

THE DEVELOPMENT OF THE LATERAL-LINE SYSTEM
OF DOROSOMA PETENENSE (GÜNTHER)

By

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PREFACE

The neuromasts of the lateral-line system of Dorosoma petenense (Günther) originate from cells of the sensory layer of the epidermis and are not preceded by sensory lines, grooves, ridges or placodes. The most important discovery of this study is that some neuromasts form a trunk lateral-line which begins to appear at 40 hours of development (68 F) and disappears before the juvenile is 17 mm. The permanent neuromasts do not evoke lateral-line bones but may regulate the time or origin of the laterosensory components of the bones.

The five cephalic canals begin as grooves and coincide in development with the enclosing laterosensory components.

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CHAPTER I

INTRODUCTION

The purpose of this investigation was to study the development of the neuromasts (and the innervation of each), cephalic canals and bones of the lateral-line system in the clupeid, Dorosoma petenense. Special emphasis was placed on the relationship between developing neuromasts and bones.

Various aspects of adult clupeid lateral-line systems have been described. Bamford (1941), Wohlfahrt (1937) and Tretyakov (1950) described the histology of pit (surface) and canal neuromasts. Wohlfahrt (1937) reported which cranial nerves supply the neuromasts, but gave no description of the association of the nerve endings with the neuromasts. Verheijen (1959), Stephens (1962), Wohlfahrt (1937), Bamford (1941), described the location of the neuromasts on the surface or in the canals. Gunter and Demoran (1961), Wohlfahrt (1937), Bamford (1941), Stephens (1962) and Tretyakov (1938) described the topography of the canals. The bones were described by Ridewood (1904), Phillips (1942), Chapman (1944 and 1948), Bamford (1941), Wohlfahrt (1937) and Stephens (1962).

Bamford's (1941) report on the lateral-line system of Clupea harengus L. described the time of appearance of the neuromasts, late development of lateral-line bones and development of the cephalic canals. However, he did not describe the origin of neuromasts (and their nerve

supply), lateral-line bones, cephalic canals or the relationship between developing neuromasts and lateral-line bones.

In cold-blooded vertebrates, other than clupeids, the lateral-line system was observed to develop from the placode of the ear (acoustico-lateralis placode) in a salmon (Beard, 1884; Wilson and Mattocks, 1897); in amphibians (Stone, 1931), in Serranus atrarius (= Centropristis striatus L.) (Wilson, 1891) and in cyclostomes and amphibians by Mitrophanow (1893, fide Wilson and Mattocks, 1897). However, Beckwith (1902), Clapp (1898), Landacre and Conger (1913) and Lekander (1949) observed the lateral-line system originating from placodes not connected with the auditory placode in Amia calva L., Batrachus (= Opsanus) tau L., Lepidosteus (= Lepisosteus) osseus (L.), and selected minnows, respectively.

Some workers (Landacre and Conger, 1913; Lekander, 1949; Neave, 1946; and Wilson and Mattocks, 1897) maintained that the placodes give rise to migrating sensory lines. Allis (1899), Holmgren and Pehrson (1949), Omarkhan (1949) and Stone (1928 and 1933) observed migrating sensory ridges originating from the placodes. Other workers (Clapp, 1899; Johnson, 1917; Lekander, 1949; and Wilson, 1891) have shown that the placodes give rise to migrating sensory furrows. However, some of the placodes develop directly into a single surface neuromast (Lekander, 1949).

Those surface neuromasts forming from the sensory lines, ridges or furrows are linked in chain-like sequence to one another by sensory cords. The sensory cords persist (Platt, 1896; Johnson, 1917; Beard, 1884; Neave, 1946; and Allis, 1899) or disappear (Stone, 1933). The

subsurface neuromasts, which form from the sensory ridges, are linked by persisting sensory cords (Omarkhan, 1949).

Neuromasts are formed by two types of sensory cells bearing kinocilia or stereocilia (Dijkgraaf, 1962); or one type bearing both kinds of cilia (Flock and Wersäll, 1962); sustentative epithelial cells; and cupulae. The cupulae have been reported by Görner (1961) to arise from the sustentative epithelial cells in amphibians. Cahn and Shaw (1962), Dijkgraaf (1962), Iwai (1963 a and b, 1964 and 1965), and Thomopoulos (1957) have traced development of cupulae to early larval and late embryonic stages but have not been able to report the origin of cupulae in fishes.

The lateral-line bones are grouped as one-component (laterosensory) and two-component (laterosensory and anasmestic) bones (Allis, 1899; Devillers, 1944; and Stensio, 1947). The laterosensory elements (Branson and Moore, 1962) originate in the dermis from one or more blastemas (Pehrson, 1940 and 1944), which may or may not fuse, forming one-component bones. Anasmestic elements (Branson and Moore, 1962) originate in the dermis and fuse with laterosensory elements to form two-component bones. The bones originate adotically and develop abotically.

