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Cranial Nerves of a Percoid Fish, *Polycentrus schomburgkii* (Family Nandidae), a Contribution to the Morphology and Classification of the Order Perciformes

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ABSTRACT

Freihofer, Warren C. Cranial nerves of a percoid fish, *Polycentrus schomburgkii* (family Nandidae), a contribution to the morphology and classification of the order Perciformes. *Occasional Papers of the California Academy of Sciences*, no. 128, 78 pages, 31 figures, 1 table, 1978.—Four cranial nerves, the trigeminus, facialis, glossopharyngeus, and vagus, of *Polycentrus schomburgkii* (Nandidae) are described and illustrated (including muscles of jaws and gill arches) in detail from cleared-and-stained nerve preparations of whole specimens and from serial sections. The nerves are described in terms of their main functional components. The descriptions are intended as a basic reference for comparative nerve studies of perciform fishes for systematic purposes. Comparisons were made with numerous other families (85 represented as nerve preparations) for particular points such as the innervation of the snout, upper jaw, cephalic lateral line canals and pitorgans, cheek musculature, and trunk lateral line systems. In many features of its cranial nerves, *Polycentrus* is a moderately generalized percoid. Compared with *Roccus*, *Archoplites*, *Kuhlia*, and *Perca*, it is more specialized in its lateral line system: the second to fourth infraorbitals apparently are fused as are the fifth and sixth, and only one canal neuromast is in each compound bone; there are more cephalic pitlines, and these have more organs; the trunk lateral line is reduced to one tubed scale but there are three longitudinal rows of scales bearing free lateralis organs (pitorgans), one row each along the bases of the dorsal and anal fins and one row halfway between the dorsal fin and the horizontal septum. These are innervated by dorsal and ventral segmental branches from a trunk lateral line nerve pattern of the basic acanthopterygian type. No communis fibers from the vagus nerve join the ramus lateralis accessorius (RLA) on top of the head; RLA is composed only of communis fibers from the facial nerve; the same observation holds for other percoids and other groups examined. Therefore, it may be necessary to use the name ramus recurrens facialis in its place. Comparisons with other groups, especially some percoids, beryciforms, atherinomorphs, and paracanthopterygians, brought out specializations in these groups which made more evident the generalized state of the nerves of *Polycentrus*. Whereas *Polycentrus* is generalized in its innervation of the snout, the carangids, rachycentrids, coryphaenids, and echeneids have a shared specialization in prenasal canals and canal bones; a shared specialization rare in teleosts, of an evident migration of an anteriormost frontal canal organ into the nasal canal occurs only in the gadoids, ophidioids, and *Stephanoberyx*; a shared specialization, apparently unique to the group, of an evident capture of a free lateralis organ by the nasal bone occurs in all berycoid families; atherinomorphs have a shared specialization of a large general cutaneous nerve to the upper jaw, but it is present also in holocentrids; a unique specialization of the nasal canal occurs also in *Scomber* and *Rastrelliger*; whereas the cheek-muscle innervation in *Polycentrus* is not distinctive, it is in atherinomorphs and in various other groups. The pattern of innervation within a muscle mass as well as the source of innervation to the muscle may be of systematic importance.

Of the four functional nerve-component systems, *Polycentrus* is specialized mostly in the lateralis system; the communis (gustatory) system is present in one of the basic percoid patterns of the recurrent facial nerve; nothing distinctive was observed in the motor system (gill-arch-muscle innervation was not compared) nor in the general cutaneous system. Generalizations drawn from observations of 85 families for the innervation of the snout and upper jaw are that (1) pitorgans on the snout and neuromasts of prenasal canals are invariably innervated from the infraorbital, not from the supraorbital trunk, and (2) general cutaneous innervation of the upper jaw is only from the infraorbital trunk (except in atherinomorphs and the holocentrids), not from the supraorbital trunk as might be expected. Reasons for utilizing cranial nerves in higher category classification are given along with suggestions for simplifying cranial nerve studies.

INTRODUCTION

In the 1960's there was a notable renewal of interest in problems of the classification of bony fishes at higher taxonomic levels. Numerous orders were shifted into new systematic positions (Rosen 1964; Greenwood, Rosen, Weitzman, and Myers 1966; Rosen and Patterson 1969; Rosen 1973). An increase in the number of higher taxonomic categories was utilized to express new and more detailed views of relationships. Much of the new classification has been influenced by the methodology proposed by Hennig (1966) for phylogenetic systematics. The entire classification of fishes is due for reexamination under the impetus of new methods and renewed interest. The largest and a most formidable group, the order Perciformes, should receive major attention.

One precept of an improved methodology of systematics should be that systematic information be drawn from several anatomical systems. Most past studies on higher category classification have utilized the skeletal system as the chief source of characters. Few have included the muscles and almost none the nerves (see Freihofer 1963). The muscles are now being used more extensively (Winterbottom 1974a and 1974b). The nerves, hopefully, will be also. A large obstacle to their use, the lack of a technique for readily viewing the nerves, has been removed. Whereas the only way to study accurately the peripheral nerves has been by tedious methods of serial sectioning and reconstruction, the nerves can now be seen in a whole specimen by means of the Sihler technique.

The Sihler technique renders a whole or hemisectioned specimen virtually transparent except for the nerves, which are stained a dark purple. Descriptive nerve studies involving little more effort than for osteological studies are now practical. The growth of a comparative literature on the nerves can begin. Of more immediate importance for getting at the taxonomic utility of the nerves than accumulating a nerve literature, which will take decades, is the formation of a reference collection of Sihler nerve preparations. Such a collection can now be assembled relatively quickly, covering a sizeable taxonomic range. Assuming that properly preserved fishes of numerous groups are available, an experienced technician working one year can produce fine nerve preparations representing 50 to 100 or more families. Properly processed Sihler preparations (see under "Methods" section for use) may last 15 to 20 years and no doubt will last longer. The reference collection, once assembled and growing, can be used for conducting surveys of promising nerve complexes.

Several nerve complexes were surveyed during the time this descriptive account of *Polycentrus* was in progress. The results are in various stages of completion and are planned for later publication. The studies embrace comparisons ranging from *Amia* up to callionymids. Sihler nerve preparations representing up to 90 families were used. Two of the nerve complexes involved the innervation of lateral line canal bones; a third was a large general cutaneous nerve of the supraorbital trunk; a fourth involved patterns of innervation to the cheek muscle mass; a fifth concerned new patterns of a gustatory nerve, the recurrent facial; and the sixth was on trunk lateral line nerve patterns.

Each of these studies revealed nerve characters of promising systematic importance. A few are apparently convergent in some groups. Two attributes of nerves giving them systematic potential were observed in these studies. One is that nerves follow their end organs (taste buds, lateral line canal organs, and muscles). The other is that, in general, each nerve innervating a lateral line canal neuromast has a certain morphological integrity connected with that bone and organ. No other nerve to a canal neuromast may enter through the substance of that bone and supply a canal organ there. This observation might be stated as a rule. As with all rules, they are always (it seems) occasionally broken, but there are always good reasons for their being broken; the exceptions to the rule, if the exceptions are valid, should prove the rule. Important for the systematist using nerves is the fact that the exceptions result in new specializations being formed. These may become characters useful to the systematist. If nerves always followed the rules, there would be fewer important systematic characters.

Some examples of what nerves do that are important to systematists come from study of the nerves and neuromasts of the canal bones. Not only may the total number of canal organs be significant for a main branch of the cephalic canal system, but the changes in the number of organs in each canal bone may be especially important. These changes involve how canal organs in a bone may increase or decrease in number. An increase in the number of organs may result from an original organ dividing into two organs which subsequently move away from each other; an organ may migrate out of its bone into another canal bone; a canal bone may, in effect, "capture" an adjacent terminal free lateralis organ. Unless the innervation to the canal organs is studied, the systematic significance of the canal bones may largely or completely escape detection.

Such facts as these plus the fact that the cranial nerves of more than 20,000 species of fishes remain to be explored should make the study of nerves of fishes a rather exciting prospect to some systematists.

The order Perciformes, to which *Polycentrus* belongs, has been divided into as many as 20 suborders (Greenwood et al. 1966) and may contain up to 7,000 species. The present report is the only detailed description of the fifth, seventh, ninth, and tenth cranial nerves of a member of this order. Accounts are needed of the cranial nerves of representatives of the other suborders, though descriptions need not be as detailed as this one for *Polycentrus*. Descriptive reference studies break the ground for ensuing comparative studies in which the mass of detail need not be reported, but only the significant differences between compared species. This report on *Polycentrus* will, hopefully, serve such a purpose for the suborder Percoidea.

METHODS

The courses of the cranial nerves are described mainly from whole specimens cleared and stained selectively for the nerves by the Sihler technique. For use of the method see Williams (1943), Freihofer (1966), Fraser and Freihofer (1971), and Freihofer et al. (1977). All myelinated nerves are stained down to very small branches. A much more accurate and complete picture of the distribution of the nerves is possible by this method than can be had from serial sections. The latter method should be used for study of the complexes of nerves and ganglia, especially those inside the cranial cavity for which it is indispensable. It is best to use both methods. Much preliminary, exploratory work on the nerves can be done for systematic purposes, however, by use of the Sihler technique together with the study of the basic nerve references.

The nerves are drawn in Figures 1 through 14 as white cords as accurately as possible on the background of the skeleton, the bones serving as reference points for the courses of the nerves. This seems the natural way to illustrate the nerves for use by systematists. The major nerve components are not drawn upon the nerves. Usually, so many components would have to be crowded into the space of each nerve and its branches that the distribution of the nerves could not be shown in the detail that they now are. The probable components for all the nerves and their branches are given in the text.

One serious problem with the preservation of specimens for Sihler processing should be emphasized. The problem is that manufacturers of formaldehyde now leave from 10 to 15% methyl alcohol in it for the purpose, they say, of "preservation of the preservative," for retarding the breakdown of formaldehyde into paraformaldehyde. Even reagent-grade formaldehyde has this amount of alcohol in it. The only grade of formaldehyde that I have been able to obtain that can compare with the purity of the formaldehyde I used before 1969, which had 1% or less alcohol content, is the grade sold as "purified formaldehyde." Thus far, I have succeeded in obtaining it only in 55-gallon drums. Specimens preserved in the other grades of formaldehyde are ruined for use in the Sihler technique. It is possible to make formaldehyde free of alcohol by heating paraformaldehyde crystals in water, using as a catalyst a drop or two of ammonium hydroxide solution (28% NH_3).

Since the intracranial courses and ganglia of the nerves as well as the brain are destroyed while macerating Sihler specimens in 2 or 3% aqueous potassium hydroxide solution, a serial-section technique was used to study these parts in *Polycentrus*. The object at the time the research was planned was to use a technique that would help clarify difficult points on ganglia and nerve anastomoses and to rely on published accounts to help resolve questions of nerve-fiber tracts and connections. The method chosen was Curtis's modification of Van Gieson's triple stain (Leach 1946). It was easy to use and gave brillantly stained and well-differentiated tissues. It is not good for fiber-tract study.

All descriptions based on Sihler preparations are from one specimen unless otherwise indicated. The nerves for the gill arches and associated muscles are from a second Sihler specimen.

Dissections of fresh formalin specimens were used to check against the serial sections on such points as the intracranial courses and ganglia of the trigeminal, facial, and vagal nerves.

Skeletal preparations cleared and stained by the alizarin method of Hollister (1934) were used for making the drawings of the cranial skeleton. All skeletal drawings were made from one specimen (CAS 12540) from Guyana.

The muscle terminology follows that of Winterbottom (1974a). The nerve terminology generally follows that of Herrick (1899). In the present work, lateralis organs are referred to as canal neuromasts if located in canals and as free lateralis organs or pitorgans if located in skin outside the canals. The term pitline is used to indicate a row of free lateralis organs, or even a single organ if that is all that is present in any area, whether or not these organs are in pits. The term nerve is loosely used to refer to an entire cranial nerve and its branches or to a bundle of nerve fibers of any size coursing independently outside of the brain or spinal cord. The root or radix of a cranial nerve is the proximal part or parts of the nerve inside the cranium and close to the brain. A nerve root is either sensory, and of a single functional component, or motor in function.

Herrick, in his work on *Menidia* (1899), *Gadus* (1900), and *Ameiurus* (1901), used a modification of the Weigert method for preparation of serial sections of nerves. The modification worked excellently for Herrick, but he found teleost tissues to be very brittle for sectioning (see Herrick 1898, and Sheldon 1914). The fixatives required a hardening time of up to 6 months and the use of osmic acid (osmium tetroxide). Using fiber diameter as a means of identifying the four nerve components, Herrick was able to follow on his serial sections the fiber bundles of the different functional components of the nerve roots, from the brain through the ganglia and out to their undifferentiated endings or end organs. His *Menidia* paper (1899) is still the best single reference on the nerves of fishes.

LITERATURE ON NERVES OF PERCIFORM FISHES

Relative to the great size of the order Perciformes, there are very few descriptive studies of the nerves of perciform fishes. Stannius (1849) and Baudelot (1883) gave observations on various cranial nerves of some perciforms. Cuvier and Valenciennes (1828) described the cranial nerves of *Perca fluviatilis* from dissections. Allis (1903) carefully described the nerves of the mackerel, *Scomber scomber*, but not completely nor in much detail. Maheshwari (1965) described the cranial nerves of the spiny eel, *Mastacembelus armatus*, and Saxena (1969a) did likewise for the nandid, *Nandus nandus*, but both of these authors used only dissection methods and omitted details in their descriptions, diminishing the systematic usefulness of their work.

The most useful references for this study were the papers by Herrick (1899, 1900, 1901), especially his monograph (1899) on the cranial nerves of *Menidia* (family Atherinidae). His *Menidia* paper pioneered the analysis of nerves of fishes according to the major types of functional nerve fibers they carry. The nerve components, as Herrick called the functional types of nerve fibers (see section on nerve components below), are the best basis for analyzing, identifying, and understanding the nerves. Other papers found useful because they were so carefully and thoroughly done were those by Allis (1897, 1903, 1910) on the bowfin, *Amia calva*, the mackerel, *Scomber scomber*, and on *Scorpaena*; Norris (1925) on the genera *Acipenser, Polyodon, Amia*, and *Lepisosteus*; Norris and Hughes (1920) on the spiny dogfish, *Squalus acanthias*; Pancratz (1930) on the toadfish, *Opsanus tau*; Manigk (1934) on *Phoxinus*; and, lastly, the most recent study by Ray (1950) on *Lampanyctus*.

