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DESCRIPTIONS AND ANALYSES OF THE CEPHALIC LATERAL-LINE
SYSTEMS OF THE CYPRINID GENUS HYBOPSIS

By

HARLEY WAYNE RENO

Bachelor of Science
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Stillwater, Oklahoma
1961

Master of Science
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Submitted to the faculty of the Graduate College of
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Scope and Method of Study: Studies on the cephalic lateral-line system of 23 species of Hybopsis were conducted. To demonstrate the lateral-line canals of Hybopsis, canals were blown free of liquid and injected with a mixture of black Indian ink and 50% 2-propanol. Heads of selected specimens of each species (H. monacha excluded) were serially sectioned for histological and cytological examination and enumeration of the canal and skin (superficial neuromasts).

Findings and Conclusions: On the basis of lateral-line canal and brain patterns, eye sizes and positions, barbel lengths, and quantitative and qualitative measurements of neuromasts (canal and skin) and taste buds, it was possible to correlate the known ecologies of some Hybopsis with specialized structures and to speculate on the ecologies of little-known species of Hybopsis.

Histological examination of the lateral-line canals of Hybopsis revealed the epithelial lining to be stratified squamous instead of simple cuboidal and pseudostratified columnar as has been suggested elsewhere. The canal epithelium in all Hybopsis except H. gracilis has few if any goblet cells; consequently, in lieu of mucus, the canals are filled with environmental water in which diatoms and protozoa live.

In face sections of canal neuromasts showed each neuromast to be segmentally connected via "cords of mesenchyme." These cords are described and discussed in relation to the ectodermal origin of the neuromasts.

The superficial neuromasts of H. crameri are unique among teleosts, for each neuromast possesses several (2-9) extracellular, protozoa-like structures. These structures were critically examined and compared with similar structures reported in neuromasts of some anurans and urodels.

The mechanisms of neuromast invagination and effects of neuromasts upon bone formation are discussed. In Hybopsis it was concluded that neuromasts do not evoke bone, but rather are passively enclosed by bone.

Tentative phylogenies for the subgenera Erimystax and Hybopsis are presented and the taxonomic status of H. harperi and H.

labrosa are questioned. It appears that H. harperi is more closely related to members of Hybopsis than to members of Erimystax and that H. labrosa is more closely related to Erimystax than to Hybopsis as currently recognized taxonomically. On the basis of much morphological evidence, it is suggested that the nine subgenera now included in Hybopsis be ressurected to full generic status.

ADVISER'S APPROVAL _____

PREFACE

Use of the cephalic lateral-line system as an index to habitats and ecological requirements of fishes has long been known. This lateral-line study of Hybopsis was conducted to; (1) correlate lateral-line structure with species ecologies; (2) predict probable ecologies of little-known species of Hybopsis; (3) investigate the neuromast-bone relationships in Hybopsis; and (4) erect tentative phylogenies for some subgenera of Hybopsis.

I am indebted to Dr. Rudolph J. Miller, my major advisor, for his assistance and encouragement during the course of this study and his critical examination of this manuscript. Drs. George A. Moore, L. Herbert Bruneau, Bryan P. Glass, and Roy W. Jones served on my advisory committee and also evaluated the manuscript. Sincere thanks is personally extended to Dr. George A. Moore, because it was his initial influence years ago which aroused my interests in fish morphology. Thanks is extended to William F. Wade, George C. Rogers, and C. Stanley Rouk for their many enlightening discussions.

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CHAPTER I

INTRODUCTION

For over a century, the lateral-line system of cold blooded aquatic vertebrates has been of special interest to zoologists, because structural and functional specializations in the system offer interesting problems in adaptive radiation. Allis (1936), Romer (1945), Stensiö (1947), and many others observed that lateral-line systems in many primitive (fossil and extant) vertebrates were well developed and frequently complex, as seen, for example, in Amia (Allis, 1889), Lepisosteus (Collinge, 1893), and Dipnoi in general (Goodrich, 1930). Apparently, from the more primitive fishes with complex lateral-line systems to higher teleosts, there has been a gradual reduction and simplification of the lateral-line system. The cephalic canals are complex with much secondary ramification in the Clupeidae (Tretzakov, 1938; Dijkgraaf, 1962; and Stephens, 1962); less complicated in the Catostomidae (Branson, 1962a); simpler in the Cyprinidae (Lekander, 1949; and Illick, 1956); and still simpler in the Poeciliidae (Gosline, 1949; and Rosen and Mendelson, 1960), Centrarchidae (Branson and Moore, 1962), and Percidae (Hubbs and Cannon, 1935).

Quantitative and qualitative changes in lateral-line systems vary from taxon to taxon, and, in some groups, taxonomic significance has been attributed to canal structure (Hubbs and Cannon, 1935; Goslin, 1949; Bailey, 1951; Illick, 1956; Moore, 1957; and Branson

and Moore, 1962). Major modifications in the system have generally resulted in loss or near loss of side branches, trunk canals, disruption of previously existing canals, or total disappearance of canals, leaving only pit lines to suggest their previous existence (Hubbs and Cannon, 1935; Lekander, 1949; Branson and Moore, 1962; Dijkgraaf, 1962; and Reno, 1966). Among modern cold blooded aquatic vertebrates, pit lines are present in the Agnatha (Wright, 1951), Elassoma (Branson and Moore, 1962), Gymnarchus (Pehrson, 1945), many specialized teleosts (Goodrich, 1930), and larval and certain adult amphibians (Wright, 1951; and Holmgren and Pehrson, 1949).

Lekander (1949) indicated that in more primitive fishes, bones associated with lateral-lines form in connection with neuromasts. These bones, usually tube-like, are secondarily transformed into "lamellar bone"; that is, dermal bone is added secondarily to the latero-sensory elements. In higher teleosts bone continues to form around lateral-line canals, but underneath, separate membranous components appear which may or may not fuse with the overlying lateral-line bones. In fishes lacking canals the lateral-line bones are generally wanting or greatly reduced in size (Branson and Moore, 1962); however, the dermal elements usually persist as normal bones (Lekander, 1949). Not all investigators agree with these phylogenetic generalizations; consequently, numerous papers have appeared elucidating the neuromast-bone relationships in various piscine and amphibian taxa. Allis (1889, 1936), Westoll (1937), Pehrson (1940, 1944), and Branson and Moore (1962) asserted neuromasts are directly responsible for bone formation, while Walther (1882), Moodie (1922), De Beer (1937), Moy-Thomas (1941), Parrington (1949), and Stephens

(1967) suggested that neuromasts lack evocating properties and that bones are derived from sources other than neuromasts. An interjacent view held by Stensiö (1947), Kapoor (1962), and Reno (1966) suggests bones are derived from two sources, i.e., neuromast activities and anasmestic forces.

Although literature on lateral-line structure and function is voluminous, comparatively little is known about the system in the Cyprinidae (Lekander, 1949; and Illick, 1956). Sagemehl (1891) briefly discussed the cephalic canals in minnows, and, a few years later, Andres (1899) discussed the same system in Tinca. Allis (1904) reviewed the canal systems in Carassius and Moxostoma. Manigk (1933) gave a detailed account of the lateral-line system in adult Phoxinus laevis, and Devillers (1944, 1947) discussed the canal system in Leuciscus rutilus. More recently, Lekander (1949) studied the lateral-line ontogeny in one cobitid and four cyprinids, i.e., Phoxinus phoxinus, Leuciscus rutilus, Alburnus alburnus, and Tinca tinca. Illick (1956) researched the cephalic canals in "... eighty-three forms including subspecies, representing thirty-eight genera." Reno (1966) analyzed the cephalic lateral-line system of Notropis volucellus and N. buechanani. Lekander (1949) and Illick (1956) pointed out that in some respects the lateral-line system of cyprinids is unique among fishes. Unlike most fishes, the supraorbital canal is incomplete; that is, connection with the postocular commissure is lacking. Similarly, the preoperculomandibular canal lacks confluence with the same postorbital canal. When these peculiarities are coupled with intrinsic canal variability (Illick, 1956; and Reno, 1966), it is evident that cyprinids in general afford

excellent material for lateral-line studies (Lekander, 1949). Among the diversified groups of minnows, the genus Hybopsis Agassiz is unusually unique and well suited for lateral-line studies, because its members are morphologically quite diverse and occupy a wide variety of aquatic environments (Moore, 1957).

Prior to the present time, studies on Hybopsis have been principally behavioral or ecological (Reighard, 1943; Marshall, 1947; Raney, 1947; and Lachner, 1950, 1952), although the barbels, cutaneous sense organs, breeding tubercles, rugosities, and olfactory apparatus of some have been investigated (Moore, 1950; and Branson, 1962b, 1963, 1966). Davis and Miller (1967) critically analyzed the gustatory apparatus and brain patterns of most species of Hybopsis in an effort to correlate structure and function with species' ecology. The aims of this study are twofold: (1) to provide additional information on phylogeny and ecological requirements of little-known species of Hybopsis; and (2) to investigate the neuromast-bone relationships in these fishes.

CHAPTER II

LATERAL-LINE STRUCTURE AND FUNCTION

Fundamentally, lateral lines develop from the acoustico-lateralis portion of the auditory placode. During ontogeny, most of the placode sinks beneath the skin to become the auditory labyrinth, while the lateral-line component persists superficially, gradually giving rise to the primary neuromast or pit line of the head and body (Allis, 1889; Landacre, 1910; Pehrson, 1922, 1940, 1944; Stone, 1928, 1933, 1937; Stensiö, 1947; Holmgren and Pehrson, 1949; Lekander, 1949; Wright, 1951; Satô, 1956; Branson and Moore, 1962; Hama, 1965; and Stephens, 1967). Lekander (1949) suggested that pit lines develop by any of three means, i.e., (1) direct maturation from the lateral-line portion of the auditory placode; (2) "budding" of primary neuromasts; or (3) spontaneous appearance independent of placodes or primary neuromasts. Stone (1933, 1935, 1937), Bailey (1937), Wright (1951), and Stephens (1967) reached similar conclusions from works on urodeles, Fundulus, anurans, and Dorosoma, respectively. Stone (1928, 1933) further demonstrated that the primary neuromast lines are polarized, the cephalic lines preceding development of trunk lines. According to Stone (1933, 1935, 1937), Speidel (1948), and Lekander (1949), some of the primary neuromasts secondarily bud or divide into smaller superficial neuromasts which generally persist as free sense organs in the skin. As free sense organs, they may be

sunken into pits or crypts (pit organs), elevated on sensory hillocks, or remain exposed as naked neuromasts (Stensiö, 1947; Lekander, 1949; Satô, 1955a, 1955b, 1956; Branson, 1961; Branson and Moore, 1962; Dijkgraaf, 1962; Reno, 1966; and Stephens, 1967). Neuromast division ceases after the primary sense organs sink below the skin and become entrenched in connective tissue tubes (Bamford, 1941). Bone primordia develop around the enclosed neuromasts and eventually form chains of embryonic lateral-line bones which may or may not fuse with the membranous components developing underneath (Stensiö, 1947; Lekander, 1949; Dijkgraaf, 1962; and many others).

Histologically, canal and superficial neuromasts are similar; that is, each is constructed of sense (receptor) and sustentacular supporting) cells (Wright, 1951; Satô, 1955b; Moore, 1956; Branson, 1961; Branson and Moore, 1962; and Reno, 1966). In an intact neuromast (Fig. 1), the centrally placed sustentacular cells extend from the basement membrane to or near the free surface of the organ, instead of terminating at the basal ends of the sense cells as some authors have reported. The more peripheral supporting cells frequently extend above the organ forming a cavity (tremognostic chamber) into which the sense hairs of the sense cells project (Branson and Moore, 1962; and Reno, 1966). Distally, each sustentacular element is intricately bound to its neighbor by a complex system of interdigitations and desmosomes (Hama, 1965; and Iwai, in press). Similar structures (intercellular bridges) were seen by Moore (1956) in Lepomis humilis, and Branson and Moore (1962) in centrarchids. The cytoplasm of these attenuate cells is homogeneous (Branson 1961; Branson and Moore 1962; and Reno 1966); however, Flock and Wersäll

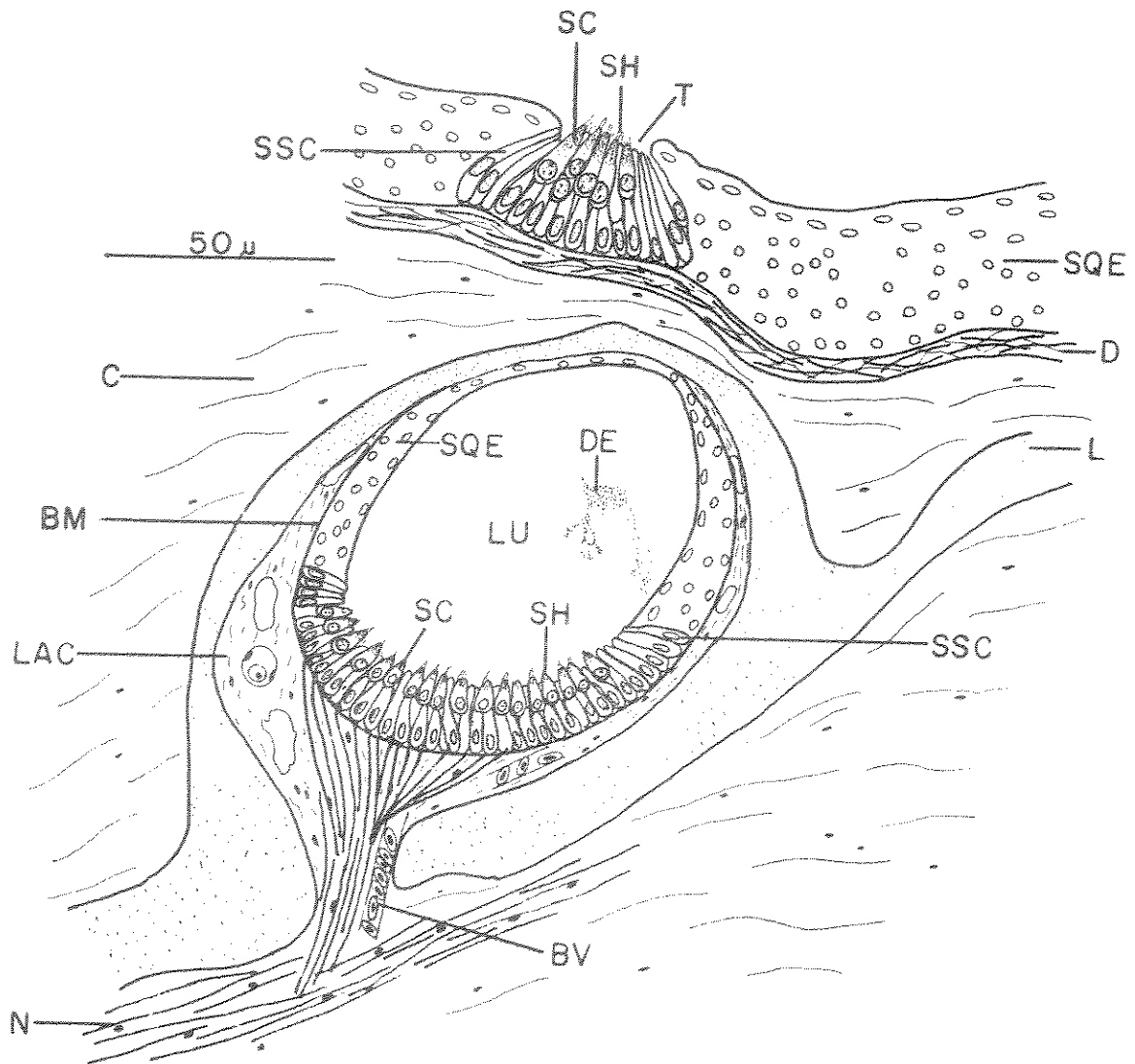


Fig. 1. Transverse section through infraorbital canal neuromast and superficial neuromast of *Hybopsis aestivalis*. BM, basement membrane; BV, blood vessel; C, connective tissue; D, dermis; DE, detritus; L, lachrymal; LAC, loose areolar connective tissue; LU, lumen of infraorbital canal; N, lateral-line nerve; SC, sense cell; SH, sense hair; SSE, stratified squamous epithelium; SSC, sustentacular cell; T, tremognostic chamber.

(1962a), Hama (1965), and Iwai (in press) revealed the ultrastructure to be granular with some supranuclear mitochondria and Golgi apparatus, and paranuclear lamination and membrane folding. Flock and Wersäll (1962a) further illustrated tiny microvilli (apparently nonfunctional) on the apical ends of these cells. The nuclei, ellipsoidal in shape, are basally placed and generally homogeneous throughout (Branson, 1961; Branson and Moore, 1962; and Reno, 1966).

Unlike the sustentacular cells, the sense cells are club-shaped and fewer in number. The large ovate nuclei are basally placed and generally contain numerous dark-staining bodies (chromatin or nucleoli). The supranuclear cytoplasm is highly granulated and apically each cell bears one to several sense hairs (Wright, 1951; Satô, 1955a; Moore, 1956; Moore and Burris, 1956; Branson, 1961; Branson and Moore, 1962; Dijkgraaf, 1962; Van Bergeijk and Alexander, 1962; and Reno, 1966). Ultrastructure studies by Trujillo-Cenóz (1959), Flock and Wersäll (1962a, 1962b), Lowenstein and Osborne (1964), Hama (1965), and Iwai (in press) disclosed that each sense cell actually bears a tuft of sense hairs (cilia); each tuft being composed of a long kinocilium and numerous (25-50) shorter stereocilia. Moreover, as reported by Flock and Wersäll (1962a) and substantiated by Iwai (in press), the kinocilia are alternately arranged on opposite sides of successive ciliary tufts, instead of being topographically polarized on the same side of consecutive tufts as in the labyrinth cristae (Lowenstein and Wersäll, 1959; Trujillo-Cenóz, 1961; and Flock and Wersäll, 1962b). At the base of each sense hair is a small axial filament which has roots in the dark staining cuticular plate immediately below the sense hair bases (Flock and Wersäll, 1962a;

Lowenstein and Osborne, 1964; and Hama, 1965). The cuticular plate is probably homologous to the blepharoplast-like granules seen by Branson (1961) in Cichlasoma cyanoguttatum, and Branson and Moore (1962) in centrarchids. Bedell (1939), Speidel (1949), and Wright (1951) attributed the supranuclear granulation to mitochondria; however, Flock and Wersäll (1962a), Lowenstein and Osborne (1964), and Hama (1965) showed that lysosomes, parts of the endoplasmic reticulum, and the striated organelle also substantially contributed to the granulation. The striated organelle, according to Lowenstein and Osborne (1964), passes from the cuticular plate down through the cytoplasm to synaptic junctions near the basal end of the cells. Although the subnuclear cytoplasm is clear, staining homogeneous throughout (Branson and Moore, 1962; and Reno, 1966), cytoplasmic inclusions, such as multivesicular bodies, synaptic bars, and folding membranes to name a few, have been reported (Flock and Wersäll, 1962a; Lowenstein and Osborne, 1964; and Hama, 1965).

Whether or not lateral-line nerves lose their myelination after penetrating the basement membrane of a neuromast is problematical (Reno, 1966). Recent evidence by Hama (1965) and others, suggests that both myelinated and nonmyelinated nerves innervate the same sense organ, the points of demyelination, probably analogous to nodes of Ranvier, occurring anywhere above or below the basement membrane. Seemingly, neurons (myelinated or not) are interspersed between sustentacular cells, eventually terminating as synaptic bulbs on the basal surfaces of the sense cells (Lowenstein and Osborne, 1964; Hama, 1965; and Iwai, in press). The synaptic bars, folding membranes, and multivesicular bodies of the sense cells are almost always

localized near the synaptic surfaces. The synaptic surfaces per se are smooth and straight or tortuous and interdigitated (Flock and Wersäll, 1962a; and Hama, 1965). According to Flock and Wersäll (1962a) and Hama (1965), the cytoplasm of the nerve endings contain clusters of small mitochondria, numerous irregular-shaped granules (probably glycogen), and varying numbers of vesicles.

That the sense hairs of a neuromast project into the base of the cupula and that the cupula-sense cells system functions as a micro-current receptor is well documented. The cupulae, possibly originating from apocrine activities of the supporting cells (Dijkgraaf, 1962; and Iwai, in press), generally persist as skin structures or are secondarily incorporated into the subdermal canals noted earlier (Dijkgraaf, 1962; Cahn and Shaw, 1962; Branson and Moore, 1962; and Iwai, 1965). Denny (1937), Cahn and Shaw (1962), Dijkgraaf (1962), and others observed the cupulae to be easily destroyed by mechanical abrasion or chemical fixation. Apparently, however, once mechanically destroyed, new cupulae are not regenerated. Reno (1966) further observed that the sense hairs of protected neuromasts (principally pit organs) remained separate and intact despite cupular destruction and that cupular shrinkage during fixation caused the sense hairs of canal organs to be drawn into cones.

With the exception of the enveloping bone, lateral-line canal walls are constructed of two layers, the inner being separated from the outer by the basement membrane (Fig. 1). According to Branson and Moore (1962) and Reno (1966), the inner layer is principally simple cuboidal which gradually changes to pseudostratified columnar epithelium in the vicinity of the sense organs. Generally, goblet

cells are found scattered throughout the epithelium (Branson and Moore, 1962; Van Bergeijk and Alexander, 1962; and Reno, 1966). However, Sharma (1964) indicated that the poreless canals of Notopterus chitala lacked mucous cells. The outer layer is loose areolar connective tissue with some blood capillaries, nerve fibers, and mast cells (Branson and Moore, 1962; and Reno, 1966). Denny (1937) and Van Bergeijk and Alexander (1962), working on Fundulus heteroclitus, observed in this layer, cords of mesenchymal tissue, and supposed the undifferentiated tissue was a "...remnant of the embryonic lateral-line anlage..." since the cells of the cord merged with and changed into the supporting cells of the neuromasts. Jakubowski (1965) observed similar cords in Lota lota and Esox lucius. However, he strongly questioned the term "mesenchymal cord," for he said, "This is supposed to be a remnant of the embryonic anlage of lateral-line neuromasts (placode),..." which is ectodermal in origin. Beard (1884) reported that the canal neuromasts of Salmo fario are segmentally arranged and connected by a cord of embryonic cells. In most instances, each neuromast, generally situated between two consecutive canal pores, is closely associated with a bone foramen through which pass the lateral-line nerves and blood vessels (Branson and Moore, 1962; Van Bergeijk and Alexander, 1962; and Reno, 1966). The vessels, according to Van Bergeijk and Alexander (1962), form extensive capillary beds under each sense organ.

The functions ascribed to the lateral-line system were extensively reviewed by Dijkgraaf (1962) and Branson and Moore (1962). Dijkgraaf (1962) described the lateral-line organs as "'distant touch' receptors" and said:

They serve to detect and locate moving animals (prey, enemies, social partners) at short range on the basis of current-like water disturbances. Their use in obstacle avoidance and rheotactic orientation is of relatively minor importance. They are not engaged in the detection of propagated sonic or infrasonic sound waves, nor are they used as temperature receptors.

Functionally, the principal difference between superficial and canal neuromasts is that the former are directly exposed to external currents, whereas the latter are effected by local currents more or less impinging vertically on the lateral lines. At such angles, a certain amount of water is forced through one or more canal pores, thus vibrating the canal fluid and neuromast cupulae (Dijkgraaf, 1962). Some question has been raised as to how much liquid actually penetrates a canal pore, especially if the pore is small and partially occluded by mucus. Under these circumstances, some intrinsic canal modifications, such as seen by Moore (1956) and Curd (1959) in Lepomis humilis and by me in Ericymba buccata (unpublished data), may serve to amplify or modify the impinging vibrations; thus, the inlet function of the pores is circumvented (Dijkgraaf, 1962).

According to Flock and Wersäll (1962b), the sense cells of lateral-line organs are stimulated by bidirectional displacement of the cupulae, while unidirectional displacement effects the sense cells of the labyrinth cristae. This means that in neuromasts, antero-posterior movement of the cupulae affects equal numbers of kinocilia, whereas the kinocilia of cristae responds to one-way deformation only (Lowenstein and Wersäll, 1959; Trujillo-Cenóz, 1961; Dijkgraaf, 1962; Flock and Wersäll, 1962b; and Iwai, in press). Each time the cupulae are flexed, the sense hairs are deformed and impulses initiated within

each sense cell. How the incipient impulses are conveyed from the sense hairs to the synaptic junctions is questionable, although the axial filaments, cuticular plate, and striated organelle of each cell undoubtedly effect impulse transmission (Lowenstein and Osborne, 1964; Hama, 1965; and Iwai, in press). The functional significance of the synaptic bars and multivesicular bodies is obscure, but their close association with the striated organelle and synaptic membranes suggest that they relay impulses across the synaptic junctions to the end organs of the innervating nerve (Lowenstein and Osborne, 1964; and Hama, 1965). Once across the synapse, impulses may be conducted through a neuromast-associated ganglion (Reno, 1966) or directly to the brain via the lateral-line nerves (Branson and Moore, 1962; Dijkgraaf, 1962; and other).

Several authors, notably Olmsted (1920), Parker and Pain (1934), and Bailey (1937), have indicated that trophic activities of lateral-line nerves are responsible for maintaining neuromast integrity. Harrison (1924), Stone (1937), Bedell (1939), and others disagreed, and argued that lateral-line organs were maintained indefinitely despite denervation. Speidel (1944a, 1944b, 1947, 1948), and Wright (1951), working independently on anurans, established that lateral-line nerves definitely influence neuromast integrity, although the effect of denervation (atrophy) is not immediate.

CHAPTER III

METHODS AND MATERIALS

In this study 450 specimens from 23 species of the genus Hybopsis were examined. Each species, except H. alta which was unavailable, was represented by two or more specimens. Two undescribed forms of the subgenus Nocomis were also studied. Specimens were obtained from collections at Cornell University (CU), Kansas University (KU), University of Michigan (UMMZ), Oklahoma State University (OAM), Tulane University (TU), University of Richmond (UR), and University of Texas (UT) with the locality data below. Parenthetical numbers represent the number of specimens examined from each collection and hyphenated numbers indicate the range of standard length in millimeters.

Hybopsis aestivalis (Girard), speckled chub: (13), 15:XI:1963, Arkansas R., Yell Co., Ark., 31.5-39.0; (2), 6:XII:1960, KU 7266, Wabash R., Clark Co., Ill., 39.5-48.0; (7), 3:IX:1963, Wabash R., Vigo Co., Ind., 32.5-37.0; (7), 23:III:1965, North Fork of Ninnescah R., Sedgewick Co., Kan., 47.0-51.0; (5), 7:IX:1964, Mississippi R., Scott Co., Mo., 24.0-25.0; (5), 16:II:1952, Pearl R., Marion Co., Miss., 35.0-39.5; (3), 23:IV:1964, KU 8064, Pecos R., Chaves Co., N. Mex., 28.0-30.0; (6), 13:IV:1963, KU 8365, Pecos R., Chaves Co., N. Mex., 18.5-27.5; (11), 17:VII:1965, North Fork of Red R., Tillman Co., Okla., 28.0-47.0; (13), 8:VII:1965, Elm Fork of Red R., Greer Co., Okla., 35.0-45.5; (3), 3:VIII:1950, UT 293, San Marcos R.,

Gonzales Co., Tex., 44.0-51.0; (12), 1:IV:1961, KU 5976, Blanco R.,
Hays-Caldwell Co., Tex., 44.0-51.0.

Hybopsis amblops (Rafinesque), bigeye chub: (1), 9:IX:1964, Piny
Cr., Izard Co., Ark., 61.0; (7), 9:IX:1964, Indian Cr., Marion Co.,
Ark., 27.0-34.5; (5), 19:IX:1963, Sugar Cr., Parke Co., Ind., 39.0-
56.5; (3), 1:V:1965, Pearl R., Marion Co., Miss., 45.0-47.0; (7),
6:IX:1964, East Fork of Pigeon R., Sevier Co., Tenn., 33.5-48.0; (7),
20:V:1959, South Indian Cr., Tenn., 47.0-53.5; (8), 31:VIII:1964,
Powell R., Claiborne Co., Tenn., 29.0-57.0.

Hybopsis bellica (Girard), southern chub: (1), 8:IX:1964,
Buttahatchie R., Marion Co., Ala., 56.0; (5), 29:VIII:1964, Ogeechee
R., Warren-Hancock Co., Ga., 42.0-107.0; (1), 7:VIII:1962, TU 29449,
Toxaway R., Transylvania Co., N. C., 154.0.

Hybopsis biguttata (Kirtland), hornyhead chub: (3), 9:IX:1964,
Kings R., Carroll Co., Ark., 57.0-93.0; (2), 2:V:1959, OAM 5722,
Barren Fork Cr., Cherokee Co., Okla., 140.5-150.5; (3), 23:VII:1950,
OAM 4506, Bidding Springs Cr., Cherokee Co., Okla., 51.0-65.5; (4),
10:X:1965, Barren Fork Cr., Cherokee Co., Okla., 34.0-116.0.

Hybopsis cahnii Hubbs and Crowe, slender chub: (2), 31:VIII:1964,
OAM 6126, Powell R., Claiborne Co., Tenn., 35.8-46.5.

Hybopsis crameri Snyder, Oregon chub: (5), 10:VI:1963, Willamette
R., Lane Co., Ore., 23.0-47.0.

Hybopsis dissimilis (Kirtland), streamline chub: (3), 4:IV:1964,
KU 8000, Buffalo R., Marion Co., Ark., 60.0-91.0; (5), 9:IX:1949,
St. Francis R., Butler Co., Mo., 54.0-82.0; (4), 7:IV:1963, KU 7641,
Current R., Shannon Co., Mo., 83.0-94.0; (3), 31:VIII:1964, Powell
R., Claiborne Co., Tenn., 53.0-63.0.

Hybopsis gelida (Girard), sturgeon chub: (2), 17:VII:1940, Mississippi R., Jackson Co., Ill., 30.0-38.8; (2), 24:VIII:1938, Mississippi R., Jackson Co., Ill., 30.0-33.0; (6), 12:VII:1952, KU 2447, Kaw R., Douglas Co., Kan., 44.0-52.0; (3), 17:VII:1940, Republican R., Dundy Co., Neb., 59.0-67.0.

Hybopsis gracilis (Richardson), flathead chub: (1), 1:IX:1941, OAM 5997, Mississippi R., Jackson Co., Ill., 41.0; (2), 24:X:1951, OAM 4700, Kaw R., Douglas Co., Kan., 114.0-147.0; (6), 10:IX:1931, Missouri R., Lafayette Co., Mo., 53.0-81.5; (8), 23:VII:1965, Yellowstone R., Dawson Co., Mont., 53.0-107.5; (6), 22:VII:1965, Redwater R., McCone Co., Mont., 63.0-83.0; (3), 25:VII:1931, UMMZ 92256, Platte R., Dawson Co., Neb., 41.0-46.0; (1), 22:VIII:1959, KU 4961, Bad R., Haakon Co., S. Dak., 61.0.

Hybopsis harperi (Fowler), redeye chub: (15), 30:V:1951, TU 2370, Russ Cr., Jackson Co., Fla., 37.0-46.0; (12), 11:IV:1955, TU 9776, Ichetuchnee Spring, Columbia Co., Fla., 44.0-54.0.

Hybopsis hypsinota (Cope), highback chub: (6), 15:II:1964, Cold Springs, Meriwether Co., Ga., 47.0-51.0.

Hybopsis insignis Hubbs and Crowe, blotched chub: (8), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 48.0-54.0.

Hybopsis labrosa (Cope), thicklip chub: (4), 24:III:1954, CU 19663, South Tyger R., Spartausburg Co., S. C., 39.0-50.0; (2), 7:IX:1964, North Fork of Saluda R., Pickens Co., S. C., 48.0-51.5.

Hybopsis leptocephala (Girard), Carolina Chub: (2), 6:IX:1964, Catawba R., Iredell Co., N. C., 34.0-50.0; (6), 6:IX:1964, Catawba R., Burke Co., N. C., 48.0-60.0; (16), 4:VII:1958, OAM 5992, Roanoke R., Montgomery Co., Va., 44.0-153.0; (4), 7:IX:1963, UR 1973, Catawba

Cr., Botetourt Co., Va., 97.0-154.0.

Hybopsis meeki Jordan and Evermann, sicklefin chub: (5), 1:VIII:1941, OAM 285, Mississippi R., Jackson Co., Ill., 21.0-26.0; (1), 10:IX:1931, Missouri R., Jackson Co., Mo., 45.0; (9), 9:IX:1940, UMMZ 152574, Missouri R., Jackson Co., Mo., 41.0-53.0.

Hybopsis Micropogon (Cope), river chub: (2), 6:IX:1964, Chattooga R., Jackson Co., N. C., 80.0-88.0; (15, 17:VII:1961, OAM 5990, Webb Cr., Sevier Co., Tenn., 49.0-134.0; (6), 31:VIII:1964, Powell R., Claiborne Co., Tenn., 47.0-49.5; (6), 2:VII:1963, UR 1755, North Fork of Holston R., Smyth Co., Va., 107.0-126.0.

Hybopsis Monacha (Cope, Spotfin Chub: (3), 23:IX:1947, UMMZ 157561, South Fork Holston R., Sullivan Co., Tenn., 44.5-51.0.

Hybopsis (Nocomis) sp.₁: (12), 5:VIII:1957, OAM 6127, Wolf Cr., Bland Co., Va., 58.0-146.0.

Hybopsis (Nocomis) sp.₂, bull chub: (15), 5:VII:1961, OAM 5991, Blackwater R., Franklin Co., Va., 50.0-121.0.

Hybopsis plumbea (Agassiz), northern chub: (1), 15:V:1964, Bluewater Cr., Carbon Co., Mont., 76.0; (7), 28:VIII:1965, Cliff Lake, Madison Co., Mont., 47.0-76.0; (3), 22:VI:1961, KU 6972, Bighorn R., Bighorn Co., Wyo., 22.0-33.0.

Hybopsis rubrifrons (Jordan), reface chub: (16), 29:VII:1964, Ogeechee R., Warren-Hancock Co., Ga., 47.0-65.0; (7), 23:VII:1962, TU 29593, Tonaway R., Pickens-Oconee Co., S. C., 55.0-59.0.

Hybopsis storeriana (Kirtland), silver chub: (7), 8:XII:1964, Wabash R., Vigo Co., Ind., 63.0-83.0; (5), 19:IX:1963, OAM 5632, Mississippi R., Scott Co., Ia., 53.0-67.0; (2), 24:VIII:1946, OAM 2426, Illinois R., Sequoyah Co., Okla. 62.5-63.0; (7), 15:IV:1949, OAM 2950,

commissure, across the posterior edge of the cranium to the junction on the other side. When the supratemporal canal was incomplete, pores were counted from the same junction to the canal's terminus lateral to the occiput. Canal systems of smaller species were illustrated with a camera lucida mounted on a binocular dissecting microscope and those of larger species pictures from proportional measurements and freehand drawings.

