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# The Lateral Line System in Larval *Ichthyophis* (Amphibia: Gymnophiona)

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**Summary.** The lateral line systems of larval caecilians of the genus *Ichthyophis* possess two types of elements, free neuromasts and ampullary organs. Free mechanoreceptive neuromasts are typical of those found in other vertebrates, and are arranged in series roughly homologous to neuromast groups in many other fishes and amphibians. In contrast to other amphibians, *Ichthyophis* larvae possess only one paired, dorsal body series of neuromasts. Regional specialization of neuromasts is evident in *Ichthyophis*. Premaxillary and anterior head neuromasts are the largest in size and total cell number. Overall, size and total cell numbers are correlated with depth of epidermis. Neuromasts on the anterior sides of the head occur in slight grooves and have apical tips situated farther below the level of the epidermis and with greater apical indentation. These features probably provide increased protection against abrasion. Apparently abnormal neuromasts are frequently found among the neuromast series. Such neuromasts contain fewer cells that lack normal apical extension, producing a sunken effect similar to that of the ampullary organ elements. The ampullary organs of *Ichthyophis* are morphologically similar to those found in various freshwater fishes and known to function as electroreceptors. These organs are not observed in the lateral line systems of members of other amphibian orders (Urodela and Anura), and we suggest that they function as electroreceptors. The sunken neuromasts of the *Ichthyophis* lateral line system may parallel the possible evolutionary development of pit organs from normal neuromasts.

## A. Introduction

Little attention has been paid to the lateral line system of the caecilians (Amphibia: Gymnophiona) and its evolutionary significance, though it has been assessed in fish and other amphibian orders. To make amphibian comparisons inclusive

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of all three orders, we present new information on the morphology of the system in the biologically little known caecilians and compare their system with that of other vertebrate lineages.

Lateral line systems are found in most species of fish, free-living amphibian larvae, and adults of some aquatic species of amphibians. The system is ancient evolutionarily, being present in Silurian-Devonian agnathous Heterostraci (Romer, 1945) and a variety of other extinct primitive fish. Among amphibians, free-living larvae of some species of all three orders have lateral line systems, and retention of these structures in the adult state is correlated with the period of the life spent in aquatic habitats. For example, pipid frogs (*Pipa, Xenopus*), which are aquatic throughout life, retain the system as adults, as do certain aquatic salamanders (*Amphiuma, Necturus*). Adult caecilians that are aquatic do not retain the system, however. Some adult salamanders (*Triturus, Taricha*) amplify the lateral line system during aquatic phases of their lives but suppress it during terrestrial periods. In contrast to amphibian species with free-living larvae, virtually all of which have lateral line systems, those species with direct development (within egg coats or in or on the body of a parent) show a different pattern. The embryos of the live-bearing *Salamandra atra* Laurenti, 1768, have lateral line systems (Escher, 1925; Fachbach, 1966); other members of the genus and the family Salamandridae have free-living larvae that have the system. Conversely, several members of the salamander family Plethodontidae, all of which are direct developers, completely lack the system (Hilton, 1947). The direct-developing caecilians of the genus *Hypogeophis* have the system as embryos (Brauer, 1897, 1899); embryos of the several viviparous species of caecilians seem to lack it entirely (pers. obs.). There appears to be a mosaic of evolutionary loss of the system correlated with (1) the aquatic habitus of the adults and (2) the degree to which the larval stage has been abandoned in a lineage.

Attention has been paid to structure (including ontogeny) and function of the lateral line system in relatively few amphibian species. The system in *Xenopus* is well documented (the literature is summarized in reviews by Dijkgraaf, 1962, 1967, and Flock, 1965) and some work has been done with *Rana* (Escher, 1925; Knouf, 1935) and *Hyla regilla* Baird and Girard, 1852 (Larsell, 1925). The external features of the lateral line systems of many salamander species are cursorily described by Hilton, (1947); the aquatic adult forms including *Necturus* (Charipper, 1928; Chezar, 1930; Dye, 1921; Platt, 1894, 1896), *Amphiuma* (Norris, 1908), and *Siren* (Norris, 1913) have been studied. Reviews of amphibian lateral line system structure with comparison to that of fish include those of Flock (1967), Holmgren and Pehrson (1949), Stensiö (1947), and Wright (1951).

Work on the lateral line system of caecilians includes a description of the lateral line system and neuromast organs of *Ichthyophis glutinosus* (Linnaeus, 1758) from Ceylon by Sarasin and Sarasin (1887a, 1887b). Working largely from the Sarasins' description, Coggi (1905) compared *Ichthyophis* 'ampulli of Lorenzini' with those of sharks. Brauer (1897, 1899) commented on the presence of lateral line organs in the direct-developing *Hypogeophis rostratus* (Cuvier, 1829) of the Seychelle Islands. He stated that the organs do not appear until relatively late in development and that they disappear long before a young hatches. Parker (1958) noted the presence of lateral line organs in larvae of *Grandisonia seychellensis* and *larvatus* (taxonomy of Taylor, 1968). Taylor (1960) described the distribution of lateral line organs on the heads of larvae of several species of south-east Asian *Ichthyophis*, and later (1970) formalized the terminology of the neuromast series for caecilians, described the series for species of the South American *Epicrionops* and for *Ichthyophis*, and stated that larvae of the ichthyophiid genus *Caudacaecilia* also have lateral line systems. Largen, et al. (1972) described the lateral line series in larvae of the Ethiopian *Geotrypetes grandisonae*, a species of particular interest because other species in the genus are live-bearers whose embryos lack lateral line systems (Parker, 1936; Wake, 1977).

No work on the cellular structure of lateral line organs has been done since that of the Sarasins. We present data on structure and innervation of the organs and evaluate the two types of organs mentioned by the Sarasins as composing the system. We compare these with the organs in other amphibians, and, generally, in fish. This work is part of the on-going studies in the laboratory of the junior author on the morphology, life history, and evolution of caecilians.

## B. Materials and Methods

Larval caecilians, representing three species of the genus *Ichthyophis*, were examined. All are from the collections of the Field Museum of Natural History, Chicago, and were collected in the Philippines, Borneo-Sarawak, Thailand, and Malaya. The specific name *mindanaoensis* was associated with the larval and certain adult specimens from the Philippines by Taylor (1960, 1968). Material from the other regions is not assignable to any described species of *Ichthyophis*. The populations from Borneo-Sarawak show considerable similarity to each other, and those from Thailand and Malaya resemble each other. Because there are marked differences between the two groups, and between these and any described species, we refer to the specimens as *Ichthyophis* sp. A and sp. B, respectively.

