Published in : Journal of Fish Biology (1997), vol. 50, n°2, pp. 227–253
DOI: 10.1111/j.1095-8649.1997.tb01355.x
Status : Postprint (Author's version)

POSTEMBRYONIC DEVELOPMENT OF THE CEPHALIC REGION IN HETEROBRANCHUS LONGIFILIS

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At hatching, *Heterobranchus longifilis* does not display any primordia of the cephalic skeleton. The latter appears 12 h post-hatching and develops in three stages up to day 16. The first stage (12 h to 2 days) involves almost exclusively the development of the chondrocranium. During the second period (days 3-8), dermal elements of the Splanchnocranium appear. The final stage is marked by resorption of the cartilages, progressively replaced by ossifications (days 10—16). At their appearance the elements of the Splanchnocranium are fused together, as are the first neurocranial elements. Later, the Splanchnocranium splits up. By the time the yolk sac is completely resorbed, the buccal and pharyngeal jaws are present, the suspensoria and hyoid bars are partially developed, and the parasphenoid partially closes the hypophyseal fenestra. These structures delimit a buccal cavity that is probably functional, i.e. capable of participating in the intake of exogenous food. Next to continue its development is principally the splanchnocranium. completing the walls of the buccal cavity. Cartilage resorption parallels the appearance of endochondral ossifications (except for the trabecular bars). Braincase closure begins to accelerate once the buccal system is complete.

KEY WORDS: postembryonic development; skeleton; catfishes; Clariidae; *Heterohranchus.*

INTRODUCTION

Heterobranchus longifilis Valenciennes, is an African catfish that seems to have a very promising future in fish farming. Sound knowledge of its biology in general should help towards mastering its successful farming. In this context, an in-depth analysis of the postembryonic development of the cephalic skeleton should contribute to understanding the direct correlations that exist between the development of structures of the head and vital functions such as breathing and feeding (Osse, 1990; Surlemont & Vandewalle, 1991). This should make it possible to match the food distributed in pisciculture more closely with the developmental status of the fry.

Most studies dealing with the development of the cephalic skeleton in teleosts have been fragmentary. They have focused either solely on the osteocranium (Jollie, 1984; Potthoff *et al.,* 1988; Vandewalle *et al.,* 1995), solely on the chondrocranium (Bhargava, 1958; Bertmar, 1959), on a few cranial elements

(Francillon, 1974; Verraes, 1977; Arratia & Schultze, 1990; Potthoff & Tellock, 1993), or on a few, sometimes distant, developmental stages (Howes & Sanford, 1987' Surlemont & Vandewalle, 1991; Kobayakawa, 1992). Reports describing the close timing of the events that mark the postembryonic development of a teleost skull are rare (Vandewalle *et al.,* 1992). The aim of the present study is to establish such a chronology for the development of the cephalic skeleton of *H. longifilis,* from hatching to day 16 (end of the larval period: presence of many adult characters—Legendre & Teugels, 1991). In addition to contributing to knowledge about the development of the cephalic skeleton in teleosts, this chronology should reveal links between the development of certain head structures and fry survival, in relation to breathing and feeding. The nomenclature used for the developing skeletal structures is based principally on the works of de Beer (1937), Daget (1964), and Paterson (1977).

MATERIALS AND METHODS

H. longifilis fry were supplied by the C.E.R.E.R. Experimental Pisciculture (Tihange, Belgium). The first group of fry was reared at 29° C. The fry were sampled (batch size varying from 40 of the youngest fry to 10 of the oldest) at hatching (24 h post-fertilization, day 0) and on days 1, 2, 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16. The corresponding average fry lengths were 2·9, 5·0, 6·7, 7·8, 8·2, 91, 10·0, 12·2, 12·7, 131, 16-5, 18 0, and 24 0 mm. A second group of fry was reared at 27° C. The fry were sampled (batch size ranging from 50 of the youngest fry to 25 of the oldest) at hatching and 12 h, 1 day, 36 h, and 2 days post-hatching (average lengths: 2·5, 3·5, 5·0, 5-7, 6·0 mm respectively). In this group, it was easier to pinpoint the initial appearance of the skeletal primordia thanks to a slower development of the fry (caused by the lower temperature) and a higher sampling frequency.

The fry were fixed in $CaCO_3$-buffered 10% formalin and trypsin-cleared. Some of the fry were stained with alcyan blue, to reveal the cartilages, and some with alizarin, to reveal the bones. The techniques used were derived from those proposed by Dingerkus & Ulher (1977); Potthoff (1984), and Taylor & Van Dyke (1985). Attempts to double-stain the fry with both dyes were unsuccessful.

Although the results present fry that have just hatched, we were in fact able to establish homologies and recognize structures by only comparing the structures of adult catfish (Nawar, 1954; Jarayam, 1970; Mahy, 1974; Taverne & Aloulou-Triki, 1974) with those of the oldest fry and then progressing by successive comparisons from the oldest fry to the youngest.

All the figures represent the average state of skeletal development in the batch or stage studied.

There may appear in the various figures some discrepancies in size and in shape between the lateral, ventral, and dorsal views of the cephalic region of the fry, because of the difficulty in positioning the fry exactly after placing them in glycerin for observation.

RESULTS

FRY REARED AT 27° C

AT HATCHING AND 12 H POST-HATCHING

No cephalic skeletal structure is visible.

DAY 1

The first cartilaginous structures have appeared [Fig. 1(a)], They all belong to the Splanchnocranium. These structures are: the hyosymplectic, the interhyal, the hyoid bar, the pars quadrata of the palato-quadrate, and Meckel's cartilage.

On each side (left and right) the structures form a single entity, with no separations between the various components.

36 H POST-HATCHING

The first cartilaginous elements of the neurocranium are in place: the trabecular bars are already fused posteriorly with the parachordal plates and each one is prolonged outwardly by a commissura basicapsularis anterior and the beginning of the lateral wall of the otic capsule [Fig. 1(b)].

The Splanchnocranium appears practically unchanged. The two main improvements are a posterior protuberance of the hyosymplectic on which the opercular will later articulate (see day 4) and the fact that Meckel's cartilages have extended forward: they now curve toward and touch each other.

DAY 2

The lateral walls of the otic capsules are well developed and the posterior part of each taenia marginalis is present. The parachordal plates are practically in contact with one another [Fig. 1(c),(d)].

The Splanchnocranium has several additions: the first four pairs of Ceratobranchials and an anterior basibranchial. The first elements to have appeared still form paired undivided entities.

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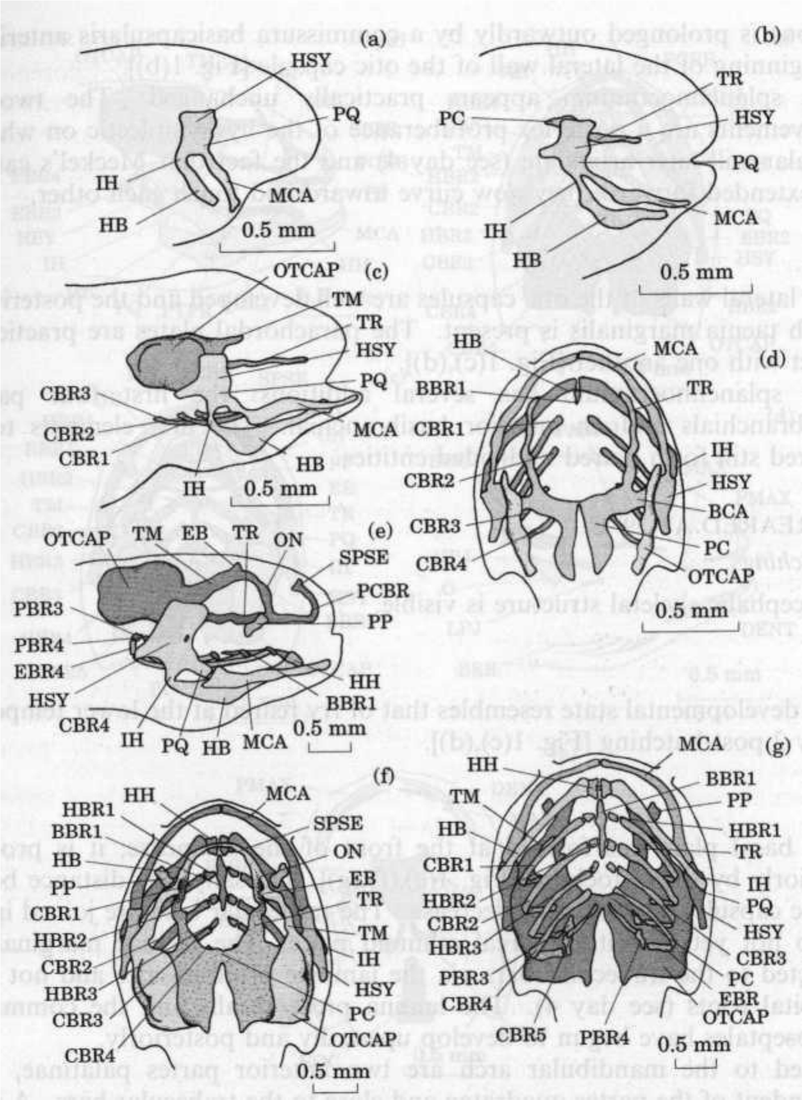
Fig. 1. *Heterobranchus longifilis :*



(a) lateral view of the chondrocranium of a 1-day-old fry reared at 27" C; (b) lateral view of a 36-hour old fry reared at 27° C; (c) lateral view and (d) dorsal view of the chondrocranium of a 2-day-old fry reared at 27° C; (e) lateral view, (f) ventral view, and (g) dorsal view of the chondrocranium of a 2-day-old fry reared at 29° C; BBRl, basibranchial 1; BCA, commissura basicapsularis anterior; CBR. Ceratobranchial; EB. epiphyseal bar; EBR, epibranchial; HB, hyoid bar; HH, hypohyal; HSY, hyosymplectic; IH, interhyal; MCA, Meckel's cartilage; ON, lamina orbitonasale; OTCAP. otic capsule; PBR, pharyngobranchial; PC, parachordal plate; PCRB, lamina precerebralis; PP, pars palatina; PQ, pars quadrata; SPSE, commissura Sphenoseptale; TM, taenia marginalis; TR, trabecular bar.

