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EARLY DEVELOPMENT OF CEPHALIC BONY ELEMENTS IN *CHRYSICHTHYS AURATUS* (GEOFFROY SAINT-HILAIRE, 1808) (PISCES, SILURIFORMES, CLAROTEIDAE)

by

PIERRE VANDEWALLE (1), PHILIPPE LALEYE (2) and BRUNO FOCANT (3)

(1) Université de Liège, Institut de Zoologie,
Laboratoire de Morphologie fonctionnelle,
22, quai Van Beneden, B-4020 Liège (Belgique) ;
(2) Université nationale du Bénin, Faculté des Sciences agronomiques,
B.P. 526, Abomey-Calavi, Cotonou (Bénin) ;
(3) Université de Liège, Institut d'Anatomie,
Laboratoire de Biologie cellulaire et tissulaire,
20, rue de Pitteurs, B-4020 Liège (Belgique).

SUMMARY

The inception and development of the bony cephalic skeleton of *Chrysichthys auratus* is described from hatching to 28 days. The larval development is divided, into morphological levels rather than following days after hatching or fry length. Fry were cleared by trypsin and stained with alizarine. The bony cephalic development passes through periods of fast and slow growth. These rates are not the same in different parts of the skull. The operculum, dentary and two branchiostegal rays are present after two days. The first bone appearing in the braincase is the parasphenoid ; many of other bones develop subsequently and at the same time : the interoperculum, maxilla, lacrimal and upper pharyngeal jaw. The splanchnocranium continues to develop at a relatively fast rate while the neurocranium grows slowly. The braincase begins to close when the bucco-pharyngeal apparatus is almost complete.

Key words : Early development, fish skull, cephalic bones, Pisces, Siluriformes, Claroteidae, *Chrysichthys*.

INTRODUCTION

Researchers have long shown interest in the postembryonic development of the cephalic skeleton of teleostean fish (PARKER, 1873 ; STÖR, 1882 ; TISCHOMIROFF, 1885 ; WINSLOW, 1897), but all investigators have not pursued the same objectives and few studies make it possible to establish the precise chronology of the events which mark the development of a teleostean skull. Knowledge of this chronology, associated with the appearance and transformation of movements during growth, is crucial to understand the changes which occur during the development of functions, such as ventilation and feeding, which are vital to fry at all stages of their existence (Osse, 1990 ; Surlemont and Vandewalle, 1991). To obtain such knowledge, we have undertaken a morpho-functional study of the postembryonic development of the cephalic region of *Chrysichthys auratus*, an African catfish of the Claroteidae family. The aim is to contribute to general knowledge on the biology of *Chrysichthys*, which in certain countries might potentially be raised as a food source (Hem, 1986 ; Hem *et al.*, 1994).

The present paper concerns a morphological study of the development of the bony skeleton of *Chrysichthys auratus* from hatching (24 hours after fertilization) to the age of 28 days. The study thus encompasses the eleutheroembryo and larval stages as defined by Krupka (1988). The nomenclature used to describe the developing skeletal structures is based principally on the work of De Beer (1937) and Daget (1964).

MATERIAL AND METHODS

C. auratus fry were obtained by semi-natural fertilization carried out at the Faculty of Agronomical Sciences at Cotonou (Benin). The fry were raised at a temperature of 27° C. Batches of 30 fry were sampled on days 1 (hatching), 2, 3, 4, 6, 8, 10, 12, 15, 18, 21, 24, and 28 post-fertilization. The fry were fixed in a $CaCO_3$-buffered 10 % formalin solution. The fry were trypsin-cleared, alizarin-red-stained, and finally stored in glycerin (Taylor and Van Dijk, 1985).

Initially, the fry developed rather synchronously, but as their age increased, they exhibited variations in their developmental state. This is why we chose to describe levels of development. Figures 1 to ten represent the levels in the development of the bony skeleton, distinguishable in the 13 batches of fry.

Although the presentation of our results begins with the youngest fry, we were actually able to establish homologies and recognize structures only by comparing them with adult Bagridae (see for example Jayaram, 1970 ; Skelton, 1981 ; Ghiot et. al., 1984) then with those of the oldest fry and progressing by successive comparisons from the oldest fry to the youngest.

RESULTS

Level 1 : 1-day-old fry (fry 1 day after fertilization or at hatching)

At hatching, no bony skull element is discernible.

Level 2 : 2-day-old fry (Fig. 1)

The first dermal ossifications have appeared : the thin, flat opercles, the small but already thick dentaries, and two pairs of branchiostegal rays.

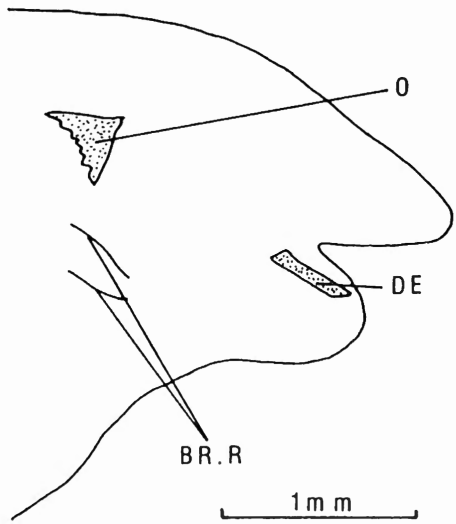

Fig. 1. — *Chrysichthys auratus.* — Lateral view of the cephalic bony elements at the second level (24 hours after hatching). Abbreviations : BR.R, branchiostegal rays ; DE, dentary ; O, opercle.

Level 3 : 3-day-old fry (Fig. 2)

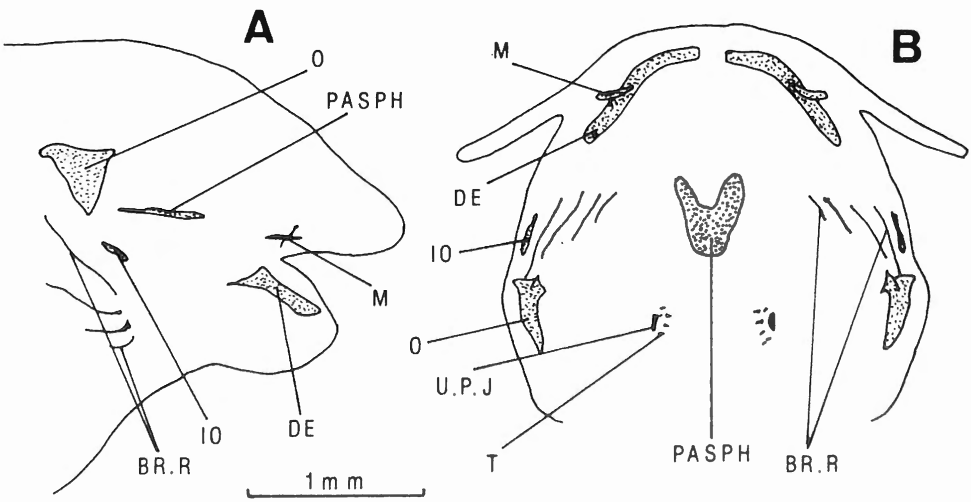

Fig. 2. — *Chrysichthys auratus.* — Lateral (A) and dorsal (B) views of the cephalic bony elements at the third level. Abbreviations : BR.R, branchiostegal rays ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; T, teeth ; U.P.J, upper pharyngeal jaw.

