, and *Noturus*, where it is the hypobranchial artery that pierces the parurohyal (Arratia and Schultze, 1990).

In *Clarias gariepinus* the first basibranchial is absent (Nawar, 1954). In their developmental study Adriaens and Verraes (1998) concluded it is most likely incorporated in the parurohyal. The present study corroborates this hypothesis: serial sections of subsequent stages show that the first basibranchial splits off from the next basibranchials, and becomes reduced. It remains, however, continuous to the dumbbell-shaped cartilage nucleus of the parurohyal. It is difficult to say whether it disappears completely or forms the dorsalmost part of the medial dorsal ridge of the parurohyal anterior to the foramen for the inferior jugular vein.

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## LITERATURE CITED

- Adriaens D, Verraes W. 1994. On the functional significance of the loss of the interhyal during ontogeny in *Clarias gariepinus* Burchell, 1822 (Teleostei: Siluroidei). *Belg J Zool* 124:139–155.
- Adriaens D, Verraes W. 1998. Ontogeny of the osteocranium in the African catfish. *Clarias gariepinus* (1822) (Siluriformes: Clariidae): Ossification sequence as a response to functional demands. *J Morphol* 235:183–237.
- Adriaens D, Verraes W, Taverne L. 1997. The cranial lateral-line system in *Clarias gariepinus* (Burchell, 1822) (Siluroidei: Clariidae): Morphology and development of canal related bones. *Eur J Morphol* 35:181–208.
- Alexander RMcN. 1964. The structure of the Weberian apparatus in the Siluri. *Proc Zool Soc Lond* 142:419–440.
- Alexander RMcN. 1965. Structure and function in the catfish. *J Zool Lond* 148:88–152.
- Aquino AE, Schaefer SA. 2002. The temporal region of the cranium of loricarioid catfishes (Teleostei: Siluriformes): Morphological diversity and phylogenetic significance. *Zool Anz* 241:223–244.
- Armbruster JW. 2004. Phylogenetic relationships of the sucker-mouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. *Zool J Linn Soc* 141:1–80.
- Arratia G. 1987. Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): Morphology, taxonomy and phylogenetic implications. *Bonn Zool Monogr* 24:1–120.
- Arratia G. 1990. Development and diversity of the suspensorium of trichomycterids and comparison with loricarioids (Teleostei: Siluriformes). *J Morphol* 205:193–218.
- Arratia G. 1992. Development and variation of the suspensorium of the primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonn Zool Monogr* 32:1–148.
- Arratia G. 2003. Catfish head skeleton: An overview. In: Arratia G, Kapoor AS, Chardon M, Diogo R, editors. *Catfishes*, Vol. 1. Enfield, USA: Science Publishers. pp 3–46.
- Arratia G, Gayet M. 1995. Sensory canals and related bones of tertiary siluriform crania from Bolivia and North America and comparison with recent forms. *J Vertebr Paleontol* 15:482–505.
- Arratia G, Huaquín L. 1995. Morphology of the lateral line system and of the skin of diplomystid and certain primitive loricarioid catfishes and systematic and ecological considerations. *Bonn Zool Monogr* 36:1–110.
- Arratia G, Menu-Marque S. 1981. Revision of the freshwater catfishes of the genus *Hatcheria* (Siluriformes, Trichomycteridae) with commentaries on ecology and biogeography. *Zool Anz* 207:88–111.
- Arratia G, Menu-Marque S. 1984. New catfishes of the genus *Trichomycterus* from the high Andes of South America (Pisces, Siluriformes) with remarks on distribution and ecology. *Zool Jahrb, Abt Syst (Oekol)*, *Geogr Biol* 111:493–520.
- Arratia G, Schultze H-P. 1990. The urohyal: Development and homology within osteichthyans. *J Morphol* 203:247–282.
- Bailey RM, Baskin JN. 1976. *Scoloplax dicra*, a new armored catfish from the Bolivian Amazon. *Occ Pap Mus Zool Univ Mich* 674:1–14.
- Bamford TW. 1948. Cranial development of *Galeichthys felis*. *Proc Zool Soc Lond* 118:364–391.
- Bhatti HK. 1938. The integument and dermal skeleton of Siluroidea. *Trans Zool Soc Lond* 24:1–102.
- Bridge TW, Haddon AC. 1893. Contributions to the anatomy of fishes. II. The air-bladder and Weberian ossicles in the siluroid fishes. *Philos Trans R Soc Lond* 184:65–333.
- Chardon M. 1968. Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann Mus R Afr Centr Sér IN-8* 169:1–277.
- Coburn MM, Grubich PG. 1998. Ontogeny of the Weberian apparatus in the armored catfish *Corydoras paleatus* (Siluriformes: Callichthyidae). *Copeia* 1998:301–311.