Specimens prepared for histological or cytological examination were fixed in 10% formalin or Bouin's fluid, decapitated, and the heads decalcified in 2 or 4% acid alcohol. After thorough decalcification, heads selected for histological study were gradually dehydrated in 2-propanol, cleared in acetone or xylene, and infiltrated in vacuo with Tissuemat. Of the two clearing agents, xylene proved the most desirable since tissues tended to harden excessively after prolonged periods in acetone. To enhance dehydration and infiltration, the heads of larger specimens were split logitudinally. After infiltration, heads were embedded in Tissuemat, cut serially with a rotary microtome at 10 μ thickness, mounted on slides, stained with Harris' hematoxylin and eosin, cleared in xylene, and mounted in Piccolyte. Heads selected for cytological study were embedded in celloidin according to Wall's (1932) method; cut with a rotary microtome at 5 or 10 μ thickness; gradually dehydrated in ethanol; stained with Harris' hematoxylin and eosin, Mallory's triply connective tissue stain, or Heidenhain's hematoxylin and phloxine; cleared in terpeneol; and mounted in Piccolyte.

Six arbitrary head regions were selected for making quantitative and qualitative measurements of superficial and canal neuromasts. The regions were: (I) anterior nasal rosette = that part of the snout which

contained the anteriormost olfactory lamellae; (II) posterior nasal rosette = that part of the snout which contained the posteriormost olfactory lamellae; (III) optic nerve head = that point in the eye where the optic nerve fully penetrated the retina; (IV) posterior sclera = that posterior point in the eye where the choroidal pigment vanished from the sections; (V) preopercle bone = that point where the preoperculomandibular canal began to bend dorsad to outline the posterior margin of the bone; (VI) junction of the postocular commissure and supratemporal canal = that point where the two canals

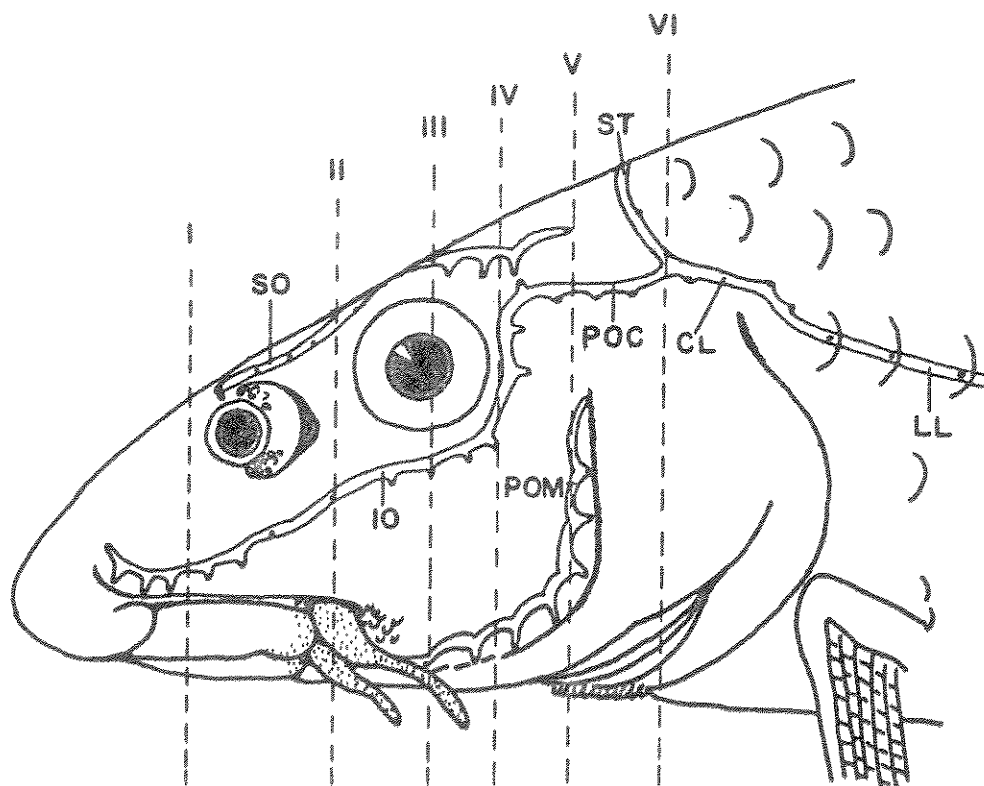


Fig. 2. Six head regions arbitrarily selected for making quantitative and qualitative measurements of superficial and canal neuromasts. I, anterior nasal rosette; II, posterior nasal rosette; III, optic nerve head; IV, posterior sclera; V, preopercle bone; VI, junction of the postocular commissure and supratemporal canal. CL, cephalic lateralis; IO, infraorbital canal; LL, lateralis; POC, postocular commissure; POM, preoperculomandibular canal; SO, supraorbital canal; ST, supratemporal canal.

coalesced into the cephalic lateralis. It must be realized that the distances between these six regions were size-dependent, varying within and between species. Moreover, the sectioning angles were not always perpendicular to the long axis of the head, thus topographical features included in any region varied frequently. Therefore, the slope and spacing of the region lines in Figure 2 are only hypothetical.

The number of integumental and canal neuromasts was calculated for each of the six regions by counting the number of neuromasts in every third section until 13 sections had been examined. In addition, neuromasts in Regions I and II were measured and their position in the canals and skin noted. For each canal organ, the maximum diameter, maximum and minimum height (that distance from the basement membrane to the organ's exposed surface), and maximum diameter of the sensory area was recorded. Maximal and minimal lengths and diameters were recorded for the sensory and sustentacular components of each canal organ. Whenever possible, the number of sense hairs per sense cell and their lengths were tabulated. Similar measurements and counts were made for superficial neuromasts and their cellular constituents. Neuromasts examined cytologically were of Regions I and II. All microscopic measurements were made with a Filar micrometer mounted on a compound, trinocular microscope. Drawings of histological materials were made from photomicrographs taken with a 35-mm camera mounted on the same microscope. The photomicrographs were later traced and reproduced as line drawings.

In 1896, Jordan and Evermann consolidated the genera Hybopsis, Nocomis, Ceraticthys, Erinemus, and Erimystax into the nominal genus Hybopsis. After consolidation, they divided Hybopsis into four subgenera and noted "...a greater number of subordinate groups could be recognized." The genera Hybopsis, Nocomis, and Erimystax were thus given subgeneric status along with the newly created Yuriria Jordan and Evermann, erected specifically for H. (Yuriria) altus (Jordan, 1880) of Mexico. The genus Erinemus was not mentioned, perhaps being accidentally omitted, for they listed Ceraticthys hyalinus Cope, 1868, under the newly acknowledged Hybopsis amblops (Rafinesque, 1820).² This species, described as Rutilus amblops Rafinesque, is the type species for Hybopsis; consequently, Erinemus hyalinus (Cope) is a junior synonym. Other species placed in the subgenus Hybopsis by Jordan and Evermann (1896) were H. labrosus (Cope, 1871b), H. hypsinotus (Cope, 1871b), H. rubrifrons (Jordan, 1876b), and H. storerianus (Kirtland, 1842).

Jordan and Evermann (1896) listed Hybopsis kentuckiensis (Rafinesque) as the only species in the subgenus Nocomis (N. nebrascensis was preceded by the senior synonym Luxilus kentuckiensis Rafinesque, 1820). They noted Semotilus biguttatus Kirtland, 1841; Nocomis bellicus Girard, 1856; Ceraticthys leptocephalus Girard, 1856; Ceraticthys leptocephalus Girard, 1856; and Ceraticthys micropogon Cope, 1865, were synonymous with Hybopsis kentuckiensis.

The subgenus Erimystax acquired several species of questionable relationship, in particular, Hybopsis tetranemus Gilbert, 1887;

²Hybopsis amblops (Rafinesque) (= H. gracilis Agassiz, 1854).

H. aestivalis (Girard, 1856); H. hyostomus (Gilbert, 1885); H. gelidus (Girard, 1856); H. meeki Jordan and Evermann, 1896; H. monacus (Cope, 1868); H. dissimilis (Kirtland, 1841); and H. watauga Jordan and Evermann (In: Jordan, 1888). Couesius and Platygobio were also changed because Couesius milneri (Jordan, 1878) became Couesius plumbeus by virtue of description of Gobio plumbeus by Agassiz, 1850; and Platy-gobio communis because Platygobio gracilis when it was recognized as a junior synonym of Cyprinus gracilis Richardson, 1836.

In their lepidological study of some cyprinids, Cockerell and Allison (1909) placed Hybopsis gelidus (Girard, 1856) in their new subgenus Macrhybopsis. Macrhybopsis remained a subgenus until Jordan (1920) listed it as a full genus with Macrhybopsis gelidus (Girard) the type species. Jordan (1918) formed the monotypic genus Extrarius for Hybopsis tetranemus Gilbert, 1887. Later Jordan (1924) reviewed the genus Hybopsis, recognizing Extrarius, Macrhybopsis, Erimystax, Erinemus, Yuriria, and Nocomis as full genera, and also erecting the new monotypic genus Erimonax for Ceraticthys monacus Cope, 1868, previously listed as Hybopsis monacus (Cope, 1868) by Jordan and Evermann (1896). In the same review Jordan said, "The name Hybopsis, in my judgement, should be restored to the Alburnops group (of Notropis), in which the name gracilis has priority over blennius, stramineus, deliciosus, missuriensis and other recognized synonyms." Hubbs (1926) concurred with Jordan's generic revision of Hybopsis and further noted Erimystax contained two species, E. dissimilis and E. watauga. Hubbs also recognized Erinemus hyalinus and stated, "This is the species usually but apparently wrongly called Hybopsis amblops."

Jordan's decision to change the species composition of Hybopsis

must have been partly influenced by others, because, in his analysis of Hybopsis (Jordan, 1929), he commented, "The analysis of the species of Hybopsis, Hydrophlox, and Cyprinella found within our limits is mainly furnished by Carl Leavitt Hubbs. These genera, with Luxilus and Lythrurus, Mr. Hubbs prefers to unite with Notropis, the oldest name applied to any of these small minnows." Those species formerly of Hybopsis, i.e., H. amblops, H. labrosus, H. rubrifrons, H. hypsinotus, and H. storerianus were placed in the newly resurrected genus Erinemus. Unfortunately, the transposition resulted in some confusion, since Jordan (1929) listed Erinemus as containing only E. hyalinus, E. labrosus, E. hypsinotus, and E. storerianus. Why E. hyalinus was listed in favor of Hybopsis amblops is problematical. The problem was further confounded when Hubbs and Ortenburger (1929b) listed Hybopsis amblops as part of Oklahoma's piscifauna. Moreover, they noted that a color sketch by Agassiz of Hybopsis gracilis (=amblops) made virtually certain that Ceratichthys hyalinus Cope was conspecific with H. amblops.

The genus Extrarius, formerly monotypic, acquired two species from Erimystax, namely Extrarius aestivalis and E. hyostomus. The genus was further enlarged by Hubbs and Ortenburger (1929a) after inclusion of Extrarius sterletus (Cope, 1876), E. marconis (Jordan and Gilbert, 1887), and the new species E. australis Hubbs and Ortenburger, 1929a.

The species Erimystax meeki in Jordan and Evermann (1896) failed to appear in Jordan 1929; consequently, only two species of Erimystax, E. dissimilis and E. watauga were recognized therein.

Nocomis kentuckinesis was not listed in Jordan (1929), whereas

both Nocomis biguttatus (Kirtland, 1841) and N. micropogon (Cope, 1865) were listed under Nocomis. This was doubtless based on Hubbs' (1926) nomenclatural revision of N. kentuckiensis, wherein N. biguttatus, N. micropogon, and the east coast relative, N. leptcephalus, were accorded full specific status. Macrhybopsis, Platygobio, and Couesius remained unchanged through 1929.

In Jordan, Evermann, and Clark (1930) the species of Hybopsis were still those of the Alburnops and Chrioeps groups, although Hybopsis gracilis, the type species of Hybopsis, was listed among them. Furthermore, Erinemus hyalinus, a junior synonym of H. gracilis, was listed among the species of Erinemus recognized earlier by Jordan (1929). Unfortunately, no explanation was offered to clarify the nomenclatural problem created by the two listings. According to Jordan, Evermann, and Clark, the genus Macrhybopsis included Macrhybopsis gelida, M. aestivalis, M. marconis, M. sterletus, M. montana (Meek),³ and M. hyostoma, most of which were taken out of Extrarius.⁴ After loss of most forms, Extrarius again became monotypic with E. tetranemus the only species listed. The species Nocomis biguttatus listed in Jordan (1929) was synonymized with N. kentuckiensis; however N. micropogon was still considered a distinct species. Couesius

³In a footnote Hubbs and Ortenburger (1929a) noted that Hybopsis montana Meek was a synonym of the barbelless Nortopsis dorsalis pipitolepis. Perhaps this information was not available to Jordan, Evermann, and Clark before their Check-list went to press.

⁴Jordan, Evermann, and Clark (1930) changed the spelling of Macrhybopsis gelida, M. monatana, and M. hyostoma from that in Jordan and Evermann (1896) so that the specific names were of the same gender as Macrhybopsis. For the same reason, similar spelling changes were made in other genera.

acquired additional forms, namely C. squamilentus (Cope, 1871a); C. greeni Jordan, 1894; C. dissimilis (Girard, 1856); and C. adustus Woolman, 1895, many of which were revived synonyms of C. plumbeus. Two additional species, Platygobio physignathus (Cope, 1876) and P. pallidus Forbes, 1883, were listed with Platygobio gracilis. The genera Yuriria and Erimonax, represented by Y. alta and E. monacus, respectively, remained monotypic as in Jordan (1924). The genus Erimystax remained as in Hubbs (1926) with E. dissimilis and E. watauga the only species.

A new genus Oregonichthys Hubbs, established for Hybopsis crameri Snyder, 1907, appeared in Jordan, Evermann, and Clark (1930) accompanied by a reference to a paper by C. L. Hubbs which was never published. Schultz and Hubbs (1961), in clarifying the nomenclatural problem, noted the genus had been mentioned earlier in Schultz (1929), and that a diagnosis appeared in Schultz (1931). Oregonichthys crameri was next listed without a diagnosis in Schultz and De Lacy (1935, fide Schultz and Hubbs, 1961), and, shortly thereafter, in Schultz (1936). The species O. cumingii (Günther, 1868) formerly Ceratichthys cumingii, listed in Jordan, Evermann, and Clark (1930) from the type only, was not listed in Moore (1957) or mentioned by Schultz and Hubbs (1961). No reason, other than dubious locality data, has been given for ignoring this species.

Except for minor shifts and groupings (e.g., Notropis harperi Fowler changed to Erimystax harperi⁵), the species composition of

⁵Erimystax harperi, originally described as Notropis harperi by Fowler (1941), was listed as Erimystax harperi by Bangham (1941). This listing was regarded as a nomen nudum by Hubbs and Crowe (1956). Marshall (1947) next listed E. harperi, but without nomenclatural justification.

Hybopsis, Erimystax, Nocomis, Extrarius, Couesius, Platygobio, Oregonichthys, and Yuriria remained rather stable for the next 20 years. Then, in 1951, Bailey placed these separate genera into the single genus Hybopsis which he said, "...is properly to be treated as feminine." Although skeptical of the merger, Hubbs and Crowe (1956) reviewed the subgenus Erimystax and described the species Hybopsis cahni, H. insignis, and H. x-punctata. In the same paper, the spelling of Hybopsis monacha (formerly Erimonax monacus) was discussed. Thus, as recognized today (Moore, 1957), the genus Hybopsis consists of the following species: H. aestivalis, H. amblops, H. bellica, H. biguttata, H. cahni, H. crameri, H. dissimilis, H. gelida, H. gracilis, H. harperi, H. hypsinota, H. insignis, H. leptocephala, H. meeki, H. micropogon, H. plumbea, H. rubrifrons, H. storeriana, and H. x-punctata.

CHAPTER V

CEPHALIC LATERAL-LINE SYSTEM OF HYBOPSIS

According to Dijkgraaf (1962), lateral-line canals presumably appeared when ancient benthic fishes evolved into free-swimming forms or when they invaded lotic environments. Conceivably, these benthic fishes possessed skin neuromasts which functioned in detecting microcurrents; however, once their successors moved into lotic environments or began to swim, the receptor function of the superficial neuromasts was probably interfered with by constant stimulation from currents passing over the body surfaces. By incorporating some of the exposed neuromasts into canals, sensory fatigue might be circumvented, although knowledge of the external environment was undoubtedly modified slightly.

Rauther (1925) first mused that most fishes with well developed lateral-line canals were fast or persistent swimmers, whereas forms with reduced or wanting canals were usually slow or intermittent swimmers, or bottom dwellers. Since 1925, other investigators have substantiated Rauther's generalizations. In particular, Dijkgraaf (1962) observed that the stream-dwelling cobitid Nemachilus barbatulus has cephalic and trunk canals, while its muddy-water cognate Misgurnus fossilis has only a few exposed neuromasts and no canals. He further indicated that the stream-dwelling Neoceratodus of Australia has closed head and trunk canals, while its swamp-dwelling relative

Lepidosiren of Brazil possesses only scattered skin neuromasts.

Branson and Moore (1962) showed that reduced canals occurred in some less active centrarchids inhabiting quiet environments. Reno (1966) observed that the lateral-line canals of the lotic species Notropis volucellus are well developed, whereas they are reduced in the sluggish-water species N. buchanani. Linder (1958) found that eggs of Etheostoma spectabile and E. radiosum fertilized in vitro developed into individuals without most or all of the lateral-line system, yet individuals from natural surroundings have normally developed canals. In the pirate perch Aphredoderus sayanus (Moore and Burris, 1956), the blind cave fish Typhlichthys osbornii (Dijkgraaf, 1962), and some sunfishes of the genus Lepomis (Branson and Moore, 1962), hyperdeveloped parts of the lateral-line system suggest that environmental limitations on other sensory modalities have been compensated for by the lateral-line system.

In general most investigators agree that reduction or simplification of the lateral-line system or hyperdevelopment of specific parts is secondary and, in many instances, indicative of environmental specialization. Gosline (1949), however, warned, "There is no way of knowing that the 'simplest' type of canal system may not be secondarily 'simple' rather than primitive. And there is no reason why a relatively specialized fish might not retain a primitive sensory system." He, along with Illick (1956), also pointed out that differences in the lateral-line system per se do not necessarily represent phylogenetic lines and that a phylogeny should be founded on information from other systems as well, because significance of any one system in phylogeny depends, in part, on how well it agrees

with other systematic characters.

In comparison with those of other taxa, the lateral-line systems of North American cyprinids are comparatively "simple"; that is, the amount of secondary branching is minimal, some canals are commonly incomplete, and, in some instances, canal reduction is maximal. Among the species of Hybopsis, the relative completeness of canals; the size, number, and position of canal pores and canaliculi; and the structure, size, and distribution of skin and canal neuromasts provide some insight into species ecology. These data, in conjunction with studies on the brain patterns and concentration of taste buds (Davis and Miller, 1967), provided substantial foundation on which to base tentative phylogenies for some subgenera within the genus Hybopsis.

The nomenclature used in describing the canals of the cephalic lateral-line system is that of Reno (1966). Unless otherwise stipulated, the canals on the left side of the head are described and, in general, the descriptions are applicable to the corresponding canals on the other side.

Subgenus Extrarius

This subgenus consists of the single species Hybopsis aestivalis which is divisible into six subspecies. In agreement with Moore (1950), no discernible lateral-line differences were observed between subspecies; therefore, the lateral-line system illustrated and described is considered representative of the species (Fig. 3).

In H. aestivalis the usual position of the infraorbital (IO) canal is altered. The canal begins far forward on the snout, gently curves posterodorsad passing below the eye, and bends dorsomesad to the level of the upper margin of the eye. Since H. aestivalis is a

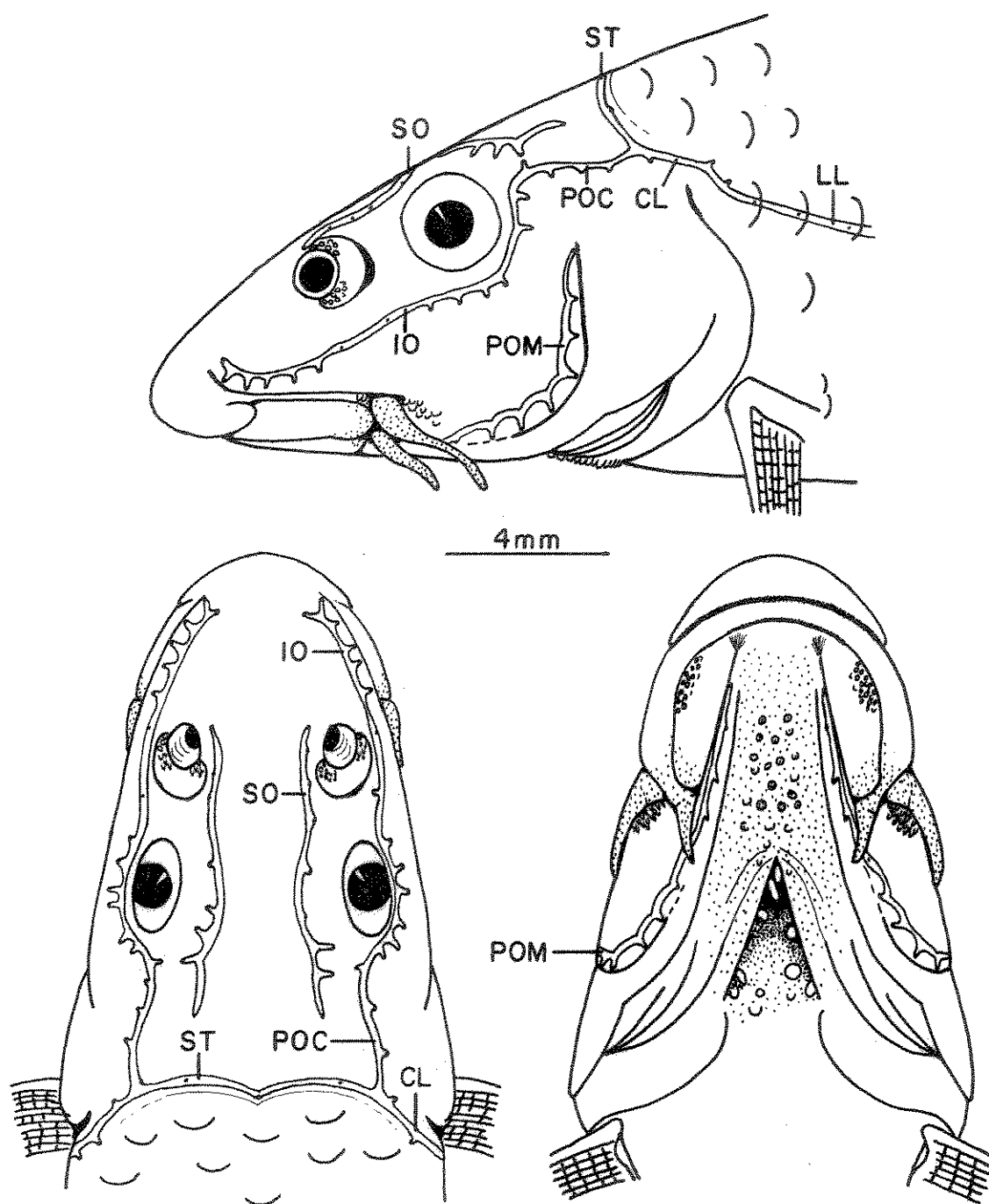


Fig. 3. Three views of *Hybopsis aestivalis* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

bottom-dweller, the tilting of the head axis slightly downward and elongation of the snout account for the lengthening and angular rotation of the IO canal. Posterodorsad to the eye, the IO canal turns sharply caudad, is now termed the "postocular commissure" (POC), continues as a straight line bending dorsomesad prior to confluence with the supratemporal (ST) canal and cephalic lateralis (CL). The POC canal has been variously called the "lateral canal" by Hubbs and Cannon (1935) and Moore (1950), "temporal canal" by Lekander (1949), "cephalic lateralis" by Branson (1961), and as part of the infra-orbital canal by Illick (1956). The CL canal is a short, chevron-shaped tube directed posteroventrad from the POC canal to the body lateralis.

The ST canal, usually conforming to the intersect curvature of the skull and trunk, branches off the POC-CL junction and either partially or wholly traverses the posterior edge of the cranium. As in most cyprinids, the supraorbital (SO) canal is incomplete; that is, it rarely intersects the POC canal. The SO canal begins slightly mesad to the anterior border of the nostril, bends mesolaterad around the nostril, arches mesolaterad over the eye, and terminates approximately midway across the parietal bone dorsomesad to the POC canal. Called the operculomandibular canal by Moore (1950), the preoperculo-mandibular (POM) canal is incomplete, at least no connection with the POC canal was observed. The POM canal, deeply embedded in the flesh of the jaw, starts slightly posterolaterad to the mandibular symphysis, passes caudad across the anteroventral tip of the preopercle, turns dorsad as a series of short arches along the posterior margin of the preopercle, and terminates near the top of the bone.

In H. aestivalis the minute lateral-line pores open directly into the canals or are displaced to the terminal ends of tubular canaliculi. Anteriorly, the canaliculi of the IO canal project downward and open along the dorsolateral margin of the upper lip. Beneath the nostril, canaliculi are usually wanting, although pores are present (compare IO canals dorsal view, Fig. 3), and below and behind the eye the canaliculi are directed ventrad and posteriad, respectively. Where the IO canal intersects the POC canal, a canaliculus projects dorso-mesad toward one from the SO canal. The other POC canaliculi are ventrally positioned, although the last, generally associated with the POC-CL junction, is sometimes displaced dorsally as a member of the ST series or caudally as one of the CL. Other CL canaliculi are usually positioned after the flexure and pointed caudad. The nasal portion of the SO canal lacks canaliculi, instead the pores open directly into the canal. Above and behind the eye, the series of laterally directed canaliculi gradually become longer caudally with the ultimate canaliculus almost reaching its IO equivalent. The parietal portion of the SO canal is considered a canaliculus for reasons to be discussed later. Canaliculi of the POM canal gradually become longer toward the posterior limits of the canal. Those on the mandible are short and directed posteromesad, while those on the preopercle are longer and oriented perpendicular to the exposed edge of the bone.

H. aestivalis is morphologically the most plastic species of Hybopsis, perhaps because it occupies the widest variety of aquatic environments. Davis and Miller (1967) showed that the brain patterns and taste bud concentrations in different forms of H. aestivalis are

indeed, highly plastic and closely correlated with habitats. Fortunately, sufficient specimens were available for statistically testing the variability of pores in each lateral-line canal. Because pore counts in fishes from certain drainages were more variable than others and the oversall number of pores in each canal small, the square root of each pore count was taken so that the transformed data were approximately normally distributed and the means and variances independent and homogeneous. The null hypothesis of no difference in pore counts between drainages was proposed and tested with the appropriate "F" value. All canals except the supratemporal, which is complete or incomplete within populations, were analyzed and only the infraorbital and preoperculomandibular canals proved significantly different at the 0.01 and 0.05 confidence levels, respectively.

Since the analyses provided little information as to which drainages contain statistically different populations, the transformed mean pore counts from each drainage were ranked and analyzed according to Duncan's New Multiple-range Test (Steel and Torrie, 1960). Once the differences were located, the transformed means were squared and plotted (Tables I and II).

Obviously the rankings given in Tables I and II are not discrete, rather overlapping as anticipated. Several points, however, warrant further elaboration.

That the rivers of the Great Plains are muddy through most months of the year and that light penetrates only the first few centimeters of the surface, leaving the major portion of the river devoid of perceptible light, is well documented. In order to thrive and fulfill basic biological requirements in such environments, some morphological

TABLE I

MEAN INFRAORBITAL CANAL PORE COUNTS FOR HYBOPSIS AESTIVALIS
FROM EIGHT RIVER DRAINAGES RANKED BY DUNCAN'S
NEW MULTIPLE-RANGE TEST

Arkansas R., Okla.	Ninnescah R., Kan.	Mississippi R., Mo.	Red. R., Okla.	Pecos R., Tex.		Pearl R., La.	Blanco R., Tex.	Wabash R., Ind.
12.7	13.0	13.5	13.6	14.1		15.5	16.0	16.2

TABLE II

MEAN PREOPERCULOMANDIBULAR CANAL PORE COUNTS FOR HYBOPSIS
AESTIVALIS FROM EIGHT RIVER DRAINAGES RANKED
BY DUNCAN'S NEW MULTIPLE-RANGE TEST

Red. R., Okla.	Ninnescah R., Kan.		Pearl R., La.	Arkansas R., Okla.	Wabash R., Ind.	Pecos R., Tex.	Mississippi R., Mo.	Blanco R., Tex.
10.9	11.0		11.5	11.6	11.7	11.8	12.1	12.4

modifications are necessary. Some forms of H. aestivalis are adapted to such conditions, and, in fact, so well so as to be the most common resident in certain localities. Seemingly, reduced visual acuity has been so successfully augmented by hyperdevelopment of cutaneous sense organs and barbels that individuals in muddy water detect the presence and palatability of food, propinquity of adversaries, and direction of currents without much difficulty. Conversely, some forms dwell in semiturbid and/or clear streams. These forms, usually possessing larger eyes, fewer gustatory organs, and smaller barbels, apparently rely more on sight in securing food and eluding enemies than the accessory sense organs used by their turbid-water cognates (Moore, 1950; and Davis and Miller, 1967).

Apparently water quality quantitatively affects the number of infraorbital canal pores, because mean pore counts from H. aestivalis of muddy rivers (Arkansas, Ninnescah, etc.) are low, higher in rivers of intermediate quality (Pecos), and still higher in semiclear or clear rivers (Pearl, Wabash, etc.). If this trend is real, the mean pore counts given for the Arkansas and Red Rivers indicate that H. aestivalis in these rivers are probably in the process of changing. Some populations of H. aestivalis in the Red River drainage exhibit high pore counts for no apparent reason unless dams constructed in the past have effectively altered turbidities so as to stimulate development of additional pores. Recent construction of dams along the Arkansas has effectively decreased turbidity levels, although insufficient time has elapsed to perceive any changes in mean pore counts. Future investigations on H. aestivalis of the Arkansas may clarify the connections between improved water quality and high pore counts.

According to Moore (1950), past turbidity levels in the Red exceeded those for the Arkansas; therefore, if the mean pore count from the Red were corrected for peculiarities, that is, the abnormally high counts disregarded, the new mean would closely approximate that of the Arkansas. Such mathematical manipulations suggest that the Pecos River is an intermediate quality stream. Indeed, Davis and Miller (1967) observed that the H. aestivalis inhabiting the Pecos are, in some respects, intermediate between and, in others, dramatically different from forms of other drainages.

Water quality effects are seemingly confounded by the data presented in Table II. The drainages which were neatly ordered in Table I are more or less randomly dispersed without regard to turbidity levels. This chaotic arrangement is perhaps the result of H. aestivalis being an epigeal species groping about with barbels and fins touching the substrate. In silty-water forms the suspended particles homogeneously affect the entire lateral-line system, whereas in semi-turbid or clear-water forms microeddies created by the barbels (?) and fins produce turbidities which, in limited areas, approximate those of muddy streams. Conceivably, this might inhibit the development of extra POM canal pores and explain the low variability in pore counts between drainages.

Unfortunately, the effects of turbidity on the lateral-line system were not clarified by quantitative estimates of canal and superficial neuromasts obtained from the few drainages sampled histologically.

Subgenus Hybopsis

At present, the subgenus Hybopsis includes the species H. amblops,

H. hypsinota, H. labrosa, H. rubrinfrons, and H. storeriana. Most manifest few modifications for specific habitat types, albeit large eyes, blunt snouts, and small barbels are characteristic of all but H. labrosa which has long barbels, small eyes, and a terete body.

To date little information is available on the ecology of the group. H. amblops, an inhabitant of small- or medium-size streams of low to moderate gradient, is usually found in pools or riffles with sand or fine gravel bottoms. Apparently, H. amblops is very susceptible to silt, pollutants, and other substances which adversely alter water quality (Trautman, 1957). H. storeriana, found in many lakes and rivers of the Great Plains, evidently prefers areas with sand and/or gravel bottoms. Although dwelling in turbid streams, H. storeriana responds negatively to excessive siltation by moving into smaller streams or less turbid microenvirons (Trautman, 1957). Information on the ecology of the other species is lacking; however, the superficial appearance of the brains and cephalic lateral-line systems, and the quantity and distribution of cutaneous sense organs permit inferences about their ecological requirements.

To develop insight into the ecology of the little known species, the cephalic lateral-line system of H. labrosa is discussed first. For the most part, each lateral-line canal begins, traverses, and terminates in approximately the same areas as those in H. aestivalis (Fig. 4). However, some peculiarities are evident and require elaboration, i.e., the ST canal is incomplete, generally terminating lateral to the occiput, and the POM canal frequently interrupted between the mandible and preopercle. In general the canaliculi are longer, pores larger, and mean pore counts per canal higher in H. labrosa than in

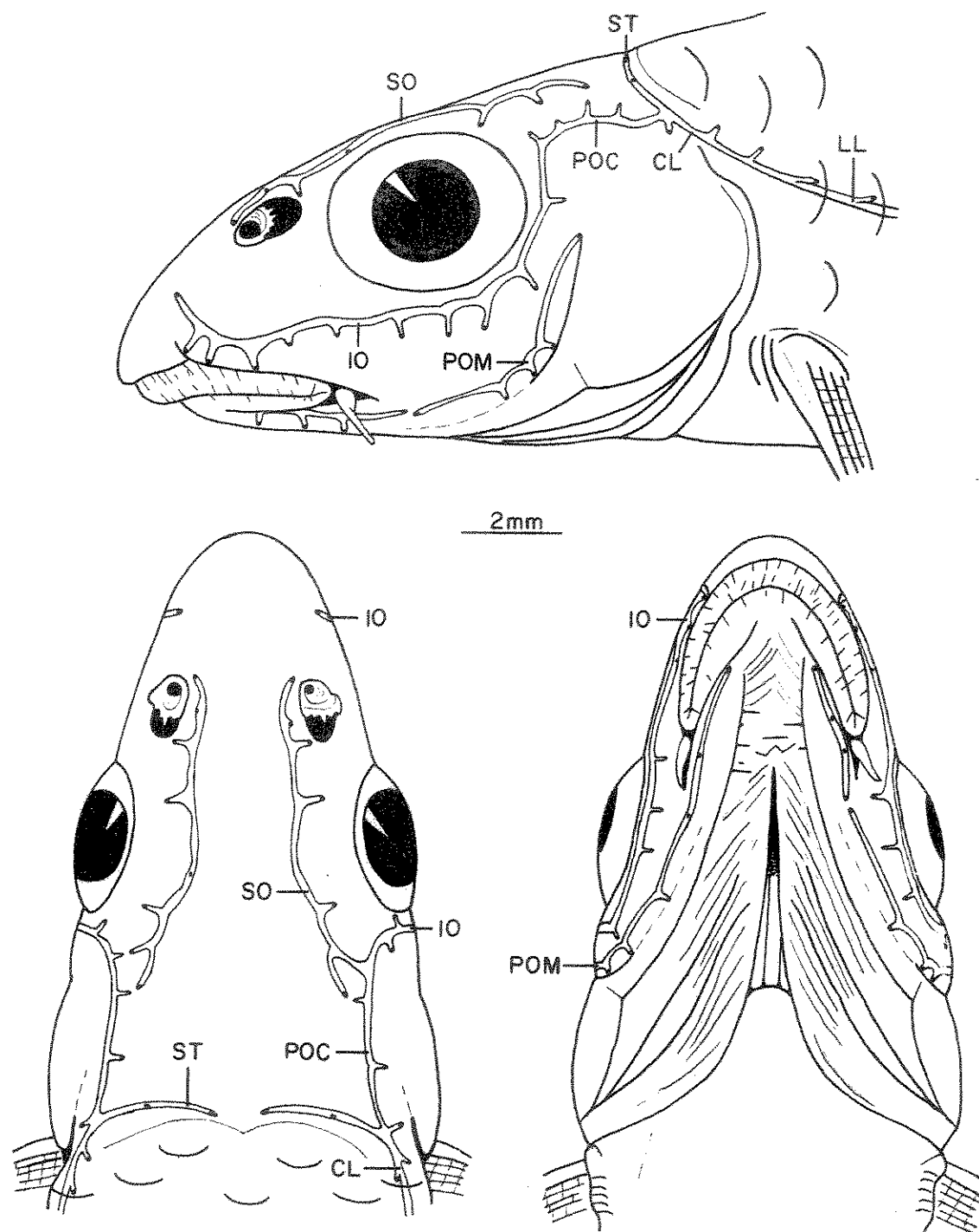


Fig. 4. Three views of *Hybopsis labrosa* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

H. aestivalis (Table III). Unfortunately, only a few specimens of H. labrosa were available for examination; consequently, some means given in Table III (e.g., supraorbital canal) are probably exaggerated and not representative of the species. Anteriorly, 3 IO canaliculi open along the margin of the upper lip, 2 or 3 downward between the nostril and eye, and 3 or 4 below and 1 behind the eye. Unlike H. aestivalis, most POC canaliculi project dorsomesad toward the SO canal, the first or second sometimes fusing with a SO cognate (compare SO canals dorsal view, Fig. 4). The terminal POC canaliculus opens ventrally from the POC-CL junction instead of being variously placed around the junction. The mandibular canaliculi of the POM canal project ventrad and those on the preopercle are reduced in size and concentrated at the bend of the preopercle. Canalicular modifications in other canals are insignificant.