The number of dermal ossifications has considerably increased. The interopercles, the maxillae, the parasphenoid, two additional pairs of branchiostegal rays, and the upper pharyngeal jaw, already bearing teeth, are present. The parasphenoid appears well developed from the start, with two diverging anterior processes. The two outer pairs of branchiostegal rays are longer and are certainly those which appeared at level 2. The upper pharyngeal jaws appear to be formed as a single piece and it is impossible to determine which pharyngobranchial constitutes them. The opercles have become shell-shaped and the dentaries have lengthened.

Level 4 : 4- and 6-day-old fry (Fig. 3)

The first endochondral ossification has appeared : the basioccipital. Its anterior limit is unclear. The premaxillae are present and already bear teeth, and there are six pairs of branchiostegal rays. The outermost pairs have thickened and lengthened. Anteriorly and dorsally, the opercles bear a protuberance which is the beginning of the articular cavity for the hyomandibula-opercular joint. The other bones already present have developed further and the dentaries bear teeth.

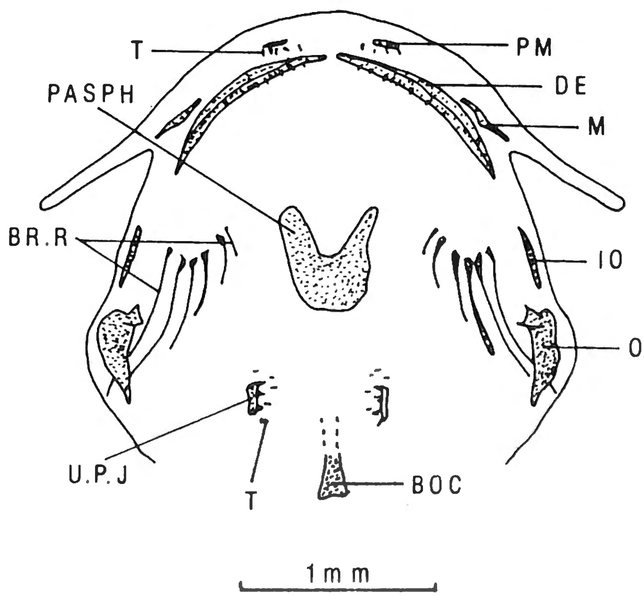

Fig. 3. — *Chrysichthys auratus.* — Dorsal view of the cephalic bony elements at the fourth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; T, teeth ; U.P.J, upper pharyngeal jaw.

Level 5 : 6- and 8-day-old fry (Fig. 4)

At this stage, there are 7 pairs of branchiostegal rays, one pair of ceratohyals, and pharyngeal teeth corresponding with the lower pharyngeal jaws. These teeth, located below the upper pharyngeal jaws, are aligned in two curved rows. The other skeletal parts are somewhat enlarged.

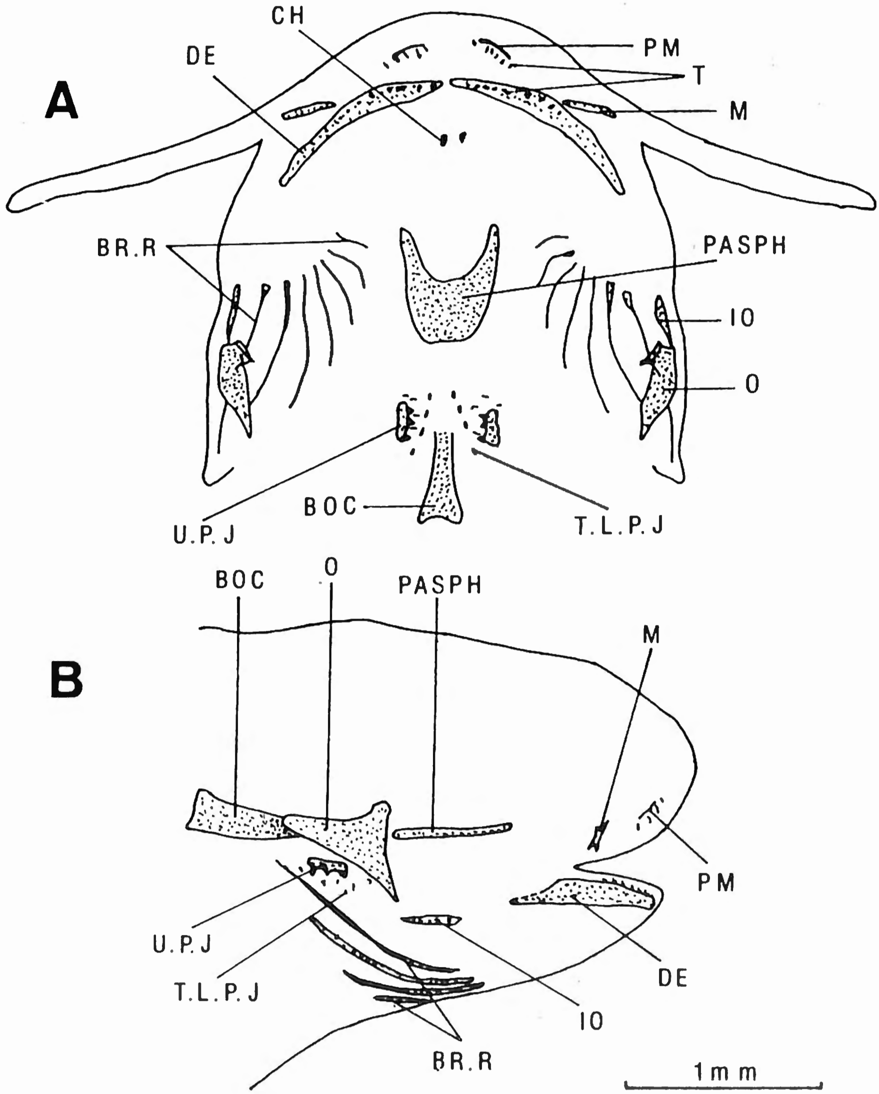

Fig. 4. — *Chrysichthys auratus.* — Dorsal (A) and lateral (B) views of the cephalic bony elements at the fifth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; T, teeth ; T.L.P.J, teeth of the lower pharyngeal jaw ; U.P.J, upper pharyngeal jaw.