The specimens were collected at various times from 1946 to 1964, were fixed in the field in formalin and stored in 70% ethanol. Distribution of the lateral line elements was determined by external observation using a Wild dissecting microscope. Only a few specimens with a well preserved epidermis and dark pigmentation allowed detailed counting of lateral line organs, and often only certain parts of the system were clearly visible on a given specimen. Specimens of *Ichthyophis* sp. A from two different populations provided the best opportunity for careful analysis, whereas specimens of *Ichthyophis sp.* B and *I. mindanaoensis* Taylor, 1960, provided limited observation of only a few parts of the system.

Histological examination was performed on one whole head of a specimen of *Ichthyophis* sp. A from North Borneo (FMNH 76340; total length of 112 mm) and on pieces of skin from a size series of specimens of *Ichthyophis* sp. A. and sp. B. The whole head was decalcified in acid alcohol for approximately five days, embedded in JB-4 plastic, sectioned at 8 µm, and stained with toluidine blue. Pieces of epidermis were carefully dissected from the specimens, with or without areas of underlying dermis, and were either embedded in JB-4 plastic and cut at 6–7 µm, or embedded in Epon 812 and cut at 1–2 µm. Both groups of sections were then stained with toluidine blue. Skin samples were taken from two specimens of *Ichthyophis* sp. A (total lengths 121 and 230 mm) and three of *Ichthyophis* sp. B (total lengths 69, 120, and 131 mm). Specimens were chosen that had well preserved skin and that together formed a reasonable size series for ontogenetic comparison. Skin containing parts of the lateral line system from the head, lower jaw, and spiracular regions was studied in each of the specimens, as was skin from middle and posterior regions of the body of one specimen of *Ichthyophis* sp. A.

## C. Results

The lateral line system of *Ichthyophis* larvae displays two distinct types of organs, free neuromasts – the Hügelorgane of Sarasin and Sarasin (1887a) – and other elements that will be referred to as ampullary organs – the Nebenohre of the Sarasins (1887a).

### *1. Free Neuromasts*

The free neuromasts in *Ichthyophis* larvae are distributed in distinct series along the head and body (Fig. 1). Externally they appear as pale spots, being most apparent when the surrounding epidermis has been damaged and sloughed, maximally exposing the unpigmented neuromast. One paired dorsal line of neuromasts occurs on the body, whereas many series of neuromasts occur on the head region. Taylor (1970) introduced a terminology for caecilian neuromast lines that, however, does not conform to terms applied to clearly homologous series in other vertebrates. We propose a modified terminology that agrees more closely with the usage for other vertebrates. Distinct series include the nasal, supraorbital, infraorbital, postorbital, oral, mandibular, gular, and supraspiracular series. An additional group of neuromasts, usually only two or three, lies between the postorbital and oral series, and another group, usually two, lies above the supraspiracular series. There are also numerous secondary rows of neuromasts leading medially from the oral row. The supraorbital row of neuromasts was divided into two series, the anterior canthals and posterior supraorbitals, by Taylor (1970), but the two are frequently continuous and are included as one series here.

These various neuromast series were consistent in all three species of *Ichthyophis* studied, although complete counts for all series could only be obtained for one species, *Ichthyophis* sp. A, from Sarawak. Although it was apparent that both *Ichthyophis* sp. B. and *I. mindanaoensis* specimens possessed all of the series, it was possible to get complete counts for only a few series in these species. Neuromast row counts are presented in Table 1. Overall, counts for specific rows were somewhat variable both within species and within a given individual when both sides were compared, and because of limited sample size, we do not treat the data statistically. However, these data do suggest appreciable interspecific and intraspecific differences in neuromast number in certain series. Two distinct populations of *Ichthyophis* sp. A from different regions of Sarawak were counted separately, and, although similar, there are some differences in series counts. Specimens from the Mengiong River in Sarawak had fewer neuromasts in their supraorbital and oral series than specimens from the Baleh river. Other series counts were similar. *Ichthyophis* sp. B and *I. mindanaoensis* specimens appeared distinct from *Ichthyophis* sp. A in having a much lower neuromast number in the supraspiracular row, and *I. mindanaoensis* appeared distinct from both other species in a low count for the postorbital row.

The free neuromasts found in *Ichthyophis* have the same basic morphology as those found in other amphibians and in fishes (see Wright, 1951 and Dijkgraaf,

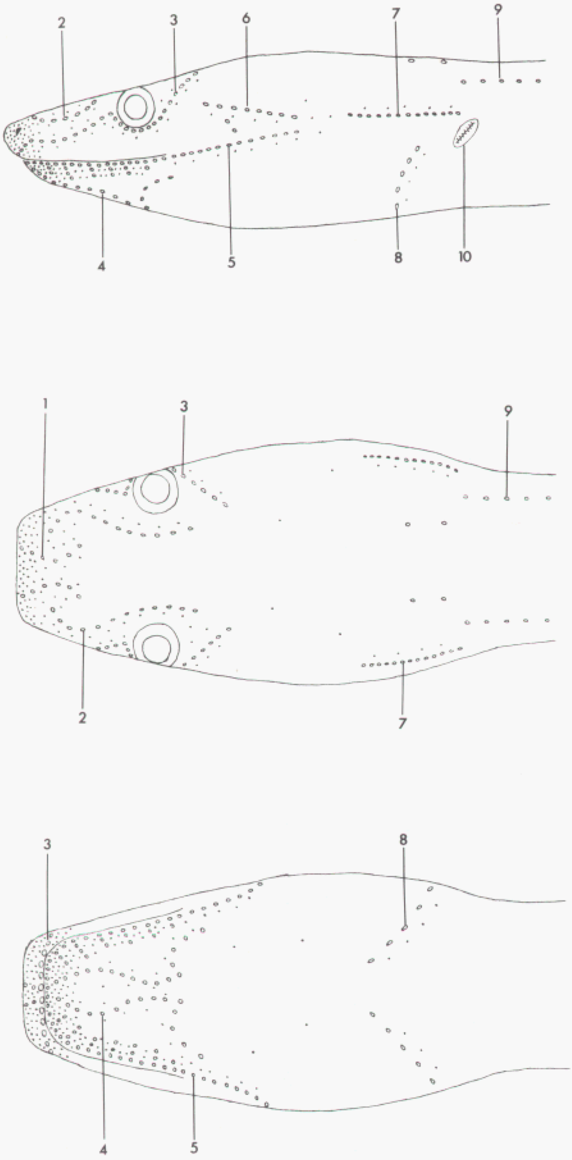


**Fig. 1.** Diagram of lateral (top), dorsal (middle), and ventral (*bottom*) views of *Ichthyophis* showing lateral line system. Free neuromasts designated by open circles and ampullary organs by dark spots. *1*, nasal series; *2*, supraorbital; *3*, infraorbital; *4*, mandibular; *5*, oral; *6*, postorbital; *7*, supraorbital; *8*, gular; *9*, body; *10*, spiracular. Approximately ×15