Opinions vary regarding the evocative powers of neuromasts over adjacent lateral-line bones, even though Pehrson (1940) has reported that the osteoblasts which form the laterosensory elements, migrate from neuromasts. Allis (1899 and 1936), Westoll (1937), Pehrson (1940 and 1944), Lekander (1949), Mori (1931), Branson and Moore (1962) and Takebe (1934) stated that the neuromasts initiate and influence complete development of lateral-line bones. Kapoor (1962) reported that

neuromasts induce the development of laterosensory elements. Reno (1966) and Stensio (1947) agreed that the neuromasts influence development of lateral-line bones but suggested that other factors are involved. deBeer (1937), Moy-Thomas (1941), Parrington (1948) and Moodie (1922) doubt the possibility of neuromasts influencing the origin or development of lateral-line bones.

Cranial nerves VII, IX and X innervate the neuromasts (Herrick, 1899; Allis, 1899; Cole, 1898; Goodrich, 1930; Landacre, 1912; Platt, 1896; and others). Both nerves and neuromasts originate from the same layer of cells (Landacre, 1912). In amphibians Speidel (1947) showed that the neuromasts and their innervation interact with one another to promote the development and longevity of each. Neuromasts do not influence their nerve supply in Ameiurus (= Ictalurus) nebulosus (Le Sueur) (Mori, 1931) or goldfish (Brocklebank, 1925).

Only the nucleus of a sensory cell is surrounded by a basket of nonmyelinated fibers in Necturus maculosus (Rafinesque) (Charipper, 1928) but in amphibians (Larsell, 1929) and Mustela canis Mitchill and Squalus acanthias L. (Johnson, 1917) the entire sensory cell is in the basket. Synaptic connections occur between the sensory cell and its nonmyelinated nerve in Lota vulgaris (= Lota lota L.) (Flock and Wersäll, 1962) and a Japanese sea eel (Hama, 1962). Reno (1966) observed unidentified swellings (possibly ganglia) beneath some neuromasts.

In the present work, the nomenclature for the lateral-line canals is based on the works of Branson and Moore (1962), Greenwood, et al. (1966), Wohlfahrt (1937), and Bamford (1941), while the nomenclature

for the ossicles agrees with that of Chabanaud (1945), Harrington (1955), Lekander (1949), Devillers (1947) and Branson and Moore (1962).

CHAPTER II

MATERIALS AND METHODS

Adults were collected by shocking on 7, 8, and 14 May 1965 in 2 to 4 feet of water (68 F) in Buncombe Creek arm of Lake Texoma. Eggs were stripped into containers 75 and 90 per cent full of lake water (68 F) and fertilized by spermatozoa stripped from males. Fifteen minutes later the water in the containers was replaced with new lake water (68 F).

Light was disregarded as a factor in incubation.

Embryos were collected from the containers at 2-hour intervals of development from the 12-hour stage to hatching (about 72 hours). Pro-larvae and small postlarvae were collected from the containers at 1-day intervals after hatching (about 3 mm) until specimens 4 1/2 to 5 mm long were obtained. Larger postlarvae were collected on 28 and 29 May 1965 by a millimeter trawl and juveniles and adults on 7, 8 and 9 June 1965 with a small-mesh seine or a 3/4-inch gill net.

All specimens were killed and fixed at the time of collection. The embryos and prolarvae were killed and fixed in Smith's fluid for 24 hours and stored in 5 per cent formalin. Postlarvae, juveniles and adults were killed and fixed in 10 per cent formalin, washed and stored in 80 per cent ethanol. Measurements were made after fixation using total length or, if a hypural plate had developed, standard length.

Eight hundred sixty-two specimens were studied at various stages of development. The stages ranged from 1 to 210 mm. The number of specimens studied at each stage before the embryonic lateral-line system was evident was two to four. When the lateral-line system first appeared the number of specimens studied at each stage was increased to eight and where variations and rapid development were occurring the number of specimens studied at each stage was increased to 20.

To study development of neuromasts, canals and bones, 422 specimens from the 12-hour stage of development to those 20 mm long were prepared by the paraffin method and sectioned at 5, 6, 8, 10, 12, 15, and 20 μ , stained in Harris', Heidenhain's or Delafield's hematoxylin and counterstained in eosin. These same methods were used to study the histology of neuromasts, canals and bones of 40 adult specimens (108-210 mm).

One hundred twenty juveniles and adults (18 to 210 mm) were stained in thionin and erythrosin B to supplement developmental studies of the neuromasts and canals. Two hundred eighty postlarvae, juveniles and adults (10 to 210 mm) were macerated in 2 to 10 percent KOH, stained in alizarin red S and cleared in glycerin to supplement study of bone development.