Level 6 : 8-, 10-, and 12-day-old fry (Fig. 5)

Additions to the neurocranium are two curved, somewhat upper exoccipital appendages, one on each side of the basioccipital. The bony lower pharyngeal jaws have appeared. Towards the front have appeared a Y-shaped urohyal and a pair of apparently double visceral ossifications which we have called ceratohyals (but these may be hypohyals). There are now nine pairs of branchiostegal rays. The parasphenoid is considerably enlarged and its anterior processes have practically disappeared. The lacrimal began to ossify.

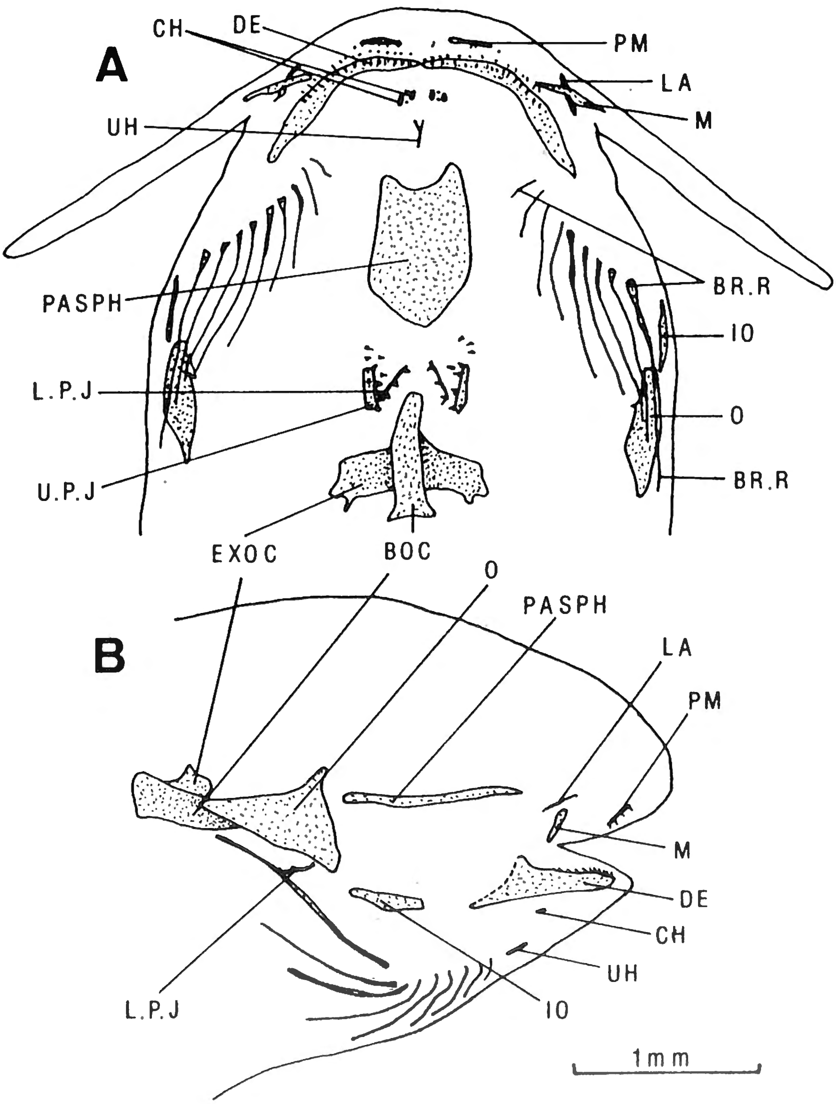

Fig. 5. — *Chrysichthys auratus.* — Ventral (A) and lateral (B) views of the cephalic bony elements at the sixth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; EXOC, exoccipital ; IO, interopercle ; LA, lacrimal ; L.P.J, lower pharyngeal jaw ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; UH, urohyal ; U.P.J, upper pharyngeal jaw.

Level 7 : 10-, 12-, and 15-day-old fry (Fig. 6)

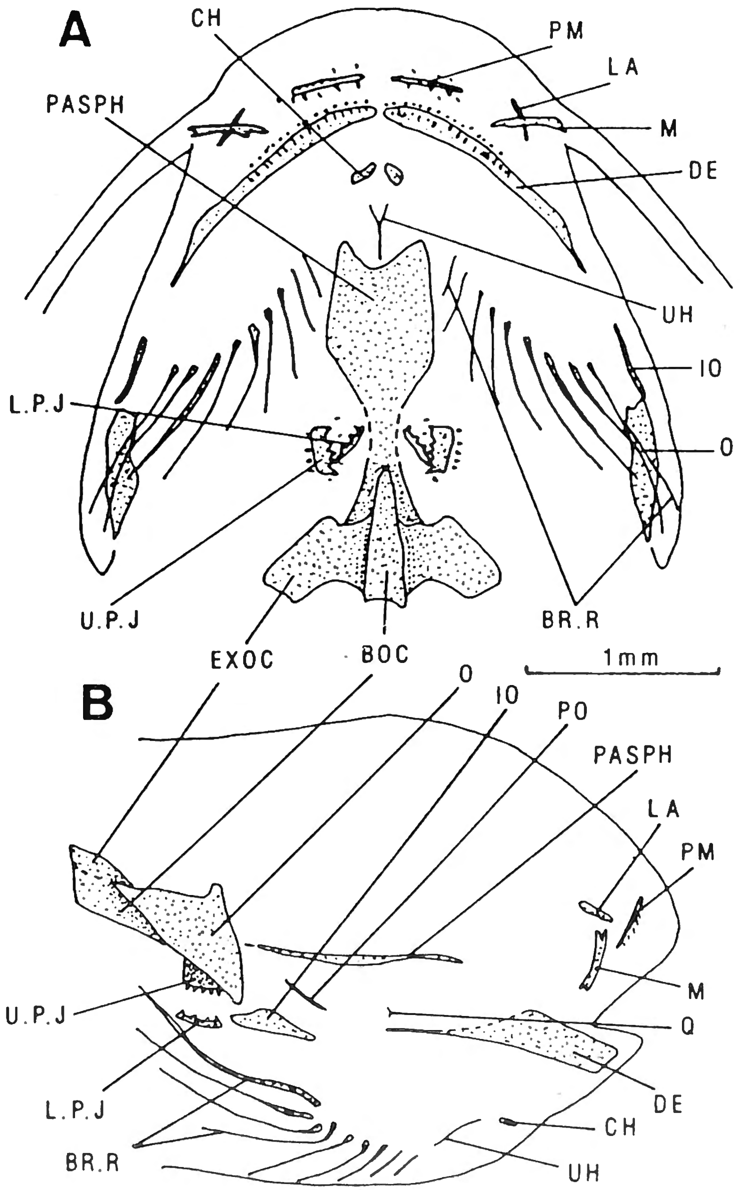

Fig. 6. — *Chrysichthys auratus.* — Ventral (A) and lateral (B) views of the cephalic bony elements at the seventh level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; Exoc, exoccipital ; IO, interopercle ; LA, lacrimal ; L.P.J, lower pharyngeal jaw ; M, maxilla ; O, opercle ; PM, premaxilla ; UH, urohyal ; U.P.J, upper pharyngeal jaw.