1962, for reviews). Each consists of three recognizable cell types – mantle cells, forming the outer rim of the neuromast, supporting cells that constitute the bulk of the organ, and sensory cells that are concentrated toward the apex (Fig. 2). The mantle cells are elongate, slender cells usually arising from the basal lamina of the epidermis and possessing elongate nuclei normally positioned

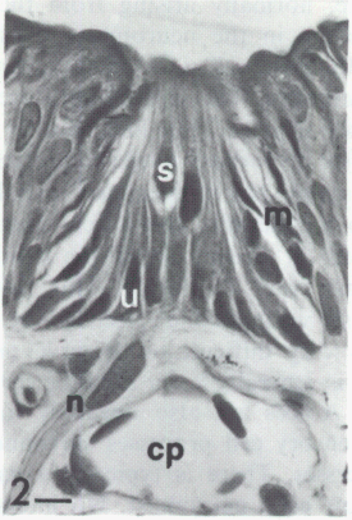
**Table 1.** Counts, ranges, and means of free neuromast number in series of three species of *Ichthyophis*. Table includes data for two distinct populations of *Ichthyophis* sp. A; one population from the Mengiong River, Sarawak, and another population from the Baleh River, Sarawak. Partial counts for *Ichthyophis* sp. B from Thailand and *Ichthyophis mindanaoensis* from the Philippine Islands also included. Superscript letters above count numbers represent individual specimens, and are included to demonstrate the variation between left and right sides of an individual

| Neuromast series | *Ichthyophis* sp. A (Mengiong River, Sarawak) | | | *Ichthyophis* sp. A (Baleh River, Sarawak) | | | *Ichthyophis* sp. B (Thailand) | | | *Ichthyophis mindanaoensis* (Philippine Is.) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Counts | Range | $\bar{x}$ | Counts | Range | $\bar{x}$ | Counts | Range | $\bar{x}$ | Counts | Range | $\bar{x}$ |
| Supraorbital | 14, $11^{b}$, $13^{b}$, $11^{c}$ $10^{c}$, 11 | 10–14 | 11.7 | 13, $15^{c}$, $14^{c}$, $16^{d}$, $17^{d}$, 16 | 13–17 | 15.2 | – | – | – | $12^{a}$, $13^{a}$ 10 | 10–13 | 11.7 |
| Infraorbital | $24^{a}$, $25^{a}$, $22^{b}$, $20^{b}$ 23 | 20–25 | 22.8 | 21, 20, $22^{d}$, $23^{d}$, 22 | 20–23 | 21.4 | $24^{a}$, $18^{a}$, 20 | 18–24 | 20.7 | $16^{a}$, $18^{a}$, 16, 20 | 16–20 | 17.5 |
| Oral | $26^{a}$, $24^{a}$, $26^{b}$, $29^{b}$ $28^{c}$, $26^{c}$ | 24–29 | 26.5 | $31^{a}$, $30^{a}$, $30^{c}$, $27^{c}$ $29^{d}$, $30^{d}$, 30 | 27–31 | 29.6 | $30^{a}$, $27^{a}$, 27 | 27–30 | 28.0 | $24^{a}$, $24^{a}$, 23, $30^{c}$ $27^{c}$, 21 | 21–30 | 24.8 |
| Postorbital | $10^{a}$, $9^{a}$, $7^{b}$, $7^{b}$, $8^{c}$ $9^{c}$, 9 | 7–10 | 8.4 | $8^{a}$, $8^{a}$, $6^{b}$, $9^{b}$, $8^{c}$ $9^{c}$, $11^{d}$, $9^{d}$ | 6–11 | 8.5 | $7^{a}$, $6^{a}$, 7 | 6–7 | 6.7 | $4^{a}$, $3^{a}$, $6^{b}$, $5^{b}$, 4 | 3–6 | 4.7 |
| Gular | $9^{a}$, $6^{a}$, $8^{b}$, $6^{b}$, $6^{c}$ $8^{c}$ | 6–9 | 7.2 | 6, $7^{c}$, $7^{c}$, $7^{d}$, $6^{d}$ 8 | 6–8 | 6.8 | – | – | – | $5^{a}$, $5^{a}$, 5 | – | 5.0 |
| Supraspiracular | $14^{a}$, $14^{a}$, $11^{b}$, $13^{b}$ $12^{d}$, $11^{c}$ | 11–14 | 12.5 | $13^{a}$, $14^{a}$, $11^{b}$, $13^{b}$ $12^{c}$, $12^{c}$, $14^{d}$, $13^{d}$ | 11–14 | 12.6 | $6^{a}$, $6^{a}$, $6^{b}$, $7^{b}$ | 6–7 | 6.2 | $6^{1}$, $7^{a}$, $9^{b}$, $7^{b}$, 6 | 6–9 | 7.0 |
| Mandibular | $16^{a}$, $16^{a}$, $16^{b}$, $14^{a}$ $18^{c}$, $20^{c}$ | 14–20 | 16.7 | $15^{a}$, $16^{a}$, $18^{c}$, $18^{c}$ $17^{d}$, $17^{d}$ | 15–18 | 16.8 | – | – | – | – | – | – |

basally. Supporting cells are also elongate, normally arising from the basal lamina, although some may occur farther up in the neuromast. These cells possess more spherical nuclei situated basally in the cell, and send long cytoplasmic extensions toward the apex of the neuromast. The sensory cells are interspersed among the extensions of the supporting cells. They have shorter extensions to the apex of the neuromast and possess spherical nuclei that often stain more lightly than those of the other cell types. Nerve fibers are seen leaving the neuromast ventrally and passing into the dermis, and a few neural cell bodies are often seen associated with the fibers directly below the neuromast. The cupula structure of typical neuromasts was not found. This would be expected in material fixed in the field and stored in alcohol, because the cupula is an extremely delicate structure that is very difficult to preserve properly (Dijkgraaf, 1962). The apex of a neuromast is generally lower than the surrounding epidermis, although this is variable. Apices are also normally indented to varying degrees, with the tips of the sensory cell processes surrounded by an elevated layer of supporting cell processes. There is typically a capillary of variable size in the dermis directly below each neuromast. No interspecific differences in general neuromast morphology were found.

