Development of the chondrocranium of the shallow-water Cape hake *Merluccius capensis* (Cast.). Part 2: Viscerocranium

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The development of the viscerocranium of *Merluccius capensis*, from the earliest identifiable stage, is described. The anterior mesenchyme gives rise to the commissura palatoquadrati, the processus pterygoideus and the lamina orbitonasalis. The lamina orbitonasalis probably represents a suprapharyngopremandibula and the processus pterygoideus an infrapharyngopremandibula. A processus basalis is absent and the processus oticus represents a processus oticus internus. The hyomandibula consists of epihyal and laterohyal portions. A single suprapharyngobranchial develops, fused on to the fourth epibranchial.

Die ontwikkeling van die visserokranium van *Merluccius capensis* word beskryf vanaf die vroegste herkenbare stadium. Die anteriormesenkiem gee oorsprong aan die commissura palatoquadrati, die processus pterygoideus en die lamina orbitonasalis. Die lamina orbitonasalis stel waarskynlik 'n suprafaringopremandibulare voor, terwyl die processus pterygoideus 'n infrafaringopremandibulare voorstel. 'n Processus basalis is afwesig en die processus oticus stel 'n processus oticus internus voor. Die hiomandibulare bestaan uit epihiale en laterohiale gedeeltes. 'n Enkele suprafaringobrangiale ontwikkel, versmelt met die vierde epibrangiale.

In this paper, the second of a two-part series on the development of the chondrocranium of *Merluccius capensis*, the development of the viscerocranium is described and discussed.

Material and Methods

These are described fully in Part 1 on the development of the neurocranium.

Results

Stage 1 (2,3 mm)

Premandibular arch

The blastemic anterior end of each processus pterygoideus is continuous with a mesenchymatous sheath (remains of the anterior mesenchyme — Bertmar 1959) which anteriorly, ventrally and laterally surrounds the planum ethmoidale (Figure 3, Part 1). The ventral part of this sheath represents the commissura palatoquadrati (Holmgren 1943).

Mandibular arch

The anteroventral, articular part of the pars quadrata (processus articularis palatoquadrati) is fully chondrified (Figure 3, Part 1). It consists of young cartilage and it is posteriorly in contact with, though not fused to, the symplectic cartilage. Of the metapterygoid portion of the pars quadrata only the ventral part is chondrified. The dorsal part is still blastemic and cannot be distinguished from the posterior extension of the processus pterygoideus. There is no processus basalis of the palatoquadrate and no early blastemic or mesenchymatous palatobasal connection between the palatoquadrate and the polar cartilage, such as described by Bertmar (1959) in *Hepsetus* and by Van der Westhuizen (1979) in *Barbus*. The posterior, mesenchymatous portion of the pars quadrata, pointing towards the trabecula, represents a processus oticus internus (Holmgren 1943; Bertmar 1959). The processus articularis palatoquadrati articulates, but is not fused with Meckel's cartilage. Similar to *Gadus* (De Beer 1937), *M. capensis* very early in its development displays the typically gadoid facies with the upturned lower jaw and the articulation far forward (Figure 3, Part 1). Meckel's cartilage is chondrified and it consists of young cartilage. Anteriorly the two cartilages of each side meet in a symphysis, strengthened by the early ossified mentomandibular bone. Dorsal to its articulation with the pars quadrata Meckel's cartilage has a distinct processus coronoideus and posteroventrally a slight processus retroarticularis (Figure 3, Part 1). There is no trace of an early, blastemic contact between Meckel's cartilage and the ceratohyal such as Bertmar (1959) describes in *Hepsetus*.

Hyoid arch

The large hyomandibula is fully chondrified and it consists of symplectic, epihyal and laterohyal (Bertmar 1959) portions (Figure 3, Part 1). The latter part is pierced by the truncus hyomandibularis of the facial nerve, which passes through the foramen hyomandibulare. The hyomandibula only has a single articulation with the auditory capsule. The interhyal (stylohyal), which consists of young cartilage, is synchondrotically fused with the hyomandibula and with the posterior end of the ceratohyal. The ceratohyal (Figure 3, Part 1 and Figure 1) is large and conspicuous and is fully chondrified throughout its length. Anteriorly the hyoid arch is continued as a separately chondrifying hypohyal (Figure 1), the anterior tip of which is still prochondral while the rest is young cartilage. The hypohyals of each side are attached to the median basihyal by means of thick mesenchyme. The basihyal is entirely prochondral and it is not separate from the first basibranchial, although there is some indication of an earlier separation.