Prolarvae were cooled by refrigeration to retard movement and aid in a search for cupulae.

The following methods for staining nerves were used several times without success in an attempt to trace the development of cranial nerves VII, IX and X: Golgi's Rapid, Cajal's Pyridine-Silver, the Bielschowsky and the Bodian (Humason, 1962) and Charles Sihler's hematoxylin stain with potash (Guyer, 1953). Illustrations were made with the aid of

photographs, camera lucida and binocular microscope. The nomenclature of Hubbs (1943) was used for early stages in life history.

CHAPTER III

THE ADULT LATERAL-LINE SYSTEM

The adult lateral-line system (Figures 1 and 2) is composed of various numbers of pit neuromasts (the two on each side of the rostrum are always present) scattered over the cephalic area and a distinct pattern of five cephalic canals enclosing 36 neuromasts located on their floors, roofs, and/or walls. The cephalic canals are, in turn, enclosed by 17 paired lateral-line (laterosensory or laterosensory and anasmestic) bones and partly enclosed by two paired lateral-line scales (laterosensory bones).

The five cephalic canals are as follows: (1) supraorbital, containing four neuromasts and enclosed by the frontal and nasal bones; (2) infraorbital, containing 10 neuromasts and enclosed by the six sub-orbitals (SO-1 to 6); (3) the preoperculo-mandibular, containing 12 neuromasts and enclosed by the preopercle, angular and dentary; (4) the cephalic lateralis, containing eight neuromasts and enclosed by the horizontal portion of the supratemporal-intertemporal, posttemporal, supracleithrum and the first two trunk scales; and, (5) the supra-temporal, containing two neuromasts and enclosed by the dorsal portion the supratemporal-intertemporal and parietal.

The extensive adorbital branches of the canals pass through openings of the bony canals, cross over one another, cross the cephalic canals from which they branch, extend onto the opercle and trunk and

Figures

1. Lateral view of the topography of the lateral-line canals and location of the neuromasts of a 32-mm specimen.
2. Lateral view of disarticulated lateral-line bones of a 120-mm specimen.

Abbreviations

A, angular; CLC, cephalic lateralis canal; D, dentary; DP, dermopterotic; F, frontal; IOC, infraorbital canal; N, nasal, P, preopercle; PA, parietal; PMC, preoperculo-mandibular canal; PT, posttemporal; R, rostral neuromasts; RL, recessus lateralis; S, sphenotic; SC, supracleithrum; SC 1, 2, scales 1, 2; S-I, supratemporal-intertemporal; SO-1 to 6, suborbitals 1 through 6; SOC supraorbital canal; STC, supratemporal canal.