Since 1960 the following authors published general descriptive accounts on some or all of the cranial nerves of fishes: Freihofer (1963, 1970, 1972); Gilmore (1972); Gupta (1972); Maheshwari (1965); Mithel (1964a, 1964b); Narawane (1965); Saxena (1966, 1967, 1969a, 1969b); Saxena and Rastogi (1968); Springer and Freihofer (1976); Vashisht and Uberoi (1965). In all these studies except my own, in which serial sections and/or Sihler whole-nerve preparations were used, dissection of preserved specimens was the only technique employed.

FAMILY NANDIDAE

Polycentrus schomburgkii Müller and Troschel, 1848, is a small spiny-rayed fish living in fresh water in northeastern South America and Trinidad. It belongs to the family Nandidae, which is one of about 70 families of the suborder Percoidea, probably the least specialized of the 20 recognized suborders of the order Perciformes (Greenwood et al. 1966), with perhaps 7,000 species.

Polycentrus is specialized for stalking its prey. Its barely perceptible swimming movements and coloration make it look rather like a dead, floating leaf when approaching its prey fish. After an investigative forward movement, instead of turning around and swimming away, *Polycentrus* usually swims backwards and downwards, which it can do for some distance unobtrusively. The lateral line shows specialization seemingly for these ways of swimming. The large, protrusible jaws are adapted for suddenly engulfing the prey. Liem (1970) has done a comparative functional anatomical study of the feeding mechanism of the Nandidae. In the rest of its morphology, except for the increase in number of dorsal and anal fin spines, *Polycentrus* appears to be a generalized percoid.

The Nandidae are of special zoogeographical interest. There are two monotypic genera (*Afronandus* and *Polycentropsis*) in Africa, two monotypic genera (*Polycentrus* and *Monocirrhus*) in South America, and one genus, the least specialized (*Nandus*), with 2 species in India and Southeast Asia. The ancestors of the African and South American genera were evidently living in the area of separation between Africa and South America when these continents drifted apart.

NAMES OF CRANIAL NERVES

There are actually eleven pairs of cranial nerves in fishes, not ten. The nervus terminalis, which has the number zero, was not discovered (Pinkus 1894) until long after the other ten pairs had been numbered. The present terminology for the cranial nerves may not be the best that could be devised, but it is so well established in the literature of vertebrates that it can hardly be uprooted.

Cranial Nerve Number	Name
0	nervus terminalis
I	nervus olfactorius (olfactory)
II	nervus opticus (optic)
III	nervus oculomotorius (oculomotor)
IV	nervus trochlearis (trochlear)
V	nervus trigeminus (trigeminal)
VI	nervus abducens (abducent)
VII	nervus facialis (facial)
VIII	nervus acusticus (auditory, acoustical)
IX	nervus glossopharyngeus (glossopharyngeal)
X	nervus vagus (vagal)

NERVE COMPONENTS

Herrick (1897, 1899, 1903) used a simple functional analysis in describing the cranial nerves of *Menidia*. His system is followed here for the cranial nerves of *Polycentrus*.

Each root of a nerve is considered to be composed of one functional component. Cranial nerves I (olfaction), II (vision), III (motor), IV (motor), VI (motor), and VIII (acousticolateralis) are very simple in that each has characteristically only one main functional component which is either sensory or motor. The other cranial nerves are more complex, containing one or more sensory and one motor root. A sensory root is either lateralis (acousticolateralis), communis, or general cutaneous in its functional component. These components are defined below. Cranial nerve V (trigeminus) has two roots: one motor and one general cutaneous; nerve VII (facialis) has four roots: two are lateralis, one is communis, and one is motor; nerve IX (glossopharyngeus) has two roots in most fishes: one motor and one communis; nerve X (the vagus together with the lateral line nerve of the trunk) has four roots: one motor, one lateralis, one communis, and a small general cutaneous root.

The cranial nerve roots are easy to follow in their courses from the brain out to the first cranial nerve ganglia, but at this point inside the cranium where most of the cranial ganglia are located, nerves V, VII, and X begin to form anastomosing complexes, one of which is the trigemino-facialis complex. This complex forms intracranially near the closely spaced trigeminal and facial foramina of the prootic bone. Four sensory roots and their ganglia and two motor roots are more or less intimately compacted. All necessary fiber interchanges are made there. Three main nerve trunks arise from the trigemino-facialis complex: the truncus supraorbitalis, truncus infraorbitalis, and truncus hyomandibularis, as well as the palatine nerve.

The cranial nerves of *Polycentrus* are analyzed into functional components as far as possible. In instances where the component could not be determined directly, its identification was made indirectly on the basis of Herrick's work on *Menidia*.

Definitions of the five functional components found variously in cranial nerves V, VII, IX, and X are listed below. Each sensory component is referred to as a system of similar fibers.

1. *General cutaneous system*. General cutaneous fibers innervate skin; in fishes they do not innervate specialized sense organs; they end only in free nerve terminations. The cell bodies are located in the Gasserian ganglion. Their fibers terminate in the central nervous system in the spinal V tract or the cells associated with it. General cutaneous fibers are part of the somatic sensory system.
2. *Communis system*. Communis fibers innervate taste buds on the lips, in the buccal and pharyngeal cavities, and wherever taste buds occur on the external surface of the body (head, fins, and trunk). The cell bodies for communis fibers are located in the geniculate ganglion. For the vagus and glossopharyngeus nerves, a second kind of fiber is associated with the communis system. These are fibers that have free, undifferentiated endings in the mucous epithelium of the pharyngeal and buccal cavities. Communis fibers end in the brain at a single center, the lobus vagi of the medulla oblongata. Communis fibers may enter this center directly through the vagus roots or indirectly through the fasciculus communis tract from the roots of the 9th and 7th cranial nerves. Communis fibers belong to the special viscerosensory system.
3. *Acousticolateralis system*. Its fibers innervate the lateral line organs and the internal ear. They terminate in the tuberculum acusticum of the medulla oblongata. The fibers belong to the special somatosensory system.
4. *Somatomotor system*. On the head, fibers of the somatomotor system innervate the extrinsic eye muscles (the four rectus and two oblique muscles) and are carried in the 3rd, 4th, and 6th pairs of cranial nerves.
5. *Visceromotor system*. On the head, fibers of the visceromotor system innervate muscles of the jaws and gill arches and are carried in cranial nerves V, VII, IX, and X. This component in the present paper is usually simply referred to as motor, since only the jaw and gill-arch muscles are discussed.

Descriptions of Nerves

Radix Profundus

Closely associated at the brain with the root of the fifth, or trigeminal, nerve, but separate from it, is the radix profundus (Figs. 14 and 31). The radix profundus supplies visceral sensory innervation to muscles which move the lens and change the diameter of the iris. This nerve divides into two diverging rami, the ramus ciliaris longus and the ramus ciliaris brevis (called the radix longus up to the point of its contact with the ciliary ganglion). Both rami receive major fibers from the fifth, or trigeminal, sympathetic ganglion and separately enter the rear of the eyeball.

In one specimen of *Polycentrus*, the radix profundus has its root origin in the medulla at the dorsal surface of the base of the trigeminal root. Both the profundus and the trigeminal roots emerge from the midlateral wall of the anterior end of the medulla, ventral to the posterior ends of the optic lobes and a little posterior to the root of the nervus trochlearis. The radix profundus remains separate from the trigeminal root for the rest of its intracranial course. In another specimen the radix profundus was applied closely to the trigeminal root for some distance from the brain, after which the two roots separated.

En route to its cranial exit, the radix profundus lies fairly close to the nervus trochlearis, both nerves usually being on the dorsal surface of a large blood vessel, with the profundus medial and a little ventral to the trochlearis, and both roots being medial to the roots and ganglia of the trigeminal and facial nerves. Not far from its cranial exit, the radix profundus bears on its dorsal surface a ganglion of about two dozen cell bodies (Fig. 14). Shortly beyond its ganglion, the profundus, now called the truncus ciliaris profundus, is crossed dorsally by the intracranial parietodorsal branch (RLA-PD) of the ramus lateralis accessorius (RLA). Shortly beyond this point, the truncus ciliaris profundus enters the trigeminal foramen, passing through it at the dorsolateral corner of the foramen. The truncus is pressed up against the wall of the foramen by the large dorsal fiber mass of the truncus supraorbitalis. The truncus ciliaris profundus moves down to lie ventral to the large horizontally elliptical fiber mass of the fifth-seventh complex that is pressed up against the prootic roof of the depression (the trigeminofacialis fossa of Allis) in which the external part of the fifth-seventh complex lies. The truncus ciliaris profundus divides into two parts. The lateral division is the ramus ciliaris longus, and the medial division is the ramus ciliaris brevis. The ciliaris longus receives a sizeable bundle of fibers from the trigeminal sympathetic ganglion lying below it. The ciliaris brevis passes ventrally and then medially through or past the trigeminal sympathetic ganglion, apparently receiving sympathetic fibers from it. On the left side of the specimen, trigeminal sympathetic nerve fibers clearly could be seen entering the ciliaris brevis, but not on the right side (Fig. 14). Leaving the trigeminal sympathetic ganglion, the ciliaris brevis, which at this point can be termed the radix longa ad ganglion ciliare or radix longa, passes medially over to the ventrolateral surface of the oculomotor nerve, which lies on top of a large blood vessel or sinus close to the prootic wall of the cranium. Some ganglion cells form at the point of contact between the oculomotor and the radix longa (Fig. 14). The radix longa courses for a short distance with the oculomotor nerve, and the two separate and each passes ventrally down opposite sides of a large blood vessel, the radix longa passing down the lateral side and the oculomotor down the medial side. About two-thirds of the way down the lateral side and after the formation of a few more ganglion cells in it, the radix longa passes medially around the large blood vessel and joins the ciliary ganglion located on the oculomotor nerve. The ramus ciliaris brevis directly departs from the ciliary ganglion and passes anterodorsally and laterally over to the rear of the eyeball in company with an ophthalmic blood vessel and penetrates the sclera close to the optic nerve and vein. Inside the sclera the ciliaris brevis passes ventrally on the side of a large vein or sinus reaching the lateroventral edge of the retina where the retractor lentis muscle attaches to the base of the iris (Fig. 15). The ciliaris brevis sends a branch anteriorly and another posteriorly along the periphery of the iris, each branch ramifying over the ventral surface of the iris.

The remainder of the ciliaris longus is described next. At the point where it has received fibers from the trigeminal sympathetic ganglion, the ciliaris longus shortly leaves the proximity of the fifth-seventh complex and passes anteroventrally through the fibrous coating separating the prootic foraminal area from the orbital cavity, enters the orbital cavity in company with an ophthalmic artery, passes laterally over to the dorsal rear of the eyeball, and enters the eyeball about two-thirds of the way middorsally above the entrance of the optic nerve (Figs. 14 and 15). The course and relationships of the radix profundus are essentially the same on both sides of the sectioned specimen.

Fifth and Seventh Cranial Nerve Roots, Trunks, and Rami

The trigemino-facialis complex is the result of six roots of the fifth and seventh cranial nerves (each nerve root carrying fibers of one functional component) coming together, forming ganglia if they are sensory roots, exchanging fibers, and then leaving again with nerve components recombined into the three main nerve trunks which innervate the anterior half of the head. These three nerve trunks are the truncus supraorbitalis, truncus infraorbitalis, and truncus hyomandibularis. The truncus supraorbitalis courses anteriorly from the rear of the orbital cavity dorsal to the eye and innervates the top of the head and the snout (Fig. 3) but not, except rarely, the upper jaw. The infraorbital trunk passes anteriorly from the rear of the orbital cavity along the ventral edge of the orbit and branches into three main rami: 1) the ramus maxillaris trigeminus to the upper jaw; 2) the ramus buccalis facialis to the lateral line organs associated with the infraorbital canal and to the adjacent skin; and 3) the ramus mandibularis trigeminus to the muscles and skin of the cheek and lower jaw (Figs. 1, 6–10). The truncus hyomandibularis facialis leaves the cranium a little further posteriorly than do the first two trunks and passes ventrally along or through the hyomandibular and preopercular bones and divides into two main rami, the ramus mandibularis facialis and the ramus hyoideus (Figs. 2 and 13). The ramus mandibularis innervates the preopercular area, the anterior part of the opercular area, and the lower jaw. The ramus hyoideus passes down the hyoid arch innervating the skin and muscles of the gill membrane and branchiostegal rays, and the posterior part of the protractor hyoidei muscle connecting the hyoid arch to the lower jaw.

The six roots of the 5th–7th complex of fishes may be examined more closely. The 5th or trigeminal nerve consists of two nerve roots, a somatic sensory root carrying nerve fibers belonging to the general cutaneous system and a visceral motor root carrying motor fibers to jaw muscles associated originally with an anterior gill slit lost in the evolution of the jaws. The 7th or facial nerve has four nerve roots, three of which are sensory and one motor. The motor root supplies visceral motor fibers to the muscles of the palate, opercle, and hyoid arch—muscles associated originally with the hyoid gill arch which are innervated by the 7th cranial nerve. The three sensory roots of the facial nerve consist of two lateralis roots, referred to as the dorsal and the ventral lateralis roots; the third is a visceral sensory root carrying fibers that innervate the taste buds and the mucosa of the mouth. Each of the sensory roots of the 5th and 7th nerves bears a large ganglion.

After leaving the posterior part (medulla oblongata) of the brainstem, the six roots of the 5th and 7th nerves converge anteriorly towards their foramina in the prootic bone, but shortly before passing through the prootic, a ganglion forms on three of the sensory roots of the facial nerve. In *Polycentrus* the Gasserian ganglion of the sensory root of the trigeminal nerve forms directly outside of the trigeminal foramen in the prootic bone. In some other fishes it forms inside the cranium. Just beyond the ganglia but still inside the cranium, the fiber bundles in all fishes begin to detach from the roots, the various fiber bundles coming together forming the three nerve trunks described above.

In *Polycentrus* the dorsal lateralis root of the 7th cranial nerve sends a large bundle of fibers into the supraorbital trunk, and the remainder of the root enters into the formation of the infraorbital trunk. The rest of the supraorbital trunk is formed by a bundle of general cutaneous fibers from the Gasserian ganglion of the 5th cranial nerve and a small bundle of communis (taste fibers) from the geniculate ganglion of the gustatory root of the 7th cranial nerve. This communis bundle then leaves the supraorbital trunk as the orbito-pectoral branch of the recurrent facial nerve.

