

# The development of the nasal capsule of the silver carp *Hypophthalmichthys molitrix* (Valenciennes)

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The development of the nasal capsule, including the procartilagenous as well as some mesenchymatous developmental stages, is described in the chinese silver carp, *Hypophthalmichthys molitrix* (Val.). In the nasal capsule a primitive feature, namely the presence of a complete paraphysial bridge was observed. The composition and possible origin of the ethmoidal plate, nasal septum and lamina orbitonasalis in fishes are discussed.

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Die ontwikkeling van die neuskapsel, insluitende die prokraakbenige sowel as sommige mesenkiemateuse ontwikkelingsstadia, word in die chinese silwerkarp *Hypophthalmichthys molitrix* (Val.) beskryf. In die neuskapsel is 'n primitiewe kenmerk, naamlik die aanwesigheid van 'n volledige parafisiale brug, waargeneem. Die samestelling en moontlike oorsprong van die planum ethmoidale, septum nasi en lamina orbitonasalis by visse word kortliks bespreek.

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The classical work of Parker (1873) and the subsequent research done by Gaupp (1906) on the development of the chondrocranium and osteocranium of *Salmo* was followed by several studies on the development of the chondrocranium of various teleosts (Jarvik 1980). The majority of these studies, however, seldom included more than three developmental stages with the result that most of these investigations are, as far as the ontogenesis of the nasal capsule is concerned, rather incomplete. A study such as that carried out by Bertmar (1959) on the characid *Hepsetus* in which the procartilagenous as well as the mesenchymatous developmental stages were included, has not yet been done on a cyprinid.

*Hypophthalmichthys molitrix* was chosen for the present study since, besides the investigations carried out by Hubendick (1942) and Tewari (1971) on the cyprinids *Leuciscus* and *Rasbora*, respectively, very little is still known about the development of the nasal capsule of cyprinid teleosts. Furthermore, because the possible use of the two phytophagous chinese carp species, *Hypophthalmichthys molitrix* and *Ctenopharyngodon idella* in the biological control of excessive growth of algae and submerged macrophytes in impoundments in the Transvaal was being investigated by the Department of Nature Conservation of this province (Schoonbee, Brandt & Bekker 1978) it was possible to obtain a complete series of developmental stages of these two cyprinid species.

According to Berg (1949) the generic name *Hypophthalmichthys* was instituted by Bleeker in 1860 and the species *molitrix* described by Valenciennes in 1844 as *Leuciscus molitrix*. In 1909 Berg placed the species *molitrix* within the genus *Hypophthalmichthys* (Berg 1949).

## Materials and Methods

Material used for this investigation was collected during October–November 1978 at the Provincial Fisheries Research Station at Marble Hall, Transvaal. After spawning had been induced (Schoonbee *et al.* 1978) fertilized eggs were collected at hourly intervals for a period of 22 h when hatching occurred. After hatching, larvae were again collected at hourly intervals for a further 6 h. From 30–120 h after fertilization larvae were collected every 6 h and thereafter daily until 60 days after fertilization. After at least 15 eggs, embryos or larvae were collected at each of the above-mentioned developmental stages, they were divided into groups of four and then fixed in 10% formalin, Bouin's solution, Smith's solution and Bodian's solution (Romeis 1968).

Twenty developmental stages ranging from 54 h to 59 days after fertilization were microtomed transversely and sagittally

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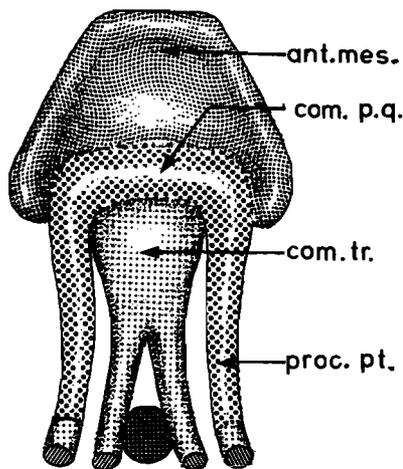
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at 8  $\mu\text{m}$  and 10  $\mu\text{m}$ , depending on the age of the specimens. Azocarmine and aniline blue-orange G were used as stains.