Fide Branson and Moore (1962) and Reno (1966), the total number of sense organs in each canal may be estimated by counting canal pores, since a single neuromast is usually positioned between two consecutive pores. However, this scheme is often erroneous, because pores deleted by canal anomalies or obliterated by outside forces result in two or more organs between consecutive pores. Also, it is sometimes difficult to distinguish between the canal proper and a canaliculus. These sources of error were circumvented by histologically counting the organs in each canal. Disregarding canal variability and extraneous modifications, the mean number of canal neuromasts (Table IV) in H. labrosa and H. aestivalis closely parallel the mean canal pore counts given in Table III. Conversely, the number and distribution of superficial neuromasts seem independent of the canal system (Table V).

TABLE III
MEAN PORE COUNTS AND RANGES FOR EACH CANAL OF THE LATERAL-LINE SYSTEM IN SPECIES OF HYBOPSIS

Species	Infraorbital	Postocular Commissure	Cephalic Lateralis	Supra- orbital	Supra- temporal	Preoperculo- mandibular
<u>Subgenus Extrarius</u>						
<u>H. aestivalis</u>	14.2 (10-19)	2.5 (1-4)	1.9 (0-4)	7.6 (6-10)	*	11.6 (10-14)
<u>Subgenus Hybopsis</u>						
<u>H. hypsinota</u>	11.3 (10-13)	3.6 (3-4)	1.0 (0-2)	7.2 (5-8)	2.3 (1-3)	3.9, 6 (3, 5-5, 7)
<u>H. rubrifrons</u>	12.0 (9-15)	2.3 (0-3)	1.0 (0-2)	8.8 (7-10)	1.5 (1-3)	10.1 (8-12)
<u>H. labrosa</u>	12.5 (10-13)	3.0 (3)	2.0 (1-3)	8.7 (5-10)	2.0 (2)	*
<u>H. amblops</u>	13.2 (9-16)	2.8 (0-4)	1.2 (0-4)	8.9 (7-11)	2.5 (1-5)	10.8 (8-14)
<u>H. storeriana</u>	13.6 (10-16)	2.8 (0-5)	1.6 (0-5)	9.5 (6-12)	4.4 (2-7)	12.4 (10-15)
<u>Subgenus Erimystax</u>						
<u>H. cahni</u>	9.3 (9-12)	2.8 (2-3)	0.8 (0-1)	7.8 (7-8)	3.0 (2-4)	7.8 (7-8)
<u>H. x-punctata</u>	10.5 (8-12)	2.9 (1-5)	2.6 (1-4)	9.3 (7-11)	5.0 (3-6)	8.1 (7-10)
<u>H. monacha</u>	11.0 (10-12)	2.9 (2-3)	2.3 (2-3)	8.0 (7-9)	4.3 (3-5)	*
<u>H. harperi</u>	11.9 (10-14)	3.1 (2-4)	2.1 (1-6)	7.9 (5-10)	1.9 (1-3)	10.1 (7-11)
<u>H. insignis</u>	11.9 (11-13)	2.0 (2)	3.0 (3)	9.6 (8-10)	5.2 (5-6)	7.9 (7-9)
<u>H. dissimilis</u>	12.5 (11-14)	3.3 (2-4)	2.9 (2-4)	10.2 (8-11)	5.5 (3-7)	8.3 (8-10)
<u>Subgenus Nocomis</u>						
<u>H. bellica</u>	11.1 (9-13)	3.8 (2-4)	2.7 (2-3)	8.0 (6-9)	6.8 (3-7)	9.5 (9-11)
<u>H. leptocephala</u>	11.4 (10-13)	4.6 (3-6)	2.6 (1-4)	8.9 (8-11)	6.8 (5-9)	9.0 (7-10)
<u>H. (Nocomis) sp.2</u>	11.5 (10-13)	3.2 (2-4)	2.5 (2-4)	9.2 (8-11)	6.4 (5-9)	9.6 (9-10)
<u>H. micropogon</u>	11.8 (9-14)	3.2 (2-5)	2.0 (0-3)	8.2 (6-10)	5.0 (4-7)	9.0 (7-10)
<u>H. (Nocomis) sp.1</u>	12.9 (11-14)	2.9 (2-4)	2.3 (2-3)	8.9 (7-11)	5.2 (4-7)	10.0 (9-12)
<u>H. biguttata</u>	13.5 (12-15)	4.6 (1-5)	2.2 (1-3)	10.3 (9-12)	6.0 (3-7)	11.4 (9-12)
<u>Subgenus Macrhybopsis</u>						
<u>H. meeki</u>	11.7 (9-13)	4.4 (3-5)	1.7 (0-3)	7.0 (5-8)	2.3 (1-4)	10.2 (8-13)
<u>H. gelida</u>	13.0 (12-14)	4.0 (3-5)	1.9 (0-3)	8.9 (8-12)	4.1 (3-5)	10.1 (7-11)
<u>Subgenus Platygobio</u>						
<u>H. gracilis</u>	11.8 (9-15)	5.1 (4-6)	2.1 (1-3)	8.4 (6-10)	5.5 (4-9)	12.8 (11-16)
<u>Subgenus Couesius</u>						
<u>H. plumbea</u>	12.8 (11-15)	3.6 (2-5)	3.0 (2-4)	8.5 (7-11)	2.4 (1-3)	*
<u>Subgenus Oregonichthys</u>						
<u>H. crameri</u>	*	*	*	*	*	*

* Accurate pore counts were unobtainable, because the canal is complete, incomplete, and/or rudimentary within populations.

Comma (,) denotes canal is incomplete.

TABLE IV
MEAN CANAL NEUROMAST COUNTS AND RANGES FOR EACH CANAL OF THE LATERAL-LINE SYSTEM IN SPECIES OF HYBOPSIS

Species	Infraorbital	Postocular Commissure	Cephalic Lateralis	Supra- orbital	Supra- temporal	Preoperculo- mandibular
<u>Subgenus Extrarius</u>						
<u>H. aestivalis</u>	13.9 (8-15)	2.4 (1-3)	2.1 (1-4)	7.9 (6-9)	*	11.2 (9-13)
<u>Subgenus Hybopsis</u>						
<u>H. hypsinota</u>	9.2 (8-12)	3.0 (2-4)	2.0 (1-3)	6.8 (6-8)	2.1 (1-3)	2.6, 3.3 (2, 5-3, 5)
<u>H. labrosa</u>	11.0 (9-12)	2.7 (2-4)	3.0 (2-4)	6.5 (6-8)	2.3 (1-3)	*
<u>H. rubrifrons</u>	11.2 (9-12)	2.8 (1-3)	2.0 (1-3)	8.1 (7-9)	2.0 (1-3)	9.4 (7-12)
<u>H. amblops</u>	11.5 (8-13)	2.0 (1-3)	3.0 (3)	8.2 (7-10)	2.0 (1-3)	10.0 (7-12)
<u>H. storeriana</u>	13.8 (11-15)	2.3 (1-4)	1.9 (1-3)	9.0 (7-12)	3.9 (1-7)	10.2 (8-12)
<u>Subgenus Erimystax</u>						
<u>H. cahni</u>	8.0 (8)	3.0 (3)	1.5 (1-2)	7.5 (7-8)	2.5 (2-3)	7.0 (7)
<u>H. x-punctata</u>	9.9 (8-11)	3.0 (2-4)	2.6 (1-3)	8.1 (6-11)	2.7 (2-5)	7.1 (6-9)
<u>H. monacha</u>	—	—	—	—	—	—
<u>H. harperi</u>	11.0 (9-13)	2.0 (1-3)	1.9 (1-4)	7.0 (5-8)	1.8 (1-3)	8.3 (6-10)
<u>H. insignis</u>	11.6 (10-13)	1.7 (1-2)	1.7 (1-2)	8.6 (7-10)	4.1 (3-6)	7.3 (5-9)
<u>H. dissimilis</u>	11.8 (8-13)	1.6 (1-4)	2.1 (1-4)	8.7 (7-10)	3.9 (2-6)	7.9 (6-9)
<u>Subgenus Nocomis</u>						
<u>H. bellica</u>	9.8 (7-11)	2.1 (2-3)	1.8 (1-3)	6.9 (5-8)	4.4 (3-6)	8.6 (7-10)
<u>H. (Nocomis) sp.1</u>	10.9 (8-13)	2.1 (1-3)	—	7.0 (6-8)	—	8.8 (7-11)
<u>H. micropogon</u>	11.0 (10-13)	3.1 (2-4)	1.9 (1-3)	7.2 (6-8)	4.1 (2-6)	8.8 (6-10)
<u>H. leptcephala</u>	11.2 (10-12)	3.6 (2-4)	—	7.6 (5-9)	4.9 (4-6)	9.2 (6-11)
<u>H. (Nocomis) sp.2</u>	11.2 (10-13)	2.9 (2-5)	2.0 (1-3)	8.7 (7-9)	6.0 (5-7)	8.9 (8-11)
<u>H. biguttata</u>	11.2 (10-13)	3.3 (1-4)	—	7.6 (5-9)	4.8 (4-5)	10.1 (8-11)
<u>Subgenus Macrhybopsis</u>						
<u>H. meeki</u>	10.6 (8-12)	3.8 (3-5)	—	5.1 (4-6)	1.8 (1-3)	8.7 (6-10)
<u>H. gelida</u>	—	—	—	—	—	—
<u>Subgenus Platygobio</u>						
<u>H. gracilis</u>	9.8 (9-11)	4.0 (4)	—	7.3 (6-8)	4.8 (3-6)	12.5 (12-13)
<u>Subgenus Couesius</u>						
<u>H. plumbea</u>	11.1 (10-12)	3.0 (2-4)	2.0 (2)	7.5 (7-9)	2.0 (1-3)	8.7 (7-9)
<u>Subgenus Oregonichthys</u>						
<u>H. crameri</u>	*	*	*	*	*	*

* Accurate canal neuromast counts were unobtainable, because the canal is complete, incomplete, and/or rudimentary within populations. Other symbols as in Table III.

TABLE V

MEAN SUPERFICIAL NEUROMAST COUNTS AND RANGES FROM SIX HEAD REGIONS IN SPECIES OF HYBOPSID

Species	I	II	III	IV	V	VI
<u>Subgenus Extrarius</u>						
<u>H. aestivalis</u>	6.8 (2-11)	4.4 (1-9)	6.4 (2-12)	4.9 (0-9)	4.4 (1-6)	1.6 (1-3)
<u>Subgenus Hybopsis</u>						
<u>H. hypsinota</u>	5.0 (5)	3.0 (3)	5.0 (5)	7.0 (7)	2.0 (2)	—
<u>H. storeriana</u>	5.0 (1-9)	2.3 (0-9)	7.0 (6-8)	4.5 (3-6)	1.2 (0-4)	0
<u>H. labrosa</u>	10.0 (10)	6.0 (6)	4.0 (4)	1.0 (1)	0	0
<u>H. rubrifrons</u>	24.0 (21-27)	8.5 (6-11)	17.0 (10-24)	22.0 (12-32)	22.0 (20-24)	5.0 (3-9)
<u>H. anbllops</u>	73.6 (25-154)	82.0 (20-140)	77.5 (28-139)	65.5 (31-94)	51.0 (27-81)	10.5 (0-28)
<u>Subgenus Erimystax</u>						
<u>H. cabni</u>	6.0 (6)	3.0 (3)	3.0 (3)	5.1 (4-6)	1.0 (1)	—
<u>H. x-punctata</u>	7.8 (4-11)	1.5 (0-3)	3.0 (2-4)	2.1 (1-3)	1.0 (0-2)	—
<u>H. insignis</u>	8.0 (3-12)	2.0 (1-3)	3.2 (1-4)	3.4 (1-5)	5.0 (1-6)	2.6 (1-3)
<u>H. dissimilis</u>	9.3 (5-14)	3.5 (2-5)	7.3 (6-8)	5.3 (2-9)	8.0 (3-14)	2.7 (2-3)
<u>H. harperi</u>	10.2 (8-12)	6.4 (2-9)	7.5 (3-13)	9.6 (7-14)	20.7 (12-30)	6.4 (3-9)
<u>H. monacha</u>	—	—	—	—	—	—
<u>Subgenus Nocomis</u>						
<u>H. lentoccephala</u>	6.5 (5-8)	2.3 (0-6)	2.0 (1-3)	2.3 (2-4)	1.8 (0-4)	0
<u>H. bellica</u>	8.8 (0-15)	2.3 (0-5)	4.0 (0-8)	4.5 (0-11)	7.0 (5-11)	2.5 (2-3)
<u>H. micropogon</u>	10.0 (8-12)	1.3 (0-3)	5.0 (3-6)	4.0 (4)	2.0 (1-3)	0
<u>H. (Nocomis) sp.2</u>	10.8 (9-13)	1.8 (0-3)	2.3 (2-3)	3.6 (2-6)	2.0 (2)	—
<u>H. biguttata</u>	14.8 (8-19)	5.2 (3-9)	4.4 (2-8)	6.9 (3-13)	6.9 (5-9)	1.2 (0-3)
<u>H. (Nocomis) sp.1</u>	21.3 (17-25)	1.3 (1-2)	2.7 (1-4)	2.3 (1-4)	5.0 (2-7)	—
<u>Subgenus Macrhybopsis</u>						
<u>H. gelida</u>	5.5 (2-9)	8.0 (6-10)	7.5 (5-10)	2.5 (2-3)	5.5 (4-7)	1.0 (1)
<u>H. meeki</u>	17.5 (4-30)	22.8 (7-41)	23.3 (13-36)	17.0 (5-40)	19.7 (3-70)	7.8 (3-15)
<u>Subgenus Platygobio</u>						
<u>H. gracilis</u>	24.4 (12-40)	7.0 (2-18)	7.6 (3-11)	6.6 (4-10)	7.6 (4-12)	1.5 (1-2)
<u>Subgenus Couesius</u>						
<u>H. plumbea</u>	11.8 (5-18)	7.7 (4-12)	12.2 (2-13)	8.4 (1-16)	8.2 (1-18)	4.8 (3-9)
<u>Subgenus Oregonichthys</u>						
<u>H. grameri</u>	27.0 (24-29)	14.0 (12-16)	20.5 (13-28)	27.0 (15-39)	42.0 (31-52)	14.5 (14-15)

I = anterior nasal rosette; II = posterior nasal rosette; III = optic nerve head; IV = posterior sclera; V = pre-opercle bone; VI = junction of postocular commissure and supratemporal canal.

In H. aestivalis the small eyes, minute canal pores, large barbels, and shovel-like head are adaptations for a benthic existence in turbid-water of moderate to fast flow. Similarly, the large barbels, larger eyes and canal pores, and general body appearance of H. labrosa suggest that it, too, is a bottom-dweller, although living in less turbid waters. The similarity of lateral-line systems and large number of cutaneous taste buds in each species (Davis and Miller, 1967) further substantiate this supposition. Moreover, the restricted distribution of superficial neuromasts (Table V) and limited geographical range indicate that the habitat of H. labrosa may be more narrow than previously anticipated. Perhaps only the head is in direct communication with the environment and the rest of the body sheltered by any of several means. With the head exposed, the presence and edibility of food, and proximity of social partners could be easily detected, yet the remainder of the body poised for response to adverse stimuli.

With respect to the other species of Hybopsis, the lateral-line systems are very similar, although conspicuously different from H. labrosa (Figs. 5-8). Unlike H. labrosa, the anteriormost segment of the IO canal in the other Hybopsis is rotated posteriad toward the anteroventral tip of the nostril and, from the edge of the upper lip, the canal extends posteriad toward the eye, eventually outlining the ventral and posterior margins of the orbit. The POC canal arches caudad, straightening prior to confluence with the ST and CL canals. In H. amblops and H. hypsinota (Figs. 6 and 8), the CL canal is posteriorly angulate and in H. storeriana and H. rubrifrons rectilinear (Figs. 5 and 7). In all Hybopsis except H. labrosa, the SO canal, beginning anteromesad to the nostril, extends straight

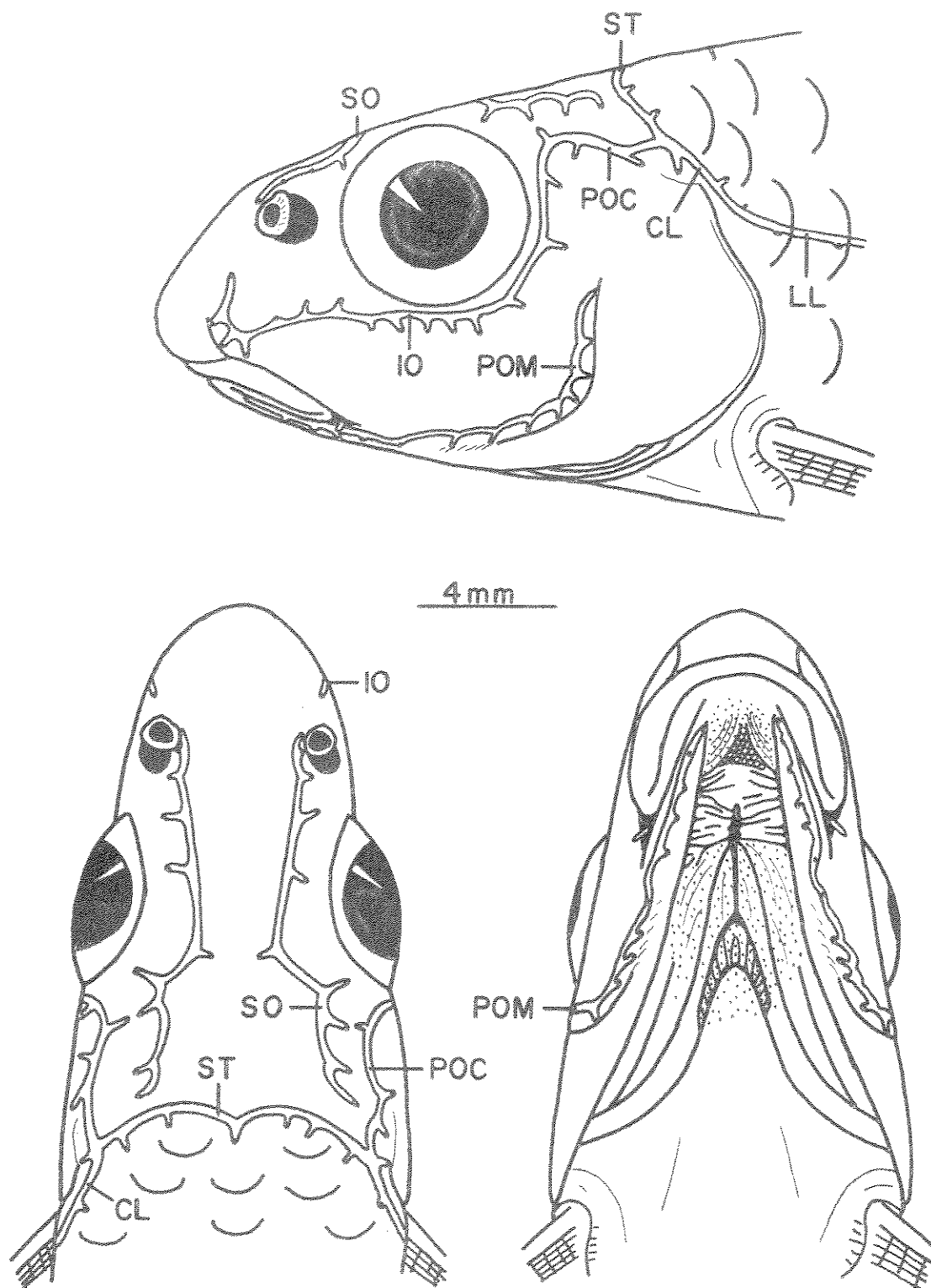


Fig. 5. Three views of *Hybopsis storeriana* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

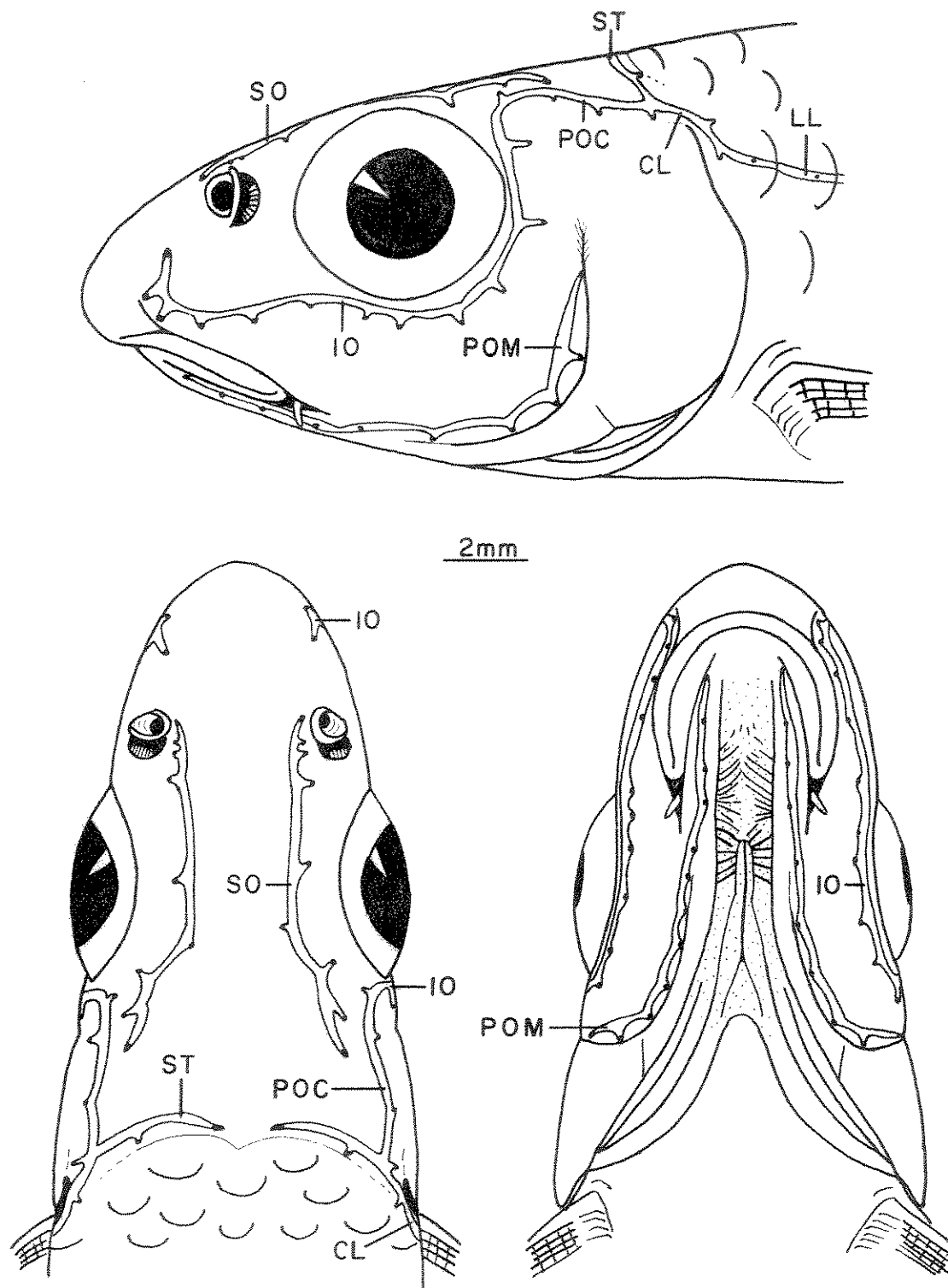


Fig. 6. Three views of *Hybopsis amblops* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

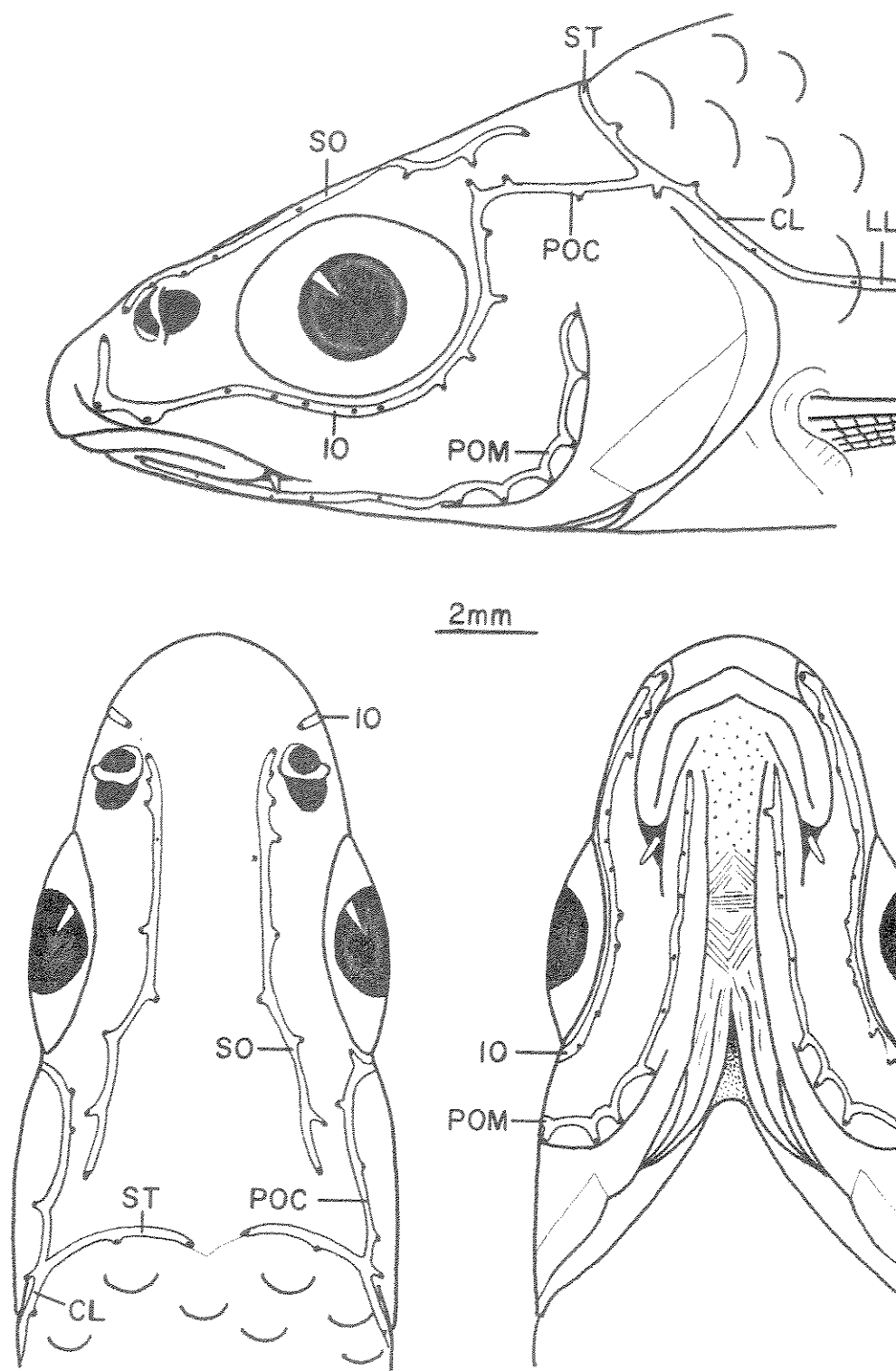


Fig. 7. Three views of *Hybopsis rubrifrons* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

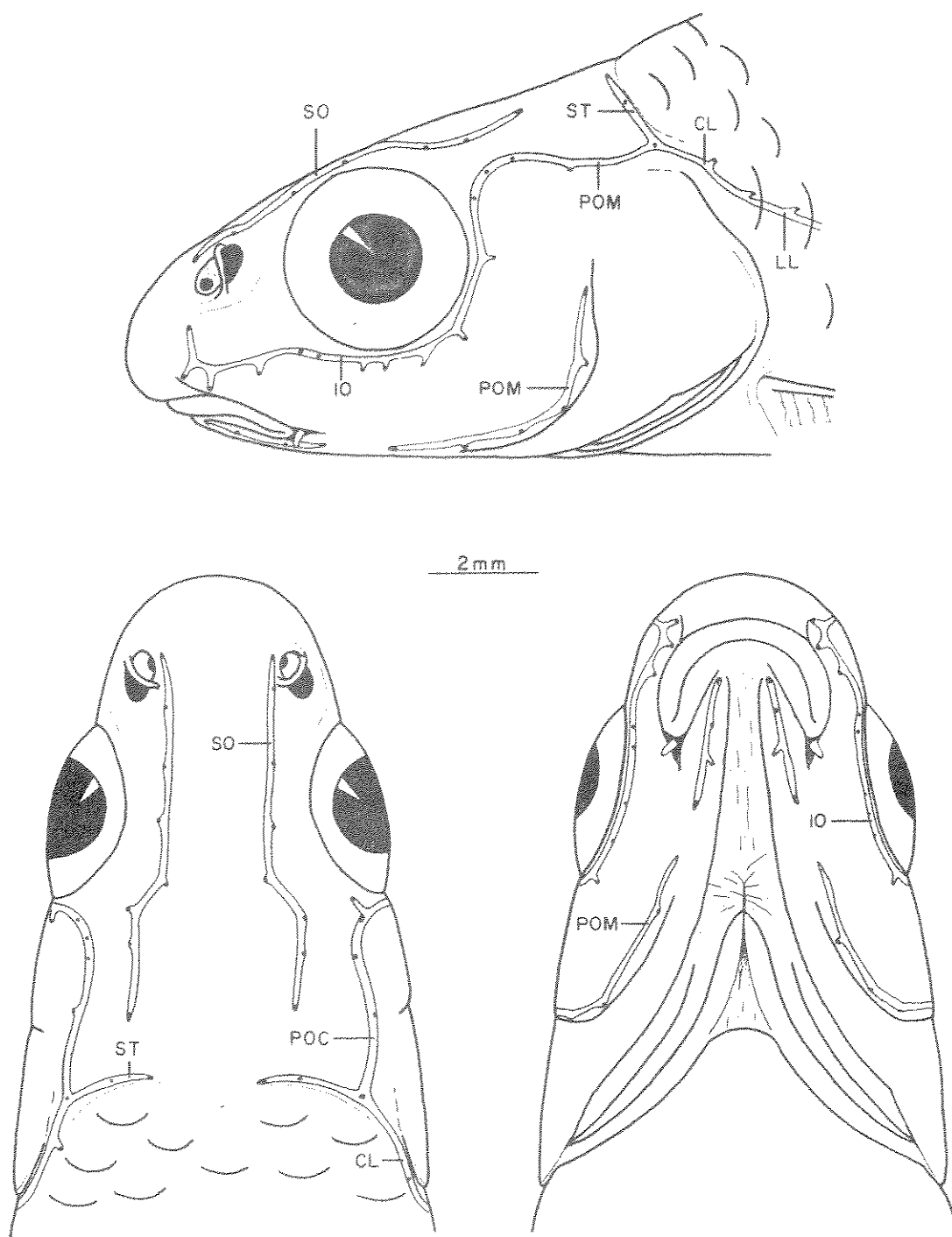


Fig. 8. Three views of *Hybopsis hypsinota* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

posteromedial over the eye, bends sharply laterad behind the eye, and terminates about midway across the parietal. The ST canal, complete in H. storeriana, is incomplete in the others, usually terminating paraocciput. The POM canal is complete in all except H. hypsinota, the interruption being between the mandible and preopercle.

Despite discontinuity in some canals, significant lateral-line differences exist between species. In the main, lateral-line heterogeneity is probably the result of differences in size, number, and arrangement of canal pores and canaliculi. As pointed out earlier, inhabitants of silty streams usually possess long canaliculi, larger pores, and, occasionally, incomplete canals. In addition, species living in lentic- or lotic-like environments exhibit lateral-line peculiarities indicative of one environment or the other. With the habitat of H. storeriana variable and often transitory, the canaliculi, as expected, are of intermediate length and the canal pores small (Fig. 5). Davis and Miller (1967) suggested that H. amblops, and perhaps H. rubrifrons and H. hypsinota, avoid high-gradient streams scoured free of sand and detritus, because of reduced visual acuity and poor ability to locate food chemically under such conditions. Since the pores are large and the canaliculi variously modified, being small in H. amblops, reduced in H. rubrifrons, and virtually absent in H. Hypsinota (Figs. 6-8), it is highly improbable that the lateral-line systems in any of these fishes could function normally in adulterated environments without soon becoming filled with debris. More specifically, the larger pores and reduced canaliculi of H. rubrifrons suggest that its streams may be of better quality, or more than likely, of lower gradient than those of H. amblops. Conceivably, H. rubrifrons

lives in stream areas where the currents are not strong nor are the surroundings lentic-like. Canal disruptions and canalicular loss indicate that H. hypsinota may be a lentic-like species; that is, it perhaps lives in pools or microenvirons where currents are practically imperceptible.

From H. storeriana to H. hypsinota, the mean number of pores and canal neuromasts per canal gradually decrease (Table III-IV). Despite higher numbers in some species (e.g., H. aestivalis), other factors than water quality may modify the structure of the lateral-line system. Structural simplification of the canals (i.e., canal descriptions, formation of gutters, etc.) tends to increase the number of superficial neuromasts, since the primary neuromasts remain in the skin rather than being secondarily incorporated into connective tissue tubes. However, superficial neuromasts are sparse in H. hypsinota, but exceedingly abundant in H. amblops and H. rubrifrons (Table V), thus indicating that none of the above factors exhibit absolute control. Perhaps some aspect of their behavior (schooling or spawning?) is facilitated by large numbers of ventral and lateral skin neuromasts.