The morphology of neuromasts in the different series of the head and body is basically the same except for size, which appears directly correlated with surrounding epidermal height. Table 2 presents data on relative sizes of neuromasts of different regions and of the surrounding epidermis. Neuromast size is somewhat variable but distinct regional differences are apparent. Neuromasts on the snout and anterior sides of the head, where the epidermis is thickest, are relatively large. A group of premaxillary neuromasts, actually an extension of the infraorbital series under the tip of the snout, includes the largest. The apices of these neuromasts are only slightly below the level of the epidermis, and there is also very slight apical indentation in these neuromasts. The entire snout region is exceptionally well-vascularized, and numerous large capillaries occur beneath the premaxillary neuromasts. The neuromasts of the anterior parts of the infraorbital, supraorbital, and oral series are also quite large. Figure 3 shows a free neuromast from the oral series of *Ichthyophis* sp. A. The tips of these neuromasts are relatively far below the level of the epidermis, and the apical indentation of these neuromasts is often striking, up to 20 μm deep. Vascularization is well developed, with single capillaries of about 50 μm diameter occurring beneath the neuromasts. These anterior neuromast rows are also interesting in that the neuromasts lie in slight grooves in the epidermis (Fig. 3), whereas other neuromasts occur in areas of flat epidermis. As one proceeds posteriorly, the neuromasts become progressively smaller and the epidermis progressively thinner. The smallest neuromasts are those of the gular, supraspiracular, and dorsal body rows. They are virtually even in height with the surrounding epidermis, and also have slight apical indentation. Relatively small capillaries, about 20 μm in diameter, are associated with these posterior neuromasts.

The various neuromast rows are innervated by the anterior and posterior lateral line nerves. The posterior lateral line nerve, closely associated with the tenth cranial nerve, innervates the supraspiracular and body neuromasts. Various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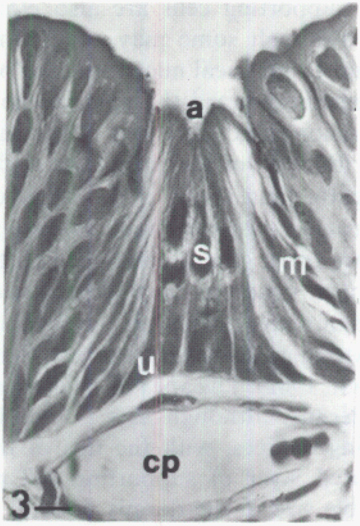
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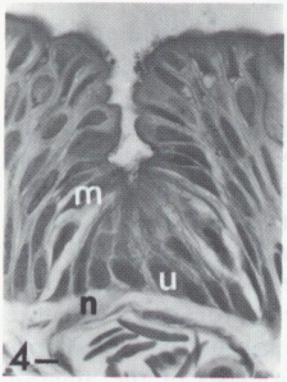
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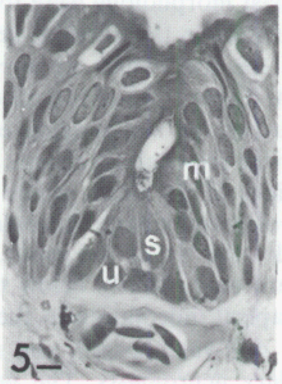
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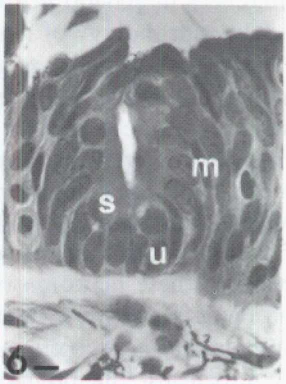
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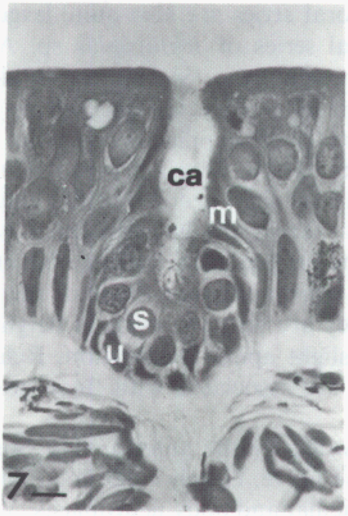
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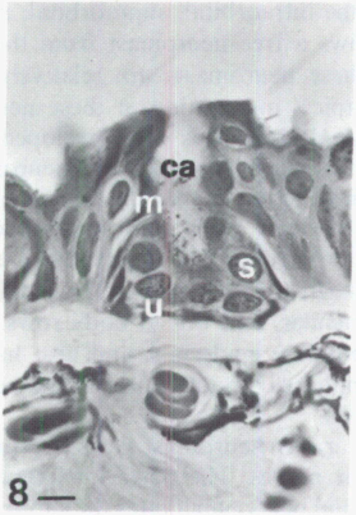
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**Table 2.** Ranges and mean values of neuromast size and epidermal height for representative neuromast series. Height and width values calculated from measurements to the nearest 5 µm from 112 mm larvae of *Ichthyophis* sp. A. Mean values rounded to the nearest 5 µm. Total cell number counted to the nearest 5 cells. Sample size of 10 for each category, except 8 for the premaxillary series

| Neuromast Series | Epidermal height (µm) | | Neuromast height (µm) | | Neuromast width (µm) | | Total cell number | | Total sensory cell number | |
|---|---|---|---|---|---|---|---|---|---|---|
| | range | $\bar{x}$ | range | $\bar{x}$ | range | $\bar{x}$ | range | $\bar{x}$ | range | $\bar{x}$ |
| Premaxillary | 120–130 | 125 | 100–110 | 105 | 120–125 | 120 | 230–255 | 245 | 15–20 | 17 |
| Anterior infraorbital | 125–140 | 130 | 90–105 | 100 | 95–105 | 100 | 165–200 | 185 | 9–12 | 11 |
| Posterior infraorbital | 105–115 | 110 | 80–95 | 85 | 85–95 | 90 | 150–175 | 65 | 6–11 | 8 |
| Supraspiracular | 70–75 | 75 | 60–70 | 65 | 60–75 | 65 | 95–115 | 105 | 4–6 | 5 |

branches of the anterior lateral line nerve innervate the remaining anterior neuromast series. The nerve terminology used here for the different branches of the anterior lateral line nerve is that of Norris and Hughes (1918) for larval *Ichthyophis*. The neuromasts of the snout and sides of the head (infraorbital series) are innervated by a buccal branch, whereas those on the top of the head (nasals and supraorbitals) are innervated by a superficial ophthalmic branch. Neuromasts of the oral, mandibular, and postorbital series are innervated by a medial external branch and the gular series by a medial internal branch.