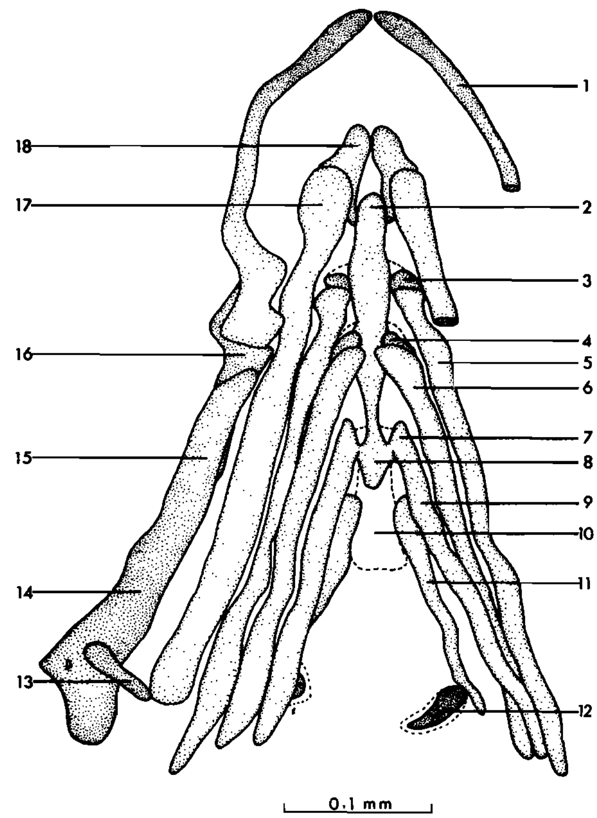

Figure 1 Graphic reconstruction of the viscerocranium. Stage 1. Ventral view. 1: Meckel's cartilage, 2: basibranchial I, 3: hypobranchial I, 4: hypobranchial II, 5: ceratobranchial I, 6: ceratobranchial II, 7: hypobranchial III, 8: basibranchial II, 9: ceratobranchial III, 10: basibranchial II anlage, 11: ceratobranchial IV, 12: fused infrapharyngobranchials, 13: interhyal, 14: hyomandibula, 15: symplectic, 16: pars quadrata, 17: ceratohyal, 18: hypohyal.

Branchial arches

Although *M. capensis* eventually develops five branchial arches, only four of these are present at this stage (Figure 1). Ventromedially, in the floor of the pharynx, the first basibranchial is chondrifying opposite the hypobranchials of the first four arches. It is mostly prochondral, except opposite the first hypobranchials, where it consists of young cartilage. From Figure 1 it is evident that the first basibranchial is derived from the basal elements of the first three branchial arches. The second basibranchial, which develops in connection with the fourth (and later the fifth) branchial arch, is still blastemic. Separate hypobranchials are present in only the first three arches. They are mostly prochondral, except for their extreme anterior portions which are blastemic. Separate hypobranchials never occur in the fourth arches. The hypobranchials are not fused with the first basibranchial but they are, as in the case of the hypohyals, closely attached to their basal element by thick mesenchyme. In all four arches ceratobranchials have chondrified, those of the first three arches consisting of young cartilage. The anterior part of the fourth ceratobranchial, which is blastemically linked to the blastemic second basibranchial, is still prochondral. Epibranchials are still lacking in all four arches and not even their blastemic anlagen are present at this stage. Dorsally, in the roof of the pharynx and immediately above the posterior ends of the fourth ceratobranchials, the infrapharyngobranchials are condensing. They consist on each side of a core of procartilage surrounded by blasteme. At this stage it is impossible to identify positively the arches to which they belong.

Stage 2 (3,4 mm)

Premandibular arch

The anterior part of the processus pterygoideus is still blastemic, but in the region of its contact with the planum ethmoidale its core is turning prochondral. Further posterior the processus pterygoideus remains blastemic up to the level of the blastemic part of the cartilago supraorbitalis anterior (Figure 6, Part 1), whereafter it becomes prochondral until it fuses with the pars quadrata. The commissura palatoquadrati is now blastemic and it is more extensive than in the previous stage. Just posterior to the articulation between the processus pterygoideus and the planum ethmoidale, the anlage of the lamina orbitonasalis can now be identified. It develops as a dorsal extension of the processus pterygoideus, in the shape of a blastemic cord reaching dorsally towards the hind boundary of the nasal placode.

Mandibular arch

The entire metapterygoid portion of the pars quadrata has chondrified (Figure 6, Part 1). The processus oticus internus is not very prominent. From it a blastemic cord reaches towards the polar cartilage. This cord might easily be mistaken for the early blastemic contact between the pars quadrata and the polar cartilage described by Bertmar (1959), Van der Westhuizen (1979), Nel (1981) and Van den Heever (1981) respectively, where the contact is between the processus basalis and the polar cartilage. The histology of this cord, however, is markedly similar to that of the primordium of the musculus rectus externus, and in *Ctenopharyngodon* Van den Heever (1981) describes a similar connection which later develops into the musculus adductor hyomandibulae internus. It is therefore accepted that the cord described above represents a muscle primordium. The dentary has started to ossify in the blasteme surrounding the anterior part of Meckel's cartilage.

Hyoid arch

Ventral to the hyomandibula the symplectic (Figure 6, Part 1), which has undergone slight perichondral ossification, is still free of the pars quadrata, although it is firmly attached to the latter by means of thick blastemic tissue. The ceratohyal has ossified perichondrally in its central and anterior sections, while its posterior part remains cartilaginous. In the anterior floor of the pharynx the basihyal (Figure 2) has now chondrified completely, as have the two hypohyals, the anterior ends of which are imbedded in thick blasteme. No indication of an earlier separation between the basihyal and the

