

POSTEMBRYONIC DEVELOPMENT OF THE CEPHALIC SKELETON IN *DICENTRARCHUS LABRAX* (PISCES, PERCIFORMES, SERRANIDAE)

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ABSTRACT

At hatching, *Dicentrarchus labrax* larvae are 3.0 mm long and devoid of any cephalic skeleton. At 3.6 mm, the Meckelian cartilage appears, after which the whole skeleton develops so slowly and gradually that clear-cut stages are impossible to define. Some cephalic elements, however, develop faster than others. Skeletal development is subject to constraints imposed by vital functions such as aquatic respiration and feeding. As the yolk sac shrinks, the branchial parts develop. By the time the vitellus is completely exhausted, the mandible, pharyngeal jaws, hyoid bar, and parts of the suspensorium and operculum are present. Though still incomplete, these structures are probably sufficient to allow ingestion of exogenous food. Further development should enable the larvae to perform suction feeding, as is typical of perciforms. Before the shift to exogenous feeding, the cartilaginous floor of the skull remains open, but the opening is then closed by the parasphenoid and basioccipital, so the brain is completely isolated from the buccal cavity. The cranial vault and ethmoid region develop later: these structures are probably less essential to fry survival than the earlier and more rapidly developing structures.

Throughout their postembryonic development, i.e., until the appearance of the first adult characters (Krupka, 1988; Haylor, 1992), fish must be equipped to survive, notably at certain critical times such as hatching and the shift to exogenous feeding. Upon hatching, the embryo comes in contact with the environment. It feeds on the nutrients contained in the yolk sac. The latter also performs a respiratory function, being highly vascularised. Within a few days of hatching, development must enable the larvae to breathe in and collect food from its environment. To perform these functions, the larvae must at least have developed an effective means of locomotion, a system for capturing and digesting prey, a new respiratory system, and nervous and sensory systems.

The prey-capture and respiratory systems are located in the head and consist notably of skeletal structures and muscle. The present work concerns the post-embryonic development of *Dicentrarchus labrax*, a teleost species of the order Perciformes.

Investigators have long shown interest in the post-embryonic development of the head region (i.e., Stöhr, 1882; Tischomiroff, 1885; Winslow, 1897; Swinnerton, 1902; Gaupp, 1903). Not all of them, however, have pursued the same goals. Many studies have focused solely on external development: recent examples include Able et al. (1986), Munehara and Mishima (1986), Nishikawa (1987), Fukuhara (1988), Krupka (1988), Baldwin et al. (1991), Kovac (1993, 1994), Ditty et al. (1994). Others have dealt solely with the osteocranium (Morris and Gaudin, 1982; Jollie, 1984; Potthoff et al., 1988; Vandewalle et al., 1995) or only with the chondrocranium (Wells, 1923; Bhargava, 1958; Bertmar, 1959). Sometimes the focus has been the whole cephalic skeleton (Kindred, 1919; Bamford, 1948; Elman and Balon, 1980; Vandewalle et al., 1992, 1997), sometimes it has been only certain cranial elements (Haines, 1937; Devillers, 1944; Corsin, 1961; Francillon, 1974; Arratia and Schultze, 1990; Potthoff and Tellock, 1993), occasionally with emphasis on

functional aspects (Verraes, 1977). Several authors have described only a few developmental stages (Srinivasachar, 1959; Howes and Sanford, 1987; Surlemont and Vandewalle, 1991; Kobayakawa, 1992). A few, finally, have tried to get a synthetic or general picture (De Beer, 1937; Daget, 1964).

Few studies devoted to the bony and cartilaginous skeleton provide a basis for accurately timing the events that mark a teleost's post-embryonic development. Yet knowledge of this timing is needed in order to understand the evolution of respiration and feeding. On a chronological basis alone it is possible to establish many correlations between the development of structures and vital requirements. This chronology is based upon the size of larvae instead of time (i.e., days after hatching). This is the first aim of the present study. The second is to increase our currently very fragmentary knowledge concerning the development of the cephalic skeleton in perciforms.

The nomenclature used here to designate developing stages and skeletal structures is based principally on the work of De Beer (1937), Daget (1964), Patterson (1977) and Kendall et al. (1984).

MATERIAL AND METHODS

Dicentrarchus labrax specimens were from the hatcheries of the "Ecloserie marine Sepia Exploitation" located at the site of the Graveline nuclear reactors (France). The larvae were raised in water ranging in temperature from 14.3°C (at hatching) to 20.6°C (latest stage). Twelve batches of 50 larvae were sampled from hatching (3.0-mm fry) to day 18 post-hatching (8.1-mm fry) and five batches of 30 larvae from day 22 (8.3 mm) to day 34 (11.2 mm). The larvae were fixed in buffered 10% formalin and trypsin-cleared. Some were stained with alcyan blue to reveal the cartilages, others with alizarin to reveal the bones. The staining techniques were derived from those of Dingerkus and Uhler (1977), Potthoff (1984) and Taylor and Van Dyke (1985). The stained larvae were then observed under a Wild M5 binocular magnifier. The drawings representing the cartilaginous or bony structures were made using a camera lucida mounted on the magnifier. Each stage is represented by a lateral view, a ventral view, and when necessary, a dorsal view.

Although our presentation of results begins at hatching, we in fact had to work backward to establish homologies and recognise structures. We compared the structures of adult perciforms (Liem, 1970; Vandewalle, 1972; Benmouna et al., 1984) with those of the oldest larvae and proceeded by successive comparisons from the oldest larvae to the youngest.

RESULTS

3.0 mm (hatching).—No cephalic skeletal structure is visible.

3.6 mm (Fig. 1A).—The mandibular arch is represented by Meckel's cartilages.

4.0 mm (Fig. 1B,C).—Several cartilaginous elements have appeared: the trabeculae, first parts of the neurocranium, and parts of the palato-quadrates, added to the mandibular arch where Meckel's cartilages have considerably developed. The hyoid arch is represented by the hyosymplectics.

4.3 mm (Fig. 1D,E).—The trabecular bars have lengthened posteriorly and fused anteriorly to constitute the beginnings of a trabecula communis and ethmoid plate. A pair of lateral cartilages has appeared, probably the first signs of the latero-dorsal walls of the otic capsules. Below these cartilages, the hyosymplectics are already well developed, particularly broad in their upper parts and touching the palato-quadrates with their lower

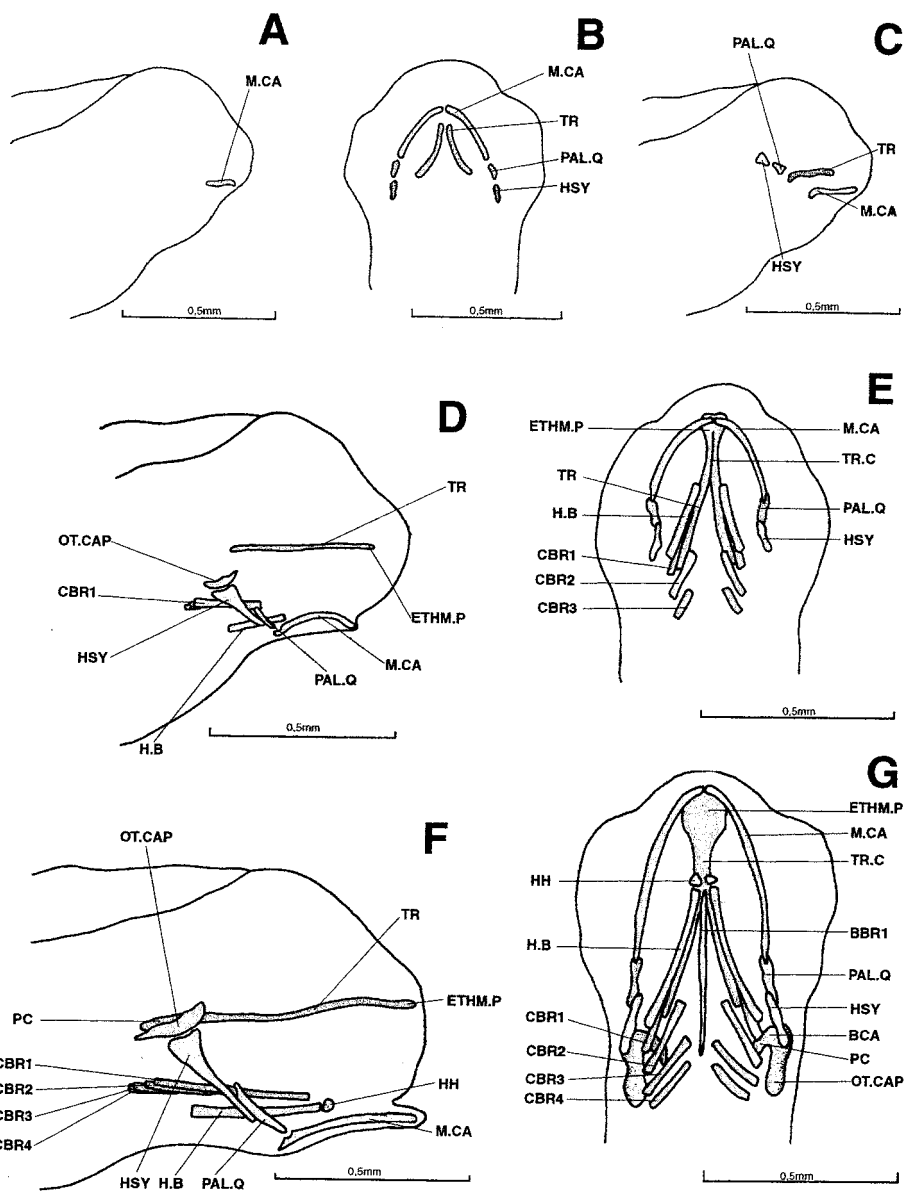


Figure 1. *Dicentrarchus labrax*: Lateral view (a) of the chondrocranium in a 3.6-mm larvae; ventral (b) and lateral (c) views of the chondrocranium in a 4.0-mm larvae; lateral (d) and ventral (e) views of the chondrocranium in a 4.3-mm larvae; lateral (f) and ventral (g) views of the chondrocranium in a 4.8-mm larvae. BBR 1: basibranchial 1; BCA: commissura bicapsularis anterior; CBR 1-4: ceratobranchial 1-4; ETHM.P: ethmoid plate; H.B: hyoid bar; HH: hypohyal; HSY: hyosymplectic; M.C.A: Meckel's cartilage; OT.CAP: otic capsule; PAL.Q: palato-quadrates; PC: parachordal plate; TR: trabecular bar; TR.C: trabecula communis.