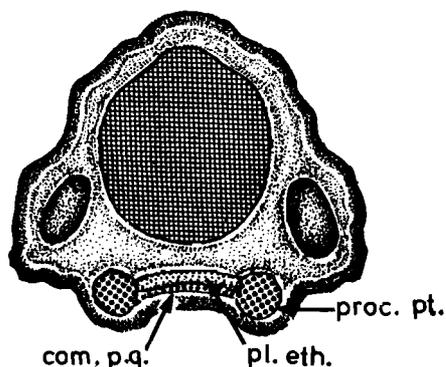
Graphical reconstructions were made from drawings of transverse sections according to the method described by Pusey (1939).

### Description of the development of the nasal capsule

In the 5,5-mm larva (60 h after hatching) the nasal capsule anlage is partly represented by a thin, horizontally orientated sheet of sparsely distributed mesenchyme cells, the anterior mesenchyme, forming a floor for the forebrain (ant. mes., Figure 1). Posterolaterally the anterior mesenchyme is continuous with the blastemal condensations of the pterygoid process (proc. pt.) and posteromedially with the blastemal condensation of the palatoquadrate commissure (com. p.q.). The latter in turn is continuous with the procartilagenous anlage of the trabecular commissure (com. tr.). The trabecular commissure is chondrified in the 5,7-mm larva and is rostrally continuous with the posterior part of the anterior mesenchyme which has now turned into procartilage, forming the caudal part of the ethmoid plate (pl. eth., Figure 2). At this stage the blastemal pterygoid processes are connected to each other and ventrally to the ethmoid plate, by the anlage of the palatoquadrate commissure (com. p.q., Figure 2). In the region where the oblique muscles of the eyes originate from the dorsal face



**Figure 1** *Hypophthalmichthys molitrix*. Dorsal view of anterior part of neurocranium of 5,5-mm larva. (ant. mes. = anterior mesenchyme; com. p.q. = palatoquadrate commissure; com. tr. = trabecular commissure; proc. pt. = pterygoid process).

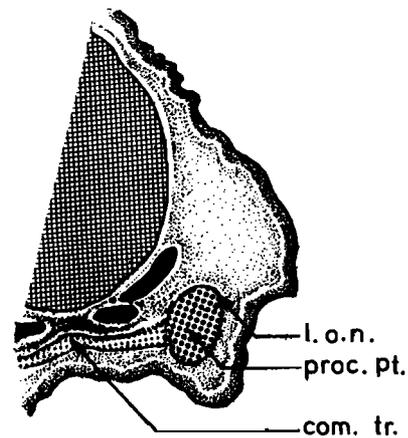


**Figure 2** *H. molitrix*. Drawing of transverse section through the ethmoid region of a 5,7-mm larva. (proc. pt. = pterygoid process; pl. eth. = ethmoid plate; com. p.q. = palatoquadrate commissure).

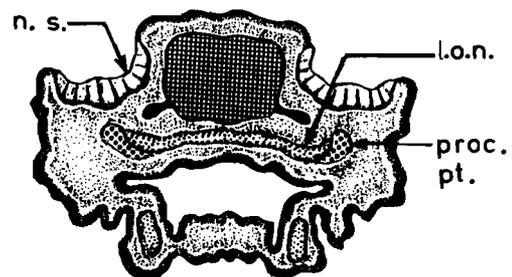
of the trabecular commissure (com. tr.), the anlage of the pterygoid process (proc. pt.) shows a dorsolaterally directed process, the anlage of the orbitonasal lamina (l.o.n., Figure 3).

As a result of chondrification of the anterior mesenchyme in a caudorostral direction the ethmoid plate in the 6,0-mm larva is considerably longer than in the 5,7-mm larva and forms a cartilaginous floor for the forebrain. The anlage of the orbitonasal lamina has now become chondrified but is still connected to the procartilagenous pterygoid process by means of a blastemal condensation (proc. pt., Figure 4). In the 7,0-mm stage the anterior edge of the ethmoid plate (pl. eth., Figure 5) reaches beyond the forebrain and its lateral parts now form a cartilaginous floor for the nasal sacs (n.s., Figure 5). At this stage a mesenchymatous condensation, the anlage of the nasal septum, appears on top of the precerebral part of the ethmoid plate (sep. n., Figure 5). This anlage of the nasal septum is chondrified in the 8,0-mm stage, forming a broad plate separating the nasal sacs (sep. n., Figure 6). The lateral parts of the ethmoid plate form a cartilaginous floor for the ventromedial parts of the nasal sacs only (pl. eth., Figure 6). At this stage a blastemal condensation is present in front of the ethmoid plate. From the medial part of this condensation the rostral cartilage originates, whereas the lateral parts give origin to the supraethmoid and premaxillary bones (ros. c., pmx., Figure 7).