As noted above, the lateral-line system develops early during ontogeny and evidently most of the neuromasts are laid down at that time. If the space between organs increases as an individual grows, the number of cutaneous neuromasts viewed histologically at any point should diminish proportionally. However, should superficial neuromasts be added periodically throughout life, the number of sense organs, when viewed microscopically, would remain constant or increase with growth. Indeed, superficial neuromasts quantitatively decrease with respect to length and, unlike cutaneous taste buds, (Davis and

Miller, 1967), few if any are added secondarily (Fig. 9).

Subgenus Erimystax

The subgenus Erimystax includes the nominal species H. cahni, H. dissimilis, H. harperi, H. insignis, H. monacha, and H. x-punctata. With the exception of H. harperi, all Erimystax appear to be bottom inhabitants adapted to riffle habitats in clear, fast-flowing streams (Davis and Miller, 1967).

In general the lateral-line systems are similar in all Erimystax but H. harperi and, because differences are minimal, it is difficult to select one species as a basis for comparison. The cephalic lateral-line system of H. monacha (Fig. 10) resembles that of H. labrosa (Fig. 4) much more than do other species of Erimystax. As in H. labrosa, the IO canal of H. monacha begins far forward on the snout, gradually arches posteroventrad connecting 3 supralabial canaliculi, passes posterodorsad to intersect several minute canaliculi below the eye, and then turns dorsad behind the eye where canaliculi are few or lacking. Since POC canaliculi are absent, evidently this canal is not as intimately associated with the SO canal as its homologue in H. labrosa (compare SO canals in Figs. 10 and 4). The CL canal of H. monacha is curved slightly posteroventrad (almost chevron-shaped) and the pores variously placed along its entirety. Unlike H. labrosa, the ST canal is complete and in both the SO canals similar, although in H. monacha, where the canal bends behind the eye, a single canaliculus projects posteromedially toward the midline of the head. As in H. labrosa, the POM canal is often interrupted between the mandible and preopercle; however, the preopercle canaliculi are more evenly spaced

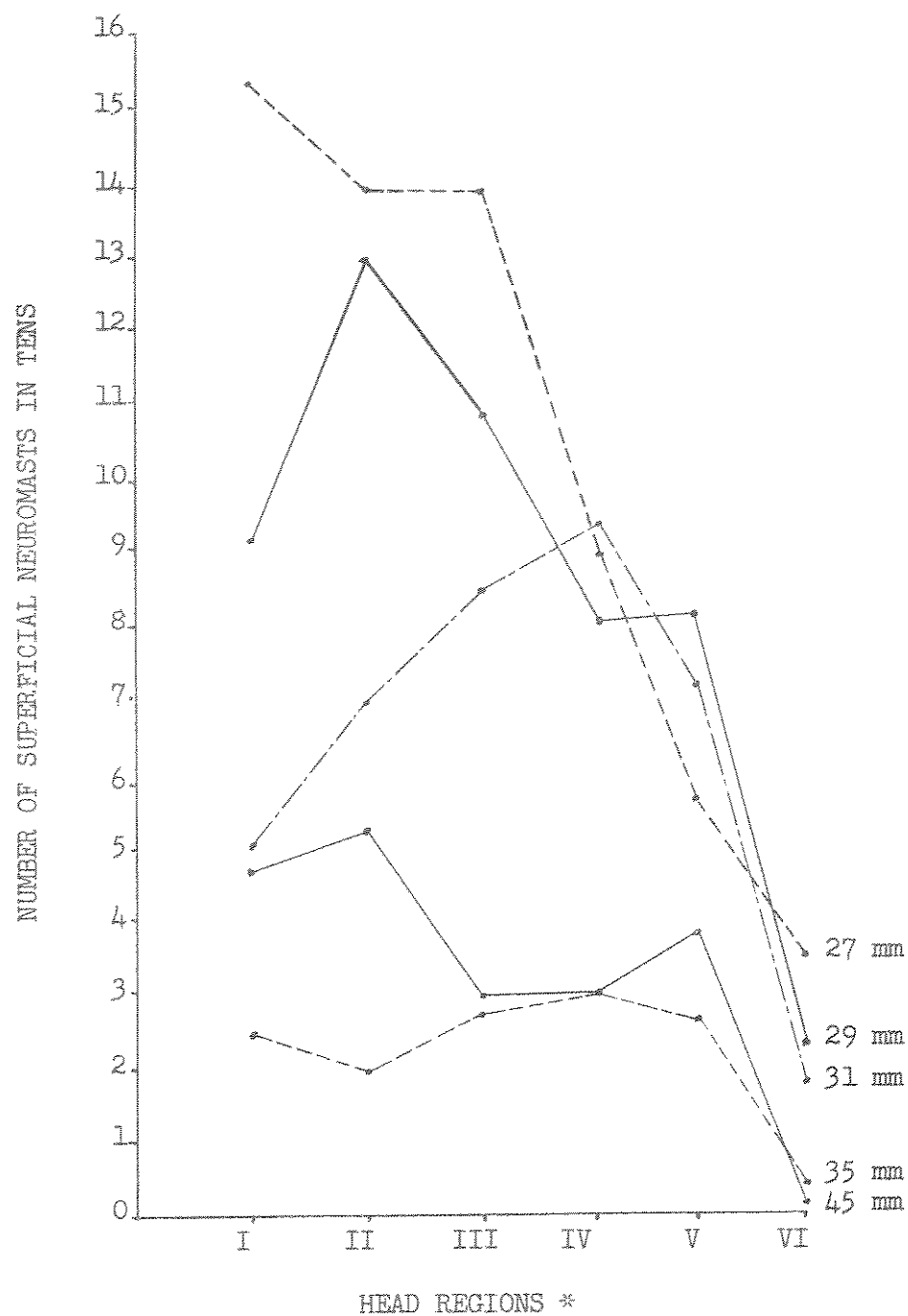


Fig. 9. Quantitative comparison of superficial neuromasts between six head regions of *Hybopsis amblops*. Measurements are standard length. *Head regions as in Fig. 2.

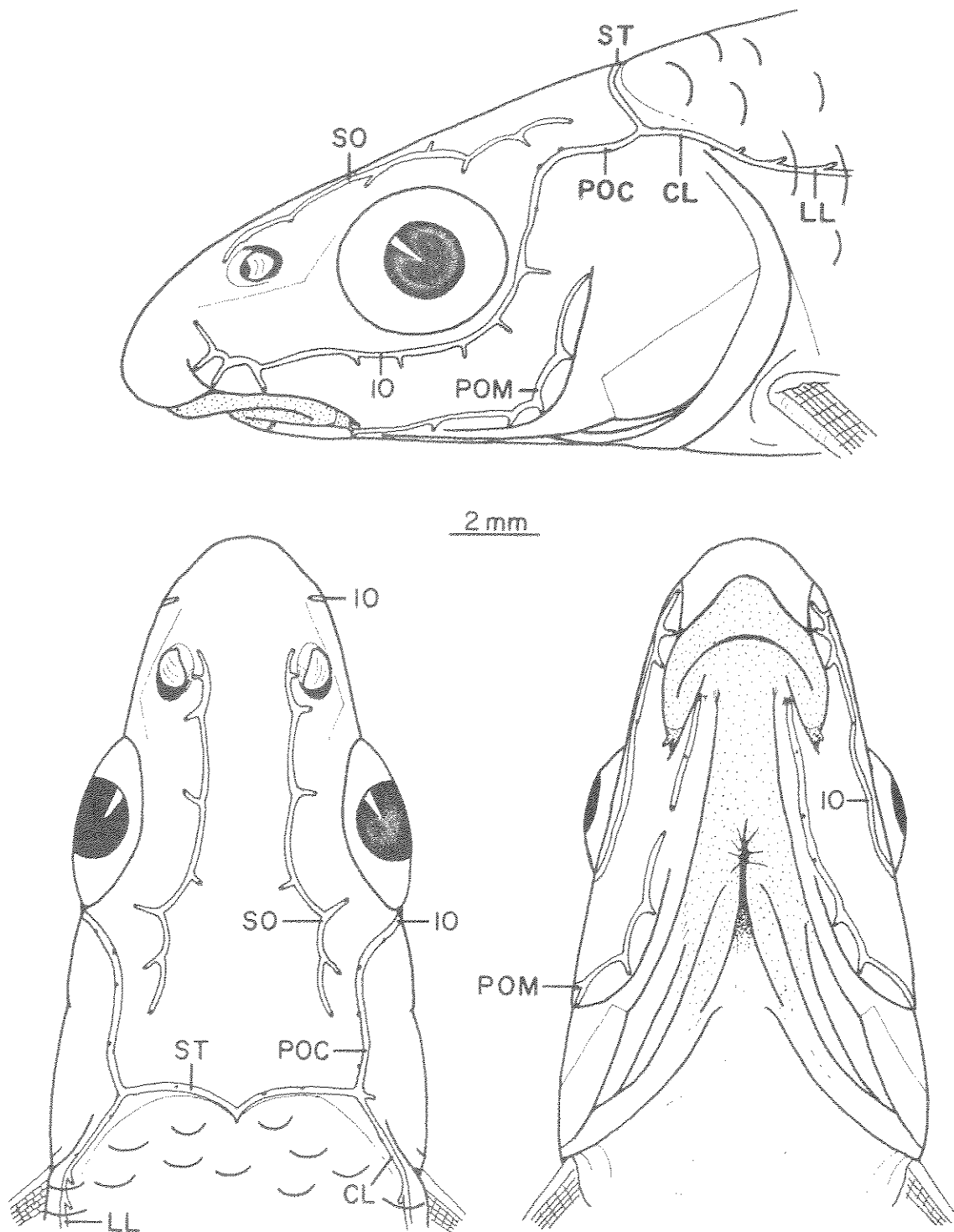


Fig. 10. Three views of *Hybopsis monacha* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

along the margin of the preopercle than in H. labrosa. Mean pore counts per canal for the two species are similar (Table III). Mean canal and skin neuromast counts were not available for H. monacha since specimens were not prepared histologically.

Since the lateral-line system of H. harperi is unique, it will be discussed separately below. Unlike H. monacha, the IO canal of the remaining species of Erimystax begins slightly rostrad to the nostril and passes ventrad toward the lip where it intersects 2 canaliculi. These canaliculi are long and slender in H. x-punctata, and H. cahni (Figs. 11-12), of medium length in H. insignis (Fig. 13), and small and, in part, contiguous in H. dissimilis (Fig. 14). The third canaliculus of the series seen in H. monacha is reduced in each and, in some, displaced posteriad. From the lip, the IO canal turns posterodorsad toward the eye, connecting several long canaliculi in H. x-punctata (The dorsal IO canaliculus pictured in Fig. 11 lateral view is considered anomalous), several smaller canaliculi in H. cahni and H. insignis, and only ventrally placed pores in H. dissimilis. In the 4 species the adorbital segment of the IO canal bears medium to long canaliculi. As in H. monacha, the POC canal of each species arches posteriad and straightens mesoposteriad prior to joining the ST and CL canals. In H. x-punctata and H. dissimilis 2 (rarely 1) canaliculi project dorsad toward members of the SO canal, whereas in H. insignis and H. cahni 1 (rarely 2) canaliculus projects dorsad. At the POC-CL junction, only H. cahni has ventrally directed canaliculi, in the other species, the canaliculi are directed posteriad. Unlike H. monacha, the CL canal of each species is rectilinear, with the canaliculi in H. x-punctata and H. insignis pointed posteromesad and in H.

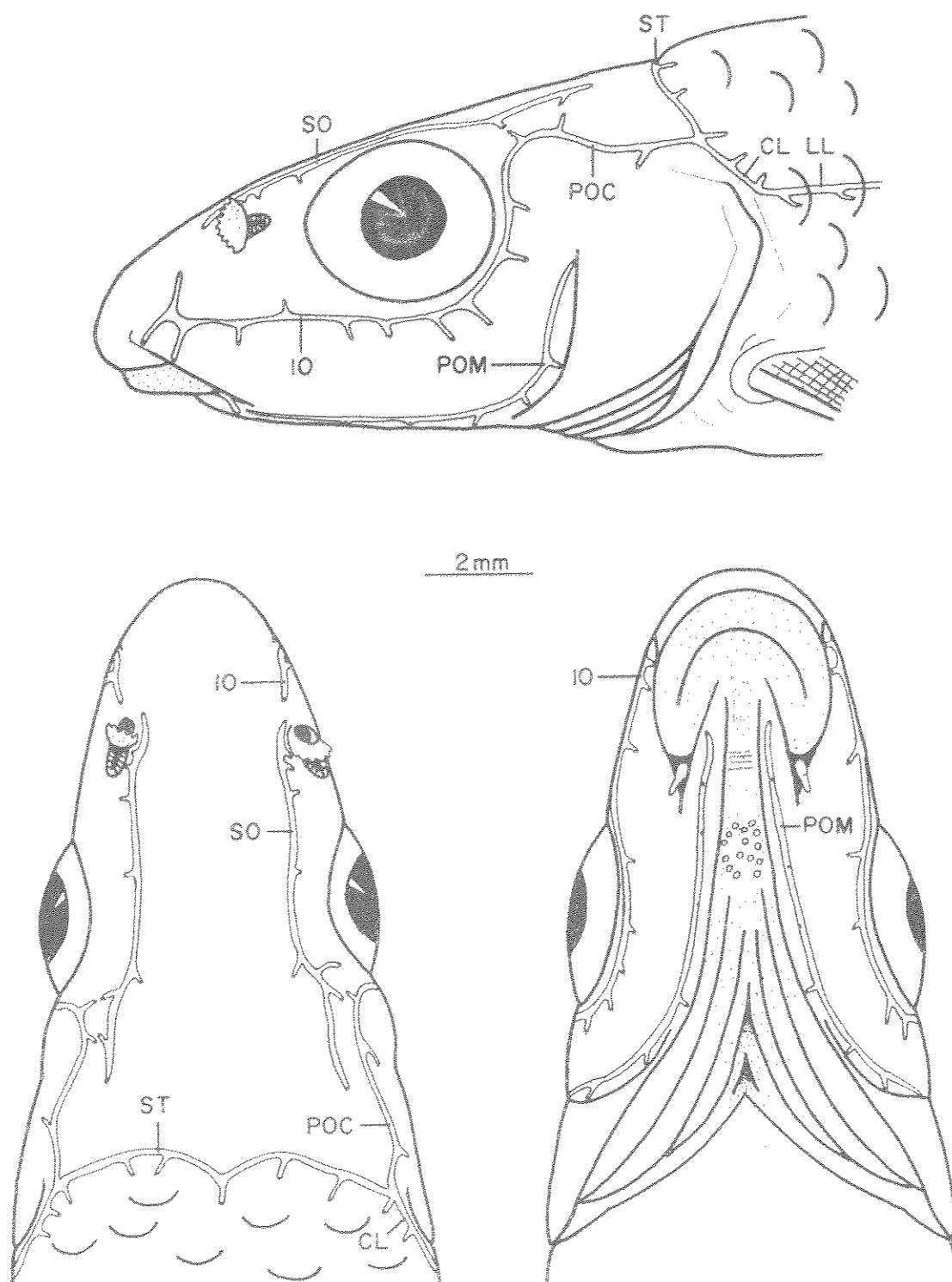


Fig. 11. Three views of *Hybopsis x-punctata* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

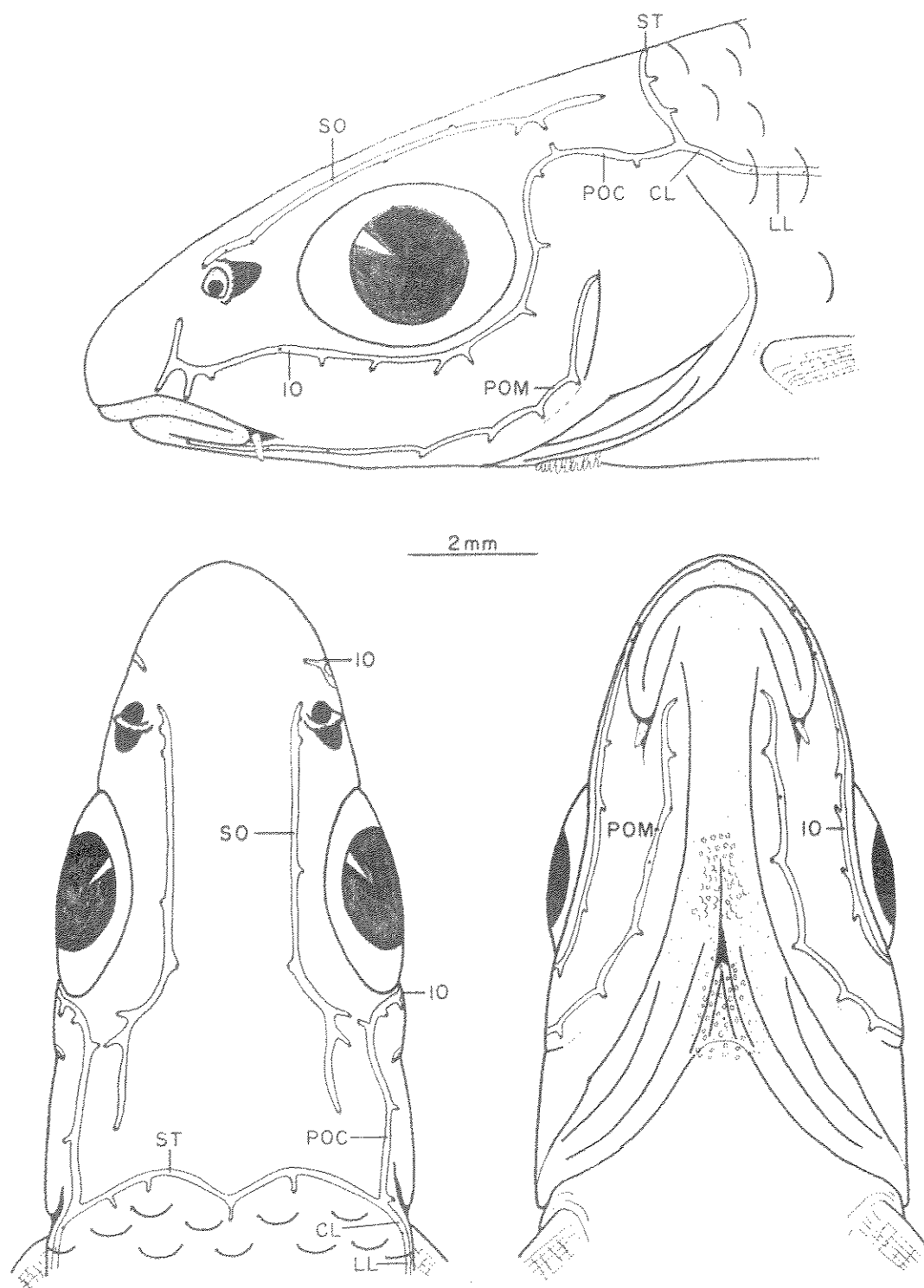


Fig. 12. Three views of *Hybopsis cahnii* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

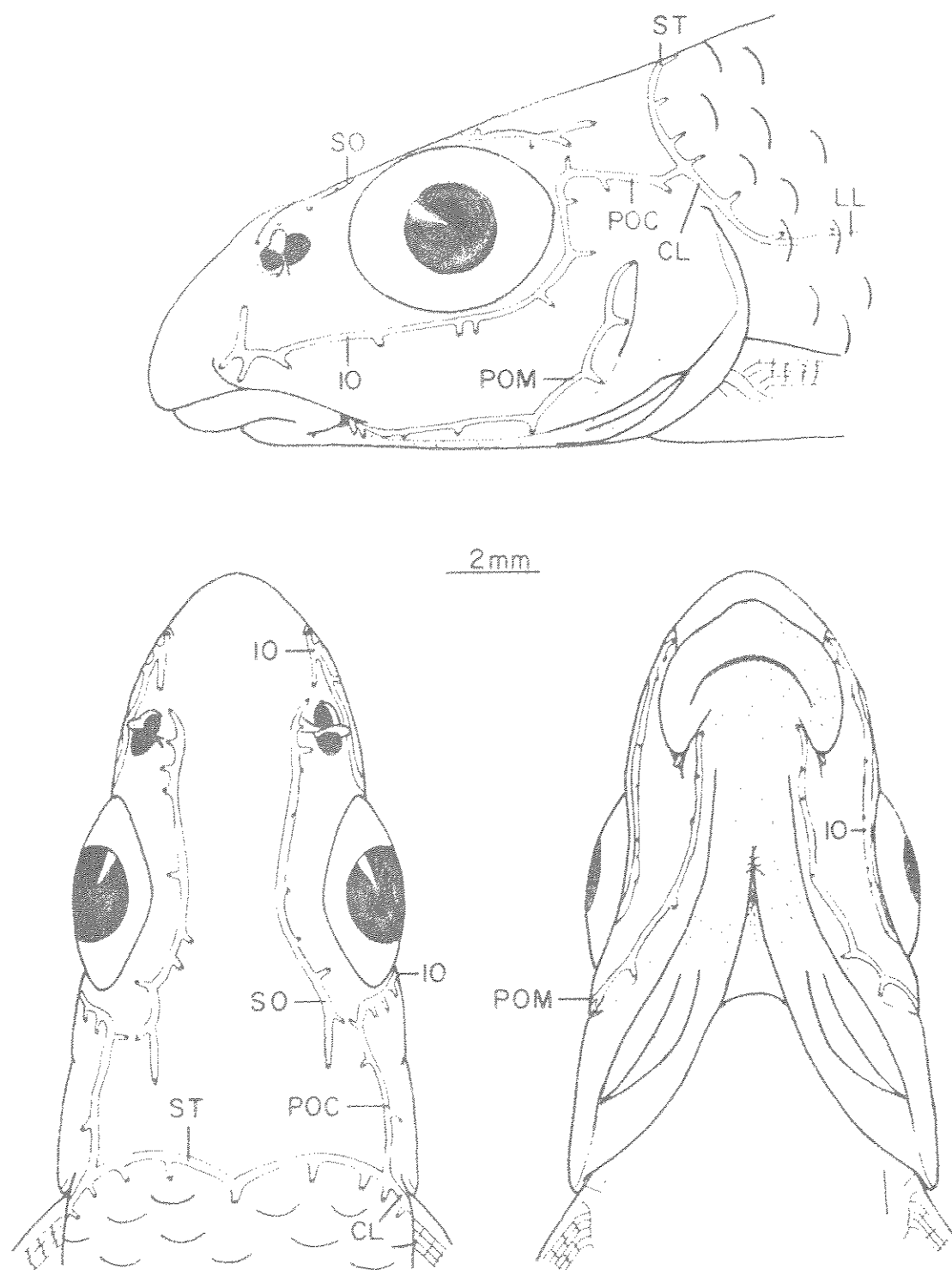


Fig. 13. Three views of *Hybopsis insignis* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

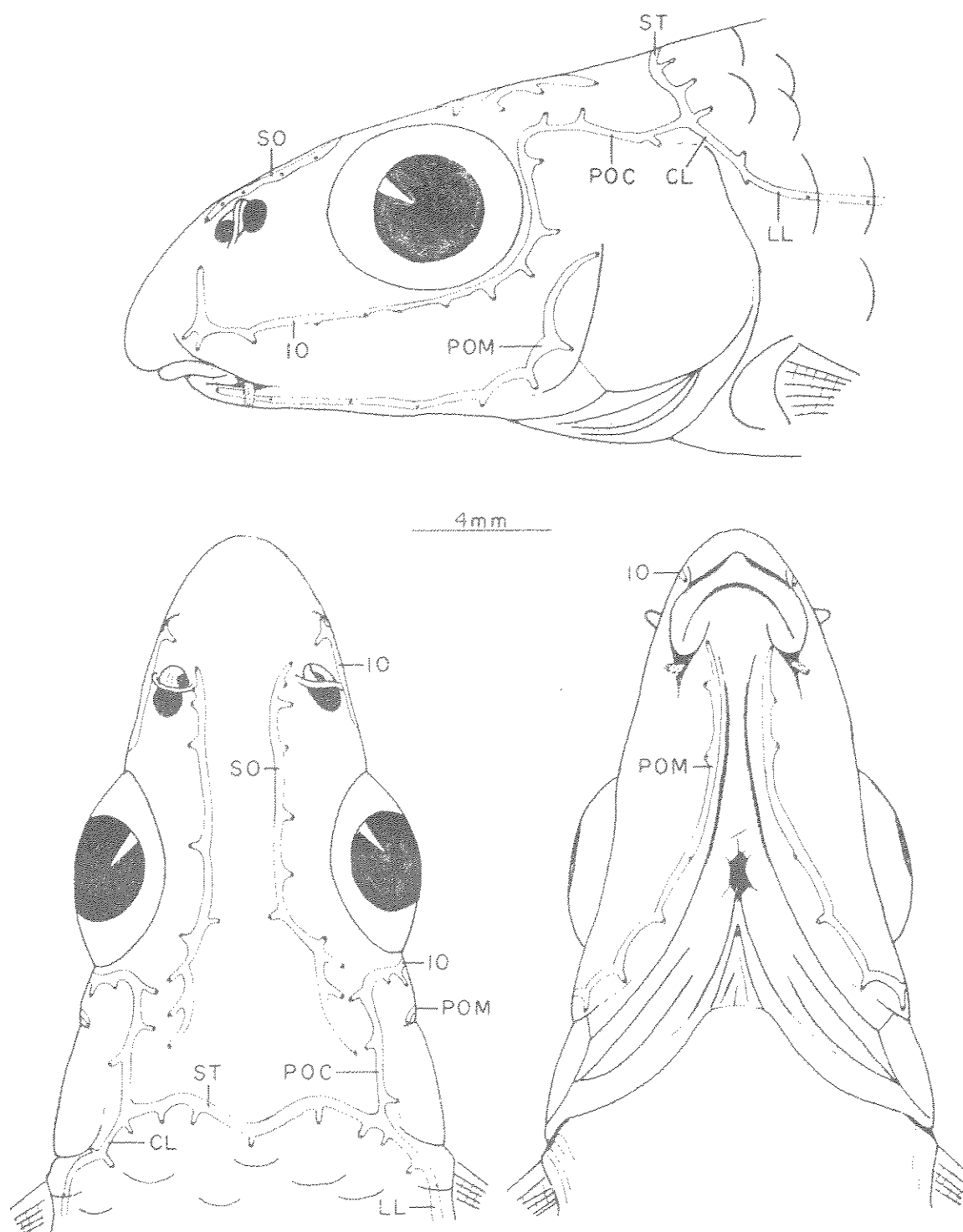


Fig. 14. Three views of *Hybopsis dissimilis* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

cahni and H. dissimilis variously placed and reduced in size. Even though the ST canal is complete, all but H. monacha, and to a lesser extent H. cahni, have long, posteriorly directed canaliculi traversing the skull-trunk intercept. In general the SO canal of the 4 species resembles that of H. monacha; however, the canaliculi gradually shorten in the following order: H. dissimilis, H. x-punctata, H. insignis, and H. cahni. With the exception of occasional discontinuity in H. monacha, the POM canal and canaliculi in the other species closely resemble those of H. monacha.

Most species of Erimystax are probably bottom dwellers and live in clear, high-gradient streams. Since most Erimystax possess large, upward projecting eyes, food is probably located by sight; however, Davis and Miller (1967) showed that in some sight-feeding is supplemented by cutaneous taste buds. Where species are sympatric (e.g., Powell River, Tennessee), competition is probably reduced by different food requirements, feeding behaviors, and/or position within the limited space of riffles. More specifically, Trautman (1957) observed H. x-punctata and H. dissimilis living in close proximity ("... within a few inches...") of each other, and noted that H. x-punctata was usually found in riffles and H. dissimilis at the base of riffles. He further suggested that H. x-punctata and H. dissimilis are apparently affected by silty conditions, since, in recent years, increasing siltation in some streams has modified their distribution. Earlier, however, Moore (1950) considered H. x-punctata a silty-water species and H. dissimilis a clear-water form. Moore and Paden (1950) specified the habitat of H. x-punctata as "... under flat rocks in shallow, fast water at the head of riffles." In such limited spaces,

turbidity levels could rise, perhaps the result of microeddy agitation of particles between and under rocks, and yet escape notice to the unaided human eye. Morphological evidence presented by Davis and Miller (1967) substantiated Moore and Paden's (1950) observations on H. x-punctata, for they wrote "... feeding is probably accomplished by probing under rocks and in crevices with its sensitive snout..." Lateral-line evidence (long canaliculi and minute canal pores), plus the concentration of superficial neuromasts toward the snout, further imply that H. x-punctata is a "turbid-water" species and that it seeks food as postulated by Davis and Miller (1967). Shorter canaliculi and larger canal pores in H. dissimilis (Fig. 14) suggest that, although it and H. x-punctata occasionally live close together, their habitat requirements are very different. Seemingly, H. dissimilis should seek out quieter waters (at the base of riffles?) where suspended particles settle quickly and turbidity levels are low. Also, the more or less even distribution of superficial neuromasts over the head (Table V) indicates that H. dissimilis lives (slightly above the bottom?) where microcurrent reception by the skin neuromasts is unabated and unmodified by surrounding obstacles.

Collections of H. cahni from the type locality in Tennessee (see Davis and Reno, 1966) revealed that H. dissimilis and H. insignis also occur at the same site. Since the ecology of H. cahni and H. insignis is little known, the environmental and morphological mechanisms which reduce competition between these species and H. dissimilis is unknown. Perhaps the minute pores, larger eyes (Fig. 12), and fewest number of taste buds, neuromasts, and canal pores (Tables III-V) effectively isolate H. cahni into a described habitat (almost lentic-like?) where

food is procured visually. Although pore and cutaneous sense organ counts are consistently higher in H. dissimilis (Table III-V; and Davis and Miller, 1967), the skin taste buds are more concentrated on the snout, lips, and enlarged gular region in H. insignis (compare Figs. 13-14). Furthermore, skin neuromasts are more lateral and ventrally placed in the latter than in the former species. It therefore seems reasonable to assume that competition between H. insignis and H. dissimilis is reduced by H. insignis groping about the riffle bottom where, as stated by Davis and Miller (1967), it "... uses its lips for food detection or discrimination." instead of relying more on visual acuity as does H. dissimilis. Without supplementary histological evidence, it is hazardous to speculate on the ecological requirements of H. monacha.

The lateral-line system of H. harperi is more like those in the subgenus Hybopsis than those in Erimystax (Fig. 15). In H. harperi the ST canal is incomplete, the POM canal short, canal canaliculi reduced or absent, and pores large. According to Marshall (1947) and Bailey, Winn, and Smith (1954), H. harperi lives in springs, small spring-fed creeks, limestone sinks, and caves in northern Florida and adjacent parts of Alabama. In such environs, waters are clear and relatively free of suspended solids; consequently, as suggested by Davis and Miller (1967), H. harperi is probably a sight-feeder where conditions permit. The possession of numerous taste buds and superficial neuromasts (Table V) and hyperdevelopment of certain canal pores (see snout and jaw portions of IO, SO, and POM canals, Fig. 15) indicate that sight perhaps has been supplemented by other systems to permit location of food and avoid obstacles in crepuscular and

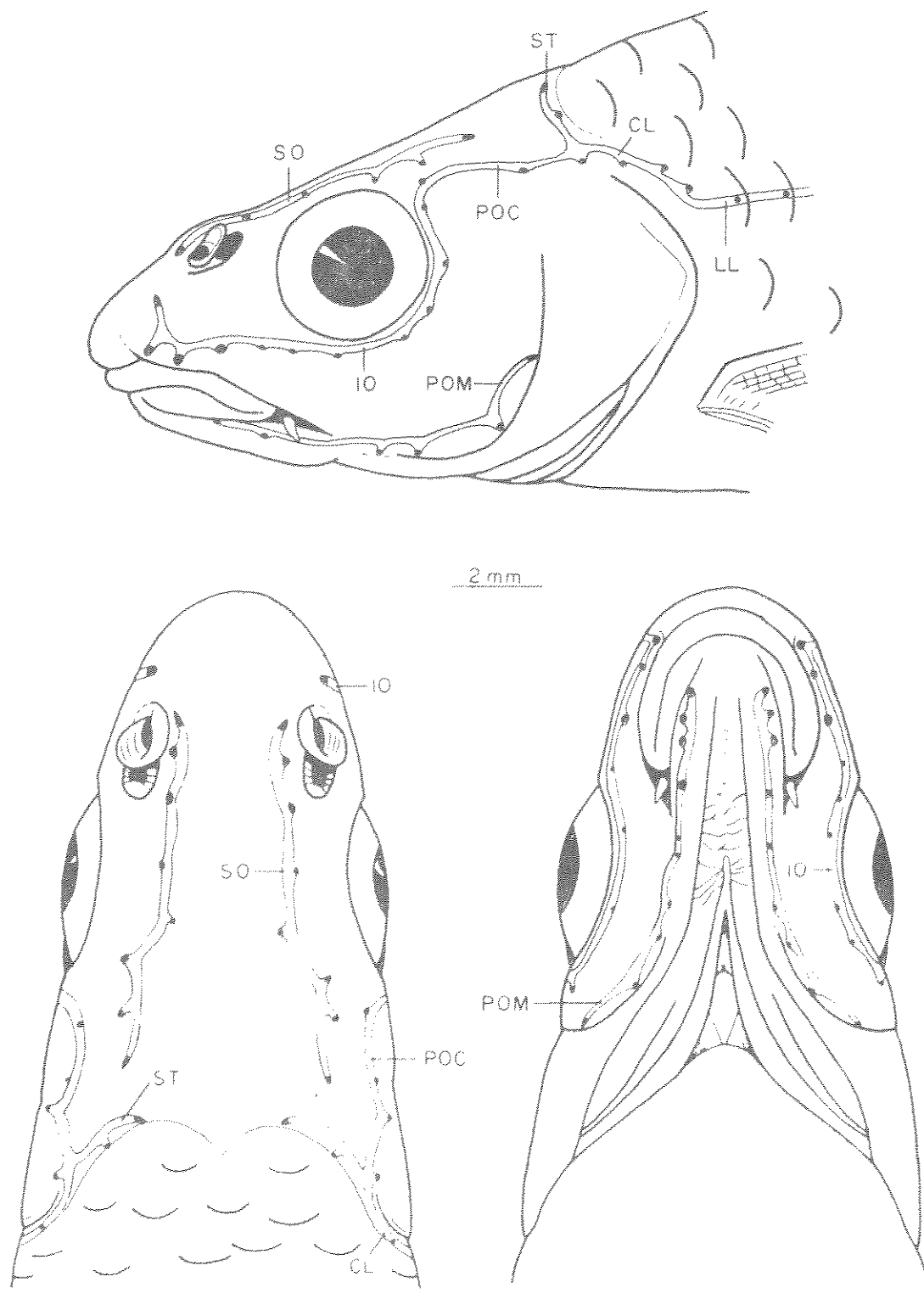


Fig. 15. Three views of *Hybopsis harperi* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

speleal environments.

Subgenus Nocomis

As recognized by Moore (1957), the subgenus Nocomis contains the nominal species H. bellica, H. biguttata, H. leptcephala, and H. micropogon. In this study two undescribed Nocomis were also considered, i.e., H. (Nocomis) sp.₁ and H. (Nocomis) sp.₂. The species H. (Nocomis) sp.₂ corresponds to H. (Nocomis) sp. of Davis and Miller (1967). These are currently being described by E. H. Lachner and R. E. Jenkins.

