Development of the chondrocranium of the shallow-water Cape hake *Merluccius capensis* (Cast.). Part 1: Neurocranium

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The development of the neurocranium of *Merluccius capensis*, from the earliest identifiable stage, is described. The anterior mesenchyme gives rise to the rostral cartilage, the lamina orbitonasalis and probably also to the planum ethmoidale. There is no true ethmopalatine articulation, only a rostropalatine articulation. The ethmopalatine articulation is represented by the preorbital ligaments. A cartilago supraentethmoidalis develops, but no processus ethmoideus. A preoptic root is absent and only a foramen olfactorium advehens is delimited. A lateral commissure and prootic process, and consequently a trigeminofacialis chamber, are absent. Both the auditory capsules and the occipital arches take part in the development of the tectum synoticum. The tectum posterius does not develop separately, but as a posterior extension of the tectum synoticum.

Die ontwikkeling die neurokranium van *Merluccius capensis* word beskryf vanaf die vroegste herkenbare stadium. Die anteriormesenkiem gee oorsprong aan die rostraalkraakbeen, die lamina orbitonasalis en waarskynlik ook aan die planum etmoidale. 'n Egte etmopalatiene gewrig ontbreek en slegs 'n rostropalatiene gewrig is teenwoordig. Die etmopalatiene gewrig word deur die preorbitale ligamente voorgestel. 'n Cartilago supraentetmoidalis ontwikkel, maar geen processus etmoideus nie. 'n Preoptiese wortel is afwesig en slegs 'n foramen olfactorium advehens word dus afgebaken. 'n Laterale kommissuur en pro-otiese uitsteeksel en derhalwe 'n trigemino-fascialiskamer, is afwesig. Beide die oorkapsels en die oksipitaalboë neem deel aan die ontwikkeling van die tectum synoticum. Die tectum posterius ontwikkel nie onafhanklik nie, maar as posterior verlenging van die tectum synoticum.

Two species of hake, *Merluccius capensis* Cast. and *M. paradoxus* Franca, known collectively as the Cape hakes, occur off southern Africa. The hakes are closely related to the Gadidae, Order Anacanthini (Botha 1980), and were previously thought to belong to this family. The contemporary view, however, is that they comprise a separate family, the Merlucciidae (Botha 1980; Inada 1981).

To the knowledge of the author the development of the chondrocranium of a hake species has never been described. The only such description of a species closely related to *M. capensis* is that of *Gadus merlangus* by De Beer (1937). His description is superficial and only covers three developmental stages.

Holmgren (1943) stresses the importance of the mesenchymatous and blastemic stages, which precede the appearance of cartilage, in the study of the development of the chondrocranium. To the knowledge of the author, since Holmgren (1943), only Bertmar (1959), Van der Westhuizen (1974, 1979), Nel (1981) and Van den Heever (1981) have given descriptions of the development of the chondrocranium in the Teleostei, which included the precartilaginous stages. In the smallest *M. capensis* larva available for the present study (2,3 mm caudal length) most of the mesenchymatous and blastemic anlagen had already been transformed into cartilage but it was still possible to identify certain important mesenchymatous and blastemic regions.

The present study of the development of the neurocranium of *Merluccius capensis*, which forms the first of a two-part series, is aimed at increasing the knowledge on development of the chondrocranium in the Teleostei, especially in species indigenous to the southern African region, of which only three have received attention to date.

Material and Methods

Forty transverse and nine sagittal serial sections were made at a thickness of 0,010 mm from *M. capensis* larvae ranging between 2,3 mm and 14,1 mm caudal length. Azocarmine was used as a nuclear stain, with Aniline Blue and Orange G as the counterstain. The smaller specimens often failed to stain with these dyes. In these instances Meyer's haematoxylin, followed by aqueous Eosin and finally Aniline Blue and Orange G were used. This method yielded adequate results — the nuclei staining purple to dark blue, the cartilage matrix light blue and bone dark blue.

Five stages in the development of cartilage were distinguished:

(i) mesenchyme — diffuse cells without definite boundaries,
(ii) blasteme — dense cell masses with clearly delineated borders,
(iii) procartilage — cells with a strong affinity for Aniline blue,
(iv) young cartilage — cartilage with small quantities of intercellular matrix and
(v) cartilage cells with relatively large quantities of intercellular matrix.

Six representative developmental stages were selected and, with the aid of photomicrographs, reconstructions were made of the neurocranium and the viscerocranium of each stage.

Results

Stage 1 (2,3 mm)

The neurocranium is extremely small, less than 0,5 mm in length.

Ethmoidal region

The most conspicuous feature of the ethmoidal region is a large, spoon-shaped planum ethmoidale (Figures 1 and 2), situated medial to the anterior boundaries of the eyes. Except for its extreme anterior portion, which is blastemic, the planum ethmoidale consists of procartilage rostrally and very young cartilage caudally, one cell layer thick. The fused anterior ends of the trabeculae form a broad, prochondral commissura trabecularis, extending anteriorly into the planum ethmoidale. Both the musculus obliquus inferior and superior insert in fasciae on the dorsal surface of the commissura trabecularis. Anteriorly and ventrally a mesenchymatous sheath surrounds the planum ethmoidale. Anteroventral to the latter this sheath is continuous with the blastemic anterior end of each processus pterygoideus forming a commissura palatoquadrati (Holmgren 1943). The blastemic processus pterygoideus is connected to the entire lateral surface of the planum ethmoidale.

Orbitotemporal region

The neurocranium is distinctly tropibasic (Figures 1 and 2). The anterior portions of the two trabeculae are fused to nearly the level of the hypophysis, forming a trabecula communis which consists of a single layer of young chondrocytes. Anteriorly the trabecula communis expands laterally on each side as the commissura trabecularis. Caudally, in the region of the hypophysis, the trabeculae are separated into two, thin, rod-like structures, each consisting of merely a single chondrocyte surrounded by matrix. Posteriorly each trabecula is fused to a polar cartilage. The latter element is traversed by the musculus rectus externus and may as such be identified as a polar cartilage (Bertmar 1959), although no evidence of an originally separate origin of the trabeculae and the polar cartilages is present at this stage. The musculus rectus

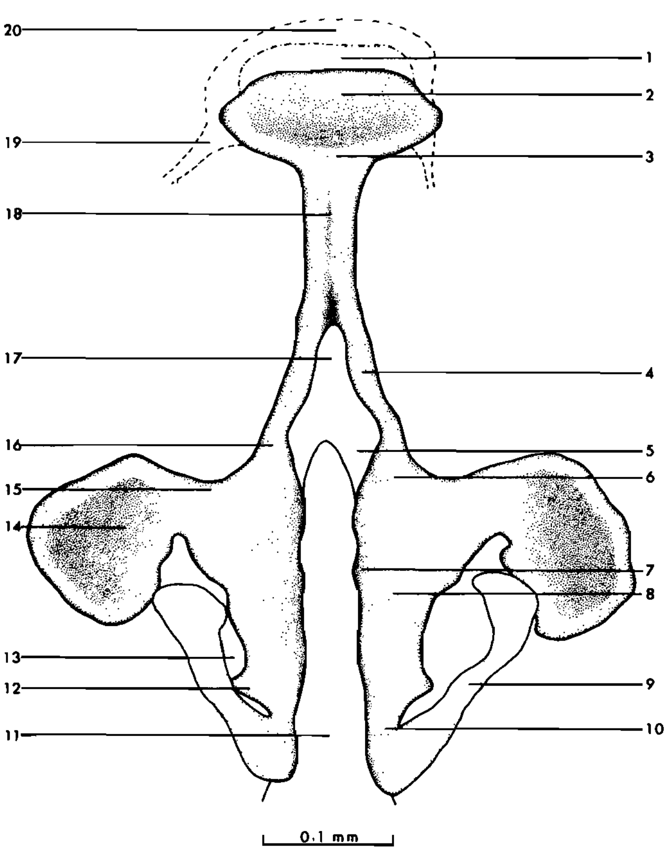

Figure 1 Graphic reconstruction of the neurocranium. Stage 1. Dorsal view. 1: prochondral part of planum ethmoidale, 2: planum ethmoidale, 3: commissura trabecularis, 4: trabecula, 5: mesenchymatous anterior parachordal, 6: anterior basiotic lamina, 7: mesotic parachordal, 8: mesotic basiotic lamina, 9: occipital arch, 10: occipital parachordal, 11: notochord, 12: occipital basiotic lamina, 13: metotic fissure, 14: auditory capsule, 15: anterior basicapsular commissure, 16: polar cartilage, 17: fenestra hypophyseos, 18: trabecula communis, 19: processus pterygoideus anlage, 20: anterior mesenchyme.

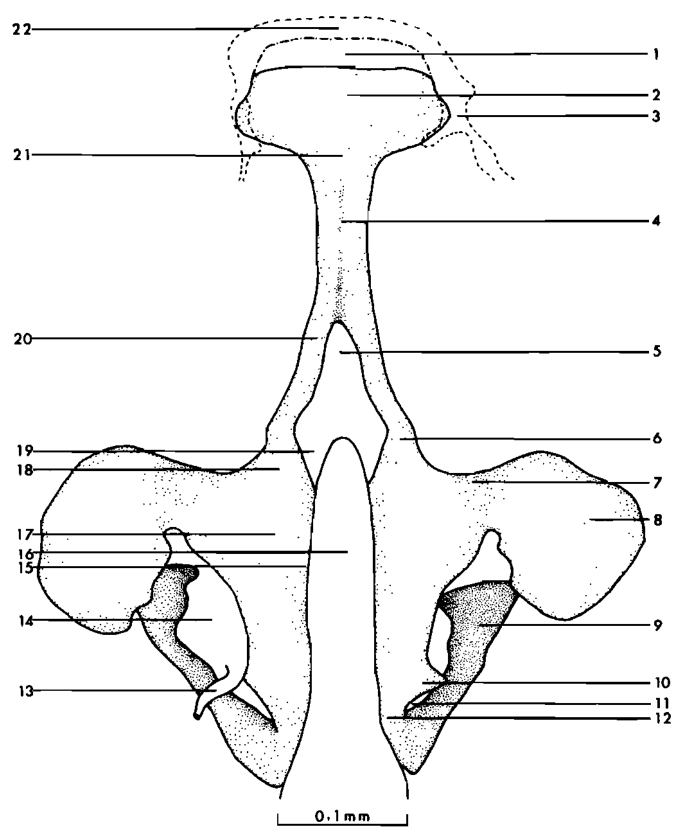

Figure 2 Graphic reconstruction of the neurocranium. Stage 1. Ventral view. 1: prochondral part of planum ethmoidale, 2: planum ethmoidale, 3: processus pterygoideus anlage, 4: trabecula communis, 5: fenestra hypophyseos, 6: polar cartilage, 7: anterior basicapsular commissure, 8: auditory capsule, 9: occipital arch, 10: occipital basiotic lamina, 11: metotic fissure, 12: occipital parachordal, 13: nervus vagus, 14: metotic fissure, 15: mesotic parachordal, 16: notochord, 17: mesotic basiotic lamina, 18: anterior basiotic lamina, 19: anterior parachordal — mesenchymatous, 20: trabecula, 21: commissura trabecularis, 22: anterior mesenchyme.

externus inserts on fasciae surrounding the anterior tip of the notochord. The fenestra hypophyseos, the gap between the two diverging trabeculae, from the fork in front to the polar cartilages and the tip of the notochord in the rear, is covered by a thin sheet of mesenchyme, separated from the brain and the hypophysis only by the dura mater. The parasphenoid is already present as a thin sliver of bone in this mesenchymatous sheet. It reaches from the fork in the trabeculae in front to the tip of the notochord in the rear. There is no trace of acrochordal tissue. A marked degree of cranial flexure is evident in the basal plate and trabeculae. The trabecula communis, however, is flexed upwards at an angle of 45 ° (Figure 3).