The most remarkable fact is the joining of the parasphenoid with the occipital region, quite conspicuous in the ventral view. The remainder of the skeletal system is growing. This is particularly obvious for the dentaries, the opercles, the exoccipitals, the ceratohyals, and the upper pharyngeal jaws.

Level 8 : 15- and 18-day-old fry (Fig. 7)

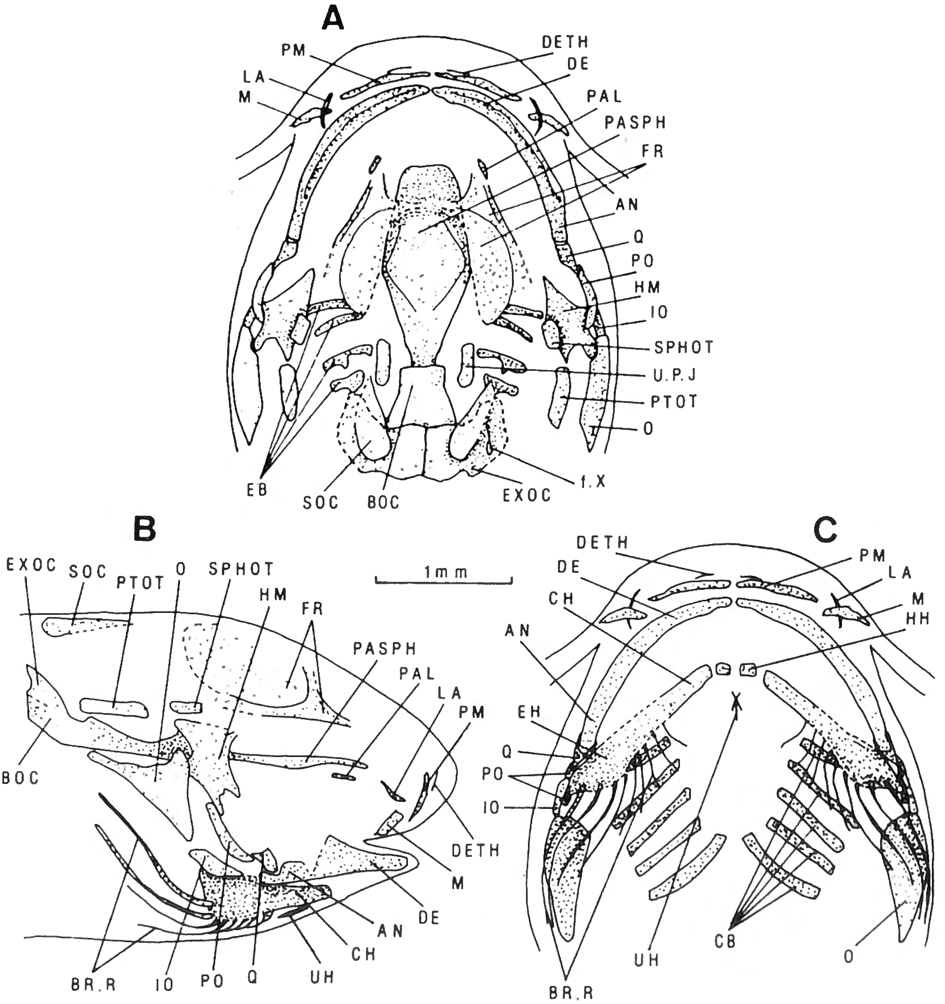

Fig. 7. — *Chrysichthys auratus.* — Presentation of the cepalic bony elements at the eigth level. (A) Dorsal view of the neurocranium, jaws, suspensorium, and dorsal part of the branchial basket; (B) lateral view of the skull; (C) ventral view of the jaws, suspensorium, hyoid bar and ventral part of the branchial basket. Dotted lines represent unclear limits. Abbreviations : AN, angular; BOC, basioccipital; BR.R, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; DE, dentary; DETH, dermethmoid; EB, epibranchial; EH, epihyal; EXOC, exoccipital; FR, frontal; f.X, foramen for the vagus nerve; HH, hypohyal; HM, hyomandibula; IO, interopercle; LA, lacrimal; M, maxilla; O, opercle; PAL, palatine; PASPH, parasphenoid; PM, premaxilla; PO, preopercle; PTOT, pterotic; Q, quadrate; SOC, supraoccipital; SPHOT, sphenotic; UH, urohyal; U.P.J, upper pharyngeal jaw.

This level is characterized by the simultaneous appearance of many ossifications. The neurocranium has progressed considerably. The frontals are already well developed, although their limits are not clear. It is possible to distinguish the sensory canals and the primordium of the epiphyseal junction. Each frontal is con-