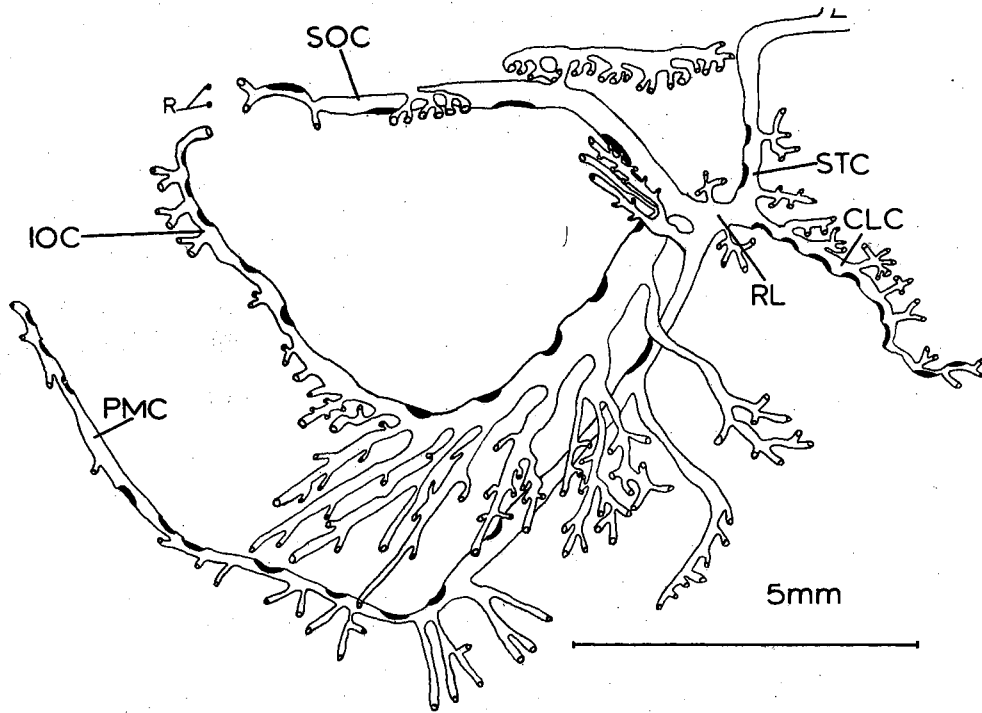


FIG.1

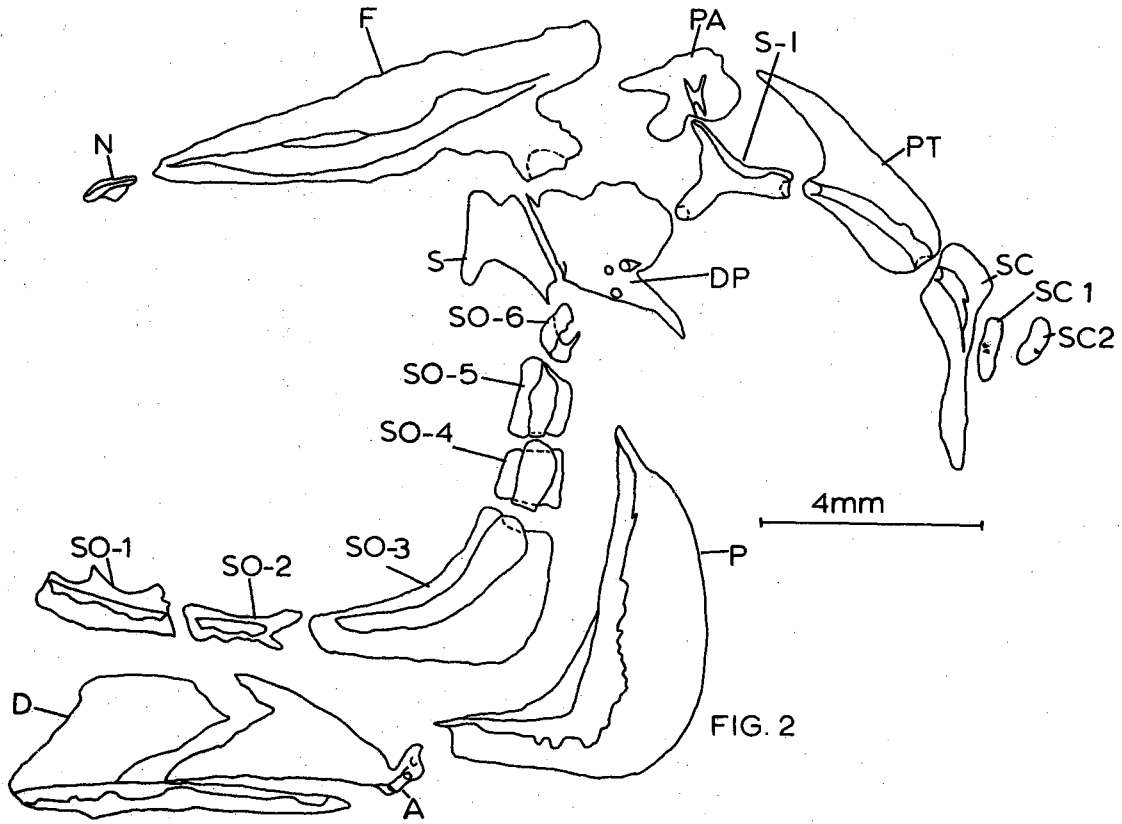


FIG. 2

terminate in small perforated hillocks. There is a one-to-one ratio between the primary branches and canal neuromasts, except in the anterior arm of the preopercle and SO-3 where the branches outnumber the sense organs. The terminal branches increase in number as the fish ages.

Except for the difference in shape, the pit neuromasts (spherical) and canal neuromasts (elongate and crescentic) are cellularly similar. Both are composed of a single type of sense cell supported on all sides, except the side facing the lumen of the canal or pit, by sustentative epithelial cells attached to the basement membrane. A representative neuromast (Figure 3), infraorbital region, has club-shaped sensory cells 10 to 12 μ in length and 1.3 to 3 μ in diameter, and elongate club-shaped sustentative epithelial cells 8 to 15 μ in length and 1.3 to 3 μ in diameter. The elongated sustentative epithelial cells, in some organs, extend from the sides of the canal toward the middle of the lumen to form a small "tremognostic chamber" (Branson and Moore, 1962).