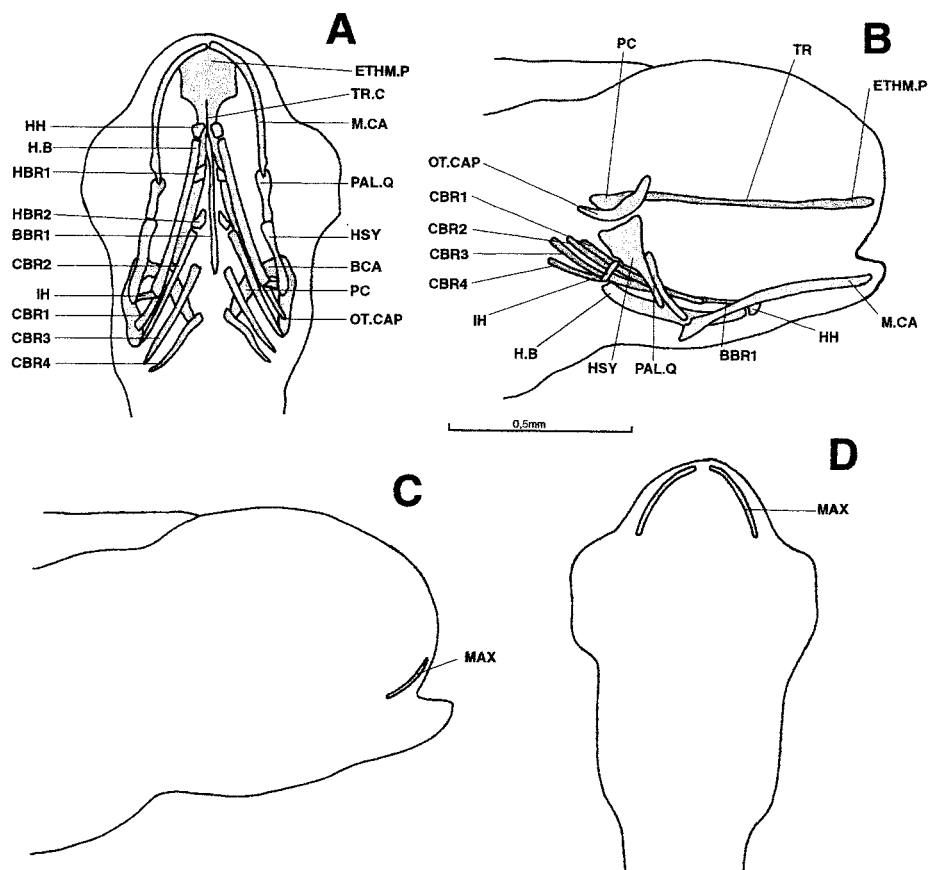


Figure 2. *Dicentrarchus labrax*: ventral (a) and lateral (b) views of the chondrocranium and lateral (c) and ventral (d) views of the osteocranium in a 5.2-mm larvae. BBR 1: basibranchial 1; BCA: commissura bicapsularis anterior; CBR 1-4: ceratobranchial 1-4; ETHM.P: ethmoid plate; H.B: hyoid bar; HBR 1-2: hypobranchial 1-2; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; MAX: maxillary; M.CA: Meckel's cartilage; OT.CAP: otic capsule; PAL.Q: palato-quadrates; PC: parachordal plate; TR: trabecular bar; TR.C: trabecula communis.

tips. The palato-quadrates point towards the rear portions of Meckel's cartilages, which exhibit a cavity already shaped like a joint socket. Meckel's cartilages, markedly curved, touch each other anteriorly. Additions to the splanchnocranium include two already well-developed hyoid bars and the first three pairs of ceratobranchials.

4.8 mm (Fig. 1F,G).—To the front of the neurocranium, the ethmoid plate has broadened. To the rear, the parachordal plates are in place. They are connected to the latero-dorsal walls of the otic capsules, probably by the almost-horizontal commissurae bicapsulares anteriores.

A pair of hypohyals has appeared in front of the hyoid bars. The branchial basket now possesses a fourth pair of ceratobranchials and a long basibranchial bar. Meckel's cartilages are straightening.

5.2 mm (Fig. 2).—The trabecular bars have lengthened posteriorly but remain separate from the parachordal plates.

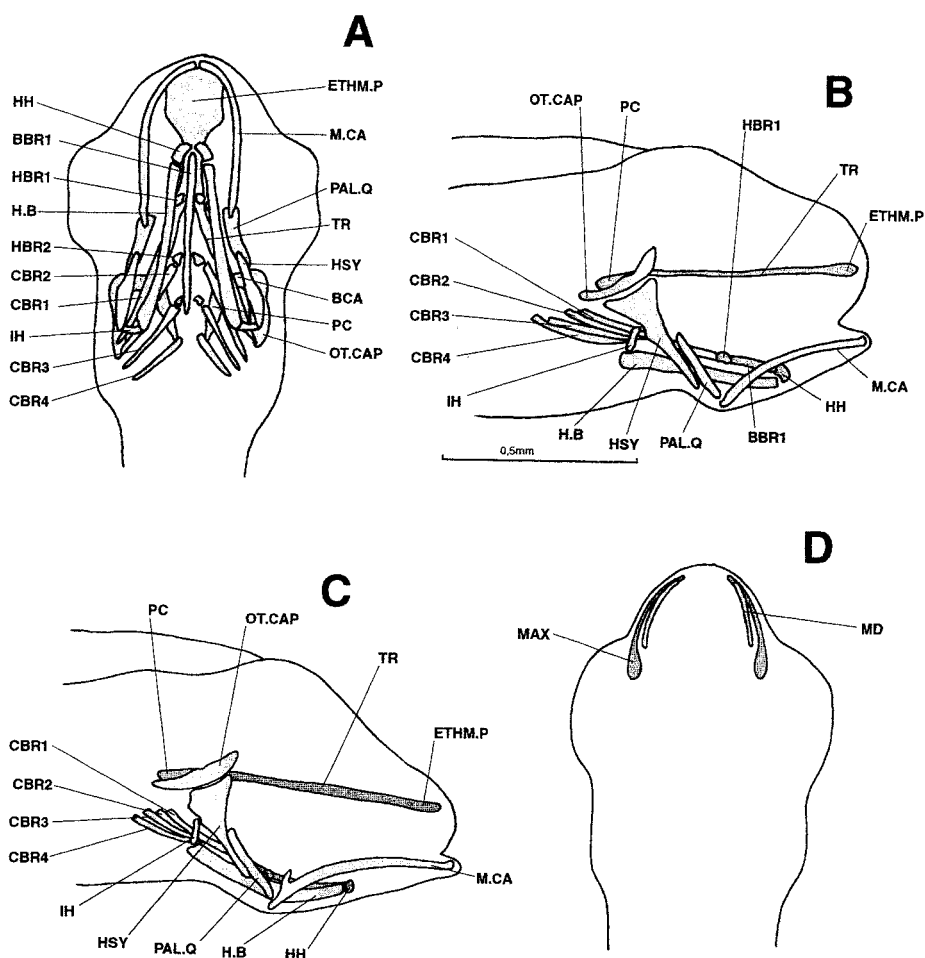


Figure 3. *Dicentrarchus labrax*: Ventral (a) and lateral (b) views of the chondrocranium in a 5.3-mm larvae; lateral view (c) of the chondrocranium and ventral view (d) of the osteocranium in a 5.7-mm larvae. BBR 1: basibranchial 1; BCA: commissura bicapsularis anterior; CBR 1-4: ceratobranchial 1-4; ETHM.P: ethmoid plate; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; MAX: maxillary; M.CA: Meckel's cartilage; MD: mandible; OT.CAP: otic capsule; PAL.Q: palato-quadrate; PC: parachordal plate; TR: trabecula communis.

The hyoid bars are connected to the hyosymplectics by a pair of independent interhyals. The branchial basket now possesses its first two pairs of hypobranchials. Meckel's cartilages are long and almost straight.

The maxillaries are present on the edge of the upper lip in the form of two small, bony rods.

5.3 mm (Fig. 3A,B).—The trabecular bars and parachordal plates are united. Anteriorly and laterally they limit the hypophyseal fenestra, which remains open in the rear. A third pair of hypobranchials has appeared in the branchial basket. The maxillaries are still the only discernible ossifications.

5.7 mm (Fig. 3C,D).—No new neurocranial element has appeared, but the existing components have enlarged.

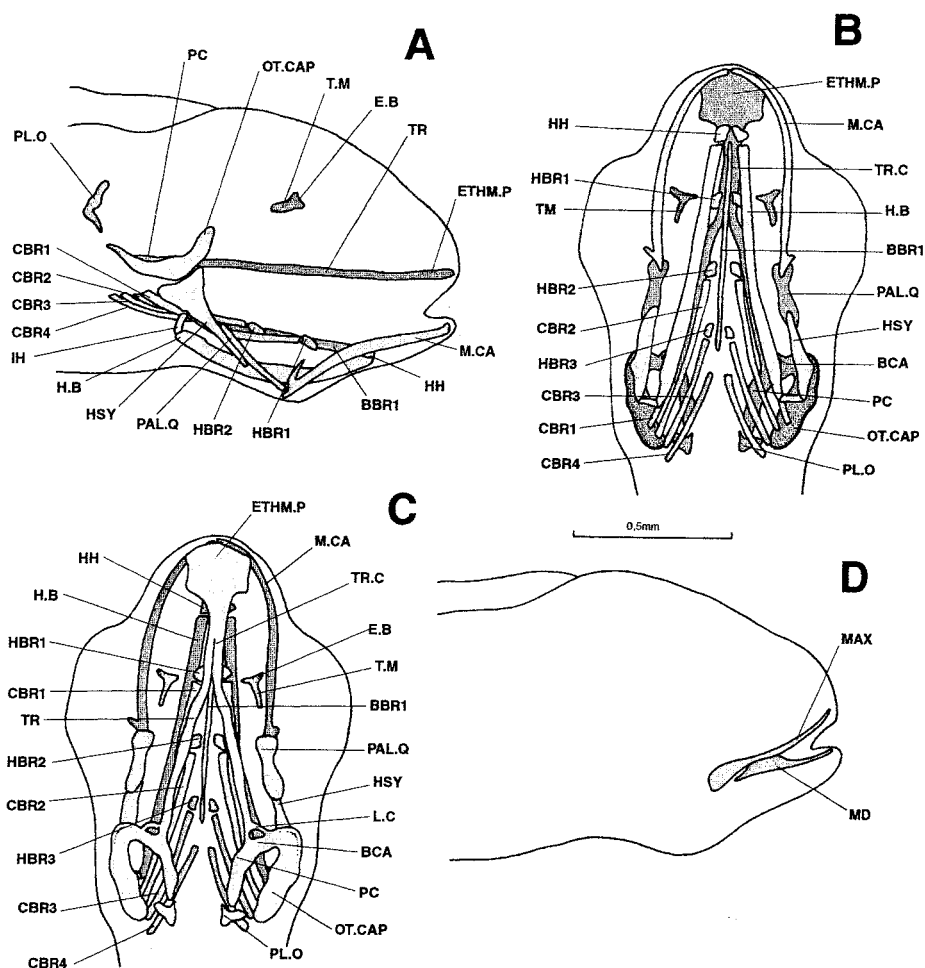


Figure 4. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium and lateral (d) view of the osteocranium in a 6.3-mm larvae. BBR : basibranchial 1; basibranchial 1; BCA: commissura bicapsularis anterior; CBR 1-4 : ceratobranchial 1-4; E.B: epiphyseal bridge; ETHM.P: ethmoid plate; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; MAX: maxillary; M.CA: Meckel's cartilage; MD: mandible; OT.CAP: otic capsule; PAL.Q: palato-quadrate; TR: trabecular bar; TR.C: trabecula communis.