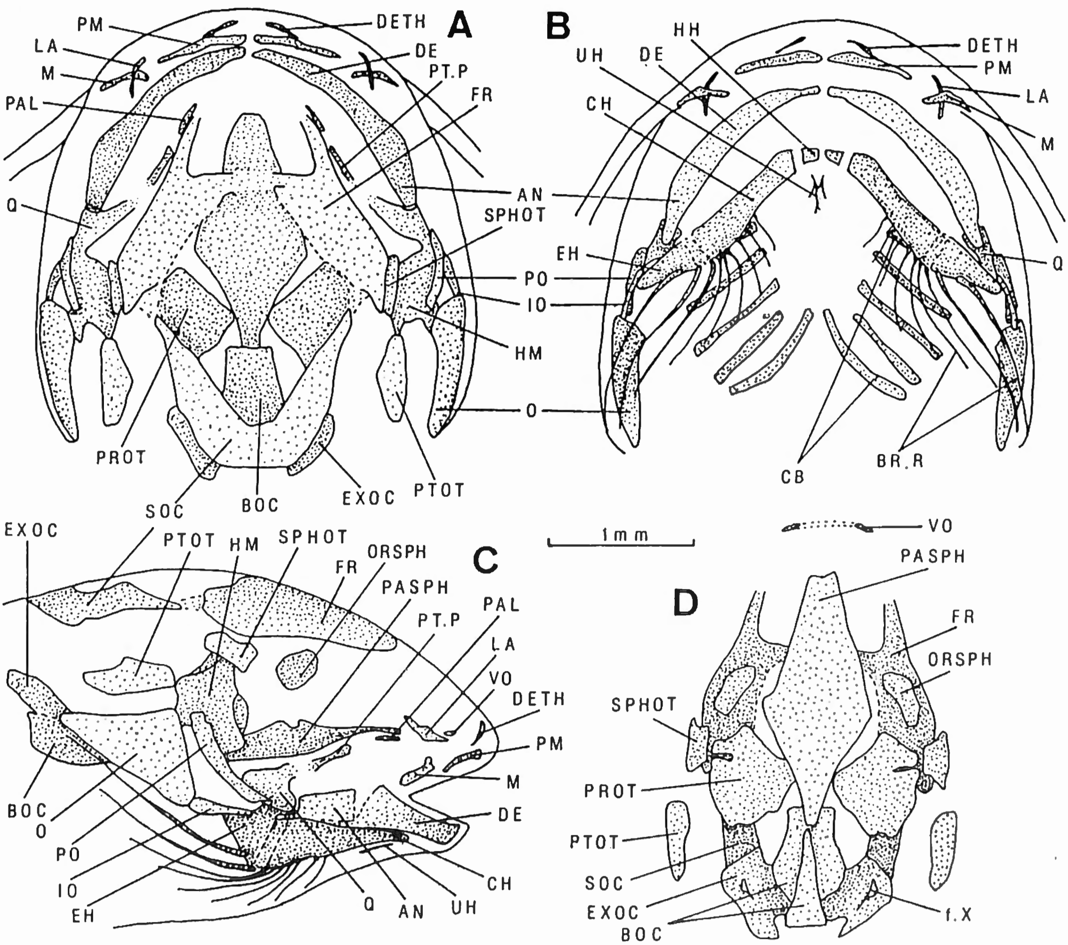

Fig. 8. — *Chrysichthys auratus.* — Presentation of the cephalic bony elements at the ninth level. (A) Dorsal view of the neurocranium, jaws and suspensorium; (B) ventral view of the jaws, the suspensorium, hyoid bar and ventral part of the branchial basket; (C) lateral view of the skull; (D) ventral view of the neurocranium. Dotted lines represent unclear limits. Abbreviations : AN, angular; BOC, basioccipital; BR.R, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; DE, dentary; DETH, dermethmoid; EH, epihyal; EXOC, exoccipital; FR, frontal; f.X, foramen for the vagus nerve; HH, hypohyal; HM, hyomandibula; IO, interopercle; LA, lacrimal; M, maxilla; O, opercle; ORSPH, orbitosphenoid; PAL, palatine; PASPH, parasphenoid; PM, premaxilla; PO, preopercle; PROT, prootic; PTOT, pterotic; PT.P, pterygoid process; Q, quadrate; SOC, supraoccipital; SPHOT, sphenotic; UH, urohyal; VO, vomer.

tinued by a « horn » which is probably the beginning of the taenia marginalis ossification. Towards the front, two small dermethmoids have appeared. Towards the back, the supraoccipital region displays two distinct ossifications and laterally the pterotics have appeared. The latter two parts, however, are independent. Ventrally, the joining of the parasphenoid and basioccipital is complete. The parasphenoid has enlarged considerably towards the front and has widened in its middle.

The lower jaw has appeared, composed of two elements : the dentary is continued by an articulo-angular, but in places, their limits are unclear. A small quadrate is also present, with the articulo-angular, it seems, already articulating with it. The preopercle is present and in contact with the hyomandibular, still incomplete in its upper portion. It already bears a posterior process pointing towards the opercle. Laterally with respect to the parasphenoid, a small palatine ossification has appeared. The hyoid arch is well developed and comprises hypohyals and two hyoid bars composed of an anterior ceratohyal region and a posterior epihyal region, separated by an indistinct ossified zone. The shape of the urohyal has become more complex. The branchial basket includes all the ceratobranchials and all the epibranchials but the pharyngobranchials are not recognizable in the upper pharyngeal jaws.

Level 9 : 18-, 21-, 24-, and 28-day-old fry (Fig. 8)

The neurocranium has received the addition of the orbitosphenoids, at the level of the orbit, and of the prootics. Towards the front, the dermethmoids have further developed and the vomerine ossifications have appeared. The limits of the frontals are more obvious, the sphenotics have come closer to the frontals and extend beneath them. There appears to be a fronto-occipital junction and the posterior regions of the supraoccipital ossifications have fused. The exoccipitals are each pierced by the foramen of the vagus nerve.

The quadrate has lengthened. Between it and the palatine has appeared an ossification corresponding to the pterygoid process. The hyomandibular extends beneath the sphenotic and the interopercle touches the opercle. Ventrally, the ceratohyal is easier to distinguish from the epihyal.

Level 10 : 24- and 28-day-old fry (Fig. 9)

The bones of the dome of the skull have all grown. The pterotic, the sphenotic, and the orbitosphenoid have all considerably developed vertically to constitute the lateral wall of the braincase. The latter is extended posteriorly by the exoccipital which stretches upward. Anteriorly, the vomerine ossifications have lengthened. At the level of the suspensorium, the novelty is the appearance of a small ossification situated latero-ventrally with respect to the palatine. This may be an ectopterygoid.