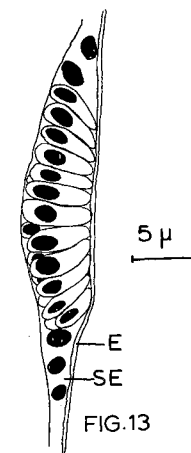
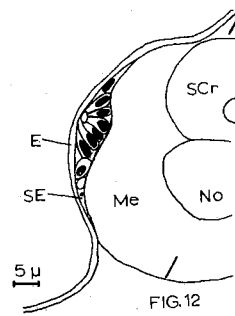
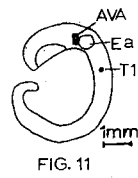
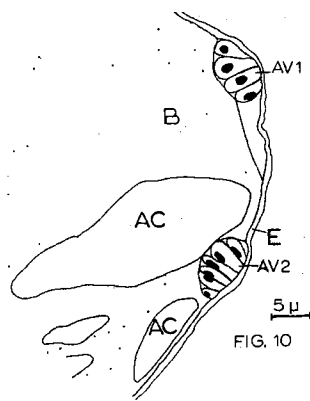
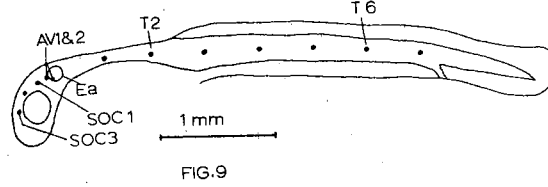
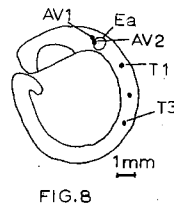
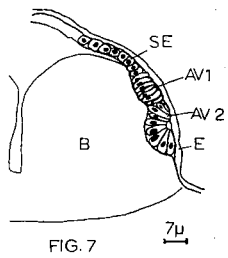
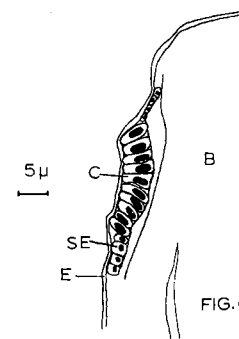
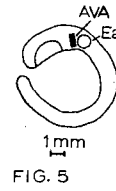
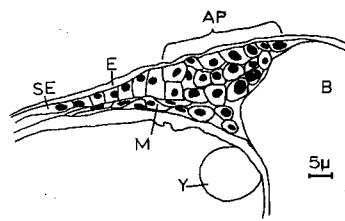
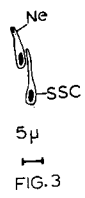
The nasal, SO-1 to 6, preopercle, supratemporal-intertemporal and the two lateral-line scales are one-component (laterosensory) bones. The other eight lateral-line bones are two-component (laterosensory and anasmestic) bones. Only the bony canals of the two-component bones are laterosensory components.

Figures

3. Cellular components of infraorbital neuromast 9.
4. Transverse section of an 18-hour embryo through the auditory placode.
5. Lateral view of a 34-hour embryo.
6. Frontal view of a 34-hour embryo through the anterior vestigial area.
7. Transverse section of a 50-hour embryo through the developing anterior vestigial neuromasts.
8. Lateral view of a 50-hour embryo.
9. Lateral view of a 3-mm prolarva.
10. Transverse section of a 3-mm prolarva through the anterior vestigial neuromasts.
11. Lateral view of a 40-hour embryo.
12. Transverse section of a 43-hour embryo through the first trunk organ.
13. Transverse section through the third trunk neuromast of a 12-mm postlarva.

Abbreviations

AC, auditory canal; AP, auditory placode; AV 1, 2, anterior vestigial neuromasts 1, 2; AVA, anterior vestigial area; B, brain; C, cell of anterior vestigial area; E, outer layer of epidermis; Ea, ear; M, mesenchyme; ME, mesoderm; Ne, sensory cell; No, notochord; SCr, spinal cord; SE, sensory layer of epidermis; SOC 1, 3, supraorbital canal neuromasts 1, 3; SSC, sustentative epithelial cell; ST 1, 2, supratemporal canal neuromasts 1, 2; T 1-7, trunk neuromasts 1-7; Y, yolk platelet.



CHAPTER IV

DEVELOPMENT AND FATE OF VESTIGIAL NEUROMASTS

All neuromasts develop from the second or sensory layer of the epidermis (Figure 4). The cells forming the first two neuromasts, ultimately located on the anterodorsal surface of the ear, are enlarging and elongating in 34-hour embryos (Figures 5 and 6) and contain a large nucleus near the base of each. The developing neuromasts separate from one another in 50-hour embryos (Figures 7 and 8) and complete their development, characterized by cell reduction, in 3-mm prolarvae (Figures 9 and 10) but disappear after the larvae reach 8 mm. Since these neuromasts never acquire sustentative epithelial cells or break through the epidermis, they probably have no function. The average length and diameter of the club-shaped cells of these spherical organs are 6μ ($5-7 \mu$) and 1.7μ (0.75 to 2.5μ), respectively. Their position gives very meager clues to their part in the lateral-line system, but possibly they may represent a remnant of the posterior dilatation, described by Bamford (1941) in Clupea harengus.