Analysis of the ontogenetic changes in the lateral line in larval life showed no significant differences between neuromasts of the smallest larva (69 mm total length) and the largest (230 mm total length). The small specimen represents a very young larva, whereas the large specimen represents a larva approaching metamorphosis (gills resorbed, skin thickened and keratinized, tentacle formed). Corresponding neuromasts were of similar size and morphology, and the innervation and vascularization appeared the same.

**Fig. 2.** Free neuromast from mandibular series of *Ichthyophis* sp. A. *m* mantle cell; *n* nerve; *s* sensory cell; *u* supportive cell; *cp* capillary. Bar represents 10 µm. **3**, Free neuromast from oral series of *Ichthyophis* sp. A. Note relatively high epidermal walls and apical identation (*a*). Bar represents 10 µm. **4**, Sunken neuromast from the oral series of *Ichthyophis* sp. A. Note lack of normal extension in the neuromast cells. Bar 10 µm. **5**, Sunken neuromast from the supraorbital series of *Ichthyophis* sp. A. Note the greater reduction in neuromast cell extension compared with Fig. 4. Oblique view giving the erroneous impression of an occluded "canal". Bar 10 µm. **6**, Sunken neuromast from the infraorbital series of *Ichthyophis* sp. A. Note reduced cellular extension. Bar 10 µm. **7**, Typical ampullary organ associated with the anterior supraorbital neuromast series in *Ichthyophis* sp. A. *ca* canal. Bar 10 µm. **8**, Ampullary organ associated with supraspiracular neuromast series of *Ichthyophis* sp. A. Note smaller size typical of more posteriorly situated ampullary organs. Bar 10 µm

Neuromast series in *Ichthyophis* were frequently found to contain unusual neuromast organs (Figs. 4, 5, and 6). These elements were noted throughout all neuromast series in all of the specimens studied, although they were most common among the anterior head rows. In one specimen, these organs composed approximately 20% of the supraorbital and infraorbital series. These elements are sunken neuromasts, and there were differing degrees of sunkenness. The arrangement and features of the cells are very similar to a normal neuromast except that long cytoplasmic extensions of the cells are absent. As seen in Figs. 4, 5, and 6, the degree of cellular extension in these sunken neuromasts is variable. Figure 4 shows an element with somewhat reduced cellular elongation, Fig. 5 is an example of greater reduction, whereas the organ in Fig. 6 has extremely reduced cell extensions. These elements occupy positions in series that would normally be occupied by a typical neuromast, and were consistently smaller than surrounding neuromasts. Those associated with the large anterior neuromasts, for example, were about 75 μm wide and contained perhaps 100 cells, of which about five would be classified as sensory. The degree of vascularization varied, with underlying capillaries often quite smaller than expected, but also occasionally of normal size. For anterior positions, for example, capillaries were found which ranged from perhaps 30 μm to about 60 μm. Innervation of these elements appeared normal, with fibers and associated cell bodies situated ventrally in the dermis. The lack of normal cell extensions in these sunken neuromasts produced in effect a canal-like structure passing through the epidermis to the neuromast cells, causing a superficial resemblance to the lateral line ampullary organs next discussed.

### 2. *Ampullary Organs*

The other element of the lateral line system of larval *Ichthyophis* is the ampullary organ. These organs resemble the flask-like ampullary organs of certain fishes, and consist of mantle, supporting, and sensory cells clustered at the base of the epidermis and connected to the surface by a canal (Figs. 7 and 8). The canal widens at its base to form a broad lumen. Elongate mantle cells, similar to those of free neuromasts, circle the periphery of the cell cluster and form the bottom edge of the canal. Normal epidermal cells usually line the top region of the canal. Supporting cells form a basal layer, although they may occur slightly above the basal lamina. Other cells, presumably sensory in function, lie above the supporting cells and border the lumen of the canal. Both supporting and sensory cells have cellular extensions leading to the lumen of the canal although they are much shorter than those of their counterparts in free neuromasts.

The spherical nuclei of the sensory cells appear slightly smaller than the nuclei of neuromast sensory cells, usually less than 10 μm in diameter, whereas those of neuromast sensory cells are normally slightly more than 10 μm in diameter. The nuclei of sensory cells in ampullary organs have a distinct granularity in contrast to the homogenous appearance of those of neuromasts. The sensory cells of ampullary organs also comprise a much greater proportion of total cell number, normally 20–25%, than those of neuromasts. No distinct cupular material was observed in the canals of the ampullary organs, although this might be due to fixation. Nerve fibers, associated with a few nerve cell bodies, leave the ampullary organs and enter the underlying dermis. Ampullary organs have poorly developed vascularization, occasionally having a small capillary lying near them, but usually none. No variation in general ampullary organ morphology was found between the different *Ichthyophis* species.

Ampullary organs are distributed primarily on the head, being most numerous on the tip of the snout (Fig. 1). They become increasingly rare as one proceeds posteriorly, and were not found in skin samples taken from middle and posterior body regions. Sarasin and Sarasin (1887a) report that ampullary organs do occur sparingly on the body. Externally, ampullary organs appear as pale spots much smaller than neuromasts, and are most conspicuous in specimens with a worn epidermis. Ampullary organs are associated with particular neuromast series and usually occur along either side of neuromast rows in a regular fashion. Occasionally they occur only along one side of a neuromast series, as in the instance of organs occurring only lateral to the supraorbital series. Ampullary organs usually number fewer than the neuromasts in the series with which they are associated. For example, supraorbital series containing 10–14 neuromasts would be paralleled by perhaps 7–9 ampullary organs. Ampullary organs are densely packed on the snout region with no obvious order to their distribution; they also show a more random distribution than neuromasts, occasionally occurring far from any neuromasts. A few normally occur, for example, on the dorsal, posterior parts of the head disjunct from any neuromast series. A few ampullary organs are also associated with the supraspiracular neuromast series.