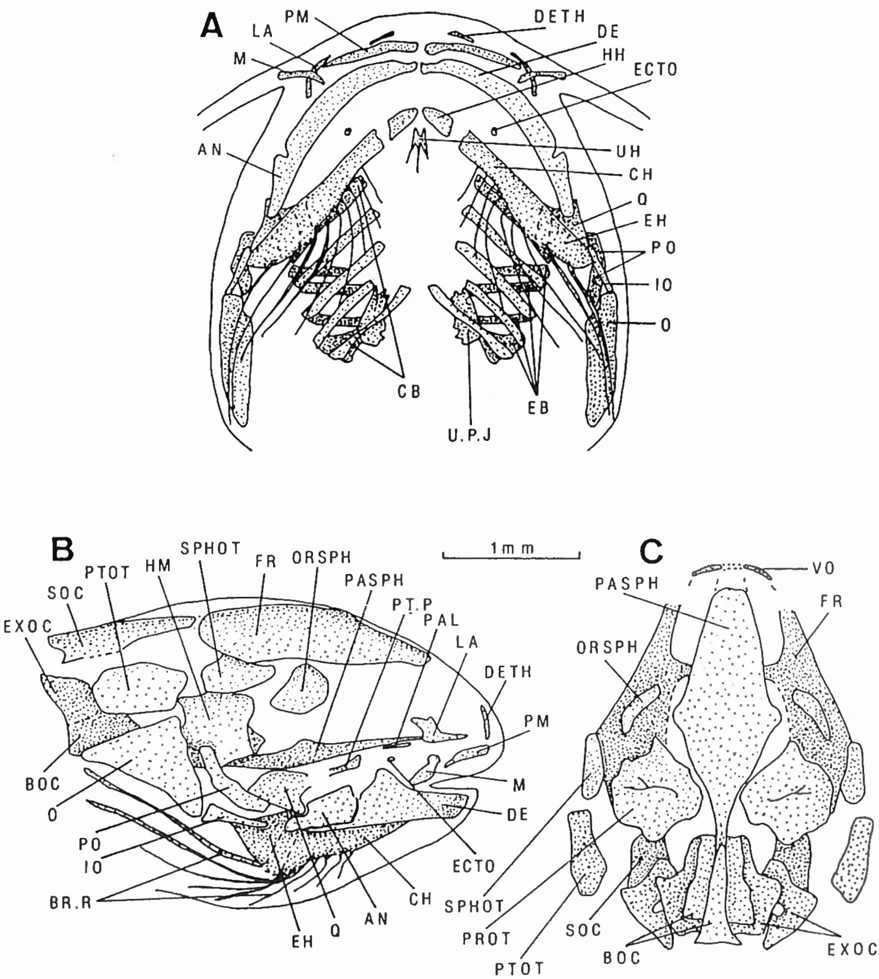

Fig. 9. — *Chrysichthys auratus.* — Presentation of the cephalic bony elements at the tenth level. (A) Ventral view of the splanchnocranium ; (B) lateral view of the skull ; (C) ventral view of the neurocranium. Dotted lines represent unclear limits. Abbreviations : AN, angular ; BOC, basioccipital ; BR.R, branchiostegal rays ; CB, ceratobranchial ; CH, ceratobranchial ; DE, dentary ; DETH, dermethmoid ; EB, epibranchial ; ECTO, ectopterygoid ; EH, epihyal ; EXOC, exoccipital ; FR, frontal ; HH, hypohyal ; HM, hyomandibula ; IO, interoperculaire ; LA, lacrimal ; M, maxilla ; O, opercle ; ORSPH, orbitosphenoid ; PAL, palatine ; PASPH, parasphenoid ; PM, premaxilla ; PO, preopercle ; PROT, prootic ; PTOT, pterotic ; PT.P, pterygoid process ; SOC, supraoccipital ; SPHOT, sphenotic ; UH, urohyal ; U.P.J, upper pharyngeal jaw ; VO, vomer.

The hypohyals and the urohyal have extended. Epibranchials 3 and 4 are in contact with the upper pharyngeal jaws, where it is still impossible to distinguish individual components.

Level 11 : 24- and 28-day-old fry (Fig. 10)

The supraoccipital ossification has practically come into contact with the frontals, which are linked by a complete epiphyseal bridge. The taenia marginalis ossification plunges toward the dermethmoid which has grown upward. Next to the latter, a nasal has appeared. The vomer is now a single piece, in contact with the parasphenoid. Laterally, two small ossifications have been added to the nasal region. These are probably two elements of the lateral ethmoid.

Posteriorly, the supraoccipital, the pterotic, and the sphenotic have almost completely united. The exoccipital and the supraoccipital are not yet truly joined. The sphenotic, the prootic, and the orbitosphenoid are still independent.

The mandible displays distinct dentaries and angulars. The quadrate has reached the pterygoid process. The hyomandibular articulates with the sphenotic and the pterotic. The hyohyals touch. The branchial basket has been enriched with two basibranchials, with dentate plates on the dorsal face of the 5th ceratobranchials and the ventral face of the upper pharyngeal jaws, and with the first gill rakers borne by the two first ceratobranchials. There are not yet any ossified hypobranchials.

DISCUSSION

It is not easy to compare the cephalic bony development in different teleosts. Few descriptions begin at hatching, the observed stages are often far apart, the living or farming conditions of the fry are variable, and finally, stages are defined differently according to the author. Having made these reservations, one can say that the postembryonic development of the skull bones of teleosts seems not to be very constant (De Beer, 1937 ; Bamford, 1948 ; Jollie, 1984 ; Matsuura and Yoneda, 1987 ; Vandewalle *et al.*, 1992a), although the first bones to appear are always the dermal elements of the splanchnocranium.

There is no bony structure in *Barbus barbus* (L., 1758) or *Clarias gariepinus* (Burchell, 1822) at hatching (Surlemont *et al.*, 1991 ; Vandewalle *et al.*, 1992a). The same is true for *Chrysichthys auratus*. In the siluriform *Clarias gariepinus*, the first bone appears after 48 hours : the opercle (Surlemont *et al.*, 1989). In another catfish, *Galeichthys felis* (Valenciennes, 1840), there is, at 8 mm, nothing but a small dentosplenial (Bamford, 1948). Tilney and Hecht (1993) report that development is very slow in *Galeichthys feliceps* (Valenciennes, 1840) and that the first bones to develop are the cleithra, followed, at 43 days, by the opercles, the dentaries, the maxillaries, and the first four pairs of branchiostegal rays. In three species of the genus *Silurus*, the maxillaries and premaxillaries appear first (Kobayakawa, 1992). In the cyprinid *Leuciscus rutilus* (L., 1758), the first ossification is the fifth ceratobranchial which is in fact the pharyngeal jaw (Hubendick, 1942). In another cyprinid, *Barbus barbus*, on the contrary, the opercle, a thin maxilla, a dentary, a small angular, and a small retroarticular appear at 8 days along with a branchiostegal ray (Vandewalle *et al.*, 1992a). In *Lophius gastrophysus* (Ribeiro) 8 mm long, there are already a maxilla, a premaxilla, a dentary, an articular, and