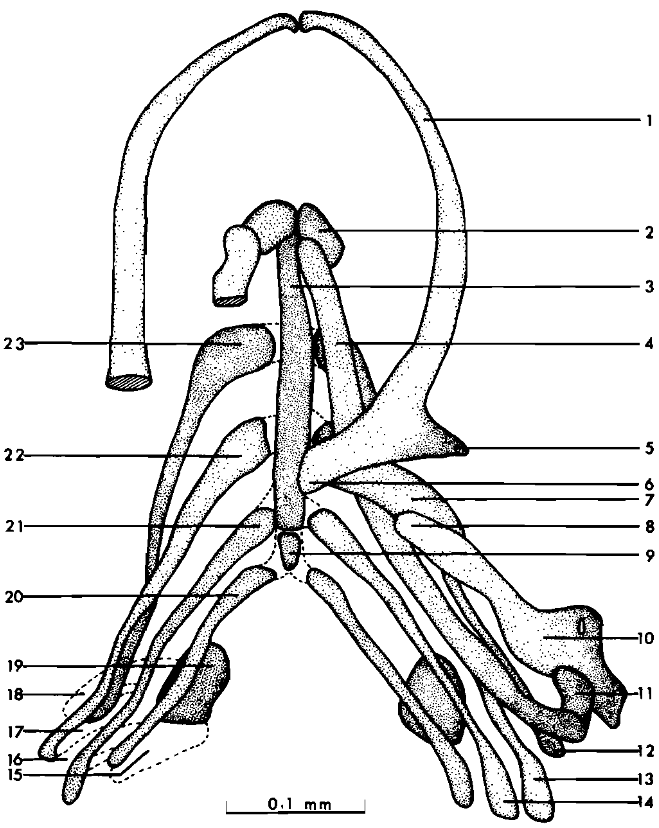

Figure 2 Graphic reconstruction of the viscerocranium. Stage 2. Ventral view. 1: Meckels's cartilage, 2: hypohyal, 3: basibranchial I, 4: ceratohyal, 5: processus coronoideus, 6: processus retroarticularis, 7: pars quadrata, 8: symplectic, 9: basibranchial II, 10: hyomandibula, 11: interhyal, 12: ceratobranchial I, 13: ceratobranchial II, 14: ceratobranchial III, 15: epibranchial IV anlage, 16: epibranchial III anlage, 17: epibranchial II anlage, 18: epibranchial I anlage, 19: fused infrapharyngobranchials, 20: ceratobranchial IV, 21: hypobranchial III, 22: hypobranchial II, 23: hypobranchial I.

first basibranchial remains.

Branchial arches

The first basibranchial is completely chondrified. The second basibranchial, which was blastemic in the previous stage, is now starting to chondrify. It does not lie on the same horizontal plane as the first, but is situated more dorsally. Anteriorly it is blastemically connected to the first basibranchial (Figure 2), its central part is turning prochondral and posteriorly it remains blastemic. The first hypobranchial is prochondral anteriorly while the rest is young cartilage. The second and the third hypobranchials remain blastemic anteriorly but become progressively chondrified caudally. Whereas it was possible to distinguish between the hypo- and ceratobranchials of the first three arches in the previous stage, this has now become impossible. The fourth ceratobranchial which lacks a hypobranchial is in direct blastemic contact with the posterior part of the second basibranchial. The fifth branchial arch is still absent. The infrapharyngobranchials have chondrified and consist of young cartilage (Figure 2). It is still impossible to determine accurately to which arches they belong, but they probably represent the infrapharyngobranchials of the first four arches. The epibranchials of the first three arches have meanwhile developed as blastemic condensations (Figure 2) which link the posterior ends of the ceratobranchials ventral to the compound infrapharyngobranchials dorsally. The first and the second epibranchials are separated posteriorly where they attach to their respective ceratobranchials, but anteriorly they form one common blasteme in contact with the infrapharyngobranchials. The third and the fourth epibranchials display a similar mode of development.

Stage 3 (4,0 mm)

Premandibular arch

The processus pterygoideus remains in blastemic contact with the lamina orbitonasalis via a thin cord which in later stages develops into the preorbital ligament (the ethmopalatine articulation). The anterior contact between the processus pterygoideus and the planum ethmoidale may now rightly be termed the rostropalatine articulation. The commissura palatoquadrati remains blastemic, albeit much reduced compared to the previous stage.

Mandibular arch

The processus articularis palatoquadrati and that part of the pars quadrata in contact with the symplectic now display signs of perichondral ossifications. The metapterygoid portion of the pars quadrata still consists of young cartilage and, to a lesser extent, of procartilage while the processus oticus internus is made up entirely of young cartilage. Meckel's cartilage is unchanged from the previous stage.

Hyoid arch

The hyomandibula still has only one broad articulation with the auditory capsule. Both its epihyal and laterohyal portions now display the advent of perichondral ossification. The anterior boundary of the foramen hyomandibulare is starting to disappear and only a thin sliver of cartilage remains anterior to the truncus hyomandibularis, where it passes through the foramen (Figure 9, Part 1). The symplectic is much thinner and longer than in the previous stage. In the region of its contact with the pars quadrata further perichondral ossifications are taking place. The symplectic is not fused with the pars quadrata, but it is firmly attached to the latter by ligaments which have formed in the blasteme surrounding the two elements. This indicates future syndesmosis. Anteroventral in the hyoid arches the hypohyals are starting to ossify perichondrally. They are still firmly attached to their respective ceratohyals, but they do not display any sign of fusion with the latter. Only the posterior ends of the two hypohyals are in contact with the median basihyal (Figure 3). The perichondral ossifications of the ceratohyals are now more pronounced.