In the 8,0-mm stage a small cartilage, the supraethmoidal cartilage, makes its appearance dorsomedially to the posterior part of the nasal sac (c. sup. ent., Figure 8). The supraethmoidal cartilage is rostrally connected to the nasal septum by a procartilagenous bar, the sphenoseptal commissure



**Figure 3** *H. molitrix*. Drawing of transverse section through the ethmoid region of 5,7-mm larva. (l.o.n. = orbitonasal lamina; proc. pt. = pterygoid process; com. tr. = trabecular commissure).



**Figure 4** *H. molitrix*. Drawing of transverse section through the ethmoid region of 6,0-mm larva. (n.s. = nasal sac; l.o.n. = orbitonasal lamina; proc. pt. = pterygoid process).

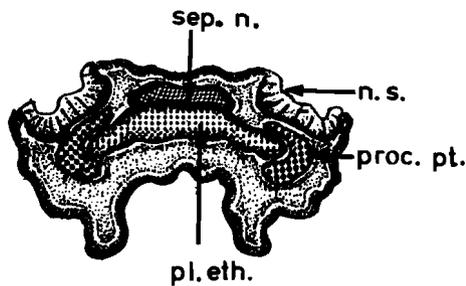


Figure 5 *H. molitrix*. Drawing of transverse section through ethmoid region of 7-mm larva. (sep. n. = nasal septum; n.s. = nasal sac; proc. pt. = pterygoid process; pl. eth. = ethmoid plate).

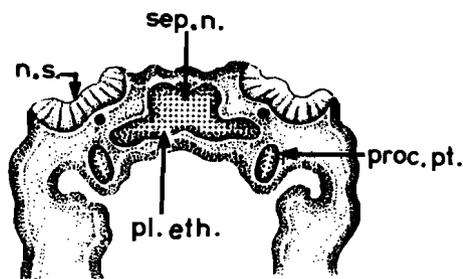


Figure 6 *H. molitrix*. Drawing of transverse section through ethmoid region of 8.0-mm larva. (n.s. = nasal sac; sep. n. = nasal septum; proc. pt. = pterygoid process; pl. eth. = ethmoid plate).

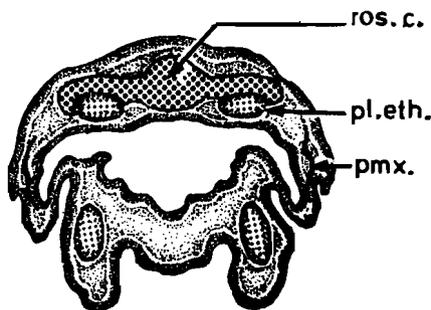


Figure 7 *H. molitrix*. Drawing of transverse section through ethmoid region of 8.0-mm larva. (ros. c. = rostral cartilage; pl. eth. = ethmoid plate; pmx. = premaxillary bone).

(De Beer 1937; taenia marginalis ethmoidalis, Hammarberg 1937) and ventrally to the orbitonasal lamina by a procartilaginous pillar, the entethmoidal process, situated directly behind the olfactory nerve. The two supraentethmoidal cartilages are interconnected above the olfactory lobes by a thin mesenchymatous bridge, the anlage of the paraphysial cartilage (c. par., Figure 8). In the 11.3-mm larva the anlage of the paraphysial cartilage has become chondrified forming a flat cartilaginous plate connecting the supraentethmoidal cartilages and the sphenoseptal commissures dorsally to the olfactory lobes (Figure 9). The entethmoidal process (proc. ent., Figure 9) is also chondrified and synchondrosially fused to the orbitonasal lamina (Figure 9).