A pointed processus dorsalis has appeared behind Meckel's cartilages.

A second pair of ossifications has developed, constituting the dentaries. The maxillaries have enlarged posteriorly.

6.3 mm (Fig. 4).—Dorsally, the neurocranium now includes the primordia of the anterior portions of the taeniae marginales and epiphyseal bridge. On each side, a small cartilaginous column has appeared at the posterior tip of the trabecular bar, linking the junction between the trabecula and parachordal plate with the front of the otic capsule. These columns are probably the commissurae laterales. Finally, the pilae occipitales are present at the rear of the braincase; they are already almost in contact with the parachordal plates.

The composition of the splanchnocranium is unchanged. The two ossifications previously present have developed further.

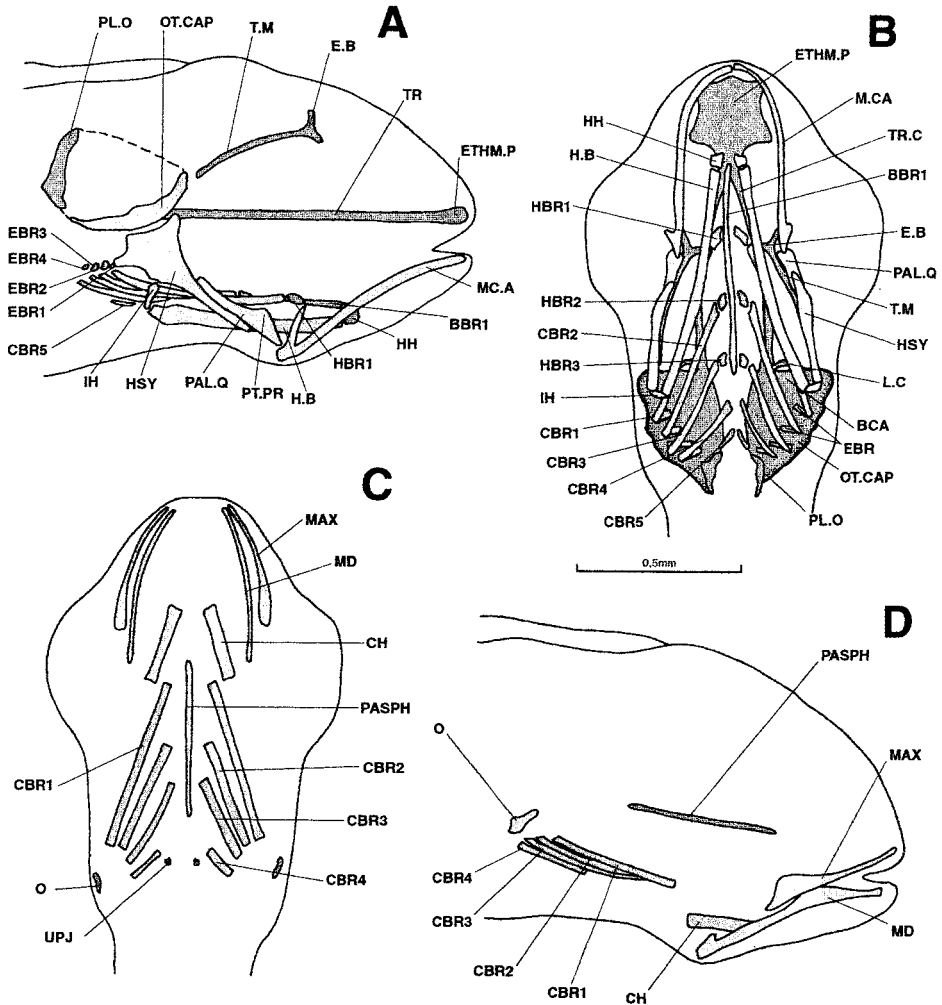


Figure 5. *Dicentrarchus labrax*: lateral (a) and ventral (b) views of the chondrocranium and ventral (c) and lateral (d) views of the osteocranium in a 6.7-mm larvae. Interrupted lines indicate the probable limit of the otic capsule. The buccal teeth are not represented in Figs. c and d. BBR : basibranchial; BCA: commissura bicipularis anterior; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; EBR: epibranchial; E.B: epiphyseal bridge; ETHM.P: ethmoid plate; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; L.C: commissura lateralis; MAX: maxillary; M.CA: Meckel's cartilage; MD: mandible; O: opercular; OT.CAP: otic capsule; PAL.Q: palato-quadrate; PASH: parasphenoid; PL.O: pila occipitalis; PT.PR: pterygoid process; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabecula communis; UPJ: upper pharyngeal jaw.

6.7 mm (Fig. 5).—The taeniae marginales have extended towards the otic capsules and the pilae orbitales are practically attached to the parachordal plates. The floor of each otic capsule has broadened, but without closing the hypophyseal fenestra to the rear. The lateral walls of these capsules are forming but their outlines are not clear.

The palato-quadrate bears a "budding" pterygoid process. To the branchial basket have been added the fifth pair of ceratobranchials and four pairs of epibranchials.

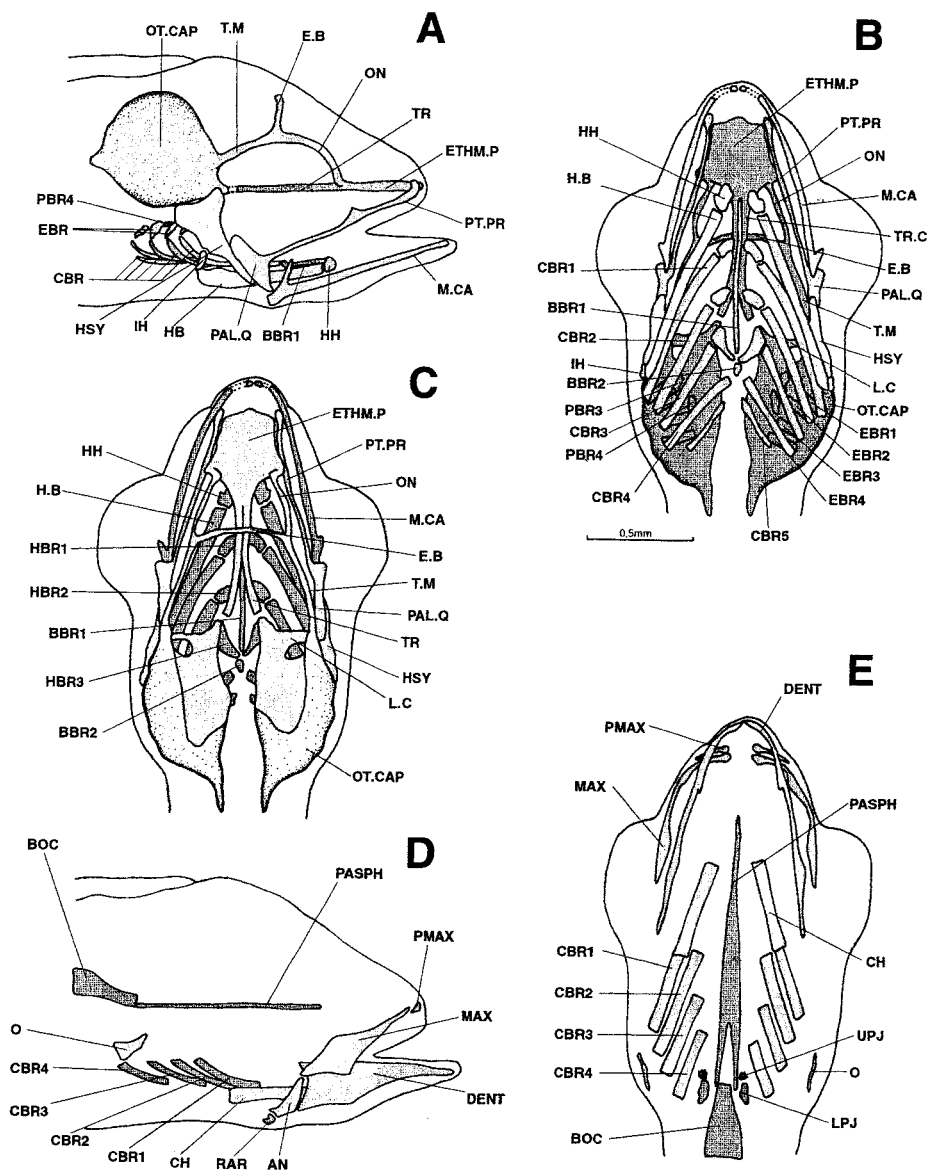


Figure 6. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium and lateral (d) and ventral (e) views of the osteocranium in a 7.6-mm larvae. The dotted lines indicate a regressing cartilaginous region. The buccal teeth are not represented in Figs. d and e. AN: angular; BBR 1-2: basibranchial 1-2; BOC: basioccipital; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; E.B: epiphyseal bridge; ETHM.P: ethmoid plate; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypophyal; HSY: hyosymplectic; IH: interhyal; L.C: commissura lateralis; LPJ: lower pharyngeal jaw; MAX: maxillary; M.CA: Meckel's cartilage; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PAL.Q: palato-quadrate; PASPH: parasphenoid; PBR 3-4: pharyngobranchial 3-4; PMAX: premaxillary; PT.PR: pterygoid process; RAR: retroarticular; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabecula communis; UPJ: upper pharyngeal jaw.

The parasphenoid, first ossification of the neurocranium, has appeared in the middle of the hypophyseal fenestra. The bony splanchnocranium displays the operculars, ceratohyals, four pairs of well-developed ceratobranchials, and a pair of small dorsal toothed plates. The latter are apparently located above the fifth pair of cartilaginous ceratobranchials, i.e., at the position corresponding to the toothed plates of the upper pharyngeal jaws. The composition of the latter is hard to determine at this stage.