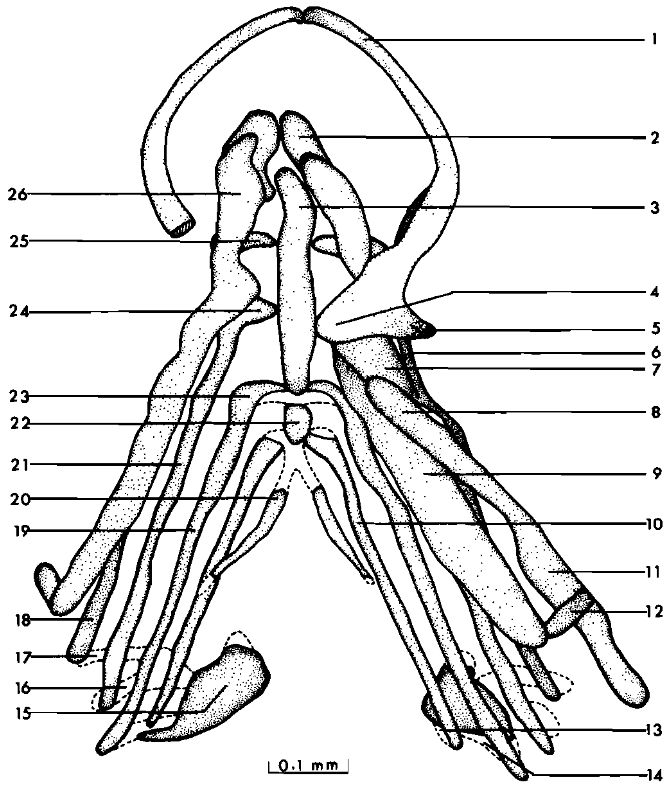

Figure 3 Graphic reconstruction of tbe viscerocranium. Stage 3. Ventral view. 1: Meckel's cartilage, 2: hypohyal, 3: basibranchial I, 4: processus retroarticularis, 5: processus coronoideus, 6: processus pterygoideus, 7: pars quadrata, 8: symplectic, 9: ceratohyal, 10: ceratobranchial IV, 11: hyomandibula, 12: interhyal, 13: blastemic epibranchial IV, 14: blastemic epibranchial III, 15: fused infrapharyngobranchials, 16: blastemic epibranchial II, 17: blastemic epibranchial I, 18: ceratobranchial I, 19: ceratobranchial III, 20: ceratobranchial V, 21: ceratobranchial II, 22: basibranchial II, 23: hypobranchial III, 24: hypobranchial II, 25: hypobranchial I, 26: ceratohyal.

Branchial arches

Both basibranchials are fully chondrified, except for the anterior part of the second, which remains blastemic where it comes into contact with the first (Figure 3). Chondrification of the fourth ceratobranchial has progressed more anteriorly and it has gained contact with the second basibranchial. The fifth ceratobranchial (Figure 3), the only element to develop in the fifth branchial arch, has now appeared. It is mostly prochondral, except anteriorly, where it is blastemic and in contact with the fourth ceratobranchial and the second basibranchial, and posteriorly, where it is also blastemic. The epibranchials (Figure 3) remain blastemic, except for the first two where prochondral centres are forming. As in the previous stage, the first two epibranchials are grouped together while the third and the fourth epibranchials develop from another, separate anlage. Except for their anteromedial part, which remains blastemic, the fused infrapharyngobranchials of each side have completely chondrified (Figure 3). Swinnerton (1902) describes a similar condition in *Gasterosteus* where the 'pharyngobranchials' (infrapharyngobranchials) form a unified plate.

Stage 4 (5,1 mm)

Premandibular arch

The processus pterygoideus articulates with the mediolateral edge only of the planum ethmoidale, rostrally its anterior end diverges from the planum. It is not fused with the planum ethmoidale, but it is connected by thick connective tissue at the rostropalatine articulation. In *Acipenser*, *Amia* and *Salmo* (Holmgren 1943) and in *Hepsetus* (Bertmar 1959) an intermediating body, which differentiates out of the blasteme which attaches the anterior end of the processus pterygoideus to the cornu trabeculae, is present. In *Amia* and in *Hepsetus* (Bertmar 1959) the intermediating body chondrifies separately to form the submaxillary cartilage. In *M. capensis* a separate intermediating body does not develop. The entire processus pterygoideus is now chondrified. Its central section, which lies in the roof of the pharynx, is undergoing perichondral ossification, and thin bone lamellae, the dermal ossifications of the endopterygoid, have also appeared in the surrounding membranes. The commissura palatoquadrati is confined to that area ventral to the planum ethmoidale which lies anterior to the rostropalatine articulation. In this region the vomer has ossified as a thin, bony plate in the commissura palatoquadrati. The preorbital ligaments are slightly more extensive, but they are still rudimentary and blastemic in nature.

Mandibular arch

Meckel's cartilage (Figure 4 and Figure 12, Part 1) is more or less unchanged from the previous stages, except for the beginning of perichondral ossification of the processus coronoideus and the processus retroarticularis. The ossifications of the dentary and the mentomandibula are more extensive. In the pars quadrata, perichondral ossifications are more advanced on its ventral surface and on the surface in contact with the symplectic. The latter cartilage is now syndesmotically attached to the pars quadrata. The metapterygoid portion of the pars quadrata is made up of a thin, vertical plate containing a single row of chondrocytes, while the processus articularis palatoquadrati is more massive and it appears circular in cross section. The processus oticus internus is more pronounced than in the previous stage.

Hyoid arch

Compared with the rest of the chondrocranium, the hyomandibula is less prominent and the angle between it and the symplectic is more acute than in the previous stage (Figure 12, Part 1). The anterior boundary of the foramen hyomandibulare has been resorbed completely and only an incisure remains for the passage of the truncus hyomandibularis. In *Gadus* (De Beer 1937) this nerve trunk leaves laterally in front of the hyomandibula, a condition which at this stage *M. capensis* is gradually approaching. According to De Beer (1937) this condition is unique in the Teleostei. Srinivasachar (1960) reports a similar erosion of the anterior boundary of the