- Daget J. 1964. Le crâne des téléostéens. I. Origine et mise en place des tissus squelettogènes chez l'embryon. Mésomésenchyme et ectomésenchyme. *Mém Mus Natl Hist Nat Sér A Zool* 31:164–340.
- de Beer GR. 1937. *Studies on the Vertebrate Head*. Oxford: Clarendon Press.
- de Pinna MCC. 1993. Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysi), PhD Thesis, City University of New York, 482 pp.
- Diogo R, Oliveira C, Chardon M. 2001. On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium. *Belg J Zool* 131:93–109.
- Fink SV, Fink WL. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zool J Linn Soc Lond* 72:297–353.
- Fink SV, Fink WL. 1996. Interrelationships of ostariophysan fishes (Teleostei). In: Stiassny MLJ, Parenti LR, Johnson GD, editors. *Interrelationships of Fishes*. London: Academic Press. pp 209–249.
- Geerinckx T, Brunain M, Adriaens D. 2005. Development of the chondrocranium in the sucker-mouth armored catfish *Ancistrus* cf. *triradiatus* (Loricariidae, Siluriformes). *J Morphol* 266:331–355.
- Gluckmann I, Hurlaux F, Focant F, Vandewalle P. 1999. Postembryonic development of the cephalic skeleton in *Dicentrarchus labrax* (Pisces, Perciformes, Serranidae). *Bull Mar Sci* 65:11–36.
- Gosline WA. 1975. The palatine-maxillary mechanism in catfishes, with comment on the evolution and zoogeography of modern Siluroidea. *Occas Pap Calif Acad Sci* 120:1–31.
- Grande L. 1987. Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. *J Vertebr Paleontol* 7:24–54.
- Harrington RW Jr. 1955. The osteocranium of the American cyprinid fish, *Notropis bifrenatus*, with an annotated synonymy of teleost skull bones. *Copeia* 1955:267–291.
- Hoedeman JJ. 1960a. Studies on callichthyid fishes: (4) Development of the skull of *Callichthys* and *Hoplosternum* (1) (Pisces-Siluriformes). *Bull Aquat Biol* 1:73–84.
- Hoedeman JJ. 1960b. Studies on callichthyid fishes: (5) Development of the skull of *Callichthys* and *Hoplosternum* (2) (Pisces-Siluriformes). *Bull Aquat Biol* 2:21–36.
- Hoffmann M, Britz R. 2006. Ontogeny and homology of the neural complex of otophysan Ostariophysi. *Zool J Linn Soc* 147:301–330.
- Howes GJ. 1983. The cranial muscles of loricarioid catfishes, their homologies and value as taxonomic characters. *Bull Br Mus Nat Hist (Zool)* 45:309–345.
- Howes GJ, Teugels GG. 1989. Observations and homology of the pterygoid bones in *Corydoras paleatus* and some other catfishes. *J Zool Lond* 219:441–456.

- Kindred JE. 1919. The skull of *Amiurus*. Ill Biol Monogr 5:1–4.
- Kobayakawa M. 1992. Comparative morphology and development of bony elements in the head region in three species of Japanese catfishes (*Silurus*: Siluridae; Siluriformes). Jpn J Ichthyol 39: 25–36.
- Lauder GV, Crompton AW, Gans C, Hanken J, Liem KF, Maier WP, Meyer A, Presley R, Rieppel OC, Roth G, Schluter D, Zweers GA. 1989. Group report: How are feeding systems integrated and how have evolutionary innovations been introduced? In: Wake DB, Roth G, editors. Complex Organismal Functions: Integration and Evolution in Vertebrates. New York: Wiley. pp 97–115.
- Lundberg JG. 1975. Homologies of the upper shoulder girdle and temporal region bones in catfishes (Order Siluriformes), with comments on the skull of the Helogeneidae. Copeia 1975:66–74.
- Lundberg JG. 1982. The comparative anatomy of the toothless blindcat. *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. Misc Publ Mus Zool Univ Mich 163:1–85.
- Mabee PM, Trendle TA. 1996. Development of the cranium and paired fins in *Betta splendens* (Teleostei: Percomorpha): Intra-specific variation and interspecific comparisons. J Morphol 227:249–287.
- McElman JF, Balon EK. 1980. Early ontogeny of white sucker. *Catostomus commersoni*, with steps of saltatory development. Environ Biol Fish 5:191–224.
- McMurrich JP. 1884. On the osteology of *Amiurus catus* (L.) gill. Zool Anz 168:296–299.
- Mo T. 1991. Anatomy and Systematics of Bagridae (Teleostei), and Siluroid Phylogeny. Koenigstein: Koeltz Scientific Books. 216 pp.
