SENSORY CANALS OF THE SNOUT OF ACTINOPTERYGIAN FISHES

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ABSTRACT. — The snout of the earliest palaeoniscoids is more modified in terms of developmental facts than is that of later actinopterygian fishes. This specialization demands that later fishes, presumably derived from the palaeoniscoids, arrived at their condition by neoteny and functional reorganization of snout elements. Inaccuracies in accounts of snout structures are also reported.

Recently Gardiner (1963) reconsidered some ideas concerning the structure of the actinopterygian snout. In his opinion the primitive condition was one of extreme shortness associated with a relatively large eye (Fig. 1A). He stated that the primitive paleoniscoid fish had two nasal openings and that these were widely separated: the anterior opening lying between the "postrostral" and the nasal bone, and the posterior opening behind the nasal bone at the anterior margin of the eye. The supraorbital canal connected with the infraorbital canal by way of a short branch of the latter and this connection passed between the nasal openings. He proposed (p. 315) that "In order to arrive at the condition seen in both holosteans and teleosts, with regard to the nostrils, it is necessary to get both of the nostrils to the lateral side of the supraorbital sensory canal." And (p. 317), ". . . in *Polypterus senegalus* we have the answer to the problem, that is that the anterior nostril migrated round the anterior edge of the nasal (bone), passing round the contained supraorbital sensory canal to end up on the posterior side of the nasal." (Fig. 2).

It is not my purpose to take issue with what Gardiner has said but rather to discuss the canal pattern as seen in several of the living "primitive" actinopterygians and teleosts and suggest that what has occurred is not well described by the term "migration"; it is more like reorganization. And, if reorganization has occurred, there might be some question as to the original state. As background for an approach to these questions, I want first to consider (briefly) the ontogeny of the nasal capsule and the lateral-line system and then the adult canal-nostril conditions.

The development of the nasal organ is generally agreed to involve an epidermal placode which invaginates. The external opening of the vesicle, at a relatively early stage, subdivides into anterior and posterior openings which quickly assume the position of the adult apertures. This