7.6 mm (Fig. 6).—On one hand, the cartilaginous skull continues to develop. The left and right parts of the braincase have broadened ventrally, laterally, and dorsally without actually joining. The taeniae marginales are in contact posteriorly with the otic capsules; anteriorly, they are extended by the laminae orbitonasales (perhaps connected to the pre-orbital roots). The laminae orbitonasales are attached to the latero-posterior tips of the ethmoid plate. The pilae occipitales are fused with the otic capsules and the epiphyseal bridge is complete. The branchial basket now displays two posterior pairs of pharyngobranchials and a small basibranchial. Lastly, the pterygoid processes have lengthened and now reach the front of the ethmoid plate.

On the other hand, certain cartilages have begun to regress. The otic capsules have separated from the trabecular bars. Meckel's cartilages are also resorbing, isolating two small, anterior cartilaginous masses.

The osteocranium now possesses a basioccipital and small premaxillaries; the lower jaw consists of distinct dentaries, angulars, and retroarticulars. The parasphenoid has broadened and bears two posterior points surrounding the basioccipital. The pharyngeal jaws, formed by the 5th ceratobranchials bearing toothed plates, lie opposite a pair of upper jaws whose composition is still hard to determine.

8.1 mm (Fig. 7).—At this stage the chondrocranium displays the first signs of a lamina precerebralis and four pairs of pharyngobranchials. Two small protuberances appear on the posterior rims of the commissurae laterales: they constitute the first signs of the pilae laterales (see 8.9-mm larvae).

Cartilage regression continues with that of the hyoid bars, which have begun to split up.

The occipital region of the neurocranium displays dorsally a pair of small ossified exoccipitals, one to each side of the basioccipital. The upper pharyngeal jaws are represented by three pairs of toothed plates which probably correspond with ossification of the three posterior pairs of pharyngobranchials.

Ossification of each quadrate has begun at the joint with the mandible. The premaxillaries curve upward to constitute the first signs of the processus ascendentes. Like the lower jaw, they are toothless or sometimes bear a single tooth. The first pair of branchiostegal rays has appeared.

8.3 mm (Fig. 8).—No new element appears in the chondrocranium, which continues to regress. Ventrally, the ethmoid and otic regions have completely separated. A major part of the central region of each ceratobranchial is resorbing, isolating the two cartilaginous extremities. The same applies to the hyosymplectics, where a hyomandibular and a symplectic region are distinguishable. The regions where the palato-quadrate articulate with the lower jaw are also disappearing.

The osteocranium now displays symplectics and an increased number of buccal teeth (4–5 per half-jaw). The parasphenoid is in contact with the basioccipital. A long urohyal has appeared between the ceratohyals.

8.9-mm (Fig. 9).—The cartilaginous braincase is beginning to close dorsally with the presence of the tectum posterius, just in front of the pilae occipitales. Ventrally, the para-

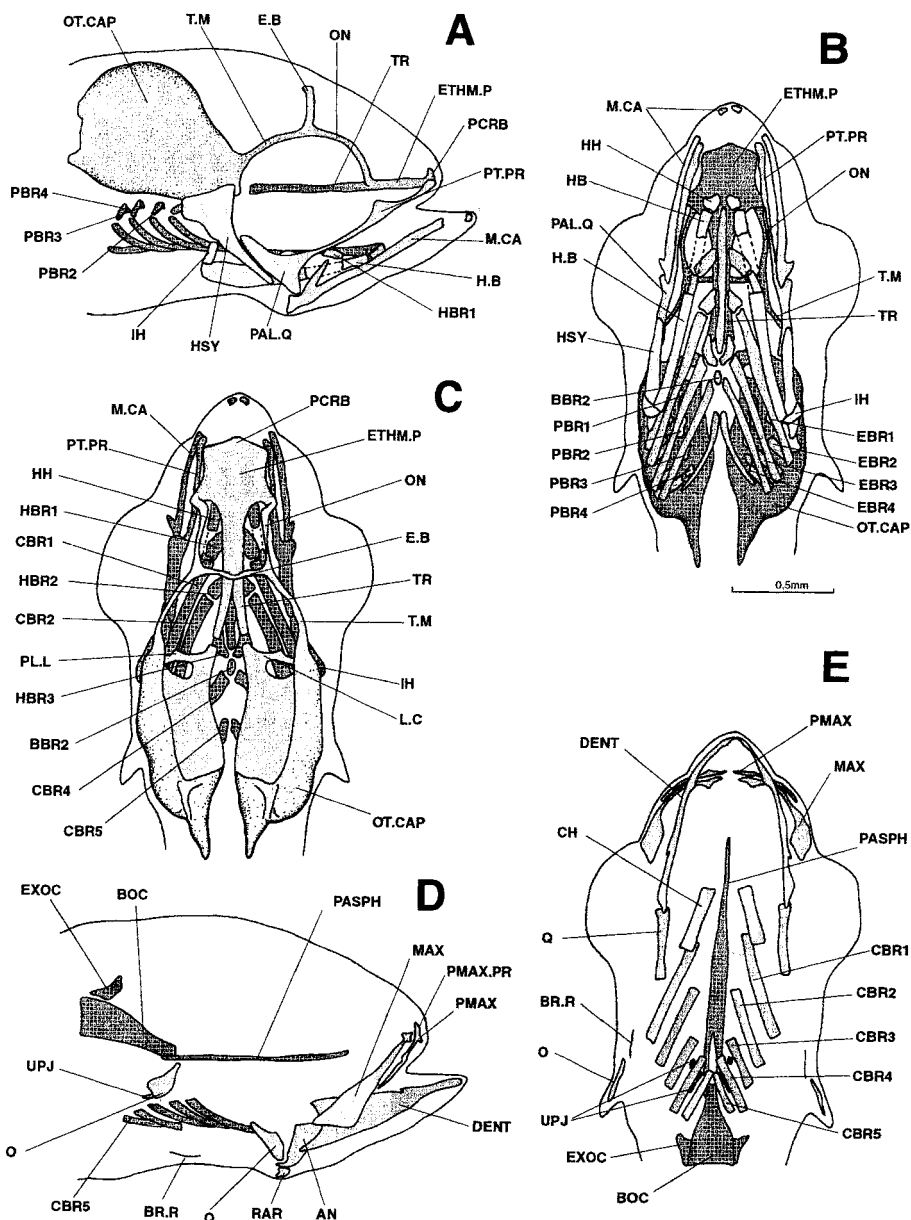


Figure 7. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium and lateral (d) and ventral (e) views of the osteocranium in an 8.1-mm larvae. The dotted lines indicate a regressing cartilaginous region. The buccal teeth are not represented in Figs. d and e. AN: angular; BBR 1-2: basibranchial 1-2; BOC: basioccipital; BR.R: branchiostegal ray; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; E.B: epiphyseal bridge; ETHM.P: ethmoid plate; EXOC: exoccipital; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; L.C: commissura lateralis; MAX: maxillary; M.CA: Meckel's cartilage; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PAL.Q: palatoquadrate; PASPH: parasphenoid; PBR 1-4: pharyngobranchial 1-4; PCRB: lamina precerebralis; PLL: pila lateralis; PMAX: premaxillary; PMAX.PR: premaxillary process; PT.PR: pterygoid process; Q: quadrate; RAR: retroarticular; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabacula communis; UPJ: upper pharyngeal jaw.

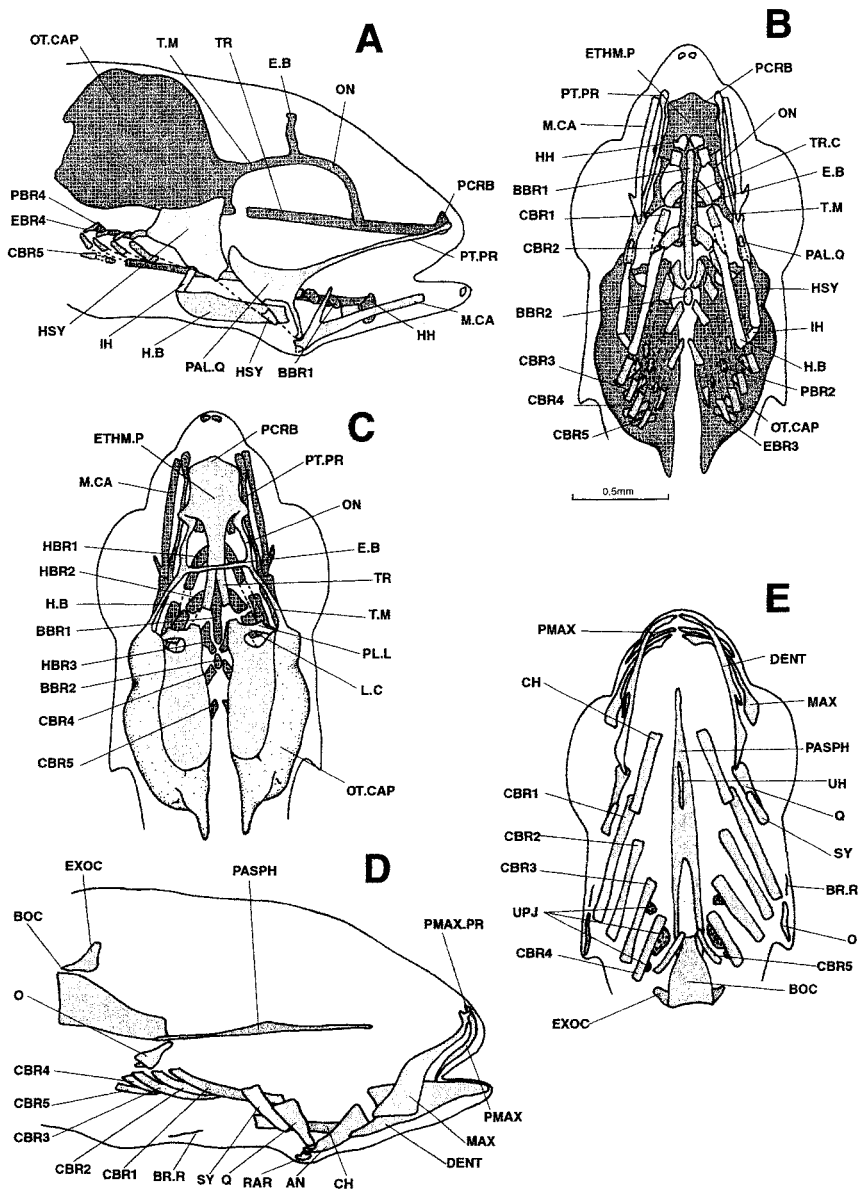


Figure 8. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium and lateral (d) and ventral (e) views of the osteocranium in an 8.3-mm larvae. The dotted lines indicate a regressing cartilaginous region. The buccal teeth are not represented in Figs. d and e. AN: angular; BBR 1-2: basiobranchial 1-2; BOC: basioccipital; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; E.B: epiphyseal bridge; ETHM.P: ethmoid plate; EXOC: exoccipital; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; L.C: commissura lateralis; MAX: maxillary; M.C.A: Meckel's cartilage; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PAL.Q: palato-quadrate; PASPH: parasphenoid; PBR 1-4: pharyngobranchial 1-4; PCR.B: lamina precerebralis; PL.L: pila lateralis; P.MAX: premaxillary; P.MAX.PR: premaxillary process; PT.PR: pterygoid process; Q: quadrate; RAR: retroarticular; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabecula communis; UH: urohyal; UPJ: upper pharyngeal jaw.