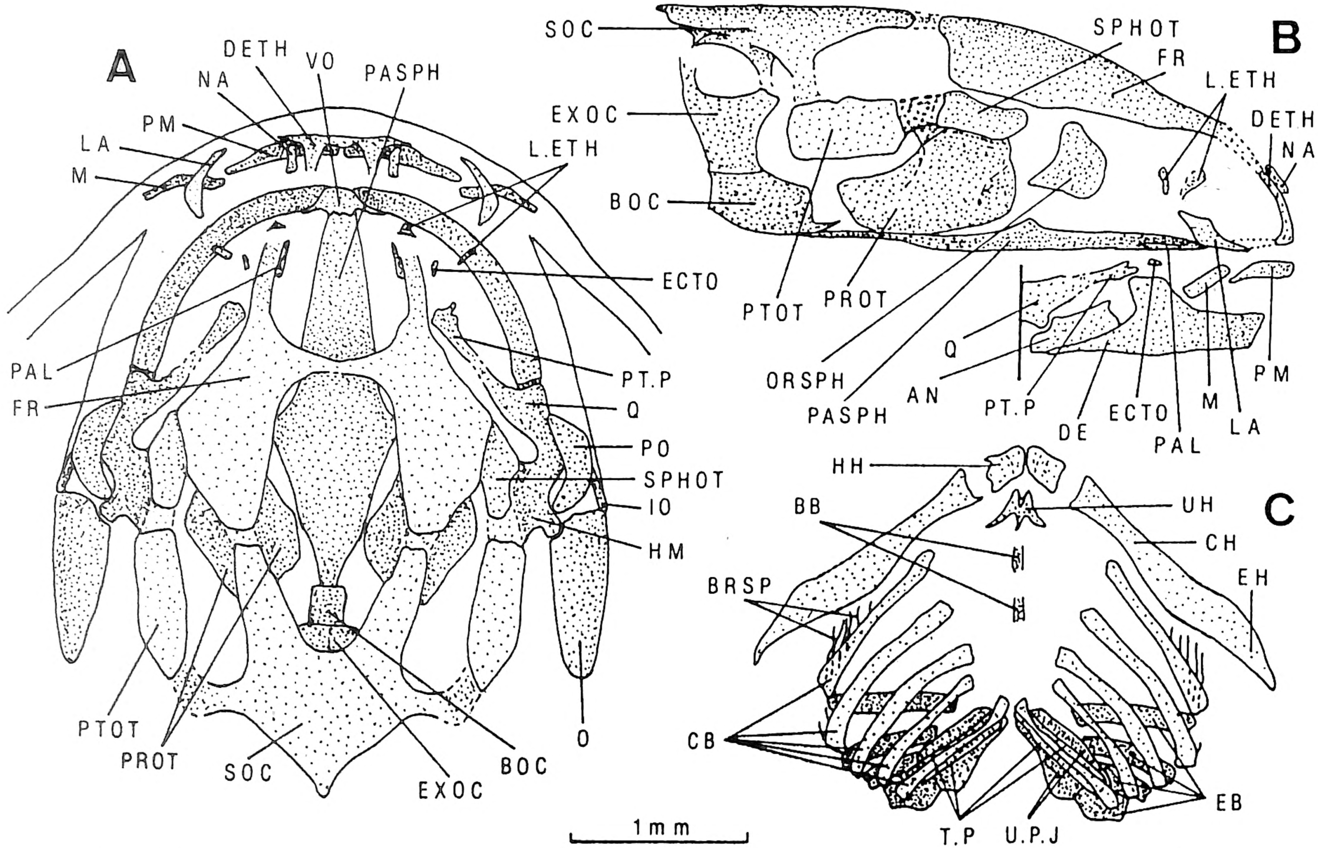

Fig. 10. — *Chrysichthys auratus*. — Presentation of the cephalic bony elements at the eleventh level. (A) Dorsal view of the neurocranium, jaws, suspensorium and operculum ; (B) lateral view of the neurocranium and anterior part of the splanchnocranium ; (C) ventral view of the hyoid bars and branchial basket. Dotted lines represent unclear limits. Abbreviations : An, angular ; BB, basibranchial ; BOC, basioccipital ; BRSP, Branchiospines or gill rakers ; CB, ceratobranchial ; CH, ceratohyal ; DE, dentary ; DETH, dermethmoid ; EB, epibranchial ; ECTO, ectoptérygoid ; EH, epihyal ; EXOC, exoccipital ; FR, frontal ; HH, hypohyal ; HM, hyomandibula ; IO, interopercle ; LA, lacrimal ; L.ETH, lateral ethmoid ; M, maxilla ; NA, nasal ; O, opercle ; ORSPH, orbitosphenoid ; PAL, palatine ; PASPH, parasphenoid ; PM, premaxilla ; PO, preopercle ; PROT, prootic ; PTOT, pterotic ; PT.P, pterygoid process ; Q, quadrate ; SOC, suparoccipital ; SPHOT, sphenotic ; T.P, tooth plate ; UH, urohyal ; U.P.J, upper pharyngeal jaw ; VO, vomer.

a preopercle (MATSUURA and YENODA, 1987). In *Nerophis aequoreus* (L., 1758), the first ossifications are the premaxilla, the maxilla, the dentary, and the angular (KADAM, 1961), while in *Salmo gairneri* (Richardson, 1836), there is first at least the opercle (VERRAES, 1977). *Chrysichthys auratus* is relatively precocious with, at two days of age, the presence of an opercle, a dentary, and two branchiostegal rays.

Throughout the eleutheroembryonic and larval periods, the splanchnocranium develops more rapidly than the neurocranium. This is a general phenomenon in teleosts (DE BEER, 1937). In *Barbus barbus*, all the ossifications of the suspensorium are present at 20 days, whilst the neurocranium still counts only four bones (VANDEWALLE *et al.*, 1992a). The buccal and pharyngeal jaws grow particularly fast. This situation is encountered also in *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991) and in many Perciforms (OTTEN, 1982 ; ISMAIL *et al.*, 1982 ; MORRIS and GAUDIN, 1982 ; POTTHOFF *et al.*, 1987 ; POTTHOFF and TELLOCK, 1993 ; WATSON and WALKER, 1992). The same is true in *Chrysichthys auratus.* In the latter species, it is noteworthy that from the time of its appearance, the maxilla is oriented towards the maxillary barbel ; from level 4 onwards, it occupies the place it has in the adult, where it supports the maxillary barbel and partially ensures its mobility (GHIOT *et al.,* 1984).

The first endochondral ossifications of the splanchnocranium of *Chrysichthys auratus* appear rather late, at level 8, but numerous ones appear all at once (hyomandibular, quadrate, palatine). In *Barbus barbus*, the quadrate appears first and progressively the rest of the endochondral suspensorium (VANDEWALLE *et al.,* 1992a). In *Chrysichthys auratus*, the shape of the quadrato-mandibular articulation seems to indicate that it is functional from the time it appears. This is not true in *Barbus barbus* (VANDEWALLE *et al.*, 1992a), where this articulation does not seem functional until the hyomandibular is present and well developed. As just mentioned, this situation arises more abruptly in *Chrysichthys auratus.* In both species, by the time the quadrato-mandibular articulation seems functional, so do the hyomandibulo-opercular and cranio-hyomandibular articulations, or nearly so. Thus, three of the four principal articulations of the suspensorium are constituted. They very likely enable the dilation of the buccal and opercular cavities which is necessary for breathing and feeding (OSSE, 1969 ; VANDEWALLE, 1979, 1980 ; LAUDER, 1983, 1985). Only the palatine region remains very incomplete. These observations agree with those of JOLLIE (1975) on *Esox lucius* (L., 1758).

The formation of the anterior region of the suspensorium varies from species to species. In all known cases, it is late. In *Barbus barbus*, the entopterygoid appears first, then the ectopterygoid and the palatine, and finally the metapterigoid. In this species, at 24 days, these different bony elements are separate from each other and the palato-ethmoideal articulation is not yet functional. In *Clarias gariepinus* (VANDEWALLE *et al.,* 1993), an entopterygoideal ossification is reported to form in front of the cartilaginous processus pterygoideus. Perhaps this ossification merely corresponds with the processus pterygoideus of *Chrysichthys auratus.* In the latter species, the palatine appears first, followed by the processus pterygoideus and finally by a small ossification which we have called ectopterygoid because of its ventro-lateral position with respect to the palatine. These three parts are not joined.

