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

Tom Geerinckx,* Marleen Brunain, and Dominique Adriaens

Evolutionary Morphology of Vertebrates, Ghent University – UGent, 9000 Ghent, Belgium

ABSTRACT The chondrocranium of the suckermouth armored catfish *Ancistrus* cf. *triradiatus* was studied. Its development is described based on specimens ranging from small prehatching stages with no cartilage visible, to larger posthatching stages where the chondrocranium is reducing. Cleared and stained specimens, as well as serial sections, revealed a cartilaginous skeleton with many features common for Siluriformes, yet several aspects of *A.* cf. *triradiatus* are not seen as such in other catfishes, or to a lesser extent. The skull is platybasic, but the acrochordal cartilage is very small and variably present, leaving the notochord protruding into the hypophyseal fenestra in the earlier stages. The ethmoid region is slender, with a rudimentary solum nasi. A lateral commissure and myodomes are present. The larger posterior myodome is roofed by a prootic bridge. The maxillary barbel is supported by a conspicuous cartilaginous rod from early prehatching stages. The ceratohyal has four prominent lateral processes. Infrapharyngobranchials I–II do not develop. During ontogeny, the skull lengthens, with an elongated ethmoid, pointing ventrally, and a long and bar-shaped hyosymplectic-pterygoquadrate plate. Meckel's cartilages point medially instead of rostrally. J. Morphol. 266: 331–355, 2005.   © 2005 Wiley-Liss, Inc.

KEY WORDS: ontogeny; skeleton; cartilage; *Ancistrus*; Loricariidae; catfishes

The ontogeny of fishes and other vertebrates merits attention for various reasons. First, a description of ontogeny and ontogenetic transformations is essential for understanding the pattern behind body plan formations. Second, this knowledge provides information that can be used in reconstructing phylogenies. Third, attention must be given to the fact that an organism must be functional at each moment, including young, growing, ever-changing, and thus "temporary" stages (Galis, 1993; Galis et al., 1994). Organisms can hardly be understood by considering only their adult forms, and study of their early ontogeny may be more revealing and is therefore very important (Balon, 1986).

An interesting case, of which very little is known at the moment, is the ontogeny and growth in the catfish family Loricariidae, or suckermouth armored catfishes. With more than 670 species (Ferraris et al., 2003), this extremely diverse South American

family is the largest within the Siluriformes and is renowned for its remarkable niche occupation, i.e., the scraping and sucking of algae and other food types off various substrates. Within the superfamily Loricarioidea, the loricariids developed a highly specialized feeding apparatus, with a ventral suctorial mouth, tilted lower jaws, and new muscle configurations that greatly increase jaw mobility as the most eye-catching adaptations (Alexander, 1965; Schaefer and Lauder, 1986). A number of studies have focused on the group, clarifying many aspects of the adult osteology and myology of the Loricariidae (a.o. Howes, 1983; Schaefer, 1987, 1988; Schaefer and Lauder, 1986).

Many questions concerning loricariid morphology are still unresolved. Virtually nothing is known about their ontogeny. One aspect was studied by Carter and Beadle (1931), who confirmed the development and function of the stomach as a respiratory organ in *Liposarcus anisitsi*. A critical question is whether a family with such aberrant adult head morphology shows the general siluriform tendencies during early development. Given the atypically siluriform adult morphology of Loricariidae, coupled with a peculiar, not completely understood feeding and respiratory behavior, one could question how this affects early life stages. In addition, hatchlings appear to be able to adhere themselves to the substrate immediately, using their sucker mouth, as noted by Riehl and Patzner (1991) in the loricariid *Sturisoma aureum*. A first step in answering questions concerning ontogeny and function in Loricariidae, and hence the ontogeny of function, is a proper

*Correspondence to: Tom Geerinckx, Evolutionary Morphology of Vertebrates, Ghent University – UGent, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium. E-mail: tom.geerinckx@ugent.be

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

No.	SL (mm)	SkL (mm)	Age (PF)	Method	Staining	Used for
1	4.8	—	2	Serial sections	T	Observation
2	5.2	—	3	Serial sections	T	3D reconstruction
3	5.6	1.24	4	Clearing	AB + AR	Drawing
4	6.0	1.39	4	Clearing	AB + AR	Drawing
5	6.1	—	4	Serial sections	T	Observation
6	6.3	1.47	5	Clearing	AB + AR	Observation
7	6.8	1.60	5*	Clearing	AB + AR	Drawing
8	7.0	—	6	Serial sections	T	Observation
9	7.4	1.82	6	Clearing	AB + AR	Drawing
10	7.7	2.00	6	Clearing	AB + AR	Observation
11	8.0	2.16	7	Clearing	AB + AR	Drawing
12	8.0	—	7	Serial sections	T	Observation
13	8.5	2.38	7	Clearing	AB + AR	Observation
14	8.7	2.45	7	Clearing	AB + AR	Observation
15	8.9	2.51	8	Clearing	AB + AR	Drawing
16	9.9	2.82	10	Clearing	AB + AR	Drawing
17	10.2	—	14	Serial sections	T	Observation
18	11.5	3.38	30	Clearing	AB + AR	Observation
19	12.4	—	43	Serial sections	T	Observation
20	12.7	3.67	48	Clearing	AB + AR	Observation

AB: alcian blue, AR: alizarin red S, PF: post-fertilization, SL: standard length, SkL; chondrocranial skull length (from tip of ethmoid plate to end of basis of occipital pilae, thus excluding tectum posterius), T: toluidine blue.
*Immediately after hatching.

knowledge of the changing morphology during ontogeny. This article deals with the development and growth of the chondrocranium in a representative loricariid species, the "bristlemouth" suckermouth armored catfish *Ancistrus* cf. *triradiatus*.

The chondrocranium of several of the ~34 siluriform families has already been described. Accounts of one or more stages in the development of the chondrocranium are published for Ariidae (*Ariopsis felis*; Bamford, 1948; *Arius jella*; Srinivasachar, 1958a), Bagridae (*Mystus vittatus, Rita* sp.; Srinivasachar 1957a), Callichthyidae (*Callichthys callichthys*; Hoedeman, 1960; *Hoplosternum littorale*; Ballantyne, 1930), Clariidae (*Clarias gariepinus*; Vandewalle et al., 1985; Surlemont et al., 1989; Surlemont and Vandewalle, 1991; Adriaens and Verraes, 1994, 1997a; *Heterobranchus longifilis*; Vandewalle et al., 1997), Claroteidae (*Chrysichthys auratus*, Vandewalle et al., 1999), Heteropneustidae (*Heteropneustes fossilis*; Srinivasachar, 1958b, 1959), Ictaluridae (*Ameiurus nebulosus*; Kindred, 1919), Pangasiidae (*Pangasius pangasius*; Srinivasachar, 1957b), Plotosidae (*Plotosus canius*; Srinivasachar 1958a), Schilbeidae (*Ailia coila*, *Silonia silondia*; Srinivasachar 1957b), and the suspensorium of Trichomycteridae (Arratia, 1990). Recent articles have shed light on generalities and trends, as well as the diversity in catfish chondrocrania (Arratia, 1992; Adriaens and Verraes, 1997a; Vandewalle et al., 1999; Adriaens and Vandewalle, 2003). The current study of the chondrocranium of a species of the family Loricariidae adds a rather aberrant type of siluriform to this list, and forms the basis of current work on the ontogeny of other structures in loricariids.

MATERIALS AND METHODS

Ancistrus cf. *triradiatus* Eigenmann, 1918 (a bristlenose catfish) was chosen for this study because of its fairly typical loricariid habitus and medium size. Until recently, Ancistrinae was recognized as one of six subfamilies in the Loricariidae (de Pinna, 1998). Armbruster (2004) lowered the Ancistrinae to the tribe Ancistrini in the subfamily Hypostominae. The systematics within the Ancistrini remain largely unresolved (de Pinna, 1998; Armbruster, 2004). Complete determination keys of *Ancistrus* itself are nonexistent, and the genus is in need of revision.

Specimens representing the major period of the early ontogeny were used to study the morphology of the chondrocranium, from early prehatching stages (no cartilage visible) to later stages in which the osteocranium becomes predominant. Various egg clutches were obtained from adults kept in a 24–26°C aquarium; all specimens were fathered by the same male. At different time intervals eggs and embryos were sedated in MS-222 and fixed in a paraformaldehyde-glutaraldehyde solution. For prehatching stages, egg scales were removed prior to fixation. Most specimens were used for in toto clearing and staining following the alcian blue / alizarin red method of Taylor and Van Dyke (1985) (Table 1). Examination of the specimens was done using an Olympus SZX9 stereoscopic microscope equipped with a camera lucida for drawing. Seven specimens were selected for serial sectioning. Toluidine blue-stained 2-μm sections (Technovit 7100 embedding, cut with a Reichert-Jung Polycut microtome) were studied using a Reichert-Jung Polyvar light microscope. A 3D reconstruction was made from serial sections of the 5.2 mm stage using the software package Amira 3.1.1 (TGS Europe, France).

RESULTS

The chondrocranium of *Ancistrus* cf. *triradiatus* is composed of cell-rich hyaline cartilage (Benjamin, 1990). Both appositional growth (proliferation of chondroblasts at the outer edge of cartilage) and interstitial growth (division of preexisting, medially located chondrocytes, and subsequent addition of matrix) are observed during development. Matrix-rich hyaline cartilage is only found in the anterior
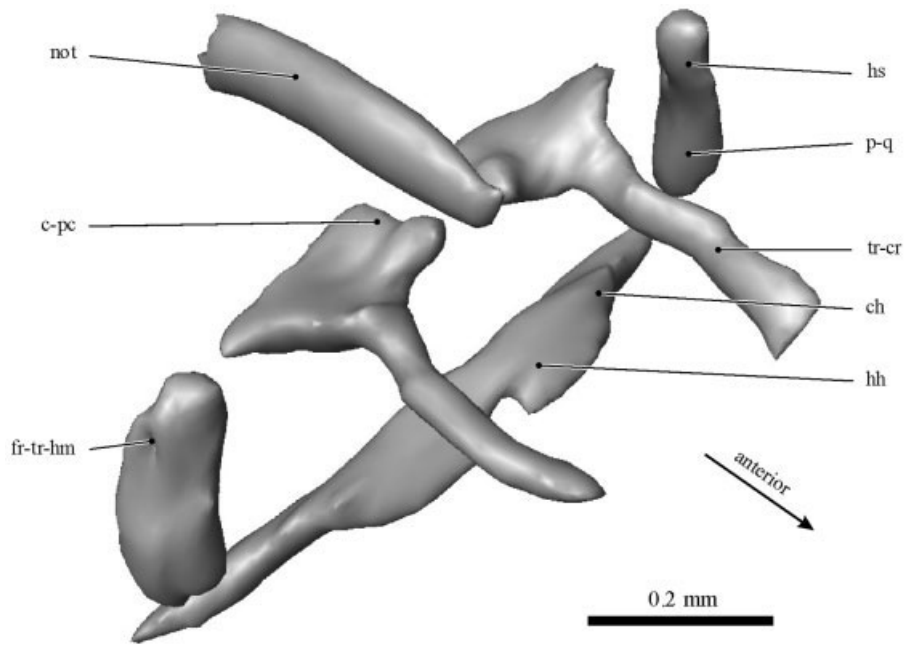
Fig. 1. 3D reconstruction of chondrocranium of *Ancistrus* cf. *triradiatus* (5.2 mm SL). Oblique dorsal view. c-pc, cartilago parachordalis; ch, ceratohyale; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; hh, hypohyale; hs, hyosymplecticum; lm-bot, lamina basiotica; not, notochord; p-q, pars quadrata of palatoquadratum; tr-cr, trabecula cranii.

cartilaginous head of the autopalatine bone in juveniles and adults, and not in the embryonic chondrocranium.

4.8 mm SL (Standard Length) Stage

Serial sections show no evidence of cartilage or chondroblast differentiation in this stage.

5.2 mm SL Stage (Fig. 1)

Neurocranium. Serial sectioning reveals the presence of a few cartilaginous structures. The anterior parts of the parachordal cartilages have formed, and in front of these the trabecular bars are well visible and continuous with the parachordal cartilages. Chondroblast differentiation at both sides of the tip of the notochord constitutes the onset of the acrochordal cartilage (Fig. 2a,b). The trabecular bars are wide apart and slightly curved, typical for platybasic teleosts, leaving a broad hypophyseal fissure. They do not touch rostrally yet. Except for the notochord, no supporting structures unite both halves of the young neurocranium. Differentiating chondroblasts are seen where the anterior otic cartilage will form.

Splanchnocranium. The equally well-stained hyoid bar is already present. The hyosymplectic-pterygoquadrate plate is less developed, but also visible to some extent. In this stage no cartilage is seen at the future location of the interhyal.

5.6 mm SL Stage (Fig. 3)

Neurocranium. Most parts of the skull floor are now at least partly formed, supporting the develop-

ing brain and separating it from the underlying structures. The parachordal cartilages, bordering the notochord, and the collateral basiotic laminae, more anteriorly, are indistinguishably fused. The curved trabecular bars become broader rostrally, where they will soon form the solum nasi; they end at the ethmoid plate. In this stage, it is impossible to distinguish the trabecular bars from the polar cartilages, as there is as yet no sign of a fissure for the arteria carotis interna yet; but, as deduced from the later stages, and by analogy with the observations of Adriaens and Verraes (1997a) and others, the posterior part probably corresponds to the polar cartilage. It is this part that connects with the basiotic lamina. The rudimentary acrochordal cartilage only covers the tip of the notochord dorsally, so that the notochord protrudes slightly into the hypophyseal fenestra. From posterior to anterior, the elements bordering the hypophyseal fenestra are: the tip of the notochord and the acrochordal cartilage, the plate-like basiotic lamina, the polar cartilages, the trabecular bars, and the ethmoid cartilage.