As with neuromasts, ampullary organs situated in anterior head regions with thick epidermis are larger than more posterior ones in areas of thinner epidermis. The largest ampullary organs are approximately 60 µm wide at the base with a total of about 80 cells, 15–20 being sensory. The smallest organs (Fig. 8) average about 45 µm wide at the base, with a cell total of around 60, 10–15 being sensory cells. The depth of the canal varied with the height of the surrounding epidermis, ranging from 200 µm on the outer surface of the snout to 50 µm farther back on the neck region. The innervation of the ampullary organs appears to follow the general pattern of the neuromasts near them. The ampullary organs associated with the supraspiracular row of neuromasts are innervated by the posterior lateral line nerve. All remaining anterior organs are innervated by various components of the anterior lateral line nerve. Those on the snout and sides of the head are innervated by a buccal branch, those on the top of the head by a superficial ophthalmic branch, those on the lower jaw and cheek region by a medial external branch, and those associated with the gular neuromast row by a medial internal branch. As with the free neuromasts, no ontogenetic differences in ampullary organ structure could be discerned between those organs of very small larvae and those of a large larva nearing metamorphosis.

## D. Discussion

### *1. Neuromast Distribution*

The arrangement of free neuromasts on the head region of *Ichthyophis*, and also of other caecilian genera as observed by Taylor (1970), is similar to neuromast distribution patterns in most other vertebrates possessing a lateral line system; i.e., the neuromasts are arranged in discrete rows (see Holmgren and Pehrson, 1942 for review). Certain urodele amphibians, such as *Necturus* (Kingsbury, 1895) and *Siren* (Reno and Middleton, 1973) have relatively broader zones of neuromast distribution, but a constriction of these areas into single rows would produce a pattern similar to that of *Ichthyophis*. The supraorbital, infraorbital, oral, and mandibular series of neuromasts are persistent throughout most vertebrates. The nasal row in *Ichthyophis* is a unique series that probably represents a medial part of the supraorbital series, which is often a broad group of neuromasts in certain urodeles, such as *Necturus* (Kingsbury, 1895). The postorbital series in *Ichthyophis* appears homologous to neuromast groups often termed jugal or postorbital in amphibians and fishes. The isolated gular series perhaps represents a posterior part of the mandibular series that often extends posteriorly in other amphibians. The supraspiracular row would appear homologous to neuromast series commonly termed suprabranchial in various fishes and amphibians. The pattern of innervation of the neuromast rows in *Ichthyophis* fits a general vertebrate pattern. The most striking feature of neuromast distribution in *Ichthyophis* concerns the presence of only one paired dorsal series along the body. Both urodele and anuran amphibians normally possess three paired body rows situated ventrally, laterally, and dorsally. The sole body row in larval *Ichthyophis* apparently corresponds with the dorsal body row of other amphibians. Taylor (1970) reported the presence of both lateral and ventral rows in certain caecilian larvae, including *Ichthyophis* species, noting that they are difficult to observe externally. However, histological examination of skin from middle and posterior body regions showed only a dorsal row. It is likely that Taylor was confusing linear arrangements of dermal glands, which often resemble neuromasts, as lateral and ventral lines. The presence of a single body series represents a unique feature of the caecilian lateral line.

The only noticeable difference in neuromast distribution between the three species of *Ichthyophis* studied involved relative numbers of neuromasts in a given series (Table 1). The number of neuromasts in a given row was found to vary both interspecifically and intraspecifically between two different populations, and also tended to vary between members of the same populations and within individuals when right and left sides were compared. Taylor (1970) published row counts for several specimens of *Epicrionops petersi* Taylor, 1968, that suggest that this genus has substantially fewer neuromasts in most series compared with the three *Ichthyophis* species. For example, the row counts for *Epicrionops* ranged from 2–4 for the postorbital series, 12–14 for the orbital series, and 16–20 for the oral series. The corresponding count ranges for all three *Ichthyophis* species combined were 3–11, 16–25, 21–31. The degree of difference seen between members of the different populations of the same species, between species of the same genus, and between genera suggests that the number of neuromasts in a particular series is a feature susceptible to evolutionary change and therefore useful to distinguish taxa or populations.

### 2. *Regional Differences in Neuromasts*

Free neuromasts in *Ichthyophis* larvae show regional differentiation in physical dimensions and total cell number. Size corresponds closely to surrounding epidermal height. Whereas greater cellular extension would be expected so that the apices of neuromasts might approach the surface of a high epidermis, increase in total cell number might not be expected. It cannot be determined if the same factors are responsible for increased epidermal height and increased neuromast size. However, large neuromasts usually had larger capillaries associated with them. Whether this greater vascularization is associated with development or a functional requirement of large size cannot be determined.

The anterior head regions possessed the thickest epidermis and, correspondingly, the largest neuromasts. This condition might be functionally important in that mechanoreceptive information concerning water displacements near the head might be especially important for such purposes as prey detection. Increased numbers of sensory cells per neuromast, combined with the greater density of neuromasts on the anterior head regions, could provide greater information and more detailed analysis of disturbances in the surrounding water. The largest neuromasts in *Ichthyophis* larvae were those of the premaxillary groups in the infraorbital series. These were correspondingly larger than nearby neuromasts in equally thick epidermis. The large size of these neuromasts may be related to their position on the ventral side of the upper lip, directly in front of the mouth, and potentially useful in prey detection.

Another aspect of regional differentiation involved the neuromasts in the infraorbital and oral series along the sides of the head. These neuromasts occurred in slight grooves in the skin, appeared to have apical tips farther below the surrounding epidermis, and tended to have more pronounced apical indentation. These specializations may provide increased protection for the neuromast and the tips of the sensory cells. Neuromasts occurring behind the head region, including the gular, supraspiracular, and body rows, were the smallest and least protected. Their apical tips were more or less level with the epidermis, and there was only slight apical indentation.

### 3. *Function of the Ampullary Organ*

The other element of the *Ichthyophis* lateral line system is the ampullary organ, unique to caecilians among the amphibians. Urodele and anuran amphibians possess only free neuromasts in their lateral line systems. The ampullary organs in caecilians are morphologically very similar to ampullary organ structures of various freshwater fishes. The ampullary organs of these fishes are considered to function primarily as electroreceptors (see Bennett, 1971, for review). The major features of a functional electroreceptive organ involve some type of channel, filled with a conducting substance, passing through electrically resistant epidermal layers and leading to electrosensitive receptor cells. Electric currents preferentially flow through the channel and receptor cells, changing the potential of the latter and in turn effecting neurotransmitter release at their synaptic junction with neural cells. The ampullary organs of most freshwater fishes follow this basic scheme with varying degrees of specialization. The ampullary organs of other freshwater fishes, such as those of the catfish *Ictalurus* (Mullinger, 1964; Roth, 1969) the lungfish *Protopterus* (Roth and Tscharntke, 1976), and the brachiopterygian *Calamoichthyes* (Roth and Tscharntke, 1976), are not specialized and closely resemble the ampullary organs seen in *Ichthyophis*. In ampullary organs of all of these forms, morphology, including general size and cellular arrangement, is very similar. Physiological experimentation by Roth (1968, 1969) found that the ampullary organs of *Ictalurus nebulosus* (Le Sueur, 1819) were approximately twenty times more sensitive to electrical square pulses than neuromasts in that species. Roth (1973) also showed that the ampullary organs of the lungfish *Lepidosiren paradoxa* Fitzinger, 1836, and brachiopterygian *Calamoichthyes calabaricus* Smith, 1865, were responsible for electroreceptive capabilities demonstrated in behavioral tests.