FRY REARED AT 29^{o} C

AT HATCHING

No cephalic skeletal structure is visible.

DAY 1

The developmental state resembles that of fry reared at the lower temperature on day 2 post-hatching [Fig. 1(c),(d)].

DAY 2

The basal plate has formed at the front of the braincase; it is prolonged posteriorly by the notochord [Fig. 1 (e),(f),(g)]. Dorsally, the distance between the otic capsules has begun to decrease. The trabecular bars are joined in front but do not yet constitute a real ethmoid plate. The taeniae marginales are connected to the trabecular bars via the laminae orbitonasales and not by the preorbital roots (see day 4). The lamina precerebralis and the commissurae sphenoseptales have begun to develop upwardly and posteriorly.

Added to the mandibular arch are two anterior partes palatinae, totally independent of the partes quadratae and close to the trabecular bars. A pair of hypohyals have been added to the hyoid bars but remain joined with them. The left and right hypohyals touch each other medially. The branchial basket displays a fifth pair of Ceratobranchials, three pairs of hypobranchials, and four pairs of epibranchials as well as the third and fourth pairs of pharyngobranchials. The basibranchial has lengthened posteriorly. On each side, Meckel's cartilage has become independent of the 'pars quadrata-hyosymplectic-interhyal-hyoid bar ' entity.

DAY 3

Dorsally, the epiphyseal bridge has begun to form and the commissurae sphenoseptales have joined with the taeniae marginales (Fig. 2). The front of the trabecular bars has fused to form a very narrow ethmoid plate. Two pterygoid processes prolong the partes quadratae anteriorly. Each hyoid bar is separate from the ' pars quadrata-hyosymplectic-interhyal ' entity. A second small basibranchial is present behind the first.

The first ossifications are present. In the neurocranium, there is a compact basioccipital and a parasphenoid, very thin at its centre and thicker laterally. The Splanchnocranium supports the dentaries and premaxillaries, both with fixed teeth, small maxillaries, tooth-bearing upper and lower pharyngeal jaws at the level of the fifth pair of ceratobranehials and fourth pair of pharyngobranchials, seven pairs of branchiostegal rays complete with joint articular process with the still-cartilaginous hyoid bars, and two operculars which are already well developed and extend posteriorly.

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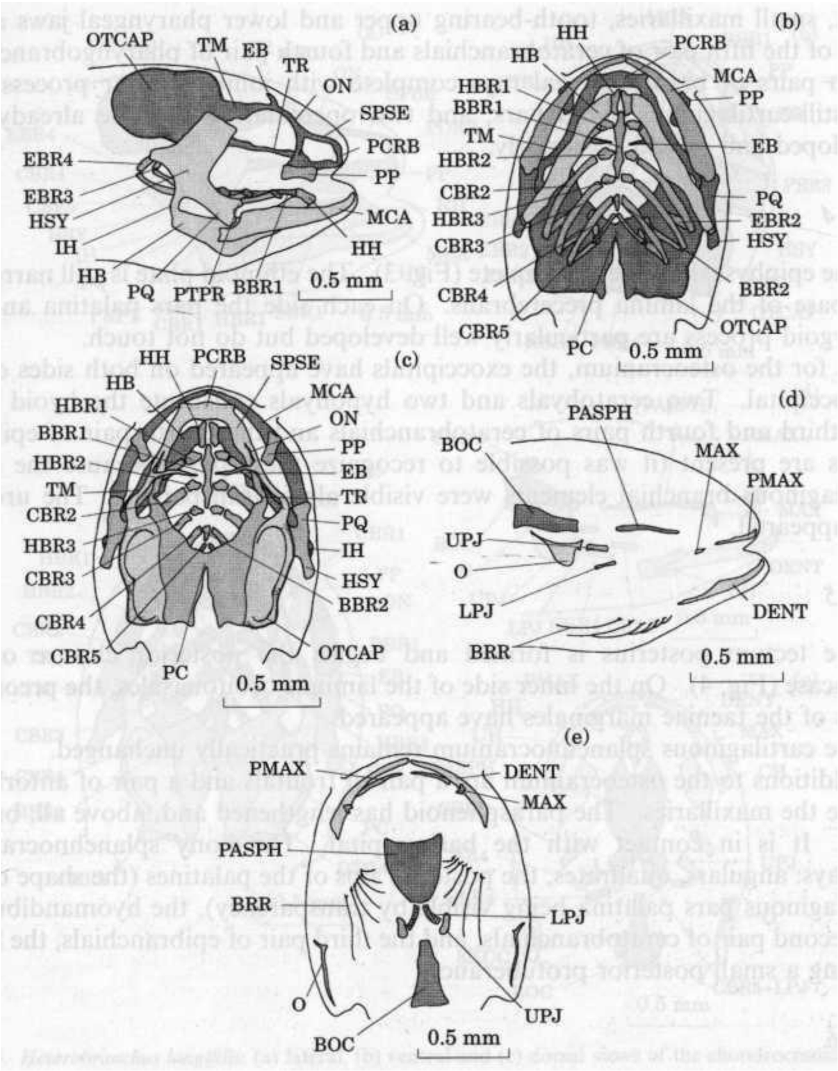
Fig. 2*. Heterobranchus longifilis:*



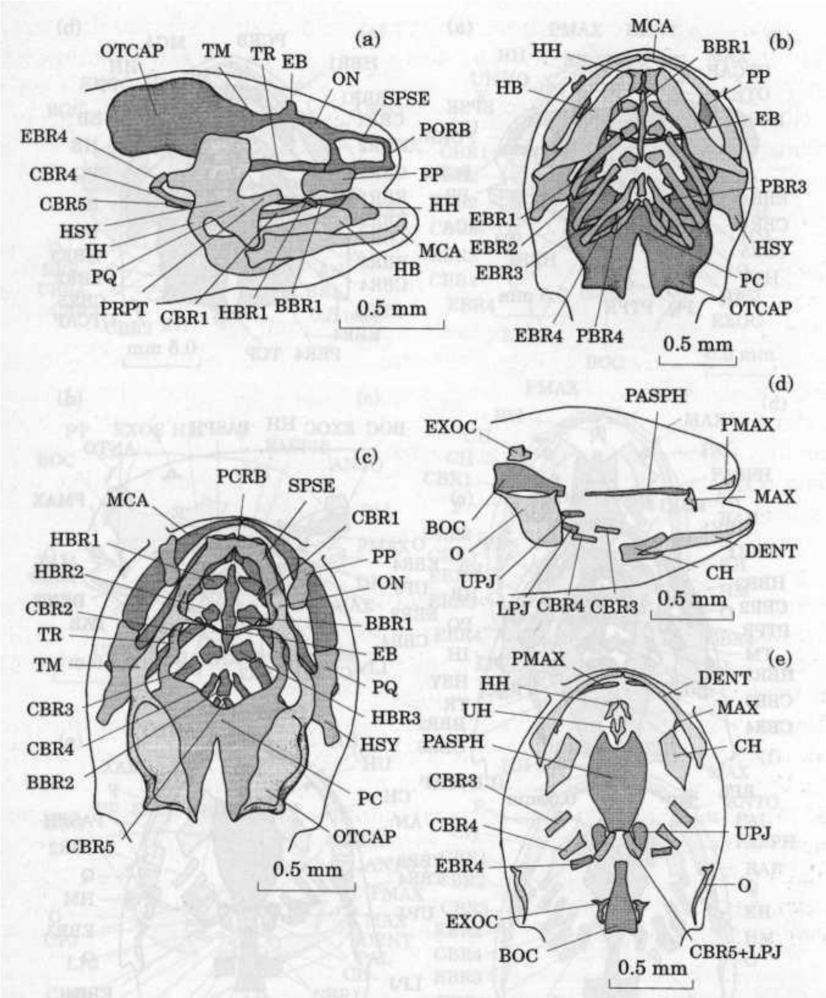
(a) lateral, (b) ventral and (c) dorsal views of the chondrocranium, and (d) lateral and (e) dorsal views of the osteocranium of a 3-day-old fry. The buccal teeth are not represented on Figs (d) and (e); BBR1, basibranchial 1; BBR2, basibranchial 2; BOC, basioccipital; BRR. branchiostegal ray; CBR, Ceratobranchial; DENT, dentary; EB, epiphyseal bar; EBR, epibranchial; HB. hyoid bar; HBR, hypobranchial; HH, hypohyal; HSY, hyosymplectic; IH, interhyal; LPJ. lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; O, opercular; ON, lamina orbitonasale; OTCAP, otic capsule; PASPH, parasphenoid; PC, parachordal plate; PCRB, lamina precerebralis; PMAX. premaxillary; PP, pars palatina; PQ, pars quadrata; PTPR. pterygoid process; SPSE, commissura sphenoseptale; TM, taenia marginalis; TR, trabecular bar; UPJ, upper pharyngeal jaws.

DAY 4

The epiphyseal bridge is complete (Fig. 3). The ethmoid plate is still narrow at the base of the lamina precerebralis. On each side the pars palatina and the pterygoid process are particularly well developed but do not touch.

As for the osteocranium, the exoccipitals have appeared on both sides of the basioccipital. Two Ceratohyals and two hypohyals constitute the hyoid arch. The third and fourth pairs of Ceratobranchials and the fourth pair of epibranchials are present (it was possible to recognize these parts because the other cartilaginous branchial elements were visible albeit transparent). The urohyal has appeared.