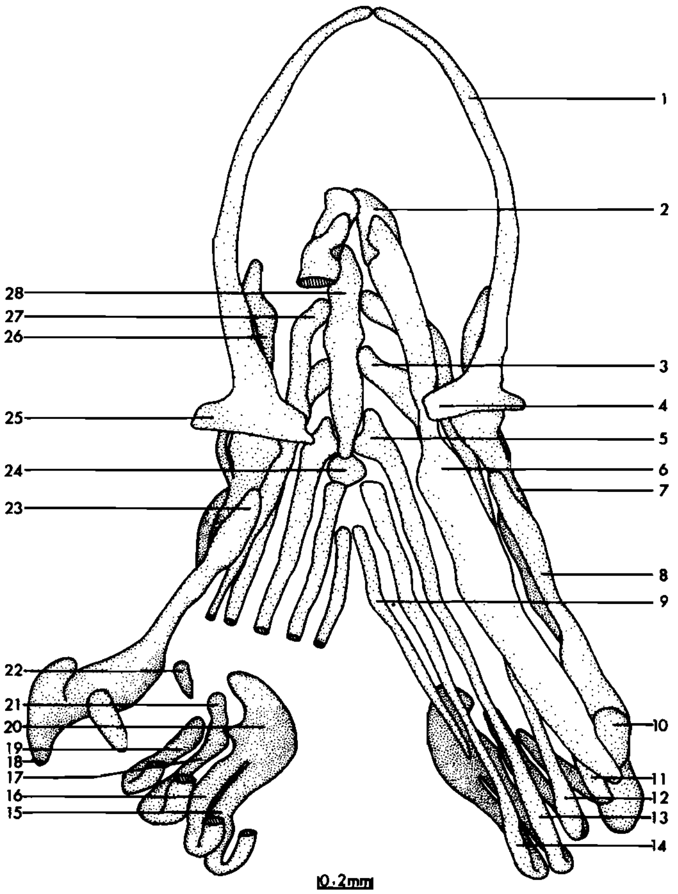

Figure 4 Graphic reconstruction of the viscerocranium. Stage 4. Ventral view. 1: Meckel's cartilage, 2: hypohyal, 3: hypobranchial II, 4: processus retroarticularis, 5: hypobranchial III, 6: ceratohyal, 7: pars quadrata, 8: hyomandibula, 9: ceratobranchial V, 10: interhyal, 11: ceratobranchial I, 12: ceratobranchial II, 13: ceratobranchial III, 14: ceratobranchial IV, 15: epibranchial IV, 16: epibranchial III, 17: epibranchial II, 18: processus opercularis, 19: epibranchial I, 20: fused infrapharyngobranchials III & IV, 21: infrapharyngobranchial II, 22: infrapharyngobranchial I, 23: symplectic, 24: basibranchial II, 25: processus coronoideus, 26: processus pterygoideus, 27: hypobranchial I, 28: basibranchial I.

foramen hyomandibulare in *Heteropneustes*. In *Mastacembelus* (Bhargava 1958) this erosion takes place on the posterior border of the hyomandibula. Dorsally the hyomandibula is synchondrotically attached to the auditory capsule, being lodged in the fossa hyomandibularis of the latter. The interhyal is similarly synchondrotically attached to both the hyomandibula and the ceratohyal. The posterior end of the ceratohyal remains unossified and now has a dorsally directed process (Figure 12, Part 1), but the central part is much reduced compared to the previous stages. Anteroventrally the two hypohyals meet in a symphysis (Figure 4). Each hypohyal is pierced by a foramen which transmits the afferent hyoidean artery. Similar foramina are reported by Berrill (1925) in *Solea* and in *Pleuronectes* and by Srinivasachar (1953) in *Ophicephalus*. Only the posterodorsal ends of the hypohyals are in contact with the basihyal, which now appears wedge-shaped in cross section. Although the hypohyals are intimately fused with the ceratohyals, the original demarcations between them may still be observed.

Branchial arches

The second basibranchial is fully chondrified and its anterior end is situated dorsal to the posterior end of the first basibranchial. The hypobranchials of the first three arches are fused with their respective ceratobranchials. The third hypobranchial now displays a prominent anteroventral process which becomes even more prominent in later stages. The fifth ceratobranchials are completely chondrified and they have lost their earlier contact with the second basibranchial (Figure 4). Their anterior ends meet in a symphysis which is strengthened by connective tissue. Relative to the other ceratobranchials, the fifth ceratobranchials have lengthened markedly. The really significant developments in the branchial arches have occurred in the epibranchials and in the infrapharyngobranchials (Figure 4). The four epibranchials have all chondrified independently. On the right side of the viscerocranium an independent first infrapharyngobranchial is present. It is not certain whether it arose separately or whether it split off from the fused infrapharyngo-elements of the previous stage. On the left side the first infrapharyngobranchial is fused to the epibranchial. On both sides the second infrapharyngobranchials are fused with the anterior (i.e. dorsal) ends of their respective epibranchials. In the third and the fourth arches the infrapharyngobranchials are fused with each other as well as with the third and the fourth epibranchials. There is still no trace of any suprapharyngobranchials.

Stage 5 (11,0) mm)

Premandibular arch

The processus pterygoideus extends much further anteriorly than in the previous stage (Figure 15, Part 1). Its anterior end diverges sharply from the planum ethmoidale anteriorly and a ligament connects it with the proximal end of the maxillary. Perichondral ossifications, which will eventually give rise to the autopalatine part of the palatine, have also commenced in the anterior part of the processus pterygoideus. Further posterior, in the region of the rostropalatine articulation, the processus pterygoideus has become dorsoventrally thickened. Further back the dermal endopterygoid and ectopterygoid are now forming as thin slivers of bone, mediodorsal and ventrolateral respectively, to the processus pterygoideus. Ventral to the planum ethmoidale the vomer has increased in size, while the commissura palatoquadrati has become considerably reduced. The preorbital ligaments are more pronounced than in the previous stage.

Mandibular arch

Most of the cartilage at the symphysis has been replaced by the mentomandibular ossification. The dentary is much enlarged. Further posterior the angular has also ossified in the blasteme which surrounded this part of

Meckel's cartilage in the previous stage. Both the processus coronoideus and the processus retroarticularis, the latter now decidedly more prominent, display extensive perichondral ossifications. These partly give rise to the posterior, articular part of the angular and to the retroarticular respectively, both of which are of mixed origin as evidenced by the presence of dermal bone lamellae in close proximity to both perichondral ossifications. In the processus articularis palatoquadrati, extensive perichondral ossifications are taking place. This part of the pars quadrata remains bulbous in cross section, whereas the metapterygoid portion is made up of a thin column of closely packed chondrocytes, the medial surface of which is starting to ossify perichondrally. Both the symplectic and that part of the pars quadrata in contact with it are heavily ossified in their contact region and they have become tightly connected by interosseus ligaments.