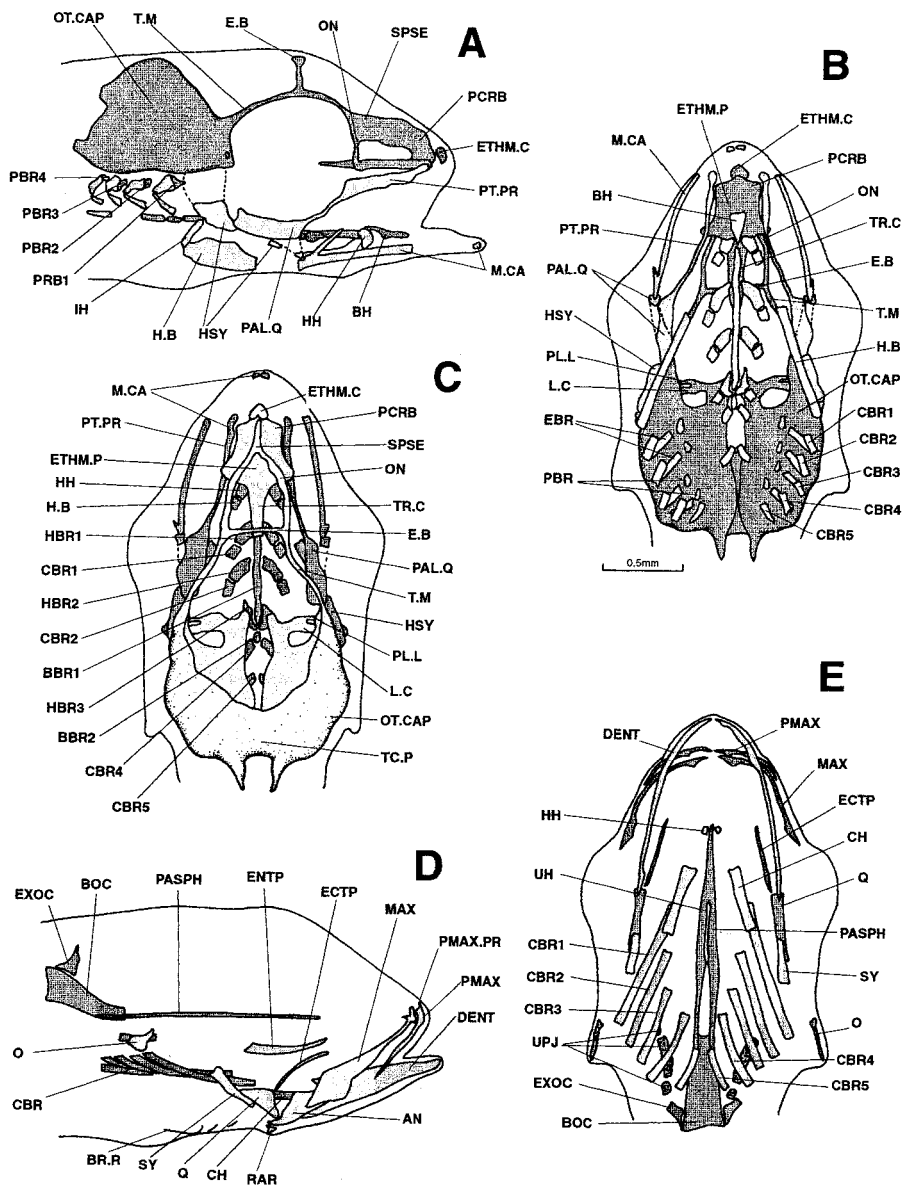


Figure 9. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium and lateral (d) and ventral (e) views of the osteocranium in an 8.9-mm larvae. The dotted lines indicate a regressing cartilaginous region. The buccal teeth are not represented in Figs. d and e. AN: angular; BBR 1-2 : basibranchial 1-2; BH: basihyal; BOC: basioccipital; CBR 1-5 : ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; ECTP: ectopterygoid; ENTP: entopterygoid; E.B: epiphyseal bridge; ETHM.C: ethmoid cartilage; ETHM.P: ethmoid plate; EXOC: exoccipital; H.B: hyoid bar 1-3: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HSY: hyosymplectic; IH: interhyal; L.C: commissura lateralis; MAX: maxillary; M.CA: Meckel's cartilage; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PAL.Q: palato-quadrato; PASPH: parasphenoid; PBR: pharyngobranchial; PCRB: lamina precerebralis; PLL: pila lateralis; PMAX: premaxillary; PMAX.PR: premaxillary process; PT.PR: pterygoid process; Q: quadrate; RAR: retroarticular; SPSE: commissura sphenoseptalis; SY: symplectic; TC.P: tectum posterius; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabecula communis; UH: urohyal; UPJ: upper pharyngeal jaw.

chordal plates have come closer together but do not yet form a basal plate. The protuberances on the commissurae laterales have continued to develop, attaching to the bases of the taeniae marginales to form the pilae laterales. The lamina precerebralis has developed upwardly and to the rear and is connected to the laminae orbitonasales and taeniae marginales via the commissurae sphenoseptales. A new cartilaginous element, single and small, has appeared in front of the ethmoid region: this is the cartilaginous pad or ethmoid cartilage, situated under the processus ascendentes of the premaxillaries in *Acanthopterygii*. A basihyal is also present.

The trabecular bars are now no more than the posterior tips of the ethmoid plate. The upper parts of the hyomandibulars are regressing. So are the palato-quadrates, which form an isolated cartilaginous island at the site of the joint with Meckel's cartilage. The central portion of each cartilaginous ceratobranchial has totally disappeared, leaving a very scattered-looking branchial basket.

The bony splanchnocranium now includes pairs of ecto- and entopterygoids and two small hypohyals. There are two additional pairs of branchiostegal rays and the number of buccal teeth has increased. The median pharyngobranchial toothed plates have lengthened.

9.9 mm (Fig. 10).—The cartilaginous neurocranium is continuing to close dorsally, from rear to front, with the formation of the tectum synoticum. A thin processus anteromedialis appears at this site, pointing towards the epiphyseal bridge. The lamina precerebralis, commissurae sphenoseptales, and laminae orbitonasales constitute a whole forming the dorso-medial part of the ethmoid region. This whole is pierced by the foramina for the olfactory nerves. In the splanchnocranium, the first pair of hypobranchials and the interhyals have begun to resorb centrally.

Most characteristic of this stage is the abundance of new bony parts in the neurocranium. In front there are a vomer, a pair of lateral ethmoids, and a pair of lacrymals. In the orbital region, the frontals have appeared. The otic region includes sphenotics, pterotics, and epiotics. Finally, the occipital region now displays a supraoccipital and a pair of posttemporals.

The bony splanchnocranium now includes the palatines, the interhyals, the preoperculars, the inter- and suboperculars, three pairs of hypobranchials, and all four pairs of epibranchials. The first, second, and third pairs of ceratobranchials bear gillrakers. The eight pairs of branchiostegal rays that characterise the adult are well developed.

11.2 mm (Fig. 11).—The cartilaginous braincase still has no basal plate. Dorsally, a taenia tecta medialis is developing from the epiphyseal bridge towards the rear, in the direction of the anterior process of the braincase.

All the bony parts previously present have enlarged. This is especially true of the pterotics, supraoccipital, preoperculars, maxillaries, and premaxillaries. The pterotics consist of two parts; the anterior part bears a portion of the bony tube of the pterotic sensory canal. The parasphenoid exhibits the lateral wings which in the adult limit the trigemino-facial chamber.

The ethmoid region now displays a pair of nasals and a mesethmoid, pleurosphenoids are present in the orbital region, a pair of parietals reinforces the otico-occipital region, and the epihyals have finally appeared. The first palatine and vomerine teeth are present.