In addition to the large bundle of lateralis fibers from the dorsal root of the 7th cranial nerve, the infraorbital trunk receives a large bundle of general cutaneous fibers from the Gasserian ganglion for the skin. It also receives the whole of the motor root of the 5th cranial nerve. Both of these trunks, the truncus supraorbitalis and truncus infraorbitalis, leave the cranium through the trigeminal foramen on the outer face of the prootic bone and then diverge on the rear wall of the orbital cavity, one trunk passing dorsoanteriorly above, the other ventroanteriorly below, the orbit.

The truncus hyomandibularis in *Polycentrus* is formed by the whole of the motor root of the 7th cranial nerve, plus a large bundle of communis fibers from the geniculate ganglion of the 7th cranial nerve, and by the whole of the ventral lateralis root of the 7th nerve. The truncus hyomandibularis usually contains a sizeable bundle of general cutaneous fibers from the Gasserian ganglion. These fibers reach the truncus hyomandibularis as the ramus communicans n. trigemini ad n. facialem. This ramus passes posteriorly in a chamber or lateral passageway that lies in the wall of the prootic between the trigeminal and facial foramina. The ramus communicans turns laterally beyond the prootic chamber and joins the truncus hyomandibularis as this trunk enters its passageway in the hyomandibular bone.

Not all of the communis fibers of the geniculate ganglion of the 7th cranial nerve go into the three trunks of the 5th and 7th cranial nerves. Some geniculate fibers form the ramus palatinus, which passes out of the cranium into the myodome and then along the medial edge of the palate next to the parasphenoid bone, innervating taste buds and the mucosa of the palate and upper jaw. In many fishes there are still other gustatory branches arising from the geniculate ganglion. These are considered together under the terms ramus lateralis accessorius (ramus recurrens facialis). The branches of this ramus course back from the head onto the trunk.

As will be seen in the detailed descriptions for *Polycentrus*, both the ramus mandibularis trigeminus of the truncus infraorbitalis and the ramus mandibularis facialis of the truncus hyomandibularis course onto the lower jaw and out to its tip. Although the trigeminal (fifth) and facial (seventh) nerves parallel each other in their courses on the lower jaw, each nerve serves a different function there. Where these rami reach the lower jaw in *Polycentrus* and in teleosts in general, the ramus mandibularis trigeminus carries only motor fibers for muscles and general cutaneous fibers for the skin of the lower jaw, while the ramus mandibularis facialis carries only lateralis fibers for free lateralis organs and canal neuromasts, and communis fibers for the taste buds and mucosa of the lower jaw.

Roots and ganglia of nervus trigeminus

The single sensory root and single motor root of the nervus trigeminus (V) are indistinguishably bound together as they arise from the midlateral wall of the medulla oblongata directly posterior to the root of the oculomotor nerve, anterior and ventral to the facial roots, and posterior to the lateral emergence of the nervus trochlearis (Fig. 29). The radix profundus lies on the dorsal surface of the trigeminal root as these two roots leave the brain. They soon separate but remain rather close for most of their intracranial courses. The trigeminal root remains unconnected to the roots and ganglia of the facialis. When close to its foramen, the compound motor and sensory trigeminal root lies dorsal to the geniculate ganglion of the facial nerve and medioventral to the dorsal lateralis ganglion of the facial nerve. The Gasserian ganglion of the trigeminal nerve forms outside the trigeminal foramen where the final interchanges between the trigeminal and facial nerves occur to form the truncus supraorbitalis and truncus infraorbitalis.

The communis root and geniculate ganglion

The communis root of the facial nerve carries gustatory fibers to taste buds in the mouth and to terminal buds on the body, and communis fibers to the mucosa of the buccal cavity. Dorsal to the facial foramen, the communis root enlarges into a round, dense mass of large and small ganglionic cells, the geniculate ganglion (Fig. 31). From the geniculate ganglion arise two ventrally directed, large fiber bundles; one is the anterior ramus palatinus which innervates taste buds on the palate and upper jaw, and the other is the communis bundle which joins the truncus hyomandibularis as this nerve passes through the facial foramen.

Several fiber bundles leave a dorsoanterior extension of the geniculate ganglion. One of these is a small bundle, the parieto-dorsal branch of the ramus lateralis accessorius (Fig. 31), which passes laterally around the ventral surface of the trigeminal root and then dorsally up the side of a blood vessel where it is joined by a similar bundle from the medial side of the geniculate ganglion. The enlarged nerve thus formed shortly comes into contact with the intracranial ganglion of the radix profundus and then passes dorsally up to the parietal bone, through which it passes. The further course of the parieto-dorsal branch of the ramus lateralis accessorius (RLA), is described in another section. There is no fiber exchange between the parieto-dorsal branch of the RLA and the radix profundus. The remainder of the dorsoanterior part of the geniculate ganglion gives rise to a fiber mass which passes through the trigeminal foramen, lying, as it does so, on the lateral surface of a mass of trigeminal fibers. As this communis bundle goes out the trigeminal foramen, it detaches fibers that course with the ramus oticus. These fibers of the geniculate ganglion constitute the orbito-pectoral branch (Fig. 31, RLA-OP) of the RLA. General cutaneous fibers leave the Gasserian ganglion outside the trigeminal foramen and also join the ramus oticus. On serial sections no fiber bundle from the geniculate ganglion was observed to pass into the infraorbital trunk, but on a dissection a fiber bundle from the geniculate ganglion appears to enter the infraorbital trunk, and another apparently enters the supraorbital trunk, but it could not be definitely determined that they do.

In summary, the fiber bundles leaving the geniculate ganglion and joining various parts of the trigemino-facialis complex are as follows: (1) a large bundle of fibers that forms the ramus palatinus; (2) a large bundle to the truncus hyomandibularis; (3) a dorsally directed intracranial branch (the parieto-dorsal branch of the RLA) to the dorsal fin; (4) a sizeable bundle that forms the orbito-pectoral branch of the RLA to the pectoral, pelvic, and anal fins; (5) a sizeable bundle, probably to the infraorbital trunk, and a small bundle, probably to the supraorbital trunk. Herrick (1899: 351) states that in *Menidia* such fibers in small numbers enter the supraorbital trunk.

Dorsal lateralis root of the facial nerve

The dorsal lateralis root forms a rather large ganglion of from small- to large-sized, compactly grouped cell bodies. On its course to its ganglion (Fig. 31), the dorsal lateralis root lies on the medial side of the internal ear and is lateral and dorsal to the trigeminal root. The ganglion is directly posterior to the intracranial profundus ganglion and medial to the geniculate ganglion. The dorsal lateralis root leaves the cranium at the dorsal corner of the trigeminal foramen. Outside the cranium, part of the root turns anterodorsally and continues against the side of the cranium as a part of the truncus supraorbitalis. Some fibers of the dorsal lateralis root leave it and pass dorsally as part of the ramus oticus. A sizeable portion, probably half of the dorsal lateralis root, leaves the root as it passes out the trigeminal foramen and crosses to the lateral side of the trigemino-facialis complex (Fig. 31); this portion then passes ventrally to become the ramus buccalis facialis of the infraorbital trunk.

Gasserian ganglion of the nervus trigeminus

The Gasserian ganglion lies entirely outside the cranial cavity in *Polycentrus* and is separate from other ganglia near it except the trigeminal sympathetic ganglion, with which it has a fiber connection (Fig. 31). The radix profundus (called the truncus ciliaris profundus after formation of its ganglion) passes into the dorsolateral part of the Gasserian ganglion and divides into the ciliaris longus and ciliaris brevis while inside the Gasserian ganglion. Gasserian cells fill spaces between fiber bundles of the trigeminal and facial roots which are effecting fiber bundle exchanges and which form the truncus supraorbitalis and truncus infraorbitalis. One arm of Gasserian cells extends dorsoanteriorly over the anterior surface of the dorsoanteriorly ascending truncus supraorbitalis, reaching almost as far as the first lateralis branch of the supraorbital trunk. A shorter, thicker arm of cells extends along the anterior surface of the truncus infraorbitalis. The lateralis fibers from the intracranial dorsal lateralis ganglion and the communis fibers from the geniculate ganglion of the facialis nerve pass anteriorly behind the Gasserian ganglion cells and form part of the supraorbital trunk. The rest of this trunk is formed by fiber bundles from the Gasserian ganglion constituting the general cutaneous component. Lateralis and communis fiber bundles from the facial roots, plus all the trigeminal motor fibers, and a large number of cutaneous fibers from the Gasserian ganglion all join and pass ventrally behind the Gasserian ganglion to form the infraorbital trunk.

Roots and ganglia of the nervus facialis

The nervus facialis arises by four roots which are fused basally giving the appearance of one root (Fig. 29). A short distance from the medulla, the basal root separates into three parts which, however, represent four facial roots, the motor facial and the ventral lateralis facial roots being so close together as to appear as one root (Fig. 31). The facial roots emerge from the medulla directly dorsal and a little anterior to the anteriormost auditory root. The facial roots are as follows, starting dorsally: the dorsal lateralis root; the communis root, which enlarges anteriorly into its geniculate ganglion; the motor root; and, most ventral, the ventral lateralis root, which arises directly ventral or medial to the anteriormost auditory root. A short distance from the brain, this ventral lateralis root comes to lie on the ventral surface of the motor root. These two roots become indistinguishably bound together. More anteriorly they leave the cranium as the truncus hyomandibularis through the facial foramen in the prootic bone. Before joining the motor root, the ventral lateralis root receives a ramus which is connected to the last two auditory roots. An intracranial connection between the auditory and facial nerves is apparently common in fishes, being found in *Menidia* (Herrick 1899), *Lampanyctus* (Ray 1950), and *Scomber* (Allis 1903). All these facialis roots near their points of origin lie over the posterior end of the lobus inferioris of their side. All the roots run anteroventrally to the trigemino-facialis foramina, where their relationships become complex in the formation of the supraorbital, infraorbital, and hyomandibular trunks.

A few ganglion cells appear on the medial side of the ventral lateralis root a short distance after the ramus from the auditory roots joins its lateral surface (Fig. 31). A little further distally the ventral lateralis and motor roots join and many ganglionic cell bodies appear on the lateral surface of the compound root, but they do not form as dense and compact a mass as occurs in the geniculate or Gasserian ganglia. The ganglionic cell bodies which are most abundant on the ventral half of the joined motor and lateralis roots (Fig. 31) are part of the ventral lateralis root. Beyond the ganglion the compound trunk of motor facialis and ventral lateralis roots passes medial to the intracranial flange of the prootic, which separates the facial and trigeminal foramina, receives communis fibers from the geniculate ganglion, and, as the truncus hyomandibularis, passes out the facial foramen.

Ramus communicans of the nervus trigeminus

The ramus communicans of the nervus trigeminus is large in *Polycentrus* and forms from the posterior end of the part of the Gasserian ganglion that extends into the prootic chamber (Fig. 31). The ramus communicans runs posteriorly in this chamber, emerges close to the facial foramen, but remains separated by large blood vessels from the truncus hyomandibularis as the latter truncus leaves the facial foramen. The truncus hyomandibularis and its ramus communicans from the trigeminal nerve pursue separate courses which converge laterally and ventrally at the medial side of the hyomandibular bone, which they enter together and course in a passageway in this bone, the ramus communicans lying on the dorsal surface of the truncus as the two go into the hyomandibular. The fibers of the ramus communicans shortly become a part of the truncus and cannot further be followed separately on the serial sections. All of the ramus communicans was observed on a Sihler preparation of *Liparis pulchellus* (Liparidae) to leave the proximity of the truncus hyomandibularis, not having become attached to that truncus, and to constitute almost the entire ramus hyoideus. In *Menidia* (Herrick 1899; fig. 3) all of the ramus communicans enters the ramus hyoideus, none apparently entering the other main division of the truncus hyomandibularis, that is, the ramus mandibularis facialis. In *Polycentrus* some general cutaneous fibers continue in the latter nerve also.

Truncus Supraorbitalis

The dorsal lateralis and communis roots of the facial nerve together with the general cutaneous root of the trigeminal nerve contribute to the formation at the trigeminal foramen of the following nerves that constitute, or are associated with, the truncus supraorbitalis: (1) the ramus oticus (general cutaneous and dorsal lateralis components); (2) the orbito-pectoral branch of the ramus lateralis accessorius (communis fibers from geniculate ganglion); and (3) the truncus supraorbitalis (dorsal lateralis and general cutaneous fibers and possibly some communis fibers). The supraorbital trunk separates into its two main rami, the ramus ophthalmicus superficialis trigeminus (general cutaneous fibers) and the ramus ophthalmicus superficialis facialis (lateralis fibers), shortly beyond the frontal commissure of the supraorbital lateralis canal.

Ramus ophthalmicus superficialis trigeminus and ramus ophthalmicus superficialis facialis

The first branch of the truncus supraorbitalis is the ramus oticus (Fig. 3, ROT). It is considered separately in the next section. The second branch of the truncus, SORB 2, supplies skin and certain scale pockets bearing free lateralis organs on the head dorsal to the orbital rim (Figs. 1, 3, and 5) and is assigned, therefore, to the ramus ophthalmicus superficialis facialis, although it carries some general cutaneous fibers. It detaches from the truncus a short distance after the orbito-pectoral branch of the ramus lateralis accessorius (RLA-OP) leaves from alongside the truncus. Branch SORB 2 runs dorsally a short way and penetrates the alisphenoid through a relatively large foramen. On other specimens the foramen for SORB 2 was occasionally in the sphenotic bone. Entering the cranial cavity, SORB 2 rises dorsally along the inner surface of the frontal bone. En route it is crossed by SORB 3 (Fig. 5) from the truncus supraorbitalis. SORB 3 passes through the frontal bone, and after crossing SORB 2, it joins with the parieto-dorsal branch of the ramus lateralis accessorius (RLA-PD). SORB 3 was absent on the other side of the specimen. Near the cranial roof, SORB 2 detaches several minute nerves which appear to innervate, in part, the meninges of the brain in the region dorsal and anterior to the anterior semicircular canal. Medial to the supraorbital canal, but at about its dorsalmost level, SORB 2 divides into SORB 2a and SORB 2b (Fig. 1). The smaller, SORB 2a, passes through the midmedial roof of the cranium, turns anteriorly, runs over the surface of the horizontal myoseptum between the dorsal and ventral cranial roof musculature, curves laterally over to the skin, turns posteriorly underneath it, and innervates free lateralis organs on one of the scale pockets. Intracranially SORB 2a gives off a tiny twig which appears to supply the meninges.