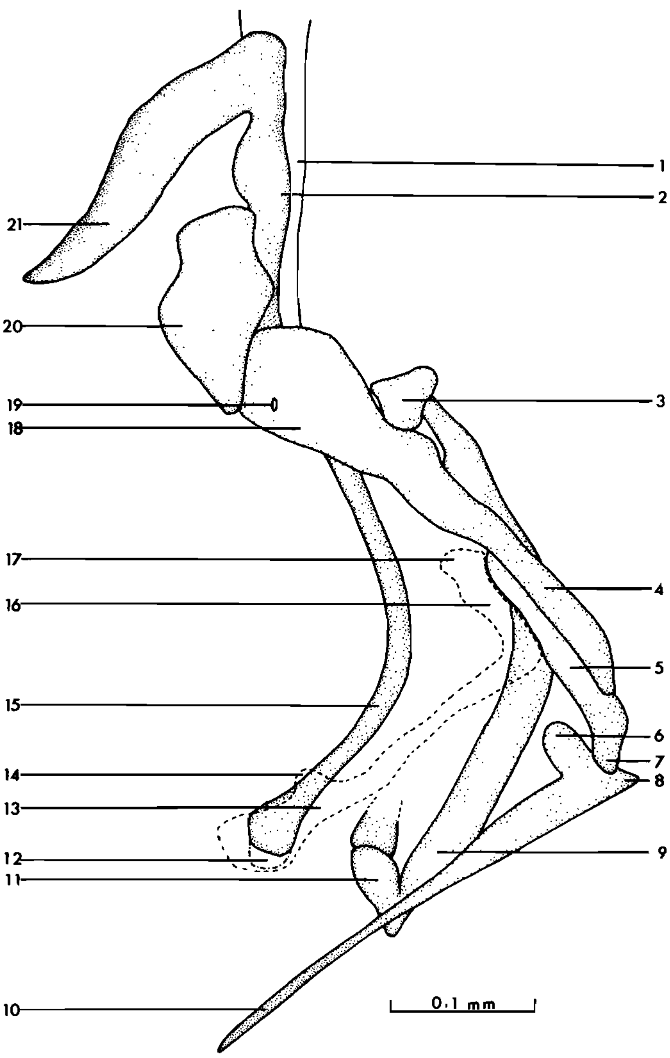

Figure 3 Graphic reconstruction of the chondrocranium. Stage 1. Lateral view (branchial arches omitted). 1: notochord, 2: mesotic parachordal, 3: interhyal, 4: symplectic, 5: pars quadrata, 6: processus coronoideus, 7: processus articularis palatoquadrati, 8: processus retroarticularis, 9: ceratohyal, 10: Meckel's cartilage, 11: hypohyal, 12: prochondral part of planum ethmoidale, 13: processus pterygoideus anlage, 14: lamina orbitonasalis anlage, 15: trabecula communis, 16: metapterygoid part of pars quadrata anlage, 17: processus oticus internus anlage, 18: hyomandibula, 19: foramen hyomandibulare, 20: auditory capsule, 21: occipital arch.

Otico-occipital region

The notochord reaches anteriorly to the junction of the trabeculae and the polar cartilages (Figures 1 and 2). It is flanked on both sides by the parachordals, which may be divided into three sections (anterior, mesotic and occipital) according to their positions relative to the facial, stato-acoustic and vagus nerves respectively (Bertmar 1959). The anterior parachordals are mesenchymatous and continuous with the mesenchyme which covers the fenestra hypophyseos. The mesotic and the occipital parachordals consist of young cartilage and they are fused with each other without any demarcation. Each polar cartilage is fused to the anterior basiotic lamina behind it, the latter also consisting of young cartilage. The anterior portion of the auditory capsule (otic cartilage) has already chondrified as a cup-shaped structure, which forms a chondral floor and side wall to the anterior and lateral semicircular canals, but the roof is still membranous. The posterior semicircular canal is only supported by a membranous floor and side wall, while its membranous roof is mediodorsally in contact with the occipital arch. Anteriorly the auditory capsule is chondrally fused with the anterior basiotic lamina by means of the anterior basicapsular commissure. As in *Gadus* (De Beer 1937) there is no lateral commissure or prootic process. All the cranial nerves up to the facial nerve pass in front of the anterior basicapsular commissure. Consequently a trigemino-facialis chamber is also absent. The occipital arch consists of young cartilage. Posteriorly it is orientated vertically, but further anteriorly the orientation gradually changes to horizontal. The occipital arch is fused with its corresponding occipital parachordal and it reaches dorsolateral to approximately the mid-point of the otico-occipital region. The fusion between the occipital arch and the occipital parachordal is not complete and a gap is left, the metotic fissure, through which the vagus nerve leaves the cranial cavity.

A posterior basicapsular commissure has not yet chondrified, and therefore the fenestra basicapsularis and the metotic fissure are still confluent. The fenestra basicapsularis is covered by a thin membrane stretching between the auditory capsule and the basiotic laminae.

Stage 2 (3,4 mm)

The neurocranium is nearly 3,5 times longer than in the previous stage.

Ethmoidal region

The anterior blastemic portion of the planum ethmoidale has chondrified and the latter now consists entirely of young cartilage. It has lost its concavity and it is flat, except for a slight medial depression on the ventral surface (Figure 5). Anteriorly the dorsal surface of the planum ethmoidale displays a slight, longitudinally orientated, medial protruberance, the first indication of a septum nasi (Figures 4 and 6). The olfactory lobes reach right forward to the small nasal septum and there is no indication of a transverse lamina precerebralis such as reported in many other teleosts (Van den Heever

1981). The anterior part of the planum ethmoidale is elevated above its posterior part and the commissura trabecularis, so that these structures lie at an angle relative to the rest of the neurocranium behind them (Figure 6). The anlage of the rostral cartilage, in the form of a dense blastemic mass, is situated anterodorsal to the planum ethmoidale. This mass is continuous with the anterior tips of the two processus pterygoidei. The latter articulate with the lateral edges of the planum ethmoidale along its entire length and they are attached to it by mesenchyme which completely envelops them. Anterior of its articulation with the planum ethmoidale the processus pterygoideus diverges laterally from the planum ethmoidale. In its region of contact with the latter, the core of the processus pterygoideus is turning prochondral, while the outer layer is still blastemic. The anterior mesenchyme (Bertmar 1959) is now more extensive and, apart from housing the future rostral cartilage and the processus pterygoidei, the proximal ends of the already ossified premaxillaries and maxillaries are also lodged here. The blastemic commissura palatoquadrati, which links the two processus pterygoidei ventral to the planum ethmoidale, is also more extensive and it is confluent anteriorly with the anterior mesenchyme. Just anterior to the junction between the planum ethmoidale and the commissura trabecularis, exactly at the point where the processus pterygoideus loses contact with the planum ethmoidale and slightly anterior of the insertion of the musculi obliqui on the commissura trabecularis, the blastemic processus pterygoideus is dorsally in contact with a blastemic cord of cells, which reaches dorsally and slightly posteriorly in the direction of the hind boundary of the nasal placode. This cord is the blastemic anlage of the lamina orbitonasalis (processus ectethmoideus — Hammarberg 1937).

Orbitotemporal region

Medial to each trabecula the arteria carotis interna can now be identified. Applying Holmgren's (1943) definition, the trabecula of *M. capensis* represents a trabecula externa as it lies lateral to the arteria carotis interna. Further back the musculus rectus externus traverses the polar cartilage dorsally, and the arteria

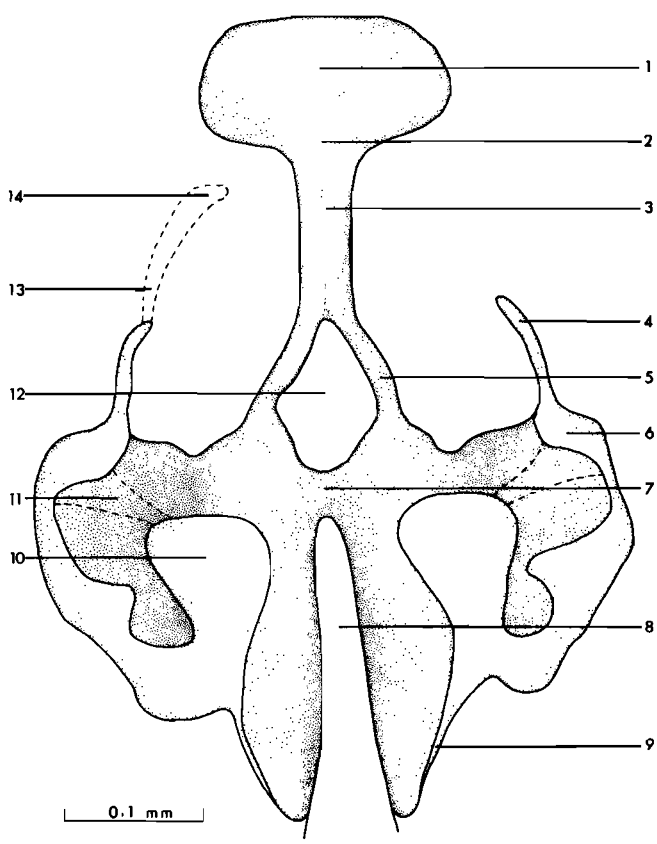

Figure 4 Graphic reconstruction of the neurocranium. Stage 2. Dorsal view. 1: planum ethmoidale, 2: commissura trabecularis, 3: trabecula communis, 4: postorbital process, 5: trabecula, 6: anterior auditory capsule, 7: prootic bridge, 8: notochord, 9: vertical part of occipital arch, 10: horizontal part of occipital arch, 11: tectum synoticum anlage, 12: fenestra hypophyseos, 13: taenia marginalis posterior anlage, 14: cartilago supraorbitalis anterior anlage.

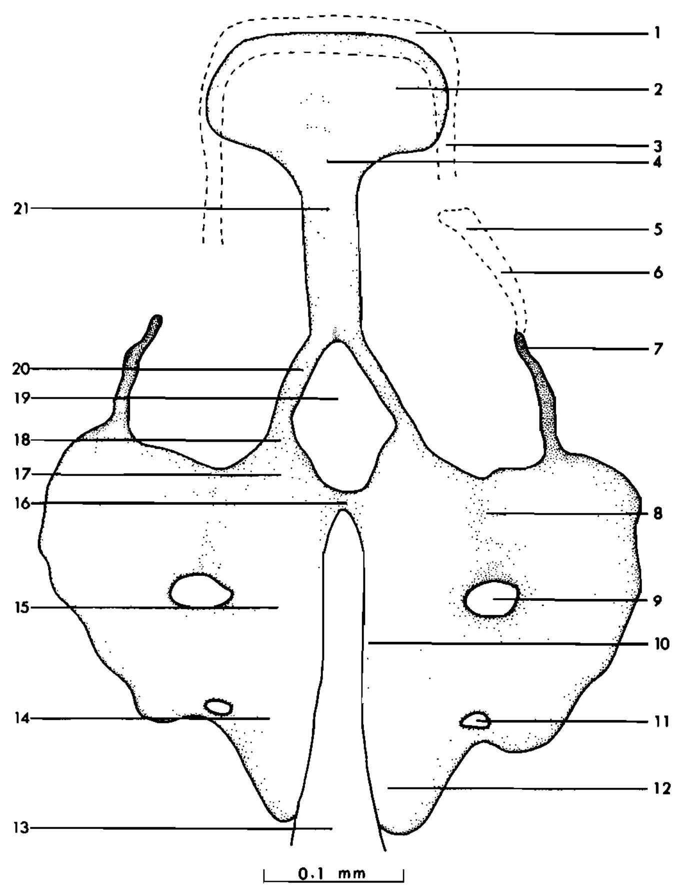

Figure 5 Graphic reconstruction of the neurocranium. Stage 2. Ventral view. 1: anterior blastemic mass, 2: planum ethmoidale, 3: processus pterygoideus anlage, 4: commissura trabecularis, 5: cartilago supraorbitalis anterior anlage, 6: taenia marginalis anterior anlage, 7: postorbital process, 8: anterior basicapsular commissure, 9: fenestra basicapsularis, 10: mesotic parachordal, 11: foramen jugulare, 12: occipital parachordal, 13: notochord, 14: occipital basiotic lamina, 15: mesotic basiotic lamina, 16: prootic bridge, 17: anterior basiotic lamina, 18: polar cartilage, 19: fenestra hypophyseos, 20: trabecula, 21: trabecula communis.