Basically, the lateral-line systems of Nocomis are similar, as are the number of canal pores and neuromasts, and number and distribution of superficial neuromasts (Tables III-V). In all Nocomis the IO canal, beginning anteroventrad to the nostril, projects ventrad to intersect 2 or 3 supralabial canaliculi. In H. bellica, H. (Nocomis) sp.₁, and H. micropogon (Figs. 16-18) the 3 supralabial canaliculi are evenly spaced and of equal length, whereas, in H. biguttata, H. (Nocomis) sp.₂, and H. leptcephala (Figs. 19-21), 2 canaliculi contact the lip and the shorter third is rotated posteriad away from the lip. In each species the IO canal slants posterodorsad toward the eye, eventually passing diagonally upward behind the eye. In 3 species postorbital canaliculi are reduced or lacking, otherwise the length of the remaining IO canaliculi gradually decrease in the following order: H. micropogon, H. (Nocomis) sp.₂, H. (Nocomis) sp.₁, H. bellica, H. biguttata, and H. leptcephala. The POC canal in all Nocomis arches mesolaterad from the IO canal to the POC-CL junction and, in all except H. biguttata, the first POC canaliculus is directed dorsad; the other canaliculi, including the one at the POC-CL junction, are

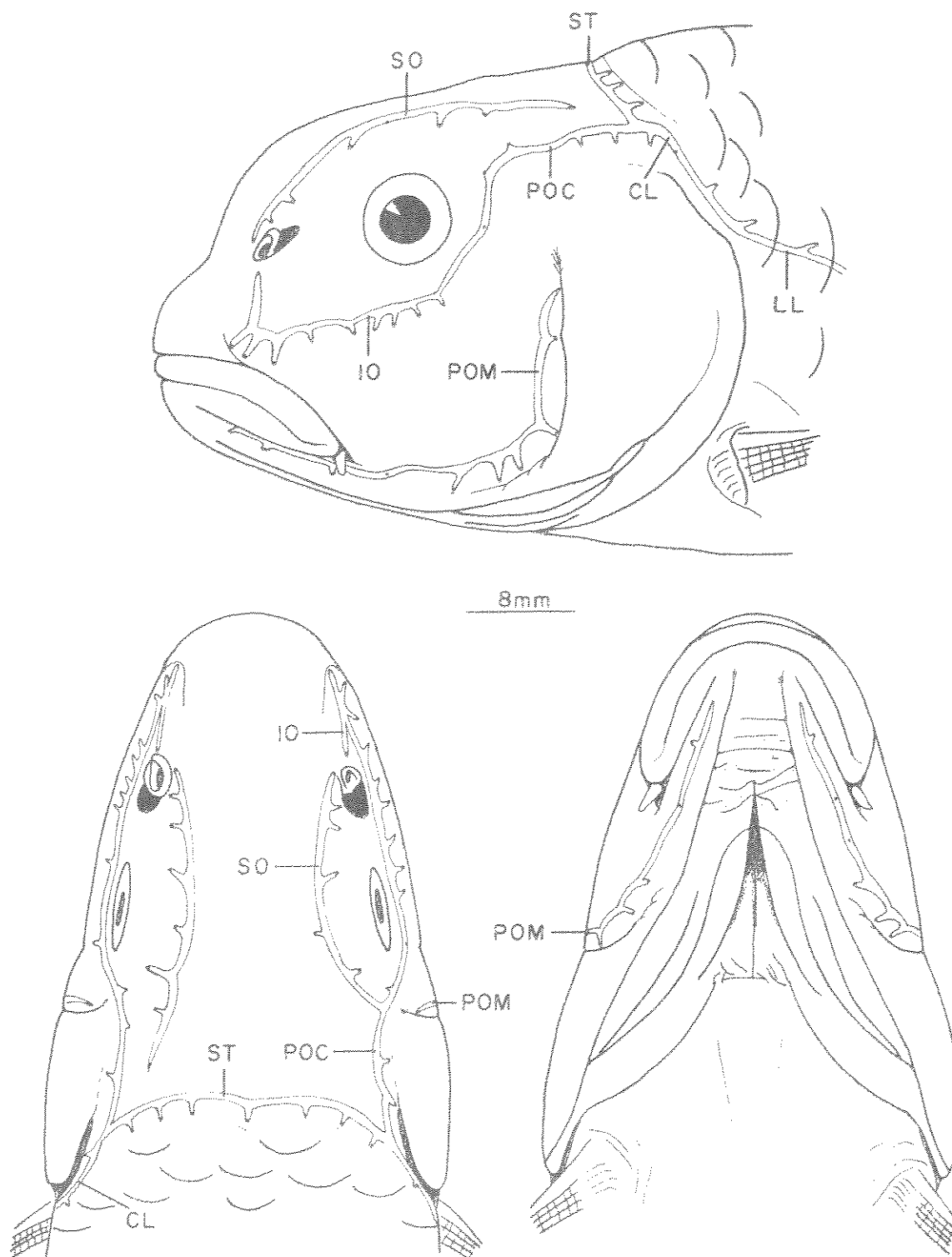


Fig 16. Three views of *Hybopsis bellica* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

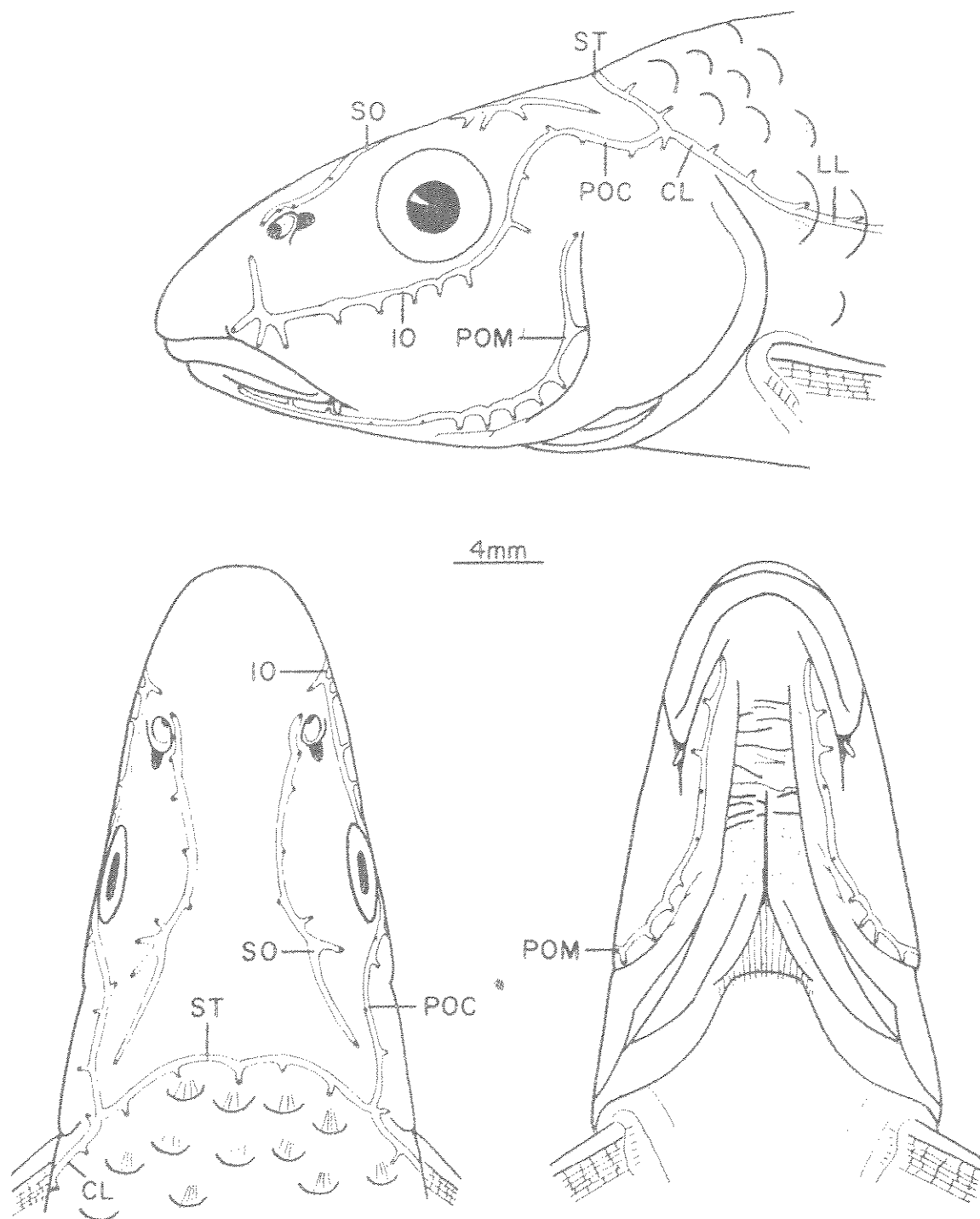


Fig. 17. Three views of *Hybopsis (Nocomis) sp. 1* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

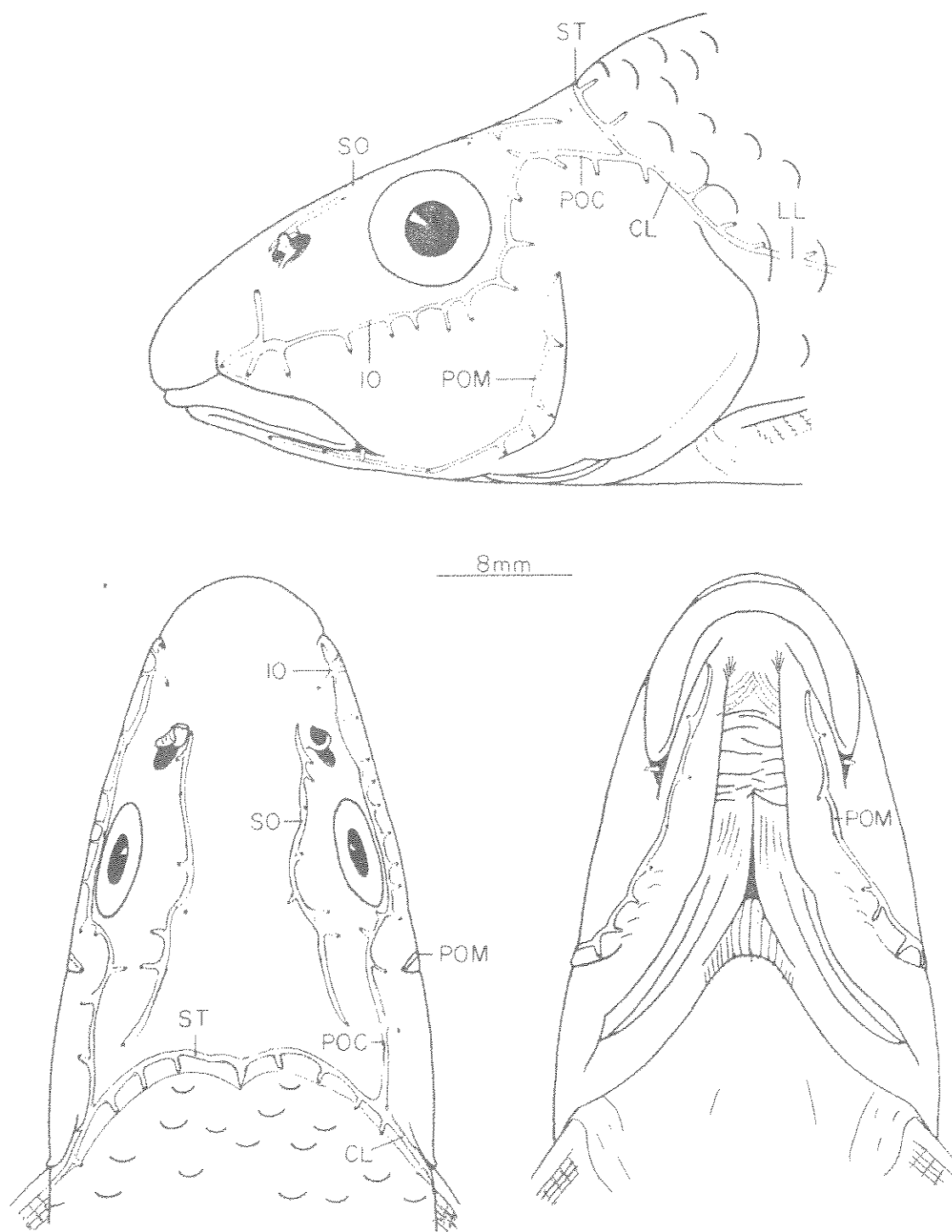


Fig. 18. Three views of *Hybopsis micropogon* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

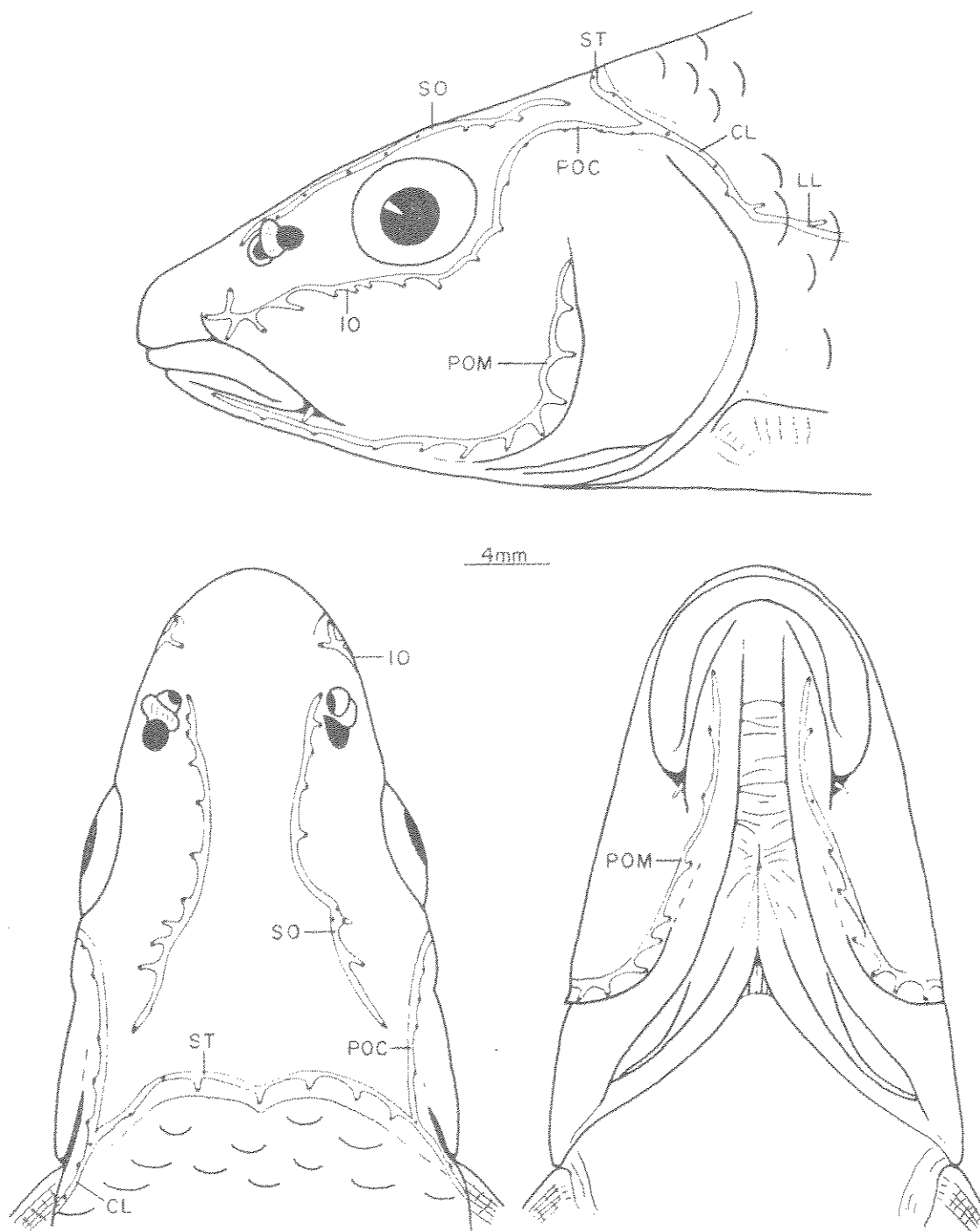


Fig 19. Three views of *Hybopsis biguttata* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

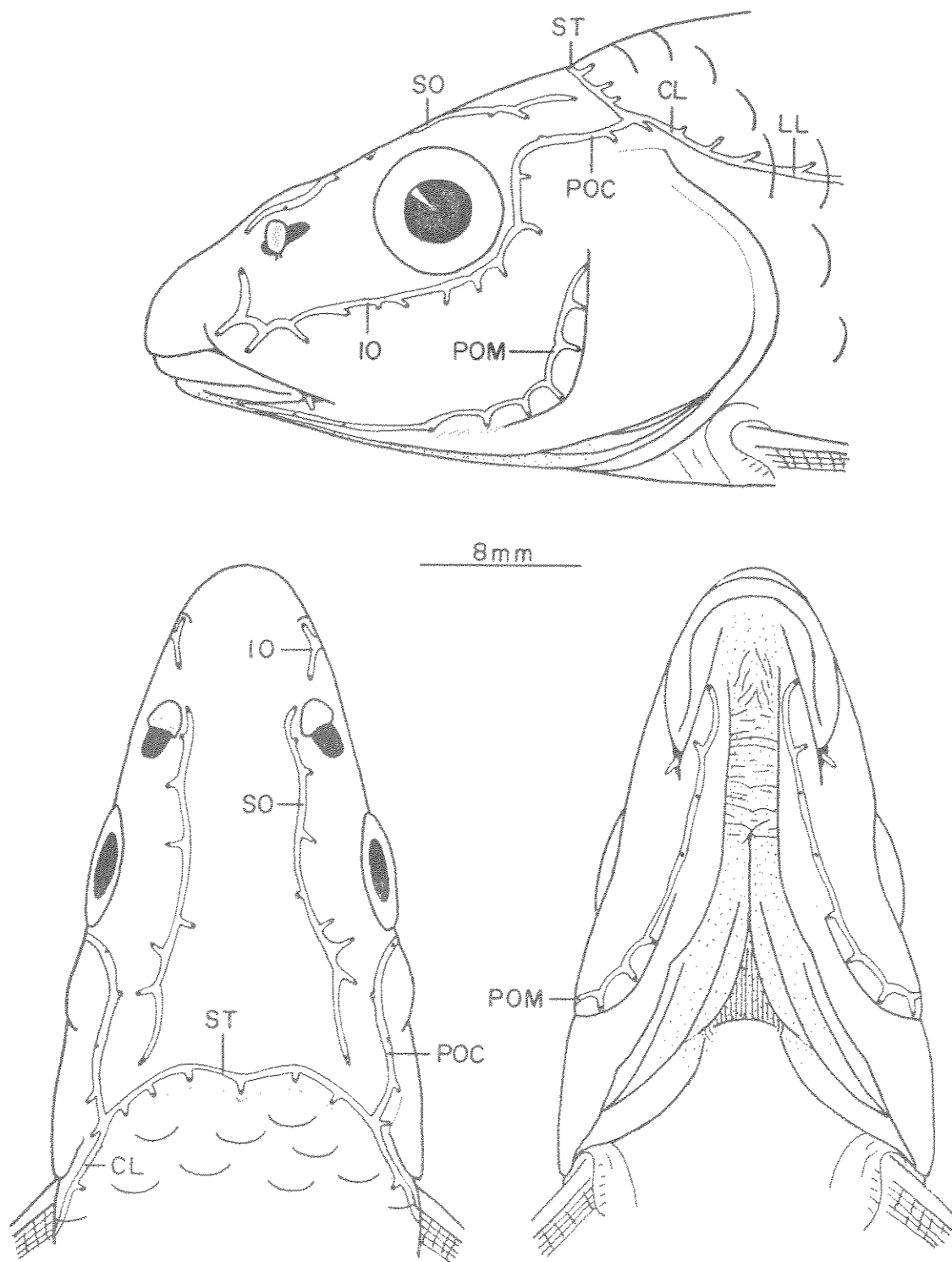


Fig. 20. Three views of *Hybopsis (Nocomis) sp.2* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

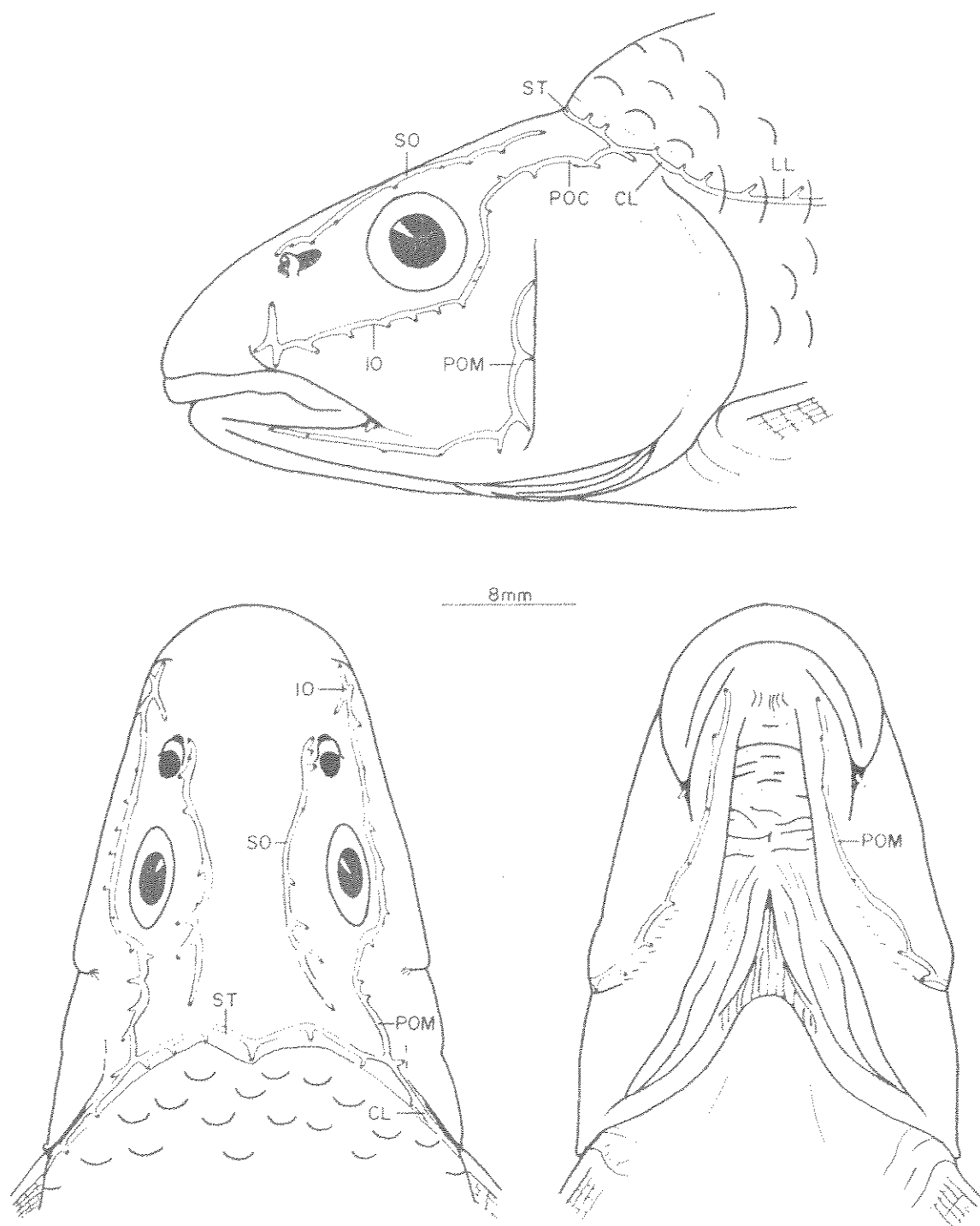


Fig. 21. Three views of *Hybopsis leptocephala* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

ventrally placed. The CL canal is straight in all except H. bellica and H. (Nocomis) sp. 1 and, in general, the canaliculi are directed posterodorsad from the canal. In all Nocomis the ST canal is complete with the canaliculi directed posteriad. As in other Hybopsis, the SO canals of Nocomis begin at the nostril and pass mesolaterad around the eye, ultimately terminating far back on the parietal. The SO canaliculi in most Nocomis are long and laterally placed, with the last closely approaching the POC canal. In all Nocomis except H. biguttata, the SO canal regularly intersected the POC canal, wherein the posterior segment of the SO canal was lacking (e.g., compare SO canals dorsal view, Fig. 16). The POM canals in all Nocomis are essentially alike; that is, differences in position, size, spacing, and number of canaliculi are minimal between species.

Morphologically quite similar, the species of Nocomis exhibit few anatomical specializations for specific habitat types. In most instances, identification of species is dependent upon the number and arrangement of nuptial tubercles in males (Moore, 1957). However, during nonbreeding seasons, tubercles are shed, thus making identification of species and recognition of sex exceedingly difficult. Davis and Miller (1967) showed that brain patterns of all Nocomis are similar and that, even though barbels are conspicuous, the paucity of taste buds casts doubt on the utility of barbels in food location. They suggested that food location is principally due to visual responses.

In general all Nocomis inhabit relatively clear streams with sand or gravel bottoms. Some species (e.g., H. leptocephala and H. micro-
pogon) inhabit medium- to large-size streams of moderate to high

gradient, while other (e.g., H. biguttata) occur in small- to medium-size streams having moderate to sluggish currents (Lachner, 1950, 1952; and Trautman, 1957). Unfortunately, the gross appearance of the lateral-line system, and number and distribution of associated sense organs offer little complementary information on these environmental generalizations.

Even though canal pores of all Nocomis are large, the length of canal canaliculi do not necessarily reflect environmental conditions. Instead, certain canaliculi are long to compensate for periodic changes in skin thickness which responds to seasonal fluctuations in hormonal levels. Numerous investigators have observed that during the breeding season, the heads of Nocomis become greatly robust and, in some instances, quite bizarre (see Fig. 16 lateral view). If the canaliculi were not long, canal communication with the exterior would be obliterated when the skin thickened. In areas where thickening is slight or nonexistent (e.g., postorbital segment of IO canal), canaliculi are reduced or lacking with the pores opening directly into the canal.

In certain localities some species of Nocomis are sympatric; however, the mechanisms of isolation are problematical. Lachner (1952) suggested interspecific competition is perhaps reduced by differences in habitat requirements of young and adults. Competition may also be lessened by variance in eye position and degree of angular vision. The ability to see downward increases in the following order: H. leptocephala, H. bellica, H. micropogon, H. (Nocomis) sp.₁, H. biguttata, and H. (Nocomis) sp.₂. Those forms unable to see downward may be bottom inhabitants, locating food (Plant material?) by means

other than sight, whereas those with greater spherical vision may swim up off the bottom, selecting food (plant and animal matter?) anywhere in the environment. According to Flemer and Woolcott (1966), and Davis and Miller (1967), H. leptocephala and perhaps H. bellica are more herbivorous than carnivorous, and, according to Iachner (1950), H. micropogon and H. biguttata ingest both plant and animal matter. Since, in some areas, H. micropogon is sympatric with either H. leptocephala or H. biguttata, the position of the eyes, plus slight differences in dietary requirements may, in part, be responsible for reducing interspecific competition.

Subgenus Macrhybopsis

The subgenus Macrhybopsis consists of two nominal species, i.e., H. gelida and H. meeki. According to Moore (1950), these fishes inhabit the turbid waters of the Missouri and Mississippi Rivers above southern Illinois and Missouri. Bailey and Allum (1962) noted both species dwell in swift water, with H. gelida usually over gravel bottoms and H. meeki over sandy areas.

Moore (1950) observed that the lateral-line systems of H. gelida and H. meeki are similar, although the ST canal is incomplete in H. meeki (Fig. 22) and complete in H. gelida (Fig. 23). He further indicated that in both species the SO canals are incomplete and that SO and POC canaliculi "... often open in close proximity." Since the other lateral-line canals of Macrhybopsis begin, traverse, and terminate in approximately the same areas as those of H. aestivalis (Fig. 3), the necessity of further verbal description is eliminated. In Macrhybopsis the canal canaliculi are the longest and the pores, in

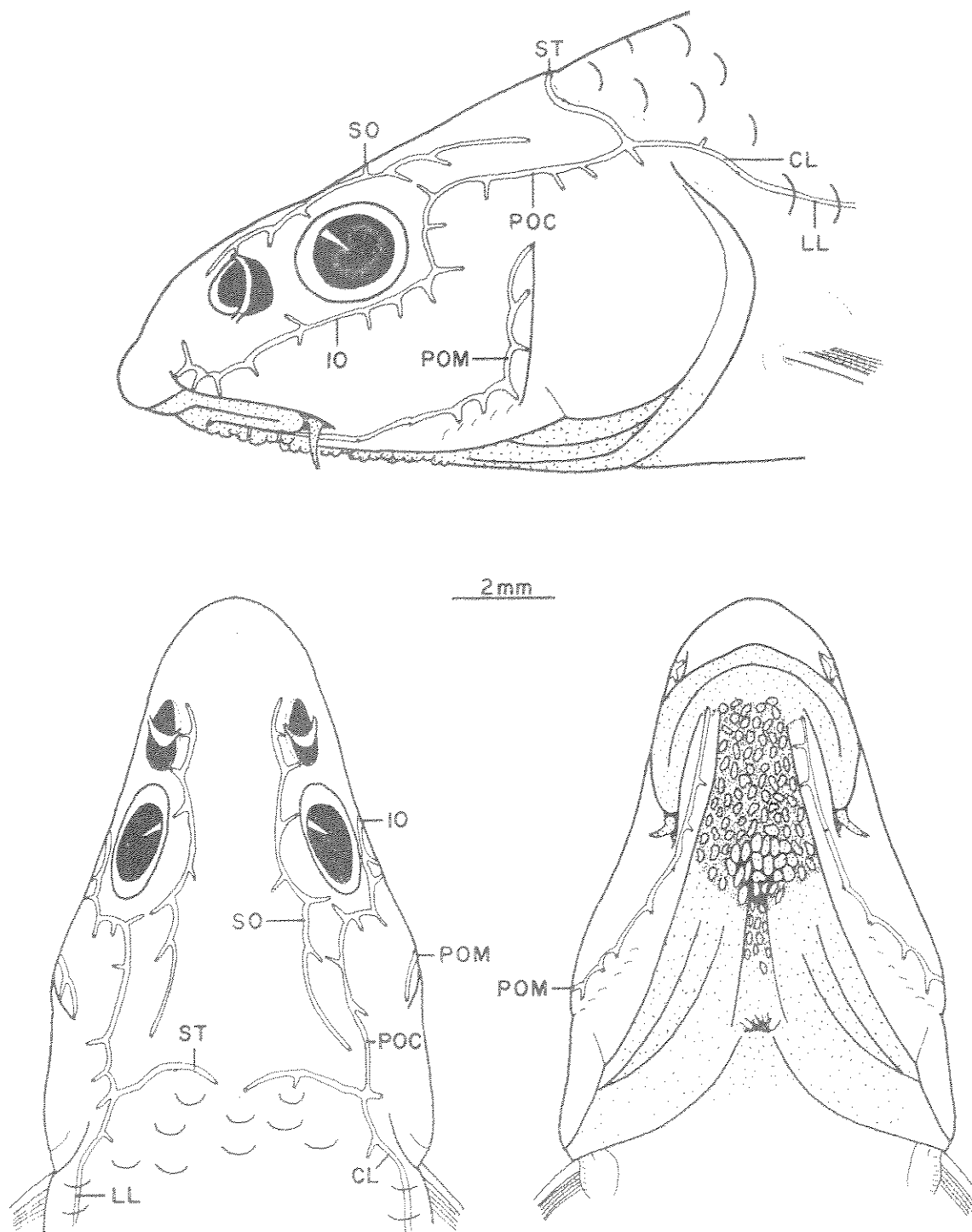


Fig. 22. Three views of *Hybopsis mseeki* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

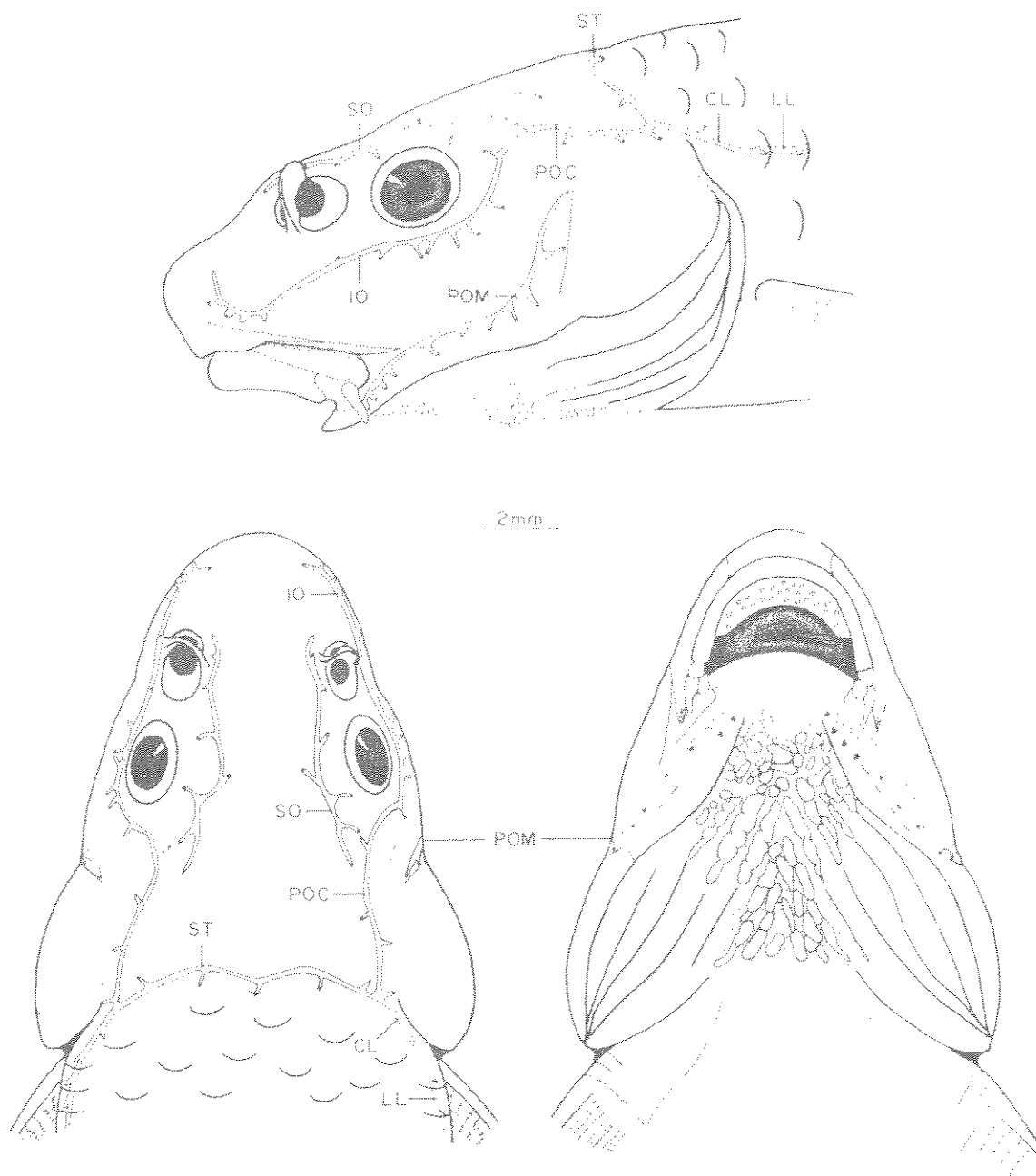


Fig. 23. Three views of *Hybopsis gelida* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

part, the smallest of all Hybopsis. Despite some enlarged POM canal pores in H. meeki and H. gelida, morphological idiosyncrasies in both close the pores and canaliculi to prevent collection of detritus in the canals. Theoretically, in H. meeki hydrostatic waves impinging upon the thin, rather flimsily constructed POM canaliculi force each pore and canaliculus shut. In H. gelida the hyperdeveloped POM canal pores, situated in grooves behind the jaw, are closed and the canaliculi pinched when the mouth is "closed" and pharyngeal cavity relaxed.