Fig. 3. *Heterobranchus longifilis:*



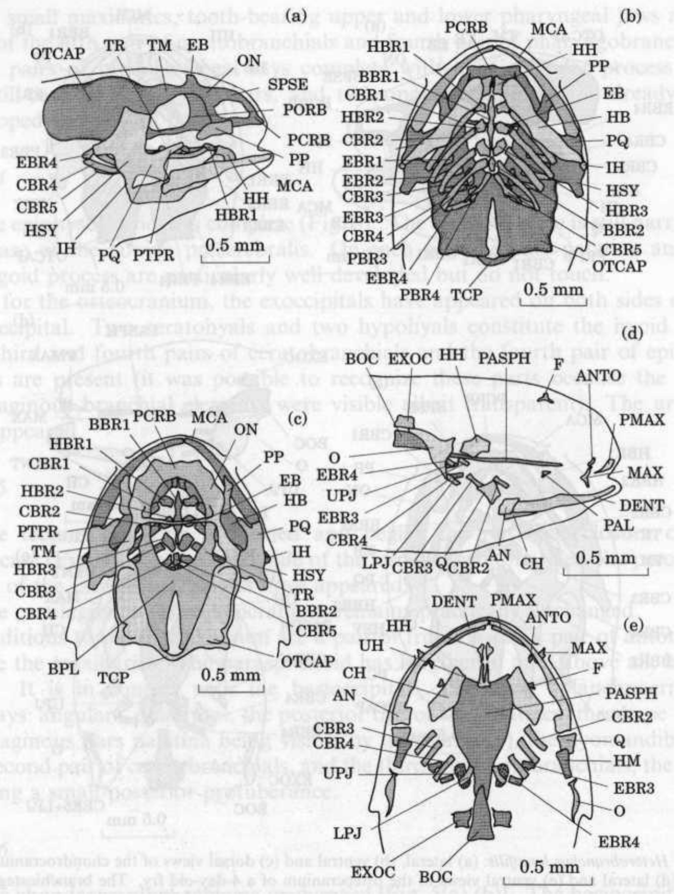
(a) lateral, (b) ventral and (c) dorsal views of the chondrocranium, and (d) lateral and (e) ventral views of the osteocranium of a 4-day-old fry. The branchiostegal rays and buccal teeth are not represented on Figs (d) and (e); BBR1, basibranchial 1; BBR2, basibranchial 2; BOC, basioccipital; CBR, Ceratobranchial; CH, ceratohyal; DENT, dentary; EB. epiphyseal bar; EBR, epibranchial; EXOC, exoccipital; HB, hyoid bar; HBR, hypobranchial; HH, hypohyal; HSY, hyosymplectic; IH, interhyal; LPJ, lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; O, opercular; ON, lamina orbitonasale; OTCAP, otic capsule; PASPH. parasphenoid; PBR. pharyngobranchial; PC. parachordal plate; PCRB, lamina precerebralis; PMAX, premaxillary; PORB, preorbital root; PP, pars palatina; PQ, pars quadrata; PRPT, pterygoid process; SPSE, commissura sphenoseptale; TM, taenia marginalis; TR. trabecular bar; UH, urohyal; UPJ, upper pharyngeal jaws.

DAY 5

The tectum posterius is formed and begins the posterior closure of the braincase (Fig. 4). On the inner side of the laminae orbitonasales, the preorbital roots of the taeniae marginales have appeared.

The cartilaginous Splanchnocranium remains practically unchanged. Additions to the osteocranium are a pair of frontals and a pair of antorbitals above the maxillaries. The parasphenoid has lengthened and, above all, broadened. It is in contact with the basioccipital. The bony Splanchnocranium displays: angulars, quadrates, the posterior tips of the palatines (the shape of the cartilaginous pars palatina being visible by transparency), the hyomandibulars, the second pair of Ceratobranchials, and the third pair of epibranchials, the latter bearing a small posterior protuberance.

Fig. 4. *Heterobranchus longifilis:*



(a) lateral, (b) ventral and (c) dorsal views of the chondrocranium, and (d) lateral and (e) ventral views of the osteocranium of a 5-day-old fry. It is hard to distinguish the angulars and retroarticulars from the dentaries in the ventral view (e). The branchiostegal rays and buccal teeth are not represented on Figs (d) and (e); AN, angular; ANTO, antorbital; BBR1, basibranchial 1; BBR2, basibranchial 2; BOC, basioccipital; BPL, basal plate; CBR, Ceratobranehial; CH, ceratohyal; DENT, dentary; EB, epiphyseal bar; EBR, epibranchial; EXOC. exoccipital; F, frontal; HB, hyoid bar; HBR, hypobranchial; HH, hypohyal; HM, hyomandibular; HSY, hyosymplectic; IH, interhyal; LPJ, lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; O, opercular; ON, lamina orbitonasale; OTCAP, otic capsule; PAL, palatine; PASPH, parasphenoid; PBR, pharyngobranchial; PC, parachordal plate; PCRB, lamina precerebralis; PMAX, premaxillary; PORB, preorbital root; PP, pars palatina; PQ, pars quadrata; PRPT, pterygoid process; Q, quadrate; SPSE, commissura Sphenoseptale; TCP, tectum posteriorus; TM, taenia marginalis; TR, trabecular bar; UH, urohyal; UPJ, upper pharyngeal jaws.

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DAY 6

The chondrocranium remains unchanged [Fig. 5(a),(b)]. The basioccipital has broadened anteriorly and is fused with the parasphenoid. Additions to the bony Splanchnocranium are the first pair of Ceratobranchials, the second pair of epibranchials, and the pair of epihyals. Nine pairs of branchiostegal rays are visible. The operculars appear to articulate with the hyomandibulars. The maxillaries have begun to penetrate into the pair of maxillary barbels.

DAY 7

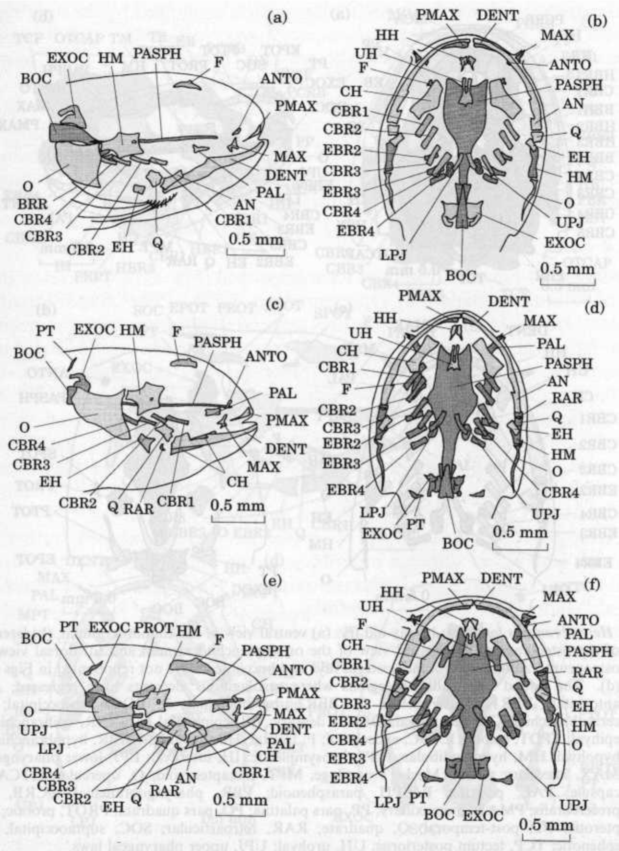
In the chondrocranium, Meckel's cartilage has been altered somewhat by the appearance of a small mediodorsal process [Fig. 5(c),(d)].

The osteocranium has progressed, now exhibiting the post-temporals, the lateral wings at the front of the basioccipital, an incipient retroarticular ossification, and fusion of each angular with the corresponding dentary.

DAY 8

The bony neurocranium now displays the primordia of the prootics [Fig. 5(e),(f)]. The first branchiospines have appeared on the second, third, and fourth pairs of ceratobranchials.

Fig. 5. *Heterobranchus longifilis:*

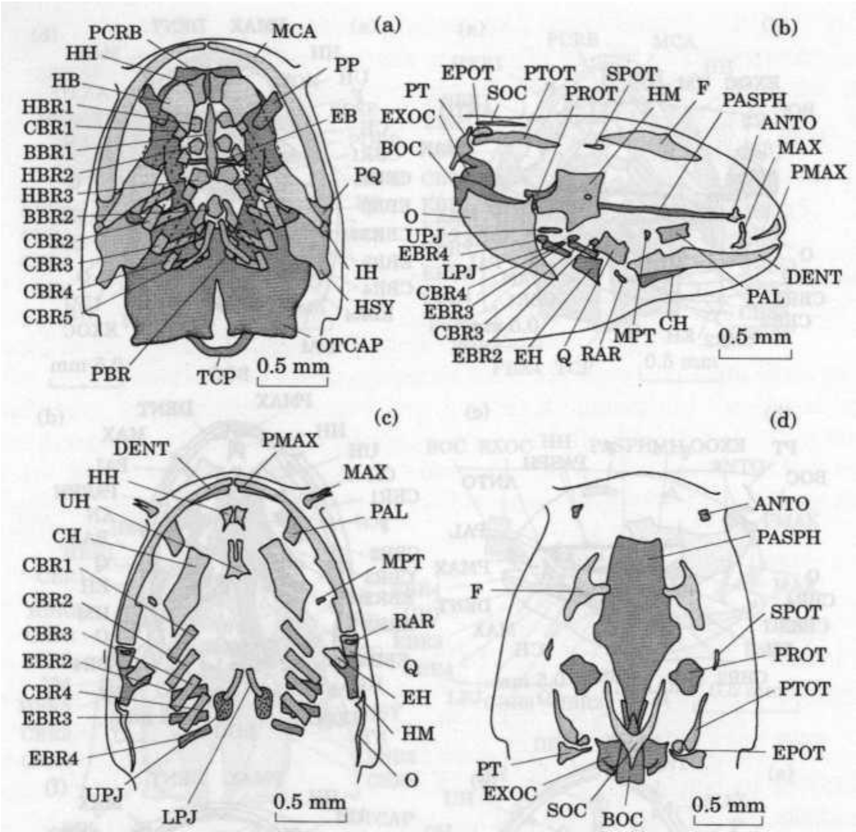


(a) lateral and (b) ventral views of the osteocranium of a 6-day-old fry; (c) lateral and (d) ventral views of the osteocranium of a 7-day-old fry; (e) lateral and (f) ventral views of the osteocranium of an 8-day old fry. The post-temporals are not represented on the ventral views (d) and (f). It is hard to distinguish the angulars and retroarticulars from the dentaries in ventral views (b), (d), and (f). The branchiostegal rays and buccal teeth are not represented; AN, angular; ANTO, antorbital; BOC, basioccipital; BRR, branchiostegal ray; CBR. Ceratobranchial; CH, Ceratohyal; DENT, dentary; EBR, epibranchial; EH, epihyal; EXOC, exoccipital; F, frontal; HH, hypohyal; HM, hyomandibular; LPJ, lower pharyngeal jaw; MAX, maxillary; O, opercular; PAL, palatine; PASPH, parasphenoid; PMAX, premaxillary; PROT, prootic; PT, post-temporal; Q, quadrate; RAR, retroarticular; UH, urohyal; UPJ, upper pharyngeal jaws.