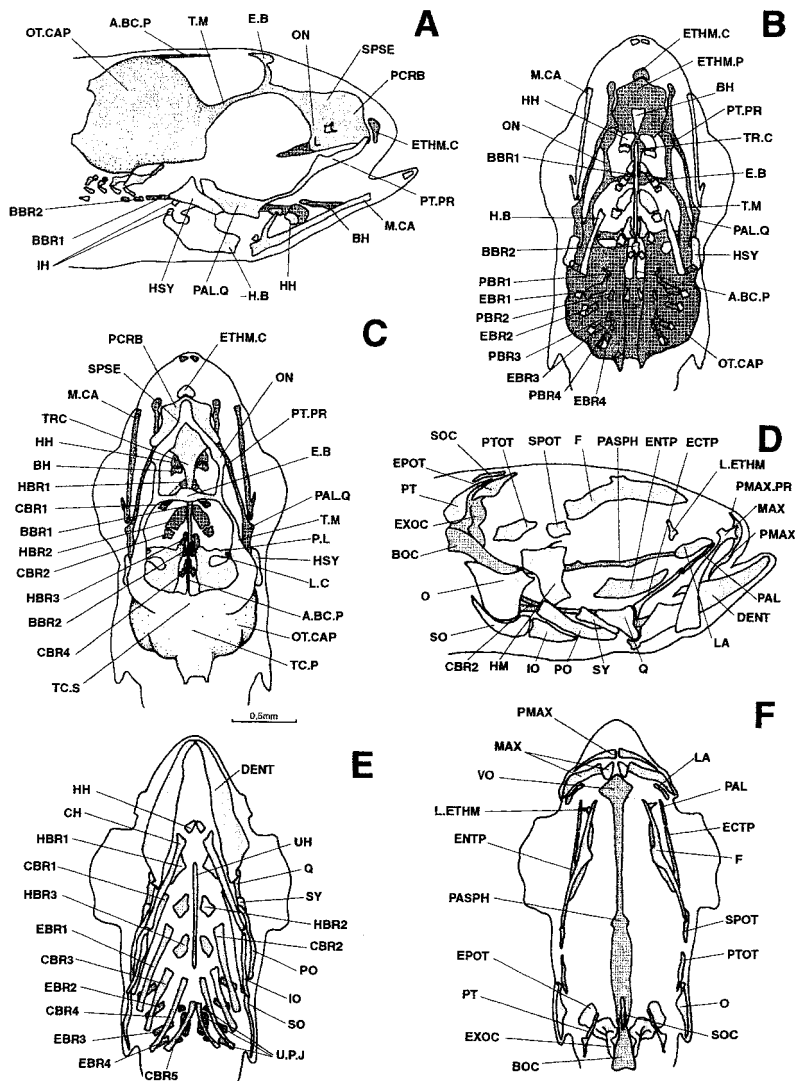


Figure 10. *Dicentrarchus labrax*: Lateral (a), ventral (b), and dorsal (c) views of the chondrocranium (d), lateral view of the osteocranium (d), ventral view (e) of the bony splanchnocranium and part of the neurocranium, and dorsal view (f) of the neurocranium in a 9.9-mm larvae. The dotted lines indicate a regressing cartilaginous region. The branchiostegal rays, gillrakers, and buccal teeth are not represented in Figs. d, e, and f. A.B.C.P: anterior process of the braincase; BBR 1-2: basibranchial 1-2; BH: basihyal; BOC: basioccipital; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; ECTP: ectopterygoid; ENTP: entopterygoid; E.B: epiphyseal bridge; EPOT: epiotic; ETHM.C: ethmoid cartilage; ETHM.P: ethmoid plate; EXOC: exoccipital; F: frontal; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HM: hyomandibular; HSY: hyosymplectic; IH: interhyal; IO: infraopercular; LA: lacrymal; L.C: commissura lateralis; L.ETHM: lateral ethmoid; MAX: maxillary; M.CA: Meckel's cartilage; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PAL: palatine; PAL.Q: palato-quadrato; PASPH: parasphenoid; PBR 1-4: pharyngobranchial 1-4; PCRB: lamina precerebralis; PL.L: pila lateralis; PL.O: pila occipitalis; PMAX: premaxillary; PMAX.PR: premaxillary process; PO: preopercular; PT: posttemporal; PTOT: pterygoid; PT.PR: pterygoid process; Q: quadrate; RAR: retroarticular; SO: subopercular; SOC: supraoccipital; SPSE: commissura sphenoseptalis; SPOT: sphenotic; SY: symplectic; TC.P: tectum posterius; TC.S: tectum synoticum; T.M: taenia marginalis; TR: trabecular bar; TR.C: trabecula communis; UH: urohyal; UPJ: upper pharyngeal jaw.

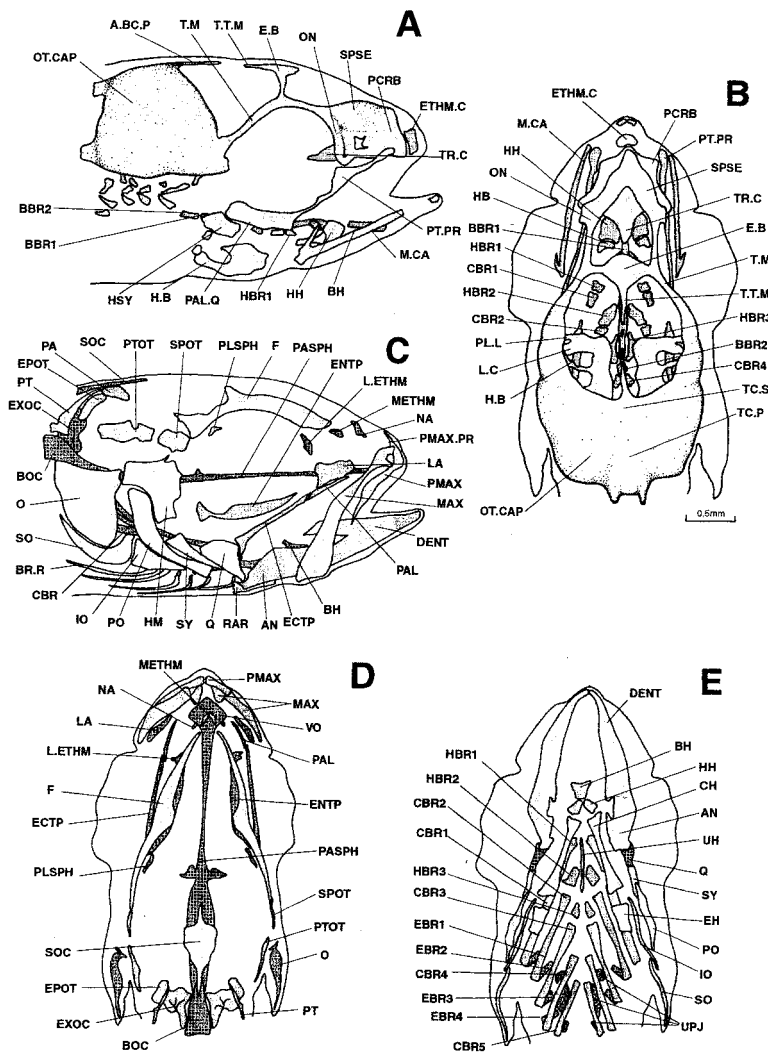


Figure 11. *Dicentrarchus labrax*: Lateral (a) and dorsal (b) views of the chondrocranium, lateral (c) view of the osteocranium, ventral view (d) of the bony splanchnocranium and part of the neurocranium, and dorsal view (e) of the bony neurocranium in an 11.2-mm larvae. The dotted lines indicate a cartilaginous region that is regressing. The branchiostegal rays, gillrakers, and buccal teeth are not represented on Figs. d, e, and f. A.B.C.P: anterior process of the braincase; AN: angular; BBR 1-2: basibranchial 1-2; BH: basihyal; BOC: basioccipital; CBR 1-5: ceratobranchial 1-5; CH: ceratohyal; DENT: dentary; EBR 1-4: epibranchial 1-4; ECTP: ectopterygoid; ENTP: entopterygoid; E.B: epiphyseal bridge; EPOT: epiotic; ETHM.C: ethmoid cartilage; ETHM.P: ethmoid plate; EXOC: exoccipital; F: frontal; H.B: hyoid bar; HBR 1-3: hypobranchial 1-3; HH: hypohyal; HM: hyomandibular; HSY: hyosymplectic; IH: interhyal; IO: infraopercular; LA: lacrymal; L.C: commissura lateralis; L.ETHM: lateral ethmoid; MAX: maxillary; M.CA: Meckel's cartilage; METHM: mesethmoid; NA: nasal; O: opercular; ON: lamina orbitonasalis; OT.CAP: otic capsule; PA: parietal; PAL: palatine; PAL.Q: palato-quadrate; PASPH: parasphenoid; PBR: pharyngobranchial; PCRB: lamina precerebralis; PLL.L: pila lateralis; PLSPH: pleurosphenoid; PMAX: premaxillary; PMAX.PR: premaxillary process; PO: preopercular; PT: posttemporal; PTOT: pterygoid; PT.PR: pterygoid process; Q: quadrate; RAR: retroarticular; SO: subopercular; SOC: supraoccipital; S.PTOT: dermopterotic; SPSE: commissura sphenoseptalis; SPOT: sphenotic; SY: symplectic; TC.P: tectum posterius; TC.S: tectum synoticum; T.M: taenia marginalis; TR: trabecular bar; T.TM: tecta taenia medialis; TC.C: trabecula communis; UH: urohyal; U.PJ: upper pharyngeal jaw.

DISCUSSION

D. labrax is a species that usually develops at a moderately high temperature. Species reared at higher temperatures develop faster (Pelosi et al., 1993; Regner and Dulcic, 1994; Vandewalle et al., 1997).

The order in which the different structures appear is presented in Table 1.

Chondrocranium.—In teleosts, the chondrocranium may begin to develop just before hatching, as in *Salmo trutta*, be partially present at hatching, as in *Heteropneustes fossilis* and *Barbus barbus*, or not form until later as in the Siluriforms *Clarias gariepinus*, *Heterobranchus longifilis*, the Cypriniforms *Leuciscus rutilus*, *Catostomus commersonii*, *Danio rerio*, the Lophiiforms *Lophius gastrophysus* or the Perciforms *Lutjanus campechanus*, *Bette splendens*, *Anisotremus davidsonii* and *Xenistius californiensis* (De Beer, 1937; Hubendick, 1942; Srinivasachar, 1959; Elman and Balon, 1980; Matsuura and Yomeda, 1987; Potthoff et al., 1988; Surlemont and Vandewalle, 1991; Watson and Walker, 1992; Vandewalle et al., 1992, 1997; Cubbage and Mabee, 1996; Mabee and Trendler, 1996). *D. labrax* falls into the third category, since the first structures begin to appear in 3.6 mm larvae (a day after hatching).

Usually, the structures of the mandibular and hyoid arches are the first cranial elements to appear with the Meckel's cartilage followed by the palato-quadrates, the hyosymplectics, and the hyoid bars in *D. labrax*. This timing is very similar to that observed in other perciforms (Potthoff et al., 1988; Watson and Walker, 1992; Potthoff and Tellock, 1993; Cubbage and Mabee, 1996). In most teleosts, these elements of the splanchnocranium are independent (Hubendick, 1942; Elman and Balon, 1980; Badenhorst, 1989b; Vandewalle et al., 1992). In most siluriforms, on the other hand, all or most of them are fused together (Kindred, 1919; Srinivasachar, 1959; Surlemont et al., 1989; Surlemont and Vandewalle, 1991; Vandewalle et al., 1997). The latter situation also arises in *Clupea harengus* (Wells, 1923). In Cypriniforms as *L. rutilus* and *C. commersonii*, the first structures to appear are the trabeculae and parachordal plates forming the base of neurocranium (Hubendick, 1942; Elman and Balon, 1980).

In most teleosts, the elements of the branchial basket are the next to complement the first structures of the splanchnocranium. The ceratobranchials develop first, generally from front to rear as in *H. fossilis* and *C. gariepinus* (Srinivasachar, 1959; Surlemont and Vandewalle, 1991), or else the first four develop simultaneously, followed by the fifth, as in *B. barbus*, *H. longifilis* and *Engraulis japonicus* (Balart, 1985; Vandewalle et al., 1992, 1997). Sometimes, all five pairs of ceratobranchials seem to appear at once, as in *Gasterosteus aculeatus*, *L. rutilus*, *C. commersonii*, *A. davidsonii*, and *X. californiensis* (Swinnerton, 1902; Hubendick, 1942; Elman and Balon, 1980; Watson and Walker, 1992). In *D. labrax*, the first ceratobranchial appears at the same time as the hyoid bar and the fifth does not appear until later, along with the epibranchials but after the hypobranchials. Then finally, in both *D. labrax* and *B. barbus* (Vandewalle et al., 1992), the pharyngobranchials appear from rear to front. In other species, the first epibranchial may appear before the rear ceratobranchials (Srinivasachar, 1959). Both pairs of pharyngobranchials appear at 7.6 mm in *D. Labrax*. They likewise do not appear until development is quite advanced in *H. fossilis*, *C. batrachus*, and *H. longifilis* (Srinivasachar, 1959; Vandewalle et al., 1997).