pseudobranchialis efferens passes below the polar cartilage after branching off from the arteria carotis interna. The two anterior parachordals have chondrified and fused dorsal to the anterior tip of the notochord to form a prootic bridge (Figures 4 and 5). The fenestra hypophyseos is thus now completely delimited by the trabecula communis, the trabeculae, the polar cartilages, the anterior basiotic laminae and the prootic bridge. The fenestra hypophyseos remains covered by the mesenchyme which houses the parasphenoid and there is no fenestra basicranialis posterior. Resorbtion of the anterior end of the notochord has commenced and it does not reach as far forward as in the previous stage. The musculus rectus externus has now shifted its insertion from the tip of the notochord, in the previous stage, to fasciae on the dorsal surface of the parasphenoid. The latter is a thin dermal bone plate medial to the trabeculae. The other rectus muscles have a common origo on the parasphenoid anterior to that of the musculus rectus externus. The blastemic anlagen of the cartilago supraorbitalis anterior and the taenia marginalis posterior (taenia marginalis postorbitalis — Bertmar 1959) are the only elements of the side wall of the neurocranium present at this stage. Posteriorly the taenia marginalis posterior is attached to the postorbital process (cartilago supraorbitalis posterior — Hammarberg 1937), of which the anterior portion is prochondral while the posterior part is' fully chondrified and fused with the auditory capsule (Figure 4). In *Hepsetus* Bertmar (1959) identifies only the blastemic anterior tip of the postorbital process as a cartilago supraorbitalis posterior.

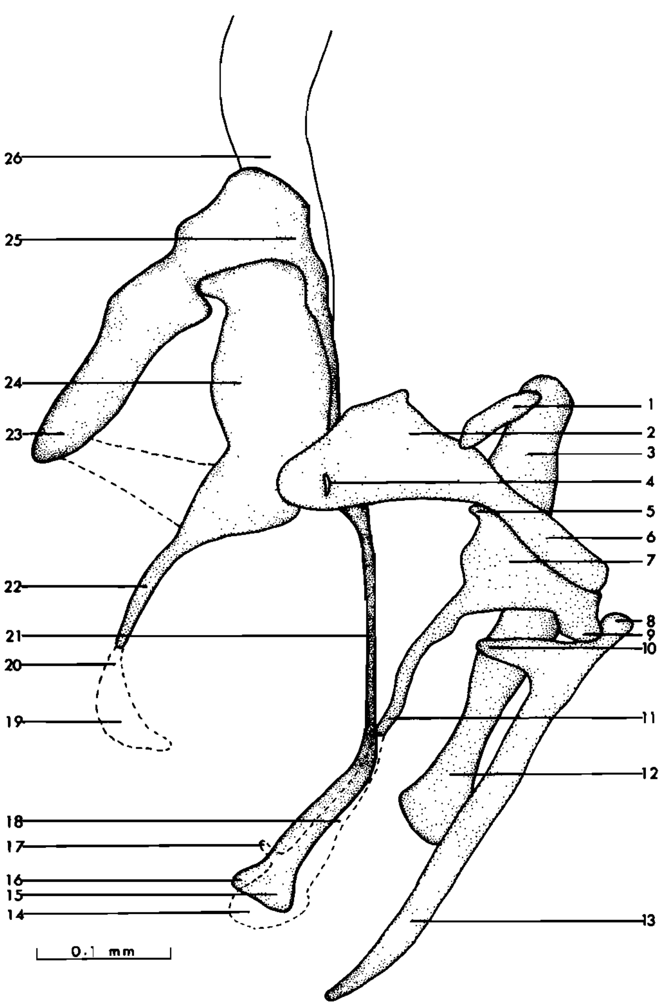

Figure 6 Graphic reconstruction of the chondrocranium. Stage 2. Lateral view (branchial arches omitted). 1: interhyal, 2: hyomandibula, 3: ceratohyal, 4: foramen hyomandibulare, 5: processus oticus internus, 6: symplectic, 7: pars quadrata, 8: processus retroarticularis, 9: processus articularis palatoquadrati, 10: processus coronoideus, 11: processus pterygoideus, 12: ceratohyal, 13: Meckel's cartilage, 14: anterior blastemic mass, 15: planum ethmoidale, 16: septum nasi, 17: lamina orbitonasalis anlage, 18: processus pterygoideus anlage, 19: cartilago supraorbitalis anterior anlage, 20: taenia marginalis anterior anlage, 21: trabecula communis, 22: postorbital process, 23: occipital arch, 24: auditory capsule, 25: occipital parachordal, 26: notochord.

Otico-occipital region

The major developmental changes in the neurocranium have occurred in this region. The notochord now displays a distinct downward flexure relative to its posterior extra-cranial part (Figure 6). With the formation of the prootic bridge, the basal plate is complete in front (Figure 5). Much of the anterior end of the notochord has been resorbed and replaced dorsally by the prootic bridge. The anterior parachordals have fused completely with the mesotic parachordals behind them and there is no discernible histological difference between the two regions. The postorbital process of the auditory capsule has chondrified. The lateral wall and the roof of the auditory capsule also display a greater degree of chondrification, especially posteriorly where a chondral floor, lateral wall and roof has now formed around the posterior semicircular canal (Figure 4). The auditory capsule does not have a medial wall and its contents are only separated from the cranial cavity by the dura mater. In the occipital region the roof of the auditory capsule has become chondrally fused with the occipital arch dorsally. The floor of the auditory capsule has fused with the occipital basiotic lamina by means of a broad, chondrified posterior basicapsular commissure. A space, the fenestra basicapsularis, is thus left between the anterior basicapsular commissure, the ventral edge of the auditory capsule, the posterior basicapsular commissure and the mesotic basiotic lamina. The occipital arch has become elongated in a rostral direction to the level of the anterior basicapsular commissure and it has gained contact with the roof of the auditory capsule anteriorly by means of a blastemic commissure. The latter commissure and the anterior part of the occipital arch represent the future tectum synoticum. The foramen for the vagus nerve, the foramen jugulare (Schreiner 1902) which is the remains of the metotic fissure (De Beer 1937) is formed by the posteriorly jutting auditory capsule, the posterior basicapsular commissure and by the occipital basiotic lamina. The dorsal fusion of the auditory capsule and the occipital arch in the occipital region extends further caudally than the posterior boundary of the posterior basicapsular commissure. Consequently the foramen jugulare is a tunnel facing obliquely posteroventrally and as such is visible only in ventral aspect. The glossopharyngeal nerve could not be traced at this stage. However, only the vagus nerve leaves the cranial cavity through the jugular foramen in Stages 2 and older. In later stages, the fenestra basicapsularis is completely obliterated by chondrification, but the relative position of the remains of this fenestra, the foramen glossopharyngeum, indicates that the glossopharyngeal nerve should leave the cranial cavity through the fenestra basicapsularis in the present stage. In *Salmo* (De Beer 1937) the posterior basicapsular commissure joins the parachordal *(sic)* in such a way as to cut off that portion of the metotic fissure lodging the glossopharyngeal nerve and incorporate it with the fenestra basicapsularis. The cod *Gadus*, which is closely related to *Merluccius*, develops in a manner similar to *Salmo* in this respect (De Beer 1937). The cartilaginous commissure, which connects the posterior part of the auditory capsule with the occipital basiotic lamina in *M. capensis*, should thus be interpreted as representing a posterior basicapsular commissure.

Stage 3 (4,0 mm)

The neurocranium is only slightly larger than in the previous stage, although major developments have occurred.

Ethmoidal region

The rostral cartilage is now prochondral and it is situated anterodorsal to the planum ethmoidale (Figure 7), somewhat in front of the septum nasi. The anterior part of the rostral cartilage is still in contact with the anterior mesenchyme which has differentiated into a mixture of mesenchyme and blasteme anterior to the planum

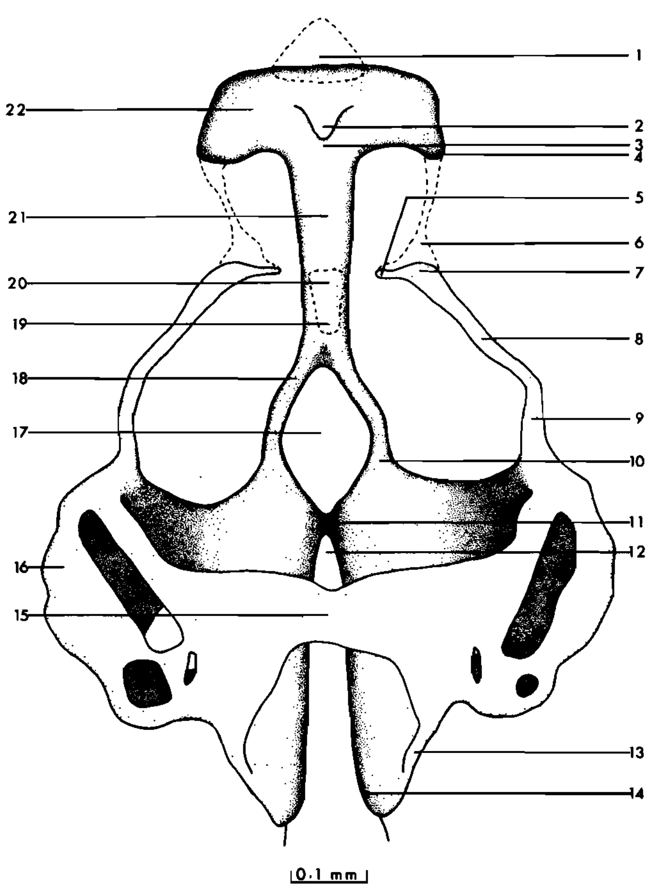

Figure 7 Graphic reconstruction of the neurocranium. Stage 3. Dorsal view. 1: rostral cartilage anlage, 2: septum nasi, 3: commissura trabecularis, 4: lamina orbitonasalis, 5: epiphysial bar, 6: taenia marginalis anterior anlage, 7: cartilago supraorbitalis anterior anlage, 8: taenia marginalis posterior, 9: postorbital process, 10: polar cartilage, 11: prootic bridge, 12: notochord, 13: occipital arch, 14: occipital parachordal, 15: tectum synoticum, 16: auditory capsule, 17: fenestra hypophyseos, 18: trabecula, 19: taenia medialis posterior anlage, 20: epiphysial cartilage anlage, 21: trabecula communis, 22: planum ethmoidale.