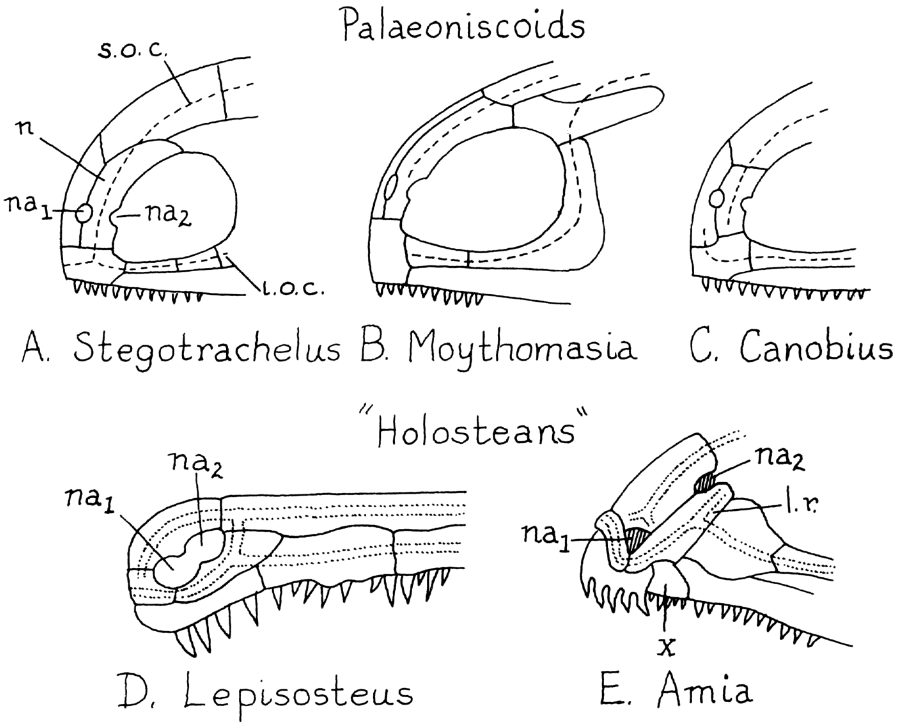

FIGURE 1. — Semidiagrammatic lateral views of the snouts of early palaeoniscoids (A, B, C) and holosteans (D, E). *n*, nasal bone; na_1, anterior nasal opening; na_2, posterior nasal opening; *m.r.*, medial rostral; *l.r.*, lateral rostral; *i.o.c.*, infraorbital canal; *s.o.c.*, supraorbital canal; *x*, unnamed bone. A, D, E. after Gardiner, 1963; B. after Jessen; C. after Moy-Thomas and Dyne, 1938.

view of the origin of the two nasal openings in fishes is uncontested. The relationship between the nasal vesicle and the mouth cavity (and Rathke's pouch) is not a part of this discussion.

Development of the lateral-line system is a more complex subject. Pehrson (1958, 1940) has considered this system in *Polypterus* and *Amia*, as has Hammarberg (1937) for *Lepisosteus* and Lekander (1949) for a number of teleosts. Several basic works on the comparative anatomy of the lateral-line system have appeared (Stensiö, 1947; Holmgren and Pehrson, 1949).

The lateral-line system appears first as a series of epidermal placodes in the postorbital and temporal region. The supraorbital and infraorbital placodes grow forward above and below the eye and subdivide into a variable number of maculae. The number of maculae is high in *Lepisosteus* (20-24 in the supraorbital line and anterior pit-line, 20-25 in the infraorbital), lower in *Amia* (6 or 7 in the supraorbital plus 2 in the anterior pit-line and 14 in the infraorbital), *Polypterus* (6 in the supraorbital, 8 in the infraorbital), and salmon (*Oncorhynchus nerka* — 8 or more in the supraorbital, 12 more-or-

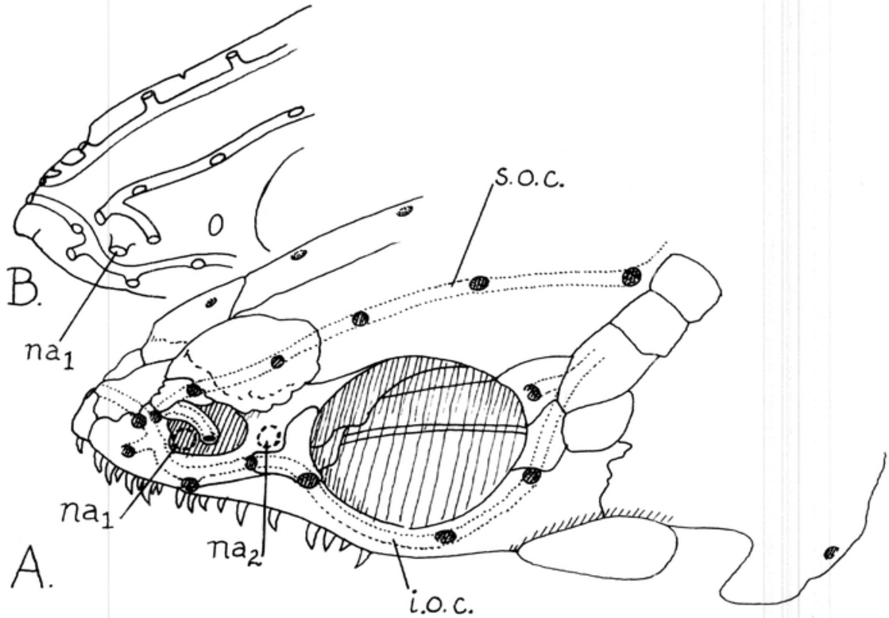

FIGURE 2. — Dorsolateral views of snout of *Polypterus* (*weeksi*?). A. Bones, canals and pores; B. details of bones removed. Abbreviations as in Fig. 1.

less in the infraorbital, and 2-3 which subdivide in the snout pit-line).