Davis and Miller (1967) indicated that brain patterns of Macrhybopsis "... are the most aberrant of any Hybopsis, approached only by turbid-water forms of Extrarius." Mean pore counts for Macrhybopsis closely correspond to those of H. aestivalis (Table III). Even though the IO canals are shorter and the POC canal longer in Macrhybopsis than in H. aestivalis, the summed IO and POC pore means for Macrhybopsis and Extrarius are very similar. However, pore count figures published by Illick (1956) are higher for Extrarius than Macrhybopsis. Mean superficial neuromast counts for H. gelida and H. aestivalis are similar, yet dramatically different from H. meeki (Table V). Since most of the H. meeki prepared histologically were juveniles, the means presented are probably exaggerated. Undoubtedly, with increased growth, the number of skin neuromasts would diminish proportionally as in H. amblops (Fig. 9). Therefore, considering the small figures more or less representative of adult H. meeki, counts for Macrhybopsis and Extrarius are similar.

Morphological similarity of certain sensory modalities in H. gelida, H. meeki, and some H. aestivalis may not represent close phylogenetic kinship, as much as convergent evolution in similar

environments. Evolutionary reactions to silty conditions have resulted in changes in body form and contour, fin shape, and brain pattern, and also reduction of eye size, and compensatory increase in cutaneous sense organs. Hubbs (1940) and Moore (1950) indicated that such changes have doubtlessly occurred countless times in response to similar environmental conditions.

Subgenus Platygobio

The monotypic subgenus Platygobio contains the nominal species H. gracilis with two subspecies H. g. gracilis and H. g. gulonella (Olund and Cross, 1961). In this study, however, subspecies were not considered.

H. gracilis ranges across Canada, from the Mackenzie River drainage eastward to Lake Winnipeg and in the United States in the Mississippi River and principal tributaries of the Great Plains. Strangely, however, except for the South Canadian River of Oklahoma, it is not found in the Arkansas and Red River basins. It is also found in the upper Rio Grande and Pecos Rivers of New Mexico. Throughout its range, H. gracilis inhabits both clear and turbid streams, being found over shifting sand bottoms or in murky pools with gravel or bedrock bases (Olund and Cross, 1961). Davis and Miller (1967) attributed the success of H. gracilis to its ability to capitalize on changing conditions, since no single sensory system is hyperdeveloped nor degenerated to an extent that utility is seriously impaired. Seemingly, the abundance of taste buds on the snout, barbels, lips, and pectoral fins constitute an adequate mechanism for food location when vision is impaired. Obviously, the ability to use

either or both taste and sight in an environment gives H. gracilis a decided advantage over other fishes which must rely on one system regardless of environmental conditions (Davis and Miller, 1967).

Basically, the lateral-line system of H. gracilis is like those of turbid-water Hybopsis, although the IO canal is not tilted downward as in certain epigeal species (Fig. 24). Typically cyprinid, the IO, POC, CL, and ST canals are complete, and the SO and POM canals incomplete. In general the canal canaliculi are moderate-to long-length and the pores minute. The number of pores and neuromasts per canal, and the number and distribution of skin neuromasts are larger than most turbid-water Hybopsis (Tables III-V). Thus, it is obvious that the lateral-line system of H. gracilis is quite conservative and yet in a way, perplexing. Why H. gracilis should need larger numbers of skin neuromasts is difficult to envision. Perhaps in silty-waters the skin neuromasts are "inoperative", but in clear-waters, they act as supplements to canal organs which would otherwise communicate with the exterior via large pores.

Subgenus Couesius

The monotypic subgenus Couesius is represented by the nominal species H. plumbea. Over much of their ranges, H. plumbea and H. gracilis are sympatric, with H. plumbea in the clear headwaters and H. gracilis in the more turbid areas downstream (Davis and Miller, 1967).

In many ways the lateral-line system of H. plumbea is indicative of a clear-water existence. The canal system is like that of H. gracilis, except that the ST canal is incomplete, canaliculi shorter,

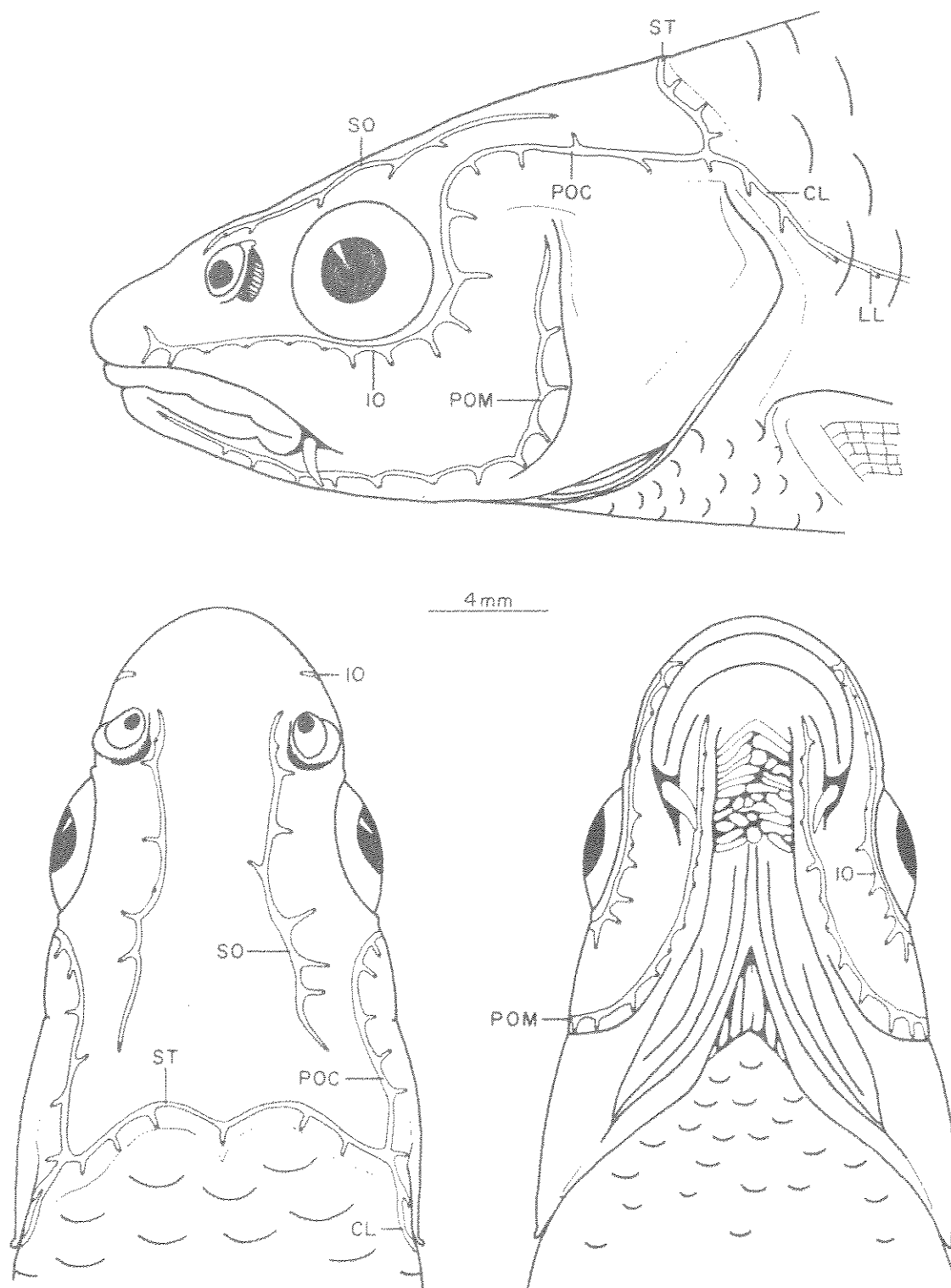


Fig. 24. Three views of *Hybopsis gracilis* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

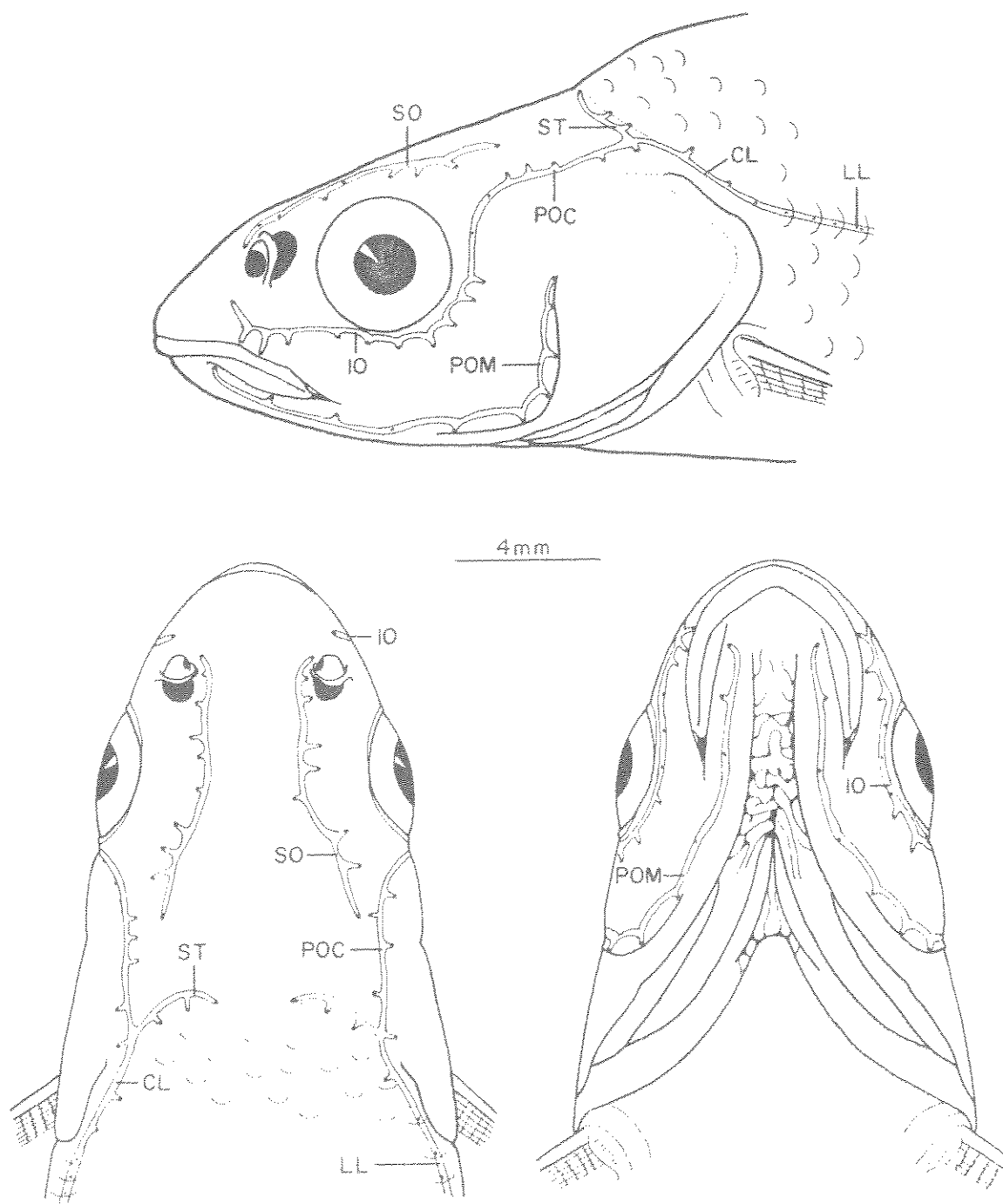


Fig. 25. Three views of *Hybopsis plumbea* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

and pores larger (Fig. 25). The number of pores and neuromasts per canal, and number and distribution of skin neuromasts in H. plumbea closely correspond to other clear-water Hybopsis, excluding, of course, skin neuromast counts from H. rubrifrons and H. amblops (Tables III-V).

Lateral-line similarity between H. plumbea and other Hybopsis is perhaps of secondary consequence. Actually, H. plumbea is morphologically quite disparate and rather dubiously related to Hybopsis. The possession of small scales and location of the barbels forward from the maxillary terminus, for example, indicate that H. plumbea is probably more closely related to Semotilus than to other subgroups within Hybopsis. A similar view is held by Mr. R. E. Jenkins.

Subgenus Oregonichthys

The monotypic subgenus Oregonichthys contains the single species H. crameri. This species, found in the Willamette and Umpqua Rivers of Oregon, is the only West Coast representative of Hybopsis. Davis and Miller (1967) summarized the characteristics of H. crameri and concluded its habitat is probably "... clear, slowly moving or standing waters, possibly with abundant vegetation."

Among Hybopsis, the lateral-line system of H. crameri is the most unique (Fig. 26). Relative completeness of the canal system varies from individual to individual, in fact so dramatically sometimes, that its sensory efficacy is questionable. Obviously, if canal variability is commonplace in H. crameri, (illustrations by Illick, 1956, indicate that it is), quantitative tabulation of pores and canal neuromasts would be futile and meaningless, and proved to be so (Tables III-IV). Illick (1956), however, did present pore counts for H. crameri, but

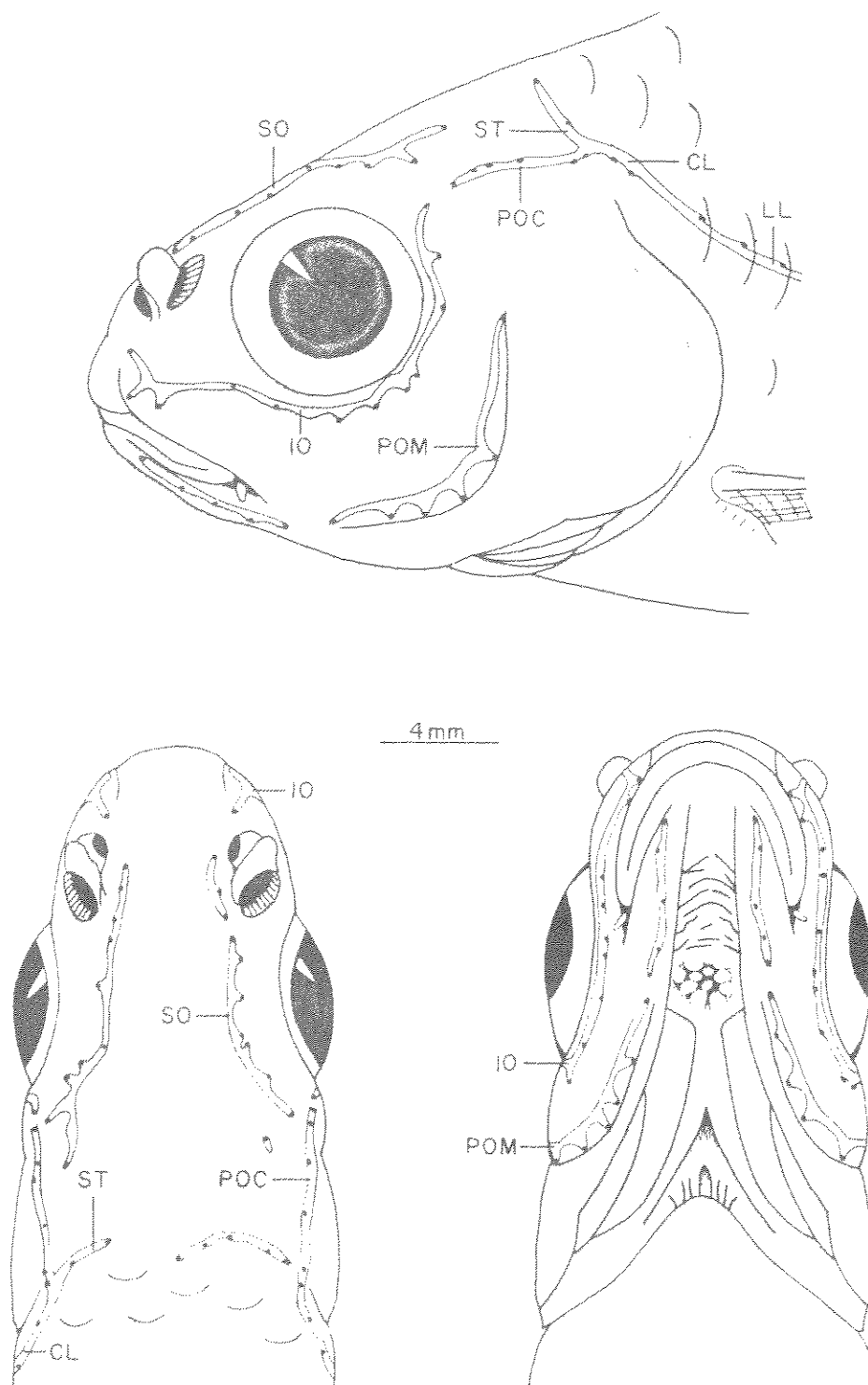


Fig. 26. Three views of *Hybopsis crameri* illustrating the canals of the cephalic lateral-line system. Abbreviations as in Fig. 2.

conceded the wide range in each count "... may be correlated with incompleteness of the canal." In H. crameri, as in other Hybopsis, large pores, reduced canaliculi, and modified or reduced canals are indicative of existence in clear, lentic-like environments. Moreover, large concentrations of skin neuromasts over certain canals (Table V) suggest lateral-line functionality has abated to such an extent that the cutaneous neuromasts are the principal lateral-line receptors. If the skin neuromasts are the principal receptors, the utility of canals probably becomes greatly reduced. Whatever the answer, it seems that selective pressures on H. crameri are structurally "pushing" the canal system toward total degeneration.

CHAPTER VI

HISTOLOGICAL OBSERVATIONS

In Hybopsis superficial neuromasts are variously shaped and either freely exposed apically or sunken into pits or crypts. Evidently, the shape of skin neuromasts is influenced by epidermal thickness, for, in areas where the epidermis is thick, organs are more slender than wide and, in thinner areas, wider than high (Figs. 27-28, respectively). In agreement with Reno (1966) the more slender neuromasts are characteristic of ventral head surfaces, whereas the other organs are indicative of dorsal and lateral surfaces. The shape and position of canal neuromasts are also variable, but, unlike centrarchids (Branson and Moore, 1962), their shapes are not species specific. Seemingly, canal neuromast shape and position are secondarily modified by development of the bony canal during postembryogenesis. Normally, neuromasts remain as originally invaginated, provided the bony canal rudiments (usually 2) develop at even increments around them and the connective tissue tubes. However, when one rudiment grows faster, the organs are flexed and secondarily rotated by the hyperactive element; hence the inconsistencies in neuromast shape and position within and between individuals and species.

Histologically and cytologically, neuromast structure in all Hybopsis is like that of H. aestivalis (Fig. 1). Basically, skin and canal neuromasts are morphologically similar, although their

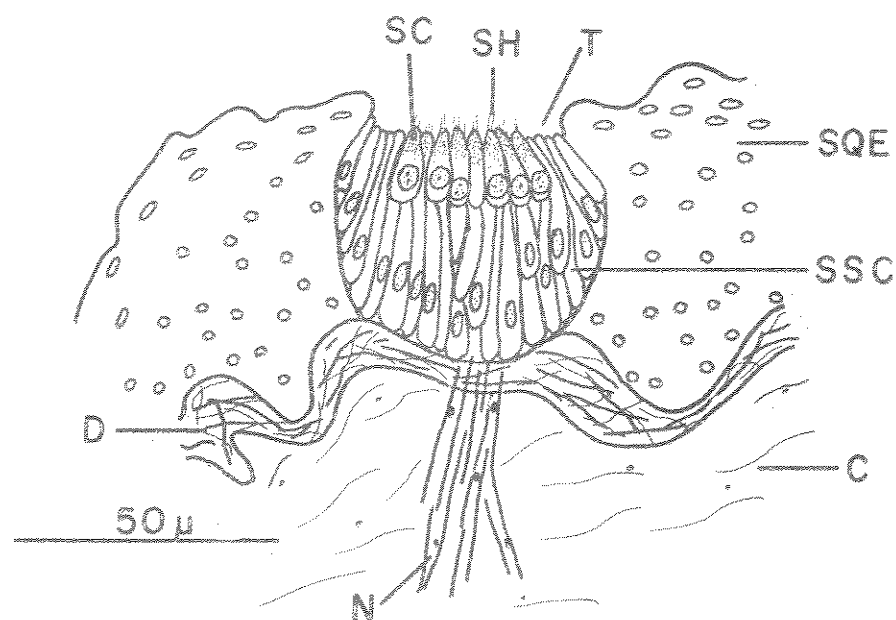


Fig. 27. A superficial neuromast from the lower jaw of Hybopsis amblops. Abbreviations as in Fig. 1.

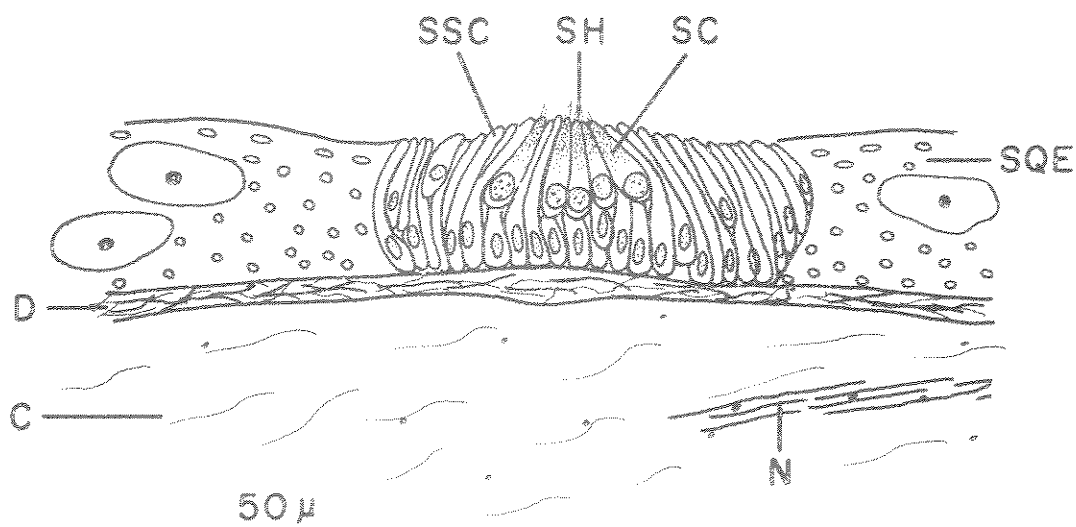


Fig. 28. A superficial neuromast from the cranium of Hybopsis amblops. Abbreviations as in Fig. 1.

quantitative and qualitative measurements differ dramatically. In general, canal organs have larger diameters and greater numbers of sense and sustentacular cells per organ (Tables VI-VII), whereas the smaller skin neuromasts possess longer cellular constituents which together give the organs greater height (Tables VIII-IX). In both types of organs the club-shaped sense cells are strongly polarized and apically bear several (2 or more) sense hairs each. The nuclei, situated basally, are large and round with several (2-7) dark-staining bodies (chromatin or nucleoli) each. Distally, the sense cell cytoplasm gradually increases in density and, at the tip, appears solid. Despite repeated examination of cell apices, blepharoplast-like granules or sense hair bases were not seen in Hybopsis. Unfortunately, sense hair length in several Hybopsis was indiscernible, but for those species with measureable sense hairs, the lengths are summarized in Tables VII and IX. Reno (1966), noting sense hair length is dependent upon two factors, viz., (1) cupula destruction during life or fixation, and (2) sectioning angles through neuromasts, indicated that either or both factors tend to reduce sense hair length. Therefore, the lengths given in Tables VII and IX are considered conservative estimates of actual hair lengths. In both types of neuromasts the attenuate sustentacular cells are elongated, extending upward from the basement membrane to the apical surfaces of the organs. The ellipsoidal nuclei, situated basally, are homogeneous and, like the cytoplasm, without inclusions. Fortuitous en face sections of canal organs in several Hybopsis showed each sense cell independently couched among the elongated sustentacular cells (Fig. 29). Curiously enough, no intercellular bridges were seen

TABLE VI

COMPARISON OF MEAN MINIMUM AND MAXIMUM ORGAN HEIGHT, MAXIMUM ORGAN DIAMETER, AND DIAMETER OF THE SENSORY AREA OF CANAL NEUROMASTS IN HYBOPSIS. PARENTHETICAL NUMBERS REPRESENT RANGES. SCALE IN MICRONS

Species	Min. Height	Max. Height	Max. Dia.	Dia. Sensory Area
<u>Subgenus Extrarius</u>				
<u>H. aestivalis</u>	7.6 (4.0-11.0)	17.4 (11.0-28.0)	74.7 (27.6-112.8)	47.5 (16.0- 72.0)
<u>Subgenus Hybopsis</u>				
<u>H. amblops</u>	9.5 (7.0-11.0)	18.4 (14.6-24.0)	84.6 (66.0-100.4)	61.2 (39.0- 76.0)
<u>H. hypsinota</u>	13.0	22.0	102.0	65.0
<u>H. labrosa</u>	7.5 (5.5- 9.8)	18.8 (14.2-27.0)	76.9 (71.0- 81.0)	58.4 (50.5- 67.0)
<u>H. rubrifrons</u>	11.3 (9.0-14.0)	21.5 (16.6-33.5)	106.8 (95.4-134.0)	73.9 (37.0- 94.0)
<u>H. storeniana</u>	12.7 (10.6-13.2)	27.4 (22.3-30.8)	113.0 (98.3-128.0)	84.2 (68.0-100.0)
<u>Subgenus Erimystax</u>				
<u>H. calmi</u>	7.7 (5.5-10.7)	17.7 (15.3-20.0)	92.5 (84.4-100.7)	58.8 (41.9- 67.1)
<u>H. dissimilis</u>	11.7 (9.4-18.0)	23.9 (22.0-29.0)	94.6 (76.5-108.0)	61.4 (43.0- 71.0)
<u>H. harperi</u>	7.8 (1.8-13.4)	25.4 (16.0-32.5)	121.5 (65.0-169.0)	92.1 (30.0-110.8)
<u>H. insignis</u>	9.8 (5.5-14.0)	23.3 (17.0-29.6)	101.0 (74.0-151.0)	64.1 (41.0-147.2)
<u>H. x-punctata</u>	12.3 (7.3-16.2)	22.0 (18.6-28.5)	82.9 (70.0- 94.6)	50.0 (44.2- 61.0)
<u>Subgenus Noconis</u>				
<u>H. bellica</u>	9.0 (4.8-15.1)	24.3 (17.0-30.0)	94.6 (66.3-119.0)	65.3 (33.0-111.0)
<u>H. biguttata</u>	17.4 (11.7-28.3)	25.8 (14.4-43.0)	86.4 (65.0-118.0)	53.2 (34.0- 80.0)
<u>H. leptocephala</u>	18.9 (14.8-27.0)	31.0 (26.0-38.7)	104.3 (65.0-138.0)	69.3 (34.6-102.0)
<u>H. micropogon</u>	14.6 (10.5-22.0)	30.6 (22.3-43.0)	99.7 (75.5-118.0)	62.3 (34.0- 72.6)
<u>H. (Noconis) sp.1</u>	19.1 (11.0-26.0)	34.8 (30.0-48.0)	124.3 (112.0-158.0)	74.9 (54.0-102.0)
<u>H. (Noconis) sp.2</u>	10.1 (9.0-11.6)	24.5 (17.2-39.5)	95.9 (79.4-130.0)	59.0 (34.0- 89.0)
<u>Subgenus Macrhybopsis</u>				
<u>H. meeki</u>	12.1 (5.2-21.3)	21.3 (17.0-31.5)	66.3 (49.0-107.6)	42.8 (22.7- 72.0)
<u>Subgenus Platygobio</u>				
<u>H. gracilis</u>	15.2 (7.3-26.0)	26.0 (15.2-37.0)	120.5 (65.0-158.0)	86.0 (43.0-119.0)
<u>Subgenus Coesius</u>				
<u>H. plumbea</u>	20.2 (15.0-29.6)	36.4 (25.0-47.0)	117.9 (81.0-139.0)	80.7 (54.0-103.6)
<u>Subgenus Oregonichthys</u>				
<u>H. crameri</u>	24.6 (22.0-29.4)	28.3 (27.0-30.0)	45.0 (36.0- 61.0)	17.9 (12.0- 28.4)

TABLE VII

COMPARISON OF THE MEAN NUMBER OF SENSE (SC) AND SUBTENTACULAR (SSC) CELLS, MEAN DIAMETER AND LENGTH OF CELLULAR CONSTITUENTS, AND LENGTH OF SENSE HAIRS (SH) PER CANAL NEUROMAST IN HYBOPSIS. PARENTHETICAL NUMBERS REPRESENT RANGES. SCALE IN MICRONS

Species	Number SC	Cell Dia.	Cell Length	Number SSC	Cell Dia.	Cell Length	SH Length
<u>Subgenus Extrarius</u>							
<u>H. aestivalis</u>	17.2 (11-33)	2.8 (1.8-5.0)	8.5 (1.2-16.0)	25.5 (11-39)	2.5 (1.5-3.8)	13.7 (5.3-25.6)	2.7 (1.8-4.0)
<u>Subgenus Hybopsis</u>							
<u>H. amblops</u>	18.0 (16-20)	3.4 (2.6-4.5)	9.1 (6.0-15.4)	27.4 (21-29)	2.8 (1.8-4.5)	14.2 (6.9-23.0)	—
<u>H. hyalinota</u>	21.0	2.1 (2.0-3.2)	12.0 (11.0-13.0)	32.0	2.8 (2.6-3.0)	18.5 (15.5-22.0)	—
<u>H. labrosa</u>	12.8 (11-18)	4.6 (2.9-5.3)	9.8 (6.0-14.5)	23.6 (19-54)	3.7 (2.8-4.5)	15.3 (7.2-24.5)	—
<u>H. rubrifrons</u>	25.5 (13-46)	3.8 (2.9-5.3)	10.1 (6.0-13.8)	34.6 (27-54)	2.9 (1.8-3.5)	16.2 (12.4-30.0)	2.4 (2.3-2.5)
<u>H. storeriana</u>	24.7 (18-28)	3.5 (2.9-4.2)	11.8 (6.8-16.0)	37.6 (35-44)	2.7 (1.8-3.3)	16.9 (11.2-28.6)	—
<u>Subgenus Primystax</u>							
<u>H. cabini</u>	15.7 (14-20)	4.6 (2.7-6.6)	9.7 (6.5-13.7)	27.2 (21-33)	4.2 (2.2-6.6)	12.0 (6.4-15.0)	—
<u>H. dissimilis</u>	21.7 (10-31)	4.2 (3.0-6.0)	13.1 (7.3-17.6)	32.0 (20-49)	3.5 (2.8-5.0)	17.5 (11.8-30.2)	2.6 (2.4-2.7)
<u>H. harperi</u>	28.1 (11-39)	4.5 (3.0-6.2)	13.0 (4.8-20.2)	35.6 (16-45)	3.7 (2.3-5.1)	16.6 (5.6-30.0)	3.7 (3.5-5.3)
<u>H. insignis</u>	21.0 (13-32)	4.6 (3.0-6.6)	12.6 (7.8-21.7)	32.8 (24-50)	3.4 (2.5-6.0)	17.3 (6.3-27.4)	2.3 (2.0-3.0)
<u>H. x-punctata</u>	21.4 (14-27)	3.8 (2.4-5.0)	12.6 (8.6-22.0)	31.1 (22-41)	3.0 (1.7-4.2)	17.6 (8.6-26.0)	1.3 (1.0-1.8)
<u>Subgenus Noconis</u>							
<u>H. bellica</u>	16.1 (10-19)	4.1 (3.0-5.4)	9.8 (6.2-15.8)	26.0 (20-30)	3.5 (2.1-4.9)	16.1 (6.6-28.9)	2.6 (1.5-4.1)
<u>H. birutata</u>	14.7 (9-27)	3.8 (2.0-6.3)	12.3 (7.3-28.3)	24.9 (20-43)	3.0 (1.6-5.5)	21.9 (10.5-43.0)	3.8 (2.0-4.4)
<u>H. leptocephala</u>	19.3 (14-26)	3.9 (2.4-5.0)	15.6 (11.0-22.0)	27.7 (19-38)	2.9 (2.5-3.3)	25.4 (18.0-38.7)	2.6 (2.3-3.0)
<u>H. micropogon</u>	22.6 (18-29)	3.6 (2.6-5.0)	15.2 (10.4-22.0)	31.3 (26-38)	2.7 (1.8-4.2)	23.6 (12.5-37.0)	2.4 (2.3-2.5)
<u>H. (Noconis) sp.1</u>	22.0 (15-30)	4.1 (2.4-5.0)	16.5 (12.0-27.0)	37.1 (27-46)	3.2 (1.9-4.4)	29.9 (18.6-48.0)	—
<u>H. (Noconis) sp.2</u>	19.9 (14-27)	3.5 (2.8-4.3)	13.3 (8.4-22.0)	29.8 (26-42)	3.1 (2.8-3.4)	18.6 (11.0-33.0)	—
<u>Subgenus Macrhybopsis</u>							
<u>H. meeki</u>	15.3 (9-23)	4.1 (2.8-6.0)	11.4 (5.4-22.0)	23.4 (16-36)	3.3 (1.8-4.8)	15.9 (5.1-40.0)	3.3 (2.0-4.5)
<u>Subgenus Platyrbio</u>							
<u>H. gracilis</u>	28.2 (15-35)	3.6 (2.0-5.0)	14.8 (6.0-20.0)	36.5 (23-53)	3.1 (2.0-4.5)	21.9 (10.1-38.0)	4.6 (2.3-5.4)
<u>Subgenus Couesius</u>							
<u>H. plumbea</u>	20.8 (16-35)	3.8 (3.3-5.0)	13.4 (11.4-29.0)	32.7 (23-42)	3.0 (2.6-3.6)	25.4 (15.0-46.5)	2.9
<u>Subgenus Oregonichthys</u>							
<u>H. crameri</u>	7.0 (6-2)	3.9 (3.0-4.2)	19.9 (15.2-22.3)	14.0 (13-16)	3.2 (2.9-3.6)	24.6 (20.6-27.0)	3.0

TABLE VIII

COMPARISON OF MEAN HEIGHT AND DIAMETER OF SUPERFICIAL
NEUROMASTS IN HYBOPSIS. PARENTHETICAL NUMBERS
REPRESENT RANGES. SCALE IN MICRONS

Species	Max. Height	Max. Dia.
<u>Extrarius</u>		
<u>H. aestivalis</u>	29.5 (22.0-29.0)	35.6 (20.4-53.0)
<u>Hybopsis</u>		
<u>H. amblops</u>	34.0 (22.3-43.0)	50.0 (35.8-80.8)
<u>H. hybsinota</u>	38.2 (36.0-40.4)	43.0 (43.0)
<u>H. labrosa</u>	22.6	40.1
<u>H. rubrifrons</u>	35.7 (22.3-43.0)	57.9 (32.0-78.0)
<u>H. storeriana</u>	26.6 (22.3-32.2)	42.1 (30.0-56.0)
<u>Erimystax</u>		
<u>H. cabni</u>	32.8 (31.8-33.2)	38.3 (33.2-43.2)
<u>H. dissimilis</u>	35.9 (33.0-53.4)	43.9 (29.4-51.0)
<u>H. harperi</u>	35.1 (25.0-45.0)	43.3 (29.0-65.2)
<u>H. insignis</u>	40.3 (32.0-53.2)	40.9 (27.6-55.0)
<u>H. x-punctata</u>	39.0 (31.6-53.4)	35.5 (24.0-48.0)
<u>Nocomis</u>		
<u>H. bellica</u>	29.7 (26.3-31.5)	31.0 (26.8-33.3)
<u>H. biguttata</u>	38.1 (22.0-48.5)	36.1 (28.0-58.0)
<u>H. leptcephala</u>	36.9 (35.0-41.0)	38.5 (30.0-52.0)
<u>H. micropogon</u>	41.0 (37.0-43.0)	44.5 (29.0-56.6)
<u>H. (Nocomis) sp.1</u>	49.7 (43.0-54.6)	47.5 (41.4-54.8)
<u>H. (Nocomis) sp.2</u>	37.3 (31.0-43.0)	39.8 (30.4-48.0)
<u>Macrhybopsis</u>		
<u>H. gelida</u>	33.4 (27.0-44.0)	33.4 (26.1-56.0)
<u>H. meeki</u>	32.4 (22.0-44.0)	48.3 (27.0-78.0)
<u>Platygobio</u>		
<u>H. gracilis</u>	30.4 (16.0-49.4)	43.5 (32.0-57.0)
<u>Couesius</u>		
<u>H. plumbea</u>	40.3 (30.8-50.0)	58.1 (35.0-99.9)
<u>Oregonichthys</u>		
<u>H. crameri</u>	35.6 (26.0-46.0)	46.9 (38.0-57.0)

TABLE IX

COMPARISON OF THE MEAN NUMBER OF SENSE (SC) AND SUSTENTACULAR (SSC) CELLS, MEAN DIAMETER AND LENGTH OF CELLULAR CONSTITUENTS, AND LENGTH OF SENSE HAIRS (SH) PER SUPERFICIAL NEUROMAST IN HYPOPSIS. PARENTHETICAL NUMBERS REPRESENT RANGES. SCALE IN MICRONS.