Hyoid arch

The hyomandibula articulates with the auditory capsule along its entire dorsal surface by only one articulation (Figure 15, Part 1). The entire hyomandibular cartilage has ossified perichondrally and the incisure has become a wide notch with the result that the epihyal and the laterohyal portions are nearly completely separated. Most of the incisure, however, is covered by mixed dermal and endochondral ossifications, leaving only a small foramen for the passage of the truncus hyomandibularis. The processus opercularis of the hyomandibula has become prominent, and syndesmotically connected to the operculum. The cartilaginous part of the symplectic has lost all contact with the cartilaginous part of the hyomandibula, owing to extensive ossifications in this region which have displaced all traces of cartilage. The interhyal has undergone syndesmosis with both the hyomandibula and the ceratohyal. The shaft of the latter, which has become heavily ossified, is even thinner than in the previous stage. Its posterior part, in the region of the pars quadrata, however, remains broad and blade-like. Although the hypohyals have completely fused with their ceratohyals, the earlier demarcation is still visible.

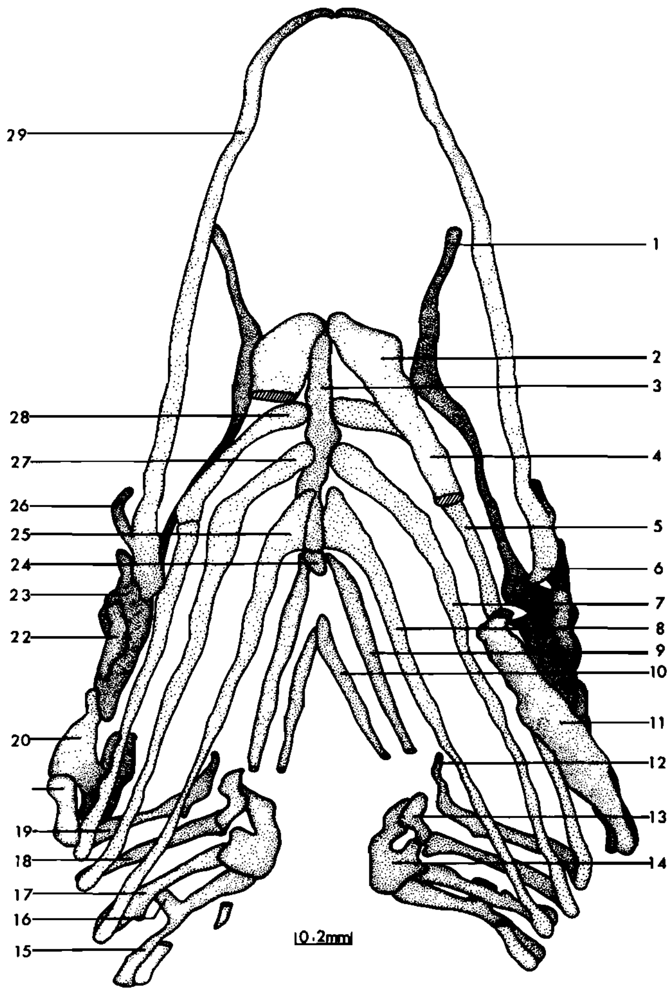

Figure 5 Graphic reconstruction of the viscerocranium. Stage 5. Ventral view. 1: processus pterygoideus, 2: hypohyal, 3: basibranchial I, 4: ceratohyal, 5: ceratobranchial I, 6: processus retroarticularis, 7: ceratobranchial II, 8: ceratobranchial III, 9: ceratobranchial IV, 10: ceratobranchial V, 11: ceratohyal, 12: infrapharyngobranchial I, 13: infrapharyngobranchial II, 14: fused infrapharyngobranchials III & IV, 15: epibranchial IV, 16: suprapharyngobranchial IV, 17: epibranchial III, 18: epibranchial II, 19: epibranchial I, 20: interhyal, 21: hyomandibula, 22: symplectic, 23: pars quadrata, 24: basibranchial II, 25: hypobranchial III, 26: processus coronoideus, 27: hypobranchial II, 28: hypobranchial I, 29: Meckel's cartilage.

Branchial arches

The independent first infrapharyngobranchial on the right side has now fused with its epibranchial. The second infrapharyngobranchial is not fused with its epibranchial, but only articulates with it as well as with the fused third and fourth infrapharyngobranchials. The latter unit is likewise not fused with the third and the fourth epibranchials, but only articulates with them. Approximately halfway along the fourth epibranchial (Figure 5), a dorsolateral process, the suprapharyngobranchial of the fourth arch, is now visible. This is the only suprapharyngobranchial that ever develops.

Stage 6 (14,1 mm)

Premandibular arch

In front of the rostropalatine articulation and medioventral to the processus pterygoideus, dermal ossifications have appeared in the membranes reaching from the processus pterygoideus to the vomer. These membranes represent the remains of the commissura palatoquadrati and the dermal ossifications are those of the dermopalatine. The latter will eventually fuse with the endochondral autopalatine to form the palatine bone of the adult. Van der Westhuizen (1979) similarly reports the dermopalatine as arising from the commissura palatoquadrati in *Barbus*.

Mandibular arch

Although the metapterygoid portion of the pars quadrata remains a thin column of closely packed chondrocytes in cross section, in lateral aspect it has become decidedly more massive than in the previous stage. Apart from the perichondral ossifications on its medial surface in the previous stage, similar ossifications have also appeared on its lateral surface.