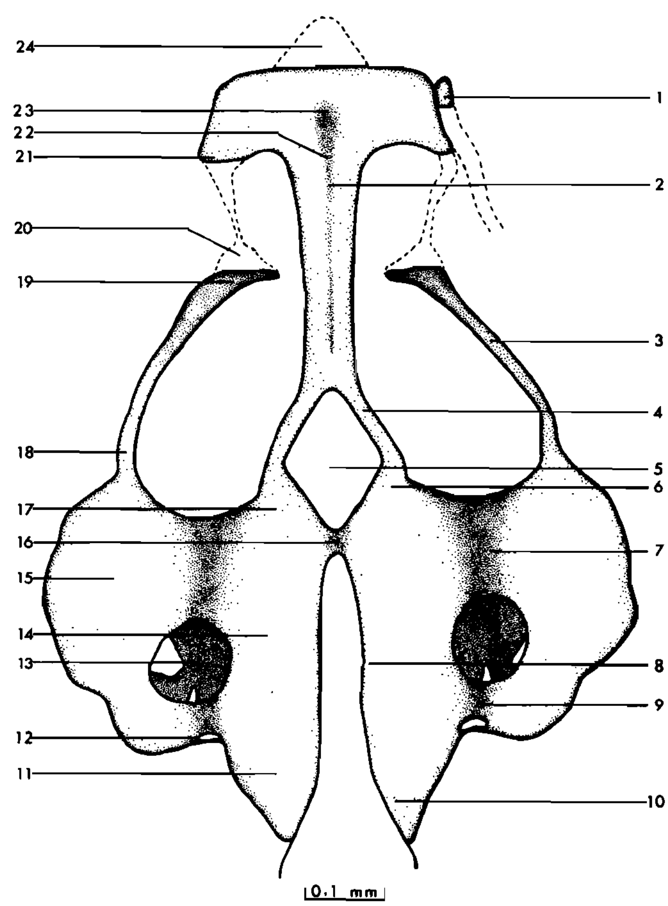

Figure 8 Graphic reconstruction of the neurocranium. Stage 3. Ventral view. 1: processus pterygoideus, 2: trabecula communis, 3: taenia marginalis posterior, 4: trabecula, 5: fenestra hypophyseos, 6: polar cartilage, 7: anterior basicapsular commissure, 8: mesotic parachordal, 9: posterior basicapsular commissure, 10: occipital parachordal, 11: occipital basiotic lamina, 12: foramen jugulare, 13: fenestra basicapsularis, 14: mesotic basiotic lamina, 15: auditory capsule, 16: prootic bridge, 17: anterior basiotic lamina, 18: postorbital process, 19: cartilago supraorbitalis anterior, 20: taenia marginalis anterior anlage, 21: lamina orbitonasalis, 22: commissura trabecularis, 23: planum ethmoidale, 24: rostral cartilage anlage.

ethmoidale. The anlage of the future ethmomaxillary ligaments, which attach the proximal ends of the maxillaries to the dorsal surface (and later also the ventral surface) of the rostral cartilage, can now also be identified in this anterior blastemic mass. The septum nasi has now enlarged considerably into a posterodorsally projecting rod of which only the rostral part is in contact with the planum ethmoidale. A conspicuous new feature of the planum ethmoidale is a distinct, posterolaterally projecting processus ethmoidalis posterior. The base of the lamina orbitonasalis has meanwhile chondrified and fused on to the dorsolateral surface of this process (Figure 9), while its dorsal extension, the commissura sphenethmoidalis, remains blastemic. The lamina orbitonasalis lies lateral to the arteria orbitonasalis and ventrally it remains in contact with the processus pterygoideus by means of a thin blastemic cord. The anterior end of the processus pterygoideus is fully chondrified (Figures 8 and 9). Posterior to its articulation with the planum ethmoidale, in the region of its blastemic contact with the lamina orbitonasalis, the processus pterygoideus, however, remains blastemic. Ventral to the planum ethmoidale the two processus pterygoidei remain interconnected by the commissura palatoquadrati, which anteriorly remains continuous with the anterior blastemic mass.

Orbitotemporal region

The trabecula communis has lengthened considerably and the cartilago supraorbitalis anterior is now situated opposite its mid-section (Figure 7), as opposed to the previous stage (Figure 4) where the cartilago supraorbitalis anterior reached forward to nearly the level of the commissura trabecularis. Both the taenia marginalis posterior and the cartilago supraorbitalis anterior have chondrified. The cartilago supraorbitalis anterior displays a dorsomedial projecting rod, the epiphysial bar (Figures 7 and 8) of which the caudal part is chondral and the rostral part blastemic. Dorsomedial to the hind part of the trabecula communis, at the future dorsal junction of the two epiphysial bars of each side, the common blastemic anlage of the epiphysial cartilage and, posterior to it, the taenia medialis posterior may now be discerned (Figures 7 and 9). Rostral to the cartilago supraorbitalis anterior the taenia marginalis anterior emanates as a blastemic extension of the latter cartilage. The rostral part of the taenia marginalis anterior then merges with the blastemic anlage of the cartilago supraentethmoidalis (Hammarberg 1937), lateral to the brain. This future chondrification centre is anteroventrally connected to the lamina orbitonasalis via the still blastemic commissura sphenethmoidalis. The mesenchyme covering the fenestra hypophyseos is less dense than in the previous stage.

Otico-occipital region

Major consolidation of the roof of the neurocranium has taken place. The blastemic bar between the anterior, horizontal part of the occipital arch and the auditory capsule in the previous stage has now chondrified. The medial margins of the anterior, vertically orientated portions of the occipital arches have similarly become chondrally fused to such an extent that a crescent-shaped tectum synoticum has formed. The auditory capsules are, however, not completely fused with the occipital arches, and three fenestrae, covered by membranes, remain dorsal to the lateral and the posterior semicircular canals on each side (Figure 7). Caudally, a large gap remains between the medial edges of the vertically orientated, posterior parts of the occipital arches and not even the blastemic anlage of a tectum posterius is present at this stage. The flexure of the notochord, where it enters the neurocranium, is now more pronounced, with the result that the occipital

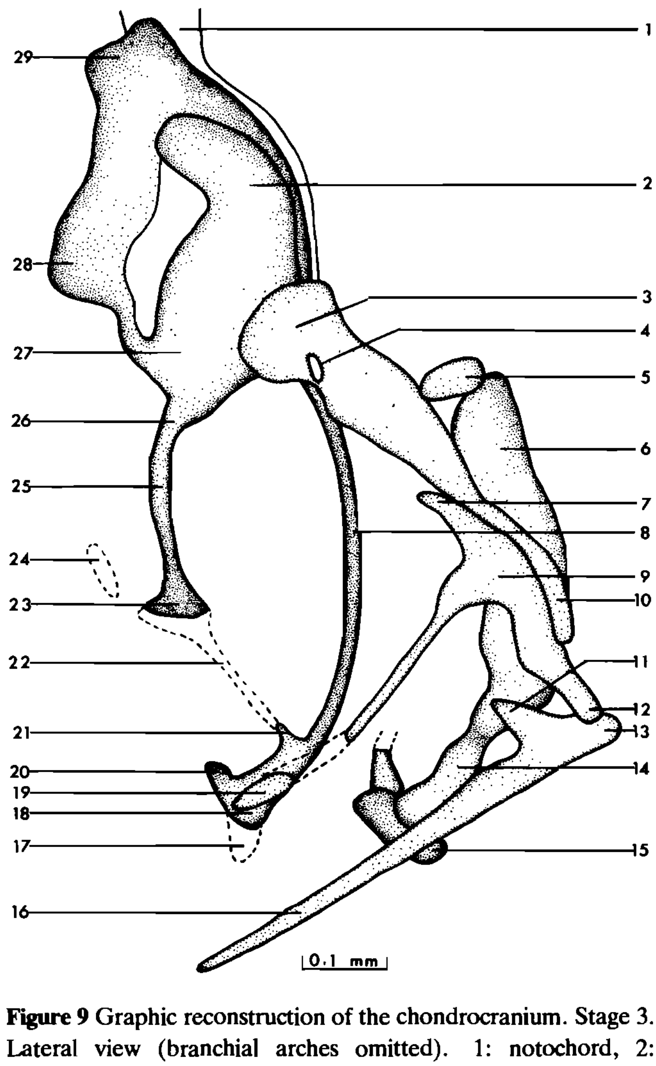

Figure 9 Graphic reconstruction of the chondrocranium. Stage 3. Lateral view (branchial arches omitted). 1: notochord, 2: auditory capsule, 3: hyomandibula, 4: foramen hyomandibulare, 5: interhyal, 6: ceratohyal, 7: processus oticus internus, 8: trabecula communis, 9: pars quadrata, 10: symplectic, 11: processus coronoideus, 12: processus articularis palatoquadrati, 13: processus retroarticularis, 14: ceratohyal, 15: hypohyal, 16: Meckel's cartilage, 17: rostral cartilage anlage, 18: planum ethmoidale, 19: processus pterygoideus, 20: septum nasi, 21: lamina orbitonasalis, 22: taenia marginalis anterior anlage, 23: cartilago supraorbitalis anterior, 24: epiphysial cartilage, 25: taenia marginalis posterior, 26: postorbital process, 27: anterior auditory capsule, 28: tectum synoticum, 29: occipital arch.

region is slightly elevated relative to the otic region (Figure 9).

Stage 4 (5,1 mm)

The neurocranium has increased 1,5 times in length and extensive developments have occurred in the ethmoidal and in the orbitotemporal regions.

Ethmoidal region

The planum ethmoidale (Figure 11) is relatively narrower and it has undergone extensive rostral growth. The angle between the planum ethmoidale and the trabecular complex is approximately the same as before (Figure 12), but the lateral wings of the planum ethmoidale are tilted upwards more than in the previous two stages. The longitudinal contact between the septum nasi and the planum ethmoidale is more extensive and the septum nasi has lengthened considerably in a posterolateral direction. It is now fused medially with a newly chondrified commissura sphenoseptalis of each side (Figure 10). The latter commissures link the septum nasi with the cartilago supraentethmoidalis of each side. The lamina orbitonasalis has also lengthened considerably. It projects posterodorsally and has fused with the cartilago supraentethmoidalis, which has now chondrified. As in *Gadus* (De Beer 1937) no preoptic root of the orbital cartilage *(sic)* chondrifies, with the result that only a foramen olfactorium advehens is delimited. The rostral cartilage is fully chondrified and it now lies directly above the septum nasi, its anterior tip still terminating in the thick anterior blasteme. The ethmomaxillary ligaments are now more prominent. The processus ethmoidalis posterior now articulates with only

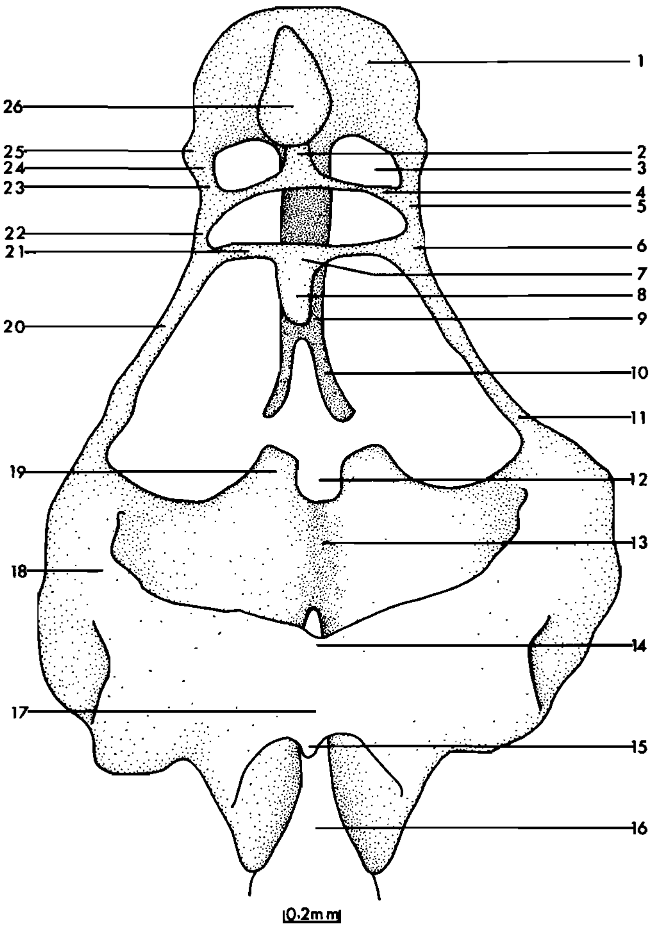

Figure 10 Graphic reconstruction of the neurocranium. Stage 4. Dorsal view. 1: planum ethmoidale, 2: septum nasi, 3: foramen olfactorium advehens, 4: commissura sphenoseptalis, 5: cartilago supraentethmoidalis, 6: cartilago supraorbitalis anterior, 7: epiphysial cartilage, 8: taenia medialis posterior, 9: trabecula communis, 10: trabecula, 11: postorbital process, 12: fenestra basicranialis, 13: basal plate, 14: tectum synoticum, 15: processus occipitalis posterior, 16: notochord, 17: tectum posterius, 18: auditory capsule, 19: polar cartilage, 20: taenia marginalis posterior, 21: epiphysial bar, 22: taenia marginalis anterior, 23: commissura sphenethmoidalis, 24: lamina orbitonasalis, 25: processus ethmoidalis posterior, 26: rostral cartilage.