DAY 10

The cartilaginous structures have begun to regress: the central parts of the first four Ceratobranchials and hyoid bars are disappearing (Fig. 6). The bony neurocranium now displays a Supraoccipital, pterotics, dermo- sphenotics, and epiotics. The anterior extremity of the processus pterygoideus has ossified and constitutes the beginning of a metapterygoid. At this stage, the opercular**s** articulate completely with the hyomandibulars.

Fig. 6. *Heterobranchus longifilis:*

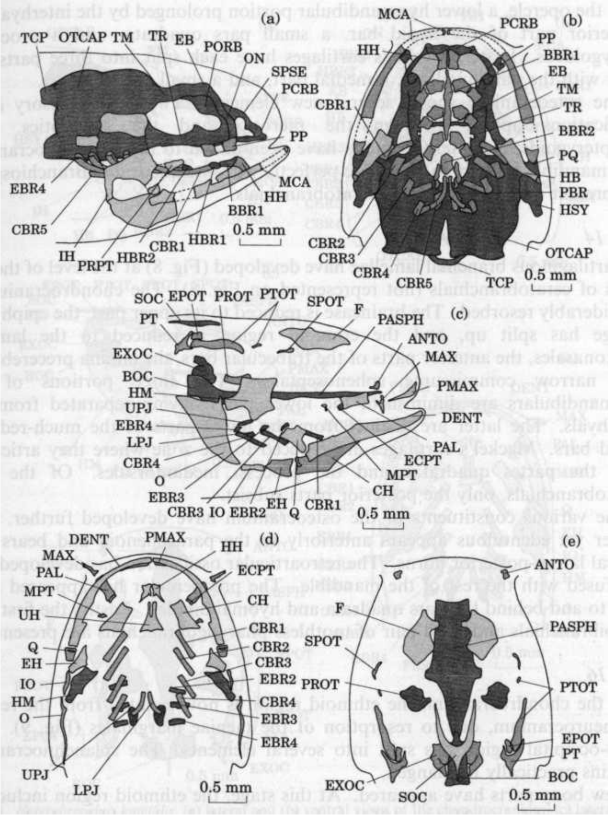


10-day-old fry: (a) ventral view of the chondrocranium, (b) lateral view of the osteocranium, (c) ventral view of the osteosplanchnocranium and (d) dorsal view of the osteoneurocranium. The branchiostegal rays and buccal teeth are not represented in Figs (b), (c), (d). The dotted lines indicate regions where cartilaginous elements have regressed; ANTO, antorbital; BBR1, basibranchial 1; BBR2, basibranchial 2; BOC, basioccipital; CBR. Ceratobranchial; CH, ceratohyal; DENT, dentary; EB, epiphyseal bar; EBR, epibranchial; EH, epihyal; EPOT, epiotic; EXOC, exoccipital; F, frontal; HB. hyoid bar; HBR, hypobranchial; HH, hypohyal; HM, hyomandibular; HSY, hyosymplectic; 1H, interhyal; LPJ, lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; MPT, metapterygoid; O, opercular; OTCAP, otic capsule; PAL, palatine; PASPH, parasphenoid; PBR, pharyngobranchial; PCRB, lamina precerebralis; PMAX, premaxillary; PP, pars palatina; PQ, pars quadrata; PROT, prootic; PTOT, pterotic; PT, post-temporal; Q, quadrate; RAR, retroarticular; SOC, Supraoccipital; SPOT, sphenotic; TCP, tectum posteriorus; UH, urohyal; UPJ, upper pharyngeal jaws.

DAY 12

The chondrocranium continues to regress (Fig. 7). Of the hyoid bars and first four pairs of Ceratobranchials, only the tips are visible. The palatines have begun to split centrally. On each side, the cartilaginous ' hyosymplectic- pars quadrata- processus pterygoideus-interhyal- hyoid bar ' entity has also split up, isolating an upper hyomandibular portion, a hyomandibular process articulating with the opercle, a lower hyomandibular portion prolonged by the interhyal, the posterior part of the hyoid bar, a small pars quadrata, and a processus pterygoideus. Lastly, Meckel's cartilages have each split into three parts: the joint with the pars quadrata, a medial part, and a small anterior part. The osteocranium shows several new elements. Two small sensory canal ossifications appear between the pterotics and the sphenotics. The ectopterygoids and interoperculars have been added to the Splanchnocranium. The mandible appears to articulate perfectly with the quadrate. Branchiospines are present on the first pair of Ceratobranchials.

Fig. 7. *Heterobranchus longifilis:*



(a) lateral and (b) ventral views of the chondrocranium, (c) lateral viewof the osteocranium, (d) ventral view of the osteosplanchnocranium and (e) dorsal view of the osteoneurocranium of a 12-day-old fry. The branchiostegal rays and buccal teeth are not represented in Figs (c), (d) and (e). The dotted lines indicate regions where cartilaginous elements have regressed; ANTO, antorbital; BBR1, basibranchial 1; BBR2, basibranchial 2; BOC, basioc- cipital; CBR, Ceratobranchial; CH, Ceratohyal; DENT, dentary; EB, epiphyseal bar; EBR, epibranchial; ECTP, ectopterygoid; EH, epihyal; EPOT, epiotic; EXOC, exoccipital; F, frontal; HB, hyoid bar; HBR. hypobranchial; HH, hypohyal; HM, hyomandibular; HSY. hyosymplectic; IH, interhyal; IO, interopercular; LPJ, lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; MPT, metapterygoid; O, opercular; ON, lamina orbitonasale; OTCAP, otic capsule; PAL, palatine; PASPH, parasphenoid; PBR, pharyngobranchial; PCRB, lamina precerebralis; PMAX, premaxillary; PORB, preorbital root; PP. pars palatina; PQ. pars quadrata; PROT, prootic; PTOT, pterotic; PT, post-temporal; PRPT, pterygoid process; Q, quadrate; SOC, Supraoccipital; SPOT, sphenotic; SPSE, commissura Sphenoseptale; TCP, tectum posteriorus; TM, taenia marginalis; TR, trabecular bar; UH, urohyal; UPJ, upper pharyngeal jaws.

DAY 14

Cartilaginous branchial lamellae have developed (Fig. 8) at the level of the five pairs of Ceratobranchials (not represented on Fig. 8). The chondrocranium is considerably resorbed. The braincase is reduced to its upper part, the epiphyseal bridge has split up, and the ethmoid region is reduced to the laminae orbitonasales, the anterior parts of the trabecular bars, the lamina precerebralis, and narrow commissurae sphenoseptales. The three portions of the hyomandibulars are diminished, the lower parts having separated from the interhyals. The latter are distinct from the lower parts of the much-reduced hyoid bars. Meckel's cartilages are reduced to the zone where they articulate with the partes quadratae and the processi mediodorsales. Of the fifth Ceratobranchials, only the posterior parts subsist.

The various constituents of the osteocranium have developed further. The vomer yet edentulous appears anteriorly to the parasphenoid and bears two typical latero-posterior horns. The retroarticular ossification has developed and has fused with the rest of the mandible. The preopercular has appeared right next to and behind the pars quadrata and hyomandibular. Lastly, the first pair of epibranchials and third pair of toothless pharyngobranchials are present.

DAY 16

In the chondrocranium, the ethmoid region is now isolated from the rest of the neurocranium, due to resorption of the taeniae marginales (Fig. 9). The otico-occipital region has split into several elements. The Splanchnocranium remains practically unchanged.

New bony parts have appeared. At this stage, the ethmoid region includes a dermethmoid *(sensu* Nawar, 1954) and already well-developed lateral ethmoids. The dermethmoid is bordered by nasals. The lachrymal is present just behind the antorbital. Two ossicles (the foremost of which appears to consist of two ossifications) complete the sub-orbital set. A pleurosphenoid (pterosphenoid according to Arratia, 1987) and a Suprapreopercular are present.