At the point of origin of SORB 2a, a larger branch, SORB 2b, runs intracranially dorsoanteriorly and soon penetrates the frontal bone medial to the frontal sensory canal. It curves over the external surface of the canal and passes laterally to skin over the posterior corner of the eye. Upon reaching the skin it divides into several branches. One branch passes onto the skin connecting the eye to the orbital rim and onto the cornea over the dorsoposterior quadrant of the eye (Fig. 16, COR 1). A smaller branch passes posteriorly and innervates a row of free lateralis organs on a scale (Figs. 5 and 17). A larger branch of SORB 2b passes anteriorly giving off about five successive short twigs each of which innervates a row of free lateralis organs on the skin of one of the scales that lies above the orbital rim, the lateralis-bearing scales forming a row which extends anteriorly from near the dorsoposterior quarter of the eye up to the frontal canal pore located in the anterior half of the orbital rim. The twig to the pore of the frontal canal near the middle of the orbital rim innervates a cluster of free lateralis organs on the membrane covering most of the canal opening.

The main body of SORB 2, at the point where it detaches SORB 2a and SORB 2b, continues intracranially in a posterior and slightly dorsal direction a little above the anterior semicircular canal and comes in contact with the ramus lateralis accessorius (RLA-PD) but is separable from it. SORB 2 passes through the parietal bone and through the thin flange of bone (Fig. 1) constituting the parietal ridge, breaking up into four branches in the ridge. These branches send twigs to various scale pockets, each scale pocket bearing a line of free lateralis organs (Fig. 17), the lateralis organ-bearing scale pockets together forming a line of free lateralis organs leading posterodorsally towards the middorsal line and ending above the rear of the supraoccipital area. It could be seen on the Sihler preparations that the sprays which these twigs form on the scale pockets are supplying specialized sense organs rather than merely being free sensory nerve endings of general cutaneous fibers in the skin. One of the four branches sends a twig dorsally and posteriorly, a few of its fibers going to the two dorsal scale pockets of the vertical row supplied by the ramus supratemporalis vagi. The remaining fibers of this branch separate into numerous small fiber groups which cross or run for a short distance with the ramus lateralis accessorius (RLA-PD), located beneath skin on top of the head, but then leave this ramus and innervate a few scales, each posterior to the vertical row supplied by the ramus supratemporalis vagi. These few scale pockets are much less strongly innervated than are those of the supratemporalis row. It is doubtful that they also bear free lateralis organs, but they could.

The remaining branches of the truncus supraorbitalis serve mainly the lateral line organs of the frontal and nasal canals (from the ramus ophthalmicus superficialis facialis) and the skin (from SORB 5 and SORB 6 of the r. oph. sup. trigeminus) near the canals. Especially interesting are the apparently lateralis branches, one from each of three of the four branches to the lateral line organs. There are patches of free lateralis organs where these branches (SORB 4, SORB 8, and SORB 11a, see Figs. 3 and 17) terminate in the skin. Each of these probable lateralis rami detaches from one of the branches that innervates a canal neuromast of the frontal or nasal bone and continues, usually rather far anteriorly, apparently to innervate free lateralis organs mainly over the anterior end of the orbital roof. One of these branches, SORB 11a (Fig. 3), detaches from the nerve (SORB 11) to the lateral line organ in the nasal bone and runs anteriorly in the canal some distance before it passes through the lateral wall of the canal and innervates the overlying skin. Its terminal branchings lie directly opposite those of a branch of SORB 6, which is apparently a completely general cutaneous nerve. Since there is a patch of free lateralis organs in this area and since SORB 6 is apparently a general cutaneous branch, it seems likely that SORB 11a is a lateralis branch supplying these free lateralis organs. It is probably the usual relationship that the same lateralis branch that supplies a canal neuromast also supplies the free lateralis organs in the skin around the adjacent canal pore.

After giving off SORB 2, the truncus is a broad, flat band of nerve fibers with no distinct bundles and is pressed close against the frontal bone in the orbital cavity. Shortly, it divides into two groups of fibers, a medial, slightly smaller one with many black nuclei, and a lateral, larger one with much lighter-stained fibers. These two divisions are the rami ophthalmicus superficialis trigeminus and facialis, respectively. The trunk at this point has come to lie near the medial side of the frontal canal, as this structure lies near the orbital rim. A lateralis branch, SORB 4 (Fig. 3), detaches from the facial part of the main truncus, enters the bone of the frontal canal, and bifurcates, one fork at a time entering the canal and innervating sensory canal organs 4 and 5 of the supraorbital canal. The two organs lie close together posterior to the frontal commissure of the supraorbital canal. The branch to each canal organ detaches a slender ramus, which is probably lateralis or perhaps both lateralis and general cutaneous in function. Each penetrates the frontal bone and innervates tissue near the orbital rim.

The truncus supraorbitalis continues anteriorly and a little laterally, lying up against the roof of the orbital cavity underneath the frontal canal, and gives off two branches (Fig. 3) of uneven size, SORB 5 and SORB 6, which together constitute most of the ramus ophthalmicus trigeminus and are general cutaneous in function. The much smaller branch, SORB 5, curves lateroanteriorly close to the edge of the orbital rim where two small twigs detach, one of which was lost in the skin connecting the orbital rim to the eyeball; the other is distributed to the orbital surface bordering the rim. The rest of SORB 5 (Fig. 16), now labeled COR 2, continues in skin directly lateral to the orbital rim, until in the anterodorsal quadrant of the orbit it turns towards the center of the eye, giving branches to skin connecting the eye and orbital rim; the rest of COR 2, which is the larger part, goes to the conjunctiva and cornea. SORB 6, which is the major portion of the ramus ophthalmicus superficialis trigeminus (r. oph. sup. tri.), and the remainder of the truncus, which is equivalent to the ramus ophthalmicus superficialis facialis (r. oph. sup. fac.; see Fig. 3), diverge rather sharply from each other, then, after some distance, approach each other and continue to the anterior end of the orbital roof where they leave together and pass out onto the snout beneath the nasal bone. The r. oph. sup. tri. courses across the ventral surface of the frontal bone in the orbital cavity and the r. oph. sup. fac. courses in a bony canal beneath or to the side of the frontal canal.

Shortly before leaving the orbital rim, SORB 6 detaches SORB 6a, which passes dorsoanteriorly up the medial side of the nasal canal and innervates skin overlying the junctions of the anterior end of the frontal canal and the posterior end of the nasal canal. The rest of SORB 6 continues anteriorly a little below the ventral side of the nasal canal. Two-thirds of the way along the nasal canal and at the ventrolateral side of it, SORB 6 gives off several branches. The first of these is a small branch, SORB 6b, which passes dorsally and innervates skin on the medial side of the nasal canal. It lies directly in front of the terminal branching of the lateralis branch SORB 11a from the main truncus supraorbitalis. The next branch, SORB 6c, larger than the SORB 6b, passes around the medial side of the nasal bone, rises to the dorsal level of this bone, and innervates skin medial to and a little behind the anterior end of the nasal bone. The remainder (SORB 6d) of SORB 6 passes to skin in front of, and lateral to, the anterior narial opening. Here it bifurcates, the dorsal fork passing medially around the front end of the nasal bone to innervate skin behind the head of the maxilla, the other fork passing anteroventrally towards the dorsal half of the shaft of the maxilla, where it innervates skin in front of the anterior narial opening and below the nasal bone. Branches SORB 6b, 6c, and 6d are essentially the same on both sides of the specimen. There is no indication that these branches innervate free lateralis organs in their vicinity. The numerous free lateralis organs located near the narial and nasal canal openings (Fig. 19) are mostly, if not completely, innervated by facialis fibers of the infraorbital trunk (Fig. 1). Further study is needed of the areas of the front end of the snout and nasal and narial openings where the truncus supraorbitalis and truncus infraorbitalis meet.

The rest of the truncus supraorbitalis, after detaching SORB 6, is the ramus ophthalmicus superficialis facialis, which carries mostly lateralis fibers but apparently also some general cutaneous fibers. The ramus, coursing in a bony passageway in the frontal bone, curves to lie medial to the frontal canal and gives off branch SORB 7 that courses along the orbital roof. SORB 7 shortly detaches branch SORB 7a that enters the frontal bone, curves medially and dorsally around the frontal canal, continues coursing anteriorly along the medial side of the canal until, a short distance behind the posterior end of the nasal bone, it rises to the skin over the frontal canal and innervates it. It could not be determined if this branch is general cutaneous or lateralis or both. The rest of SORB 7 courses anteriorly along the lateral side of the frontal canal and divides into four diverging, anteriorly directed branches; two of these emerge on the dorsal surface of the head, supplying skin in front of the anterior pore of the frontal canal, one branch passing anteriorly across the floor of the pore. Another of the branches continues along the lateral side of the frontal canal and innervates skin at the ventroanterior corner of the anterior pore of the frontal canal. The two other branches pass anteriorly almost up to the end of the orbital cavity, where they penetrate the frontal bone and pass to the skin anterior to the frontal pore. These branches of SORB 7 all innervate skin, none apparently innervate free lateralis organs, as far as could be determined, and are classed as general cutaneous branches. Only a few scattered free lateralis organs are found in the anterior third of the supraorbital rim area.

The ramus ophthalmicus superficialis facialis continues anteriorly in bone at the medioventral side of the frontal canal. Halfway along its orbital course, it detaches branch SORB 8, which innervates the third supraorbital canal organ. Some distance further SORB 9, innervating the second supraorbital canal organ, is detached. At the point where SORB 6 touches it, the ramus ophthalmicus superficialis facialis gives off SORB 10, which rises dorsoanteriorly along the medial wall of the frontal canal. From SORB 10 a twig is sent to skin outside the frontal canal, the rest going dorsally to innervate skin dorsal to the posterior end of the nasal bone. Directly beyond this branch, a smaller branch (not illustrated) is sent to skin a little anterior to the preceding branch. Branch SORB 10 apparently carries cutaneous fibers of the trigeminal ramus rather than lateralis fibers of the facial nerve. The ramus ophthalmicus superficialis facialis next passes through the frontal bone and continues medial to the nasal canal which it penetrates and detaches SORB 11 which innervates SO 1, the first canal neuromast of the supraorbital canal and the only lateral line organ in the nasal canal. Extending beyond SORB 11 is a thick, straight branch, SORB 11A, which runs anterolaterally, penetrates the lateral wall of the nasal canal two-thirds along its length, and ends in a darkly stained spray of terminal fibers on the surface of the skin on the side of the canal. Free lateralis organs are located in this area, which SORB 11A apparently innervates.

Truncus Infraorbitalis

The truncus infraorbitalis has three main divisions: division IO1, the ramus buccalis facialis; division IO2, the ramus mandibularis trigeminus; and division IO3 the ramus maxillaris trigeminus. Divisions IO2 and IO3 are closely bound together for some distance after leaving the area of the trigeminal foramen.

Ramus buccalis facialis

Division IO1, the ramus buccalis facialis, carries mainly lateralis fibers innervating the canal organs of the infraorbital series of bones, these lateralis fibers having come from the dorsal lateralis root of the facial nerve. In *Polycentrus* the ramus buccalis also carries a general cutaneous component, the fibers of which come from the Gasserian ganglion of the trigeminal nerve. They supply the skin of the cheek area and preopercular regions as well as skin on or near the infraorbital bones. The lateralis fibers of the ramus buccalis supply four canal neuromasts enclosed within the lachrymal canal as well as a neuromast enclosed in the canal of each of the second and third bones of the infraorbital series (Figs. 1 and 3). The fourth infraorbital, that on the sphenotic bone, has its neuromast innervated by a branch of the ramus oticus, a nerve which is not considered by Herrick (1899) to belong to either the supraorbital or infraorbital trunks but to lie in between the two. Free lateralis organs are distributed along the lower edge of the second and third infraorbital bones, along the posterior one-fifth of the lachrymal, and on the membrane of the second pore of the lachrymal (Fig. 17). The ramus buccalis facialis innervates these naked lateralis organs. The ramus buccalis also apparently innervates free lateralis organs medial or dorsal to the anterior and posterior ends of the nasal bone and a patch of these organs that lies in skin lateral and ventral to the anterior and posterior narial openings (Figs. 1, 3, and 17). A patch of free lateralis organs innervated by the ramus buccalis also occurs on the anterior end of the maxilla, ventral to the anterior nostril. Some branches to canal neuromasts detach a branch that innervates free lateralis organs near an adjacent canal pore. An example is the neuromast branch for the second neuromast and second pore of the lachrymal canal (Fig. 1, IO1d2).

The ramus buccalis, division IO1 of the truncus infraorbitalis, forms from the dorsal lateralis root of the facial nerve and moves through the dorsolateral corner of the trigeminal foramen and through the trigemino-facialis complex outside the foramen. A fairly large contribution of general cutaneous fibers from the Gasserian ganglion joins it as the ramus buccalis passes ventrally down the lateral side of the trigemino-facialis complex and lateral to the rest of the truncus infraorbitalis.

The first branch is IO1a (Fig. 1) to the lateralis organ in the fourth infraorbital bone (the sixth organ of the infraorbital canal). The ramus buccalis shortly divides, the larger part remaining as the ramus buccalis, the smaller part, IO1b, in turn divides into four branches, all being apparently the general cutaneous fibers going to skin of the cheek area. The first of these is branch 1h (Fig. 1), which passes under the posterodorsal end of the second infraorbital bone and across the cheek underneath skin near the sensory canal of the preopercle. Branch 1h turns sharply ventrally and innervates skin in front of and on top of the preopercle about midlength of the canal. Branch 1g passes directly posteriorly and crosses the preopercular canal, innervating skin. Branch 1f is short. It passes under the second infraorbital and ends in skin partway across the cheek towards the preopercle. The fourth branch, 1e, after contacting a thick branch of IO2b from the ramus mandibularis trigeminus (IO2), passes under the second infraorbital and extends almost in a straight line over to the preopercle, where it breaks up in skin overlying the canal of this bone. Branch IO2b of the ramus mandibularis trigeminus is mentioned here because it should be part of the ramus buccalis although it detaches from IO2, the r. mand. trigeminus. No comparison of this branch was made on other specimens. Branch IO2b also passes under the second infraorbital bone about midway along the length of this bone after having been in contact with branch 1e of the ramus buccalis. Branch IO2b divides into cheek branches 1c and 1d, both of which pass ventroposteriorly over the cheek, supplying apparently general cutaneous innervation to skin over to and on top of the preopercular canal.