Aside from the general resemblance of *Ichthyophis* ampullary organs to those of electroreceptive fishes, other evidence suggests electroreceptive function of the ampullary organs. Functional differences between neuromast amd ampullary receptors are suggested by the different nuclear size and staining characteristics of the two cell types. Close examination of the presumed cupular structure was not possible, so it cannot be determined if the cupular substance simply filled the canal or actually extended somewhat from the epidermal surface. Even assuming some type of cupular extension that could be affected by water disturbances, it is difficult to attribute a useful mechanoreceptive function to these ampullary organs. The long canal would certainly severely dampen any oscillations in the cupular substance, reducing the effect on any sensory cells at the base of the canal. Pit organs parallel and are intermixed with numerous normal neuromasts, further suggesting separate functions.

Additional support for the proposed electroreceptive function of the ampullary organs of *Ichthyophis* is provided by the natural history of the larval caecilians. Vision is apparently reduced in these animals and they forage nocturnally. As a rule, electroreceptive capabilities appear frequently in fishes living in conditions of reduced visibility (Bennett, 1971). In such conditions, sensitivity to weak electrical signals, produced by other animals, could be useful in terms of prey or predator detection. Roth and Tscharntke (1976) speculate that ampullary organs in lungfishes and brachioptergians, that frequently rise to the water surface to breathe, may be useful in informing these fishes of the distance between their mouth tip and the water surface. As the mouth approaches the water surface, a distortion of the electric field around the mouth would occur that could be sensed by the ampullary organs. Larval *Ichthyophis* have lungs, and it is likely that they also gulp air at the water surface. A final piece of evidence that supports the proposed electroreceptive function of *Ichthyophis* ampullary organs concerns their localization on the head region. Ampullary organs of the fishes are also concentrated on the head region.

### *4. Evolution of Ampullary Organs*

The organs referred to as "sunken" neuromasts found among the neuromast series probably represent unusual neuromasts, though they superficially resemble pit organs. These organs are most common in the anterior head series, and in one specimen represented about 20% of the supraorbital series. Similar neuromast elements have been described in various urodeles, such as *Necturus* (Kingsbury, 1895; Malbranc, 1876). Malbranc (1876) suggested that these neuromasts represented developing organs; Kingsbury (1895) noted, however, that such elements occurred in specimens of different ages. Similarly, sunken neuromasts occurred in *Ichthyophis* larvae of different ages. This situation sheds doubt on the possibility that these represent developing neuromasts, because all members of the series appear to develop at one specific time. It is possible that the sunken neuromasts represent regenerating neuromasts that might have previously sustained damage. However, among the *Ichthyophis* specimens examined there was no sign of previous damage in the region of sunken neuromasts. The surrounding epidermis seemed in typical condition, and nearby neuromasts appeared normal. Such sunken neuromasts were normally scattered along the neuromast rows, rather than clumped together. If these neuromasts represent previously damaged neuromasts, one would expect to find a general region of regenerating neuromasts rather than isolated regenerating organs. It seems probable that the occurrence of sunken neuromasts is a developmental phenomenon specific to individual neuromasts.

Vascularization of sunken neuromasts often was unusually low or lacking. We infer a correspondence between degree of vascularization, extent of cellular elongation, and cell number in neuromasts, at least as a partial explanation for these sunken neuromasts. It is possible that cellular extension, with its accompanying increase in cytoplasm and need for filamentous support, requires a high degree of vascularization. Wickham (1974) has suggested that the elongation of salamander neuromast cells requires a large amount of filamentous protein material to act as a support system within the cytoplasm, and that there is a high turnover rate for the protein. Lack of sufficient vascularization might result in insufficient filamentous material to act as a support system for cellular extension and result in the sunken neuromasts observed.

The "sunken" neuromasts, assuming that they are truly abnormal and not regenerating neuromasts, represent a hypothetical stage in the evolution of ampullary organs from normal neuromasts. Lissmann (1967) and Bennett (1971) have suggested that ampullary organs developed from insinking neuromasts that eventually lost mechanoreceptive capabilities and became specialized for electroreception. The presence of kinocilia in some ampullary receptor cells that they observed lends support to this hypothesis. The sunken neuromasts of *Ichthyophis*, and perhaps of some urodele amphibians, may demonstrate the developmental plasticity associated with the lateral line system that gave rise to pit organs from normal neuromast elements.

These observations on *Ichthyophis* show that the caecilian lateral line possesses unique features compared with the lateral line systems of other amphibians. Physiological and behavioral investigation of ampullary organ function could provide conclusive evidence as to whether or not certain larval caecilians may have electroreceptive capabilities. Substantial differences in neuromast distribution and the presence of ampullary organ elements in the lateral line system represent other fundamental differences between caecilians and the other amphibian orders.

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## References

Bennett, M.V.L.: Electroreception. In: Fish physiology, Vol. V (W.S. Hoar and D.J. Randall, eds.), pp. 493–574. New York-London: Academic Press 1971

Brauer, A.: Beiträge zur Kenntnis der Entwicklungsgeschichte und der Anatomie der Gymnophionen. Zool. Jahrb. Anat. **10**, 389–472 (1897)

Brauer, A.: Beiträge zur Kenntnis der Entwicklung und Anatomie der Gymnophionen. II. Die Entwicklung der äußeren Form. Zool. Jahrb. Anat. **13**, 477–508 (1899)

Charipper, H.A.: Studies on the lateral-line system of Amphibia I. Cytology and innervation of the lateral-line organs of *Necturus maculosus*. J. comp. Neurol. **44**, 425–447 (1928)

Chezar, H.H.: Studies on the lateral-line system of Amphibia II. Comparative cytology and innervation of lateral-line organs in the Urodela. J. comp. Neurol. **50**, 159–175 (1930)

Coggi, A.: Le ampolle di Lorenzini nei Gimnofioni. Monit. Zool. Ital. **16**, 49–56 (1905)

Dijkgraaf, S.: The functioning and significance of the lateral-line organs. Biol. Rev. **38**, 51–105 (1962)