### Discussion

During the development of the nasal capsule a gradual anterior shifting of the nasal sacs, relative to the forebrain, takes place. In *Hypophthalmichthys* this shifting is less pronounced than in *Salmo* (De Beer 1937). During the development in *Salmo*

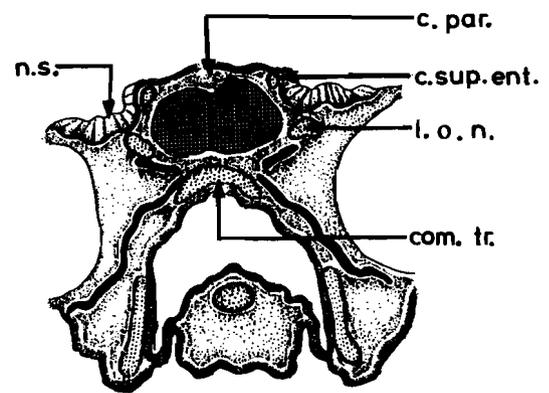


Figure 8 *H. molitrix*. Drawing of transverse section through ethmoid region of 8.0-mm larva. (n.s. = nasal sac; c. par. = paraphysial cartilage; c. sup. ent. = supraentethmoidal cartilage; l.o.n. = orbitonasal lamina; com. tr. = trabecular commissure).

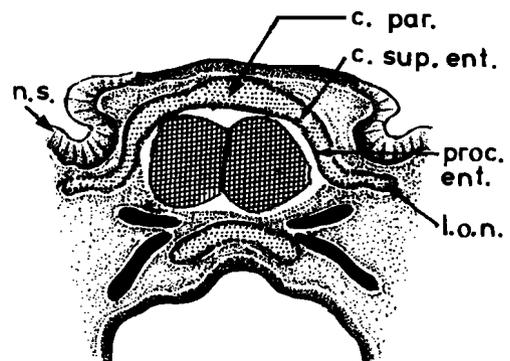


Figure 9 *H. molitrix*. Drawing of transverse section through ethmoid region of 11.3-mm larva. (n.s. = nasal sac; c. par. = paraphysial cartilage; c. sup. ent. = supraentethmoidal cartilage; proc. ent. = entethmoidal process; l.o.n. = orbitonasal lamina).

(De Beer 1927) the forebrain is gradually withdrawn from the ethmoidal region with the result that the olfactory nerve eventually transgresses the cavum orbitonasale before entering the cranial cavity through the foramen olfactorium evehens. In *H. molitrix* the entethmoidal process, which forms the posterior wall of the foramen olfactorium evehens, is fused to the lamina orbitonasalis and is not connected to the trabecula. Since the entethmoidal process and the lamina orbitonasalis lie in the same transverse plane, a cavum orbitonasale is absent in *H. molitrix* and the olfactory nerve runs directly from the nasal sacs, through the foramen olfactorium evehens to the forebrain.

As far as the morphology of the nasal capsule of recent actinopterygians is concerned, De Beer (1937 p.396) mentions that in the Holostei and Teleostei '... the nasal capsule has neither roof nor side wall, and is nothing more than a fossa with a hind wall (lamina orbitonasalis), medial wall (nasal septum), and floor (trabecular or ethmoidal plate)'. Jarvik (1980) agrees with De Beer (1937). Hammarberg (1937) on the other hand, who made a thorough investigation of the development of the nasal capsule of *Lepisosteus*, found that apart from the ethmoid plate, the nasal septum and the lamina orbitonasalis, several other cartilaginous elements contribute to the morphology of the nasal capsule of the Holostei.

Concerning the development of the ethmoid plate, Norman (1926) found that in teleosts it arises from a direct fusion of the anterior parts of the trabeculae. In the holosts *Amia*