The parachordal cartilages are connected with the otic capsule by means of the anterior basicapsular commissure at the level of the anterior otic cartilage. The posterior otic cartilage is continuous with the anterior one, and only distinguishable from it because it already carries a median process that later will give rise to the basivestibular and posterior basicapsular commissures (see below). It also is less stained, indicating that it might have developed later than the anterior otic cartilage. The occipital pilae arise from the caudal ends of the parachordal cartilages and contact the posterior otic cartilages. The metotic fenestra, a large opening bordered by
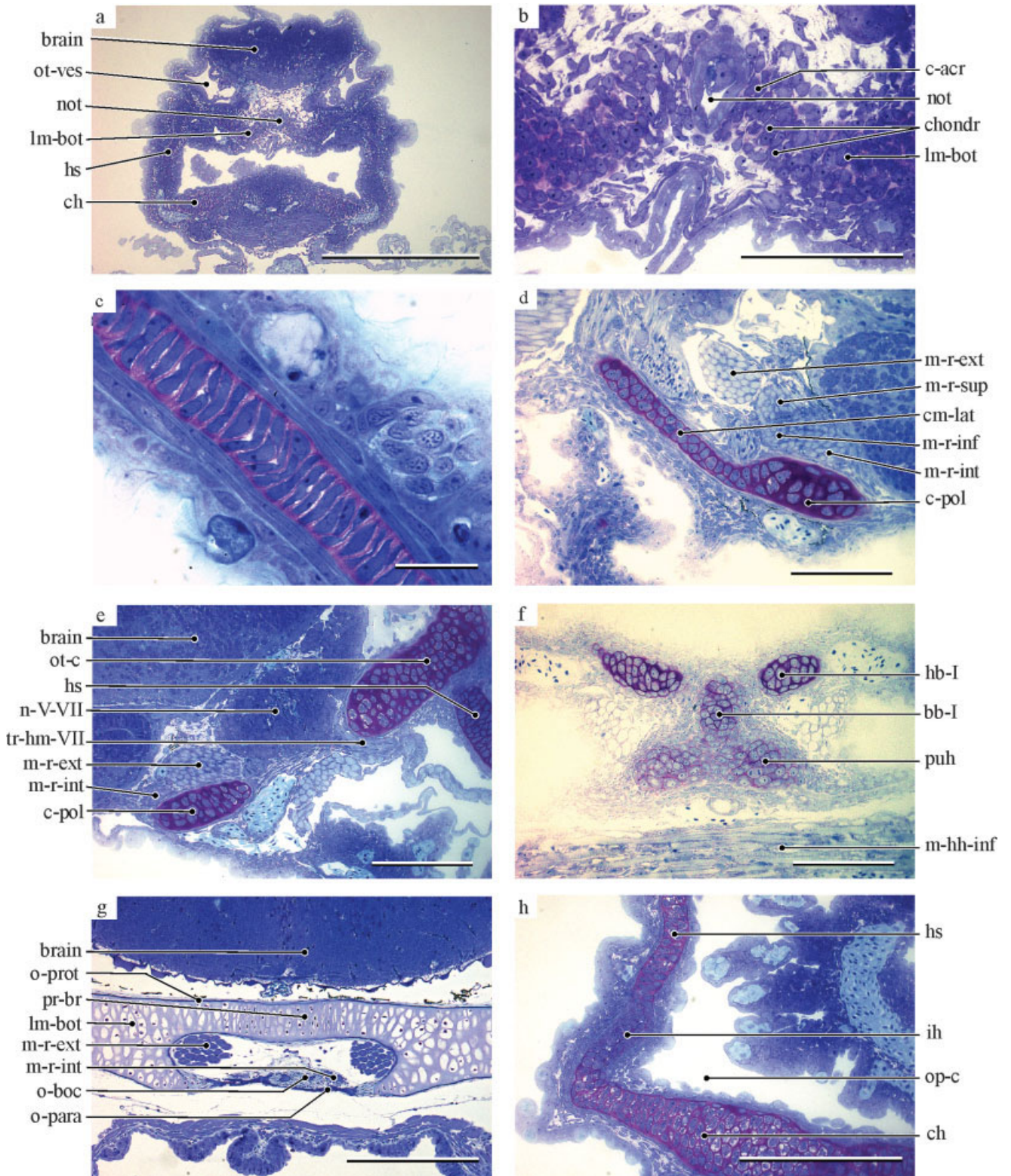
Figure 2

the parachordal cartilage medially, the anterior basicapsular commissure rostrally, the otic capsule laterally, and the occipital pila caudally accommodates the glossopharyngeal (IX) and vagal (X) nerves (as seen in serial sections of the 5.2 and 6.1 mm specimens). The lateral part of the otic capsule becomes closed now, except for a lateroventral opening in the capsule floor.

The taenia marginalis starts to grow at the rostral end of the anterior otic cartilage. Near its origin a small foramen is present in the anterior otic cartilage. A part of the otic branch of the facial nerve, innervating the sensory canal, is seen passing through it in serial sections of the 6.1 mm and all later stages.

Splanchnocranium. A short maxillary barbel cartilage is present at the base of the rudimentary maxillary barbel. Meckel's cartilage has arisen and bears a conspicuous coronoid process, which points dorsorostrally. The hyosymplectic-pterygoquadrate plate is continuous with the interhyal and the ceratohyal-hypohyal bar, and, albeit very weakly, with Meckel's cartilage (this matrix-poor articular cartilage connection is only seen in serial sections). The hyosymplectic part has a foramen for the hyomandibular trunk of the facial nerve. Both hypohyals are continuous at the midline, whereas Meckel's cartilages are not. No signs of the branchial basket are visible yet.

6.0 mm SL Stage (Fig. 4)

Neurocranium. The notochord still protrudes slightly into the hypophyseal fenestra (as in the previous stage, the acrochordal cartilage only covers the dorsal side of the tip of the notochord). The
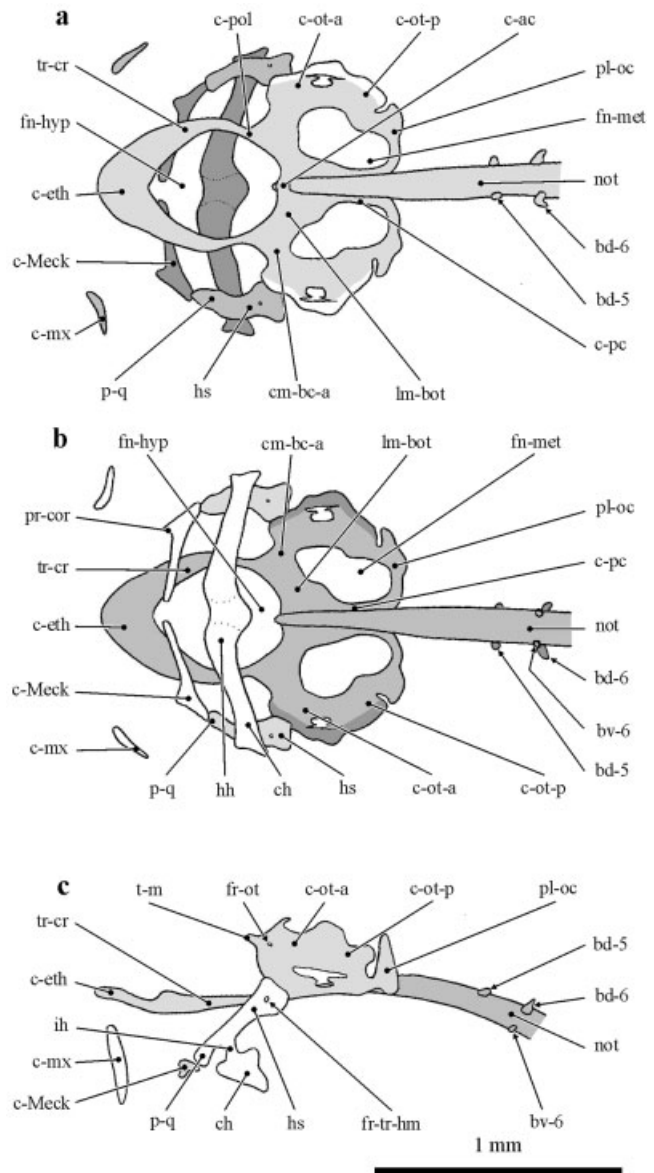

Fig. 2. *Ancistrus* cf. *triradiatus*. **a:** Section of 5.2 mm stage at the level of the notochord tip, indicating first cartilaginous structures (scale bar = 500 μm). **b:** Detail of same section, showing chondroblasts secreting first cartilage matrix (purple) (scale bar = 100 μm). **c:** Maxillary cartilage of 8.0 mm stage, showing flattened chondrocytes with little matrix between them, but surrounded by a thick layer of darker stained matrix (scale bar = 20 μm). **d:** Right lateral commissure of 8.0 mm stage. Connection to otic capsule is not visible on this section (scale bar = 100 μm). **e:** Fenestra posterior to right lateral commissure of 8.0 mm stage, at passage of truncus hyomandibularis nervus facialis (scale bar = 100 μm). **f:** Anterior end of branchial region of 8.0 mm stage (scale bar = 100 μm). **g:** Posterior myodome of 12.4 mm stage (scale bar = 200 μm). **h:** Interhyal of 6.1 mm stage (scale bar = 200 μm). bb-I, basibranchiale I; c-ac, cartilago acrochordalis; c-pol, cartilago polaris; ch, ceratohyale; chondr, young chondrocytes; cm-lat, commissura lateralis; hb-I, hypobranchiale I; hs, hyosymplecticum; ih, interhyale; lm-bot, lamina basiotica; m-r-ext, musculus rectus externus, m-r-inf, musculus rectus inferior; m-r-int, musculus rectus internus; m-r-sup, musculus rectus superior; n-V-VII, root of facial and trigeminal nerves; not, notochord; o-boc, os basioccipitale; o-para, os parasphenoideum; o-prot, os prooticum; op-c, opercular cavity; ot-cap, otic capsule; ot-ves, otic vesicle; pr-br, prootic bridge; puh, double cartilaginous nucleus of parurohyale; tr-hm-VII, truncus hyomandibularis nervus facialis. Alcian blue / alizarin red.

Fig. 3. Chondrocranium of *Ancistrus* cf. *triradiatus* (5.6 mm SL). **a:** Dorsal view. **b:** Ventral view. **c:** Lateral view. bd-5/6, basidorsal of fifth/sixth vertebra; bv-6, basiventral of sixth vertebra; c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-ot-a, cartilago oticalis anterior; c-ot-p, cartilago oticalis posterior; c-pc, cartilago parachordalis; c-pol, cartilago polaris; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; fn-hyp, fenestra hypophysea; fn-met, fenestra metotica; fr-ot, foramen ramus oticus nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-bot, lamina basiotica; not, notochord; p-q, pars quadrata of palatoquadratum; pl-oc, pila occipitalis; pr-cor, processus coronoideus; t-m, taenia marginalis; tr-cr, trabecula cranii.

metotic fenestra is slightly constricted by a lateral projection of the parachordal cartilage and a broad medial process of the posterior otic cartilage. Serial sections of the 6.1 mm SL specimen show that this broad process encloses the glossopharyngeal nerve,
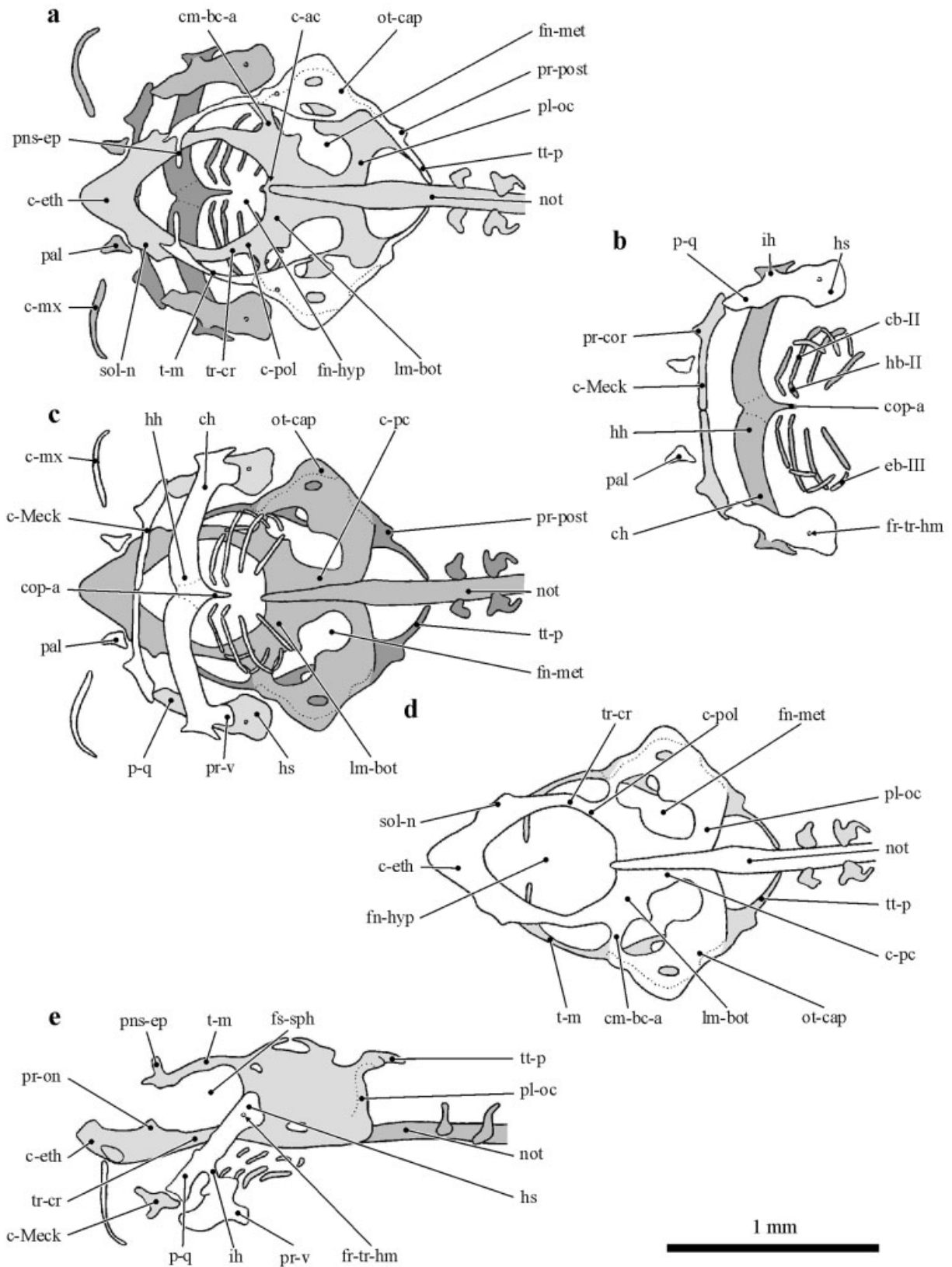
Fig. 4. Chondrocranium of *Ancistrus* cf. *triradiatus* (6.0 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Lateral view. c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; cb II, second ceratobranchiale; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cop-a, anterior copula; eb III, third epibranchiale; fn-hyp, fenestra hypophysea; fn-met, fenestra metotica; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fs-sphen, fissura sphenoidea; hb II, second hypobranchiale; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-bot, lamina basiotica; not, notochord; ot-cap, otic capsule; p-q, pars quadrata of palatoquadratum; pal, palatinum; pl-oc, pila occipitalis; pns-ep, pons epiphysialis; pr-cor, processus coronoideus; pr-on, processus orbitonasalis; pr-post, processus postoticus of otic capsule; pr-v, ventral process of ceratohyale; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

thus proving its double nature, i.e., the combined onset of the basivestibular and posterior basicapsular commissures (see next stage for details on these commissures).