In development the maculae, as small epidermal placodes, sink down into the underlying tissues, first forming a pit, then a groove (along the course of the original sensory line placode), and then a looping canal with ends opening at the surface. The macula lies at the deepest point of the U-shaped canal thus formed. These canal units (each with its separate organ) then join one with another to form a continuous canal but retain a surface pore where adjacent ends have joined. The surface pores may later divided to form complex dendritic systems.

Some sensory organs may remain at the surface in grooves, or in pits, to form the pit-lines and these may be continuous with, or separate from, the canals. Part of this system, normally forming canals, may develop only to the pit-line stage. As a generality one can say that any connections achieved anteriorly between the supraorbital and infraorbital canals are secondary ones, as are connections across the midline between any of the canals.

Comparative study of sharks, dipnoans, crossopterygians and actinopterygians shows that the relationship between the supraorbital canal and the infraorbital canal varies as does the relationships between these lines and the nasal openings (Fig. 3). Only in the crossopterygians does the supraorbital canal connect with the infraorbital canal medial to the anterior nasal opening, while in actinopterygians, as suggested by Gardiner, the connection may have been between the two openings. In sharks the connection is behind the nasal capsule. The dipnoans are unique in several ways (Panchen, 1967): the two canals in question do not appear to join; the supraorbitals connect across the snout (as in holocephalans); and both canals pass above and lateral to the olfactory openings (as in holocephalans, but the infraorbital canals do not meet at the midline as in that group).

Because of the known variation in relationships in the actinopterygians, the snout in this group should be rechecked. In order to do this the adult condition and some of the developmental stages of *Polypterus, Acipenser, Polyodon, Lepisosteus,* and *Oncorhynchus* (*O. nerka, O. kisutch* also *Salmo gairdneri, Salmo trutta, Salvelinus frontinalis, Salvelinus namaycush*) are redescribed. Of the above, only *Amia* is represented by a more-or-less full set of stages, *Lepisosteus* and *Oncorhynchus* by a sample of stages, and the others are known only as adults or from accounts in the literature. *Polypterus* is considered first since Gardiner