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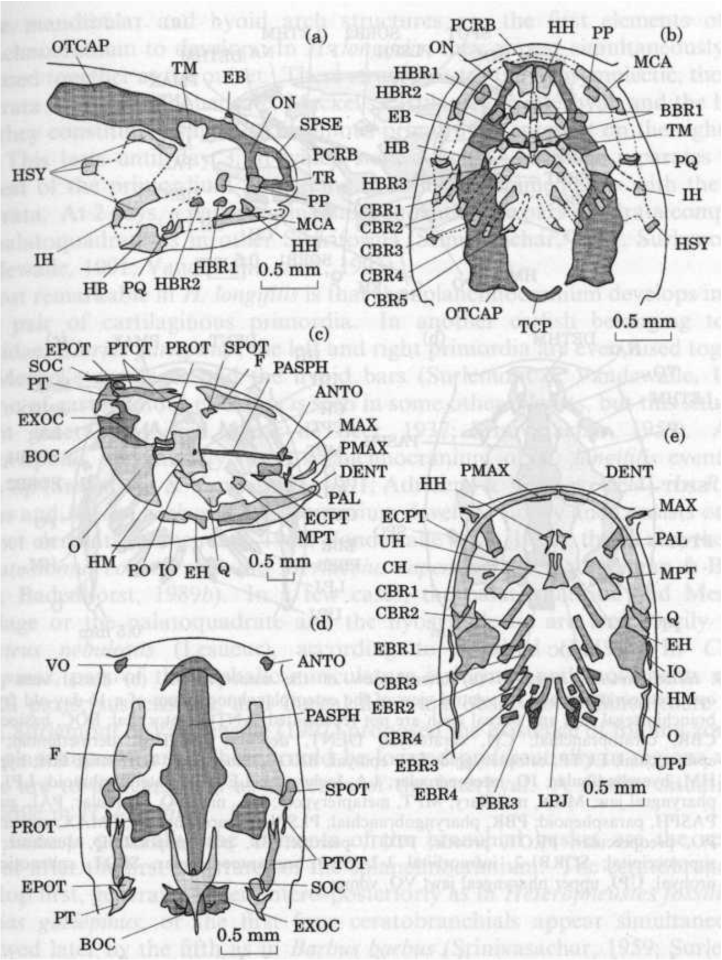
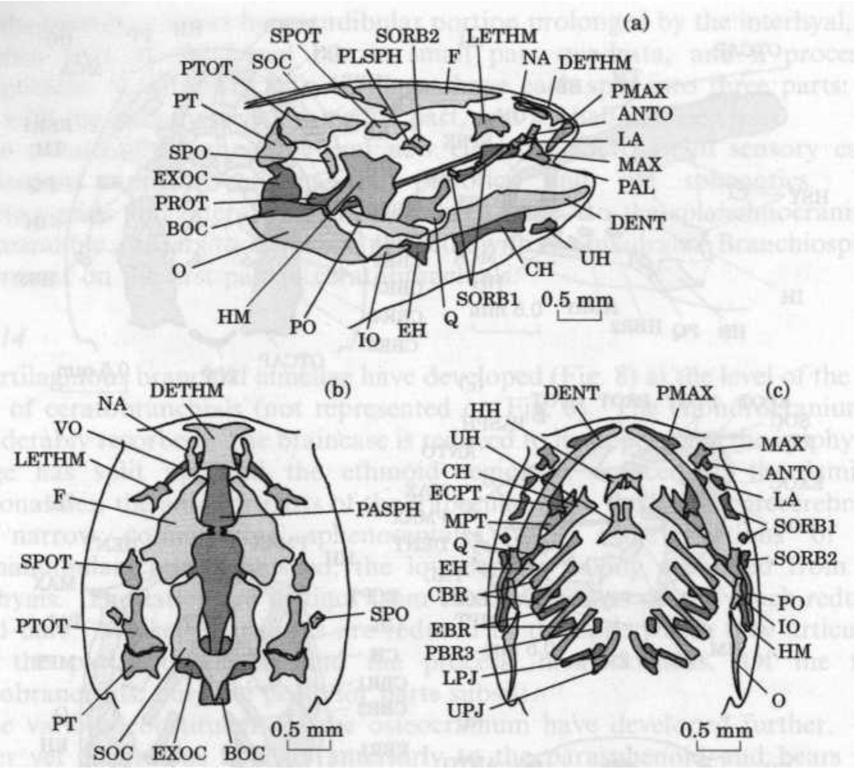
Fig. 8. *Heterobranchus longifilis:*



(a) lateral and (b) ventral views of the chondrocranium, (c) lateral view of the osteocranium, (d) dorsal view of the osteosplanchnocranium and (e) ventral view of the osteosplanchnocranium of a 14-day-old fry. The branchiostegal rays and buccal teeth are not represented in Figs (c), (d) and (e). The dotted lines indicate regions where cartilaginous elements have regressed; ANTO, antorbital; BBR1, basibranchial 1; BOC. basioccipital; CBR, Ceratobranchial; CH, Ceratohyal; DENT, dentary; EB, epiphyseal bar; EBR, epibranchial; ECTP, ectopterygoid; EH, epihyal; EPOT, epiotic; EXOC, exoccipital; F, frontal; HB, hyoid bar; HBR, hypobranchial; HH. hypohyal; HM, hyomandibular; HSY. hyosymplectic; IH, interhyal; IO, interopercular; LPJ, lower pharyngeal jaw; MAX, maxillary; MCA, Meckel's cartilage; MPT, metapterygoid; O, opercular; ON, lamina orbitonasale; OTCAP, otic capsule; PAL, palatine; PASPH, parasphenoid; PBR, pharyngobranchial; PCRB, lamina precerebralis; PMAX, premaxillary; PO, preopercular; PP, pars palatina; PQ, pars quadrata: PROT, prootic; PTOT, pterotic; PT. post-temporal; Q, quadrate; SOC, Supraoccipital; SPOT, sphenotic; SPSE, commissura Sphenoseptale; TCP. tectum posteriorus; TM, taenia marginalis; TR. trabecular bar; UH, urohyal; UPJ, upper pharyngeal jaw; VO, vomer.

Fig. 9. *Heterobranchus longifilis:*



(a) lateral view of the osteocranium, (b) dorsal view of the osteoneurocranium and (c) ventral view of the osteosplanchnocranium of a 16-day-old fry. The branchiostegal rays and buccal teeth are not represented; ANTO, antorbital; BOC, basioccipital; CBR, Ceratobranchial; CH, ceratohyal; DENT, dentary; DETHM, dermethmoid; EBR, epibranchial; ECTP, ectopterygoid; EH, epihyal; EXOC, exoccipital; F, frontal; HH. hypohyal; HM, hyomandibular; IO, interopercular; LA, lachrymal; LETHM, lateral ethmoid; LPJ, lower pharyngeal jaw; MAX, maxillary; MPT, metapterygoid; NA, nasal; O, opercular; PAL, palatine; PASPH, parasphenoid; PBR, pharyngobranchial; PLSPH, pleurosphenoid; PMAX. premaxillary; PO, preopercular; PROT, prootic; PTOT, pterotic; PT, post-temporal; Q, quadrate; SOC, Supraoccipital; SORB1-2, infraorbital 1-2; SPO, Suprapreopercular; SPOT, sphenotic; UH, urohyal; UPJ, upper pharyngeal jaw; VO, vomer.

DISCUSSION

It is hard to compare the appearance and development of the various skeletal structures in teleosts because of major differences in the morphological state at hatching, the timing of development according to species-related or individual peculiarities, and the conditions of maintenance in the laboratory.

Furthermore, authors do not agree as to the significance and definition of stages, and few studies cover all events from hatching onward.

Published in : Journal of Fish Biology (1997), vol. 50, n°2, pp. 227–253
DOI: 10.1111/j.1095-8649.1997.tb01355.x
Status : Postprint (Author's version)

CHONDROCRANIUM

Teleosts vary considerably as to the state of the chondrocranium at hatching. In *Salmo trutta* L., development of the chondrocranium begins well before hatching (de Beer, 1937). In species such as *Heteropneustes fossilis* (Bloch) and *Barbus barbus* (L.), the chondrocranium is partially present at hatching (Srinivasachar, 1959; Vandewalle *et al.,* 1992), while it does not appear until later in species such as *Rutilus rutilus* L., *Catostomus commersoni* (Lacépède) or *Clarias gariepinus* Burchell (Hubendick, 1942; Elman & Balon, 1980; Surlemont & Vandewalle, 1991). *H. longifilis* falls into the latter category, since the first structures begin to appear a few hours post-hatching.

The mandibular and hyoid arch structures are the first elements of the Splanchnocranium to develop. In *H. longifilis,* they appear simultaneously and are fused together at the outset. These structures are the hyosymplectic, the pars quadrata of the palatoquadrate, Meckel's cartilage, the interhyal, and the hyoid bar; they constitute a single cartilaginous primordium, present on the right and left. This lasts until day 3, at which stage Meckel's cartilage separates from the rest of the primordium and seems to articulate immediately with the pars quadrata. At 2 days, a pars palatina independent of the pars quadrata completes the palatoquadrate as in other Siluriforms (Srinivasachar, 1959; Surlemont & Vandewalle, 1991; Vandewalle *et al.,* 1993).