The third (first trunk) neuromast to occur was first observed in 40- to 43-hour embryos posterior to the ear (Figures 11 and 12). As the embryo elongates, the number of these trunk neuromasts increases sequentially, but the time interval between sequences is irregular (Figures 11 and 8). The total number of trunk neuromasts, four to seven (Figure 9), was never observed to increase after hatching, and

where they occur they are perpendicular to myosepta. After hatching the neuromasts form a disc and their oblong cells become 5 μ in length and 1.3 to 2.0 μ in diameter in 12-mm specimens (Figure 13). These apparent vestiges of the trunk lateral-line disappear before the juveniles reach 17 mm and, like the neuromasts above, never contain sustentative epithelial cells or break through the epidermis, and are probably functionless.

The discovery of the presence of trunk neuromasts in larvae of D. petenense is the first such discovery in fresh-water clupeids. Trunk neuromasts have also been discovered in an adult marine clupeid, C. pilchardus (Verheijen, 1959). In the entire suborder Clupeiodei, the two species mentioned above are the only clupeoids reported to have trunk neuromasts.

Perhaps other clupeoid larvae or embryos have trunk neuromasts at some period of development. If so, such new evidence should be used to confirm the subdivisions of the suborder Clupeiodei (Greenwood, et al., 1966) or be used to revise the suborder on the basis of trunk neuromasts being present or absent in different species of clupeoid larvae. If trunk neuromasts are present and their numbers are constant, the revision should also group the species according to the number of neuromasts present.

Denticipitoids and clupeoids are closely related (Greenwood, et al., 1966) for among the more important characteristics shared by both is the branching of the lateral-line system onto the opercle (Clausen, 1959 and Berg, 1940). One of the characteristics that separates the two suborders is the lack of a trunk lateral-line in clupeoids. The presence of newly discovered trunk neuromasts in larvae of D. petenense

should support more strongly the phyletic studies and provisional classification of the clupeomorphs (Greenwood, et al., 1966) by revealing that the denticipitoids and clupeoids are more closely related than previously supposed.

CHAPTER V

DEVELOPMENT OF PERMANENT NEUROMASTS, CANALS AND BONES

The first permanent neuromasts observed are three supraorbital ones in 3-mm specimens (Figure 9). The next neuromast to appear is the most anterior one of the preoperculo-mandibular canal in 10- to 11-mm specimens (Figure 14). This neuromast is followed by the next three mandibular and the first five infraorbital neuromasts in 11- to 13-mm specimens (Figure 15) and the last two mandibular, six preopercular, eight cephalic lateralis, two supratemporal, fourth supraorbital and last five infraorbital neuromasts in 12- to 14-mm specimens (Figure 16). The neuromasts, at first spherical in shape, elongate after becoming enclosed in cephalic and bony canals. As the neuromasts become enclosed in cephalic and bony canals, they may rotate on a given axis (Figures 23 and 24).

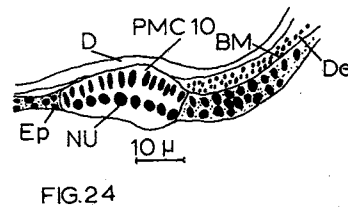
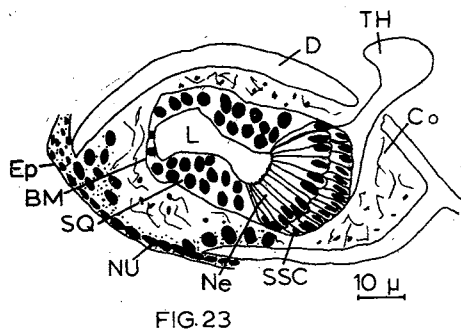
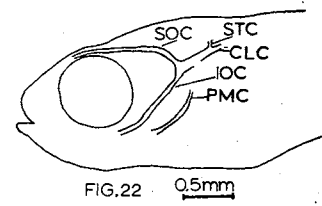
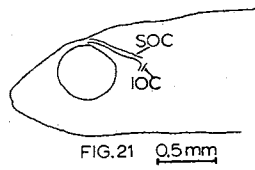
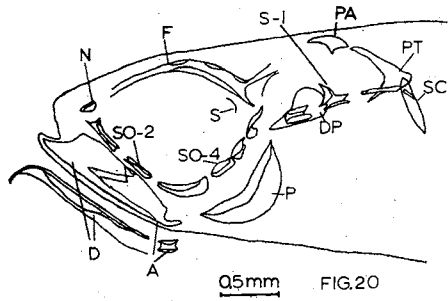
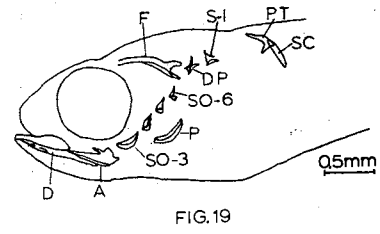
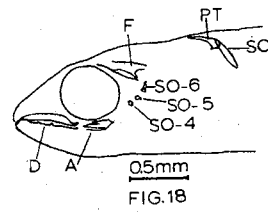
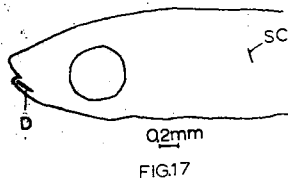
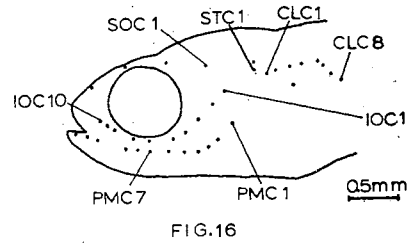
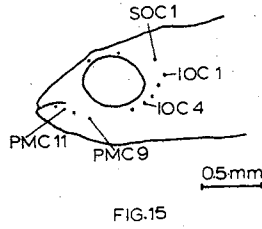
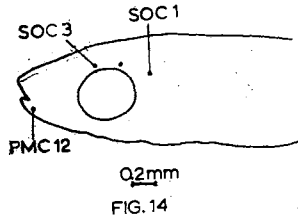
No osseous blastemas or primordia appear before ossification of the lateral-line bones. All lateral-line bones originate as single, enlarging lamellar ossifications before forming a bony canal, except for the nasal, S0-6 and S0-2, which immediately form as bony canals (Figures 18 and 20). Except for the dentary, posttemporal and supra-cleithrum, the major portions of the lateral-line bones develop abotically.