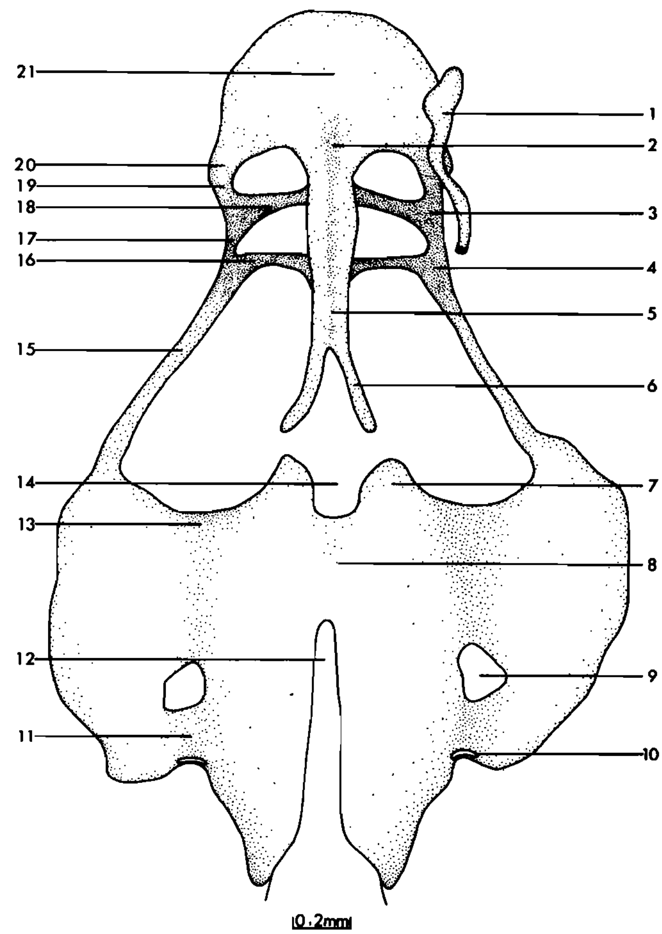

Figure 11 Graphic reconstruction of the neurocranium. Stage 4. Ventral view. 1: processus pterygoideus, 2: commissura trabecularis, 3: cartilago supraentethmoidalis, 4: cartilago supraorbitalis anterior, 5: trabecula communis, 6: trabecula, 7: polar cartilage, 8: basal plate, 9: fenestra basicapsularis, 10: foramen jugulare, 11: posterior basicapsular commissure, 12: notochord, 13: anterior basicapsular commissure, 14: fenestra basicranialis, 15: taenia marginalis posterior, 16: epiphysial bar, 17: taenia marginalis anterior, 18: commissura sphenoseptalis, 19: lamina orbitonasalis, 20: processus ethmoidalis posterior, 21: planum ethmoidale.

the mediolateral edge of the planum ethmoidale.

Orbitotemporal region

The entire side wall and most of the roof of the neurocranium has formed. The commissura sphenoseptalis connects the septum nasi with a newly chondrified element, the cartilago supraentethmoidalis (Hammarberg 1937) (Figure 10), which is situated at the junction of the commissura sphenoseptalis, the commissura

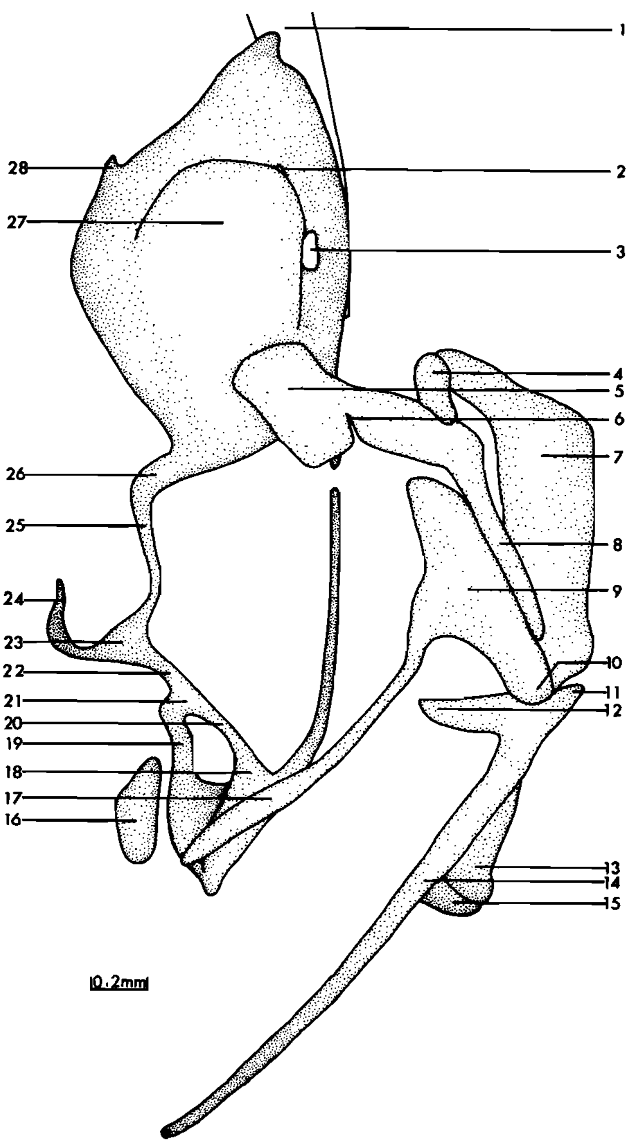

Figure 12 Graphic reconstruction of the chondrocranium. Stage 4. Lateral view (branchial arches omitted). 1: notochord, 2: foramen jugulare, 3: fenestra basicapsularis, 4: interhyal, 5: hyomandibula, 6: incisura hyomandibularis, 7: ceratohyal, 8: symplectic, 9: pars quadrata, 10: processus articularis palatoquadrati, 11: processus retroarticularis, 12: processus coronoideus, 13: hypohyal, 14: Meckel's cartilage, 15: basihyal, 16: rostral cartilage, 17: processus pterygoideus, 18: lamina orbitonasalis, 19: septum nasi, 20: commissura sphenethmoidalis, 21: cartilago supraentethmoidalis, 22: taenia marginalis anterior, 23: cartilago supraorbitalis anterior, 24: taenia medialis posterior, 25: taenia marginalis posterior, 26: postorbital process, 27: auditory capsule, 28: processus occipitalis posterior.

sphenethmoidalis and the taenia marginalis anterior, all of which are now fully chondrified. An examination of sections of larvae intermediate in development between the present and the previous stage indicates that the cartilago supraentethmoidalis and the lamina orbitonasalis give rise to the commissura sphenethmoidalis, wheras only commissura sphenoseptalis originates from the cartilago supraentethmoidalis. There is no preoptic root, nor is there any trace of an interorbital septum, either blastemic or membranous. In the dorsal mid-line, directly above the epiphysis, the epiphysial cartilage and the taenia medialis posterior have chondrified (Figures 10 and 12). Similarly chondrified is the epiphysial bridge which connects the cartilago supraorbitalis anterior with the epiphysial cartilage medially. The epiphysial cartilage and the taenia medialis posterior develop from a blastemic anlage entirely independent from the epiphysial bridge. The latter arises from the chondrification centre of the cartilago supraorbitalis anterior. The floor of the neurocranium in this region already displays evidence of the advent of resorbtion of certain chondral structures. The trabeculae have lost their contact with the polar cartilages as a result of resorbtion (Figures 11 and 12) and the trabeculae and the trabecula communis have straightened. No trace is left of the mesenchyme which had covered the fenestra hypophyseos in the previous stages. It has been completely replaced by the parasphenoid which is in contact with both trabeculae along their entire medial surfaces.

Otico-occipital region

The flexure of the notochord has straightened out and very little evidence of cranial flexure remains in this region (Figure 12). The posterior, vertically orientated parts of the occipital arches are in the process of fusing in a posterior direction to form a tectum posterius, which here does not develop separately from, but rather as a posteriorly directed expansion of, the tectum synoticum. Posteromedially the tectum posterius displays a slight processus occipitalis posterior. The occipital arches are laterally completely fused with the roofs of the auditory capsules and all the fenestrae have been obliterated (Figure 10). Posterior to where the stato-acoustic nerve emerges from the metencephalon, the roof and the floor of the auditory capsule have medially formed a vertical, chondrified septum semicircularis lateralis, which partially separates the lateral semicircular canal from the cranial cavity and the rest of the auditory capsule. In the region of the posterior semicircular canal, the septum is continued posteriorly in the form of a rod stretching obliquely between the floor of the auditory capsule and the occipital arch, where the latter is fused dorsally to the auditory capsule to form the septum semicircularis posterior. There is no true medial wall to the auditory capsule and, except for these septa and the dura mater, the cavities of the auditory capsules and the cranial cavity are confluent. The ventrolateral surface of the anterior part of the auditory capsule has a slight indentation, a fossa hyomandibularis, in which the hyomandibula lodges. Lateral to this articulation the anterior part of the auditory capsule displays a slight lateral ridge, the crista parotica, on its ventrolateral edge. Most of the prootic bridge has been resorbed resulting in a large fenestra basicranialis, confluent with the fenestra hypophyseos, between the two anterior basiotic laminae (Figures 10 and 11). This fenestra is covered ventrally by the parasphenoid. A posterior myodome does not develop and the rectus muscles insert on the parasphenoid in front of and medial to the orbital cartilages. Resorbtion of the notochord is more advanced. Its anterior tip now only reaches to the level of the anterior edge of the tectum synoticum. In front of the tip of the notochord the mesotic parachordals have fused in the ventral mid-line of the basal plate. On the ventral surface of the latter the fenestra basicapsularis is being obliterated by chondrification of the blastemic membrane which covers it. This membrane is pierced by the root of the glossopharyngeal nerve where it passes out of the cranial cavity.

Stage 5 (11,0 mm)

The neurocranium is twice the length of the previous stage and as a whole it has a slightly more slender appearance (Figure 13). Perichondral ossification has commenced in certain areas.