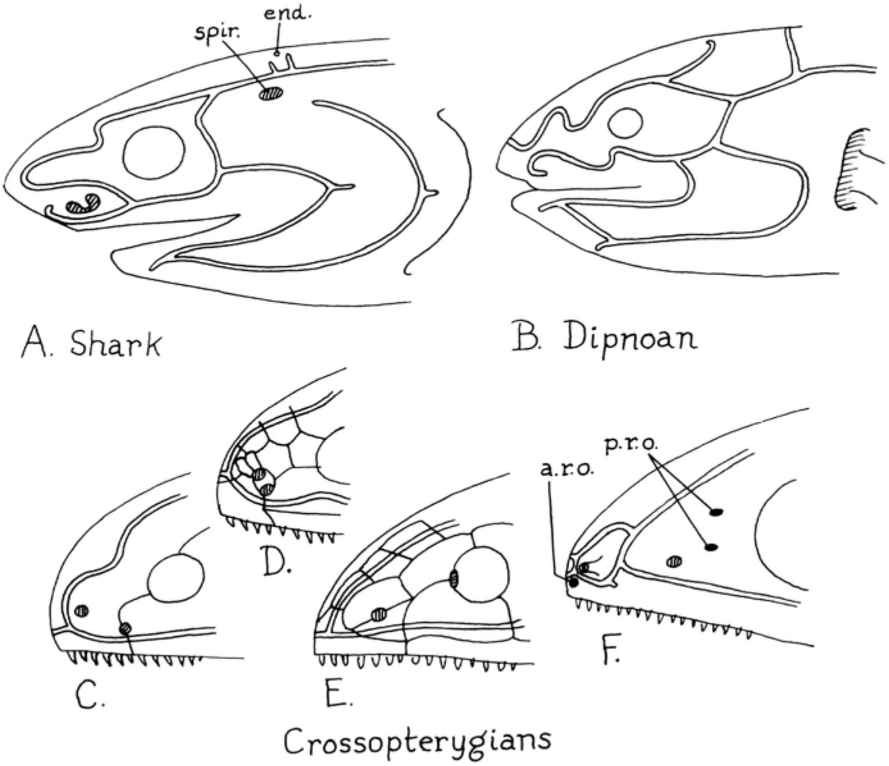

FIGURE 3. — Lateral views of heads and snouts of A. *Chlamydoselachus*; B. *Protopterus*; C. *Porolepis*; D. *Holoptychius*; E. *Eusthenopteron*; F. *Latimeria*. *end.*, endolymphatic duct pore; *spir.*, spiracle; *a.r.o.*, anterior rostral organ opening; *p.r.o.*, posterior rostral organ opening; others as in Fig. 1. A. modified from Allis, 1923; C, D, E. after Jarvik, 1966; F. after Millot and Anthony, 1958.

viewed this as a transitional stage in the shifting of the nostril relationship.

In my three specimens of *Polypterus* (*weeksi*?) (Fig. 2) the penultimate pore of the supraorbital canal surfaces in the bone next to a pore of the infraorbital canal. These two tubes join to form a single opening through the overlying skin. As suggested by Gardiner, this is a secondary condition. However, from here the supraorbital canal is reflexed posterolaterally (as remarked by Jarvik, 1942, and Pehrson, 1958) to end at a surface pore behind the base of the tube of the anterior nasal opening. I question that there has been migration of the anterior nasal opening; rather there has been a looping of the supraorbital canal to achieve a new connection medial to the anterior opening.

In *Lepisosteus*, contrary to Gardiner's account, the supraorbital canal (Fig. 4A) connects with the infraorbital between the narial openings as well as behind them. These connections are by well-defined canals in the soft tissue, canals which open to the surface by many small pores (achieved by subdivision of the original single opening).

The canal connection between the nasal openings can be compared with the one seen in palaeoniscoids, while the posterior one is probably a special feature associated with the long snout. Both connections involve the lateral rostral element. The reflexed anterior end of the supraorbital canal compares with that seen in *Polypterus* but differs in that a connection medial to the anterior nasal opening is not developed (even by way of pores to the surface).

In *Amia* (Fig. 4B) a connection between the supraorbital and infraorbital canals is developed relatively late in ontogeny (200 mm specimen). This connection passes between the nasal openings but is not comparable to that of the palaeoniscoid as the greater part of the canal is an upward extension of the infraorbital canal on the lateral rostral bone. As in the preceding genera, the anterior end of the supraorbital canal is turned lateroposteriorly and as in *Polypterus* ends at a pore above the base of the anterior nasal tube. Again no con-

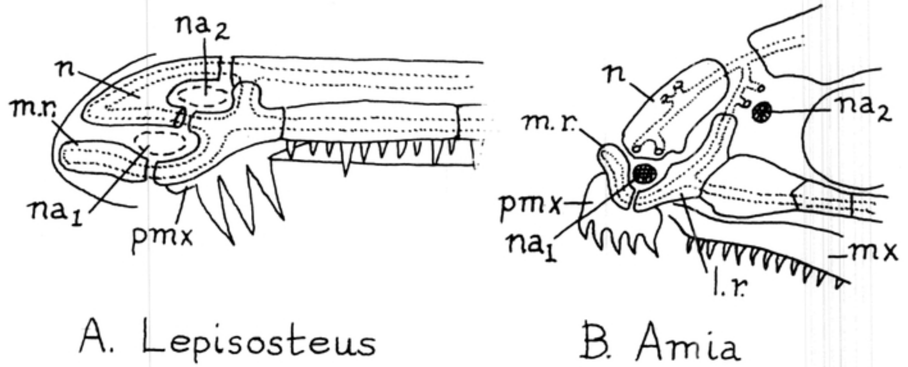

FIGURE 4. — Semidiagrammatic views of snouts of *Lepisosteus* (A) and *Amia* (B). Note differences when compared with Fig. 1, D and E.

nection exists medial to the anterior nasal opening although there is a relatively long tube to the surface here.