The ramus buccalis next detaches branch IO1c, which shortly divides into IO1c1 (Figs. 1 and 3), which supplies the lateralis organ located halfway along the length of the second infraorbital, and IO1c2, which in turn gives off two branches. The first branch, COR6, innervates conjunctiva and cornea of the posteroventral part of the eyeball and skin connecting the eyeball and the second infraorbital bone. The rest of IO1c2 passes under the second suborbital, emerges at the ventral edge of this bone, rises to skin, and divides into branches 3b and 3c. Branch 3b passes anteriorly, innervating a series of four or five free lateralis organs in a row. It anastomoses with branch 3d. Branch 3c turns posteriorly and innervates a row of four or five lateralis organs along the ventral edge of the anterior half of the second suborbital bone. The rest of the ramus buccalis continues anteriorly over the floor of the orbital cavity medial to the infraorbital bones and gives off branch IO1d, which passes anteriorly giving off branches to the suborbital bones and skin of the cheek. The first branch of IO1d (not labeled in Fig. 1) leaves IO1d near the anterior end of the second infraorbital and divides into three branches. Branches 1a and 1b pass ventrally down the cheek, innervating skin below the eye and anterior to the preopercular canal. Branches 3d and 3e both supply a row of free lateralis organs lying at the ventral edge of the anterior end of the second infraorbital bone and about three or four organs extending onto the ventral edge of the posterior end of the lachrymal (Fig. 1). Branch 3e is not continuous with branch 3f, although they are shown continuous in Fig. 1. Branch 3d anastomoses posteriorly with 3b. The last branch of the ramus buccalis to supply free lateralis organs in the infraorbital row is branch 3f, which innervates four organs in a row anterior to those innervated by 3e. The four organs lie a little above the ventral edge of the lachrymal bone well posterior to the canal of this bone. The next branch, IO1d2, detaching almost at the same point as branch 3f, passes anteriorly some distance and innervates the second lateralis organ in the lachrymal as well as the membrane over the second lachrymal canal pore. The branch innervating the pore membrane detaches from IO2d2 inside the lachrymal canal. The next branch of IO1d is 3g (Fig. 1), which passes to the exterior of the lachrymal bone and anteriorly some distance, reaching the membrane over the third pore of the lachrymal. Branch 3g innervates the patch of free lateralis organs on this membrane. Here is another example of a lateralis branch to a canal organ detaching also a branch to free lateralis organs on the membrane of the adjacent canal pore. The last two branches of IO1d each innervate a canal neuromast located near the third lachrymal pore and its membrane.

After detaching IO1d, the ramus buccalis continues anteriorly some distance and divides into IO1e and IO1f about halfway along the lachrymal (Fig. 1). Branch IO1e shortly gives off a branch (not labeled) on either side of itself before passing to the first canal organ in the lachrymal. The first of these branches is a thin nerve that passes anterolaterally medial to the lachrymal bone. It crosses under the branch to the first lateral line canal organ and emerges from under the lachrymal, where the large articulating surface of the maxilla comes in contact with the anteromedial surface of the lachrymal (Fig. 1). The nerve supplies skin in this area, especially the fold of skin that lies directly ventral to the first indentation on the anterior leading edge of the lachrymal bone adjacent to the articulating head of the maxilla. The second of the two branches of IO1e continues anterodorsally medial to the lachrymal and then almost straight dorsally near the posterior edge of the lachrymal where it innervates the skin covering the olfactory organ and olfactory chamber. From the appearance of its tiny spraylike endings as seen on Sihler whole-mount nerve preparations, this branch innervates free multicellular sense organs located on the skin. The distribution of such organs as seen on serial sections and from whole formalin specimens (Fig. 19) coincides with the location of the spraylike endings just mentioned. The serial sections show the organs to be free lateralis organs.

Branch IO1f, which arises at the same point as IO1e (Fig. 1), continues anterodorsally, passes ventral to the lateral ethmoid and a little lateral and dorsal to the palatine bone and along the medial wall of the nasal sac. At a point about on the same dorsal level as the first dorsal pore of the lachrymal, IO1f1 is detached and passes dorsally and then anteriorly medial to the lachrymal. It apparently innervates only skin on the anterodorsal part of the lachrymal. Branch IO1f continues anterodorsally and divides medial to the first pore of the lachrymal. One of these branches (IO1fa; Fig. 1) passes dorsally, medial to the posterior end of the nasal bone, and innervates the membrane over the posterior nasal canal pore and some skin anterior to it. The terminal spraylike endings of these branches on Sihler preparations indicate innervation of free multicellular sense organs on the skin. The distribution of free lateralis organs as seen on serial sections coincides with the distribution of the spraylike endings of the nerves. There is little doubt that they are innervating free lateralis organs.

Branch IO1fb (Fig. 1) continues for a short distance anterodorsally and medial to the lachrymal before dividing into two branches. One branch passes anterolaterally to innervate skin overlying the dorsal edge of the head of the maxilla and skin ventral to the anterior narial opening where there are free lateralis organs (Fig. 19). The other branch passes dorsally up the medial side of the nasal canal and ends in skin medial and dorsal to the anterior end of the nasal canal. There is a patch of free lateralis organs here, which this branch evidently supplies.

Ramus maxillaris trigeminus

The ramus maxillaris trigeminus of the truncus infraorbitalis has two main branches, the ramulus maxillaris superioris to the snout and symphyseal area of the upper jaw and the ramulus maxillaris inferioris to the upper jaw. In *Polycentrus*, at least in the specimen on which the descriptions are based, the superior ramulus is not a separate nerve but courses, to whatever extent it is present, with the ramus buccalis facialis. The inferior ramulus (IO3; Fig. 1) to the upper jaw is moderately developed. It innervates the skin of the premaxilla and maxilla. The following description covers only the inferior ramulus.

The ramulus maxillaris inferioris trigeminus leaves the floor of the orbital cavity about halfway across it and passes anterolaterally and ventrally of the palatine bone, then across the lateral side of the palatine but medial to the lachrymal, giving off as it does two small branches (not shown in Fig. 1) which anastomose with branch IO1f of the ramus buccalis facialis. The next branch, IO3a, leaves the inferior ramulus maxillaris and sends a branch to skin on the lachrymal, dorsal to the second and third pores of the lachrymal canal. The remainder of the IO3a (Figs. 1 and 16) is branch COR 4, which continues onto the anteroventral quadrant of the eye, innervating skin on the edge of the eye and then the conjunctiva and cornea.

The main part of the inferior ramulus (IO3) continues anteriorly lateral to the palatine and crosses the medial side of the alveolar shaft of the maxilla a little ventral to the curved process of the maxilla in which the premaxillary ascending process rides. As the inferior ramulus (IO3) leaves the maxilla, it receives the main part of the palatine nerve. The ramulus courses parallel and ventral to the ascending process of the premaxilla, lying between membranes of the upper jaw (Fig. 1). The external membrane is the skin and the internal membrane is the mucosal lining of the mouth, both having become modified into a stretchable, thin, tough pair of membranes. Before reaching the premaxilla, branch IO3b is detached medial to the lachrymal as IO3 passes beyond the palatine (Fig. 1). Branch IO3b also runs between the jaw membranes, passes lateral to the A_1 tendon which fastens the cheek muscles to the maxilla, and runs close to the dorsal edge of the maxilla towards its distal end. Two-thirds along the maxilla, IO3b crosses onto the lateral surface of this bone and shortly divides into three branches. A small branch runs anterodorsally into the jaw membrane anterior to the maxilla, another ends in skin over the shaft near the distal end of the maxilla, and the main part of IO3b continues to the distal end of the maxilla, coursing along the ventral edge of the ligamentous connection between the distal ends of the maxilla and premaxilla. Branch IO3b ramifies in folds of skin in this region. After passing beyond the maxilla on its way to the premaxilla, IO3 receives, as mentioned, the anterior end of the palatine nerve. The juncture of the two nerves varies somewhat on different specimens and on the two sides on the same specimen. On one side, the palatine nerve crosses IO3 but then continues alongside it, the two nerves remaining separate for some distance before joining. On the other side, the two nerves remain separate for some distance, except for a small branch, until after IO3 bifurcates at two-thirds of the way toward the shaft of the premaxillary bone. The palatine nerve then joins the dorsal fork, IO3c (Fig. 1). The dorsal fork and the palatine nerve continue as one nerve towards the base of the ascending process, giving off twigs at right angles, which run in the thin membrane of the upper jaw and innervate it. Just before IO3c passes medial to the shaft of the premaxilla, it breaks up into two large and several small nerves. The largest branch IO3c1, passes onto the medial side of the premaxilla, penetrates the premaxilla at the edge of the alveolar region, and emerges on its dorsal (external) surface and divides, one branch going towards the symphysis of the upper jaw and out onto the lip. The rest of IO3c1 innervates teeth and lip tissue adjacent to the symphysis. Branch IO3c1 is the main innervation to the lip tissue in front of the symphysis. The fair-sized remainder of IO3c innervates the teeth and adjacent tissue of the rest of the premaxillary. It sends a small branch to the premaxillary oral flap and a small branch to the premaxillary membrane (neither branches shown in Fig. 1) and then passes across the medial surface of the shaft of the premaxillary until it reaches the alveolar region, where it turns distally and runs in the gum tissue between the middle rows of teeth, supplying the teeth and gums out to the end of the tooth region.

The posterior fork, IO3d, formed from the bifurcation of IO3, slants anteroventrally across the jaw membrane and reaches the lateral surface of the premaxilla about one-third of the way along its shaft, giving off en route two branches which supply the area of the lip distal to that supplied by the dorsoanterior fork. The rest of the posterior fork passes in skin diagonally across the premaxilla, giving off branches to the upper lip; leaving the premaxilla one-third of the way from its distal end, it innervates the posterior end of the lip. Branch IO3d must carry predominantly general cutaneous fibers. Of the three main branches of the compound IO3 and palatine nerves, the branch to the alveolar region is the smallest.

The conspicuous part of the superior maxillary ramulus, the branch to the symphyseal region of the upper jaw that is apparently generally present in many teleosts, is absent in *Polycentrus*. The rest of the superior ramulus that innervates the skin of the anterior end of the snout no doubt courses as parts of branches IO1fa and IO1fb of the ramus buccalis.

Ramus mandibularis trigeminus

The ramus mandibularis trigeminus (IO2) courses for some distance bound to the rest of the truncus infraorbitalis. It leaves the truncus and turns ventrally. Medial to the second infraorbital bone, it detaches its first branch, IO2a, the ramus opercularis trigeminus (Fig. 1) and continues towards the cheek muscles and the lower jaw.

Ramus opercularis trigeminus

The ramus opercularis trigeminus, IO2a, passes posteriorly towards the hyomandibular, curves dorsally, crosses the anterior edge of this bone a little ventral to its anterior articulating head, continues posteriorly close to the lateral surface of the hyomandibular and divides en route into a dorsal and a ventral branch. The ventral branch breaks up to supply the levator arcus palatini muscle near its insertion. The dorsal branch passes through this muscle to innervate the adjacent dilatator operculi muscle. The main arm of the dorsal branch then innervates the dilatator fibers that pass under the dorsal end of the preopercle (Figs. 1 and 22).

After the ramus mandibularis trigeminus (IO2) has passed ventrally below the second infraorbital bone, it detaches IO2b (Fig. 1), a thin nerve that passes laterally across the floor of the orbital cavity. At the inner edge of the third infraorbital, it anastomoses with the anteriormost, fourth branch of IO1b of the ramus buccalis. From the anastomosis three nerves spread out (only 3b and 3c shown in Fig. 1) as they pass under the infraorbital bone and run under skin across the cheek area, as has been described in a preceding section, giving off branches en route and ending in skin covering the preopercular canal. These nerves do not appear to end in the spray typical for branches that innervate free lateralis organs. There are no free lateralis organs in this area. These nerves undoubtedly belong to the general cutaneous system. A second and smaller nerve, not illustrated, detaches at the same place as IO2b, diverges anteriorly from IO2b, and passes out as another cutaneous branch down the cheek.

Innervation of cheek muscle

A fair-sized branch, IO2c (Fig. 6), passes laterally and a little ventrally through the adductor mandibulae muscle mass a short distance below the orbit. The nerve breaks up into a fairly large posterior branch which supplies the ventrolateral part of the anterior half of muscle A_1. However, a sizeable portion (not labeled) of IO2c rises to skin not far below the orbit where it divides into numerous branches which pass under the third infraorbital to innervate the skin in its vicinity. One rather large branch of IO2c curves sharply ventrally (shown in Fig. 6 but not labeled) and passes under the skin of the cheek toward the preopercular canal, giving off what apparently are cutaneous branches to skin. It ends in skin over the anterior end of the preopercular canal. The terminal branches in the skin are very fine.

The next branch, IO2d, arises a short distance further, passes anteriorly, and breaks up in the anterodorsal half of the A_1 portion of the adductor mandibulae muscle, which it innervates (Fig. 6). A smaller branch of IO2d passes posteriorly and shortly divides, the posterior branch supplying the more posterolateral part of A_1, the anterior branch going to the more ventrolateral part of the anterior half of A_1.

The fifth branch, IO2e, quite large, leaves the ramus mandibularis trigeminus at the same point as does IO2d and passes ventroposteriorly (Fig. 6). The first branches to come off IO2e anteriorly form a rather dense ramification on the most medial side of the muscle mass. These branches lie medial to the main trunk of the ramus mandibularis trigeminus (IO2) and appear to supply mainly the muscle fibers which insert by way of the prearticular tendon (TA_3; see Fig. 24). Branches from the posterior side of IO2e supply the more lateral and ventral fibers of the posterior part of A_1 in this region, fibers which insert on the ventral end of the maxillary tendon (TA_1; see Fig. 24). Most of the rest of IO2e passes anteroventrally towards the tendon connecting the mentalis (Aw) division of the adductor mandibulae, supplying en route the ventroanterior fibers of this muscle, that is, those which mainly constitute A_2. Some of the more dorsolateral muscle fibers which IO2e innervates insert on the ventral end of the maxillary tendon. After giving off IO2d and IO2e, the main trunk of IO2, the ramus mandibularis trigeminus, continues anteroventrally, passing between the body of the cheek muscle mass along a rather clear-cut separation between what has been designated as divisions A_1 and A_2 of the jaw muscles. As the main ramus reaches the anterior edge of the quadrate a little above its articulating head where IO2 is covered laterally by fibers of A_2, the nerve forms three large subdivisions. The most ventral of these, the ramulus mandibularis cutaneus trigeminus (IO2f; see Fig. 6), passes directly anterior to the articulating head of the quadrate onto the lateral surface of the posterior end of the articular bone.