Species	Number SC	Cell Dia.	Cell length	Number SSC	Cell Dia.	Cell length	SH length
<u>Subgenus Extrarius</u>							
<u>H. aestivalis</u>	7.5 (5-11)	2.9 (2.0-4.0)	17.7 (14.0-23.6)	11.7 (9-15)	2.4 (1.6-4.0)	27.4 (22.0-38.0)	2.7 (1.8-3.3)
<u>Subgenus Hybopsis</u>							
<u>H. arbleps</u>	8.1 (4-11)	4.1 (3.0-6.0)	18.4 (10.4-22.3)	13.8 (8-19)	3.5 (2.6-5.3)	30.1 (21.0-43.0)	3.2 (2.6-4.3)
<u>H. hypsinota</u>	7.5 (7-8)	3.0 (3.0)	22.7 (21.0-23.1)	11.5 (11-13)	2.6 (2.3-2.8)	37.0 (35.0-40.0)	—
<u>H. labrosa</u>	6.0 (6)	4.8 (4.0-5.3)	15.2	13.0 (13)	3.3 (2.8-3.9)	27.2 (26.0-28.3)	—
<u>H. rubrifrons</u>	6.0 (8)	3.2 (3.1-3.3)	16.5 (15.0-18.0)	17.5 (14-21)	2.8 (2.6-2.9)	28.3 (27.8-29.0)	—
<u>H. storeriana</u>	5.5 (5-6)	3.8 (3.5-4.0)	17.2 (17.0-17.4)	10.0 (10)	3.6 (3.4-3.7)	28.0 (25.0-31.0)	2.0
<u>Subgenus Erimystax</u>							
<u>H. bahni</u>	4.0 (3-5)	3.6 (3.3-3.8)	16.5 (16.0-17.0)	9.0 (8-10)	3.8 (3.5-4.1)	26.7 (22.3-31.0)	—
<u>H. dissimilis</u>	8.5 (6-11)	4.0 (2.4-5.0)	19.3 (16.0-22.0)	13.2 (8-15)	2.9 (2.1-3.8)	31.2 (29.0-37.4)	—
<u>H. harperi</u>	7.7 (6-12)	3.6 (2.9-4.4)	18.7 (13.0-22.8)	11.9 (9-19)	2.9 (2.3-3.2)	30.9 (22.3-38.4)	3.3 (2.6-3.6)
<u>H. insignis</u>	7.2 (5-12)	4.1 (2.9-5.4)	20.9 (17.0-24.8)	14.0 (9-26)	3.2 (2.8-3.4)	36.0 (26.4-43.0)	—
<u>H. x-punctata</u>	7.0 (7)	3.0	18.0	10.0 (10)	2.5	34.0	2.1
<u>Subgenus Nocomis</u>							
<u>H. bellica</u>	5.8 (5-6)	4.4 (3.9-5.9)	15.5 (13.7-17.2)	8.8 (7-10)	3.6 (3.0-4.2)	27.5 (22.3-32.4)	—
<u>H. bifuttata</u>	8.9 (5-11)	4.0 (3.0-5.0)	19.9 (12.2-27.0)	11.1 (8-21)	3.2 (2.6-4.0)	36.6 (22.0-52.0)	3.1 (2.5-4.0)
<u>H. leptocephala</u>	7.7 (7-9)	3.7 (3.0-4.1)	21.8 (20.5-23.0)	11.8 (11-12)	2.7 (2.1-3.0)	39.2 (35.0-41.4)	2.9 (2.8-3.0)
<u>H. microporon</u>	7.6 (6-8)	3.9 (3.2-4.6)	21.6 (20.0-22.0)	13.0 (11-16)	2.5 (2.4-2.8)	41.2 (37.0-44.0)	2.7 (2.3-3.1)
<u>H. (Nocomis) sp. 1</u>	6.6 (5-8)	4.4 (3.6-5.0)	23.1 (20.0-30.0)	10.0 (8-13)	3.3 (2.9-3.6)	47.5 (42.0-56.0)	3.0
<u>H. (Nocomis) sp. 2</u>	6.4 (5-7)	2.6 (2.0-3.6)	22.5 (21.0-26.0)	11.3 (9-14)	3.1 (2.0-3.0)	37.7 (31.0-47.0)	2.1
<u>Subgenus Maerhybopsis</u>							
<u>H. meeki</u>	8.2 (5-13)	4.0 (1.2-6.3)	20.1 (13.0-29.2)	14.9 (6-27)	3.6 (2.5-6.5)	30.0 (15.6-43.0)	3.5 (2.5-5.2)
<u>H. gelida</u>	6.2 (3-9)	3.2 (1.3-4.6)	14.0 (10.1-17.1)	11.3 (6-18)	3.2 (2.1-5.0)	23.6 (18.6-34.9)	2.8 (1.5-4.1)
<u>Subgenus Platygobio</u>							
<u>H. gracilis</u>	7.1 (5-10)	3.1 (2.0-5.0)	17.5 (7.0-29.0)	10.6 (7-13)	2.8 (2.0-3.6)	32.9 (16.0-59.0)	2.6 (2.0-3.1)
<u>Subgenus Couesius</u>							
<u>H. plumbea</u>	8.2 (7-16)	4.1 (3.2-5.0)	23.4 (20.3-29.4)	14.0 (7-16)	3.0 (2.8-4.1)	36.1 (27.0-46.0)	3.0
<u>Subgenus Oronichthys</u>							
<u>H. crameri</u>	5.6 (5-10)	4.6 (4.0-6.8)	24.2 (14.0-30.0)	11.1 (8-13)	3.6 (2.9-4.8)	32.9 (26.0-43.0)	3.7 (2.6-4.0)

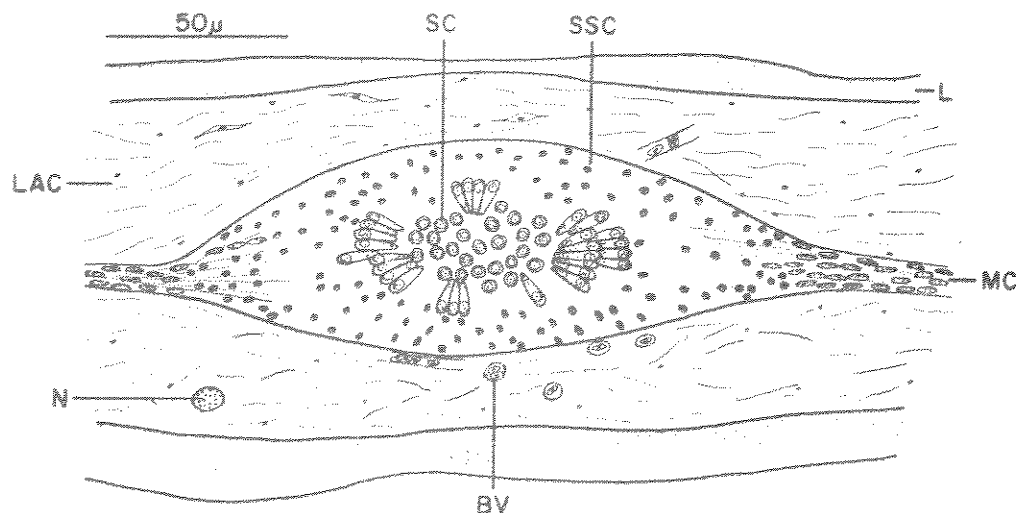


Fig. 29. En face section of an infraorbital canal neuromast of *Hybopsis harperi*. MC, "mesenchymal cord". Other abbreviations as in Fig. 1.

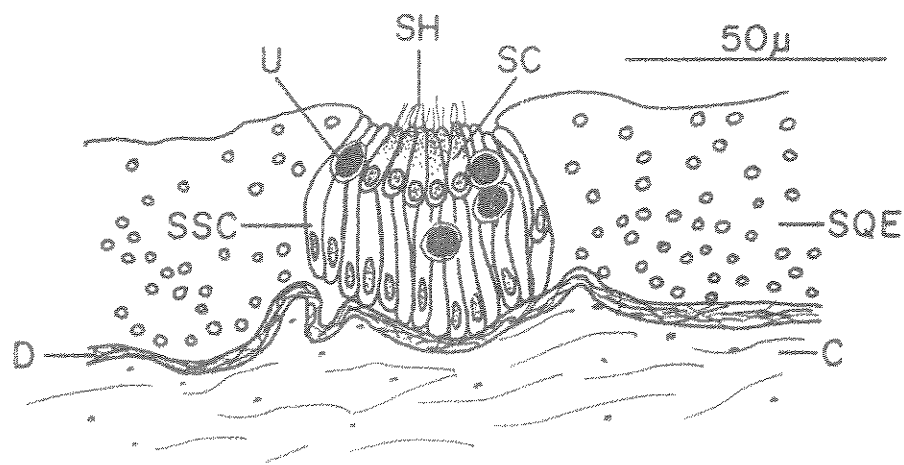


Fig. 30. A superficial neuromast of *Hybopsis crameri*. U, unidentified extracellular structure. Other abbreviations as in Fig. 1.

binding supporting cells together; however, according to Guyer (1953), Davenport (1960), and Bloom and Fawcett (1962), the demonstration of intercellular bridges requires slightly different histological techniques than used in this study.

In agreement with Beard (1884), Denny (1937), Van Bergeijk and Alexander (1962), and Jakubowski (1965), the canal neuromasts of Hybopsis appear segmentally arranged, for "cords of mesenchyme" were observed extending from the long axes of organs sectioned en face (Fig. 29). Apparently, the cords are very thin (1-2 cells thick) and, by virtue of being thin, impossible to see in sagittal and cross sectional view. Ham (1965) noted that mesenchymal and fibroblast cells are amorphous, and that, without special techniques (tissue culture, silver impregnation, etc.), cell shapes are difficult to demonstrate; consequently, the cellular nature of the cords was indiscernible, but the shape, structure, and spacing of nuclei conformed to that described by Denny (1937), Van Bergeijk and Alexander (1962), and Ham (1965). Where the cords joined the neuromasts, the cells of both merged one into the other. Numerous fibers were seen interspersed throughout the cords, and, even though cord nuclei ceased at the neuromast limits, the fibers entered, dispersed, and eventually disappeared within neuromasts. Denny (1937) and Van Bergeijk and Alexander (1962) indicated that the mesenchymal cord locally differentiates into canal organs and, thereafter, serves as a cell reservoir for neuromasts. The functional significance of the fibers is questionable and, since no similar structures have heretofore been observed, any comment would be purely speculative. Although not demonstrated, the cords may contain some contractile elements which,

via the fibers, slightly alter neuromast shape and position. To actively alter shape and position would certainly be advantageous, particularly when one considers that impinging vibrations could be modified (amplified or damped) and/or that annoying elements which frequent the canal be dissipated. This latter facet of canal "structure" will be more fully explored later.

It is interesting that in Hybopsis the size of canal neuromasts corroborates earlier suppositions concerning environmental and hormonal effects upon the lateral-line system. In turbid-water species such as H. aestivalis, H. x-punctata, and H. meeki, canal neuromasts are small and probably of limited use since external vibrations are doubtlessly inhibited by the small canal pores and long canaliculi. Conversely, in clear-water forms like H. amblops, H. rubrifrons, and H. harperi, canal organs are large and free to receive unmodified stimuli through the large pores and short canaliculi. Those species inhabiting both turbid and clear waters (e.g., H. gracilis, H. storeriana, etc.) also have large canal organs, but organ efficiency remains questionable since the canaliculi and pores are of medium size. Conversely, what can be deduced about clear-water forms like Nocomis which have large canal neuromasts, long canaliculi, and medium-size pores, or H. crameri with a degenerate lateral-line system? In juvenile Nocomis the canals, canaliculi, and pores are like other clear-water Hybopsis, but, at maturity, the canaliculi lengthen in response to hormonal modification of the integument. Doubtless, in juveniles the system functions as in other clear-water Hybopsis, but in adults reception is probably reduced to a more limited capacity. In H. crameri canal degeneration is so acute that canal organs are no longer needed; instead their function has

been secondarily usurped by the larger skin neuromasts (compare Tables VI and VIII).

In H. crameri several (2-9) extracellular structures were observed between the sense cells of each skin neuromast. These protozoa-like structures were green colored regardless of stain, homogeneous throughout, and individually surrounded by a lucid layer (Fig. 30). Charipper (1928), Chezar (1930), Dawson (1936), and Bedell (1939) observed some bright orange, granulated structures in the neuromasts of various amphibian larvae, and, from in vivo studies, suggested that the granules were modified secretory or excretory products of the sense cells. Whether or not the extracellular structures in H. crameri are homologous to those in amphibians is unknown, but heretofore no similar structures have been reported in fishes. Should someone have access to live material, in vivo and ultrastructure studies could perhaps clarify the identity of these peculiar neuromast structures in H. crameri.

In Hybopsis canal walls are composed of two layers, the inner being separated from the outer by the basement membrane (Fig. 1). Branson and Moore (1962) Sharma (1964), and Reno (1966) indicated that the inner canal layer of various fishes is simple cuboidal with pseudostratified columnar epithelium adjacent to neuromasts. In Hybopsis, however, the inner layer is stratified squamous throughout. A similar epithelial lining is characteristic of Dorosoma (Stephens, 1967) and Ericymba (unpublished date). Re-evaluation of Notropis volucellus and N. buchanai revealed their canals to also be lined with stratified squamous epithelium. Since neuromasts originate in and invaginate from the epidermis, carrying part of the epithelium with them, and since adult tissues do not metamorphose into other specialized types (Balinsky, 1961; and Ham, 1965)

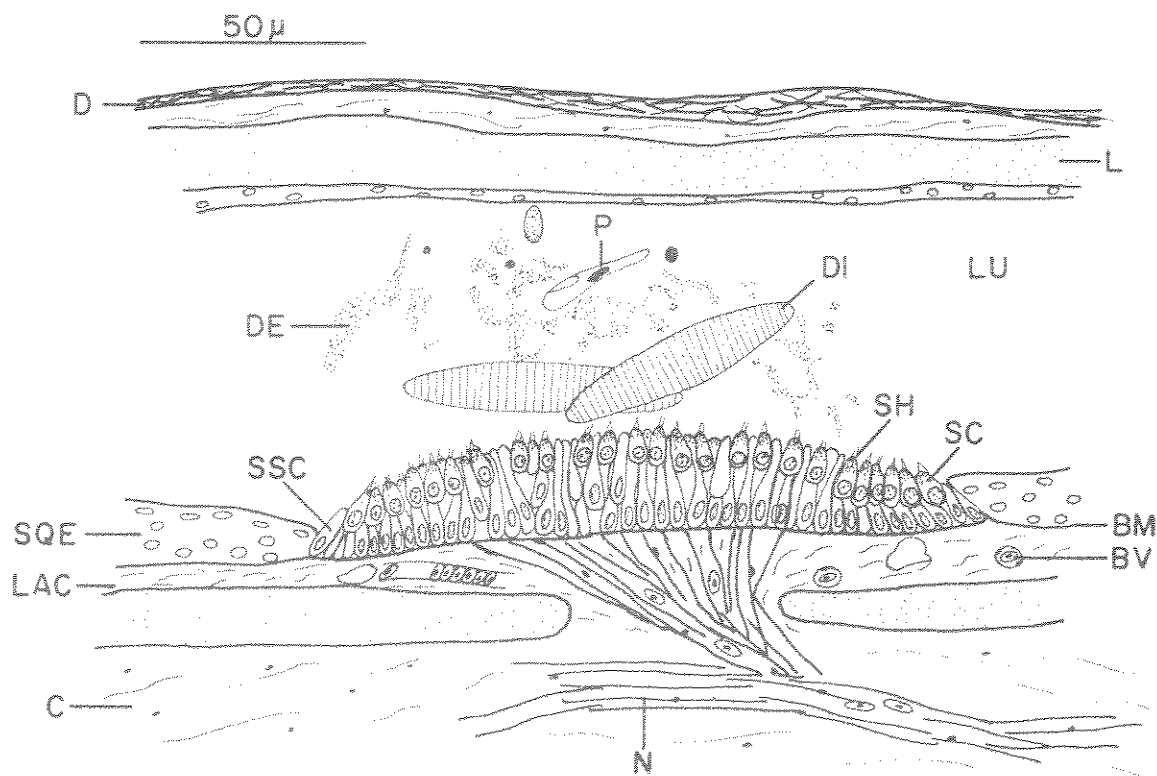


Fig. 31. Longitudinal section through the infraorbital canal and neuromast of *Hybopsis insignis*. DI, diatoms; P, protozoa. Other abbreviations as in Fig. 1.

it is not surprising that canals are lined with stratified squamous tissue. Unlike other cyprinids, all *Hybopsis* except *H. gracilis* have few if any goblet cells in the canal epithelium; as a result, the canals are virtually mucus-free. In lieu of mucus, the canals are filled with environmental water, thus creating a natural haven for microorganisms. Indeed, protozoa (primarily ciliates) and various motile algae (diatoms and desmids) were observed in canals of all *Hybopsis* except *H. gracilis* (Fig. 31). In *Hybopsis* the outer canal layer is loose areolar connective tissue. In general, beneath each canal neuromast is a bony foramen through which the lateral-line nerve and capillaries pass (Figs. 1 and 31). Upon penetrating the foramen, the unmodified nerve (without ganglia) suffuses through the loose areolar

tissue, eventually piercing the basement membrane at the base of the neuromast. Whether individual neurons lose their myelination before, while, or after penetrating the basement membrane was not determined. Like the lateral-line nerve, the capillaries suffuse through the loose areolar layer and, upon reaching the basement membrane, form a complicated rete under the organ as reported by Van Bergeijk and Alexander (1962) in Fundulus heteroclitus and Jakubowski (1965, 1966) in Lota lota, Esox lucius, and some Cobitidae.

Fundamentally, lateral-line bones originated from any of three sources, viz., (1) tropic activities of neuromasts, (2) combined actions of neuromasts and anasmestic forces, or (3) sources other than neuromasts. Allis (1889), Pehrson (1922, 1944), Westoll (1937), Lekander (1949), and Branson and Moore (1962) showed in several unrelated taxa that, during ontogeny, specific skin neuromasts (primary neuromasts) invaginate beneath the skin surface and become established in connective tissue tubes. Sometime thereafter, osteoblasts amass beneath the organs, forming a series of bone primordia. At times, specific invaginated neuromasts are secondarily lost or destroyed; however, where primordia become established prior to neuromast destruction, bones continue to develop, but without canals or neuromasts. Furthermore, when neuromasts fail to invaginate altogether, bones do not develop. Stensió (1947) showed in primitive vertebrates (fossil and extant) that each invaginated neuromast becomes enclosed by a bone primordium. The primordia usually fuse into bony plates and secondarily acquire anasmestic components which, he said, are elements that "... enter into the formation of the exoskeleton of the head..." Kapoor (1962) showed in Ophicephalus punctatus that latero-

sensory elements arise from underlying bony plates (e.g., membranous frontal) and later fuse into bony tubes around the neuromasts and connective tissue canals. He concluded that neither membranous bones nor latero-sensory elements originated from morphogenetic activities of canal neuromasts; instead neuromasts are limited to the evocations of bones in their immediate neighborhoods. Renc (1966) observed in two Notropis that bony tubes and sense organs are sometimes independent of their anasmestic associates. He concluded that neuromasts are active in evocating bony canals, but passive in initiating ossicular development. Moodie (1922) showed in some fishes and amphibians that calcium salts deposited in the inactive connective tissue of canals eventually resulted in formation of bony tubes. He surmised that the connective tissue tubes rather than invaginated neuromasts are responsible for bone formation. Parrington (1949) postulated for some primitive vertebrates that dermal bone precursors are in position before lateral-line organs are established and capable of initiating any evocation. Apparently, the position of canals is influenced by dermal bones rather than dermal bones being determined by canals and neuromasts. De Beer (1937) and Moy-Thomas (1941) asserted that origin of dermal bone is not dependent upon neuromast activities, because, in higher vertebrates, homologous bones develop without lateral-line tubes. Apparently, in lower forms, neuromasts serve only to localize, not evoke, the development of dermal bones. Wohlfahrt (1967) demonstrated in Clupea pilchardus that some canal neuromasts develop without secondarily forming bone primordia and Stephens (1967) observed in Dorosoma petenense that certain bony elements, supposedly evoked by neuromast activities, formed without

sense organs.

In Hybopsis the lateral-line system is probably the last system to form. For example, in H. aestivalis, specimens under 19 mm standard length lack fully formed canals, and, in Nocomis, canals are wanting in individuals less than 36 mm standard length. In these and other Hybopsis, however, the lateral-line bones are almost always fully formed before closure of the canals. The canals, although normally fused with bones, are sometimes freely suspended in the overlying subcutaneous connective tissue. This occurrence is not unusual, since canals, either bone or connective tissue, commonly traverse bones via grooves or depressions as seen in Ameiurus (Moodie, 1922), Lepomis humilis (Curd, 1959), Centrarchidae (Branson and Moore, 1962), Cycleptus (Branson, 1962a), and two Notropis (Reno, 1966). Canal neuromasts are normally enclosed by bone and solidly fused with lateral-line ossicles, but, like canals, occasionally become independent of bones.

The mechanisms of neuromast invagination in Hybopsis are little understood. Apparently, neuromasts and part of the epidermis are invaginated by latero-sensory elements (usually 2) growing outward from underlying bony plates. As the elements grow, the skin covering each is pushed upward, while the tissues and sense organs between elements are gradually "invaginated" and later enclosed by them. Where neuromasts are displaced laterally, the growing elements still effect invagination of the sense organs and epidermis, although the incipient tubes with neuromasts become established outside the bony components of the canals (Fig. 32). Without neuromasts, the tissues between developing elements do not invaginate; consequently, bony

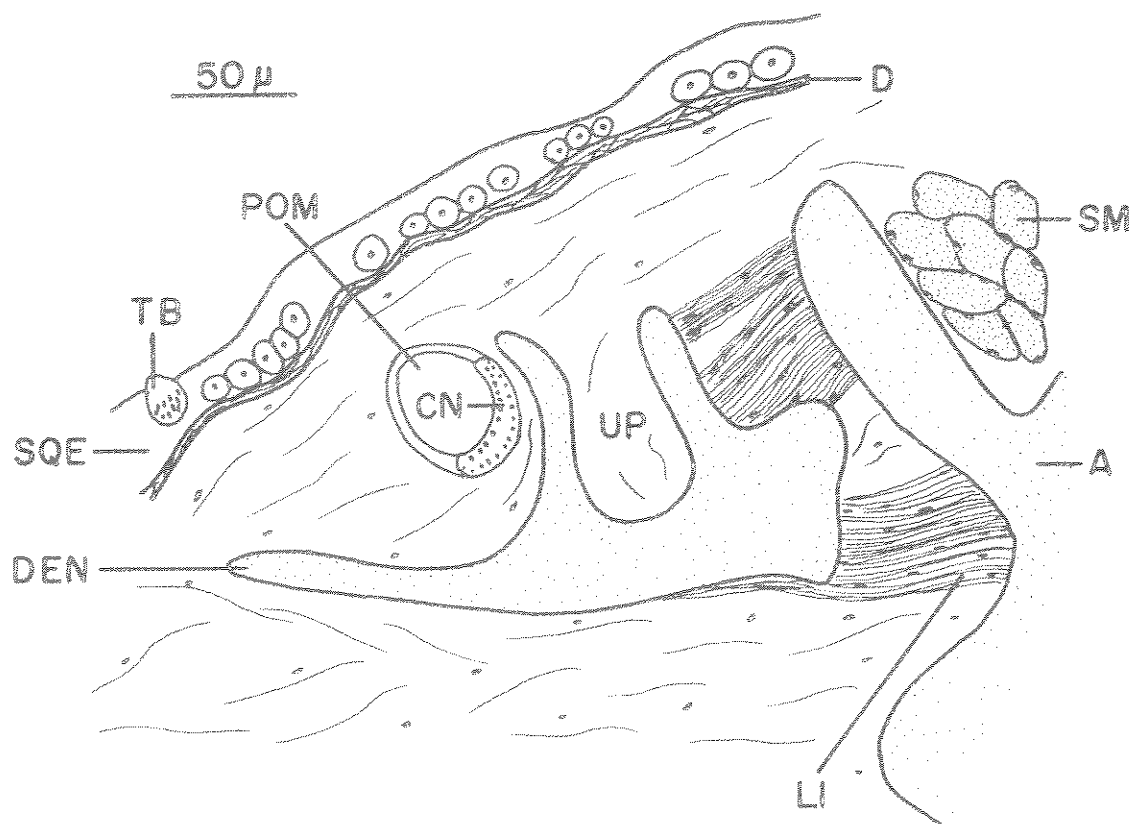


Fig. 32. Transverse section through preoperculomandibular canal of *Hybopsis leptocephala*. A, angular (after Harrington, 1955); CN, canal neuromast; DEN, dentary; LI, ligament; SM, striated muscle; TB, taste bud; UP, usual position of POM canal. Other abbreviations as in Fig. 1.

tubes form without sense organs, epithelial linings, or lumina. The development of bony canals with neuromasts independent of lateral-line bones suggests a second type of organ invagination and canal formation. Evidently, some canals or portions of canals (e.g., formation of the rudimentary dermosphenotic bone at the junction of the IO and POC canals) invaginate without the assistance of underlying latero-sensory elements. After invagination, the process of canal ossification is different from that given above, viz., direct deposition of ostein in the walls of the connective tissue tubes. Occasionally, the bony tubes become so closely associated with lateral-line bones that

deposition of bone between them results in fusion. When this happens, it is impossible to ascertain which of the two mechanisms obtained in canal formation.

Generally, among cyprinids the SO and POC canals are separate, with several groups and species manifesting closely apposed SO and POC canaliculi (Lekander, 1949; and Illick, 1956). Lekander (1949) suggested that ancestral cyprinids probably possessed joined SO and POC canals and that, in succeeding morphotypes, the connections between canals gradually disappeared. As the disruptions became more permanent, the SO canals lengthened posteriad over parts of the frontal and parietal bones. Incipient neuromasts, derived from cranial pit lines, progressively invaded the elongated canal parts and, thereafter, acquired latero-sensory elements which generally fused with the underlying membranous bones. In Hybopsis, the SO and POC canals are separate, but in most species they are closely allied via canaliculi. In H. labrosa, H. bellica, and others, connections between the SO and POC canals appear commonplace, while in still other species (e.g., H. biguttata, H. gracilis, H. plumbea, etc.), displaced or nonexistent POC canaliculi permanently isolate the canals. Furthermore, although not seen, in H. gelida, H. meeki, and other forms with long canaliculi, long life (comparatively speaking, of course) and continued growth no doubt occasionally result in fusion of the two canals. Following this line of reasoning, one might suggest that the immediate ancestors of Hybopsis had connected SO and POC canals which, through time, eventually separated. In Hybopsis those SO canal portions, elongated posteriad, are probably modified canaliculi, since most parts are connective tissue rather than bone. Seemingly, neuro-

masts have secondarily immigrated into these tubes and, in most instances, have become encased by bone. However, bony tubes not only form around organs but also around parts of the connective tissue canals as well. Thus, in any Hybopsis, a series of bony tubes ("drain-pipe" bones of Moodie, 1922) may form which may or may not secondarily amalgamate into a continuous tube. If neuromasts are responsible for bone evocation, what evokes the bony elements between organs? Apparently, sources other than neuromasts initiate formation of these latero-sensory elements, and if this be true, there is reason to question the evocating powers of neuromasts. On the basis of these and the other observations discussed earlier, it is doubtful whether neuromasts are directly responsible for bone formation in Hybopsis. Perhaps, as suggested by Lekander (1949) for higher teleosts, bones of Hybopsis arise from sources (direct genetic evocation?) other than neuromasts, and bony tubes develop only to protect the organs.

CHAPTER VII

PHYLOGENIES AND INTERGENERIC RELATIONSHIPS

Since Hybopsis appears to be a heterogeneous assemblage of questionably related species and groups, it is difficult, if not impossible, to construct a single phylogeny for the entire group; however, it does seem possible to erect phylogenies for some subgenera. Following Gosline (1949) and Illick (1956), the sequential phylogenies for Hybopsis and Erimystax are not based solely on lateral-line evidence, but on several other factors as well. It is important that most authorities consider complete lateral-line canals primitive and reduction of canals, canaliculi, and/or canal neuromasts steps toward specialization (Myers, 1958; Branson and Moore, 1962; and many others). One factor sometimes used in establishing phylogenies is distribution and habitat. According to Ross (1957) and Branson and Moore (1962), correlation between ecological and morphological characteristics frequently enhance elucidation of phylogenetic relationships within a taxon or taxa.

Apparently the subgroups Hybopsis and Erimystax are more closely related to each other than to other subgenera of Hybopsis. Both probably arose from the same free-swimming inhabitant of turbid, semiturbid, or intermittently turbid streams (Fig. 33). This hypothetical stem-type probably resembled H. labrosa (Fig. 4), but, unlike H. labrosa, it perhaps had a complete ST canal, continuous POM canals,

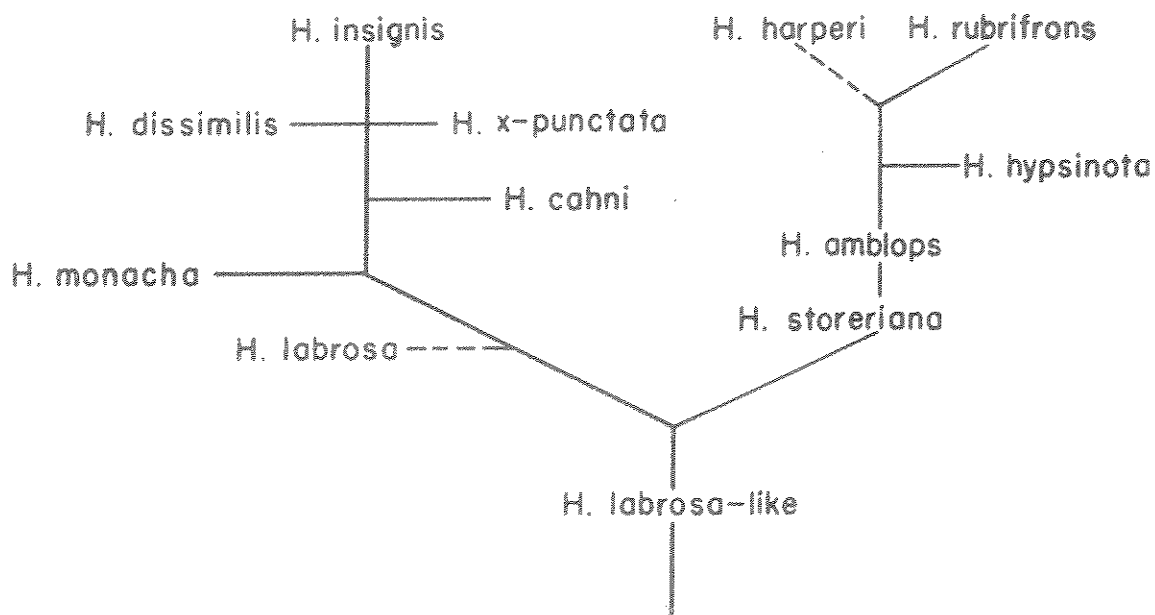


Fig. 33. Hypothetical dendrograph for *Hybopsis*, subgenera *Erimystax* and *Hybopsis*.

short barbels, and greater numbers of skin neuromasts. Davis and Miller (1967) suggested that, on the basis of greater numbers of skin taste buds, similarity in brain patterns, and living in turbid-water environments, *H. labrosa* and *H. storeriana* are primarily taste-feeders, whereas, with fewer skin taste buds, larger eyes, similar brain patterns and living in clear-water environments, *H. amblops*, *H. rubrifrons*, and *H. hypsinota* are sight-feeders. However, they questioned the close kinship of *H. labrosa* to *H. storeriana* and other *Hybopsis*, for they wrote, "The marked distinctiveness of *H. labrosa* suggests that it has either diverged from the adaptive pattern established by other members of the subgenus *Hybopsis*, or that it may not actually be as closely related, phylogenetically, as the present classification indicates." Consequently, *H. labrosa* is probably a specialized form (owing to long barbels, incompleteness in some canals, few skin neuromasts, and limited distribution) which diverged

from the main line of Hybopsis evolution.