Most remarkable in *H. longifilis* is that the Splanchnocranium develops in 12 h as a pair of cartilaginous primordia. In another catfish belonging to the Clariidae, *Clarias gariepinus,* the left and right primordia are even fused together via Meckel's cartilages and the hyoid bars (Surlemont & Vandewalle, 1991). Fusion of cartilaginous elements is seen in some other teleosts, but this situation is not general (Kindred, 1919; de Beer, 1937; Srinivasachar, 1959). As in *C. gariepinus,* the initially fused Splanchnocranium of *H. longifilis* eventually splits up (Surlemont & Vandewalle, 1991; Adriaens & Verraes, 1994). In *Rutilus rutilus* and *Barbus barbus,* the suspensorium develops slowly and consists only of distinct elements (Hubendick, 1942; Vandewalle *et al.,* 1992); this is also the case in *Catostomus commersoni* and *Merluccius capensis* Castelnau (Elman & Balon, 1980; Badenhorst, 1989*b*). In a few cases, the palatoquadrate and Meckel's cartilage or the palatoquadrate and the hyosymplectic are temporarily fused [*Ameirus nebulosus* (Lesueur), according to Kindred (1919)]. In *Clarias gariepinus,* part of the cephalic musculature is formed and movements of the buccal parts, suspensoria, and buccal floor are observable. Since there is no joint, Surlemont & Vandewalle (1991) proposed the existence of folding zones in the Splanchnocranium. These would be located preferentially in regions where joints are to appear, such as the ends of the interhyal. A similar situation is probable in *H. longifilis.*

In teleosts generally, the elements of the branchial basket are the next to appear after the first structures of the Splanchnocranium. The Ceratobranchials develop first, generally either antero-posteriorly as in *Heteropneustes fossilis* and *Clarias gariepinus,* or the first four Ceratobranchials appear simultaneously, followed later by the fifth as in *Barbus barbus* (Srinivasachar, 1959; Surlemont

& Vandewalle, 1991; Vandewalle *et al.,* 1992). In some species, all five Ceratobranchials appear at the same time *[Gasterosteus aculeatus* L., according to Swinnerton (1902); *Rutilus rutilus,* according to Hubendick (1942); *Catostomus commersoni,* according to Elman & Balon (1980)]. *Heterobranchus longifilis* appears to follow the same pattern as *Barbus barbus* (Vandewalle *et al.,* 1992), but the development of *H. longifilis* is so fast that the simultaneity of the appearance of the first four Ceratobranchials may be only apparent. Four epibranchials and two pharyngobranchials appear together shortly afterward (day 2). Given their positions facing epibranchials three and four, the pharyngobranchials probably belong to the third and fourth arches. In other species the first epibranchial sometimes appears before the posterior Ceratobranchials (Srinivasachar, 1959). In *H. longifilis,* the branchial basket displays at 2 days all the elements found in many adult Siluriforms (Nawar, 1954; Srinivasachar, 1959). In adult specimens, however, the third pharyngobranchial is much larger than the fourth.

In *Heterobranchus longifilis,* the trabecular bars, the bases of the lateral walls of the otic capsules, the parachordal plates, and the commissurae basicapsulares anteriores all appear at the same time, just after the first elements of the Splanchnocranium. At the outset they are fused. It seems to be a general rule in teleosts that the first structures of the neurocranial floor appear before the rest of the neurocranium. The trabeculae and parachordal plates always appear first. Sometimes they rapidly fuse together, as in *Salmo trutta* (after de Beer, 1937), sometimes they are fused at the outset, as in *Heteropneustes fossilis* (after Srinivasachar, 1959), *Clarias gariepinus* (after Surlemont & Vandewalle, 1991), and *Galeichthys felis* Valenciennes (after Bamford, 1948), and sometimes fusion does not take place until later, as in *Rutilus rutilus, Catostomus commersoni* and *Barbus barbus* (Hubendick, 1942; Elman & Balon, 1980; Vandewalle *et al.,* 1992). In 5·5-mm long *Clupea harengus* L., and 5·2-mm long *Clarias gariepinus* specimens, all the primordia of the neurocranium constitute a single cartilaginous unit (Wells, 1923; Surlemont & Vandewalle, 1991).

As development progresses, the order in which the elements of the neurocranium appear and their rate of development are variable. In *Anguilla anguilla* L., for example, the ethmoid and orbital regions develop before the otic capsules (de Beer, 1937); while in *Heteropneustes fossilis, Clarias gariepinus,* and *Heterobranchus longifilis,* the floor of the braincase develops first, followed by the anterior part (Srinivasachar, 1959; Surlemont & Vandewalle, 1991).

In *H. longifilis, Galeichthys felis* and *Heteropneustes fossilis* the chondrocranium develops a basal plate quite early, by fusion of the anterior parts of the parachordal plates (Bamford, 1948; Srinivasachar, 1959). The basal plate is late to appear in *Ameirus nebulosus, Salmo trutta, Merluccius capensis* and *Barbus barbus* (Kindred, 1919; de Beer, 1937; Badenhorst, 1989«; Vandewalle *et al.,* 1992). Dorso-posterior closure of the neurocranium by the tectum posterius is slow in all seven of the species just mentioned. In all these species the base of the neurocranium thus appears to develop earlier than its roof.

While the general composition of the chondrocranium appears fairly constant, there are nevertheless some specific variations. Both *Heteropneustes fossilis* and

Barbus barbus, for instance, display a basihyal in the hyoid arch (Srinivasachar, 1959; Vandewalle *et al.,* 1992), that is absent in *H. longifilis.*

Among teleosts, the shape of the ethmoid plate in the anterior region is variable. In *Barbus barbus,* the plate is formed by the anterior fusion of the two trabecular bars (Vandewalle *et al.,* 1992). In *Ameirus nebulosus, Catostomus commersoni, Rutilus rutilus* and *Nerophis aequoreus* L., it then develops into an actual platform (Kindred, 1919; Elman & Balon, 1942; Hubendick. 1942; Kadam, 1961). In *H. longifilis,* the ethmoid plate appears to consist only of the base of the lamina precerebralis and remains narrow at least until day 14.

In *H. longifilis,* as in *Heteropneustes fossilis* (after Srinivasachar, 1959), the bases of the taeniae marginales appear quite early, extending from the antero-dorsal part of the otic capsule on each side. They continue to develop forward to produce the base of the epiphyseal bridge as in *Distichodus brevipinnis* Giinther, *Merluccius capensis* and *Barbus barbus,* forming the limits of two fontanels (Daget, 1959; Badenhorst, 1989*a*; Vandewalle *et al.,* 1992). In *Salmo trutta Heterotis niloticus* (Cuvier), and *Catostomus commersoni,* parts of the epiphyseal bridge and taeniae marginales appear dorsally, isolated in the middle of the orbit. The latter then proceeds to develop posteriorly, finally joining with the front of the otic capsules (de Beer, 1937; Daget & D'Aubenton, 1957; Elman & Balon, 1980). *Anguilla anguilla* and *Heteropneustes fossilis* display a peculiarity at this level: the taeniae marginales do not appear to be linked dorsally by an epiphyseal bridge (de Beer, 1937; Srinivasachar, 1959).

In *Barbus barbus,* the lamina precerebralis, taeniae marginales, and trabecular bars are linked *via* the laminae orbitonasales, which seem to be directly associated with the preorbital roots of the taeniae marginales (Vandewalle *et al.,* 1992). In *H. longifilis,* on the other hand, the preorbital roots don't develop until later, independently of the laminae Orbitonasales.

In *H. longifilis,* as well as in *Heteropneustes fossilis* and *Clarias gariepinus,* the pilae laterales and commissurae laterales are not developed and thus do not divide the sphenoid fenestrae into three (Srinivasachar, 1959). In other species, the commissurae basicapsulares anteriores appear at the beginning of development, so the fenestrae basicapsulares anteriores are initially visible, then disappear (Badenhorst, 1989*a*). In *Haplochromis elegans* Trewawas, and *Barbus barbus,* these fenestrae are limited but the sphenoid fenestrae are not divided (Verraes & Ismail, 1980; Vandewalle *et al.,* 1992). In *Salmo trutta,* the commissurae basicapsulares anteriores remain distinct, thus limiting a fenestra basicapsularis anterior, and the commissurae laterales divide the sphenoid fenestra in two, as in *Nerophis aequoreus* (de Beer, 1937; Kadam, 1961).

H. longifilis has no tectum Synoticum completing the roof of the braincase in front of the tectum posterius, nor does it have, as do *Mormyrus rume* Valenciennes, *Anisotremus davidsonii* (Steindachner), and *Xenistius Californiensis* (Steindachner) (Daget & D'Aubenton, 1960; Watson & Walker, 1992), any taenia tecta medialis formed from the mediordorsal extensions issuing posteriorly from the braincase roof and anteriorly from the epiphyseal bridge. In the latter species there are thus two posterior fontanels. In *Salmo trutta,* *Merluccius capensis* and *Barbus barbus,* a taenia tecta medialis also develops but it seems to arise only at the level of the epiphyseal bridge (de Beer, 1937; Badenhorst, 1989*a*; Vandewalle *et al.,* 1992). The hypophyseal fenestra limited by the parachordal plates and trabecular bars is wider in *H. longifilis.* At 5 days, the chondroneurocranium of *H. longifilis* is already complete and as developed as that of *Barbus barbus* at 24 days (Vandewalle *et al.,* 1992). It will remain at this level of construction until day 12, increasing only in size.

Regression of the cartilages begins at different developmental stages in different species. In *H. longifilis,* the first signs of resorption appear at 10 days. Resorption can thus be considered a late occurrence in this species, beginning with the central parts of the Ceratobranchials and hyoid bars. In *Merluccius capensis,* the posterior part of the trabecular bars regresses first, very rapidly isolating, ventrally, the anterior and posterior parts of the neurocranium; next the first four pairs of Ceratobranchials and the Ceratohyals begin to regress, along with Meckel's cartilages (Badenhorst, 1989*b*). In *Barbus barbus,* regression also begins with the ventral separation of the anterior and posterior parts of the neurocranium, followed by regression of the fifth Ceratobranchials (Vandewalle *et al.,* 1992).

In *H. longifilis,* Meckel's cartilage regresses at two places, splitting into three discernable pieces. One piece is situated at the anterior extremity. Isolation of a cartilaginous element in front of the mandible is a fact that may shed some doubt on the purely dermal origin of the dentaries. The latter might have absorbed the small, anterior cartilaginous elements and thus have a double origin, like the palatines. Concomitant with regression of Meckel's cartilages are the left and right cartilaginous primordia, which split into five parts: the hyomandibular, the process through which the opercular articulates with it, the medial part of the hyomandibular with which the interhyal remains fused, the posterior part of the hyoid bar, and the pars quadrata. In *Barbus barbus,* the parts of the suspensorium do not begin to regress until later, each hyosymplectic splitting into a hyomandibular and a Symplectic (Vandewalle *et al.,* 1992).