The solum nasi can now be discerned as an anterior differentiation of the trabecular bars. The orbitonasal process grows upward on this solum nasi, toward the fully grown taenia marginalis. The latter branches, almost at the level of the orbitonasal process, in a medial extension, being the onset of the epiphysial bridge, and a short stub extending anteriorly. This minute stub could be called the (rudimentary) taenia marginalis "anterior," as opposed to the taenia marginalis "posterior," caudal of the epiphysial bridge. It will, however, branch near its origin in the next stage, reducing the taenia marginalis anterior almost completely. The sphenoid fissure is situated between the trabecular bar and the taenia marginalis.

The postotic process is formed at the posterior end of the posterior otic cartilage, where it borders the occipital pilae. The occipital pilae form the occipital arch, from which the tectum posterius is developing. Like the epiphysial bridge, it is not yet continuous at the midline.

Splanchnocranium. The palatine is visible. The posterior part of this cartilaginous element arises first, articulating with the solum nasi of the neurocranium. The maxillary barbel cartilage has lengthened. It consists of a row of flattened chondrocytes with little matrix between them, but surrounded by a thick layer of more darkly stained matrix (Fig. 2c). The pterygoquadrate-hyosymplectic, which articulates with the neurocranium at the level of the anterior otic cartilage, is still continuous with the interhyal and the ceratohyal-hypohyal bar, which bears a conspicuous ventral process. The pterygoquadrate-hyosymplectic now bears a rudimentary pterygoid process. Meckel's cartilages are fusing medially. The exact location of the boundary between ceratohyal and hypohyal elements cannot be made until the onset of ossification, as there is no clear hyoid artery incision in the chondrocranium of *Ancistrus* cf. *triradiatus*. The position of this incision can be used in distinguishing both elements in these early stages (Adriaens and Verraes, 1997a). The future position of the ossa hypohyale and ceratohyale (not shown) is used to distinguish both cartilage elements. Both hypohyals are still merged, and continuous with a medial bar comprising the first and second basibranchial. These elements are all fused from the beginning and will only later separate (see later stages). No other basibranchials are present in this specimen. This bar, however, proves to be longer in the serial sections of the 6.1 mm specimen, up to the level of the third branchial arch, so most probably it includes the third basibranchial and thus corresponds to the anterior copula. Ceratobranchials I–IV and hypobranchials I–II are present. Of these elements, ceratobranchials I–III

are more intensely stained with alcian blue, so probably arise first during ontogeny. Serial sections of a 6.1 mm stage suggest that corresponding cerato- and hypobranchials I–II arise as one unit. Epibranchials I–III are also present.

6.8 mm SL Stage (Fig. 5)

Neurocranium. The skull floor has now become more solidly chondrified, with a broadened solum nasi, and the onset of anterior lengthening of the ethmoid cartilage (this lengthening will go on during further ontogeny). A small precerebral process is present on the tip of this ethmoid plate. This structure starts as two separate projections (6.0 mm stage), soon fusing, but keeping two distinct tips (6.8 mm and 7.4 mm stages). This is also corroborated by serial sections of the 7.0 mm SL specimen. In the skull roof, the anterior tip of the taenia marginalis develops further, with the rudimentary epiphysial bridge still growing (although still not touching medially), and a bipartite stub at its anterior end. This stub (referred to in the previous stage as the rudimentary taenia marginalis anterior) branches into a small mediorostral sphenoseptal commissure, growing in the direction of the precerebral process, and a lateroventral spheno-ethmoidal commissure, which grows toward a dorsal projection of the skull floor, the orbitonasal process. When contact is established, a compound transverse plate, the orbitonasal lamina, is formed. A reinforcement in the corner between the spheno-ethmoidal commissure and the taenia marginalis fuses with a more caudal projection of the skull floor, forming the preorbital base, and leaving a small foramen for the ophthalmic branch of the trigeminal nerve. Both latter connections are established somewhere between the 6.8 mm and 7.4 mm SL stages. Examination of serial sections of a 7.0 mm stage reveals that the orbitonasal lamina is fully formed and the preorbital base nearly so. There is no apparent acrochordal cartilage in this stage, leaving both sides of the skull floor separated in this region.

The metotic fenestra has been divided into several small fenestrae. The two medial processes of the posterior otic cartilage (as seen in serial sections of the 6.1 mm stage) have connected to the lateral extension of the parachordal cartilage, forming the basivestibular commissure and the posterior basicapsular commissure. The posterior basicapsular fenestra, between these two commissures, accommodates the glossopharyngeal nerve (n. IX). The anterior basicapsular fenestra, between the anterior basicapsular and the basivestibular commissure, will shrink and disappear almost completely later during ontogeny. More caudally, two posterior, obliquely oriented foramina are situated between the posterior basicapsular commissure and the occipital pila. These are also remnants of the larger metotic fenestra; they are separated by a thin strut of car-
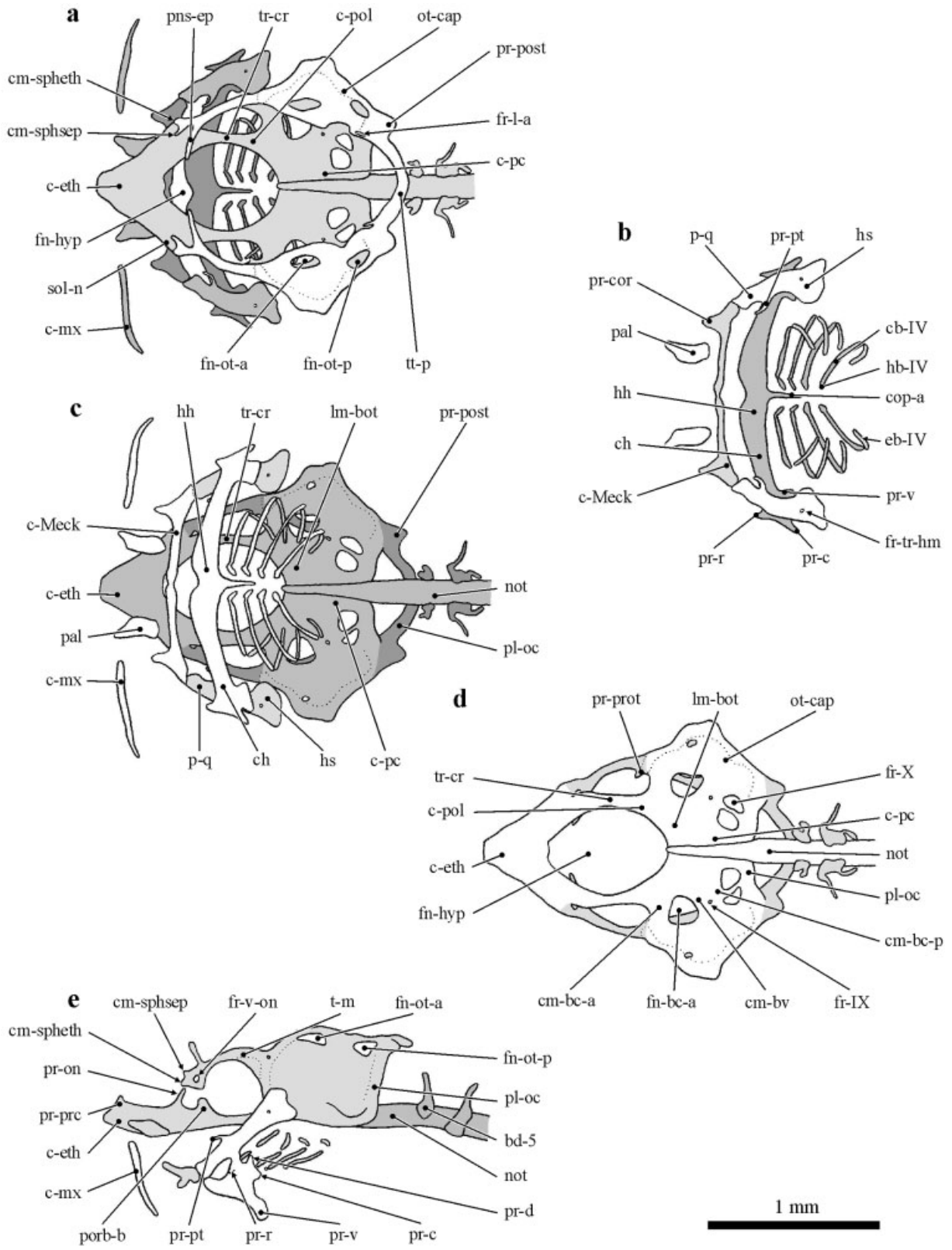
Figure 5

tilage. The medial one will soon disappear; the lateral one stays throughout ontogeny and accommodates the vagal nerve (n. X). Serial sections of a 6.1 mm stage prove that no nerve or blood vessel passes through the lateral opening in the otic capsule floor, lateral of the anterior basicapsular fenestra and anterior of the lateral semicircular septum. It seems to be closed by a membrane. Later it will form the recess for the utriculus of the inner ear. The lateral semicircular septum (dotted lines in Fig. 7) connects the floor and the roof of the otic capsule, and is surrounded by the horizontal semicircular canal.

Anteriorly, only observed at the left side, a small blastema arises from the otic capsule (Fig. 5d). This is the prootic process, described by Swinnerton (1902), Bertmar (1959), and Daget (1964) as the onset of the lateral commissure (see Discussion for details). Dorsally, the otic capsule has two large fenestrae, not observed in other siluriform chondrocrania. One is situated more or less between the anterior and posterior otic cartilages (which now can no longer be distinguished), the other in the second half of the posterior otic cartilage, close to the postotic process. The names anterior and posterior otic fenestra are proposed for these structures. The tectum posterius is complete, both parts having fused medially, and closes the foramen magnum. At the dorsomedial margin of the otic capsules, anterior to the tectum posterius, small extensions can be seen that might correspond to a rudimentary tectum synoticum (see Discussion). As proved by later stages, however, they do not grow significantly.

Splanchnocranium. The pterygoid process, only a short projection in the 6.0 mm stage, now further

develops on the anterior edge of the pterygoquadrate-hyosymplectic complex, which remains bar-shaped on lateral view throughout development. The ceratohyal part of the hyoid bar now bears four distinct processes near its lateral end: a small one oriented rostrally; one oriented dorsally, behind the interhyal connection; one oriented caudally; and a very large one oriented ventrally, pointing in the direction where the branchiostegal rays will develop (and articulate).

Hypobranchials III–IV and epibranchial IV are added to the branchial basket. All hypobranchials are continuous with the corresponding ceratohyals. Basibranchials I to III, composing the first copula, are present and confluent with the hyoid bar.

7.4 mm SL Stage (Fig. 6)

Neurocranium. In this stage all major components of the cartilaginous skull have formed. Remarkably, and opposed to the situation in previous stages, the acrochordal cartilage is well developed in this stage, also covering the rostral and ventral sides of the tip of the notochord.

The sphenoid fenestra is now well demarcated. The epiphysial bridge is completed, so now prepineal and postpineal fontanelles can be discerned. The former is still continuous with the foramen filae olfactoriae, as the sphenoseptal commissures and the forked precerebral process still do not touch. The orbitonasal lamina grows laterally, forming a prominent transverse sheet. Ventral of the foramen of a branch of the orbitonasal vein, the larger orbitonasal foramen (for the orbitonasal artery) is now separated from the foramen filae olfactoriae. In the orbitonasal lamina a rostrocaudal foramen is now clearly seen, accommodating the superficial ophthalmic branch of the trigeminal nerve.

The prootic process of the otic capsule has formed the lateral commissure on the right side, but is still growing on the left side (see also Fig. 2d). It grows from the rostroventral edge of the anterior otic cartilage to the rostral end of the polar cartilage, thus dividing the sphenoid fenestra into a large anterior fenestra and a small posterior fenestra (Fig. 2e). The taenia marginalis develops a postorbital process, including the foramen for the otic branch of the facial nerve. In this and in the next stages the asymmetrical rudiments of the tectum synoticum sometimes demarcate a small foramen where the lateral accessory branch of the facial nerve passes.

Caudal reinforcement of the skull starts with fusion of the tectum posterius and the paired cartilaginous precursors of the neural arch of the fifth and/or sixth vertebra (see Discussion).