Table 1. Timing of the appearance of the various skeletal structures in *Dicentrarchus labrax*.

Stages (mm)	Cartilages	Ossifications
Hatching	no skeletal structure is visible	
3.6	appear: Meckel's cartilage	
4.0	appear: trabecular bars, palato-quadrates, hyosymplectics	
4.3	appear: bases of the dorso-lateral walls of the otic capsules, trabecula communis, hyoid bars, ethmoid plate, ceratobranchials 1-2-3	
4.8	appear: parachordal plates, commissurae bicapsulares anteriores, hypohyals, ceratobranchials 4, basibranchial 1	
5.2	appear: interhyals, hypobranchials 1-2	maxillaries
5.3	appear: hypobranchials 3	
5.7	appear: processus mediodorsales of Meckel's cartilages	lower jaw
6.3	appear: commissurae laterales, pilae occipitales, bases of the epiphyseal bridge and taeniae marginales	
6.7*	appear: first signs of the pterygoid processes, ceratobranchials 5, epibranchials 1-2-3-4	parasphenoid, operculars, ceratobranchials 1-2-3-4, ceratohyals, first pair of upper-pharyngeal-jaw toothed plates
7.6**	appear: complete lateral walls of the otic capsules, laminae orbitonasales (preorbital roots of the taeniae marginales), epiphyseal bridge, pharyngobranchials 3-4, basibranchial 2; regress: posterior parts of the trabecular bars, central parts of Meckel's cartilages	basioccipital, premaxillaries, angulars, dentaries, retroarticulars, lower pharyngeal jaws
8.1	appear: lamina precerebralis, pharyngobranchials 1-2; beginnings of the pilae laterales; regress: central parts of the hyoid bars	exoccipitals, quadrates, ceratobranchials 5, 2 pairs of upper-pharyngeal-jaw toothed plates, 1st pair of branchiostegal rays, processus ascendens on each premaxillary, teeth on the premaxillaries and dentaries
8.3	regress: central parts of ceratobranchials 1-2-3-4, between the hyomandibular and symplectic regions, regions where the quadrates articulate with Meckel's cartilages	symplectics, urohyal
8.9	appear: tectum posterius, pilae laterales commissurae sphenoseptales, basihyal, ethmoid cartilage regress: upper parts of the hyomandibular regions	ectopterygoids, entopterygoids, hypohyals, 2 additional pairs of branchiostegal rays
9.9	appear: tectum synoticum, extension of the braincase regress: central parts of hypobranchials 1, of the interhyals	supraoccipital, posttemporals, vomer, lateral ethmoids, frontals, lacrymals, sphenotics, pterotics, epiotics, hyomandibulars, palatines, interhyals, hypobranchials 1-2-3, epibranchials 1-2-3-4, suboperculars, interoperculars, preoperculars, gillrakers on ceratobranchials 1-2-3, 5 pairs of branchiostegal rays
11.2	appear: taenia tecta medialis regress: central parts of the interhyals	nasals, mesethmoids, pleurospenoids, parietals, epihyals, palatine and vomerine teeth.

* very marked reduction of the yolk sac and presence of food in the digestive tube

** disappearance of the yolk sac

The appearance of the trabecular bars as the first structures of the neurocranium floor, before the rest of the neurocranium, appears as a general rule in teleosts. They are followed by the parachordal plates.

As development continues, the order in which the elements of the cartilaginous neurocranium appear and the rate at which they develop are variable. In *Anguilla vulgaris*, the ethmoid and orbital regions develop before the otic capsules (De Beer, 1937), while in some Siluriforms, the braincase floor is the first to develop, followed by the anterior portion (Srinivasachar, 1959; Surlemont et al., 1991; Vandewalle et al., 1997). In *D. labrax*, and in more Perciforms and *B. barbatus*, both parts develop more or less simultaneously (Vandewalle et al., 1992). In Perciforms, notably *D. labrax*, the braincase is not isolated from the splanchnocranium by formation of a basal plate in front of the notochord. In Siluriforms, the basal plate develops early in the chondrocranium, by fusion of the anterior parts of the parachordal plates (Bamford, 1948; Srinivasachar, 1959; Surlemont and Vandewalle, 1991; Vandewalle et al., 1996). The basal plate appears late in Cypriniforms and *Ameiurus nebulosus* (Kindred, 1919; Badenhorst, 1989a; Vandewalle et al., 1992; Cabbage and Mabee, 1996).

In its general outline, the structure of the chondrocranium may appear fairly constant, but variations do exist. In *D. labrax*, there appears an independent cartilage, also present in others perciforms, at the front of the ethmoid region (in the adult, this special part, called the ethmoid cartilage, plays a role in enabling the premaxillary to move with respect to the neurocranium). These parts appear to be absent in the Perciforms *L. campechanus*, *C. undecimalis*, and *B. splendens* (Potthoff et al., 1988; Potthoff and Tellock, 1993; Mabee and Trendler, 1996). In the anterior region, the shape of the ethmoid plate is variable. In *D. labrax* and *B. barbatus*, it is formed by anterior fusion of the two trabecular bars (Vandewalle et al., 1992). It then develops into an actual platform as in *A. nebulosus*, *L. rutilus*, *N. aequoreus*, and *C. commersonii* (Kindred, 1919; Hubendick, 1942; Kadam, 1961; Elman and Balon, 1980). In *H. longifilis*, the ethmoid plate remains narrow and appears merely as the base of the lamina cerebrealis (Vandewalle et al. 1997).

The taeniae marginales and epiphyseal bridge also appear to develop differently in different species. In the Siluriforms *H. fossilis* and *H. longifilis*, the Cypriniforms *B. barbatus* and *Merluccius capensis*, the taeniae marginales develop very early, from the anterodorsal parts of the otic capsules (Srinivasachar, 1959; Badenhorst, 1989a; Vandewalle et al., 1992, 1997; Cabbage and Mabee, 1996). They then extend forward to form the base of the epiphyseal bridge. In *D. labrax*, parts of the epiphyseal bridge and taeniae marginales appear dorsally, isolated in the middle of the orbit. Each taenia marginalis then extends toward the rear to join with the front of the otic capsule. This mode of development is also seen others Perciformes. *H. fossilis* displays a peculiarity at this level: the taeniae marginales are not linked dorsally by formation of the epiphyseal bridge (Srinivasachar, 1959). The lamina precerebrealis, taeniae marginales, and trabecular bars are connected via the laminae orbitonasales, apparently directly linked to the preorbital roots of the taeniae marginales in both *D. labrax* and *B. barbatus* (Vandewalle et al., 1992). In *H. longifilis*, on the other hand, the preorbital roots develop later, independently of the laminae orbitonasales (Vandewalle et al., 1997).

In *D. labrax*, the latero-ventral sphenoid fenestrae are each divided in three by the pila lateralis and commisura lateralis; the two latter structures do not appear in *H. fossilis*, *C. gariepinus*, and *H. longifilis* (Srinivasachar 1959; Surlemont and Vandewalle 1991; Vandewalle et al., 1997).

In *D. labrax*, a tectum synoticum completes the braincase vault in front of the tectum posterius, and a taenia tecta medialis is formed by mediodorsal extensions issuing posteriorly from the cranial vault and anteriorly from the epiphyseal bridge. A similar situation is seen in others Perciformes (Watson and Walker, 1992). In *M. capensis* and *B. barbatus*, a taenia tecta medialis also develops, but it seems to issue only from the epiphyseal bridge (Badenhorst, 1989a; Vandewalle et al., 1992). In *H. longifilis* there appears no primordium of a taenia tecta medialis (Vandewalle et al., 1997). In *D. labrax*, the hypophyseal fenestra is narrow and open posteriorly. This contrasts with the situation in *B. barbatus* and *H. longifilis*, where it is broad, long, and limited by the parachordal plates and trabecular bars (Vandewalle et al., 1992; Vandewalle et al., 1997). *D. labrax* thus displays a tropitric skull.

Regression of the cartilaginous parts exists in many teleosts, but it begins at different developmental sizes in different species (Wells, 1923; De Beer, 1937; Vandewalle et al., 1995, 1997). In *D. labrax*, the phenomenon starts when all parts of the chondroneurocranium are not yet present and the splanchnocranium lacks at least the basihyal. The posterior part of the trabecular bars regresses first, ventrally isolating, very rapidly, the anterior and posterior parts of the neurocranium as in *M. capensis* and *B. barbatus* (Badenhorst, 1989a; Vandewalle et al., 1992). In *H. longifilis*, regression starts when the chondrocranium is practically complete, beginning with the central parts of the ceratobranchials and hyoid bars (Vandewalle et al., 1997).

Meckel's cartilages regress differently according to the species studied. In *D. labrax*, they split in two, one part being small and isolated in front. In *H. longifilis*, Meckel's cartilage splits into three parts, one of which is again situated at the front end (Vandewalle et al., 1997). Isolation of a cartilaginous element at the front of the mandible may shed some doubt as to the purely dermal origin of the dentary bones. These might have absorbed the small, anterior cartilaginous elements and thus have a dual origin, like the palatines, for instance, which each include an auto- and a dermo-palatine. In *B. barbatus*, Meckel's cartilage remains whole beyond the larval stage (Vandewalle et al., 1992).

Regression of the neurocranium, which begins very early in *D. labrax* with the separation of the trabecular bars from the parachordal plates, does not progress any further during the larval stage in this species or *B. barbatus* (Vandewalle et al., 1992). In *H. longifilis*, on the other hand, regression of the neurocranium simultaneously affects the otic capsules, trabecular bars, and parachordal plates (Vandewalle et al., 1997).

Osteocranium.—The development of the bony skull varies considerably among teleosts (De Beer, 1937; Bamford, 1948; Jollie, 1984; Matsuura and Yomeda, 1987).

At hatching, there is usually no ossified element. *D. labrax* follows this rule. *G. felis* and *P. antarticum* appears as an exception, since at hatching they already possess operculars, dentaries, and premaxillaries (Tilney and Hecht, 1993; Voskoboinikova, 1994).

The dermal splanchnocranium appears to ossify first. The operculars and the parts forming the buccal jaws (maxillary, premaxillary and dentary) develop earliest, followed by the pharyngeal jaws or their toothed plates. In *D. labrax* the maxillaries and premaxillaries are superposed at the outset, as in the others perciformes (Otten, 1982; Kohno et al., 1983; Potthoff et al., 1988; Oozeki et al., 1992; Watson and Walker, 1992; Potthoff and Tellock, 1993; Voskoboinikova, 1994; Mabee and Trendler, 1996) as well as *L. gastrophysus* and *B. barbatus* (Matsuura and Yomeda, 1987; Vandewalle et al., 1992), all which species have a protractile mouth at the adult stage. There is thus no transient, "primitive" state in which the premaxillaries and maxillaries are adjacent. This situation does

arise in *E. lucius* and *O. kisutch* (Jollie, 1975, 1984). In *D. rerio*, The first structures to appear are those of neurocranium (parasphenoïde, exoccipital and basioccipital) (Cubbage and Mabbee, 1996).