The delayed construction of the anterior portion of the suspensorium is probably related to the absence of a functional necessity during the larval period, since specimens can carry out their essential functions, notably breathing and feeding, with a suspensorium whose posterior part alone is complete.

In *Chrysichthys auratus* as in many other species (JOLLIE, 1975 ; VERRAES, 1977 ; SURLEMONT and VANDEWALLE, 1991 ; VANDEWALLE *et al.*, 1992a), the opercle is present at an early stage of development. In the adult, this element is essential to gill ventilation because it contributes to creating the water current from front to back within the buccal and opercular cavities (OSSE, 1969 ; ELSHOUD-OLDENHAVE and OSSE, 1976 ; VANDEWALLE, 1979). This respiratory requirement probably appears very early in fry.

As in *Barbus barbus* (VANDEWALLE *et al.*, 1992a), *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991), and many Perciforms as well (WATSON and WALKER, 1992 ; POTTHOFF *et al.*, 1987, 1988), the first ossifications of the branchial basket to appear in *Chrysichthys auratus* are the pharyngeal jaws. In all cases, they bear teeth very early. They are present before or at the time feeding on exogenous food begins. Their early ossification meets the need to grasp the food to be transformed and to be transported towards the oesophagus, a function which they perform in adults (SIBBING, 1982 ; LIEM, 1986 ; LIEM and SANDERSON, 1986 ; VANDEWALLE *et al.*, 1992b, 1995). Cartilaginous skeletal elements probably suffice to fulfill, as in *Barbus barbus*, the respiratory function of the rest of the branchial basket (VANDEWALLE *et al.*, 1992b) or, as in *Cyprinus carpio* (L., 1758), a suction feeding (OSSE, 1990).

In *Chrysichthys auratus*, the neurocranium develops more slowly than the splanchnocranium, without being as delayed as in *Barbus barbus* (VANDEWALLE *et al.*, 1992a). Except for the early ossification of the anterior region of the notochord or basioccipital, only the parasphenoid appears very early, as in the other species known in this respect (VERRAES, 1974 ; SURLEMONT and VANDEWALLE, 1991 ; VANDEWALLE *et al.*, 1992a ; WATSON and WALKER, 1992 ; OOZEKI *et al.*, 1992). As it develops, it constitutes the ceiling of the buccal cavity. It very probably closes the hypophyseal fenestra as in *Barbus barbus* (VANDEWALLE *et al.*, 1992a). and *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991). Its presence is justified by the necessity of separating, by means of a rigid bony element, the buccal cavity from the front of the braincase, thus enabling the fry to ingest solid food without it pressing on the brain.

The second step of the construction of the neurocranium is the formation of the entire cranial floor, by joining of the notochord or basioccipital with the parasphenoid and the appearance of the exoccipitals. At this time a bony roof of the braincase is totally non-existant. The same order of development has been observed in *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991), *Barbus barbus* (VANDEWALLE *et al.*, 1992a), two haemulid species (WATSON and WALKER, 1992), and *Sillago japonica* (Temminck et Schlegel) (OOZEKI *et al.*, 1992). This most likely meets the necessity of isolating the brain from the underlying organs and structures without compromising rapid growth.

The third step is the development of the cranial roof, whereas the anterior region of the neurocranium is still almost nonexistant. This time gap in the elaboration of the neurocranium is even more marked in *Barbus barbus* (VANDEWALLE *et al.*, 1992a) and it seems to exist in many teleosts (WATSON and WALKER, 1992; TILNEY and HECHT, 1993). At this stage of development, effective protection of the brain probably becomes a necessity, while the anterior region shelters no essential structure.

CONCLUSIONS

The development of the cephalic bony skeleton in *Chrysichthys auratus* is not uniform. It is as if development had to meet survival needs which appear hierarchically in time. At hatching, the highly vascularized yolk sac fulfills the nutritional function and probably at least part of the respiratory function. The shift to ingestion of exogenous food requires the formation of buccal and pharyngeal jaws. This new type of food requires a well-delimited buccal cavity so as not to interfere with the development of other structures, notably the brain. Hence the parasphenoid, then the rest of the braincase floor, form the limit between the braincase and the buccal cavity, preventing any physical or mechanical interaction between them. The efficiency of food ingestion is reinforced by construction of the postero-ventral part of the cheek. At the same time, the dorsal protection of the cranium develops. It seems that the strengthening of the anterior portion of the neurocranium and of the splanchnocranium is not yet a necessity.

The postembryonic development of other species may not respond to the same necessities. In *Haplochromis elegans*, for instance, the frontal bone appears very early, shortly after the primordium of the parasphenoid (VERRAES and ISMAIL, 1980; ISMAIL *et al.*, 1982), and in *Nerophis oequoreus*, the supraoccipital and frontal bones develop at the same time as the ethmoideal region.

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DESCRIPTION OF *ENCENTRUM DIETERI* sp. nov. (ROTIFERA, DICRANOPHORIDAE) FROM THE HIGH ARCTIC, WITH REDESCRIPTION OF *E. BIDENTATUM* (LIE-PETTERSEN, 1906) AND *E. MURRAYI* BRYCE, 1922

by

WILLEM H. DE SMET
Departement Biologie
Universiteit Antwerpen, University Centre of Antwerp,
Groenenborgerlaan 17, B-2020 Antwerpen, Belgium

SUMMARY

Encentrum dieteri sp. nov. (Rotifera, Monogononta : Dicranophoridae) collected from littoral marine algae of two fjords in Spitsbergen, Svalbard, is described and illustrated. *E. murrayi* Bryce, 1922 is reported for the first time since its description from Spitsbergen ; it is redescribed and illustrated. Also described and illustrated is *E. bidentatum* (Lie-Pettersen, 1906) ; *E. linnhei* Scott, 1974 is synonymised with *E. bidentatum.*

Keywords : Rotifera, taxonomy, *Encentrum*, new species, Arctic, Svalbard.

INTRODUCTION

The rotifer genus *Encentrum* Ehrenberg, 1838 is, with about 90 species, the most species-rich of the Dicranophoridae. However, the validity of many of these species is questionable because of poor descriptions and illustrations. Also a considerable number of species have not been reported since their description.

The study of the genus has long been neglected due to difficulties in obtaining well-preserved specimens and insufficient sampling efforts of its habitats. As most of the dicranophorids, *Encentrum* species mainly occur in periphytic and interstitial habitats of the littoral zone, both marine and freshwater. The genus is considered to be cold stenotherm with predominantly temperate distribution.

In this paper *Encentrum dieteri* sp. nov. is described from littoral algae of a fjord on the west coast of Spitsbergen (Svalbard), *E. murrayi* Bryce, 1922 is reported for the first time since its description and redescribed, and *E. linnhei* Scott, 1974 is synonymised with *E. bidentatum* (Lie-Pettersen, 1906).