Splanchnocranium. Hypo- and ceratobranchials I–II become separated; III–IV will remain continuous until ossification. A fifth pair of ceratobranchials is present (this is the only element of the fifth branchial arch to appear). As for the basibranchials, two cartilaginous structures are present:

Fig. 5. Chondrocranium of *Ancistrus* cf. *triradiatus* (6.8 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Lateral view. bd-5, basidorsal of fifth vertebra; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; cb IV, fourth ceratobranchiale; ch, ceratohyale; cm-bc-a, commissura basicapsularis anterior; cm-bc-p, commissura basicapsularis posterior; cm-bv, commissura basivestibularis; cm-spheth, commissura spheno-ethmoidalis; cm-sphsep, commissura sphenoseptalis; cop-a, anterior copula; eb IV, fourth epibranchiale; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophysea; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fr-l-a, foramen ramus lateralis accessorius nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-v-on, foramen vena orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; hb IV, fourth hypobranchiale; hh, hypohyale; hs, hyosymplecticum; lm-bot, lamina basiotica; not, notochord; 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-c, caudal process of ceratohyale; pr-cor, processus coronoideus; pr-d, dorsal process of ceratohyale; pr-on, processus orbitonasalis; pr-post, processus postoticus of otic capsule; pr-prc, processus praecerebralis; pr-prot, processus prooticus; pr-pt, processus pterygoideus; pr-r, rostral process of ceratohyale; pr-v, ventral process of ceratohyale; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.
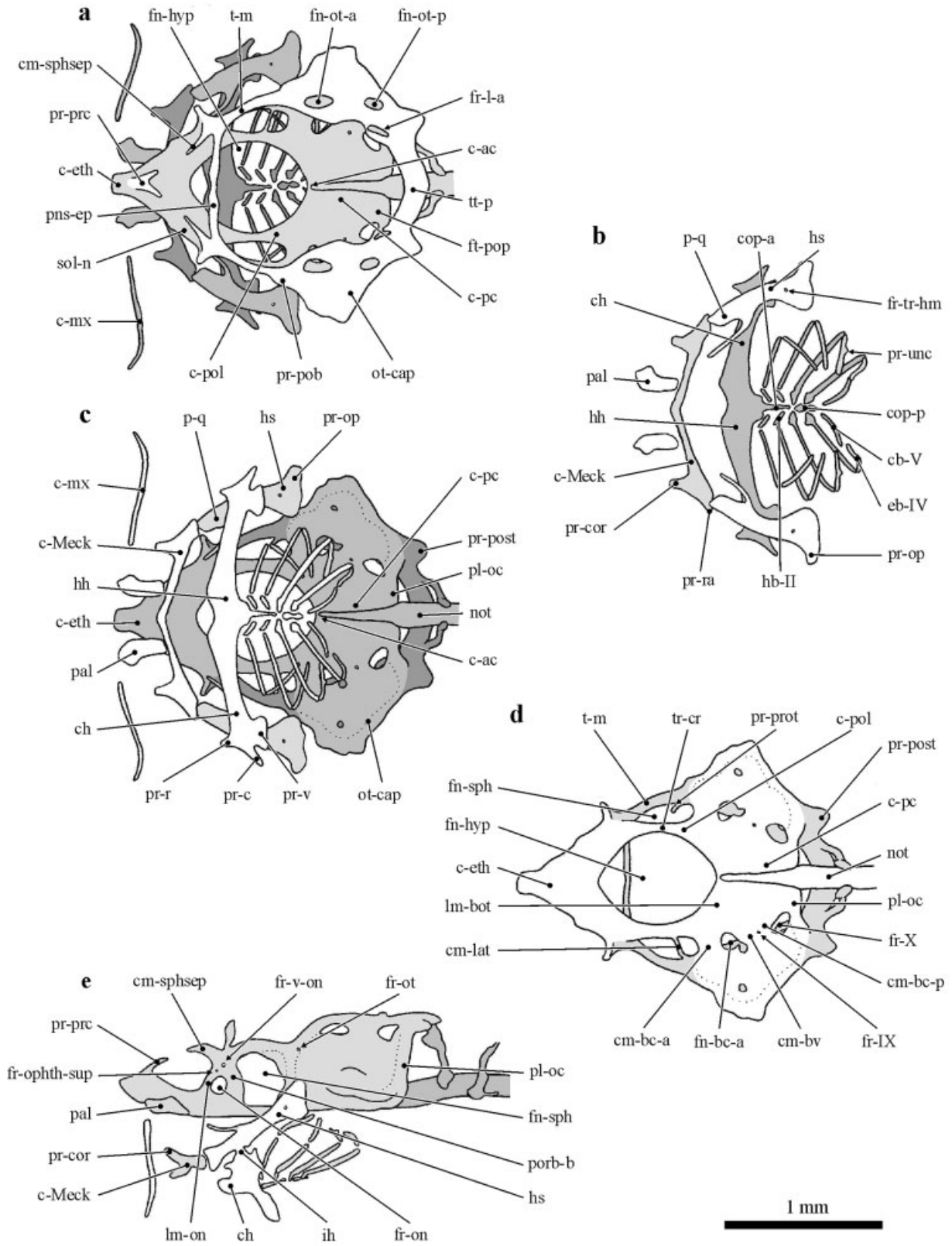
Figure 6

the first one consists of basibranchials I–III, and is still weakly connected to the hyoid bar; the second one consists of basibranchials IV–V. These two compound elements correspond to the anterior and posterior copula, respectively. A small uncinate process develops on the third epibranchial.

8.0 mm SL Stage (Fig. 7)

Neurocranium. The notochord in the cranium has now shrunken to half its postcranial diameter. The prepineal fontanelle and the foramina filae olfactoriae are now completely separated by the fusion of the sphenoseptal commissures and the (double) precerebral process. A transverse reinforcement starts to grow between both tips of the precerebral process, forming a precerebral lamina. The acrochordal cartilage is seen only underneath the rostral tip of the notochord. The lateral commissure is complete on both sides. Slightly more caudally, another small blastema appears on the rostroventral edge of the anterior otic cartilage. It is also visible in the following stages, but not at both sides. It never connects to the skull floor. The anterior part of the skull is lengthening more and the ethmoid plate develops a ventral protuberance at the rostral tip. The anterior basicapsular fenestra shrinks and splits off a small caudal fenestra, which will disappear later during ontogeny.

Fig. 6. Chondrocranium of *Ancistrus* cf. *triradiatus* (7.4 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Lateral view. c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; cb, ceratobranchiale; 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 fourth epibranchiale; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophysea; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fn-sph, fenestra sphenoidea; fr-l-a, foramen ramus lateralis accessorius nervus facialis; fr-on, foramen orbitonasalis; fr-ophth-sup, foramen ramus ophthalmicus superficialis nervus trigeminus; fr-ot, foramen ramus oticus nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-v-on, foramen vena orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; ft-pop, fontanella postpinealis; hb II, second hypobranchiale; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; lm-bot, lamina basiotica; lm-on, lamina orbitonasalis; not, notochord; 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-c, caudal process of ceratohyale; pr-cor, processus coronoideus; pr-op, processus opercularis of hyosymplecticum; pr-pob, processus postorbitalis of taenia marginalis; pr-post, processus postoticus of otic capsule; pr-prc, processus praecerebralis; pr-prot, processus prooticus; pr-r, rostral process of ceratohyale; pr-ra, processus retroarticularis; pr-unc, processus uncinatus of third epibranchiale; pr-v, ventral process of ceratohyale; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

The tectum posterius grows stronger, broadening in an anterior but mostly a posterior direction, so that the dorsal connection between both otic capsules is reinforced.

Splanchnocranium. As the snout region of the neurocranium lengthens the pterygoquadrate-hyosymplectic becomes more elongate as well. The hyosymplectic bears a conspicuous opercular process. The retroarticular process of Meckel's cartilage is very small, only visible as a small stub caudolateral of the articulation with the quadrate. The thin connection of articular cartilage between Meckel's cartilage and the quadrate is no longer seen in serial sections of the 8.0 mm SL specimen. The center of the hyoid bar is only slightly stained by alcian blue, indicating that the hypohyals are becoming separated.

The anterior copula of the branchial basket is shrinking, as basibranchial I is becoming reduced and basibranchial III becomes separated. Two infrapharyngobranchials have appeared; their location confirms that they are infrapharyngobranchials III and IV. Just behind the medial ends of the hypohyals a double, dumbbell-shaped cartilaginous nucleus is present, which will later become part of the bony parurohyal. In serial sections of the 8.0 mm stage, it is seen that it is continuous with the first basibranchial, which is not well seen in the stained specimen (and further reduces in the next stages) (Fig. 2f).

8.9 mm SL Stage (Fig. 8)

Neurocranium. No major transformations occur in the cartilaginous neurocranium during this stage. The rostrocaudal elongation of the snout region proceeds, as does the reinforcement of the occipital region: the tectum posterius becomes more and more extended posteriorly. The prepineal fontanelle becomes smaller, as the precerebral lamina extends backwards.

The outline of the hypophyseal fenestra changes: a median fissure appears between the trabecular bar and the polar cartilage, accommodating the internal carotid artery. The appearance of this fissure seems to be the result of allometric growth of the trabecular bars and the polar cartilages: they simply broaden everywhere except at the site of the fissure.

The lateral end of the orbitonasal lamina grows slightly rostrally, around the nasal sac, while the articular facet of the solum nasi for the palatine becomes ever more prominent.

Serial sections of the 8.0, 10.2, and 12.4 mm stages allow a reconstruction of the main nerve paths in the sphenoid region (Fig. 9). The olfactory nerve exits via its separate foramen. The sphenoid fenestra is penetrated by the optic, oculomotor, trochlear, and abducens nerves, as well as by the main part of the trigeminal and facial nerves. The hyomandibular trunk and opercular branch of the
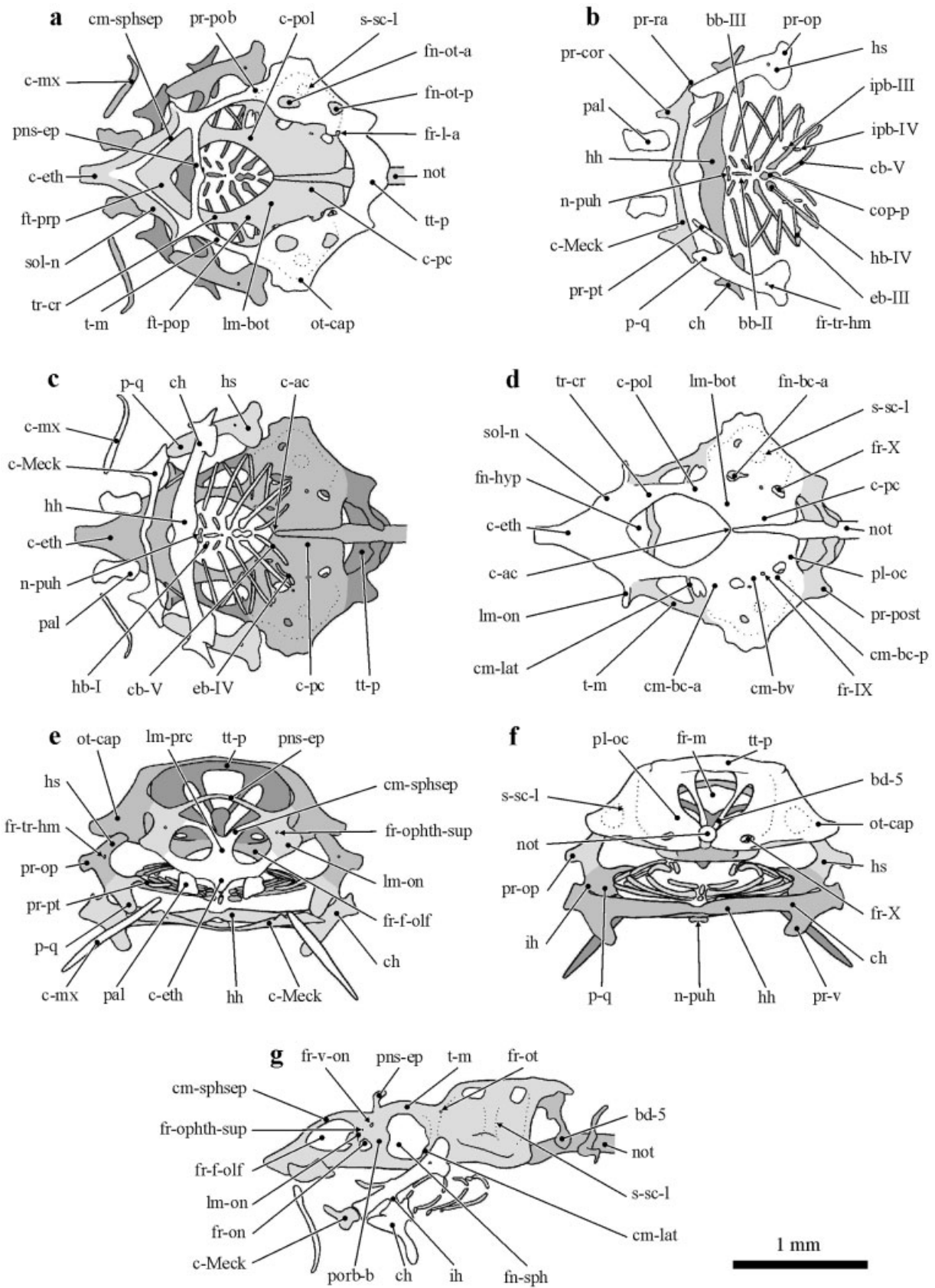
Figure 7

facial nerve exit posterior to the lateral commissure (as do a vein and an artery, probably the orbital artery [de Beer, 1927]), and the otic branch rises and leaves the skull via the postpineal fontanelle, close to the taenia marginalis. One division of the otic branch pierces this taenia at the level of the postorbital process. Two branches of the trigeminal nerve pass through the orbitonasal lamina; one part (unclear homology) passes through a groove at the ventral side of the lamina (but goes through a ventral foramen in the right side of the 10.2 mm stage); the other (superficial ophthalmic branch) always pierces the dorsal part of the lamina. Two other foramina in this region are not penetrated by any nerves: the orbitonasal foramen accommodates the orbitonasal artery, and a more dorsal foramen accommodates a branch of the orbitonasal vein.

Splanchnocranium. The medial connection between the hypohyal parts of the hyoid bar is now completely invisible in the stained specimen: the bar is no longer continuous. In serial sections of a 10.2 mm specimen, however, it is still visible as a frail and thin rostral sheet. The connection between Meckel's cartilages has disappeared. Their coronoid processes, however, are becoming more substantial. The first basibranchial seems to have been reduced completely.