- Nawar G. 1954. On the anatomy of *Clarias lazera*. I. Osteology. J Morphol 94:551–585.
- Nawar G. 1955. On the anatomy of *Clarias lazera*. III. The vascular system. J Morphol 97:179–214.
- Orton GL. 1955. Some aspects of ecology and ontogeny in the fishes and amphibians. Am Nat 89:193–203.
- Patterson C. 1975. The braincase of the pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. Philos Trans R Soc Lond Biol Sci 269:275–579.
- Patterson C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In: Andrews SM, Miles RS, Walker AD, editors. Problems in Vertebrate Evolution. London: Academic Press. pp 77–121.
- Radermaker F, Surlemont C, Sanna P, Chardon M, Vandewalle P. 1989. Ontogeny of the Weberian apparatus of *Clarias gariepinus* (Pisces, Siluriformes). Can J Zool 67:2090–2097.
- Regan CT. 1911. The classification of the teleostean fishes of the order Ostariophysi. II. Siluroidea. Ann Mag Nat Hist 8:553–577.
- Reif WE. 1982. Evolution of dermal skeleton and dentition in vertebrates. The odontode regulation theory. Evol Biol 15:287–368.
- Reissner E. 1859. Über die Schwimmblase und den Gehörapparat einiger Siluroiden. Arch Anat Phys Wiss Med Leipz 421–438.
- Retzer ME, Page LM. 1996. Systematics of the stick catfishes. *Farlowella* Eigenmann & Eigenmann (Pisces: Loricariidae). Proc Acad Nat Sci Phila 147:33–88.
- Schaefer SA. 1987. Osteology of *Hypostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). Contrib Sci 394:1–31.
- Schaefer SA. 1988. Homology and evolution of the opercular series in the loricarioid catfishes (Pisces: Siluroidei). J Zool Lond 214:81–93.
- Schaefer SA. 1997. The neotropical cascudinhos: Systematics and biogeography of the *Otocinclus* catfishes (Siluriformes: Loricariidae). Proc Acad Nat Sci Phila 148:1–120.
- Schaefer SA, Aquino AE. 2000. Postotic laterosensory canal and pterotic branch homology in catfishes. J Morphol 246:212–227.
- Schaefer SA, Lauder GV. 1986. Historical transformation of functional design: Evolutionary morphology of feeding mechanisms in loricarioid catfishes. Syst Zool 35:489–508.
- Surlemont C, Vandewalle P. 1991. Développement postembryonnaire du squelette et de la musculature de la tête de *Clarias gariepinus* (Pisces, Siluriformes) depuis l'éclosion jusqu'à 6.8 mm. Can J Zool 69:1094–1103.
- Taylor WR, Van Dyke GC. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.
- Tilney RL, Hecht T. 1993. Early ontogeny of *Galeichthys feliceps* from the south east coast of South Africa. J Fish Biol 43:183–212.
- Vandewalle P, Huysseune A, Aerts P, Verraes W. 1994. The pharyngeal apparatus in teleost feeding. In: Bels VL, Chardon M, Vandewalle P, editors. Advances in Comparative and Environmental Physiology. Heidelberg: Springer-Verlag. pp 59–92.
- Vandewalle P, Lalèyé P, Focant B. 1995. Early development of cephalic bony elements in *Chrysichthys auratus* (Geoffroy Saint-Hilaire, 1808) (Pisces, Siluriformes, Claroteidae). Belg J Zool 125:329–347.
- Vandewalle P, Gluckmann I, Baras E, Huriaux F, Focant B. 1997. Postembryonic development of the cephalic region in *Heterobranchius longifilis*. J Fish Biol 50:227–253.
- Vandewalle P, Gluckman I, Wagemans F. 1998. A critical assessment of the Alcian blue/Alizarine double staining in fish larvae and fry. Belg J Zool 128:93–95.
- Vandewalle P, Chikou A, Lalèyé P. 1999. Early development of the chondrocranium in *Chrysichthys auratus*. J Fish Biol 55: 795–808.
- Verraes W. 1974. Discussion on some functional-morphological relations between some parts of the chondrocranium and the osteocranium in the skull base and the skull roof, and of some head parts during postembryonic development of *Salmo gairdneri* Richardson, 1836 (Teleostei: Salmonidae). Form Funct 7:281–292.
- Wagemans F, Focant B, Vandewalle P. 1998. Early development of the cephalic skeleton in the turbot. J Fish Biol 52:166–204.
- Weisel GF. 1967. Early ossification in the skeleton of the sucker (*Catostomus macrocheilus*) and the guppy (*Poecilia reticulata*). J Morphol 121:1–18.