Ramulus mandibularis cutaneus trigeminus

The first branch detached en route, IO2f1, passes medially around the anterior edge of the quadrate. It ends in a dense, localized ramification of branches (Fig. 10) in the tendinous mucosa which lies on the inside of the mouth directly in front of the anterior edge of the quadrate near the articulation head of the bone. This tendinous mucosa fans out towards the ventral end of the maxillary tendon. Branch IO2f1 may innervate stretch receptors located in the jaw membranes in this region. Just before IO2f reaches the quadrate, three branches of IO2f are given off. One of these, IO2f2, runs dorsally beneath the skin covering the ventral area of the cheek (Fig. 6; only the stub of this branch is shown) and which fastens onto the articular bone. One twig innervates this skin. A more dorsal twig innervates the skin area directly posterior to the ventral end of the maxillary tendon.

A second of the three branches, IO2f3 (Fig. 6; stump only of branch shown), runs beneath skin posteriorly, gives off a small twig to skin lying over the articulating head of the quadrate, and then continues dorsally a short distance, parallel to the ventral edge of the quadrate and bifurcates. One of the two forks extends posteriorly to the ventral end of the maxillary tendon and ends in very fine branches in the skin near the area supplied by IO2f1. The other, larger fork slants posteroventrally over the preopercular canal and ends in fine branches in skin directly dorsal to the ventral opening of the preopercular canal. It innervates skin close to that innervated by a branch of the ramus mandibularis facialis of the truncus hyomandibularis, TH16, but TH16 (Fig. 2) has terminal sprays typical of nerves supplying free lateralis organs in the skin, whereas for the smallest distal branches of the larger fork of IO2f3, the terminations as viewed on Sihler specimens are very delicate, widely forked twigs and apparently are of the general cutaneous component.

The last of the three branches, IO2f4 (Fig. 6), passes anteriorly over the lateral side of the posterior end of the articular, gives off a small ventral branch to skin, then slants dorsally and shortly bifurcates, with fork IO2f4b passing close to the dorsal edge of the articular. A short distance up the articular, IO2f4b gives off a small branch that enters the fold of bone constituting the dorsal edge of the articular. This nerve passes to the end of the dorsal edge and onto the ventral surface of the cartilaginous pad between the posterior end of the alveolar process of the dentary and the anterior end of the dorsal edge of the articular. It breaks up into tiny branches in this region. The rest of IO2f4b continues up the dorsal articular process, detaches a branch which passes onto the cartilaginous pad, and then continues in a curved course anteriorly along the ventral edge of the alveolar process of the dentary, gradually becoming smaller. It is apparently a cutaneous nerve. A second branch, which was given off at the same time as this branch from IO2f4, also passes to the cartilaginous pad where it could not be followed. The third branch of IO2f4b curves anterodorsally along the lateral surface of the broad anterior articulating shaft of the articular bone, becomes thinner as it approaches the posterior edge of the body of the dentary, and disappears between the lateral wall of the dentary and the anterior shaft of the articular.

The other fork of the general cutaneous branch of IO2f4, branch IO2f4a (Fig. 6), extends anteriorly under skin above the articular segment of the mandibular lateral line canal, giving off occasional branches which run downward in the skin over the canal. It becomes progressively smaller until it disappears in skin. Branch IO2f4 is apparently all general cutaneous.

Shortly after IO2f passes onto the articular, it is joined by TH16, a branch from the ramus mandibularis facialis of the truncus hyomandibularis. Branch TH16 could be carrying either lateralis or cutaneous fibers or both. Branch IO2f from the r. mandibularis trigeminus would be carrying general cutaneous fibers but not motor fibers. Since IO2f and TH16 distribute to the same areas and IO2f carries only or mostly general cutaneous innervation, it is not likely that TH16 is carrying this component. More likely, since it detaches from the r. mandibularis externus (Fig. 2) which carries lateralis fibers mainly or only, TH16 must carry lateralis fibers, which it supplies to free lateralis organs of the articular and preopercular areas. The compound nerve (TH16 + IO2f), after a short distance, detaches IO2f5 (Figs. 6 and 9), which passes posteroventrally directly ventral to the articulating head of the quadrate. Branch IO2f5 shortly sends a small branch which contributes to the innervation of the skin over the posterior opening of the lateral line canal in the articular bone. Branch IO2f5 passes medial to the lateral line canal and comes out under skin covering the posterior process of the articular and angular bones. Here it breaks up into several branches. Branch IO2f5a turns anteriorly beneath skin at the posteroventral surface of the articular, where it disappears as fine branches; the other branches come off the remainder of IO2f5. Branch IO2f5b (Fig. 6) divides into an anterior branch, which passes in skin of the articular ventral to its sensory canal, and into a long, thin posterior branch which runs posteriorly in the ligament connecting the interopercle to the angular and articular. It passes further onto the interopercle, where it anastomoses with a branch from the ramus hyoideus and gives off en route another branch, IO2f5d (Fig. 6), which passes dorsally, medial to the ventral end of the preopercle. Branch IO2f5d anastomoses with the r. mandibularis facialis of the truncus hyomandibularis. Branch IO2f5e passes posteriorly underneath the ventral edge of the preopercle, giving off branches to skin on the interopercle. A larger branch, IO2f5c, continues across the interopercle-articular ligament and onto the ventral skin covering the articulation between the interopercle, articular, and angular bones, and the bases of the anteriormost branchiostegal rays. Branch IO2f5 is undoubtedly partly general cutaneous and partly lateralis, since it is a branch of the compound nerve formed by TH16 (lateralis) and IO2f (general cutaneous). There are free lateralis organs in the area.

The remainder of IO2f, after detaching the above branches, enters the articular segment of the mandibular lateral line canal and detaches IO2f6, a small branch (Fig. 9) which ends in a dense and very finely divided network on the surface of skin covering the articular segment of the mandibular canal. About halfway anteriorly along the articular, the remainder of IO2f breaks up into branches IO2f7, IO2f8, and IO2f9. Branch IO2f7 (Figs. 6 and 9) passes posteromedially and supplies skin over the medial ventral surface of the articular. Two long anterior branches of IO2f8 course in skin over the articular and dentary canals. There is a row of free lateralis organs in this skin and a patch of them at the junction of the articular and dentary canals. It could be observed directly that these branches of IO2f8 innervated these free lateralis organs. The longer branch of IO2f8 ends in skin and membrane around lateral line canal pore number four of the dentary. No free lateralis organs were observed in this area (Fig. 17). The branches of IO2f7 and IO2f9 ending in skin over the ventral surface of the articular and dentary medial to the lateralis canal apparently are of a general cutaneous component and would be from the r. mandibularis trigeminus, not from the r. mandibularis facialis.

The lateralis fibers for IO2f8 are apparently all from the r. mandibularis facialis of the truncus hyomandibularis via TH16, which joins IO2f above the quadrate's articulating head. Herrick (1899: fig. 3, V–VII.I) found with fairly good certainty such a source of innervation for a small number of free lateralis organs over the canal of the articular bone in *Menidia*.

Returning in the description of the main trunk of the r. mandibularis trigeminus (IO2) to the point where it detaches IO2f (Figs. 7, 9, and 10), it is seen than the ramus mandibularis trigeminus passes anteriorly medial to the muscle fibers that insert on the A_2–Aw common tendon, and onto the medial side of the articular, crossing at about midpoint of the posterior edge of this bone. IO2 continues anteriorly and a little ventrally on the medial surface of the articular, detaching en route four branches rather close together which innervate subdivisions for the mentalis muscle (Fig. 7). The subdivisions are shown in Figures 23 and 24. Shortly beyond the branches to the mentalis muscle, the r. mandibularis trigeminus (IO2) detaches the ramulus mandibularis internus trigeminus (IO2g; Fig. 7). The remainder of IO2 continues anteriorly as the ramulus mandibularis externus trigeminus (IO2h; Fig. 8). The internal trigeminal ramulus (IO2g; Fig. 7) crosses Meckel's cartilage and runs forward with the ramus mandibularis facialis of the truncus hyomandibularis. Branch IO2g innervates the protractor hyoidei and intermandibularis muscles, and adjacent skin on the outside, and the mucous lining on the inside of the lower jaw.

Ramulus mandibularis externus trigeminus

After detaching IO2g, the ramulus mandibularis externus trigeminus (IO2h) continues anteriorly some distance and, near the teeth, it detaches IO2h1 (Fig. 10), which carries general cutaneous fibers. IO2h1 is shortly joined anterodorsally by TH19a carrying communis fibers. The two branches course together towards the inner edge of the alveolar region of the dentary, where the compound nerve divides. An anterior branch, TH19a4 (Fig. 8), enters the dentary beneath the inner rows of teeth and courses towards the symphysis of the lower jaw, supplying teeth and apparently tissue surrounding the teeth. Two posterior branches run along the inner edge of the alveolar region, TH19a3 in bone under the teeth and Th19a2 next to the alveolar region but in the skin (Fig. 8). The latter nerve breaks up into several parallel branches, one of which, a little posterior to the teeth, drops ventrally and innervates an area of mucosa lining the inside of the lower jaw. A thin branch, TH19a1 (Fig. 8), detaches from TH19a shortly after the latter leaves TH19 and runs forward to an area a little posterior and lateral to the symphysis, where it ends in skin. Shortly before it breaks up, TH19a1 is joined by a long anterior branch of TH19b1 (Fig. 8). Branches of TH19 should be carrying communis fibers for taste buds and mucosa.

After detaching IO2h1, the remainder of the ramulus mandibularis externus trigeminus (IO2h) (Fig. 8) courses anteriorly to near the end of the dentary and detaches a fairly stout branch, IO2i, at the curve of the lower jaw. Branch IO2i goes to the anterolateral corner of the dentary, near the symphysis, and probably carries mostly general cutaneous fibers. It passes through the dentary directly above the attachment of the labial cartilage of the lower lip and directly divides into three large and several small branches which supply the lower lip. The largest of these branches follows the curve of the labial cartilage posteriorly, giving off branches to the posterior half of the lip. One of these branches curves posteriorly across the dorsal surface of the lip and runs in skin of the lip above the teeth of the dentary. Branches pass laterally and anteriorly supplying the anterior half of the lip. After detaching IO2i, the rest of IO2h continues anteriorly as IO2j (Fig. 8), which passes under the teeth, has a connection with TH19b1, and, near the symphysis, comes close to and probably joins with the rest of TH19b, which carries communis fibers from the r. mandibularis internus facialis.

Ramulus mandibularis internus trigeminus

Branch IO2g (Figs. 7 and 10) of the r. mandibularis trigeminus (IO2) remains to be described. The rest of the r. mandibularis facialis (branches TH19 through TH25) are described in another section along with the rest of the r. mandibularis facialis and the truncus hyomandibularis. The ramulus mandibularis internus trigeminus (IO2g) innervates the protractor hyoidei (geniohyoideus), the intermandibularis muscles, and the skin of the anterior end of the lower jaw in the area of these muscles. It carries a lateralis contribution from the r. mandibularis externus facialis, which innervates free lateralis organs between the anterior ends of the dentary bones. Just before the main trunk of the r. mandibularis trigeminus (IO2) reaches the dorsal side of Meckel's cartilage, about halfway along the articular bone, branch IO2g is detached. IO2g passes ventrally around the cartilage and comes to lie on the medial surface of the r. mandibularis facialis, runs with it for some distance on the ventral surface of Meckel's cartilage, leaves the r. mandibularis facialis, and continues dorsoanteriorly medial to the cartilage. After branch TH19 is detached (Fig. 10) from the r. mandibularis facialis (see section on the truncus hyomandibularis for description of TH19), the remainder of the r. mandibularis facialis (lateralis fibers from the ramulus mandibularis externus facialis) plus the trigeminal branch IO2g (general cutaneous and motor fibers) continue anteriorly medial to Meckel's cartilage. The facial and trigeminal parts of this nerve cannot be separated. En route to the muscles and skin of the floor of the lower jaw, branches TH20 to TH24 are detached. These branches mainly constitute the remainder of the r. mandibularis externus facialis, although some cutaneous innervation of the trigeminus courses with them. Only branches IO2g2 and IO2g2a (Fig. 8), which innervate the protractor hyoidei and the intermandibularis muscles, respectively, and overlying skin are labeled as deriving from IO2g of the r. mandibularis trigeminus. Branch IO2g2 passes anteromedially (Fig. 8) and detaches IO2g2a, which continues anteriorly and is almost contiguous at the midventral line with a similar branch from the opposite side, the two together innervating the intermandibularis muscle (Figs. 8, 9, and 10). The remainder of IO2g2 enters the protractor hyoidei muscle, courses posteriorly in it near the medial edge of the muscle, and sends lateral branches into the muscle. Near the point of divergence of the two parts of the protractor hyoidei where the belly of each muscle is crossed by a myoseptum, the remainder of branch IO2g2 of each side meet. There appears to be some crossing of the nerve fibers of each side over to the opposite side as branch IO2g2 continues posteriorly in the protractor hyoidei, IO2g2 finally overlapping, as far as could be determined: the anterior extent of the ramus hyoideus passes anteriorly from the hyohyoideus muscle.

Ramus Oticus

The ramus oticus forms intracranially from a larger bundle of fibers from the dorsal lateralis root and a smaller bundle from the ventral lateralis root, both being roots of the facial nerve.

The two bundles join, pass out the lateral side of the trigeminal foramen, and receive general cutaneous fibers from the Gasserian ganglion. The compound nerve passes laterodorsally over the surface of the orbital cavity and into a foramen in the sphenotic bone. En route to this foramen, a branch is detached which innervates the next-to-last lateral line canal organ of the infraorbital series, organ 6. In Figure 1 this branch is labeled IO1a and is shown as detaching from the ramus buccalis facialis. Usually this branch is associated with the ramus oticus (Freihofer 1963: fig. 5). A cutaneous branch (not shown in Fig. 1) extends from IO1a underneath the infraorbital bone and ramifies in skin posterior to this bone. Upon emergence from the sphenotic bone, the ramus oticus (Fig. 5) lies underneath the last infraorbital bone. It detaches a lateralis branch innervating the single lateralis organ in the last infraorbital, which lies over the sphenotic, and also detaches a branch (not shown in Fig. 1) which passes from under this last infraorbital. It innervates skin overlying the dilator operculi muscle. The rest of the ramus oticus, along with the orbito-pectoral branch of the ramus lateralis accessorius (RLA-OP), which joins it in the porous passageway through the sphenotic, enters a bony passageway at the lateral side of the pterotic canal, shifts medially, and enters the pterotic canal, where it innervates two lateral line canal organs lying close together. The orbito-pectoral branch of the ramus lateralis accessorius continues on and is described in a later section.