Regression of the neurocranium is not observed until 14 days in *H. longifilis,* but several structures are affected simultaneously: the bases of the lateral walls of the otic capsules, the trabecular bars, and the parachordal plates. Meckel's cartilage regresses concomitantly: the posterior part is reduced to its joint with the quadrate, the processus mediodorsalis becomes separated from the central part, and the anterior part disappears completely. The processus mediodorsalis might become the corono-meckelian. By day 16, the ethmoid region is entirely separated from the braincase. Although regression of the branchial basket begins at 10 days with the Ceratobranchials, it is surprising to note that regression of these elements is not yet complete by day 14, whereas the cartilaginous pharyngobranchials and epibranchials have disappeared.

OSTEOCRANIUM

The bony development of the cephalic skeleton is quite variable in teleosts (de Beer, 1937; Bamford, 1948; Jollie, 1984; Matsuura & Yoneda, 1987).

Published in : Journal of Fish Biology (1997), vol. 50, n°2, pp. 227–253
DOI: 10.1111/j.1095-8649.1997.tb01355.x
Status : Postprint (Author's version)

At hatching, there is no ossified element in *H. longifilis, Clarias gariepinus, Barbus barbus,* or *Chrysichthys auratus* (Geoffroy Saint-Hilaire) (Surlemont & Vandewalle, 1991; Vandewalle *et al.,* 1992; Vandewalle *et al.,* 1995). *Galeichthys felis* appears as an exception, since the dentaries, operculars, and premaxillaries are already present at hatching in this species (Tilney & Hecht, 1993).

The first bones to appear generally belong to the dermal Splanchnocranium. In *Clarias gariepinus* and *Oncorhynchus mykiss* (Walbaum), the operculars appear first, followed by the premaxillaries, the maxillaries, the dentaries, the inferior and superior pharyngeal tooth plates (Verraes, 1977). In *Chrysichthys auratus,* ossification of the skull begins with the dentaries, the operculars, and two pairs of branchiostegal rays, followed by the maxillaries and operculars (Vandewalle *et al.,* 1995); the pharyngeal tooth plates do not appear until the next stage along with the first buccal teeth. In three *Silurus* species, the maxillaries and premaxillaries appear first (Kobayakawa, 1992). The pharyngeal jaws come first in *Rutilus rutilus* (after Hubendick, 1942). In *Lophius gastrophysus* Ribeiro, there directly appears a pair each of maxillaries, premaxillaries, dentaries, operculars, and Suboperculars (Matsuura & Yoneda, 1987). In *Xenistius Californiensis,* the maxillaries appear first, followed by the premaxillaries and dentaries (Watson & Walker, 1992). In *Anisotremus davidsonii,* the first to appear are the premaxillaries, maxillaries, dentaries, preoperculars, and operculars (Watson & Walker, 1992). In *Nerophis aequoreus,* the first ossifications are a pair each of maxillaries, premaxillaries, dentaries, and angulars (Kadam, 1961). In the Cyprinid *Barbus barbus,* it's the operculars, maxillaries, and dentaries that develop first, followed by the pharyngeal jaws (fifth Ceratobranchials) (Vandewalle *et al.,* 1992). At the start of development in *Esox lucius* L., only the maxillaries are present, closely followed by the premaxillaries (Jollie, 1975).

In *H. longifilis,* the first ossifications are elements of the dermal Splanchnocranium. The maxillaries, dentaries, premaxillaries, operculars, and upper and lower pharyngeal jaws appear simultaneously at 3 days. The dentaries and maxillaries are particularly well developed. In *H. longifilis,* as in *Silurus* sp., *Clarias gariepinus,* and *Chrysichthys auratus,* the maxillary is placed, at the outset, at the base of the barbel as in the adult, and thus does not contribute to forming the contour of the mouth (David, 1936; Poll, 1942; Tilak, 1963; Schaefer, 1990; Surlemont & Vandewalle, 1991; Kobayakawa, 1992; Vandewalle *et al.,* 1995). This means there is no transient primitive state where the premaxillaries and maxillaries are juxtaposed. In all species with a protractile mouth whose development is at least partially known *(Haplochromis elegans, Lophius gastrophysus, Lutjanus campechanus* (Poey), *Anisotremus davidsonii* and *Xenistius Californiensis, Sillago japonica* Temminck & Schlegel, *Barbus barbus* and *Centropomus undecimalis* (Bloch)], the maxillaries and premaxillaries are superposed from the time they are formed (Otten, 1982; Matsuura & Yoneda, 1987; Potthoff *et al.,* 1988; Watson & Walker, 1992; Oozeki *et al.,* 1992; Vandewalle *et al.,* 1992; Potthoff & Tellock, 1993). The primitive situation thus seems to exist only in those species which retain it in adulthood. In *Esox lucius* and *Oncorhynchus kisutch* (Walbaum), the maxillaries and premaxillaries are indeed juxtaposed from the time of their appearance to adulthood (Jollie, 1975, 1984).

In *H. longifilis,* the pharyngeal jaws appearing on day 3 bear teeth. It is hard to determine whether the tooth plates are purely dermal or whether there is already an ossified cartilaginous component. At this stage, moreover, the tooth-bearing upper pharyngeal jaws are larger than the cartilaginous pharyngobranchials three and four and might thus each be supported by these two elements together. Not until day 14, when a second dorsal ossification appears opposite the first in continuation of epibranchial three, can one assert that the tooth plate is supported solely by pharyngobranchial four, as in adult Clariidae (Nawar, 1954).

The first ossifications of the cartilaginous Splanchnocranium of *H. longifilis* are the ceratohyals, hypohyals, third and fourth Ceratobranchials, and fourth epibranchials. Then antero-posteriorly appear the remaining cerato- and epibranchials. From the time it appears, the third epibranchial bears an uncinate process as in the adult (Nawar, 1954; Vandewalle *et al.,* 1995). The first epibranchial appears late, at 14 days.

In many teleosts, after ossification of the pharyngeal jaws, the first four Ceratobranchials are simultaneously added to the branchial basket, either just before or concomitantly with the epibranchials.

In Siluriforms, the first endochondral ossifications of the suspensorium appear after the first dermal elements, progressively replacing the existing cartilaginous skeleton. In *H. longifilis,* the quadrates, hyomandibulars, and palatines are the next to ossify after the Ceratobranchials. The Symplectics are absent in this species up to day 16, as in many adult Siluriforms (Nawar, 1954; Jayaram, 1970; Mahy, 1974; Taverne & Aloulou-Triki, 1979). The same applies to three *Silurus* species and to *Chrysichthys auratus* (Kobayakawa, 1992; Vandewalle *et al.,* 1995). In the latter, the suspensorium and branchial basket begin to ossify at the same time. In many non-Siluriform teleosts, the hyomandibulars and palatines develop later, after the dermal bones of the suspensorium (entopterygoids, ectopterygoids). In *Lophius gastrophysus,* the palatines and quadrates are the first ones present, followed by the hyomandibulars (Matsuura & Yoneda, 1987). *Barbus barbus* first displays ossification of the quadrate, then of the ento- and ectopterygoids, and finally of the hyomandibular and palatine (Vandewalle *et al.,* 1992). In *Nerophis aequoreus,* the quadrates appear at the same time as the first dermal structures of the Splanchnocranium (Kadam, 1961). In *Esox lucius,* the hyomandibulars, symplectics, and quadrates all appear at the same time but quite a bit later than the ectopterygoids (Jollie, 1975).

In *H. longifilis,* as in *Chrysichthys auratus,* two new ossifications of the suspensorium appear after those of the hyomandibular, quadrate, and palatine (Vandewalle *et al.,* 1995). We have called them the metapterygoid and ectopterygoid. The first, probably situated at the tip of the cartilaginous processus pterygoideus, occupies a place corresponding to that of the metapterygoid of adult Clariidae (Nawar, 1954). Vandewalle *et al.* (1993), however, have called a similar structure found in 15-mm *Clarias gariepinus* the entopterygoid, because the ossification seems external to and independent of the processus pterygoideus. The second ossification is situated behind and below the palatine, which is the usual location of an ectopterygoid and considered as such by Tilak (1963), Mahy (1974), and Taverne & Aloulou-Triki (1974). Yet several authors call this ossification 'entopterygoid' (Nawar, 1954; Howes, 1985; Kobayakawa, 1992), ' dermopalatine ' (Vandewalle *et al.,* 1993), or perhaps ' bone 4 of Mc Murrich ' (Arratia, 1987).

The joints of the suspensorium appear to become functional quite quickly, as soon as endochondral ossification begins. In *H. longifilis,* the quadrato-mandibular joint appears at 5 days, the hyomandibulo-opercular joint at 6 days. These events occur in the same order in *Chrysichthys auratus* (after Vandewalle *et al.,* 1995). In *Barbus barbus,* the quadrato-mandibular and hyomandibulo-opercular joints become functional simultaneously (Vandewalle *et al.,* 1992).

Development of the neurocranium begins rapidly, almost always with the appearance of the parasphenoid immediately after that of the first dermal structures of the Splanchnocranium (Kadam, 1961; Ismail *et al.,* 1982; Jollie, 1984). Growth of the parasphenoid seems related to the shape of the hypophyseal fenestra, which it probably closes progressively. The parasphenoid broadens in species with a platytrabic skull such as *H. longifilis, Oncorhynchus kisutch, Clarias gariepinus, Barbus barbus, Chrysichthys auratus* (Jollie, 1984; Surlemont & Vandewalle, 1991; Vandewalle *et al.,* 1992; Vandewalle *et al.,* 1995). It remains narrow in species with a tropitrabic skull such as *Astatilapia elegans* Trewawas, *Anisotremus davidsonii* and *Xenistius Californiensis* (Verraes *et al.,* 1982; Watson & Walker, 1992). In other species, the parasphenoid may appear at the same time as the dermal parts of the Splanchnocranium, as in *Nerophis aequoreus* and three *Silurus* species (Kadam, 1961; Kobayakawa, 1992). In *Esox lucius,* the vomer appears at the same time as the parasphenoid, just after the first dermal bony structures (Jollie, 1975).