Thus in these genera, the anterior end of the supraorbital canal is turned laterally or posterolaterally; however, a sutural connection between the nasal and rostral bones is lacking (although Gardiner, footnote p. 317, described a bridge as "occasional" in *Lepisosteus*). In both *Amia* and *Lepisosteus* a lateral rostral bone, with an upward extending canal, is distinctive. Another important point here is that the commonly used illustrations in the literature (as in Gardiner, *see* Fig. 1 D, E) contain inaccuracies relative to the interrelationships of these canals or the bony cover of the snout. In *Amia* the bones are not sutured but separated by connective tissue. Further such figures conceal other facts such as that the "premaxillae" of these fishes are distinctly different. This difference runs much deeper than whether or not canal bones are fused to the premaxilla.

The canal situation seen in these fishes is in part shared with other living kinds. In *Acipenser* (or *Scaphirynchus* — Grassé 1958, fig. 696; Norris, 1924, 1925) a bony tube lies in the tissue between the anterior and posterior nasal openings. This tube can be compared with that seen in *Polypterus*; its canal does not connect with the intraorbital, nor does the canal continue much beyond this bone (as shown in Goodrich, 1930, fig. 298; Gardiner, 1963, fig. 20A; or in *Polyodon* as shown by Collinge, 1894, pl. 39, fig. 3). The course of the supraorbital canal in the chondrosteans is that of a palaeoniscoid, however, the lateral rostral bone, where connection between the supraorbital line and the infraorbital line might occur, is near the tip of the elongated snout (Pehrson, 1944, and personal observation). The snout with its transverse connection of the infraorbital canals develops early in the sturgeons, before the extension of the supraorbital canal between the nasal openings.

In *Oncorhynchus* (*Salmo* or *Salvelinus*) the supraorbital canal ends above the nasal sac and the infraorbital below that sac. There is a surface pit-line continuation of the infraorbital canal upward in front of the anterior nasal opening and across the snout. The pit-lines of either side appear to join at the midline. The supraorbital canal does not have any definite relation to this pit-line (it may open into the groove of the pit-line). In the teleost *Elops* (Nybelin, 1956) the infraorbital canals connect across the snout but the supraorbital canal, lying above or medial to the nasal sac, does not connect with the infraorbital. There is no clear evidence in these teleosts of the supraorbital canal bending laterally or posterolaterally to pass between the nasal openings, although in early stages of the salmon there is a suggestion of such a bend. An infraorbital branch extends upward on the lateral rostral (antorbital) bone in *Elops* but not in the salmon where only a groove is sometimes observed.

It is evident that some of the teleosts (it is difficult to talk about such a group since it is as yet only poorly understood and extremely heterogeneous anatomically) differ from the more primitive genera in that the sensory canals open to the surface by large pores, and in that the development of the nasal capsule proceeds only to a slight separation of the anterior and posterior nasal openings. From the ontogeny of *Amia* (Allis, 1889; Pehrson, 1922, 1940) it can be said that the lack of separation of nasal openings and lack of subdivision of the surface pores are neotenic trends or secondary simplifications. Reduction of canal development is carried to the extreme in *Cobitis taenia* in which the sensory organs remain on the surface (Lekander, 1949). The forward growth of the supraorbital canal medial to the nasal openings, without forming a loop, suggests a secondary condition also. Failure to connect with the infraorbital canal cannot be viewed as exceptional.