Next there appear the first deep ossifications of the splanchnocranium, which progressively replace the existing cartilaginous skeleton. In *D. labrax*, the quadrates appear first, followed by the symplectics. The hyomandibulars and palatines appear later, after the dermal bones of the suspensorium, i.e., the entopterygoids and ectopterygoids. In *L. gastrophysus*, the palatines and quadrates come first, the hyomandibulars appearing at the next stage (Matsuura and Yomeda, 1987). *B. barbatus* also shows delayed development of the hyomandibular (Vandewalle et al., 1992). In *N. aequoreus*, the quadrates appear at the same time as the first dermal structures of the splanchnocranium (Kadam, 1961). In *E. lucius* the hyomandibulars, symplectics, and quadrates appear simultaneously but somewhat later than the other structures, notably the ectopterygoids (Jollie, 1975).

The ectopterygoids and entopterygoids are usually considered to be dermal ossifications and the metapterygoid to be an endochondral one (Devillers, 1958; Daget, 1964). Watson (1987), surprisingly, describes the metapterygoid as the only dermal bone of the suspensorium in *Enchelyurus brunneolus*, although this bone is usually considered endochondral and although Watson and Walker (1992) report a cartilaginous stage for the ectopterygoid and entopterygoid in two Perciformes Haemulidae species. Matsuoka (1987) believes that in Sparidae, the quadrato-ptyergoido-palatine complex derives from two cartilaginous primordia, while Potthoff and Tellock (1993) report that only the ectopterygoid is dermal in *C. undecimalis*. If we compare, in *D. labrax*, the positions of the cartilaginous and bony elements, only the ectopterygoid might be considered to have an endochondral origin, while the entopterygoid is clearly dermal.

Ossification of the hyoid system begins, in all known cases, with the center of the hyoid bar, which becomes the ceratohyal. Next to appear are the two hypohyals, before or along with the posterior ossification of the hyoid bar or epihyal. The branchiostegal rays appear gradually, always from rear to front; the first ray is present well before the first ossification of the hyoid bar (Potthoff et al., 1988; Surlemont and Vandewalle, 1991; Watson and Walker, 1992; Vandewalle et al., 1992; Potthoff and Tellock, 1993; Vandewalle et al., 1995). In some cases there appears a third anterior ossification of the hyoid bar (Tilney and Hecht, 1993). In other cases, only a hypohyal seems to ossify (Tilney and Hecht, 1993; Vandewalle et al., 1995, 1997; Cubbage and Mabbee, 1996). Finally, the cartilaginous interhyal may in some cases never ossify; it may even disappear completely (Adriaens and Verraes, 1994). In *D. labrax*, the only peculiarity is the absence of an interhyal ossification at 40 d; it will appear later, since adult serranids possess an interhyal bone (Benmouna et al., 1984).

Ossification of the branchial basket is somewhat variable among teleosts. In several perciformes, all five ceratobranchials appear together, along with the first pharyngeal toothed plates; then come the epibranchials, pharyngobranchials, and hypobranchials. Finally, the axes of the basibranchials also ossify. The gillrakers appear first on the first bony ceratobranchial, then towards the rear on the epibranchials (Potthoff et al., 1988; Watson and Walker, 1992; Potthoff and Tellock, 1993; Mabbee and trendler, 1996). In *D. labrax*, the timing is somewhat different: the first four ceratobranchials ossify as the upper toothed plates appear, a little before the bony tooth-bearing fifth ceratobranchials and before the rest of the branchial basket. In the Ostariophysi whose development is known in this respect, the pharyngeal teeth and jaws always appear well before the other bony

branchial elements (Surlemont and Vandewalle, 1991; Vandewalle et al., 1992, 1995, 1997; Cubbage and Mabee, 1996). In all cases, the pharyngeal tooth-bearing elements appear at the same time as the buccal teeth, or nearly so.

Development of the neurocranium begins rather early, almost always with the appearance of the parasphenoid just after the first dermal structures of the splanchnocranium. This bone's growth seems related to the shape of the hypophyseal fenestra, which it gradually closes. The parasphenoid remains narrow in *D. labrax*. It rapidly broadens in *O. kisutch*, *B. barbus*, *A. davidsonii* and in Siluriformes (Jollie, 1984; Surlemont and Vandewalle, 1991; Vandewalle et al., 1992; Watson and Walker, 1992; Tilney and Hecht, 1993; Vandewalle et al., 1995, 1997; Cubbage and Mabee, 1996).

The second braincase bone to appear very early in development is the basioccipital. In *B. barbus*, it even appears just before the parasphenoid, and in *X. californiensis*, both bones appear simultaneously (Vandewalle et al., 1992; Watson and Walker, 1992). Shortly after the basioccipital, the exoccipitals appear in *D. labrax*, *B. barbus*, and *C. auratus* (Vandewalle et al., 1992, 1995). In *N. aequoreus* (Kadam, 1961) and *E. lucius* (Jollie, 1975), the exoccipitals and basioccipital appear simultaneously, but later in development. In *O. kisutch* and *D. rerio*, the exoccipitals develop along with the parasphenoid, after the first dermal parts of the splanchnocranium (Jollie, 1984; Cubbage and Mabee, 1996). In *H. longifilis*, the first step in bony development is the simultaneous appearance of the parasphenoid, basioccipital, and exoccipitals (Vandewalle et al., 1997).

The neurocranium then continues to develop in *D. labrax*, but more slowly than the splanchnocranium. The usual pattern is for the braincase vault to develop later, with the appearance of the supraoccipital, posttemporals, and epiotics, together with the pterotics and sphenotics. Then the front of the neurocranium, notably the frontals, is formed. The order in which these parts appear differs according to the species. In *A. davidsonii*, the frontal appears first, followed by the pterotic; in *X. californiensis*, the opposite occurs (Watson and Walker, 1992). In three *Silurus* species studied, *B. barbus*, and *C. auratus*, the supraoccipitals, pterotics, and sphenotics appear at the same time as the frontals (Kobayakawa, 1992; Vandewalle et al., 1992, 1995). In *H. longifilis*, the frontals develop first, then the rear of the neurocranium (Vandewalle et al., 1997). In *O. kisutch* and *G. felis*, the posttemporals and frontals appear at the same time as the parasphenoid (Jollie, 1984; Tilney and Hecht, 1993), while in *E. lucius*, they appear just after it (Jollie, 1975).

The bony cephalic skeleton then continues its development with the appearance of the front parts of the neurocranium and further development of the parts already present.

It is easy to see, by comparing alcyan-blue- and alizarin-stained individuals at the same developmental stage, that the deeper skeletal ossifications appear where cartilage regression is to occur. Ossification begins before regression. For the splanchnocranium, this correspondence is seen with the ceratobranchials, the ceratohyals, and parts of the suspensorium. The dentary is well formed by the time Meckel's cartilage begins to regress. According to Huysse (1990), this regression occurs only at the level of the tooth-bearing parts. Construction of the cartilaginous neurocranium is still under way and only the trabecular bars show signs of regression. But in this particular case, no bony structure of endochondral origin is yet in place. The parasphenoid, early-appearing dermal bone, is ventral with respect to such structures.

General consideration.—In teleosts, the different parts of the skull develop at different rates.

Whatever the variations among teleosts, development of the skull must always meet the survival requirements of the larvae. In *D. labrax* hatchlings, respiration is cutaneous and the highly vascularised yolk sac plays an important role in this process. Feeding, moreover, is endogenous. No skeletal structure is *a priori* necessary to support these two essential functions. The yolk sac resorbs slowly in *D. labrax*, in accordance with the gradual appearance of the skeletal structures. As the sac shrinks, the branchial system develops from front to rear, with the appearance of the first four cartilaginous ceratobranchials, the main bearers of respiratory filaments in the adult. The fifth ceratobranchials, having no respiratory function, form later and participate in feeding. Once the yolk sac has disappeared, cutaneous respiration is probably much reduced, but by then the branchial basket also possesses epibranchials (Table 1). Respiration in an aquatic medium requires the creation of a water current from front to rear (Hughes and Shelton, 1958; Ballintijn, 1969; Osse, 1990). This is possible in *D. labrax*, since 7.6-mm larvae possess a suspensorium articulating with the neurocranium, a hyoid bar hanging from the hyosymplectic, and the beginnings of an operculum. The very gradual ossification of the branchial basket suggests that cartilaginous structures can adequately carry out respiration.

Total resorption of the vitellus makes it necessary for the fry to switch from endogenous to exogenous feeding. This means the buccal cavity must be able to take up food from the external environment. First of all, this cavity must be limited, to avoid damage to other parts of the head such as the brain. In 7.6-mm larvae, the cartilaginous braincase is not yet closed ventrally, but the presence of the parasphenoid and basioccipital bones complements it and makes it rigid, dorsally limiting the buccal cavity. This should reduce the mechanical relations between the buccal cavity and the brain. Next, the mandible and the strong tooth-bearing pharyngeal jaws should be able to ensure food processing. A protractile mouth typical of perciforms (Liem, 1970, 1979; Lauder and Liem, 1981) does not develop until the larvae reach 8.1 mm, with the formation of an ascending process on the premaxillary. To be functional, such a mouth should also possess an ethmoid cartilage, indispensable to enable the premaxillary to slide along the neurocranium. A suspensorium (even cartilaginous), a hyoid bar, and an opercular are probably sufficient both for aquatic respiration and to constitute the beginnings of a suction feeding typical of evolved fish (Muller and Osse, 1984; Lauder, 1985), but one would expect the efficiency of this system to be far from optimal. This suggests that exogenous feeding probably begins at 7.6 mm with prey seizing and that efficient suction feeding appears gradually, with ossification of the endochondral structures and the appearance of all the bony elements of the suspensorium and operculum.

Yet other functional constraints govern construction of the cephalic skeleton. Late closure of the cranial vault probably reflects the need for the brain to grow. On the other hand, the development of certain cephalic structures such as the ethmoid region might not be subject to such crucial or obvious constraints, and their late appearance should not compromise fry survival.

Differences between teleost species in the development of the cephalic skeleton may reflect different survival requirements. Yet as observed by Vandewalle et al. (1997), one general rule does appear to emerge: the parasphenoid, the basioccipital, and the first dermal ossifications of the splanchnocranium appear at the time the yolk sac disappears or just after. All species must indeed solve the same survival problem linked with the switch from endogenous to exogenous feeding.

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