A second bone of the braincase floor appears very early in development: the basioccipital. In *Barbus barbus,* it even appears just before the parasphenoid (Vandewalle *et al.,* 1992). In *B. barbus* and *Chrysichthys auratus,* the exoccipitals appear shortly after the basioccipital (Vandewalle *et al.,* 1992, 1995), while in *Nerophis aequoreus* they appear at the same time as the basioccipital but later in development (Kadam, 1961). The latter pattern also applies to *Esox lucius* (after Jollie, 1975). In *Oncorhynchus kisutch,* the exoccipitals appear at the same time as the parasphenoid, and thus after the first dermal structures of the Splanchnocranium (Jollie, 1984). In *H. longifilis,* the first stage of development of the bony neurocranium begins on day 3 with the parasphenoid and basioccipital, concomitantly with the first dermal structures of the Splanchnocranium.

After the appearance of the exoccipitals (day 4) and frontals (day 5), construction of the bony neurocranium then proceeds more slowly in *H. longifilis* than that of the bony Splanchnocranium. It isn't until quite late that the braincase roof develops, with the appearance of the post-temporals, supra-occipitals, and epiotics, accompanied first by formation of the pterotics and sphenotics, then by construction of the front of the neurocranium, notably the frontals. In some species such as *Anisotremus davidsonii* and *Xenistius Californiensis,* the primordia of the frontals and of several other parts of the braincase appear quite early (Watson & Walker, 1992). In *Barbus barbus* (after Vandewalle *et al.,* 1992), three *Silurus* species (Kobayakawa, 1992), and *Chrysichthys auratus* (after Vandewalle *et al.,* 1995), the Supraoccipitals, pterotics, and sphenotics all develop concomitantly with the frontals. In *Oncorhynchus kisutch* and *Galeichthys felis* (Jollie, 1984; Tilney & Hecht, 1993), the post-temporals and frontals appear at the same time as the parasphenoid, whereas in *Esox lucius* they appear just after it (Jollie, 1975).

The later development of the rest of the bony skeleton involves the appearance of the front of the neurocranium, particularly the ethmoid region, and enlargement of the parts already present.

It is easy to note, by comparing individuals at the same developmental stage but stained with either alcyan blue or alizarin, that many ossifications of the endochondral skeleton appear where regression of cartilages is about to occur. Ossification begins before regression. In the Splanchnocranium, this correspondence can be seen at the level of the Ceratobranchials, Ceratohyals, and parts of the suspensorium. The cartilages regress while the ossified elements are already in place. The dentary is well formed by the time Meckel's cartilage begins to regress. In the *H. longifilis* neurocranium, the braincase begins to regress in its latero-ventral part when the exoccipitals, sphenotics, pterotics, and prootics are already present. There is one remarkable exception which concerns the floor of the neurocranium: the trabecular bars regress before any bony structure of endochondral origin is present at that level, the parasphenoid being a membrane bone that appears early between the trabecular bars.

CONCLUSIONS

Unlike that of some other teleosts (de Beer, 1937), the cephalic skeleton of *H. longifilis* is absent at hatching. Like *Clarias gariepinus,* however, *H. longifilis* makes up quickly for its late start, first with the appearance of part of the Splanchnocranium, then immediately with the formation of the first neurocranial elements. At the outset, the cartilaginous primordia are fused, forming one Splanchnocranial and one neurocranial skeletal entity on each side. Not until later (day 2) does the Splanchnocranium begin to split up into its constituents.

Development of the cephalic skeleton is not uniform in *H. longifilis* (Table I). We distinguish a first stage during which the cartilaginous structures arise, a second stage characterized by the appearance of the initial, principally dermal, bony structures, and a last stage marked by cartilage resorption and an increase in the number of bony elements. This succession of stages in early development does not appear, or at least not so clearly, in the other teleosts studied in this respect.

Formation of the *H. longifilis* skull must meet the survival requirements of the fry. At hatching, as in many other teleosts, respiration is cutaneous and the highly vascularized yolk sac plays an important role in this process. The food supply, furthermore, is endogenous. There appears to be no need, *a priori,* for any skeletal structure.

As the yolk sac is resorbed, the importance of cutaneous respiration should diminish. As it does, aquatic branchial respiration should increase, as suggested by the appearance of the first four Ceratobranchials. These are doubtless sufficient, for a time, to ensure the necessary complementary respiration. The fifth Ceratobranchials, whose role has rather to do with food ingestion, develop later. By day 3, the yolk sac has disappeared. Cutaneous respiration is probably very limited, but by then the epibranchials have been added to the branchial basket.

Resorption of the yolk sac forces the fry to switch from an endogenous to an exogenous food supply (Table I). This implies an organization of the buccal cavity enabling the fry to take up food from the external aquatic medium. The buccal cavity must be clearly limited to ensure efficient food ingestion without damage to the other parts of the head, e.g. the brain. Accordingly, the parasphenoid and basioccipital are present at 3 days. The former is already quite broad and closes at least partially the hypophyseal fenestra, while the latter reinforces the braincase floor. Any physical and mechanical interactions, due to food ingestion, between the buccal cavity and the brain should thus be minor. The buccal jaws individuate, ossify, and articulate with the pars quadrata. The bony tooth-bearing pharyngeal jaws develop, thus constituting a system for seizing and processing food. At the same time the suspensorium broadens, then becomes reinforced by ossifications and the opercular appears; these developments enable the fry to begin to ingest food by sucking it in, a mechanism typical of animals living in an aquatic medium (Lauder, 1985).

The efficiency of suction feeding should increase progressively with the construction of the cheeks, opercles, and buccal roof.

The first ossifications of the branchial basket are the pharyngeal jaws, involved in food ingestion. The remainder ossifies gradually in an original fashion, posteriorly to anteriorly. Although it seems difficult to justify this development, it might have something to do, in the case of the epibranchials at least, with air breathing, a phenomenon existing in most Clariidae (Moussa, 1956; Hughes & Munshi, 1973). The organs of aerial respiration consist principally of two pairs of arborescent structures borne by the fourth and second epibranchials. The posterior respiratory structures, more developed than the anterior ones, may appear before the latter, thus explaining why the fourth epibranchials appear first. The second epibranchials would ossify later with the appearance of the anterior air-breathing structures. In this context it seems justified that the first epibranchials, which bear no respiratory arborescences, appear later.

Table 1. *Heterobranchus longifilis: timing of the appearance and development of the cephalic skeletal structures*

Age (days or h)	Cartilages	Ossifications
Hatching	No skeletal structures	
Day 1 (27° C)	Appear: hyosymplectics-interhyals-hyoid bars-pars quadrata-Meckel's cartilages	
36 h (27° C)	Appear: trabecular bars, parachordal plates, commissurae basicapsulares anteriores, bases of the latero-dorsal walls of the otic capsules	
Day 2 (27° C)	Appear: first signs of the taeniae marginales, Ceratobranchials 1-2-3-4,	
Day 1 (29° C)	basibranchial 1	
Day 2 (29° C)	Appear: basal plate, laminae orbitonasales, lamina precerebralis, commissurae sphenoseptales, pars palatina, hypohyals, Ceratobranchials 5, hypobranchials 1-2-3, epibranehials 1-2-3-4. pharyngobranehials 3-4, separation of Meckel's cartilage from the pars quadrata	
Day 3*	Appear: processi pterygoidei, basibranchial 2, Meckel's cartilage separates from the rest of the suspensorium	Basioccipital, parasphenoid, maxillaries, dentate premaxillaries, dentate dentaries, operculars, upper and lower dentate pharyngeal jaws, 7 pairs of branchiostegal rays
Day 4	Appears: epiphyseal bridge	Exoccipitals, ceratohyals, hypohyals, Ceratobranchials 3-4, epibranehials 4, urohyal

Day 5	Appear: tectum posterius, preorbitals roots of the taeniae marginales	Frontals, lachrymals, angulars, quadrates, palatines, hyomandibulars, Ceratobranchials 2, epibranehials 3
Day 6		Ceratobranchials 1, epibranehials 2, epihyals, 2 pairs of branchiostegal rays
Day 7	Appear: ascending processes of Meckel's cartilages	Posttemporals, retroarticulars
Day 8		Prootics, branchiospines on Ceratobranchials 2-3-4
Day 10	Regress: central part of Ceratobranchials 1-2-3-4, central part of hyoid bars	Supraoccipital, pterotics, sphenotics. epiotics, metapterygoids
Day 12	Regress: central part of palatines, splitting into hyosymplectics, quadrates, interhyals, hyoid bars, hyomandibulo-opercular joint process, Meckel's cartilages divided in three	Ectopterygoids, interoperculars, branchiospines on Ceratobranchials 1
Day 14	Appear: branchial lamellae Regress: braincase floor, anterior part of Ceratobranchials 5, epibranehials, and pharyngobranehials	Vomer, pre-operculars, epibranchials 1. pharyngobranehials 3
	Regress: taeniae marginales, splitting of the braincase into three parts	Lachrymal, suborbital 2, pleurosphenoid, Suprapreopercular

* Resorption of the yolk sac.

The other skeletal structures in the head of *H. longifilis* may not be subject to such crucial or obvious functional imperatives. Their late appearance or slow development should thus not compromise fry survival.

The many differences between teleosts in the development of the cephalic skeleton may reflect specific survival requirements. One feature, however, appears common to all: the appearance of the parasphenoid and/or basioccipital, and of the first dermal ossifications of the Splanchnocranium, just before or concomitantly with the disappearance of the yolk sac. All species must indeed solve the same survival problem linked with the change in food supply.

We thank J. C. Philippart for permitting the use of the specimens on which this study has focused, and K. Broman for translating the text into English. This work was supported by grant no. 2.4508.94 from the Belgian Fonds National de la Recherche Scientifique de Belgique. BF is a Research Associate of the Fonds National de la Recherche Scientifique de Belgique.

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