Figures

14. Lateral view of a 10-mm postlarva with neuromasts.
15. Lateral view of a 12-mm postlarva with neuromasts.
16. Lateral view of a 13-mm postlarva with neuromasts.
17. Lateral view of a 10-mm postlarva with lateral-line bones.
18. Lateral view of a 12-mm postlarva with lateral-line bones.
19. Lateral view of a 13-mm postlarva with lateral-line bones.
20. Lateral view of a 16.25-mm juvenile with lateral-line bones and ventral view of developing dentary and angular bony canals.
21. Lateral view of a 12-mm postlarva with developing canals.
22. Lateral view of a 13-mm postlarva with developing canals.
23. Transverse section of PMC 10 in a 24-mm specimen.
24. Transverse section of PMC 10 in a 10-mm specimen.

Abbreviations

A, angular; BM, basement membrane; CLC, cephalic lateralis canal; CLC 1, 8, cephalic lateralis canal neuromasts 1, 8; Co, connective tissue; D, dentary; De, dermis; DP, dermopterotic; EP, epidermis; F, frontal; IOC, infraorbital canal; IOC 1, 4, 10, infraorbital canal neuromasts 1, 4, 10; L, lumen; N, nasal; Ne, sensory cell; Nu, nucleus; P, preopercle; PA, parietal; PMC, preoperculomandibular canal; PMC 1, 7, 9-12, preoperculomandibular canal neuromasts 1, 7 and 9 through 12; PT, posttemporal; S, sphenotic; S 1, 2, scales 1, 2; SC, supracleithrum; SCr, spinal cord; S-I, supratemporal-intertemporal; SO-2 to 6, suborbitals 2 through 6; SOC, supraorbital canal; SOC 1, 3, supraorbital canal neuromasts 1, 3; SQ, stratified squamous epithelium; SSC, sustentative epithelial cell; STC 1, supratemporal canal neuromast 1; STC, supratemporal canal; TH, branch of hyomandibular nerve.



The first bones to appear are the anasmestic components of the dentary and supraclathrum in 10- to 11-mm specimens (Figure 17). In 11- to 12-mm specimens (Figure 18) the frontal (both components), S0-6, 5 and 4 and anasmestic components of the angular and posttemporal appear, and in 12- to 14-mm specimens (Figure 19) S0-3, the preopercle, supratemporal-intertemporal and both components of the dermopterotic are present. The nasal, S0-1 and 2, anasmestic components of the parietal, and both components of the sphenotic appear in 15- to 17-mm specimens (Figure 20).

The laterosensory components of the angular, dentary, posttemporal and supraclathrum appear in 15- to 17-mm specimens (Figure 20). The laterosensory element of the parietal and the two lateral-line scales form in 19- to 20-mm specimens.

There is little order in the origin of the lateral-line bones. However, the formation of their laterosensory elements is systematic in that the bones closest to the ear are first to develop laterosensory elements while those most distant form laterosensory elements last.

The five cephalic canals, originating as grooves (Figures 21 and 22), and their branches develop in conjunction with the bony canals. At times the cephalic canals complete a portion of their development ahead of the bony canal (Figure 23).