Ramus Palatinus

The ramus palatinus carries communis fibers for the mucosa of the palate and its taste buds, and for taste buds of the upper jaw. The ramus leaves the geniculate ganglion of the facial nerve and passes above the anterior end of the facial foramen. Intracranially the ramus palatinus apparently divides into an anterior and a posterior ramus, this division not being discernible on serial sections or on Sihler preparations. It may be that both rami arise separately from the geniculate ganglion. Two rami are identifiable outside the cranium. The anterior ramus is the main one. The posterior ramus leaves the cranium with the truncus hyomandibularis as branch TH1 (Fig. 4) to the pseudobranch area. The anterior palatine ramus drops sharply ventrally and a little anteriorly, passing through its foramen in the prootic bone, and enters the prootic chamber connecting the trigeminal and facial foramina. It directly enters the wall of the prootic and passes anteroventrally next to the lateral prootic wall of the posterior myodome chamber. It courses in a bony space outside that of the myodome. Leaving the wall of the prootic, it passes through the parasphenoid rather close to the anterior edge of the prootic wing of this bone. It continues next to the top edge of the parasphenoid, gradually shifts ventrally, and finally comes to lie alongside the parasphenoid directly above the origin of the adductor arcus palatini muscle. The first branch (not illustrated) passes anterodorsally in the palatal mucosa, continues halfway anteriorly across the adductor arcus palatini, and curves laterally. It sends several long branches posteriorly that innervate the mucosa of the posterior area of the palate. On the other side of the specimen, a branch was given off from the right anterior palatine ramus that courses near the middle of the parasphenoid bone for about half the length of this bone, and innervates mucosa. The next branch, P2, is given off a little before the main ramus passes anteriorly beyond the end of the palatal roof (Fig. 4). Branch P2 passes laterally reaching the dorsal surface of the palatine bone near its anterior end. It detaches en route a branch that courses straight posteriorly some distance, innervating the mucosa of the palate. The rest of P2 bifurcates at the palatine bone. The anterior fork gives off several twigs; some innervate anterior palatine teeth. One branch continues anteriorly across the ventral surface of the palatine ligament connecting the palatine and prevomer and innervates mucosa in this area. Another branch from P2 passes anteriorly across the ventral surface of the articulation pad of the maxillary with the prevomer and innervates mucosa in this area. Another branch serves the prevomer area.

The posterior, larger fork of P2 courses parallel and medial to the palatine teeth and gives off a small nerve at the posterior extent of these teeth, the nerve passing anteriorly beneath teeth. The rest of the posterior fork continues onto the ectopterygoid bone, where branches supply mucosa and teeth. Numerous small branches occur in the mucosa medial to the anterior end of the palatine bone and dorsal to the palatine-prevomer ligament. The rest of the anterior ramus palatinus, after detaching P2, courses anteriorly, passes beneath the process of the maxillary in which the premaxillary spine moves, and continues parallel to the ascending process of the premaxilla and the ramus maxillaris trigeminus (IO3; Fig. 1). The anterior palatine ramus finally joins the dorsal fork of the ramus maxillaris trigeminus (Fig. 1).

On the other side of the specimen, the anterior ramus palatinus joins the maxillary ramus (IO3) proximal to the splitting of IO2 into primary branches to the alveolar region of the premaxillary ramus.

Truncus Hyomandibularis

All of the nerve fibers and components of the truncus hyomandibularis are derived from the roots of the facial nerve except the general cutaneous fibers which come from the trigeminal nerve via the ramus communicans and also some sympathetic fibers from the facial sympathetic ganglion.

There are four main branches of the truncus hyomandibularis. These are (1) the ramus opercularis profundus; (2) the ramus opercularis superficialis facialis; (3) the ramus hyoideus; and (4) the ramus mandibularis facialis, which has two main divisions: the ramus mandibularis facialis externus and the r. mand. fac. internus.

The ramus opercularis profundus facialis carries visceral motor component fibers and innervates the muscles of the palate and those moving the hyomandibular bone and opercle, muscles whose origin is medial to these bones.

The ramus opercularis superficialis facialis carries lateralis and general cutaneous fibers. In *Polycentrus* it innervates the dorsalmost two canal organs of the mandibulo-preopercular canal and free lateralis organs on certain scales: one scale near the dorsal end of the preopercle; another on the opercle near the operculo-hyomandibular articulation; and a third on the anterior end of the side of the subopercle.

The ramus hyoideus facialis follows a course mainly along the ventral edge of the hyoid arch, ending a little beyond the anterior end of the arch. In *Polycentrus* it contains all or nearly all of the general cutaneous fibers that join the truncus hyomandibularis from the Gasserian ganglion of the trigeminal nerve via the ramus communicans. It also carries visceral motor fibers for the branchiostegal muscles. The ramus hyoideus apparently carries no lateralis or communis fibers. Almost all of the ramus hyoideus innervates the hyoid arch, a small part of it apparently continuing into the posterior end of the protractor hyoidei muscle, where it appears to anastomose with a posteriorly coursing branch of the ramus mandibularis trigeminus which innervates most of the latter muscle.

The ramus mandibularis facialis contains lateralis and communis fibers, but apparently none or few general cutaneous fibers and no motor fibers. It has three main branches. One of these is a lateralis branch, the ramus buccalis accessorius (TH 10; Fig. 2), which in *Polycentrus* innervates free lateralis organs around some pores of the preopercular canal, a vertical row of free lateralis organs on the cheek in front of the preopercular canal, and free lateralis organs along the third and fourth infraorbital bones. Another is the ramus mandibularis facialis externus, which is a lateralis branch that separates from the remainder of the r. mandibularis facialis at the symplectic bone, the remainder of the r. mandibularis facialis at this point being the r. mandibularis facialis internus. These two rami rejoin beyond the symplectic but remain more or less distinct entities, componentwise, but such distinctness is not evident externally. The ramus mandibularis facialis externus is so named because it courses closer to the external surface of the lower jaw, where it supplies lateralis organs in the mandibular canal and free lateralis organs in skin on the lower jaw. The last of the three branches is the ramus mandibularis facialis internus, which courses separately from the r. mandibularis facialis externus in the region of the symplectic, rejoining the r. mandibularis facialis externus, in most but not all fishes, medial and anterior to the symplectic. It carries communis fibers for taste buds located mainly at the anterior end of the lower jaw, and those on the lower lip and gum area of the teeth.

In *Polycentrus* there are apparently few or no cutaneous fibers in the r. mandibularis facialis beyond the preopercle. Herrick (1899) found a similar condition for the atherinid *Menidia*.

In the labeling of Figures 2 and 8–13, all of the branches of the truncus hyomandibularis are numbered consecutively, and given the prefix TH, and occasionally a name where one is available.

In *Polycentrus* the ventral lateralis and motor roots of the facial nerve pass through the facial foramen as one combined trunk, the truncus hyomandibularis (Fig. 31). As the truncus leaves the facial foramen, it receives a bundle of fibers from the facial sympathetic ganglion.

Directly after leaving the cranium, a small nerve, TH1 (Fig. 4), the posterior palatine ramus, detaches from the truncus and passes anteriorly and laterally at a level dorsal and anterior to the pseudobranch, where it is joined by a nerve of equal size coming from the nervus glossopharyngeus, forming what is called a Jacobson's anastomosis. Herrick (1899) used the term ramus pretrematicus facialis for branch TH1 in *Menidia* but later (1901) changed to the noncommittal term, the posterior palatine ramus. The compound facial and glossopharyngeal nerve continues its course through the adductor arcus palatini muscle (Fig. 26) to skin at the posterior roof of the mouth in front of the pseudobranch, where the compound nerve breaks up into five branches. None of these branches was observed to course onto the hyoid arch. Nerve fibers from the glossopharyngeus innervate the pseudobranch (Laurant and Dunel 1966), but no innervation of this organ, a very vascular, glandlike structure in *Polycentrus*, could be observed by the methods employed.

Ramus opercularis profundus facialis

The next two branches from the truncus, TH2 and TH3 (Figs. 2 and 4), arise together at the same point from the truncus but course in opposite directions. Together they constitute the ramus opercularis profundus of the facial nerve. Branch TH2 courses anteriorly through the adductor arcus palatini muscle, innervating it. Branch TH3 (Fig. 4) extends posteriorly medial to the head of the hyomandibular bone. In passing beneath the membrane connecting the posterior end of the adductor arcus palatini muscle and the adductor hyomandibularis muscle, TH3 detaches several very small nerves which innervate this membrane, which contains only a few muscle fibers (Figs. 4 and 26). It then enters the adductor hyomandibularis muscle near its insertion and divides. One division of TH3 gives off three small nerves which run dorsally in the adductor hyomandibularis muscle, innervating it. The other division also contributes to this muscle. The two divisions of TH3 are next connected by a small branch, and immediately several rather large branches detach and pass dorsally in the posterior part of the adductor hyomandibularis. The lateral of the two divisions of TH3 passes through the middle of the levator opercularis muscle, sending branches into this muscle, except for two small branches which join with branches of the vagus coursing down the medial surface of the opercle. One of these vagal branches apparently supplies the anterior part, and the other the posterior part, of the uppermost portion of the hyoidei adductores muscle. It has not been possible to verify this observation. The lateral division of TH3 crosses, at right angles, three branches of the vagus and continues into the body of the levator opercularis muscle, where it breaks up into a dorsal and a ventral branch of about equal size and a middle, small branch. All run posteriorly in the muscle.

No other branches leave the truncus before it passes through its foramen into the hyomandibular bone. As it enters this bone, the ramus communicans from the Gasserian ganglion joins the tr. hyomandibularis on its posterior surface (Fig. 2; r com V).

Shortly after entering its canal in the hyomandibular and turning ventrally, the tr. hyomandibularis detaches the ramus opercularis superficialis facialis (Fig. 2; TH4).

Ramus opercularis superficialis facialis

The ramus opercularis superficialis facialis (Fig. 2; TH4) directly supplies the twelfth, or last, lateral line organ of the mandibulo-preopercular canal. The rest of the opercular facial ramus sends a branch which passes directly posteriorly and, just in front of the opercle and a little below the operculo-hyomandibular joint, divides into TH4aa and TH4bb. The ventrally directed branch TH4bb passes onto the lateral surface of the opercle a little below the articular head, enters a foramen near the leading edge of the opercle, emerges on its lateral surface, and shortly detaches branch TH4bb1 and, a short distance further, branch TH4bb2, which soon rejoin and supply the pocket of a large scale. About 15 free lateralis organs were observed on a scale in this area (Fig. 17). The rest of TH4bb passes ventrally, crosses the anteroventral corner of the opercle, continues onto the subopercle a little posterior to the interopercle, and innervates free lateralis organs in the skin of this region. There are 15 such organs at this location (Fig. 17). Branch TH4aa passes dorsally, lateral to the hyomandibulo-opercular articular head, and ends in skin a little below the point where the preopercular, pterotic, and supratemporal canals open. The terminal twigs of this branch appear the same as those which supply free lateralis organs in the skin elsewhere. There are six or more free lateralis organs in this area (Fig. 17). Branch TH4aa apparently supplies these organs.

Branch TH5 leaves the hyomandibular, penetrates the preopercular lateral line canal, and after a short distance, innervates lateral line canal organ number 11 of the mandibulo-preopercular canal.

A short distance further TH6, a thin branch, detaches and passes posteriorly onto the anterior edge of the surface of the opercle that articulates with the preopercle (Fig. 2). Branch TH6 courses down the articulating edge, sending a branch laterally onto the opercle, where it appears to end by several tiny branches in a scale pocket dorsal to the pocket supplied by TH4bb1. It does not appear to innervate free lateralis organs nor are there any at this location on six whole, formalin-preserved specimens examined. A tiny twig is sent from TH6 into skin over the ligament which connects the preopercle to the interopercle. A small cutaneous branch, TH7 (Fig. 2), was present on one side of the specimen but not the other.

About three-fourths of the way toward the articulation of the interhyal with the hyomandibular and symplectic bones, the truncus hyomandibularis detaches TH8, which supplies lateralis organ number 10 of the mandibulo-preopercular canal. The truncus next directly gives off the sizeable ramus hyoideus (TH9), which passes down near the posterior edge of the hyoid arch and detaches several cutaneous branches to skin over the anteroventral ends of the opercle and subopercle, and the ventral half of the interopercle as well as branches to the hyoidei muscles and to the branchiostegal membrane. The rest of the truncus shortly divides into the rami mandibularis facialis externus and internus.

Ramus hyoideus

The ramus hyoideus (TH9; Fig. 2) continues ventrally towards the interhyal, but before reaching this bone it leaves the hyomandibular, turns posteroventrally paralleling the interhyal and gives off en route a thin branch, TH9A (Figs. 2 and 13). Branch TH9A crosses the distal end of the interhyal and passes onto the posteromedial surface of the epihyal, where it breaks up in the mucous lining of the mouth. The main part of the ramus hyoideus (TH9) passes around the posterior edge of the interhyal-epihyal articulation and detaches TH9B (Fig. 2), which passes a short distance to a point above the posterodorsal end of the interopercle, where it divides into TH9B0 and TH9B1 (Fig. 2). Branch TH9B1 goes through the broad ligament connecting the interopercle to the shaft of the hyomandibular and shortly divides into four branches, TH9B1a through TH9B1d (Fig. 2), treated together, and into branch TH9B1e. Branch TH9B1a sends long thin branches innervating skin covering the joint between the interopercle and opercle. Branch TH9B1b courses up the anterior edge of the opercle and anastomoses with a descending branch of the vagus and with TH6. These branches apparently supply general cutaneous innervation overlying the anterior edge of the opercle. Branch TH9B1c passes to skin covering the joint between the subopercle and the opercle, one small branch ending in this joint. Branch TH9B1d courses posteriorly above and somewhat parallel to the ventral end of the opercle; another branch of TH9B1d passes over the joint and curves posteriorly along the ventral edge of the opercle for a short distance, anastomoses with a branch of TH9B02, and detaches several twigs which pass down over the subopercle a short distance, innervating skin. The remainder of TH9B1, after detaching branches TH9B1a through TH9B1d, is TH9B1e, which passes along the medial side of the dorsal edge of the interopercle, continues anteroventrally, and turning horizontally, passes medial to the preopercle. About midway across the interopercle, TH9B1e curves ventrally, continues anteroventrally across the medial surface of the interopercle, detaching as it does at least five branches which emerge from under skin on the lateral surface of the interopercle below the preopercle. These branches supply the skin of ten scale pockets on the exposed lateral surface of the interopercle. No free lateralis organs were observed on any of these scales on the six whole specimens examined. The anteriormost terminal branch of TH9B1e anastomoses with a branch from IO2f5b (Fig. 2), a general cutaneous branch from the r. mandibularis trigeminus.