Fig. 7. Chondrocranium of *Ancistrus* cf. *triradiatus* (8.0 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Rostral view. **f:** Caudal view. **g:** Lateral view. bb II/III, second/third basibranchiale; bd-5, basidorsal of fifth vertebra; c-ac, cartilago acrochordalis; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; cb V, fifth ceratobranchiale; 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 III/IV, third/fourth epibranchiale; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophysea; fn-ot-a, fenestra otica anterior; fn-ot-p, fenestra otica posterior; fn-sph, fenestra sphenoidea; fr-f-olf, foramen fila olfactoria; fr-l-a, foramen ramus lateralis accessorius nervus facialis; fr-m, foramen magnum; fr-on, foramen orbitonasalis; fr-ophth-sup, foramen ramus ophthalmicus superficialis nervus trigeminus; fr-ot, foramen ramus oticus nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-v-on, foramen vena orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; ft-pop, fontanella postpinealis; ft-prp, fontanella praepinealis; hb I/IV, first/fourth hypobranchiale; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; ipb III/IV, third/fourth infrapharyngobranchiale; lm-bot, lamina basiotica; lm-on, lamina orbitonasalis; lm-prc, lamina praecerebralis; n-puh, chondroid nucleus of parurohyale; not, notochord; 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-cor, processus coronoideus; pr-op, processus opercularis of hyosymplecticum; pr-pob, processus postorbitalis of taenia marginalis; pr-post, processus postoticus of otic capsule; pr-pt, processus pterygoideus; pr-ra, processus retroarticularis; pr-v, ventral process of ceratohyale; s-sc-l, septum semicirculare laterale; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

9.9 mm SL Stage (Fig. 10)

Neurocranium. There is little shape difference with the previous stage. The tip of the notochord becomes squeezed between the parachordal cartilages. The anterior basicapsular fenestra has disappeared. Due to the lengthening of the skull and the fully grown tectum posterius, the ratio of the chondrocranial skull length to skull height is now 4, compared to 2.9 in the 6.0 mm stage. In general, the chondrocranium is now slowly being replaced by the osteocranium.

Splanchnocranium. Just below the anteroventral end of the palatine a small submaxillary cartilage has appeared. This is also visible in serial sections of the 8.0 mm specimen. The cartilaginous nucleus of the parurohyal is no longer stained by alcian blue, but can still be seen on sections of the 10.2 and 12.4 mm stages. The second copula and the central shafts of the epi- and ceratobranchials are also no longer stained.

DISCUSSION

Compared to other siluriforms in which the chondrocranium has been studied and of which data of the prehatching period and of the first appearance of the chondrocranium are available, the cartilaginous cephalic skeleton of *Ancistrus* cf. *triradiatus* is already remarkably well developed at hatching. A comparable state of development has been observed in the non-siluriform three-spined stickleback *Gasterosteus aculeatus* and the brown trout *Salmo trutta fario* (Swinnerton, 1902; de Beer, 1927). But even compared to these two species, *A.* cf. *tririadiatus* has a more developed chondrocranium at the moment of hatching, even though it has a much shorter prehatching period. Obviously there is a tendency that species hatching very early lack chondrocranium elements at hatching. In *Heterobranchus longifilis*, *Clarias gariepinus*, and *Chrysichthys auratus*, African catfishes, no cartilaginous structures are present at hatching, which occurs about 1 day after fertilization (Vandewalle et al., 1997, 1999; Adriaens et al., 1997a). It would be interesting to elaborate on the state of development of the cranium at key moments (hatching, complete resorption of yolk sac) in different species, but it is difficult to obtain the needed amount of data for more species. As in most siluriforms for which data are available, in *A.* cf. *triradiatus* the first elements of the neurocranium and the splanchnocranium appear more or less simultaneously.

Neurocranium

Skull floor. The first structures to arise in the chondrocranial skull of *Ancistrus* cf. *triradiatus* are the parachordal cartilages and the trabecular bars. As in other siluriforms, the skull is platybasic, in contrast to the derived tropibasic skull type in most
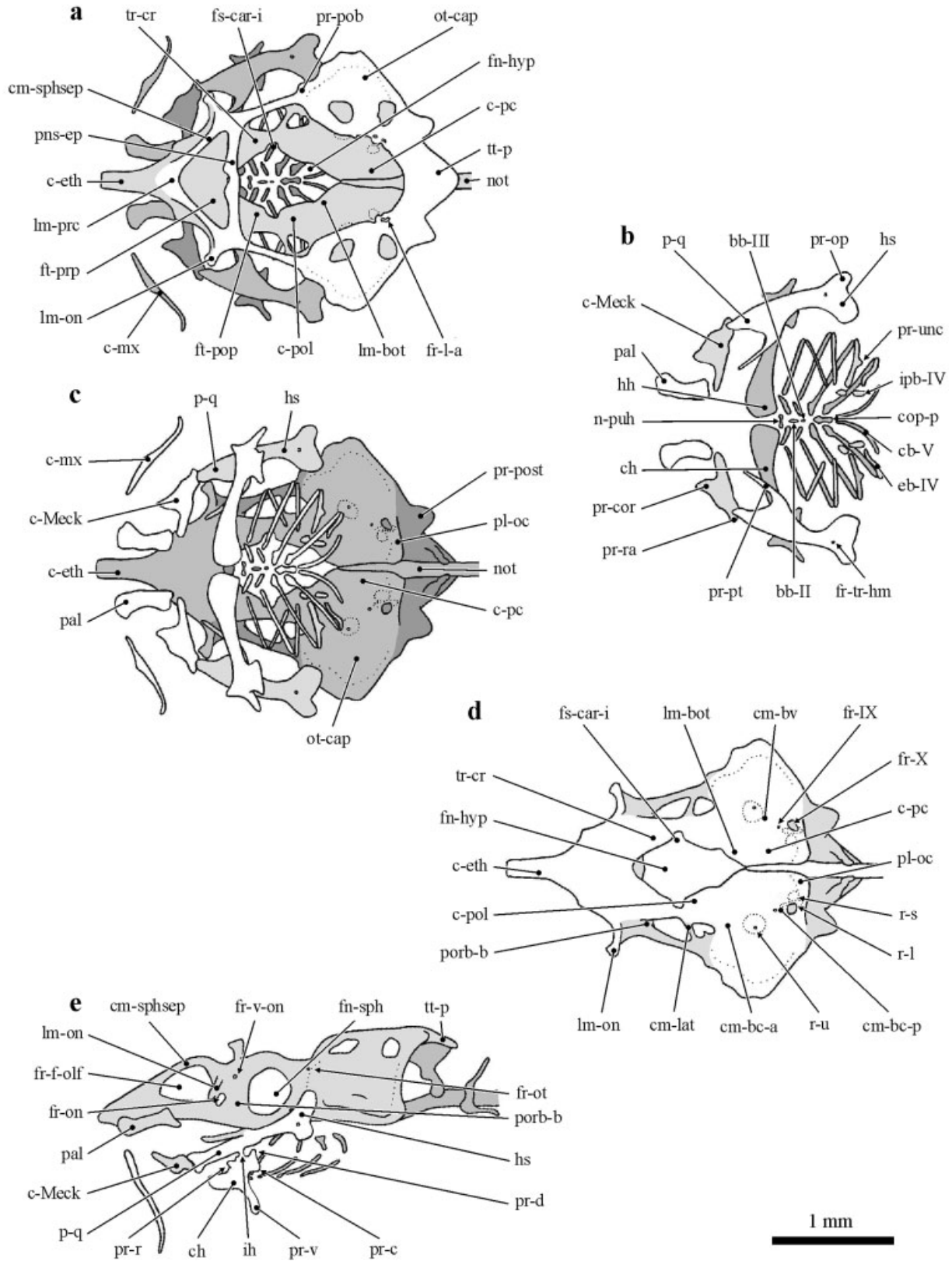
Figure 8

other teleosts (variation in the degree of trabecular fusion does exist) (Swinnerton, 1902; Bhargava, 1958; Verraes, 1974a; Wagemans et al., 1998). In some siluriforms, the ethmoid plate may be broad and can consequently be incorrectly considered a trabecula communis (Srinivasachar, 1958a). The platybasic skull type has been linked to the reduced eye size that is typical of catfishes (Verraes, 1974b; Adriaens and Verraes, 1997b).

In all examined siluriforms, including *Ancistrus* cf. *triradiatus*, each trabecular bar and the collateral parachordal cartilage arise as one part. In teleosts, this is not a general rule (Swinnerton, 1902; de Beer, 1927; Vandewalle et al., 1992).

The notochord becomes more or less surrounded by the basal plate, which develops from the fusion of the parachordal cartilages. In silurifoms, this plate usually starts as a small acrochordal cartilage, covering the dorsal, ventral, and/or rostral side of the tip of the notochord to various extents.

In *Ancistrus* cf. *triradiatus*, the acrochordal cartilage, which herein can be considered the most rostral part of the basal plate, is variably present in the various stages examined in this study. The presence of cartilaginous tissue dorsal, ventral, or rostral of the tip of the notochord was determined in the cleared and stained specimens: 5.6 mm: dorsal; 6.0 mm: dorsal; 6.8 mm: nothing; 7.4 mm: dorsal, ven-tral and rostral; 8.0 mm: dorsal; 8.9 mm: dorsal and rostral; 9.9 mm: dorsal and rostral. The absence of cartilage above or below the notochord might be due to insufficient alcian blue staining; the cartilage there is usually only one or two cell layers thick. In the specimens that underwent serial sectioning the presence of this cartilage also proved to be highly variable, but when present, was always quite visible: 5.2 mm: nothing; 6.1 mm: dorsal and almost ventral; 7.0 mm: dorsal and ventral; 8.0 mm: dorsal; 10.2 mm: dorsal and rostral, 12.4: dorsal and rostral.

In other siluriforms, the acrochordal cartilage has been reported to consist of a hypochordal or an epichordal bridge, or a combination, also covering the rostral tip of the notochord (Kindred, 1919; Bamford, 1948; Srinivasachar, 1957a,b; Adriaens and Verraes, 1997a). The notochord actually protrudes into the hypophyseal fenestra only in the earliest stages of *Ancistrus* cf. *triradiatus*, a situation also seen in *Ariopsis felis, Arius jella*, and *Callichthys callichthys* (Bamford, 1948; Srinivasachar, 1958a; Hoedeman, 1960), but not in *Clarias gariepinus* (Adriaens and Verraes, 1997a). Two hypotheses could explain the rostral position of the acrochordal cartilage in the later stages: the tip of the notochord degenerates early (as stated by Goodrich, 1958), or the acrochordal cartilage extends rostrally during development. In the sea trout *Salmo trutta trutta*, de Beer (1937) saw the formation of the prootic bridge out of a membrane situated rostral and dorsal of the notochord tip, thus at the position of the dorsally situated part of the acrochordal cartilage, or epichordal bridge, in *A.* cf. *triradiatus*. Here the onto-genetic series suggests that the basiotic laminae of both sides add to the acrochordal cartilage, thus narrowing the end of the hypophyseal fenestra and giving rise to the epichordal or prootic bridge, as seen in the 9.9 stage (Fig. 10).

The trabecular bars in teleosts usually undergo transformations for the passage of the paired internal carotid artery, which is situated caudally in the hypophyseal fenestra, rostromedial of the polar cartilage. In several siluriforms the artery moves to a more lateral position and cartilage resorption affects the inner side of the bars so as to accommodate it (e.g., *Clarias gariepinus* [Adriaens and Verraes, 1997a]). In *Chrysichthys auratus* and the non-siluriform *Barbus barbus*, the bars even reduce completely at the level of this artery (Vandewalle et al., 1992, 1999); in *Scophthalmus maximus* the trabecula communis goes through the same complete reduction (Wagemans et al., 1998). No evidence of cartilage reduction is present in *Ancistrus* cf. *triradiatus*. Although the outline of the hypophyseal fenestra does change, and a median fissure appears, the appearance of this fissure is the result of allometric growth of the trabecular bars: the bars just broaden everywhere except there, and the hypophyseal fenestra becomes narrower. No cartilage resorption is seen in the serial sections. In the brown

Fig. 8. Chondrocranium of *Ancistrus* cf. *triradiatus* (8.9 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Lateral view. bb II/III, second/third basibranchiale; c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; cb V, fifth ceratobranchiale; 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-p, posterior copula; eb IV, fourth epibranchiale; fn-bc-a, fenestra basicapsularis anterior; fn-hyp, fenestra hypophysea; fn-sph, fenestra sphenoidea; fr-f-olf, foramen fila olfactoria; fr-l-a, foramen ramus lateralis accessorius nervus facialis; fr-on, foramen orbitonasalis; fr-ot, foramen ramus oticus nervus facialis; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-v-on, foramen vena orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; fs-car-i, fissura arteria carotis interna; ft-pop, fontanella postpinealis; ft-prp, fontanella praepinealis; hb III, third hypobranchiale; hh, hypohyale; hs, hyosymplecticum; ih, interhyale; ipb IV, fourth infrapharyngobranchiale; lm-bot, lamina basiotica; lm-on, lamina orbitonasalis; lm-prc, lamina praecerebralis; n-puh, chondroid nucleus of parurohyale; not, notochord; 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-c, caudal process of ceratohyale; pr-cor, processus coronoideus; pr-d, dorsal process of ceratohyale; pr-op, processus opercularis of hyosymplecticum; pr-pob, processus postorbitalis of taenia marginalis; pr-post, processus postoticus of otic capsule; pr-pt, processus pterygoideus; pr-r, rostral process of ceratohyale; pr-ra, processus retroarticularis; pr-unc, processus uncinatus of third epibranchiale; pr-v, ventral process of ceratohyale; r-l, recessus lagenae; r-s, recessus sacculi; r-u, recessus utriculi; tr-cr, trabecula cranii; tt-p, tectum posterius.
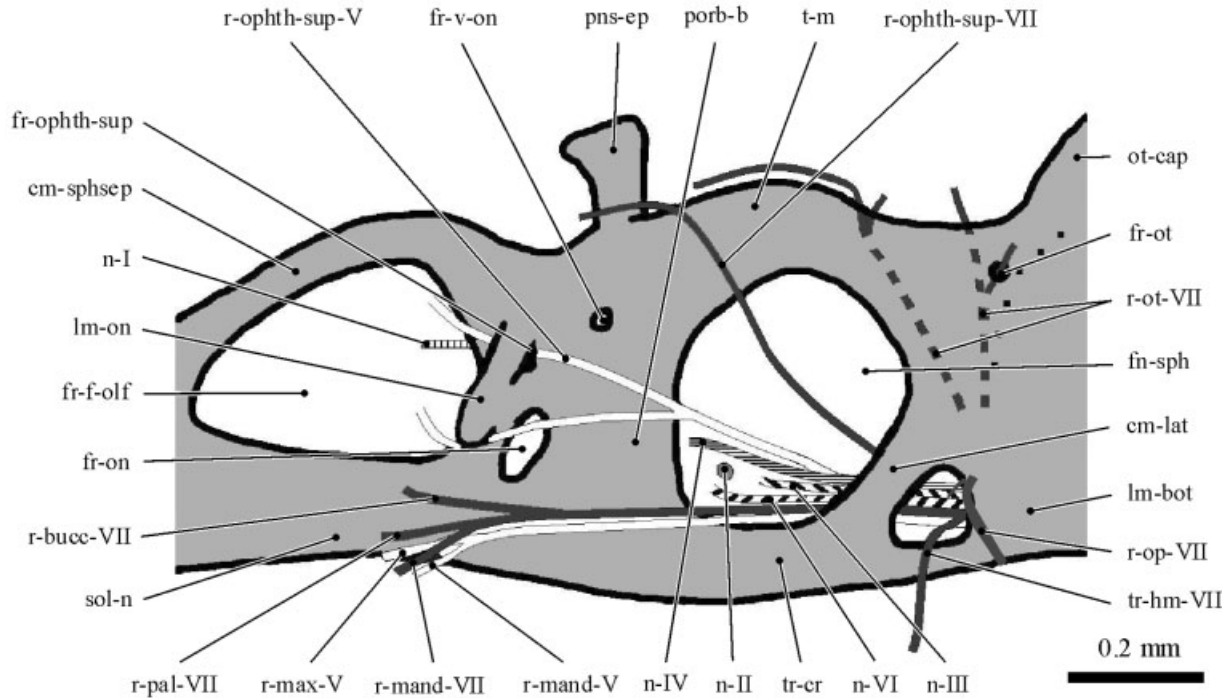
Fig. 9. Lateral view of sphenoid region of the neurocranium (8.9 mm SL), with schematic indication of main nerves. cm-lat, commissura lateralis; cm-sphsep, commissura sphenoseptalis; fn-sph, fenestra sphenoidea; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-ophth-sup, foramen ramus ophthalmicus superficialis nervus trigeminus; fr-ot, foramen ramus oticus nervus facialis; fr-v-on, foramen vena orbitonasalis; lm-bot, lamina basiotica; lm-on, lamina orbitonasalis; n-I, nervus olfactorius; n-II, nervus opticus; n-III, nervus oculomotorius; n-IV, nervus trochlearis; n-VI, nervus abducens; ot-cap, otic capsule; porb-b, preorbital base; pns-ep, pons epiphysialis; r-bucc-VII, ramus buccalis nervus facialis; r-mand-V, ramus mandibularis nervus trigeminus; r-mand-VII, ramus mandibularis nervus facialis; r-max-V, ramus maxillaris nervus trigeminus; r-op-VII, ramus opercularis nervus facialis; r-ophth-sup-V, ramus opthalmicus superficialis nervus trigeminus; r-ophth-sup-VII, ramus opthalmicus superficialis nervus facialis; r-ot-VII, ramus oticus nervus facialis; r-pal-VII, ramus palatinus nervus facialis; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tr-hm-VII, truncus hyomandibularis nervus facialis.