Ethmoidal region

The planum ethmoidale has undergone considerable rostral growth (Figure 13) and the angle between it and the trabeculae further posterior has been reduced to the extent that it now slopes downwards relative to the trabeculae (Figure 15). The ventral surface of the planum ethmoidale is supported by an extensively

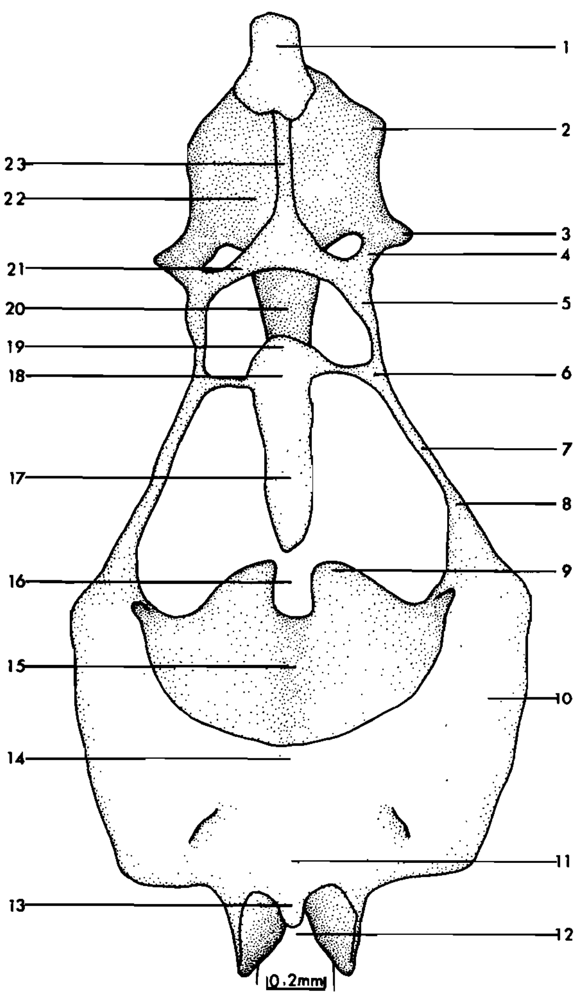

Figure 13 Graphic reconstruction of the neurocranium. Stage 5. Dorsal view. 1: rostral cartilage, 2: cornu trabeculae, 3: processus ethmoidalis posterior, 4: lamina orbitonasalis, 5: taenia marginalis anterior, 6: cartilago supraorbitalis anterior, 7: taenia marginalis posterior, 8: postorbital process, 9: polar cartilage, 10: auditory capsule, 11: tectum posterius, 12: notochord, 13: processus occipitalis posterior, 14: tectum synoticum, 15: basal plate, 16: fenestra basicranialis, 17: taenia medialis posterior, 18: epiphysial cartilage, 19: taenia medialis anterior, 20: trabecula communis, 21: commissura sphenoseptalis, 22: planum ethmoidale, 23: septum nasi.

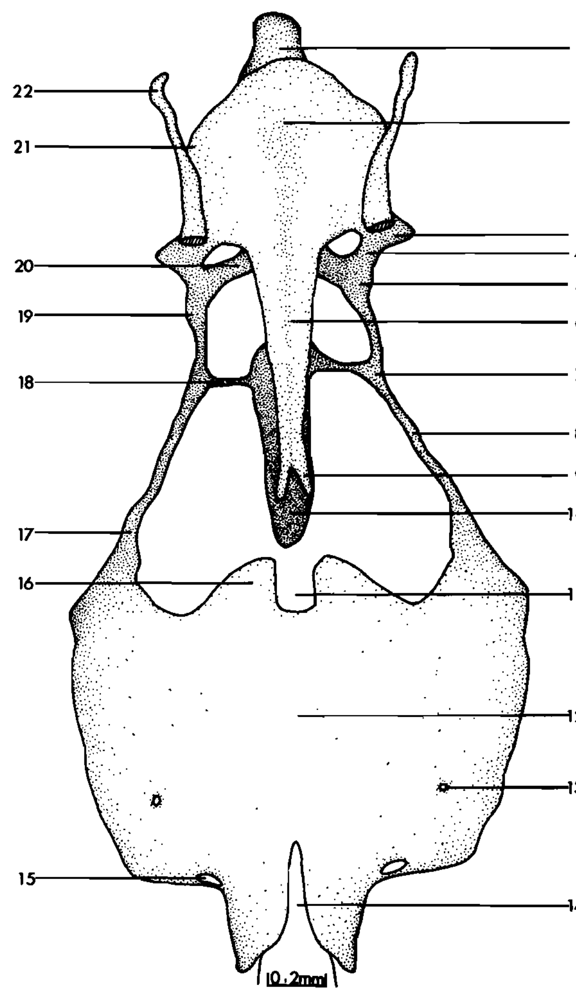

Figure 14 Graphic reconstruction of the neurocranium. Stage 5. Ventral view. 1: rostral cartilage, 2: planum ethmoidale, 3: processus ethmoidalis posterior, 4: lamina orbitonasalis, 5: cartilago supraentethmoidalis, 6: trabecula communis, 7: cartilago supraorbitalis anterior, 8: taenia marginalis posterior, 9: trabecula, 10: taenia medialis posterior, 11: fenestra basicranialis, 12: basal plate, 13: foramen glossopharyngeum, 14: notochord, 15: foramen jugulare, 16: polar cartilage, 17: postorbital process, 18: epiphysial bar, 19: taenia marginalis anterior, 20: commissura sphenoseptalis, 21: cornu trabeculae, 22: processus pterygoideus.

ossified vomer. The rostral cartilage is more massive and it has shifted forward to the extent that only its posterior half lies dorsal to the septum nasi. Anteriorly it is in contact with the ligaments which participate in the symphysis between the proximal ends of the two premaxillaries. These ligaments developed out of the anterior blasteme. Also differentiated in this blasteme are the strong ethmomaxillary ligaments which attach the anterior, proximal ends of the maxillaries to the rostral cartilage dorsally and ventrally. The processus ethmoidalis posterior has grown considerably in a lateral direction (Figures 13 and 14). Just anterior to its junction with the lamina orbitonasalis, the extreme ventrolateral edge of the processus ethmoidalis posterior is connected to the processus pterygoideus immediately ventral to it by means of the preorbital ligament. There is no true ethmopalatine articulation. The processus pterygoideus articulates with only the mediolateral edge of the planum ethmoidale, which now displays a slight lateral process, the cornu trabeculae. The contact between the processus pterygoideus and the cornu trabeculae of the planum ethmoidale constitute the rostropalatine articulation. The septum nasi is more prominent. The junction of the septum nasi and the commissura sphenoseptalis of each side is relatively further forward than in earlier stages, with the effect that these commissures now reach obliquely anterodorsal towards the septum nasi (Figure 13). The lateral growth of the processus ethmoidalis posterior has caused the lamina orbitonasalis, which previously projected posterodorsally, to reach obliquely dorsomedial towards the cartilago supraentethmoidalis.

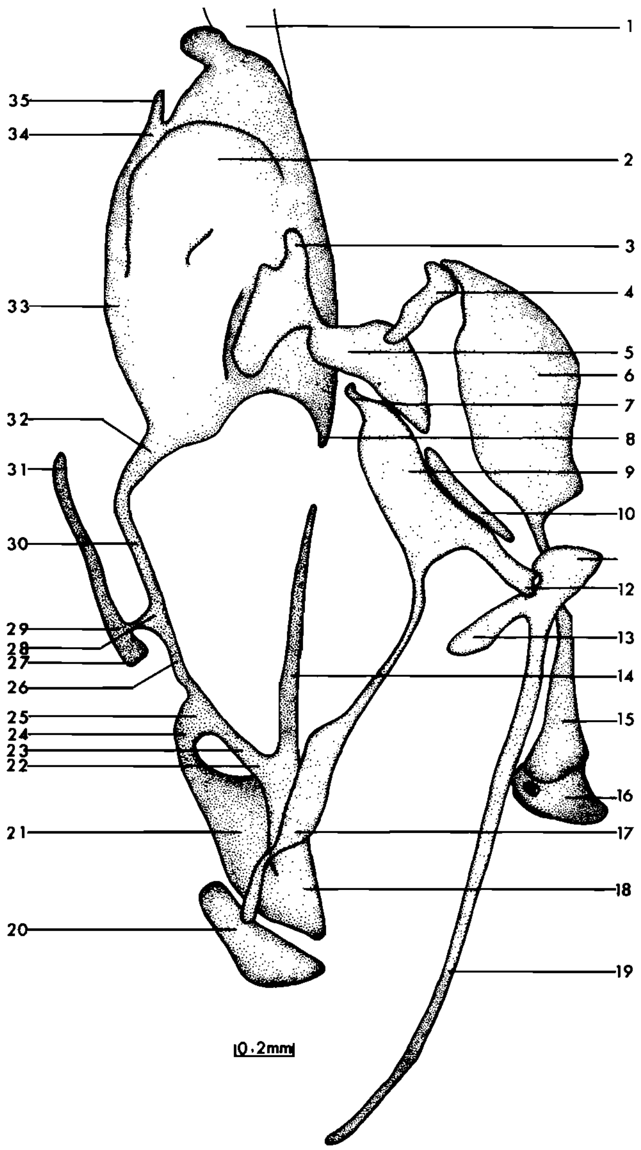

Figure 15 Graphic reconstruction of the chondrocranium. Stage 5. Lateral view (branchial arches omitted). 1: notochord, 2: auditory capsule, 3: processus opercularis, 4: interhyal, 5: hyomandibula, 6: ceratohyal, 7: processus oticus internus, 8: polar cartilage, 9: pars quadrata, 10: symplectic, 11: processus retroarticularis, 12: processus articularis palatoquadrati, 13: processus coronoideus, 14: trabecula communis, 15: ceratohyal, 16: basihyal, 17: processus pterygoideus, 18: planum ethmoidale, 19: Meckel's cartilage, 20: rostral cartilage, 21: septum nasi, 22: lamina orbitonasalis, 23: commissura sphenethmoidalis, 24: commissura sphenoseptalis, 25: cartilago supraentethmoidalis, 26: taenia marginalis anterior, 27: taenia medialis anterior, 28: cartilago supraorbitalis anterior, 29: epiphysial cartilage, 30: taenia marginalis posterior, 31: taenia medialis posterior, 32: postorbital process, 33: tectum synoticum, 34: tectum posterius, 35: processus occipitalis posterior.

Orbitotemporal region

The anterior fontanelle in the roof of the neurocranium has increased considerably in size relative to the rest of the neurocranium, owing to extensive rostrocaudal growth of the taenia marginalis anterior. In contrast, the taenia marginalis posterior does not display the same extensive increase in length and its relative dimensions are not much different from those of the previous stage. The taenia medialis posterior has increased both in width and in length and it now extends caudal to nearly the level of the polar cartilages, thus covering at least the anteromedial part of the large, posterior fontanelle in the roof of the neurocranium. The epiphysial cartilage has developed a rostrally projecting, fairly broad taenia medialis anterior, which mediodorsally partly covers the anterior fontanelle. Resorbtion of the posterior ends of the trabeculae is more advanced and they now appear as two short, rod-like posterior extensions of the trabecula communis. The entire trabecular complex follows the downward slope of the planum ethmoidale, so that the whole complex is flexed downwards relative to the basal plate behind it (Figure 15). The anterior part of the auditory capsule encroaches even more into the orbitotemporal region than before.

Otico-occipital region

Compared with the previous stages this region of the neurocranium is both dorsoventrally and laterally flattened, lending it a distinctly more slender appearance (Figure 15). The notochord has undergone further resorbtion (Figure 14) and it now barely reaches anteriorly past the foramen jugulare. The area previously occupied by the now resorbed notochord is filled by the medially fused mesotic parachordals.