In Gardiner's presumed primitive palaeoniscoid the supraorbital canal traversed the nasal bone and joined, or nearly joined, the infraorbital canal (Fig. 1A-C). He suggested that primitively these canals joined, but that this connection was later lost and the ends of the canals shifted apart. The area of connection of these canals should be that of the lateral rostral bone although such an element is evident only in a few palaeoniscoids.

If the sequence suggested by Gardiner is correct, we must assume that the nasal capsule and lateral-line system were well established and highly evolved structures when first encountered in the fossil record, not in the process of being developed, as one might suppose. These advanced features are associated with a well-defined cranial pattern of bones — again the argument that in these fishes the pattern of bones was in the course of development from a mosaic seems improbable. The modified conditions seen in other osteichthyan fishes and sharks (Fig. 3) suggest that they too are not primitive. The several patterns observed in the osteichthys imply an early radiation involving snout design. Romer (1958) made the comment that actinopterygian fishes were eye feeders and crossopterygians nose feeders. From these observations, there is the possibility that internal nares were common to all osteichthys at the beginning. Modification of the primitive nasal set-up was thus greatest in the dipnoans and most conservative in the rhipidistian crossopterygians. Presumably the gap between the premaxillary and maxillary teeth (and bones) marks the pathway of the primitive internal nasal opening.

Gardiner has supposed that primitively there was a large number of sensory organs, as in sharks (supraorbital canal in *Squalus*, 68; *Laemargus*, 80+; *Heptanchus* and *Chlamydoselachus*, 46-48 according to Ewart, 1895; Ewart and Mitchell, 1895; Norris and Hughes, 1920; Daniel, 1934; Allis, 1923) or acanthodians. Thus strong reduction in the number of organs was assumed to have marked the common ancestor of the teleostomes, or occurred in parallel fashion in each of the teleostome groups. It is probable that the primitive condition, before the origin of the osteichthys, was characterized by a large number of organs, some of which were involved in the canal system and condensed to form the larger sensory organs of the ancestral palaeoniscoid. The large number of organs in sharks may be a part of their evident regression related to the loss of bony armor and its replacement by the fine placoid shagreen.

What we see in the later evolution of the actinopterygians is in each case a different set of features; some of the components can be viewed as neotenic while others appear to be reorganizational or functional refinements. The snout appears to lengthen in some groups while the relative size of the eye is decreased. These structural changes can be related to changes in the feeding mechanism and some parallelisms are evident.

In summary there is no evidence to support the use of "migration" in reference to either or both nostrils, and certainly there is no evidence of movement of a nostril around the end of the supraorbital canal or "nasal" bone. What is involved is best described as ontogenetic reorganization. The relationship of the supraorbital canal to the nostrils in chondrosteans, *Amia*, *Lepisosteus*, and *Polypterus* supports Gardiner's view that originally this canal passed between them, whether or not it connected with the infraorbital canal. Any connection between the supraorbital and infraorbital canals would necessarily be formed in ontogeny after the separation of the original nasal opening into anterior and posterior nares. If this was the condition in the ancestral actinopterygian, it was not a primitive one but rather an evolved state which later regressed in the evolution of the group. All trace of the route of the supraorbital canal between the nasal opening has been lost in some of the living fishes and in others new secondary connections between the canals may be formed medial to the anterior naris, or elsewhere. These changes probably can be tied in with lengthening of the snout, increased kinetism in the snout, reduction in relative size of the eye, and the developmental dynamics of the canal system.

In terms of the snout the earliest palaeoniscoid appears to have been an armored group already specialized in terms of its nasal apparatus and lateral-line system. Some of the later palaeoniscoids and living fishes must have been derived either from a prepalaeoniscoid ancestor in which these features had not yet developed or, more probably, from the palaeoniscoids by reduction in armor and remodeling of the various snout components and features.

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Manuscript received May 31, 1968.