(Pehrson 1922) and *Lepisosteus* (Hammarberg 1937) the trabeculae are first joined anteriorly by a narrow transverse rod, the commissura trabecularis. This rod later expands to form the ethmoid plate. Hammarberg (1937) also mentions that the caudal lengthening of the ethmoid plate is brought about by a further rostrocaudal joining of the trabeculae to form a trabecula communis. In *Salmo* the anterior parts of the trabeculae fuse to form an extensive trabecula communis which expands in front into the ethmoid plate (De Beer 1937). Holmgren (1943), on the other hand, showed that during the mesenchymatous stage the trabeculae in *Salmo* are widely separated and their anterior ends are continuous with a broad sheet of mesenchyme which he called the frontal mesenchyme. As chondrification sets in, a commissura trabecularis develops between the anterior parts of the two trabeculae. Holmgren (1943) further mentions that a trabecula communis and an ethmoid plate are then formed but he does not elaborate. Bertmar (1959), in his study of the ontogenesis of the chondrocranium of *Hepsetus* also found a mesenchyme plate in front of the trabeculae which he called the anterior mesenchyme. The frontal parts of the trabeculae, after chondrification, fuse to form a trabecula communis. Rostrally to the trabecula communis, the posterior part of the mesenchyme chondrifies as the commissura trabecularis. Further chondrification of the caudal part of the anterior mesenchyme gives rise to the ethmoid plate. In his study of the ethmoidal region in *Amia* Bjerring (1972) refers to protochondral ethmobasals which are continuations of the cartilaginous trabeculae. The two ethmobasals are connected throughout their entire lengths by the ethmobasal commissura. With development the ethmobasal commissura chondrifies, forming, together with the ethmobasals, a flat structure, the ethmoid plate (Bjerring 1972).

In *H. molitrix* the development of the trabecula communis, the commissura trabecularis and the ethmoid plate agrees with that described for *Salmo* and *Hepsetus* by Holmgren (1943) and Bertmar (1959) respectively. Consequently in *Salmo*, *Hepsetus* and *Hypophthalmichthys* the anterior part of the trabeculae does not give rise to the ethmoid plate; the latter is derived from the anterior mesenchyme.

Because it was not possible to distinguish between ecto- and endomesenchyme in *H. molitrix*, the origin of the anterior mesenchyme could not be determined. According to Bertmar (1959) the endomesenchyme cells of teleosts do not contain yolk granules that become reabsorbed during chondrification, as is the case in the Selachii and Dipnoi. As a result of this and also because the prootic mesoderm in the Teleostei is not clearly segmented (Bertmar 1959) it is very difficult to determine the origin of the anterior mesenchyme in this group. Recently Bjerring (1972, 1977), using the relationship between the horizontal and ascending dental plates and the infra- and suprapharyngeal elements of the visceral arches, suggested that the ethmoid plate represents the fused infrapharyngeals of the premandibular and terminal visceral arches.

Concerning the development of the nasal septum Norman (1926) found in *Siphonostoma* that it chondrifies at a relatively late stage of development and that it originates separately from the ethmoid plate. Although the septum comes into contact with the ethmoid plate at a later stage during development it does not fuse with it. In *Lepisosteus* Hammarberg (1937) describes a dorsal projection of the ethmoid plate, situated behind the olfactory nerve and lateral to the forebrain, as the processus entethmoideus. The base of each of the two processus entethmoidei forms a cartilaginous rod, the taenia marginalis ethmoidalis (commissura sphenoseptalis, De Beer

1937) that runs caudorostrally and these two rods fuse with one another anteriorly to form the nasal septum. In the 7,0-mm stage of *H. molitrix*, a mesenchymal plate forms on top of the already chondrified precerebral part of the ethmoid plate. In the 8,0-mm stage this mesenchymal plate is chondrified forming a synchondrosis between the nasal septum and the ethmoid plate. Bjerring (1977) homologizes the nasal septum with fused suprapharyngoterminals.

The hind wall of the nasal capsule in fishes is formed by the lamina orbitonasalis (De Beer 1937; Jarvik 1980). Concerning the origin of the lamina orbitonasalis Holmgren (1943) established that this structure in selachians, like the visceral skeleton, originates from ectomesenchyme. Jarvik (1954) in his study of the endoskeleton of *Eusthenopteron* homologizes the lamina orbitonasalis with a suprapharyngopremandibular. Since the lamina orbitonasalis and part of the pterygoid process in *H. molitrix* develop from a common blastema it is possible that the lamina orbitonasalis in *H. molitrix* represents part of the visceral skeleton that has become incorporated into the neurocranium.

The two cartilagine supraentethmoidales in *H. molitrix* are connected dorsally to the brain by a well-developed transverse commissure, the paraphysial bridge. Although well developed in the Holostei (Hammarberg 1939), a paraphysial bridge is absent in all other teleosts hitherto investigated. The paraphysial bridge forms part of the cranial tectum probably derived from the sclerotomes of the terminal metameres.

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