Except for the foramen glossopharyngeum, the fenestra basicapsularis has similarly been completely obliterated by chondrification of the blastemic membrane which had covered it in the previous stage, resulting in a completely chondrified basal plate. Posteriorly the vertically orientated occipital arches display a greater degree of medial fusion in a caudal direction (Figure 13), with the effect that the tectum posterius and the processus occipitalis posterior reach much further caudally. This fusion gives rise to a distinct mediodorsal crest, the forerunner of the supraoccipital crest of the supraoccipital bone, which later ossifies perichondrally in the region. In the auditory capsule the bar which formed a partial septum semicircularis posterior has chondrified further to form a complete septum. The septum semicircularis anterior is now starting to develop and is present as an oblique rod connecting the anterior roof of the auditory capsule with the anteroventral part of the septum semicircularis lateralis.

Stage 6 (14,1 mm)

The neurocranium has increased in length by approximately 10%. Although the perichondral ossifications have become more extensive, the original boundaries of the various cartilages have not been affected anywhere.

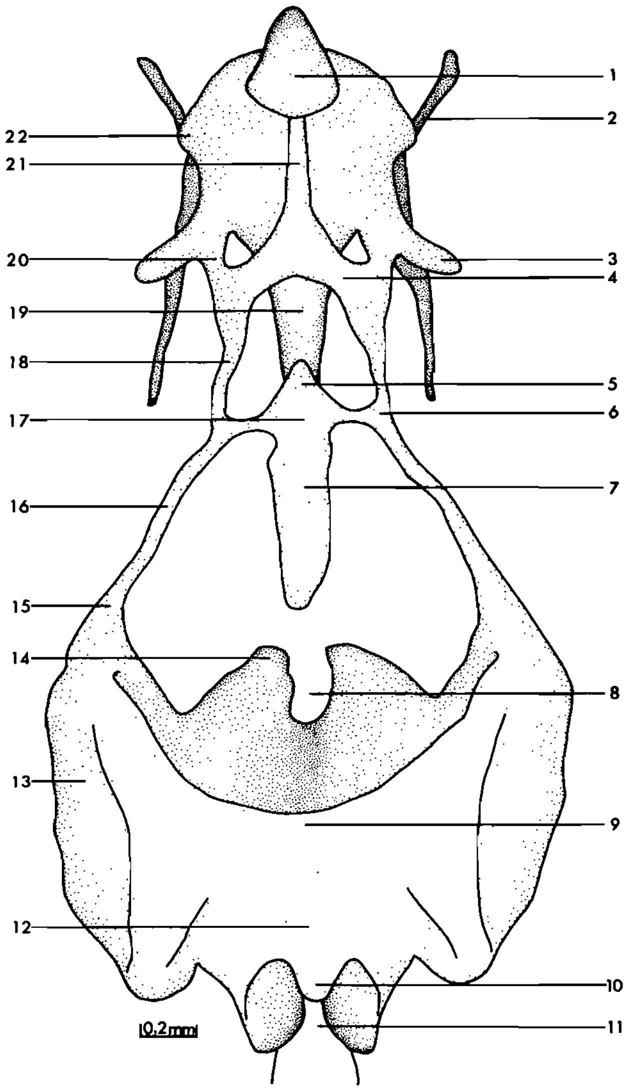

Figure 16 Graphic reconstruction of the neurocranium. Stage 6. Dorsal view. 1: rostral cartilage, 2: processus pterygoideus, 3: processus ethmoidalis posterior, 4: commissura sphenoseptalis, 5: taenia medialis anterior, 6: cartilago supraorbitalis anterior, 7: taenia medialis posterior, 8: fenestra basicranialis, 9: tectum synoticum, 10: processus occipitalis posterior, 11: notochord, 12: tectum posterius, 13: auditory capsule, 14: polar cartilage, 15: postorbital process, 16: taenia marginalis posterior, 17: epiphysial cartilage, 18: taenia marginalis anterior, 19: trabecula communis, 20: lamina orbitonasalis, 21: septum nasi, 22: cornu trabeculae.

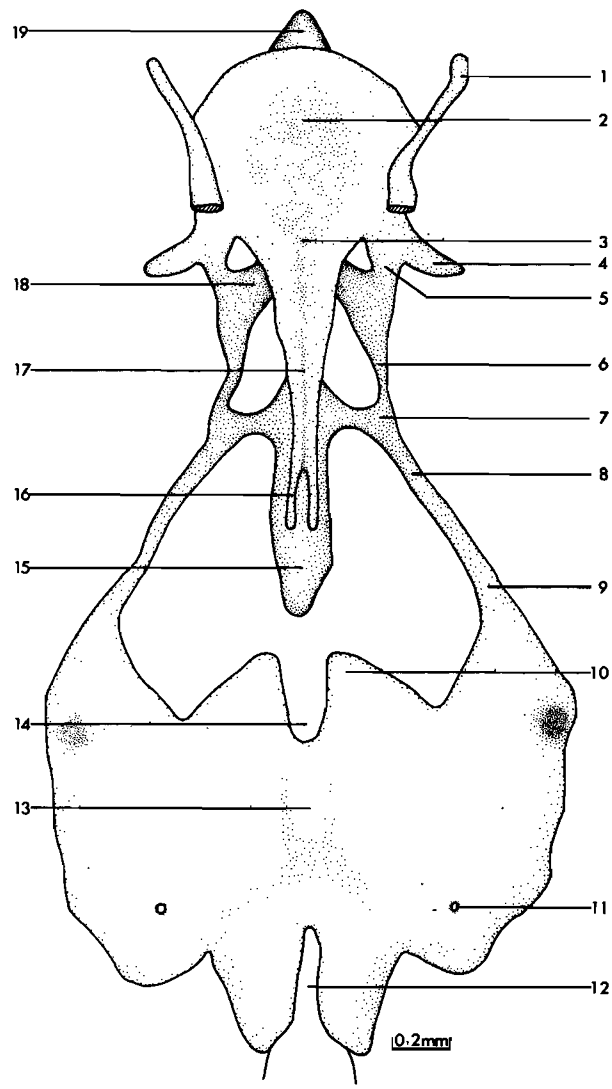

Figure 17 Graphic reconstruction of the neurocranium. Stage 6. Ventral view. 1: processus pterygoideus, 2: planum ethmoidale, 3: commissura trabecularis, 4: processus ethmoidalis posterior, 5: lamina orbitonasalis, 6: taenia marginalis anterior, 7: cartilago supraorbitalis anterior, 8: taenia marginalis posterior, 9: postorbital process, 10: polar cartilage, 11: foramen glossopharyngeum, 12: notochord, 13: basal plate, 14: fenestra basicranialis, 15: taenia medialis posterior, 16: trabecula, 17: trabecula communis, 18: commissura sphenoseptalis, 19: rostral cartilage.

Ethmoidal region

The processus ethmoidalis posterior has lengthened considerably in a posterolateral and a somewhat ventral direction. The cornu trabeculae has similarly extended laterally, but not to the same extent as its posterior counterpart. A further interesting development is the shift that has taken place in the rostropalatine articulation (Figure 18). Whereas the processus pterygoideus previously made contact with the lateral edge of the cornu trabeculae, it now articulates with the ventrolateral edge of the latter process. On the dorsal and lateral surfaces of the septum nasi and on the dorsal surface of the planum ethmoidale, perichondral ossifications have occurred. These ossifications will eventually give rise to the mesethmoid. The processus ethmoidalis posterior displays similar ossifications on its ventral, dorsal and lateral surfaces which, together with perichondral ossifications of the lamina orbitonasalis, will later give rise to the endochondral part of the lateral ethmoid.

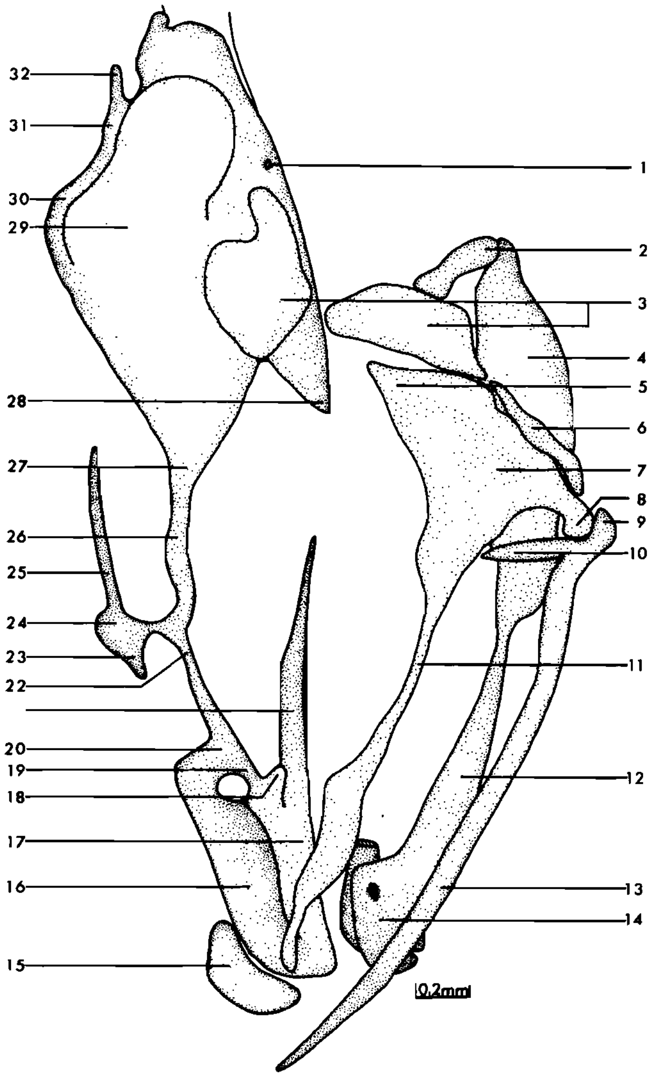

Figure 18 Graphic reconstruction of the chondrocranium. Stage 6. Lateral view (branchial arches omitted). 1: foramen glossopharyngeum, 2: interhyal, 3: hyomandibula, 4: ceratohyal, 5: processus oticus internus, 6: symplectic, 7: pars quadrata, 8: processus articularis palatoquadrati, 9: processus retroarticularis, 10: processus coronoideus, 11: processus pterygoideus, 12: ceratohyal, 13: Meckel's cartilage, 14: hypohyal, 15: rostral cartilage, 16: septum nasi, 17: planum ethmoidale, 18: processus ethmoidalis posterior, 19: commissura sphenethmoidalis, 20: commissura sphenoseptalis, 21: trabecula communis, 22: taenia marginalis anterior, 23: taenia medialis anterior, 24: epiphysial cartilage, 25: taenia medialis posterior, 26: taenia marginalis posterior, 27: postorbital process, 28: polar cartilage, 29: auditory capsule, 30: tectum synoticum, 31: tectum posterius, 32: processus occipitalis posterior.

Orbitotemporal region

Resorbtion of the trabeculae has not proceeded to the same extent as in the previous stage but, because of lack of growth of the trabecula communis, the trabeculae are now situated much further anteriorly. The insertions of the rectus eye muscles are unchanged from the previous stages as a posterior myodome fails to develop. Owing to the fact that preoptic roots also fail to develop an orbitosphenoid is absent. There is also no basisphenoid.

Otico-occipital region

No major changes have occurred in this region of the neurocranium. In all the previous stages, except the first stage where it was still absent, the dorsal fusion between the posterolateral part of the occipital arch and the posteromedial part of the auditory capsule overlapped the posterior basicapsular commissure dorsally to such an extent that the foramen jugulare was in the shape of a tunnel facing obliquely posteroventrally. In the present stage the dorsal fusion extends just as far posterior as does the posterior basicapsular commissure, with the effect that the foramen jugulare here faces posteriorly and is thus not visible in either dorsal or ventral aspect (Figures 16 and 17).