bullhead *Ameiurus nebulosus* and *Ariopsis felis*, the bars seem to become narrower. Whether they completely reduce is not clear (Kindred, 1919; Bamford, 1948). Srinivasachar (1957b) reported the artery in a small foramen in the trabecular bar in the gangetic ailia *Ailia coila*. Remarkably, in *Hoplosternum littorale* and *Callichthys callichthys* a constriction of the hypophyseal fenestra is present, anterior of where the trabecular fissure would be expected (Ballantyne, 1930; Hoedeman, 1960). No information was given, however, on the position of the internal carotid artery.

At the level of the nasal sacs in siluriforms, each trabecular bar often forms a broad solum nasi. However, in *Ancistrus* cf. *triradiatus* it fails to grow significantly after the 6.8 mm stage, leaving the nasal sacs without a real floor, as is also the case in *Arius jella* and *Plotosus canius* (Srinivasachar, 1958a). Srinivasachar also noticed that there is considerable variation in both the ventral and lateral support of the nasal sacs (the latter due to a variably developed rostral extension of the orbitonasal lamina, almost absent in *A.* cf. *triradiatus*).

The ethmoid plate is an unpaired, horizontal plate originating from, and uniting the tips of the trabec-

ular bars. Swinnerton (1902) distinguished two separate primordia of the ethmoid plate at the tip of each young trabecular bar in the non-siluriform *Gasterosteus aculeatus*. In *Ancistrus* cf. *triradiatus* it is V-shaped anteriorly; more posteriorly, it is flat, as in most catfishes. In *Ameiurus nebulosus*, much of it is also V-shaped (Kindred, 1919). The ethmoid plate of *A.* cf. *triradiatus* is rather narrow, with a long, rostral extension. This extension is unique in catfish chondrocrania described thus far, and is related to the specialized jaws: the upper jaws of larval and adult Loricariidae are situated well in front of the lower jaws, the latter being turned backwards. Hence, the supporting structures of the upper jaws are relatively elongated.

There are no ethmoid cornua (pre-ethmoid cornua of Adriaens and Verraes [1997a]) at both sides of the tip. There are, though, two more caudal processes at the rostral end of the solum nasi that might be homologous to the ethmoid cornua of other siluriforms, although the vicinity of the articular facet for the palatine contradicts this hypothesis.

Skull roof. A major component of the skull roof in *Ancistrus* cf. *triradiatus* is the taenia marginalis (alisphenoid cartilage of Kindred [1919]; anterior

process or supraorbital bar of Ballantyne [1930]; orbital cartilage of Srinivasachar [1957a,b, 1958a], and Hoedeman [1960]). As is a generality in siluriforms, it originates from the anterior end of the otic capsule, and not as a separate element, as can be observed in many other teleosts (de Beer, 1927; Adriaens and Verraes, 1997a).

The absence of a real taenia marginalis anterior, in front of the epiphysial bridge, as observed in *Ancistrus* cf. *triradiatus*, also conforms to a trend in siluriforms (a short taenia marginalis anterior persists in *Arius jella* and *Plotosus canius*, which both have fairly long and narrow chondrocrania [Srinivasachar, 1958a]). It is present in many other teleosts (e.g., *Hepsetus odoe* [Characiformes; Bertmar, 1959]). Also as is typical for siluriforms (Srinivasachar, 1957a), the taenia marginalis posterior (part behind the bridge) does not become discontinuous.

A well-developed taenia tecti medialis posterior is not present in siluriform chondrocrania. In *Ancistrus* cf. *triradiatus* the shape of the epiphysial bridge at the midline varies, and in the 8.0 mm stage a small posterior curvature may be seen. This has also been detected in *Rita* sp. and *Clarias gariepinus* (Srinivasachar, 1957a; Adriaens and Verraes, 1997a), but in these catfishes it is a small rudiment compared to the situation in various non-siluriform skulls (an extreme example is *Heterotis niloticus*, with four separate fontanelles [Daget and d'Aubenton, 1957]).

The posterior part of the skull roof in *Ancistrus* cf. *triradiatus* consists of no more than a tectum posterius originating from the occipital pilae, which rise from the rear part of the parachordal cartilages. The closure of this bridge-like structure around the time of hatching is the first dorsal fortification of the cartilaginous skull and corresponds to the formation of the foramen magnum. A tectum synoticum, formed by a fusion of the posterior otic cartilages, is absent in *A.* cf. *triradiatus*, as in *Callichthys callichthys* (Hoedeman, 1960) and *Clarias gariepinus* (Adriaens and Verraes, 1997a). Kindred (1919) and Srinivasachar (1957a,b, 1958a) mention a "practically reduced" tectum synoticum, indistinguishably fused with the tectum posterius. They provide no data from early embryonic stages, which could help distinguish the origin of both parts. The occipital pilae are those parts situated behind the vagal nerve foramen in the skull floor, but more dorsally the difference is more difficult to see when no early stages are available. In *A.* cf. *triradiatus*, the posterior otic fenestra is situated in the skull roof, anterior to the occipital pila. The small median outgrowths of the otic capsule noticed in most stages described herein (after hatching) may, however, correspond to rudiments of the tectum synoticum. Similar projections were noticed by Bamford (1948) in *Ariopsis felis*, who also considered them to represent this tectum synoticum. There, a longitudinal groove is present at each side along the posterior end of the otic capsule, accommodating the lateral accessory branch of the facial nerve. This branch goes from the ganglionic mass of the facial nerve to the dorsal body musculature, exiting the skull before the tectum posterius, and lying on top of the postotic process. In various stages of *A.* cf. *triradiatus* this nerve penetrates the rudimentary tectum synoticum, or passes through a small slit (e.g., Fig. 5a).

The fusion of the tectum posterius with elements of the first vertebrae in ostariophysans, as well as the ontogeny of the Weberian apparatus, is still a problematic topic, although many aspects have been resolved (Fink and Fink, 1981; Radermaker et al., 1989; Coburn and Futey, 1996). The ontogeny of the Weberian apparatus and the complex vertebrae, however, will not be discussed here. Among catfishes this fusion seems variable, or, at least, difficult to interpret: Kindred (1919) noticed a close contact between the tectum posterius and the third neural arch in *Ameiurus nebulosus*; Bamford (1948) mentioned the role of the third and fourth supradorsals of either side fusing into one mass of cartilage, including the third radial, in *Arius jella*. In *Ancistrus* cf. *triradiatus*, the anteriormost basidorsals seem to fuse with the corresponding supradorsals (Fig. 6e). These are not seen as separate cartilages in early stages. The next basidorsal and basiventral correspond to the first vertebra developing (large) ribs (pers. obs.), which Regan (1911) and later authors named the sixth vertebra. This suggests that the anteriormost basidorsals might be part of the fifth vertebra.

Skull wall. The skull wall in the ethmoid and orbital regions in *Ancistrus* cf. *triradiatus*, as in other teleosts, consists of vertical commissures connecting the ethmoid plate and trabecular bars with the taeniae marginales. The origin of these commissures can be single (growing from one of the above structures) or double (a dorsal and a ventral part growing toward each other). The anteriormost of these commissures has two possible points of origin: in *Heteropneustes longifilis* a broad transverse process, the precerebral lamina, rises from the anterior edge of the ethmoid cartilage, forks, and grows toward the anterior ends of both taeniae (Vandewalle et al., 1997). In *Clarias gariepinus*, most of it originates from the taeniae, where a sphenoseptal commissure emerges rostrally (Adriaens and Verraes, 1997a), and connects with the small precerebral lamina. The result looks much the same in both cases, and the broad lamina seems to be correlated to the broad ethmoid plate (as in *Callichthys callichthys* also [Hoedeman, 1960]). In *A.* cf. *triradiatus*, both points of origin contribute equally. Moreover, its ethmoid cartilage is narrow, and the precerebral process does not form a real lamina, but forks from the start (6.0 mm stage; Fig. 6). Later (10.0 mm stage), an oblique sheet (also called the precerebral lamina) fills the anterior end of what has become the prepineal fontanelle, as in the silonid catfish *Silonia*
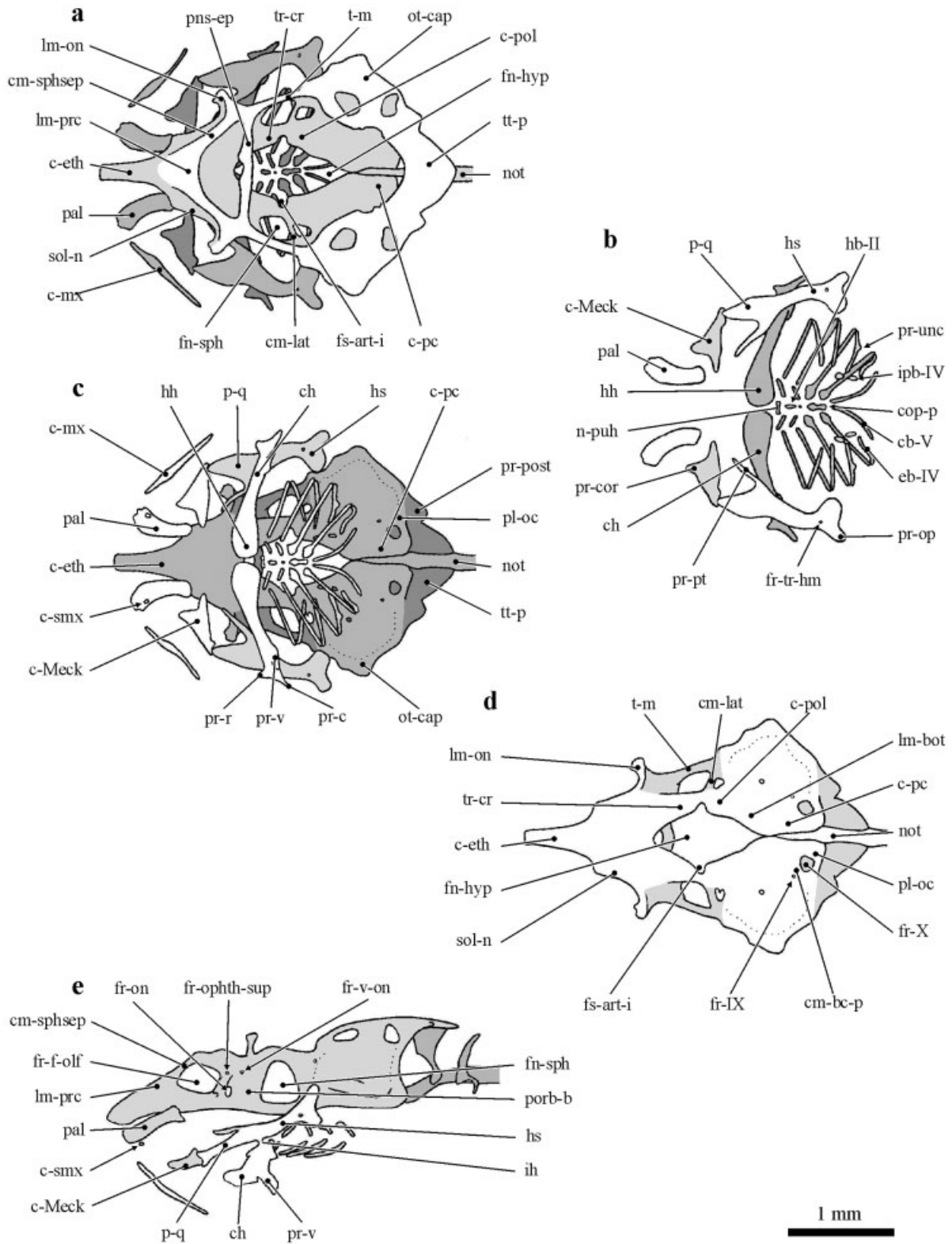
Figure 10

silondia, the yellowtail catfish *Pangasius pangasius* and *Rita* sp., and in the striped dwarf catfish *Mystus vittatus*, where it has become so large that it has been called the tectum or the tegmen cranii (Srinivasachar, 1957a,b). In the latter species, and in *Ailia coila* and *Arius jella*, a posterior mediosagittal

extension of the precerebral process, the internasal septum, separates (the anterior parts of) both nasal sacs. The precerebral lamina and the internasal septum can be considered homologous (Daget, 1964), and sometimes appear to grow very allometrically. *Rita* sp. of 12 mm TL has no septum at all (Srinivasachar, 1957a), while adult *Rita rita* (Hamilton) (formerly *R. buchanani*) has an unmistakable cartilaginous internasal septum (Bhimachar, 1933). An internasal septum is absent in *A*. cf. *triradiatus*. It is fairly common in tropibasic skulls (de Beer, 1927).