CHAPTER VI

DISCUSSION

Lateral-line neuromasts of D. petenense are not evocators of anasmestic components. The neuromasts in the immediate area of the anasmestic components of the posttemporal, supracleithrum, and angular, appear after the components (compare Figures 15 and 18). Neuromasts are never present when anasmestic components of the dermopterotic (compare Figures 16, 19 and 20) and parietal originate. Also, the neuromast present near the origin of the anasmestic component of the frontal is not in the immediate area of the initial ossification. The neuromasts do not evocate the laterosensory components because the laterosensory elements of the parietal and dermopterotic develop in the absence of neuromasts. An illustration by Wohlfahrt (1937) showing functional neuromasts of the rostral canal not enclosed by bone in C. pilchardus corresponds to the findings that neuromasts are not evocators of lateral-line bones in D. petenense.

The neuromasts appear to be one of the factors influencing development of laterosensory components in D. petenense, as recorded by Kapoor, 1962; Reno, 1966; Stensio, 1947; Moy-Thomas, 1941; and Takebe, 1934 in other fishes. The laterosensory components do not enclose neuromasts developing at opposite ends of the preoperculomandibular canal until the most adotically-positioned neuromast of that canal appears, then the laterosensory components develop in sequence

abotically. The adotical neuromast appears to regulate the time of formation of the laterosensory components. The neuromasts of the other cephalic canals originate adotically and develop abotically as do the later sequentially-developing laterosensory components that enclose them. Thus, it can be strongly suspected that all neuromasts have some influence over the time of origin of the laterosensory components which enclose them.

That neuromasts are evocators of components of lateral-line bones of D. petenense cannot be supported here. However, the possibility that ancestors had neuromasts with powers of evocating lateral-line bones but lost these powers during evolution to another part of the body through mutations and/or chromosomal aberrations, should be considered. Since there is evidence for the evocative powers of neuromasts in extant species (Lekander, 1949; Allis, 1899; Pehrson, 1922, 1940, and 1944), the latter idea must be considered even if only in speculation.

Parrington's (1948) theory that fields, eventually centers of ossification of lateral-line bones, affect development of neuromasts can neither be confirmed nor denied in D. petenense. Moodie's (1922) contention that canals initiate development of lateral-line bones is not supported in D. petenense for here lateral-line canal origin occurs after the origin of the laterosensory components.

CHAPTER VII

SUMMARY

In Dorosoma petenense, thirty-six canal neuromasts are present on each side of the head, located on the floors, roofs or walls of the cephalic canals which are enclosed in 17 paired lateral-line bones and partly enclosed by two lateral-line scales. Pit organs (surface neuromasts) are scattered over the surface in various numbers. Two are always present on each side of the rostrum.

The cellular composition of pit and canal neuromasts is the same. The ovate sensory cells are 10 to 12 μ in length and 1.3 to 3 μ in diameter, and the oblong sustentative epithelial cells are 8 to 15 μ in length and 1.3 to 3 μ in diameter. The number of sensory hairs, more than two per cell, was not confirmed. "Tremognostic chambers" (Branson and Moore, 1962) were observed, but no cupulae, ganglia near the sensory cells, or protoplasmic plates were found.

The five cephalic lateral-line canals are the supraorbital, infraorbital, preoperculomandibular, supratemporal and cephalic lateralis, continuous with one another by way of the recessus lateralis and supratemporal commissure. The development of the cephalic canals, originating as grooves, coincides with that of the laterosensory components.

The extensive branches of the cephalic canals extend over the surface of the head onto the opercle. With few exceptions, there is a one-to-one ratio between the primary external branches and the neuromasts.

All neuromasts of the lateral-line system develop independently and directly from the sensory layer of the epidermis. There is no acoustico-lateralis placode, lateral-line placode or sensory line, groove or ridge giving rise to the neuromasts. Two vestigial neuromasts appear on the head. Also, four to seven vestigial neuromasts appear on the trunk, forming a vestigial trunk lateral-line. The vestigial trunk lateral-line further substantiates the affinity of the clupeids with the denticipitids. Those permanent neuromasts which become enclosed by cephalic canals may rotate about a given axis.

The nasal, SO-1 to 6, preopercle, supratemporal-intertemporal and lateral-line scales are one-component (laterosensory) bones. The angular, dentary, frontal, posttemporal, supracleithrum, dermopterotic, sphenotic and parietal are two-component (laterosensory and anasmestic) bones.

The osteoblasts for the lateral-line bones and scales are located in the dermis. The lateral-line bones and scales originate from single centers of ossification in a random pattern of appearance and predominantly grow abotically. The bones are not evocated by the neuromasts, but the time of origin of their laterosensory components is influenced by them.

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