Hyoid arch

The separation between the cartilaginous epihyal and laterohyal portions of the hyomandibula is now complete (Figure 18, Part 1). These two elements, however,

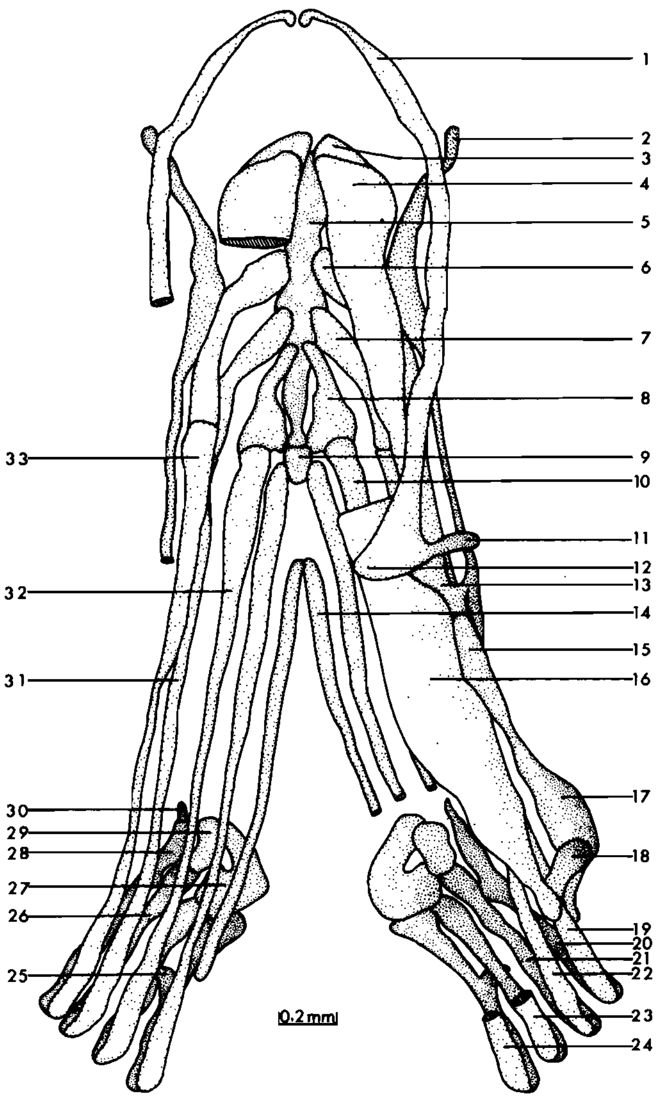

Figure 6 Graphic reconstruction of the viscerocranium. Stage 6. Ventral view. 1: Meckel's cartilage, 2: processus pterygoideus, 3: hypohyal, 4: ceratohyal, 5: basibranchial I, 6: hypobranchial I, 7: hypobranchial II, 8: hypobranchial III, 9: basibranchial II, 10: ceratobranchial IV, 11: processus coronoideus, 12: processus retroarticularis, 13: pars quadrata, 14: ceratobranchial V, 15: symplectic, 16: ceratohyal, 17: hyomandibula, 18: interhyal, 19: ceratobranchial IV, 20: epibranchial IV, 21: epibranchial III, 22: ceratobranchial III, 23: ceratobranchial II, 24: ceratobranchial I, 25: suprapharyngobranchial IV, 26: epibranchial II, 27: fused infrapharyngobranchials III & IV, 28: epibranchial I, 29: infrapharyngobranchial II, 30: infrapharyngobranchial I, 31: ceratobranchial II, 32: ceratobranchial III, 33: ceratobranchial I.

remain in contact with each other by means of mixed dermal and perichondral ossifications on the medial and the lateral surfaces of the hyomandibula, which have fused with the perichondral ossifications of the epihyal and laterohyal portions. The foramen hyomandibulare, through which the dorsal part of the arteria hyoidea (Nel 1980) and the truncus hyomandibularis pass, is thus now made up solely of bone.

Branchial arches

The anteroventral processes of the third hypobranchials now meet in a symphysis below the ventral aorta (Figure 6). Each process then curves posterodorsally around the ventral aorta to fuse with its basibranchial dorsal to the latter. The fifth ceratobranchials have gained contact with the second basibranchial via thin, tenuous pharyngeal ligaments (Mujib 1967; Inada 1981). On the dorsal surfaces of the fifth ceratobranchials, the lower pharyngeals, which in the adult form a large, triangular toothplate (Inada 1981), have started to develop. Similar dermal teeth are also present on the ventral surface of the fused third and fourth infrapharyngobranchials. These, together with toothplates on the other infrapharyngobranchials later form the upper pharyngeals (Inada 1981) of the adult fish.

Discussion

Branchial arches

In the Teleostei normally five branchial arches occur, of which the fifth usually consists of only a ceratobranchial. In *Anguilla* (Norman 1926), *Salmo* (De Beer 1927), *Carrassius* (Hsueh 1934), *Ophicephalus* (Srinivasachar 1953), *Hepsetus* (Bertmar 1959), *Clarias* (Srinivasachar 1960), *Rasbora* (Tewari 1971), *Barbus* (Van der Westhuizen 1974) and *Ctenopharyngodon* (Van den Heever 1981) the first four arches contain separate cerato- and hypobranchials. Separate fourth hypobranchials occur as transitory rudiments during the ontogeny of *Leuciscus* (Hubendick 1942). In members of other genera, e.g. *Gasterosteus* (Swinnerton 1902), *Solea* (Berrill 1925), *Notopterus* (Omarkhan 1950), *Mastacembelus* (Bhargava 1958), *Hydrocyon* (Aziz 1960), *Heteropneustes* (Srinivasachar 1960) and *Hypophthalmichthyes* (Nel 1981) separate hypobranchials are confined to the first three arches. *M. capensis* and other hake species belong to the latter group, an observation which is confirmed by Mujib (1967), Rojo (1976) and Inada (1981) in their descriptions of the adults of various hake species.