The next vertical commissure is the orbitonasal lamina (preorbital process or ectethmoid cartilage of Ballantyne [1930]; orbitonasal lamina sensu largo of Adriaens and Verraes [1997a]), a transverse sheet composed of a ventrolateral outgrowth of the taenia marginalis, the spheno-ethmoidal commissure, and a dorsal process of the solum nasi, the orbitonasal process (orbitonasal lamina sensu stricto of Adriaens and Verraes [1997a]). The term orbitonasal process is introduced herein to avoid confusion. The compound nature of the orbitonasal lamina, as seen in *Ancistrus* cf. *triradiatus*, has been confirmed by Adriaens and Verraes (1997a) in *Clarias gariepinus* as well. The lamina often carries a laterorostral process that protects the nasal sacs laterally; in *A*. cf. *triradiatus* this is rudimentary. Hoedeman (1960) mistakenly called the first rudiments of the orbitonasal lamina the sphenoseptal commissure (see above). In several siluriforms, this is the first preotic vertical commissure to develop (Ballantyne, 1930; Adriaens and Verraes, 1997a; Vandewalle et

Fig. 10. Chondrocranium of *Ancistrus* cf. *triradiatus* (9.9 mm SL). **a:** Dorsal view. **b:** Dorsal view of splanchnocranium. **c:** Ventral view. **d:** Ventral view of neurocranium. **e:** Lateral view. c-eth, cartilago ethmoideum; c-Meck, cartilago Meckeli; c-mx, cartilago maxillaris; c-pc, cartilago parachordalis; c-pol, cartilago polaris; c-smx, cartilago submaxillaris; cb V, fifth ceratobranchiale; ch, ceratohyale; cm-bc-p, commissura basicapsularis posterior; cm-lat, commissura lateralis; cm-sphsep, commissura sphenoseptalis; cop-p, posterior copula; eb IV, fourth epibranchiale; fn-hyp, fenestra hypophysea; fn-sph, fenestra sphenoidea; fr-f-olf, foramen fila olfactoria; fr-on, foramen orbitonasalis; fr-ophth-sup, foramen ramus ophthalmicus superficialis nervus trigeminus; fr-tr-hm, foramen truncus hyomandibularis nervus facialis; fr-v-on, foramen vena orbitonasalis; fr-IX, foramen nervus glossopharyngeus (fenestra basicapsularis posterior); fr-X, foramen nervus vagus; fs-car-i, fissura arteria carotis interna; hb II, second hypobranchiale; hh, hypohyale; hs, hyosymplecticus; ih, interhyale; ipb IV, fourth infrapharyngobranchiale; lm-bot, lamina basiotica; lm-on, lamina orbitonasalis; lm-prc, lamina praecerebralis; n-puh, chondroid nucleus of parurohyale; not, notochord; 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-c, caudal process of ceratohyale; pr-cor, processus coronoideus; pr-d, dorsal process of ceratohyale; pr-op, processus opercularis of hyosymplecticum; pr-pob, processus postorbitalis of taenia marginalis; pr-post, processus postoticus of otic capsule; pr-pt, processus pterygoideus; pr-r, rostral process of ceratohyale; pr-unc, processus uncinatus of third epibranchiale; pr-v, ventral process of ceratohyale; sol-n, solum nasi; t-m, taenia marginalis; tr-cr, trabecula cranii; tt-p, tectum posterius.

al., 1997). However, in *A*. cf. *triradiatus* another, more medial commissure, the preorbital base (preoptic root of Srinivasachar [1957b]; lamina preorbitalis of Vandewalle et al. [1999]) appears almost simultaneously. In most siluriforms, it is formed well after the orbitonasal lamina, but serial sections of the 7.0 mm stage show their almost synchronized formation. The preorbital base, too, consists of a dorsal part, originating from the taenia marginalis, and a ventral part, rising from the trabecular bar.

Fenestrae in this region are variably present in siluriforms, and have received various names, causing some terminology confusion. In *A*. cf. *triradiatus*, as in all siluriforms, the most rostral of these fenestrae is the foramen for the fila olfactoria (olfactory foramen or foramen I), innervating the nasal organ. When the orbitonasal lamina, bordering it posteriorly, is situated more rostrally, as in *Mystus vittatus* and *Arius jella*, the foramen reduces to a very small opening, directed more rostrocaudally (Srinivasachar, 1957a, 1958a).

An orbitonasal foramen (orbital foramen of Kindred [1919]; preoptic fontanelle or foramen of Srinivasachar [1957b]) is most often present between the orbitonasal lamina and the preorbital base in catfishes. In *Ancistrus* cf. *triradiatus*, it becomes smaller during ontogeny as the preorbital base enlarges and is pierced by the orbitonasal artery. Depending on the size of the preorbital base and its position relative to the orbitonasal lamina, the direction of the orbitonasal foramen may be rostrocaudal or mediolateral (and sometimes becoming very large), leading to misinterpretations (Adriaens and Verraes, 1997). Figure 11 shows the different orientations of the foramen, due to the size of the preorbital base. The foramen seems to be completely absent in Bagridae (Srinivasachar, 1957a).

Two more foramina are present in this region in *Ancistrus* cf. *triradiatus*: dorsal of the orbitonasal foramen a small foramen is seen in the preorbital base, containing a branch of the orbitonasal vein, as observed in serial sections of 7.0 mm and later stages, and seen by Bamford (1948) in *Ariopsis felis* as well. Another foramen pierces the orbitonasal lamina rostrocaudally, accommodating a part of the superficial ophthalmic branch of the trigeminal nerve, which innervates the skin of the dorsal snout region (not to be confused with the identically termed branch of the facial nerve, which runs caudal of it and innervates the supraorbital lateral line organs). A second part of this branch, innervating the skin lateral of the naris, passes below the lateral side of the lamina, through a small ventral slit, or through a foramen (in the right side of the 10.2 mm stage): this varies between examined specimens. The foramen for the superficial ophthalmic branch is generally featured in siluriforms, except for *Rita* sp. (Srinivasachar, 1957a). In Srinivasachar's article a ventral groove in the lamina carries the so-called profundus branch of the same nerve. Still according
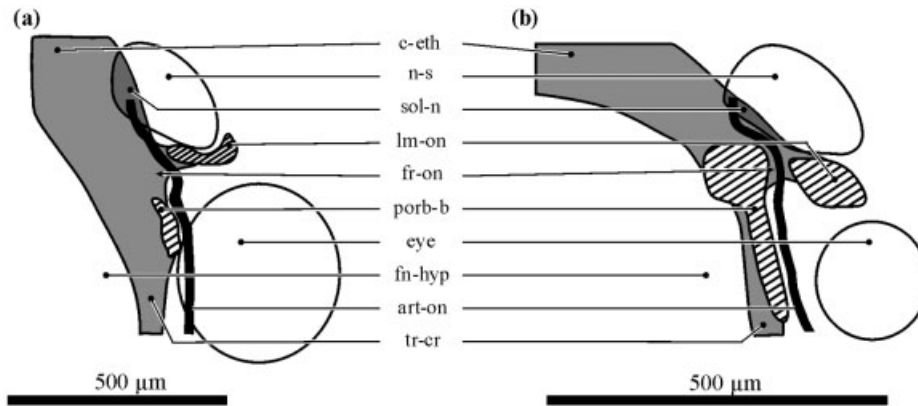
Fig. 11. Dorsal view of right orbitonasal region of *Ancistrus* cf. *triradiatus* (8.0 mm SL) and *Clarias gariepinus* (8.4 mm SL), based on serial sections. Anterior toward top. Dorsal elements are removed; orbitonasal lamina and preorbital base are cut through. art-on, arteria orbitonasalis; c-eth, cartilago ethmoideum; fn-hyp, fenestra hypophysea; fr-on, foramen orbitonasalis; lm-on, lamina orbitonasalis; n-s, nasal sac; porb-b, preorbital base; sol-n, solum nasi; tr-cr, trabecula cranii.

to that author, in *Mystus vittatus* one part of the nerve runs through a groove at the dorsal side of the lamina; another part runs through a foramen. In *Arius jella*, Srinivasachar (1958a) mentions the course of the superficial ophthalmic and profundus branches through two distinct dorsal foramina in the orbitonasal lamina. The identity of this "profundus" branch should be investigated, as it is normally characterized by a path ventral to the eye musculature and its nerves, and is absent in the black bullhead *Ameiurus melas*, and in most bony fishes (Workman, 1900).

The optic, oculomotor, trochlear, trigeminal, abducens, and facial nerves exit the skull via the sphenoid fenestra in all siluriforms, as is typical in teleosts. The only exception known so far is *Ailia coila*, in which Srinivasachar (1957b) noted a separate foramen for the oculomotor nerve in the preorbital base. As can be seen in all posthatching stages, *Ancistrus* cf. *triradiatus* shows a very peculiar feature in having a vertical structure identical to the lateral commissure, as observed in several fishes, although not in other siluriforms (de Beer, 1937) (Fig. 2d). Lateral of the trigemino-facialis chamber it originates as a prootic process from the anterior otic capsule, connecting with the anterior end of the polar cartilage. Only the hyomandibular trunk and opercular branch of the facial nerve (immediately giving rise to the hyomandibular and opercular branches), an artery (possibly the orbital artery) and a vein exit behind it (Fig. 2e). The lateral commissure in *Gasterosteus aculeatus* and *Hepsetus odoe* (Swinnerton, 1902; Bertmar, 1959) is formed in exactly the same way. In *Salmo trutta fario*, it is formed from two sides: a postpalatine process originates from the basiotic lamina and connects to the prootic process (de Beer, 1927). The absence of a lateral commissure was previously considered typical in catfishes (de Beer, 1937; Daget, 1964), but is obviously present in *A.* cf. *triradiatus*. A second,

small blastema posterior to the prootic process (as seen in the older stages described herein) is variably present, and does not seem to correspond to any other structure described in teleosts. Serial sections reveal it as a very thin, almost membranous projection.

In general, catfishes are believed to lack true myodomes accommodating the eye muscles, as seen in most other teleosts (de Beer, 1937). This might be due to the lesser eye sizes, and consequently smaller extrinsic eye muscles in catfishes (Arratia, 2003). Nonetheless, *Ancistrus* cf. *triradiatus* possesses a posterior myodome resembling very well the configuration as described by de Beer (1937) in *Salmo trutta trutta* (Fig. 2g). The external rectus muscle enters the myodome laterally and penetrates deepest into it. The internal rectus muscle also penetrates into it, and inserts on the developing parasphenoid bone. The inferior rectus muscle enters the braincase, but not the canal formed by the parasphenoid bone and the prootic bridge, and attaches on the basiotic lamina. Meanwhile, the superior rectus muscle inserts on this lamina anterior to the passage of the other three muscles into the braincase. The internal rectus muscle lies medial to the external one, while in *S. trutta trutta* it lies underneath it. This myodome can also be seen in adult *A.* cf. *triradiatus*. A smaller, anterior myodome is present too, housing the obliquus eye muscles: both superior and inferior obliquus muscles enter the braincase through the orbitonasal foramen and attach on the solum nasi.

McMurrich (1884:297) observed a rudimentary, "almost aborted" posterior myodome-like structure in *Ameiurus nebulosus*. Kindred (1919) saw no evidence of this in 10 and 32 mm stages of the same species: the rectus muscles insert on the lateral surface of the trabecula in the posterior part of the orbit. Similarly, Srinivasachar (1957b) mentioned the absence of a posterior myodome in 8 and 18 mm

stages of (a.o.) *Silonia silondia*, while Bhimachar (1933) observed a small myodome in adults of the same species (then named *Silandia gangetica*). In developmental studies on catfishes, the only mention of a small anterior myodome as in *Ancistrus* cf. *triradiatus* is in *Rita* sp. by Srinivasachar (1957a). Loricariidae have relatively large eyes, needed in clear waters where these fishes often occur, especially since loricariids lack most barbels (only the maxillary barbels are more or less developed). Adriaens and Verraes (1997b) found that, on average, after Callichthyidae, Pimelodidae, and Schilbeidae, Loricariidae have the largest eyes among siluriforms. Schaefer (1997) and Aquino (1998) described myodomes in adult hypoptopomatin loricariids.

In the auditory capsule of teleosts, the anterior otic cartilage generally develops first, very soon giving rise to the posterior one (de Beer, 1927; Goodrich, 1958; Daget, 1964; Adriaens and Verraes, 1997a). In *Ancistrus* cf. *triradiatus* this sequence is also suggested by the presence of chondroblasts in the 5.2 mm stage where the anterior otic cartilage will form. In the 5.6 mm stage, the anterior part is clearly more developed, being much better stained by alcian blue.

The initial fusion of the posterior otic cartilage with the skull floor differs from the sequence noticed in *Salmo trutta fario* and *Clarias gariepinus* (de Beer; 1927; Adriaens and Verraes, 1997a), since it first contacts the bases of the occipital pilae (5.6 mm), and only later touches the parachordal plate directly (6.8 mm). As in other teleosts, no nerve or other structure passes through the anterior basicapsular foramen (Daget, 1964). The foramen is absent in some catfishes, like *Ameiurus nebulosus* (Kindred, 1919) and *Silonia silondia* (Srinivasachar, 1957b). In the latter species, and in *Pangasius pangasius* and *Ailia coila*, both nerves exit through the same opening (Srinivasachar, 1957b), which might point to the absence of the posterior basicapsular commissure. In *Ancistrus* cf. *triradiatus*, the posterior cerebral vein does not exit the skull via the foramen for the vagal nerve, which, as Goodrich (1958) postulates, is the case in most fishes. In *A.* cf. *triradiatus* it passes laterally through the foramen magnum.