In the otic region, the postorbital process and the anterior part of the auditory capsule display the beginning of perichondral ossification which will give rise to the sphenotic. Further posterior the pterotic is starting to ossify perichondrally on the inner and the outer surfaces of the floor and the lateral wall of the auditory capsule in the region of the lateral semicircular canal. Similar ossifications are taking place in the region of the posterior semicircular canal to form the epiotic, while the prootic has started to ossify in the polar cartilage, the anterior basiotic lamina and in the medial part of the anterior basicapsular commissure. Posterior to the ossification of the prootic, the opisthotic is ossifying perichondrally in the floor of the auditory capsule.

In the occipital region the exoccipitals have also started to ossify in the vertically orientated parts of the occipital arches. Similar ossifications have also appeared in the occipital parachordals. These will eventually fuse and form the basioccipital. Dorsally in this region, the tectum synoticum and the tectum posterius are ossifying to form the supraoccipital.

Discussion

Ethmoidal region

Planum ethmoidale

In the earliest stage of *M. capensis* available for the present study (2,3 mm) the planum ethmoidale and the commissura trabecularis are already present. The anterior end of the planum ethmoidale is still blastemic, its central section is prochondral and further posterior it consists of young cartilage. The anterior blastemic portion is continuous rostrally with a sheath of mesenchymatous tissue which surrounds the planum ethmoidale anteriorly, laterally and ventrally. The lateral edges of the planum ethmoidale are in contact with the blastemic anterior ends of the processus pterygoidei, which on their part are also anteriorly and ventrally in contact with this mesenchymatous sheath. As in *Barbus* (Van der Westhuizen 1979), *Hypophthalmichthyes* (Nel 1981) and *Ctenopharyngodon* (Van den Heever 1981) the rostral cartilage condenses in this anterior mesenchymatous mass, which also encloses the proximal ends of the premaxillaries and the maxillaries. Bertmar (1959) only mentions the maxillaries developing here in *Hepsetus*.

The anterior mesenchymatous mass of *M. capensis* corresponds to the rostral part of the anterior mesenchyme which is left in *Hepsetus* (Bertmar 1959) after the chondrification of the planum ethmoidale and the commissura trabecularis has taken place. The ventral mesenchymatous commissure linking the blastemic anterior ends of the processus pterygoidei corresponds to the commissura palatoquadrati which Holmgren (1943) describes in *Salmo*. In view of the progressively rostrally differentiated planum ethmoidale of *M. capensis* and the other mentioned similarities, it seems feasible that the planum ethmoidale and the commissura trabecularis of *M. capensis* develop in the same way as in *Hepsetus* (Bertmar 1959), *Barbus* (Van der Westhuizen 1979), *Hypophthalmichtyes* (Nel 1981) and *Ctenopharyngodon* (Van den Heever 1981).

In *M. capensis* only the rostropalatine articulation occurs, the ethmopalatine articulation being represented by the preorbital ligament, which attaches the processus pterygoideus to the processus ethmoidalis posterior.

Lamina orbitonasalis

In *M. capensis* the lamina orbitonasalis and the processus pterygoideus develop from a common blasteme lateral to the commissura trabecularis and in contact with the commissura palatoquadrati. In the 3,4-mm stage the blastemic processus pterygoideus is in contact dorsally with a blastemic cord of cells which reach posterodorsally in the direction of the posterior region of the nasal placode. This cord is the anlage of the lamina orbitonasalis. Later the lamina orbitonasalis chondrifies and fuses dorsolaterally on to the processus ethmoidalis posterior, but it remains connected to the processus pterygoideus by means of a thin, blastemic cord which develops into the preorbital ligament. This ligament, which constitutes the ethmopalatine articulation in *M. capensis*, as in *Ctenopharyngodon* (Van den Heever 1981), corresponds to the orbital ligament of the Selachii (Holmgren 1943).

De Beer (1937) comes to the conclusion that the lamina orbitonasalis is not part of the original neurocranial wall and that the true cranial wall is represented by the preoptic root.

Holmgren (1940) suggests that the lamina orbitonasalis and the rest of the visceral skeleton of the Selachii develop from ectomesenchyme and that the lamina orbitonasalis of the Teleostei corresponds with that of the Selachii (Holmgren 1943). He further demonstrates that the posterior part of the commissura palatoquadrati in *Salmo*, *Esox* and *Lepidosteus* becomes incorporated in the ventral surface of the planum ethmoidale, and therefore considered that the commissura palatoquadrati represents an earlier separate element of visceral origin.

Jarvik (1954), in his investigation of the extinct crossopterygian *Eusthenopteron*, comes to the conclusion that the serial arrangement of the tooth plates in the roof of the mouth and in the pharynx of *Eusthenopteron* is indicative of a similar serial arrangement in the primary elements of the three prootic visceral arches. He considered that this arrangement corresponds to the serial arrangement of these elements in the branchial arches, where each arch dorsally possesses an infrapharyngo-, suprapharyngo- and epi-element. In the three prootic arches, the infrapharyngo- and the suprapharyngo-elements have become incorporated in the neurocranium. In the premandibular arch the infrapharyngo-element is represented by the intermediating body, which Holmgren (1943) describes in *Salmo*. The intermediating body gives rise to the commissura palatoquadrati. Bertmar (1959) agrees with Jarvik (1954), but maintains that the intermediating body is part of the epipremandibula (processus pterygoideus), and that the infrapharyngopremandibula is represented by only the lateral half of the commissura palatoquadrati.

Septum nasi

There is considerable variation in the form and in the development of the septum nasi in the Actinopterygii. Usually the fore brain is initially situated in the ethmoidal region, and as soon as it starts to retract into the orbital region, as in *M. capensis*, the septum nasi develops as a median, longitudinal wall of cartilage. The development of the septum nasi of *M. capensis* proceeds along similar lines to that of *Gadus* (De Beer 1937). The septum nasi arises as a dorsal protruberance on the mediodorsal surface of the planum ethmoidale and in later stages it expands rostrally into a thin, high septum and posterodorsally into a rod-like structure which eventually establishes contact with a commissura sphenoseptalis of each side.

In *M. capensis* where the eyes are relatively small in the adult, an anterior myodome is absent. In the larval stages the oblique eye muscles insert on fasciae dorsal to the commissura trabecularis, and just posterior to the septum nasi.

Rostral cartilage

Recent studies on *Barbus* (Van der Westhuizen 1979), *Hypophthalmichthyes (Nel 1981) and Ctenopharyngodon* (Van den Heever 1981) indicate that the rostral cartilage develops in the anterior mesenchyme. The commissura palatoquadrati, which gives rise to the rostral cartilage, differentiates in the anterior mesenchyme.

The development of the rostral cartilage of *M. capensis* proceeds along similar lines. It condenses in the mesenchyme situated anterior to the planum ethmoidale, this mesenchyme being continuous with the commissura palatoquadrati. The anterior mesenchyme also gives rise to the premaxillaries, and it is thus feasible that the rostral cartilage might represent fused premaxillary cartilages in *M. capensis*.

Orbitotemporal region

Side wall and roof of the neurocranium

A preoptic root fails to develop in *M. capensis* and the following chondrification centres are identified: a cartilago supraentethmoidalis, a cartilago supraorbitalis anterior and a postorbital process as well as a separate, medial anlage of the epiphysial cartilage. In *Amia*, *Lepidosteus* and *Gasterosteus* (Hammarberg 1937) the epiphysial cartilage also arises independently of the cartilago supraorbitalis anterior.

In *M. capensis*, as in *Cyclopterus* and *Esox* (Hammarberg 1937), the epiphysial cartilage develops a taenia medialis anterior and, as in *Amia*, *Clupea*, *Esox*, *Gasterosteus*, *Lepidosteus*, *Salmo* (Hammarberg 1937) and *Ctenopharyngodon* (Van den Heever 1981), a taenia medialis posterior.

As in *Cyclopterus* and *Esox* (Hammarberg 1937) a processus entethmoideus is absent in *M. capensis*, despite the presence of a cartilago supraentethmoidalis, which usually gives rise to this structure. The processus entethmoideus is usually well developed in the Teleostei (Hammarberg 1937), but it is absent in *Gasterosteus* (Swinnerton 1902), *Clupea* (Wells 1923), *Salmo* (De Beer 1927) and *Mastacembelus* (Bhargava 1958) as well as in *Cyclopterus* and *Esox*.

Trabeculae and polar cartilages

The present investigation can shed no light upon the problem of the origin of the trabeculae in the Teleostei. In the earliest stage of *M. capensis* (2,3 mm) the trabeculae are already fully chondrified and fused anterior to form a trabecula communis. Similarly in this stage the polar cartilage has already fused with the trabecula and with the anterior basiotic lamina and it is impossible to state whether a separate blastemic anlage of this element occurs.

Otico-occipital region

Parachordals and basiotic laminae

The basal plate of *M. capensis* does not display any segmentation and it is not possible to distinguish either histologically or morphologically between the parachordals and the basiotic laminae.

Tectum synoticum and tectum posterius

In *Hepsetus*, Bertmar (1959) finds that the occipital arches fuse medially with each other and laterally with the anterior parts of the auditory capsules to form the tectum synoticum. A tectum posterius is absent in *Hepsetus*. Van der Westhuizen (1979), Nel (1981) and Van den Heever (1981) report a similar mode of development. The occipital arches also become fused medially to form the tectum synoticum, while the tectum posterius develops further caudally through fusion of the occipital arches medially, but in continuity with the tectum synoticum.

M. capensis displays a similar mode of development. In the 2,3-mm stage the two occipital arches are separate and display no sign of fusion with either the auditory capsules or with each other. In the 3,4-mm stage the occipital arches have become elongated in an anterior direction and have established contact anterolaterally with the anterior parts of the auditory capsules by means of two blastemic commissures. In the next stage (4,0 mm) these commissures chondrify and fuse and the two occipital arches also fuse anteromedially with each other to form the tectum synoticum. Further posteriorly the two occipital arches remain separate. In later stages the tectum posterius is formed in continuity with the tectum synoticum by progressive rearward fusion of the vertically orientated parts of the occipital arches.

Summary

(i) The anterior mesenchyme gives rise to the rostral cartilage, the commissura palatoquadrati, the processus pterygoideus, the lamina orbitonasalis and probably also to the planum ethmoidale.

(ii) The lamina orbitonasalis and the processus pterygoideus develop from a common blasteme, situated lateral to the commissura trabecularis, and in contact with the commissura palatoquadrati. The lamina orbitonasalis probably represents a suprapharyngopremandibula and the processus pterygoideus an infrapharyngopremandibula.

(iii) There is no true ethmopalatine articulation, only a rostropalatine articulation between the processus pterygoideus and the cornu trabeculae. The ethmopalatine articulation is represented by the preorbital ligaments which attach the processus pterygoideus to the processus ethmoidalis posterior.

(iv) In the orbitotemporal region the following chondrification centres are present in the roof and side wall of the neurocranium: a cartilago supraentethmoidalis, a cartilago supraorbitalis anterior, a postorbital process and a separate medial anlage of the epiphysial cartilage.

(v) A cartilago supraentethmoidalis is present but no processus entethmoideus develops.

(vi) A preoptic root is absent and only a foramen olfactorium advehens is delimited.

(vii) In the earliest stage investigated the trabeculae are fully chondrified and fused anteriorly to form a trabecula

communis. The polar cartilages are similarly chondrified and fused with the trabeculae and basiotic laminae respectively.

(viii) A lateral commissure and prootic process, and consequently a trigemino-facialis chamber, are absent.

(ix) In the earliest stage investigated, the basal plate is complete and it is not possible to distinguish histologically or morphologically between basiotic laminae and parachordals.

(x) Both the auditory capsules and the occipital arches take part in the development of the tectum synoticum. The tectum posterius does not develop separately, but as a posterior extension of the tectum synoticum.

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