Most teleosts thus far investigated possess four separate epibranchials. In *Hepsetus* (Bertmar 1959) and in *Barbus* (Van der Westhuizen 1974), however, a fifth epibranchial chondrifies independently and it later fuses on to the posterior end of the fourth epibranchial. Vestigial elements corresponding to fifth epibranchials are also described in *Alepocephalus* and *Alosa* by Gegenbaur (1878) and in *Citharinus* by Sagemehl (1885), while Nel (1981) finds separately chondrified epibranchials in all five arches of *Hypophthalmichthyes*. In *M. capensis* four epibranchials chondrify, a number which is constant for the genus *Merluccius* (Mujib 1967; Inada 1981). The epibranchials of *M. capensis* arise from two separate blastemes, the first of which gives rise to the first and second epibranchials, and the second to the third and fourth epibranchials. The infrapharyngobranchials vary considerably in number and in their independence of one another amongst the Teleostei. Separate infrapharyngobranchials I–IV (mostly described as 'pharyngobranchials') are present in *Anguilla* (Norman 1926), *Carrassius* (Hsueh 1934), *Salmo* (De Beer 1927), *Notopterus* (Omarkhan 1950), *Hepsetus* (Bertmar 1959) and *Hypophthalmichthyes* (Nel 1981). In *Mastacembelus* (Bhargava 1958), *Barbus* (Van der Westhuizen 1974) and *Ctenopharyngodon* (Van den Heever 1981) the first infrapharyngobranchial is absent, while the second to the fourth occur as independent elements. In *Heteropneustes* (Srinivasachar 1960) only the third and the fourth infrapharyngobranchials are present, fused with one another. A similar situation occurs in *Solea* (Berrill 1925) and in *Ophicephalus* (Srinivasachar 1953), except that separate first and second infrapharyngobranchials are also present. In *Rasbora* (Tewari 1971) all the infrapharyngobranchials (I–IV) are fused, and in *Gasterosteus* (Swinnerton 1902) the first is absent and the second to fourth elements are fused. In *Hippocampus* (Kadam 1958) only three infrapharyngobranchials are present (similar to the number of epibranchials) and of these the first and the second are fused, while the third remains independent. The present study reveals that the first infrapharyngobranchial of *M. capensis* fuses with its epibranchial and that it remains independent of the other infrapharyngo-elements. The second infrapharyngobranchial does not fuse with its epibranchial, but only articulates with it and with the fused third and fourth infrapharyngobranchial. These are also not fused with their respective epibranchials and only articulate with them.

Amongst the Osteichthyes independent suprapharyngobranchials have only been described in *Acipenser* (Holmgren 1943). In all other cases the suprapharyngobranchials have been shown to be confined to dorsal processes of the epibranchials: *Polypterus* (Van Wijhe 1882), *Lepidosteus* (Hammarberg 1937) and *Amia* (Holmgren 1943). Not many authors explicitly describe suprapharyngobranchials in the Teleostei. Swinnerton (1902) mentions small dorsal processes on the third and fourth epibranchials, but he does not identify them as pharyngo-elements. In *Hepsetus*, Bertmar (1959) describes suprapharyngobranchials in all four arches as dorsal processes of their epibranchials. *Barbus* (Van der Westhuizen 1974) has only two suprapharyngobranchials, situated on the third and fourth epibranchials, whereas *Hypophthalmichthyes* (Nel 1981) and *Ctenopharyngodon* (Van den Heever 1981) have four and three suprapharyngobranchials, situated on the first to the fourth and on the second to the fourth epibranchials respectively.

In *M. capensis* a suprapharyngobranchial is confined to the fourth arch, where it develops as a dorsolateral process of the fourth epibranchial approximately midway along the latter's length.

Hyoid arch

Hyomandibula

In the youngest stage of *M. capensis* available (2,3 mm), as in *Barbus* (Van der Westhuizen 1974) the hyomandibula is already fully chondrified and this investigation can shed no light upon its phylogeny.

Symplectic and stylohyal

In the youngest stage of *m. capensis* (2,3 mm), as in *Barbus* (Van der Westhuizen 1974) the stylohyal is already present as an independent, separate element and it is not possible to ascertain whether it has a dual origin in this species.

Mandibular arch

Palatoquadrate

In the youngest stage of *M. capensis* available (2,3 mm) both the processus coronoideus and the processus articularis palatoquadrati are fully chondrified and it is therefore impossible to comment on their homologies with visceral arch elements. The species also does not possess a processus oticus externus, or a processus basalis, thus making it very difficult to speculate on their origin or on the composition of the palatoquadrate.

Meckel's cartilage

According to Bertmar (1959) neither hypo- nor basimandibulae seem to be described in the Teleostei, the consensus opinion apparently being that Meckel's cartilage represents only a ceratomandibula. In *Hepsetus* he describes a symphysial blasteme which is formed very early between the anterior ends of Meckel's cartilages. It does not chondrify, but forms a tendinous tissue which he is unwilling to homologize with a basimandibula. The present study on *M. capensis* can shed no light upon the problem. In the youngest stage (2,3 mm) the entire Meckel's cartilage is chondrified and the two cartilages meet in a symphysis in which perichondral ossifications are already occurring.

Premandibular arch

This arch is discussed in Part 1.

Summary

(i) A processus basalis is absent and the processus oticus represents a processus oticus internus.

(ii) The hyomandibula consists of epihyal and laterohyal portions.

(iii) A single suprapharyngobranchial develops, fused on to the fourth epibranchial.

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