Dijkgraaf, S.: Biological significance of the lateral line organs. In: Lateral line detectors (P. Cahn, ed.), pp. 83–95. Bloomington: Indiana Univ. Press 1967

Dye, W.J.P.: The relation of the lateral line organs of *Necturus* to hearing. J. comp. Psychol., **1**, 469–471 (1921)

Escher, K.: Das Verhalten der Seitenorgane der Wirbeltiere und ihrer Nerven beim Übergang zum Landleben. Acta Zool., Stockh., **6**, 307–414 (1925)

Fachbach, G.: Stimulation des Seitenliniensystems bei dem (uterus) entnommenen Alpensalamander-Larven (*Salamandra atra*). Zool Anz. **29**, 97–106 (1966)

Flock, Å.: Electron microscope and electrophysiological studies on the lateral line canal organ. Acta oto-lar. Suppl. **199**, 1–90 (1965)

Flock, Å.: Ultrastructure and function in the lateral line organs. In: Lateral line detectors (P. Cahn, ed.), pp. 163–197. Bloomington: Indiana Univ. Press 1967

Hilton, W.J.: Lateral line sense organs in salamanders. Bull. Soc. Calif. Acad. Sciences **46**, 97–110 (1947)

Holmgren, N., Pehrson, T.: Some remarks on the ontogenetical development of the sensory lines on the cheek in fishes and amphibians. Acta Zool. **30**, 249–314 (1949)

Kingsbury, B.F.: The lateral line system of sense organs in some American Amphibia, and comparison with the dipnoans. Trans. Amer. Micr. Soc. **17**, 115–146 (1895)

Knouf, R.A.: The developmental pattern of ectodermal placodes in *Rana pipiens*. J. Comp. Neuro. **62**, 17–71 (1935)

Largen, M.J., Morris, P.A., Yalden, D.W.: Observations on the caecilians *Geotrypetes grandisonae* Taylor (Amphibia: Gymnophiona) from Ethiopia. Mon. Zool. Italiano, NS Supplemento IV, No. **8**, 185–205 (1972)

Larsell, O.: The development of the cerebellum in the frog (*Hyla regilla*) in relation to the vestibular and lateral-line systems. J. comp. Neurol. **39**, 249–289 (1925)

Lissman, H.: Some general comments. In: Lateral line detectors (P. Cahn, ed.), pp. 411–414. Bloomington: Indiana Univ. Press 1967

Malbranc, M.: Von der Seitenlinie und ihren Sinnesorgangen bei Amphibien. Zeitsch. F. Wiss. Zool. **26**, 24–86 (1876)

Mullinger, A.M.: The fine structure of ampullary electric receptors in *Amiurs*. Proc. roy. Soc. B **160**, 345–359 (1964)

Norris, H.W.: The cranial nerves of *Amphiuma means*. J. comp. Neurol. Psych. **18**, 527–568 (1908)

Norris, H.W.: The cranial nerves of *Siren lacertina*. J. Morph. **24**, 245–338 (1913)

Norris, H.W., Hughes, S.P.: The cranial and anterior spinal nerves of the caecilian amphibians. J. Morph. **31**, 489–557 (1918)

Parker, H.W.: The caecilians of the Mamfe Division, Cameroons. Proc. Zool. Soc. London **1936**, 135–163 (1936)

Parker, H.W.: Caecilians of the Seychelles, a description of a new species. Copeia **12**, 71–76 (1958)

Platt, J.B.: Ontogenetische Differenzierung des Ektodermis in *Necturus*. Arch. mikr. Anat. **43**, 911–964 (1894)

Platt, J.B.: Ontogenetic differentiations of the ectoderm in *Necturus*. Pt. II. Quart. J. micr. Sci. **38**, 485–547 (1896)

Reno, H.W., Middleton, H.H.: Lateral-line system of *Siren intermedia* le Conte (Amphibia: Sirenidae) during aquatic activity and aestivation. Acta zool. Stockh. **54**, 21–29 (1973)

Romer, A.S.: Vertebrate Paleontology, 2nd ed., 687 pp. Univ. Chicago Press, Chicago (1945)

Roth, A.: Electroreception in the catfish, *Amiurus nebulosus*. Z. vergl. Physiol. **61**, 196–202 (1968)

Roth, A.: Elektrische Sinnesorgane beim Zwergwels *Ictalurus nebulosus* (*Amiurus nebulosus*). Z. vergl. Physiol. **65**, 368–388 (1969)

Roth, A.: Electroreceptors in Brachiopterygii and Dipnoi. Naturwissenschaften **60**, 106 (1973)

Roth, A., Tscharntke, H.: Ultrastructure of the ampullary electroreceptors in Lungfish and Brachiopterygii. Cell Tiss. Res. **173**, 95–108 (1976)

Sarasin, P., Sarasin, F.: Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon in den Jahren 1884–1886. Zur Entwicklungsgeschichte über die Anatomie der Ceylonische Blindwuhle *Ichthyophis glutinosus*. Part II, pp. 41–94. C.W. Kreidel's Verlag. Wiesbaden (1887a)

Sarasin, P., Sarasin, F.: Einige Puncte aus der Entwicklungsgeschichte von *Ichthyophis glutinosus (Epicrium gl.)*. Zool. Anz. **10**, 194–197 (1887b)

Stensiö, E.: The sensory lines and dermal bones of the cheek in fishes and amphibians. K. Vet. Akad. Handl. Stockholm. Ser. 3, **24**, 1–195 (1947)

Taylor, E.H.: On the caecilian species *Ichthyophis monochrous* and *Ichthyophis glutinosus* with descriptions of related species. Univ. Kansas Sci. Bull. **40**, 37–120 (1960)

Taylor, E.H.: The Caecilians of the World: A Taxonomic Review. Univ. Kansas Press. Lawrence, Ka. pp. 1–848 (1968)

Taylor, E.H.: The lateral-line sensory system in the Caecilian family Ichthyophiidae (Amphibia: Gymnophiona). Univ. of Kansas Science Bulletin **48**, 861–868 (1970)

Wake, M.H.: The reproductive biology of caecilians: an evolutionary perspective. In: Reproductive Biology of the Amphibia. (S. Guttman and D. Taylor, eds.), pp. 73–108. Plenum Press 1977

Wickham, M.G.: Large inclusions in receptor cells in the amphibian lateral line. Am. J. Anat. **138**, 465–480 (1974)

Wright, M.R.: The lateral line system of sense organs. Quart. Rev. Biol. **26**, 264–280 (1951)

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