At closure, the anterior basicapsular fenestra in *Ancistrus* cf. *triradiatus* becomes filled only by a very thin cartilage layer, forming the recess for the utriculus of the inner ear (as shown in Fig. 8d). The recess for the sacculus is situated caudomedial of the posterior basicapsular foramen. The recess for the lagena is situated medial of the foramen for the vagal nerve. These last two recesses or grooves are generally present in siluriforms (Srinivasachar, 1958a).

Also often present (but not in all catfishes) are swellings or prominences in the otic capsule, indicating the path of the internal semicircular canals (Srinivasachar, 1957b); these are visible in *Ancis-trus* cf. *triradiatus*. In addition, a vertical pillar of cartilage, the lateral semicircular septum, is situated at the inner side of the horizontal semicircular canal (Fig. 7f). The anterior and posterior semicircular septa, present in some catfishes (Srinivasachar, 1957b, 1958a), are rudimentary, as the lateral so-called cavum labyrinthi opens widely into the medial cavum cranii, exactly as in *Ameiurus nebulosus* (Kindred, 1919).

The foramen for the otic branch of the facial nerve is variably present in Siluriformes: it is seen in the anterior otic cartilage in *Silonia silondia* and *Pangasius pangasius* (Srinivasachar, 1957b), in the postorbital process of the taenia marginalis near its origin in the otic capsule in *Ameiurus nebulosus, Ailia coila, Arius jella, Callichthys callichthys*, and *Clarias gariepinus* (Srinivasachar, 1957a; b; 1958a; Hoedeman, 1960; Adriaens and Verraes, 1997a), and is absent in *Rita* sp., *Mystus vittatus, Plotosus canius,* and the stinging catfish *Heteropneustes fossilis* (Srinivasachar, 1957a, 1958a, 1959). In *C. gariepinus*, the foramen is formed as the taenia marginalis becomes broader and encloses the medially situated otic branch (Adriaens and Verraes, 1997a). In *Ancistrus* cf. *triradiatus*, the branch splits, and only the lateral part goes through the postorbital process.

Even in early prehatching stages of *Ancistrus* cf. *triradiatus* a maxillary barbel cartilage is present. This maxillary barbel of Loricariidae connects and supports the upper and lower lips that make up the typical sucker mouth. In the literature, no evidence is found of such an early presence of the cartilage in other catfishes (in which the maxillary barbel is always present). The early presence is thought to be related to the fact that young *A.* cf. *triradiatus* can suck themselves onto a substrate immediately after hatching, something requiring a well-developed sucker mouth.

Mandibular barbels are absent in Loricariidae, hence supporting cartilages are not present. They are, however, fairly common in other catfishes, and can often be seen in the cartilaginous skeleton. *Hoplosternum littorale* and *Callichthys callichthys*, both Callichthyidae and thus Loricarioidea, have a pair of tiny cartilage rods, attached to the lateral borders of the ethmoid plate and supporting the maxillary barbels (Ballantyne, 1930; Hoedeman, 1960). Ballantyne (1930), Bamford (1948), Srinivasachar (1957b, 1958b), and Hoedeman (1960) emphasized the development of cartilages supporting the mandibular barbels in *H. littorale, Ariopsis felis, Ailia coila, Clarias gariepinus*, and *C. callichthys*.

Splanchnocranium

In *Ancistrus* cf. *triradiatus*, the palatine of the premandibular arch arises independently from the pterygoid process of the pterygoquadrate (palatal bar of the mandibular arch), and stays a separate

element, a situation considered a synapomorphy among siluriforms (Arratia, 1992; Vandewalle et al., 1999). An exception occurs in *Arius jella* (Srinivasachar, 1958a), where both elements fuse; in *Callichthys callichthys* the elements almost touch (Hoedeman, 1960). In *A.* cf. *triradiatus*, the palatine elongates during ontogeny, and will articulate with the maxillary and the premaxillary bones, situated far rostrally.

Below the anterior tip of the palatine a small separate cartilage develops at around 8.0 mm SL (as seen in serial sections); it is not stained by alcian blue until the 10.0 mm stage. Adriaens and Verraes (1997a) described this submaxillary cartilage in *Clarias gariepinus*, where it appears together with the bony maxilla, and facilitates the palatine-maxillary mechanism. The head of the maxilla in *Ancistrus* cf. *triradiatus* starts to ossify at 8.0 mm, so a similar function is assumed here.

Meckel's cartilages (mandibular cartilages of Ballantyne [1930]) arise independently in *Ancistrus* cf. *triradiatus*, then fuse, and then disconnect (when the bony elements of the lower jaw develop). This sequence is not seen in other siluriforms: the cartilages never fuse in *Ariopsis felis, Silonia silondia, Pangasius pangasius, Mystus vittatus, Rita* sp., *Callichthys callichthys,* and *Heteropneustes longifilis* (Bamford, 1948; Srinivasachar, 1957a,b; Hoedeman, 1960; Vandewalle, 1997); they most often touch, though, or are joined by connective tissue. In *Ameiurus nebulosus, Arius jella, Plotosus canius, Clarias gariepinus*, and *Chrysichthys auratus* they are fused from the start, and only later separate (Kindred, 1919; Srinivasachar, 1958a; Adriaens and Verraes, 1997a; Vandewalle, 1999). In the latter two species, they are fused to the pterygoquadrate-hyosymplectic plate as well. The position of Meckel's cartilages in *A.* cf. *triradiatus* is notably different from the situation in other catfishes, as they point medially instead of rostrally. This is coupled to the caudomedial position of the ventrally oriented dental bones in juvenile and adult specimens. This position of the lower jaw is an adaptation for the scraping of algae from substrates, and for efficiently using the typically loricariid sucker mouth while breathing. The sucker mouth has to be functional at hatching, a requirement that is thought to have had a large impact on the evolution of this part of the chondrocranium. The median fusion of Meckel's cartilages supports the lower jaws and the lower lip as soon as they start to move, up to the moment that ossification occurs.

Compared to other siluriforms, the body of the suspensorium of *Ancistrus* cf. *triradiatus* is a rather narrow and straight bar, elongating during ontogeny, as well as becoming tilted, with the pterygoquadrate acquiring a more rostral position. The suspensorium of catfishes has been a point of interest, as its development and fusion of different parts is remarkable among teleosts (Arratia, 1990, 1992). At least partial fusion of the suspensorium, i.e., of the hyosymplectic with the quadrate, may be a synapomorphy of siluriforms (Arratia, 1992; Vandewalle et al., 1999). The most extensive fusion is seen in *Clarias gariepinus*, where the young splanchnocranium, including Meckel's cartilages, hyoid bars, and the first copula, consists of one part, fused with the neurocranium at the level of the hyosymplectic (Surlemont et al., 1989; Adriaens and Verraes, 1997a). The fusion with the neurocranium is also present in certain Loricarioidea, like Trichomycteridae (Arratia, 1990), and, even more intensely, the callichthyid *Callichthys callichthys* (Hoedeman, 1960). A weakly chondrified zone connects the suspensorium to the neurocranium in *A.* cf. *triradiatus*, but this is not visible in in toto stained preparations. In *A.* cf. *triradiatus*, the foramen for the hyomandibular branch of the facial nerve is present in the center of the hyosymplectic from the start; in many other siluriforms the nerve runs anterior to the hyosymplectic and then becomes captured by the growing hyosymplectic (Kindred, 1919; Srinivasachar, 1957b; Adriaens and Verraes, 1997a), or sometimes stays ahead of it, in a groove or not (Srinivasachar, 1957a,b, 1958a), or starts posterior of the hyosymplectic, later ending up in a foramen as well (Bamford, 1948).

The interhyal in *A.* cf. *triradiatus* (stylohyal of de Beer [1927]) connects the suspensorium with the ceratohyal, and is a strip of weakly chondrified cartilage tissue, being more broadly fused to the ceratohyal than with the hyosymplectic (Fig. 2h). The interhyal is strongly fused with the hyosymplectic in catfishes as *Silonia silondia, Pangasius pangasius, Ailia coila, Heteropneustes fossilis,* and *Clarias gariepinus* (Srinivasachar, 1957b, 1959). It is soon seen as a separate element in *Mystus vittatus, Rita* sp., *Arius jella*, and *Plotosus canius* (Srinivasachar, 1957a, 1958a).

The four processes of the ceratohyal in *Ancistrus* cf. *triradiatus* are thought to have various functions. The large ventral process, common among siluriforms, albeit usually smaller, articulates with the branchiostegal rays. The other three are not known from other siluriforms: the dorsal process grows to the hyosymplectic, and might well reinforce the more anterior hyoid-interhyal-hyosymplectic articulation (e.g., Fig. 8e); the anterior and posterior processes broaden the lateral end of the hyoid bar, where it will later grow into the vicinity of the preopercular bone, attached to the ossified suspensorium.

The true nature of the parurohyal dumbbell-like nucleus caudoventral of the hypohyals (Fig. 2f) is not clear; ensuing study of its link with the first basibranchial and its role in the formation of the parurohyal of *Ancistrus* cf. *triradiatus* during ossification will help clarify the possible homology of this part with elements of the parurohyal described by Arratia and Schultze (1990).

As all catfishes, *Ancistrus* cf. *triradiatus* has no separate basihyal (Arratia and Schultze, 1990; Adriaens and Verraes, 1997a). The hypohyals fuse with the first basibranchials, which, like the other branchial elements, arise in a rostrocaudal sequence, as is the case in all siluriforms, but not in teleosts generally (Vandewalle et al., 1997).

The basibranchials in *Ancistrus* cf. *triradiatus* are organized in two copulas: the anterior copula starts continuous with the hyoid bar, and consists of basibranchials I–III. Later, it becomes separated from the hyoid bar; the first basibranchial disappears, while the other two will ossify independently. The posterior copula arises separately and comprises basibranchials IV and V. This grouping is seen in several other siluriforms as well, e.g., *Ariopsis felis, Clarias gariepinus*, and *Heterobranchus longifilis* (Srinivasachar, 1958a; Adriaens and Verraes, 1997a; Vandewalle et al., 1997). Vandewalle et al. (1997) mistakenly called the two copulas basibranchial one and two. In *Silonia silondia* and *Pangasius pangasius*, the posterior copula is homologous with the fifth basibranchial only (Srinivasachar, 1957b).

The overall appearance of the other branchial elements varies among catfishes. An example is the degree of fusion of the hypobranchials and the ceratobranchials of the third arch: in *Clarias gariepinus* the hypobranchials become separated from the corresponding ceratobranchials (Adriaens and Verraes, 1997a), in *Ancistrus* cf. *triradiatus* they remain fused with the ceratobranchials, and in *Plotosus canius* both hypobranchials are fused with each other in the midline (Srinivasachar, 1958a). This might be related to the presence and size of the copulas in this region; in *Pangasius pangasius*, where the fourth basibranchial seems to be rudimentary or absent, hypobranchials IV are also fused in the midline (Srinivasachar, 1957b).

Infrapharyngobranchials I and II are not present in *Ancistrus* cf. *triradiatus*. Among catfishes, the number of infrapharyngobranchials may range between two and four (Adriaens and Verraes, 1997a). Diplomystidae have four separately ossifying infrapharyngobranchials (Arratia, 1987). In *Silonia silondia* and *Arius jella*, the posterior two become fused; in *Plotosus canius*, only the first one remains separate (Srinivasachar, 1957b, 1958a). In *Clarias gariepinus*, the first two are fused, while the last two stay apart (Adriaens and Verraes, 1997a). In *A.* cf. *triradiatus*, the first two infrapharyngobranchials are completely lost, complying with a reductional trend Adriaens and Verraes (1997a) observed among catfishes.

CONCLUSION

Many features of the cartilaginous skull of *Ancistrus* cf. *triradiatus* have been described in most other catfish species as well, and can be considered general characteristics of the siluriform chondrocranium (Adriaens and Verraes, 1997; Vandewalle et al., 1999). However, several aspects of *A.* cf. *triradiatus* are not seen as such in other catfishes, or to a lesser extent.

Like all catfishes, *Ancistrus* cf. *triradiatus* has a platybasic skull from the start. The hypophyseal fenestra is closed by the ethmoid plate first. Opposed to many other species, the notochord protrudes into the fenestra in the first stages, and the acrochordal cartilage is small and variably present. The skull is broad, although the ethmoid region is relatively narrow, with a very small solum nasi, leaving the nasal sacs rather unprotected until ossification. As expected for a broad platybasic skull, a precerebral lamina is present instead of a transverse septum. The orbitonasal lamina is formed by both the spheno-ethmoidal commissure of the taenia marginalis and the orbitonasal process of the solum nasi. A lateral commissure and myodomes are described; this has not been seen in siluriforms thus far. The larger posterior myodome is roofed by a prootic bridge as described by de Beer (1937) in *Salmo trutta trutta*. On serial sections of various stages, no cartilage reduction is seen in the trabecular bar for the passage of the arteria carotis interna; the fissure is formed by allometric growth. Initially, before the formation of the basivestibular and posterior basicapsular commissures, the posterior otic cartilage touches the parachordal plates only indirectly, via the occipital pilae. The anterior basicapsular fenestra, when closed, becomes the recess for the utriculus of the inner ear. The otic capsule lacks a real tectum synoticum and has two large dorsal fenestrae. The tectum posterius fuses with the supradorsals of a vertebra, presumably the fifth. The supporting cartilage rod for the maxillary barbel is prominent from early stages on, probably related to the strong support needed for the lips of the typical loricariid sucker mouth, which is functional from hatching on.

The splanchnocranium is typically siluriform with a separated palatine, a compound hyosymplectic-pterygoquadrate plate, continuous with the interhyal and the hyoid bar. However, it is not continuous with Meckel's cartilages, that arise separately, soon fuse, and later separate again. Meckel's cartilages in *Ancistrus* cf. *triradiatus* point medially instead of rostrally, as in other catfishes. This is an adaptation to the necessity of a fully functional sucker mouth in hatchlings.

The ceratohyal has four prominent lateral processes. Two copulas with all five basibranchials are present, but the first basibranchial soon disappears, and the fourth and fifth do not separate. Only hypobranchials I–II separate from the ceratobrachials. Infrapharyngobranchials I–II do not develop.

Both neurocranium and splanchnocranium elongate during ontogeny, with a reinforced posterior region, a narrow, elongated, and ventrally pointing

ethmoid plate, a long and slender palatine, and a long bar-shaped suspensorium. The shape changes of the ethmoid and suspensorial region are interpreted as modifications for the typical loricariid head configuration.

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