A complete ST canal, medium-size canaliculi, and a few other lateral-line percularities, coupled with a wide distribution and life in turbid environments, make H. storeriana (Fig. 5) the most logical candidate for position nearest the hypothetical stem-type for the Hybopsis group. Over much of its range, H. storeriana is sympatric with H. amblops, although the former generally dwells in more turbid waters and the latter in clear waters (Moore and Paden, 1950; and Trautman, 1957). In H. amblops (Fig. 6) reduction of canaliculus length, expansion of canal pores, incompleteness of the ST canal, increased numbers of skin neuromasts, and fewer numbers of skin taste buds suggest that it descended directly from H. storeriana. Moore (1957) indicated that H. amblops is trans-Mississippi River in distribution, ranging as far east as Alabama and Georgia, where its range is allopatric with H. rubrifrons and, to a lesser extent, with H. hypsinota. Since the lateral-line systems of H. rubrifrons and H. hypsinota are similar to H. amblops (compare Figs. 6-8), although the POM canal of H. hypsinota is interrupted, perhaps H. amblops once extended eastward from its present range into the Santee drainage of the Carolinas. Later, it retreated westward, leaving behind the specialized form H. hypsinota. Likewise H. rubrifrons differentiated in the Altamaha and Savannah drainage of Georgia and South Carolina. My data suggest that H. amblops gave rise to H. hypsinota before H. rubrifrons and that continued isolation over a longer period of time has resulted in greater phylogenetic divergence between H. amblops and H. hypsinota. Conversely, the later appearance of H. rubrifrons and rather recent isolation from H. amblops (?) is responsible for the

close morphological kinship between these two species.

According to Hubbs and Crowe (1956) and Moore (1957), H. amblops, H. hypsinota, and H. harperi sometimes lack barbels. Comparison of the brain patterns (Davis and Miller, 1967), lateral-line systems, and other morphometric data (Tables III-IX) of these species with those of H. rubrifrons (Figs. 6-8 and 14) reveals a striking similarity between them, even though H. harperi is presently considered a member of Erimystax. Conversely, making the same comparison between members of Erimystax and H. harperi (Figs. 10-14) reveals a striking dissimilarity between them. Moreover, Moore (1957) gave the range of H. harperi as being in "...northern Florida and adjacent parts of Georgia and Alabama," which is some distance south of the nearest Erimystax (H. monacha) in the Tennessee River system. Therefore, it seems that H. harperi is more closely allied to Hybopsis than Erimystax. Perhaps H. amblops once ranged southward into Florida, giving rise at that time to the closely related but highly specialized form H. harperi.

Divergence of H. labrosa from Hybopsis perhaps signifies that it is more closely related to Erimystax than currently recognized taxonomically. Indeed, similarity in brain patterns, lateral-line systems, body shapes, and other morphometric data substantiates a close kinship between them. It seems likely, however, that Erimystax evolved directly from the more primitive H. labrosa-like ancestor described earlier rather than from H. labrosa per se (Fig. 33). Erimystax appears to be phylogenetically divisible into two groups, the first being represented by H. monacha and the second by H. cahni, H. dissimilis, H. insignis, and H. x-punctata. Evidently, H. monacha,

like H. labrosa, diverged from the main line of Erimystax evolution, since it independently acquired many of the lateral-line characteristics found in H. labrosa (compare Figs. 4 and 10). Members of the second group probably emerged when the anterior portion of the primitive IO canal rotated posteriad (compare Figs. 4, 10-13). This particular character is one of the major differences separating members of the second group from H. labrosa and H. monacha. Within the second group, phylogenetic relationships are enigmatic, particularly when it is considered that most species are sympatric and morphologically very similar. However, on the basis of rareness (Davis and Reno, 1966), limited distribution (Moore, 1957), and slight differences in lateral-line systems, H. cahni may be somewhat more removed phylogenetically from the other three species.

While the phylogenies presented are tentative, it is certain that H. harperi and H. labrosa manifest some peculiarities which suggest that their present taxonomic positions are inappropriate. The possibility of relocating H. harperi in Hybopsis and H. labrosa in Erimystax as suggested in Figure 33 should definitely be considered by future students of these groups.

Biologists generally agree that taxonomic categories above the species level are more or less subjective. Accordingly, taxonomic categories recognized by one scientist may not necessarily correspond with those of another scientist. As defined by Mayr, Linsley, and Usinger (1953), a genus is "...a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap." Ordinarily, species within a genus individually occupy more or less well-

defined ecological niches with a greater or lesser degree of overlap; thus, the genus is a group of closely related species (i.e., derived from a common ancestor) adapted for a particular mode of life (Mayr, Linsley, and Usinger, 1953). While this definition is loosely worded, and indeed necessarily so for obvious reasons, it provided a method for categorizing related species into natural groups and conveys standard conceptions about generic composition. The genus may, however, become a confused and meaningless unit if inappropriate characters are utilized to delineate such groups.

The lumping of nine nominal genera into Hybopsis illustrates this point. Apparently, the possession of barbels is the single universal character these fishes have in common (Moore, 1957), even though each group is morphologically distinct. Perhaps the most easily recognized subgenus included in Hybopsis is Nocomis. Characteristically, all Nocomis exhibit seasonal changes in color and tuberculation, build elaborate nests (Raney, 1947), are large (300 mm; Moore, 1957), and inhabit clear streams. Likewise, their lateral-line systems are unique: In juveniles, canals are similar to other clear-water Hybopsis, but in adults they are dramatically modified to compensate for seasonal changes in facial integuments (Figs. 16-21).

The subgenus Couesius, characterized by barbels forward from the maxillary terminus and small scales, is unique because no other Hybopsis has facial features and/or lateral-line systems similar to H. (Couesius) plumbea (Fig. 25). If Couesius is actually best considered a Hybopsis, then it seems logical to also include Semotilus and perhaps even Rhinichthys in Hybopsis, since both also have barbels. At the present time, Couesius is being considered for separation from

Hybopsis and alliance with Semotilus, Gila, Chrosomus, and Phoxinus (correspondence between Drs. R. M. Bailey and R. J. Miller).

The subgenus Oregonichthys is geographically isolated from other Hybopsis. Its limited range, deep and compressed body, inconspicuous barbels, and unique lateral-line system (Figs. 26 and 29) cast serious doubt on any phylogenetic affinities with other subgroups of Hybopsis.

While the lateral-line system of H. (Platygobio) gracilis (Fig. 24) is similar to some Hybopsis, the presence of large numbers of canal goblet cells suggests considerable uniqueness, particularly when it is considered that other Hybopsis have few if any such cells in their canals.

Davis and Miller (1967) noted that Extrarius is perhaps the most plastic, widely distributed, and locally differentiated subgenus within Hybopsis. According to Mayr (1963), in every wide spread, actively evolving genus or species, there are geographic populations which have differentiated little from each other, others that are as different as subspecies, others that have almost reached species level, and finally still others that are full species. Sometimes these remain allopatric in other cases the most distinct ones secondarily overlap the ranges of their close relatives. Extrarius appears to be actively evolving new forms, for the brain patterns, number of barbels (usually 1 or 2, rarely 3 or more pairs per individual), and number of pores per lateral-line canal vary slightly in some localities and dramatically elsewhere.

Even though Macrhybopsis and Erimystax resemble Extrarius (compare Figs. 3, 10-14, and 22-23), morphological similarity is probably a reflection of environmental similarity, rather than close kinship.

Finally, the subgenus Hybopsis is unique, its lateral-line systems being primarily adapted to clear-water environments (Figs. 5-8, and 15). The frequent absence of barbels in some species of the subgenus Hybopsis and their appearance in Notropis amnis Hubbs and Greene suggest that Hybopsis and some Notropis are closely related; more so, in fact, than Hybopsis is to some of its congeneric subgenera.. Hubbs (1951) wrote, "The minnow that Notropis amnis perhaps most closely resembles in superficial appearance is Hybopsis amblops (Rafinesque)... Were it not for the very peculiar mouth structure of N. amnis, which H. amblops hardly shares, one might even postulate that amnis was derived from amblops by loss of the small maxillary barbel. That possibility is not wholly excluded, for H. a. winchelli occasionally lacks the barbel on one or even both sides and the mouth structure somewhat approaches that of N. amnis."

Gill (1876) once remarked, "It certainly cannot be in conformity with nature to place genera at almost extremes of the family simply on account of the presence or absence of barbels... The barbels, being only tags of skin proceeding from the integument of the maxillary bones, have very little systematic value compared with the barbels, and especially the maxillary barbes of the Siluroids." Perhaps, if Gill were alive today, he would modify his statement to include, as not being "...in conformity with nature...", the lumping of separate barbeled genera into one genus. Since the lumping of several genera into Hybopsis, some workers have viewed the merger with skepticism. For example, Hubbs and Crowe (1956) indicated that, "For several reasons the re-expanded genus Hybopsis rests on an unsteady basis, ..." Moore (1957) found it difficult to characterize the genus

Hybopsis, because subgroup morphologies are markedly different and habitat requirements exceedingly diverse. Davis and Miller (1967) said that the polytypic genus Hybopsis, as recognized today, "... probably constitute(s) and unnatural grouping." Recent correspondence between Drs. G. A. Moore and E. A. Lachner have questioned the authenticity of recognizing certain subgroups of Hybopsis as subgenera rather than full genera. Lateral-line evidence presented here also tends to question the subgeneric status of some of these groups. On the basis of morphological evidence presented by Davis and Miller (1967) and me, and the skepticism voiced by the above scientists, I suggest that the subgenera now included in Hybopsis be resurrected to full generic status.

LITERATURE CITED

- Agassiz, J. L. R. 1850. Lake Superior: Its physical character, vegetation, and animals, compared with those of other and similar regions. 428 pp.
- _____. 1854. Notice of a collection of fishes from the southern bend of the Tennessee River, in the State of Alabama. Amer. J. Sci. 67:297-308, 353-365.
- Allis, E. P. 1889. The anatomy and development of the lateral-line system in Amia calva. J. Morphol. 2:463-540.
- _____. 1904. Sensory canals and related bones in fishes. Int. Mech. Anat. Physiol. 20:125-170.
- _____. 1936. Comparison of the latero-sensory lines, the snout and cranial roofing bones of the Stegocephali with those in fishes. J. Anat. 70(2):293-316.
- Andres, A. 1899. Anatomia della Tinca con referenza ad altre Cyprinidae. Milano.
- Bailey, R. M. 1951. A check list of fishes of Iowa with keys for identification. In: Iowa fish and fishing. Harlan and Speaker, Iowa State Conserv. Comm., pp. 187-238.
- _____. and M. O. Allum. 1962. Fishes of South Dakota. Misc. Publ. Zool. Univ. Mich. 119:1-131.
- _____. H. E. Winn, and C. L. Smith. 1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Natur. Sci. Phila. 106:109-164.
- Bailey, S. W. 1937. An experimental study of the origin of lateral-line structures in embryonic and adult teleosts. J. Exp. Zool. 76:187-233.
- Balinsky, B. I. 1961. An introduction to embryology. W. B. Saunders, Philadelphia, Pa.
- Bamford, T. W. 1941. The lateral line and related bones of the herring (Clupea harengus L.). Amer. Mag. Natur. Hist. 8:414-438.
- Bangham, R. V. 1941. Parasites of fresh-water fish of southern Florida. Proc. Fla. Acad. Sci. 5:289-307.

- Beard, J. 1884. On the segmental sense organs of the lateral line, and on the morphology of the vertebrate auditory organ. *Zool. Anz.* 7:123-126.
- Bedell, S. G. 1939. The lateral-line organs of living amphibian larvae with special reference to orange colored granules of the sensory cells. *J. Comp. Neurol.* 70:231-247.
- Bloom, W. and D. W. Fawcett. 1962. A textbook of histology. 10th. ed. W. B. Saunders, Philadelphia, Pa.
- Branson, B. A. 1961. The lateral-line system in the Rio Grande perch, Cichlasoma cyanoguttatum (Baird and Girard). *Amer. Midl. Natur.* 65:446-458.
- _____. 1962a. Comparative cephalic and appendicular osteology of the fish family Cottotomidae. Part I; Cycleptus elongatus (LeSueur). *Southwest. Natur.* 7(2):81-153.
- _____. 1962b. Observations on the breeding tubercles of some ozarkian minnows with notes on the barbels of Hybopsis. *Copeia* 1962(3):532-539.
- _____. 1963. The olfactory apparatus of Hybopsis gelida (Girard) and Hybopsis aestivalis (Girard) (Pisces: Cyprinidae). *J. Morphol.* 113(2):215-229.
- _____. 1966. Histological observations on the sturgeon chub, Hybopsis gelida (Cyprinidae). *Copeia* 1966(4):872-876.
- _____ and G. A. Moore. 1962. The lateralis components of the acoustic-lateralis system in the sunfish family Centrarchidae. *Copeia* 1962(1):1-108.
- Cahn, P. H. and E. Shaw. 1962. The first demonstration of lateral line cupulae in the Mugiliformes. *Copeia* 1962(1):109-114.
- Charriper, H. A. 1928. Studies on the lateral-line system of Amphibia. I. Cytology and innervation of the lateral-line organs of Necturus maculosus. *J. Comp. Neurol.* 44(4):425-447.
- Chezar, H. H. 1930. Studies on the lateral-line system of Amphibia. II. Comparative cytology and innervation of the lateral-line organs in the Urodela. *J. Comp. Neurol.* 50(2):159-175.
- Cockrell, T. D. A. and E. M. Allison. 1909. The scales of some American Cyprinidae. *Wash. D. C. Proc. Biol. Soc.* 22:157-163.
- Collinge, W. E. 1893. The lateral canal system of Lepidosteus osseus. *Proc. Birmingham Natur. Hist. Phil. Soc.* 8:263-272.

- Cope, E. D. 1865. Description of new Ceratichthys taken in the Conestogo. Proc. Acad. Natur. Sci. Phila. 1865:277.
- _____. 1868. On the distribution of freshwater fishes in the Allegheny region of southwestern Virginia. J. Acad. Natur. Sci. Phila. 6:207-247.
- _____. 1871a. Report on recent reptiles and fishes, obtained by the naturalist of the Hayden Expedition for the survey of Wyoming and contiguous territories in 1870. Hayden's Geol. Sur. Wyo. 1870: 432-442.
- _____. 1871b. Partial synopsis of the freshwater fishes of North Carolina. Proc. Amer. Phil. Soc. 11:448-495.
- _____. 1876. Report upon the collection of fishes made in portion of Nevada, Utah, California, Colorado, New Mexico, and Arizona during the years 1871, 1872, 1873, and 1874. Wheeler's Geol. Surv. 5:635-703.
- Curd, M. R. 1959. The morphology of abnormal lateral-line canals in the centrarchid fish Lepomis humilis (Girard). Proc. Okla. Acad. Sci. 39:70-75.
- Davenport, H. A. 1960. Histological and histochemical technics. W. B. Saunders, Philadelphia, Pa.
- Davis, B. J. and R. J. Miller. 1967. Brain patterns in minnows of the genus Hybopsis in relation to feeding habits and habitat. Copeia 1967(1):1-39.
- _____. and H. W. Reno. 1966. Rediscovery of the slender chub, Hybopsis caini, at the type locality, Clairborne County, Tennessee. Southwest. Natur. 11(2):307.
- Dawson, A. B. 1936. Changes in the lateral-line organs during the life of the newt, Triturus viridescens. A consideration of the endocrine factors involved in the maintenance of differentiation. J. Exp. Zool. 74(3):295-303.
- De Beer, G. R. 1924. Notes on the pacodes and the ophthalmic nerves. Quart. J. Microsc. Sci. 68:661-665.
- _____. 1937. The development of the vertebrate skull. Oxford Univ. Press, Oxford, England.
- Denny, M. 1937. The lateral-line system of the teleost, Fundulus heteroclitus. J. Comp. Neurol. 68(1):49-65.
- Devillers, Ch. 1944. Le système sensoriel cephalique du Gardon (Leuciscus rutilus L.). Bull. Soc. Fr. 68-69:94-97.
- _____. 1947. Recherches sur le crâne dermique des Teleostéens. Ann. Paléontol. 33:1-94.

- Dijkgraaf, S. 1962. The functioning and significance of the lateral-line organs. *Biol. Rev.* 38:51-105.
- Flemer, D. A. and W. S. Woolcott. 1966. Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the blue gill, Lepomis m. macrochirus Rafinesque. *Chesapeake Sci.* 7(2):75-89.
- Flock, Å. and J. Wersäll. 1962a. Synaptic structures in the lateral line canal organ of the teleost fish Lota vulgaris. *J. Cell Biol.* 13(2):337-343.
- _____ and _____. 1962b. A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors. *J. Cell Biol.* 15(1):19-27.
- Forbes, S. A. 1883. In: A synopsis of the fishes of North America, by D. S. Jordan and C. H. Gilbert. *Bull. U. S. Natur. Mus.* 16:1-1018.
- Fowler, H. W. 1941. A collection of fresh-water fishes obtained in Florida, 1939-1940, by Francis Harper. *Proc. Acad. Natur. Sci. Phila.* 92:227-244.
- Gill, T. 1876. Report on ichthyology (Appendix L). In: Report of explorations across the Great Basin of the Territory of Utah for a direct wagon-route from Camp Floyd to Genoa, in Carson Valley in 1859, by Capt. J. H. Simpson. Gov't. Print. Office, Washington, D. C. pp. 386-435.
- Gilbert, C. H. 1885. A list of fishes collected in the East Fork of White River, Indiana, with descriptions of two new species. *Proc. U. S. Natur. Mus.* 7:199-205.
- _____. 1887. Third series of notes on Kansas fishes. *Bull. Washburn Coll. Lab. Natur. Hist.* 1:207-211.
- Girard, C. 1856. Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States of America, west of the Mississippi Valley, from specimens in the Museum of the Smithsonian Institution. *Proc. Acad. Natur. Sci. Phila.* 1856:165-213.
- Goodrich, E. S. 1930. Studies on the structure and development of vertebrates. Vol. II. Dover Publ. Reprint, New York, N. Y.
- Gosline, W. A. 1949. The sensory canals of the head in some cyprinodont fishes, with particular reference to the genus Fundulus. *Occas. Pap. Mus. Zool. Univ. Mich.* 519:1-21.
- Günther, A. 1868. Catalogue of the fishes in the British Museum. Vol. VII. Taylor and Francis, London, England.

- Guyer, M. F. 1953. Animal micrology. Univ. Chicago Press, Chicago, Ill.
- Ham, A. W. 1965. Histology. J. B. Lippincott, Philadelphia, Pa.
- Hama, K. 1965. Some observations on the fine structure of the lateral line organ of the Japanese sea eel, Lyncozymbra nystromi. J. Cell Biol. 24:193-210.
- Harrington, R. W. 1955. The osteocranium of the American cyprinid fish, Notropis bifrenatus, with an annotated synonymy of teleost skull bones. Copeia 1955(4):267-290.
- Harrison, R. G. 1924. Neuroblast versus sheath cell in the development of the peripheral nerves. J. Comp. Neurol. 37:123-205.
- Hayden, F. V. 1863. Reptiles, fishes, and recent shells (Chapter XVII). In: On the geology and natural history of the upper Missouri. Trans. Amer. Phil. Soc. 12:177-182.
- Holmgren, N. and T. Pehrson. 1949. Some remarks on the ontogenetical development of the sensory lines on the cheek in fishes and amphibians. Acta Zool. 30:249-314.
- Hubbs, C. L. 1926. A check-list of the fishes of the Great Lakes and tributary waters, with nomenclatorial notes and analytical keys. Misc. Publ. Mus. Zool. Mich. 15:1-77.
- _____. 1940. Speciation of fishes. Amer. Natur. 74:198-211.
- _____. 1951. Notropis amnis, a new cyprinid fish of the Mississippi fauna, within two subspecies. Occas. Pap. Mus. Zool. Univ. Mich. No. 530, 30 pp.
- _____ and M. D. Cannon. 1935. The darters of the genera Hololepis and Villora. Misc. Publ. Mus. Zool. Univ. Mich. 30:1-93.
- _____ and W. R. Crowe. 1956. Preliminary analysis of the American cyprinid fishes, seven new, referred to the genus Hybopsis, subgenus Erimystax. Occas. Pap. Mus. Zool. Univ. Mich. No. 578, 8 pp.
- _____ and A. I. Ortenburger. 1929a. Further notes on the fishes of Oklahoma with descriptions of new species of Cyprinidae. Publ. Univ. Okla. Biol. Surv. 1(2):17-43).
- _____ and _____. 1929b. Fishes collected in Oklahoma and Arkansas in 1927. Publ. Univ. Okla. Biol. Surv. 1(3):47-112.
- Illick, H. J. 1956. A comparative study of the cephalic lateral-line system of North American Cyprinidae. Amer. Midl. Natur. 56:204-223.

Iwai, F. 1965. Notes on the cupulae of free neuromasts in larvae of the goldfish. *Copeia* 1965(3):379.

_____. In press. The structure of naked neuromasts in larvae of the cyprinodontid fish, Oryzias latipes (Temminch and Schlegel).

Jakubowski, M. 1965. Cutaneous sense organs of fishes. II. The structure of lateral-line organs in the burbot (Lota lota L.) and pike (Esox lucius L.). *Acta Biol. Cracov.* 8:87-99.

_____. 1966. Cutaneous sense organs of fishes. Part III. The lateral-line organs in some Cobitidae. *Acta Biol. Cracov.* 9:71-80.

Jordan, D. S. 1876a. A manual of the vertebrate animals of the northern United States. 1st. ed. A. C. Clury, Chicago, Ill.

_____. 1876b. A partial synopsis of the fishes of upper Georgia. *Ann. Lyceum Natur. Hist. N. Y.* 11:307-377.

_____. 1877. Notes on Cottidae, Etheostomatidae, Percidae, Centrarchidae, Aphododeridae, Dorysomatidae and Cyprinidae, with revisions of the genera and descriptions of new or little known species. *Bull. U. S. Natur. Mus.* 10:1-68.

_____. 1878. Report on the collections of fishes made by Dr. Elliot Coues U. S. A. in Dakota and Montana during the seasons of 1873 and 1874. *Bull. Hayden's Geol. Surv. Territ.* 4:777-799.

_____. 1880. Notes on a collection of fishes obtained in the streams of Guanajuato and in Chapala Lake, Mexico, by Prof. A. Duges. *Proc. U. S. Natur. Mus.* 2:298-301.

_____. 1882. Report on the fishes of Ohio. *Rept. Geol. Surv. Ohio* IV. pp. 735-1002.

_____. 1888. Description of fourteen species of fresh-water fishes collected by the U. S. Commission in the Summer of 1888. *Proc. U. S. Natur. Mus.* 11:351-362.

_____. 1894. Description of a new species of cyprinoid fish (Couesius greeni) from the headwaters of Frazer River in British Columbia. *Proc. U. S. Natur. Mus.* 16:313-314.

_____. 1918. New general of fishes. *Proc. Acad. Nat. Phila.* 70:341-344.

_____. 1920. The genera of fishes. Part IV. Stanford Univ. Series, Stanford, Calif.

_____. 1924. Concerning the genus Hybopsis of Agaaz. *Copeia* 1924(130):51-52.

- _____. 1929. Manual of the vertebrate animals of the northeastern United States. 13th, ed. World Book Co., Yonkers-on-Hudson, N. Y.
- _____. and B. W. Evermann. 1896. Fishes of North and Middle America. Part I. Bull. U. S. Natur. Mus. 47:1-954.
- _____. and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of Venezuela and Columbia. Rept. U. S. Bur. Fish. No. 1055, 670 pp.
- _____. and C. H. Gilbert. 1887. List of fishes collected in Arkansas, Indian Territory and Texas, in September, 1884, with notes and descriptions. Proc. U. S. Natur. Mus. 9:1-25.
- Kapoor, A. S. 1962. Development of latero-sensory canal bones in the fish Ophicephalus punctatus. Copeia 1962(4):854-855.
- Kirtland, J. P. 1841. Descriptions of fishes of the Ohio River and its tributaries. Boston J. Natur. Hist. 3:338-352.
- _____. 1842. Descriptions of Acipenser rubicundus, A. platyrhynchus and Rutilus storerianus. Proc. Boston Soc. Natur. Hist. 1:71.
- Lachner, E. A. 1950. The comparative food habits of the cyprinid fishes Nocomis biguttatus and Nocomis micropogon in western New York. J. Wash. Acad. Sci. 40(7):229-236.
- _____. 1952. Studies of the biology of cyprinid fishes of the chub genus Nocomis of northeastern United States. Amer. Midl. Natur. 48(2):433-466.
- Landacre, F. L. 1910. The origin of the cranial ganglia in Ameiurus. J. Comp. Neurol. 20:309-411.
- Lekander, B. 1949. The sensory line system and the canal bones in the head of some Ostariophysi. Acta Zool. 30(1):1-131.
- Linder, A. D. 1958. Behavior and hybridization of two species of Etheostoma (Percidae). Trans. Kan. Acad. Sci. 6:195-212.
- Lowenstein, O. and M. P. Osborne. 1964. Ultrastructure of the sensory haircells in the labyrinth of the ammocoete larva of the lamprey, Lamprolaima fluviatilis. Nature 204:197-198.
- _____. and J. Wersäll. 1959. A functional interpretation of the electronmicroscope structure of the sensory hairs in the cristae of the elasmobranch Raja clavata in terms of directional sensitivity. Nature 184:1807-1808.
- Manigk, W. 1933. Der Trigemino-facialiskomplex und die Innervation der Kopfseitenorgane der Elritze (Phoxinus laevis). Z. Morphol. Ökol. Tierernähr. 28:65-106.

- Marshall, N. 1947. The spring run and cave habits of Erimystax harperi (Fowler). Ecology 28:68-75.
- Mayr, E. 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass.
- _____, E. G. Linsley, and R. L. Usinger. 1953. Methods and Principles of systematic zoology. McGraw-Hill, New York, N. Y.
- Moodie, R. L. 1922. The influence of the lateral-line system on the peripheral osseous elements of fishes and Amphibia. J. Comp. Neurol. 34:319-355.
- Moore, G. A. 1950. The cutaneous sense organs of barbled minnows adapted to life in the muddy waters of the Great Plains region. Trans. Amer. Microsc. Soc. 69:69-95.
- _____. 1956. The cephalic lateral-line system on some sunfishes (Lepomis). J. Comp. Neurol. 104:49-56.
- _____. 1957. Fishes. In: Vertebrates of the United States. A. P. Blair, et al. McCraw-Hill, New York, N. Y. pp. 33-210.
- _____. and W. E. Burris. 1956. Description of the lateral-line system of the pirate perch, Aphredoderus sayanus. Copeia 1956(1): 18-20.
- _____. and J. M. Paden. 1950. The fishes of the Illinois River in Oklahoma and Arkansas. Amer. Midl. Natur. 44:76-95.
- Moy-Thomas, J. A. 1941. Development of the frontal bones of the rainbow trout. Nature 147:681-682.
- Myers, G. S. 1958. Trends in the evolution of teleostean fishes. Stanford Ichthyol. Bull. 7:27-30.
- Olumsted, J. N. D. 1920. The results of cutting the seventh cranial nerve in Ameiurus nebulosus (LeSueur). J. Exp. Zool. 31(4):369-401.
- Olund, L. J. and F. B. Cross. 1961. Geographic variation in the North American cyprinid fish, Hybopsis gracilis. Univ. Kan. Publ. Mus. Natur. His. 13(7):323-348.
- Parker, G. H. and V. L. Paine. 1934. Progressive nerve degeneration and its rate in the lateral-line nerve of the catfish. Amer. J. Anat. 54:1-25.
- Parrington, F. R. 1949. A theory of the relations of the lateral lines to dermal bones. Proc. Zool. Soc. London 119(1):65-78.
- Pehrson, T. 1922. Some points in the cranial development of teleostomian fishes. Acta Zool. 3:1-63.

- _____. 1940. The development of dermal bones in the skull of Amia calva. Acta Zool. 21:1-50.
- _____. 1944. The development of latero-sensory canal bones in the skull of Esox lucius. Acta Zool. 25:135-157.
- _____. 1945. The system of pit organ lines in Gymnarchus niloticus. Acta Zool. 26:1-8.
- Rafinesque-Schmaltz, C. S. 1818. Description of two new genera of North American fishes, Opsanus and Notropis. Amer. Mon. Mag. Crit. Rev. 2(3):203-204.
- _____. 1820. Ichthyologia Ohiensis. Lexington, Kent.
- Raney, E. C. 1947. Nocomis nests used by other breeding cyprinid fishes in Virginia. Zoologica 32(3):125-132.
- Rauther, M. 1925. Die Syngnathiden des Golfs von Neapel. Fauna und Flora Golfes Neapel. 36 Naples: Stazione Zoologica.
- Reighard, J. 1943. The breeding habits of the river chub, Nocomis micropogon (Cope). Pap. Mich. Acad. Sci. 1942(2):397-423.
- Reno, H. W. 1966. The infraorbital canal, its lateral-line ossicles and neuromasts, in the minnows Notropis volucellus and N. buchanani. Copeia 1966(3):403-413.
- Richardson, J. 1836. Fauna Boreali-Americana. Part 3, The Fish. Richard Bently, London, England.
- Romer, A. S. 1945. Vertebrate paleontology. 2nd. ed. Univ. Chicago Press, Chicago, Ill.
- Rosen, D. E. and J. R. Mendelson. 1960. The sensory canals of the head in poeciliid fishes (Cyprinodontiformes), with reference to dentitional types. Copeia 1960(3):203-210.
- Ross, H. H. 1957. Evolutionary development in the leafhoppers, the insect family Cicadellidae. Syst. Zool. 6:87-97.
- Sagemehl, M. 1891. Beiträge zur vergleichenden Anatomie der Fische. IV. Das Cranium der Cyprinoiden. Morphol. Jahrb. 17:491-595.
- Sato, M. 1955a. Studies on the pit organs of fishes. III. The distribution of the large pit organs. Bull. Mar. Biol. Sta. Asamushi 7:57-68.
- _____. 1955b. Studies on the pit organs of fishes. I. Histological structure of the large pit organs. Jap. J. Zool. 11(3):111-120.
- _____. 1956. Studies on the pit organs of fishes. IV. The distribution, histological structure, and development of the small pit

- organs. Annot. Zool. Jap. 29(4):207-212.
- Schultz, L. P. 1929. Check-list of the freshwater fishes of Oregon and Washington. Publ. Fish. Univ. Wash. 2(4):47.
- _____. 1931. Key to the fishes of Washington and Oregon with a glossary to technical terms. Univ. Wash. Bookstore, Seattle, Wash.
- _____. 1936. Keys to the fishes of Washington, Oregon and closely adjoining regions. Univ. Wash. Publ. Biol. 2(4):103-228.
- _____ and C. L. Hubbs. 1961. Early nomenclatural history of the nominal cyprinid genus Oregonichthys and of the blennioid, Pholis schultzi, fishes of western North America. Copeia 1961(4):477-478.
- Sharma, M. S. 1964. The cephalic lateral-line system in Notopterus chitala (Ham.). Copeia 1964(3):530-533.
- Snyder, J. O. 1907. The fishes of the coastal streams of Oregon and northern California. Bull. U. S. Bur. Fish. 27:155-190.
- Speidel, C. C. 1944a. The regeneration of denervated lateral-line organs. Anat. Rec. 68:458.
- _____. 1944b. The trophic influence of specific nerve supply on special sensory organs, as revealed by prolonged survival of denervated lateral-line organs. Anat. Rec. 68:458.
- _____. 1947. Reinnervation phenomena as revealed by prolonged observations of vagus nerve stumps and associated sense organs. Anat. Rec. 97:371-372.
- _____. 1948. Correlated studies of sense organs and nerves of the lateral-line in living frog tadpoles II. The trophic influence of specific nerve supply as revealed by prolonged observations of denervated and reinnervated organs. Amer. J. Anat. 82:277-320.
- _____. 1949. Correlated studies of sense organs and nerves of the lateral-line in living frog tadpoles III. Experiments on the orange granules and sense hairs of denervated and innervated organs. J. Morphol. 85:113-139.
- Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics with special reference to biological sciences. McGraw-Hill, New York, N. Y.
- Stensiö, E. A. 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. K. Svenska Vetensk. Handl. 24:1-195.
- Stephens, R. R. 1962. The cephalic lateral-line system of the gizzard shad, Dorosoma cepedianum (LeSueur). Unpublished M. S. Thesis, Univ. Okla. 40 pp.

- _____. 1967. Development of the lateral-line system of Dorosoma petenense (Günther). Unpublished PH. D. Dissert., Okla. State Univ. 31 pp.
- Stone, L. S. 1928. Primitive lines in Amblystoma and their relation to the migratory lateral-line primordia. J. Comp. Neurol. 45:169-190.
- _____. 1933. The development of the lateral-line sense organs in amphibians observed in living and vitally stained preparations. J. Comp. Neurol. 57:507-540.
- _____. 1935. Experimental formation of accessory organs in mid-body lateral-line of amphibians. Proc. Soc. Exp. Biol. N. Y. 33:80-82.
- _____. 1937. Further experimental studies of the development of lateral-line sense organs in amphibians observed in living preparations. J. Comp. Neurol. 68(1):83-115.
- Trautman, M. B. 1957. The fishes of Ohio. Ohio State Univ. Press, Columbia, Ohio.
- Tretyakov, D. K. 1938. Seismosensory canals on the head of the Clupeidae. Zool. Zh. 17:763-776.
- Trujillo-Cenóz, O. 1959. Estructura de los neuromastos de Cnesterodon decemmaculatus. Ann. Fac. Med. Montevideo 44(3/4):469-475.
- Van Bergeijk, W. A. and S. Alexander. 1962. Lateral line canal organs on the head of Fundulus heteroclitus. J. Morphol. 110(3):333-346.
- Walls, G. L. 1932. The hot celloidin technic for animal tissues. Stain Tech. 7:135-145.
- Walther, J. 1882. Die Entwicklung der Deckknochen am Kopfskelett des Hechtes, Esox lucius. Jene. Z. Naturwiss. 16:
- Westoll, T. S. 1937. On the cheek-bones in teleostome fishes. J. Anat. 71(3):362-382.
- Wahlfahr, T. A. 1937. Anatomische Untersuchungen über die Seitenkanäle der Sardine (Clupea pilchardus Walb.). Z. Morphol. u. Ökol. Tiererrachr. 33:381-411.
- Woolman, A. J. 1895. Report on a collection of fishes from the rivers of central and northern Mexico. Bull. U. S. Fish. Comm. 14:55-66.
- Wright, M. R. 1951. The lateral line system of sense organs. Quart. Rev. Biol. 26(3):264-280.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Thesis: DESCRIPTIONS AND ANALYSES OF THE CEPHALIC LATERAL-LINE
SYSTEMS OF THE CYPRINID GENUS HYBOPSIS

Major Field: Zoology

Biographical:

Personal Data: Born in Oakland, California, February 13, 1939,
the son of Dorris G. and Margaret I. Reno.

Education: Graduated from Oakland High School, Oakland, California, in 1957; received Associate of Science degree from Connors State Agriculture College, 1959; received Bachelor of Science degree, 1961, and Master of Science degree, 1963, with majors in Zoology from Oklahoma State University, Stillwater, Oklahoma; completed requirements for Doctor of Philosophy degree, July, 1967.

Professional Experience: Dingell-Johnson Trainee, California Fish and Game, Redding, California, Summer, 1961; Graduate Teaching Assistant, Oklahoma State University, Stillwater, Oklahoma, 1962-1967; and Graduate Teaching Assistant, University of Oklahoma Biological Station, Willis, Oklahoma, Summer, 1963.

Member: Sigma Xi, Phi Kappa Phi, Phi Sigma, American Society of Ichthyologists and Herpetologists, American Society of Mammologists, Southwestern Association of Naturalists, American Association for the Advancement of Science, and Oklahoma Academy of Science.