The details of these branches of TH9B differ on the two sides of the specimen, but the same areas are served by similar branches.

Branch TH9B0 arises at the same point as TH9B1. It passes ventrolaterally onto the posteromedial surface of the interopercle where it bifurcates. The posteroventral fork, TH9B02, sends a branch to the anterolateral surface of the subopercle where it innervates skin along the ventroanterior half of the medial surface of the subopercle. It does not supply free lateralis organs. Another branch of TH9B02 goes to skin covering the articulating surfaces between the subopercle and interopercle and to skin on the anteromedial surface of the subopercle. Branch TH9B03 runs anteriorly on the medial side of the interopercle and crosses the central area of this bone, where it is joined by a branch from TH9C of the ramus hyoideus (Fig. 13). The combined nerve shortly bifurcates: fork TH9B04 continues towards the ventral edge of the interopercle, supplying skin medially in this region. It continues anteriorly near the ventral edge of the preopercle and into skin on the ventromedial surface of the posterior end of the lower jaw at the junction of the interopercle, angular, and articular bones. The other fork, TH9B05, runs ventrally close to the ventral edge of the interopercle, turns anteriorly and dorsally, and courses beyond the interopercle onto the fold of skin connecting the ventral edge of the lower jaw and the protractor hyoidei muscles, which form, in part, the floor of the mouth. The branch innervates this skin and sends a branch towards the angulo-interopercular joint.

Branches TH9B1 and TH9B0 apparently should be assigned to the general cutaneous component. The medial side of the interopercle is supplied mainly by branch TH9B03, whereas the lateral side of the interopercle is supplied mostly by TH9B13.

Branch TH9C (Figs. 13 and 2), which leaves the ramus hyoideus (TH9) beyond TH9B, innervates the portion of the hyoidei adductores muscle connecting the sixth branchiostegal ray to the opercle (Fig. 13). Immediately after arising, TH9C detaches a thin branch, TH9C1 (Fig. 13), which passes to the medial side of the interopercle, where in part it anastomoses with a branch of TH9B0 and then continues as a small nerve which runs forward to the articulating head of the sixth branchiostegal ray and then along this ray innervating apparently muscle and skin in this area. The rest of TH9C supplies the dorsalmost portion of the hyoidei adductores muscle, as already mentioned. A few branches of TH9C cross onto the medial side of the sixth ray and into the muscle spanning the sixth and fifth rays. A few twigs innervate the branchiostegal membrane spanning the distal ends of the fifth and fourth rays.

The remainder of the ramus hyoideus (Figs. 2 and 13) continues anteriorly along the ventral edge of the epihyal and across the medial side of the sixth branchiostegal ray, giving off en route a very thin, long nerve (not shown) which runs posteriorly in the first (dorsalmost) segment of the hyoidei adductores muscle. The tissue was broken in this region, but the nerve apparently rejoins the main branch of TH9C. As the ramus hyoideus crosses the sixth ray, another nerve, TH9D (Fig. 13), is given off which passes posteriorly across the sixth, fifth, and fourth rays, decreasing in size as it supplies the muscle and skin connecting these rays. As it crosses the fourth branchiostegal ray (counting the anteriormost ray first), the ramus hyoideus divides into TH9E and TH9F. Branch TH9E passes around the anterior edge of the third branchiostegal ray and into the posterior end of the protractor hyoidei (geniohyoideus) muscle, which it innervates, and then anastomoses with the posterior end of branch IO2g2 of the ramus mandibularis trigeminus supplying the major part of the protractor hyoidei muscle. A branch (not illustrated) of TH9 in the protractor hyoidei area runs back to the bases of the branchiostegals and appears to innervate the tendons and muscle fibers of the hyohyoidei abductores (H AB: Fig. 25). Branch TH9f supplies the anteriormost segment of the hyoidei abductores (H AB) and the muscle and skin connecting the first and second rays. Small twigs are detached from TH9 as it crosses the fifth to second rays, which innervate the muscle slips of the hyoidei adductores that originate on the ventral edge of the ceratohyal.

Ramus mandibularis facialis

The truncus hyomandibularis (Figs. 2 and 13), after detaching TH8 and the ramus hyoideus (TH9), is referred to at this point as the ramus mandibularis facialis. It courses away from the side of the preopercular canal and towards the point where the interhyal articulates with the symplectic, passing a little anterior to that point. Shortly it detaches TH10, the ramus buccalis accessorius facialis.

Ramus buccalis accessorius facialis

The ramus buccalis accessorius (Fig. 2, TH10) rises through the adductor mandibulae muscle to the skin, where it bifurcates: one fork, (TH10A; Fig. 2), turns dorsally and courses beneath skin up to the second suborbital bone where, near the posterior end of this bone, TH10A innervates a series of free lateralis organs that continues posteriorly near the ventral edge of the third suborbital (Figs. 2 and 17). The other fork, TH10B, runs ventroanteriorly, paralleling the preopercular canal, and shortly gives off branch TH10B1, a fairly large nerve which passes anterodorsally a short distance and divides into a dorsal and a ventral branch which together course vertically supplying a series of free lateralis organs in the skin of two large scale pockets. A third scale pocket in the series is supplied by TH10B2, which arises more ventrally from TH10B. The free lateralis organs on these three scales form a vertical row (PCL; Fig. 17). During its course down the preopercle, TH10B has a small connection with the r. mandibularis facialis, crosses the anterior arm of the preopercular canal, and detaches TH10B3 and TH10B4. Branch TH10B4 innervates free lateralis organs in the membrane over the pore of the anterior end of the preopercular canal, and branch TH10B3 innervates a cluster of free lateralis organs at the second preopercular canal pore. Branch TH10, therefore, supplies apparently only free lateralis organs. These free lateralis organs include those around the second pore of the preopercular canal plus a vertical row of about 20 organs extending dorsally up the cheek area (Fig. 2) and some free lateralis organs adjacent to the junction of the second and third suborbital bones. Branch TH10 should be termed the ramus buccalis accessorius. It may be a remnant of the ramus canalis lateralis system (Freihofer 1972). A similar nerve is present in other percoids.

Ramus mandibularis externus facialis and ramus mandibularis internus facialis

After giving off TH10, the rest of the ramus mandibularis facialis passes directly anterior to the proximal end of the interhyal, at which point it detaches TH11 (Fig. 2), which innervates the fourth canal organ of the preopercle (counting from anteriorly), the ninth organ of the mandibulo-preopercular canal. The r. mandibularis facialis next crosses the medial surface of the proximal end of the symplectic and divides into two parts, the r. mandibularis internus facialis and the r. mandibularis externus facialis, the internus portion continuing anteroventrally directly in front of the symplectic and the externus portion passing down the posterior side of the symplectic. The r. mandibularis internus approaches the externus beyond the distal end of the symplectic bone, the two rejoining on the medial surface of the articular head of the quadrate. Halfway down the quadrate, the r. mandibularis internus sends a long, thin nerve, TH12a, dorsally up the inner wall of the mouth to the mucosa covering the anterior end of the adductor arcus palatini, where the nerve could not be followed. It presumably innervates taste buds, communis fibers being the main, if not sole, component in the r. mandibularis internus. Further along its course, not far from where it rejoins the r. mandibularis externus, two more thin branches leave the r. mandibularis internus (TH12). One branch (TH12b, not illustrated) is soon joined by another twig also detached from TH12. Branch TH12b passes anteriorly on the medial surface of the quadrate to near the anterior edge of this bone and then turns dorsally onto the pterygoid bone and passes among the small patch of pterygoid teeth, where it appears to anastomose with a branch of the palatine nerve. Branch TH12c (not illustrated), which arises at the same point as TH12b, passes ventrally and then laterally around the posterior end of the angular and the articular bones anastomoses with the posterior end of IO2f (branch IO2f5d). Branches very similar to TH12a and TH12B were observed on Sihler preparations of several other percoid fishes. On the opposite side of the specimen, a branch corresponding to TH12a detaches more proximally along the r. mandibularis internus (TH12) and goes to the same area of skin in the roof of the mouth.

Some distance beyond the detachment of TH10, branch TH13 leaves the r. mandibularis facialis at the point of its division into the internal and external facial rami and passes towards the preopercular canal and bifurcates at the edge of the canal (Fig. 2): TH13a sends off one branch which ends in the external skin near the fourth pore of the preopercular canal; another branch passes under the canal and divides, one fork ends in skin at the anterior and posterior sides of the fourth pore of the canal. The other fork, TH13b, courses a short distance anteriorly along the dorsal edge of the horizontal arm of the preopercular canal and sends a branch laterally under the canal. This branch also splits into two branches under the canal, one branch innervating skin at the anterior side of the third pore of the canal, the other innervating skin of the posterior side of this same pore. No free lateralis organs were observed on preserved specimens in the vicinity of the third and fourth pores of the preopercular canal, yet branch TH13b should be suspected of carrying lateralis fibers since the r. mandibularis facialis externus carries mainly or only this component. The anterior of the two branches to the third pore sends a branch to skin at the posterior side of the second pore of the preopercular canal. There are free lateralis organs at this pore. TH13 also sends a branch into skin dorsal to the canal. The small remaining part of TH13 anastomoses with TH10. The next two branches, TH14 and TH15, in succession supply sensory canal organs eight and seven of the mandibulo-preopercular canal located between canal pores four and three and canal pores three and two, respectively. A little before the lateralis branch to the first preopercular sensory canal organ arises, a fairly large nerve, TH16, comes off the r. mandibularis externus facialis. TH16 rises to the skin, passes anteroventrally beneath the skin parallel to the posterior edge of the quadrate, and courses around the anterior edge of the articular head of the quadrate, where it anastomoses with IO2f of the ramus mandibularis trigeminus (IO2). The further course of TH16 is described as a part of IO2f. TH16 appears to constitute part of IO2f5 and apparently carries lateralis fibers, judging from all the other branches of TH10 (the r. buccalis accessorius). Branch IO2f of the r. mandibularis trigeminus carries only general cutaneous fibers. The last branch of the r. mandibularis facialis before it is joined by TH12, the r. mandibularis facialis internus, is TH17, a lateralis branch to the first sensory canal organ of the preopercle (Fig. 2). After detaching TH17, the ramus mandibularis externus facialis continues its anteroventral course, running along the posterior edge of the quadrate bone directly beneath the mucosal lining of the mouth and directly dorsal to the preopercular canal. The ramus mandibularis externus passes over the articular head of the quadrate bone and receives the ramus mandibularis internus (TH12) as it does so. Once again referred to as the r. mandibularis facialis, the compound nerve passes onto the medial surface of the articular bone; then keeping between the mandibular canal and Meckel's cartilage, the ramus runs beneath mucosa for about two-thirds of the way towards the symphysis of the lower jaw, giving off several branches en route (Fig. 10). The first branch, TH17a, innervates the only sensory canal organ of the articular. The r. mandibularis facialis then passes between tendons TA_2 and TA_1 which insert the adductor mandibulae muscles on the articular bone (Fig. 24). About halfway between the third and fourth pores of the sensory canal of the dentary, branch TH18 (Fig. 10) passes to the fourth lateralis canal organ of the dentary. A short distance further, the r. mandibularis facialis receives a large nerve, the ramulus mandibularis externus trigeminus (IO2g), from the ramus mandibularis trigeminus (IO2). Branch IO2g, carrying visceral motor and general cutaneous fibers, courses for some distance with the ramus mandibularis facialis, carrying lateralis and communis fibers, and then a number of branches arise carrying various combinations of these functional components to the anterior end of the lower jaw (Fig. 10). Just before branch TH20 leaves the compound r. mandibularis facialis and IO2g, a small nerve, TH18a, apparently carrying communis fibers, passes dorsally beneath skin of the medial side of the dentary up towards the posterior extension of the alveolar process, where it innervates mucosa in this region. Branch TH20 enters the mandibular canal and innervates the third lateralis organ of the dentary. Before innervating this canal organ, three nerves to the external surface of the dentary arise from TH20 (Figs. 8–10). The first of these, TH20a (Fig. 8), passes posterolaterally around the canal, emerges medial to the canal and runs posteriorly beneath skin on the ventral surface of the dentary. It is probably mostly, if not completely, general cutaneous and not lateralis in function. Branch TH20b curves anterolaterally around the dentary canal and runs anteriorly and then posteriorly for some distance under skin on the external surface of the dentary, medial to the canal. It also is apparently a general cutaneous branch. The third branch, TH20c, runs anteriorly on the external surface of the dentary canal almost up to the third pore of the dentary, where it bifurcates; the medial fork passes around the canal and sends one branch anteriorly and another posteriorly. The anterior of these two branches could not be followed, but the posterior one emerges in skin on the ventral surface of the dentary and runs back medial to the canal. The lateral fork likewise runs posteriorly beneath skin but lateral to the sensory canal. All these branches coming off of TH20 appear to belong to the general cutaneous system. Apparently no free lateralis organs occur in the skin over the dentary canal where these branches terminate.

At the point of origin of TH20, the rest of the compound r. mandibularis facialis plus IO2g divides into two main branches, TH19 and TH21 (Fig. 10). Branch TH19 apparently carries communis fibers from the r. mand. internus facialis that supply the taste buds on the lower lip, labial cartilage, and gum area of the teeth as well as other branches to the floor of the anterior end of the mouth. Its branches are described after those of TH21.

Branch TH21 (Fig. 10) contains the visceral motor and general cutaneous fibers carried by IO2g from the r. mandibularis trigeminus as well as lateralis fibers from the r. mandibularis externus facialis for the large patch of free lateralis organs near the tip of the lower jaw. It probably carries few or no communis fibers. A number of branches, TH22 to TH25, arise from TH21. Branch TH22, containing mainly the lateralis portion and some general cutaneous fibers of TH21, continues forward along the medial side of the lateral line canal of the dentary and detaches TH22a to the second canal neuromast of the dentary not far from the symphysis of the lower jaw (Figs. 8–10). The remainder of TH22, after detaching TH22a, continues anteriorly in skin over the ventral surface of the mandibular canal. Halfway towards the second pore of this canal, the remainder of TH22 bifurcates (neither fork illustrated), one fork passing laterally and one medially around the canal, both emerging on the ventral surface of the dentary. The medial fork innervates skin medial to the second pore of the canal. The lateral fork sends a branch anteriorly and one posteriorly, innervating skin lateral to the canal.

Branch TH23, the next most medial branch arising from TH21, courses some distance anteriorly in mucosa covering the dorsal surface of the dentary, penetrates the bone, enters the dentary canal, and innervates the first canal neuromast of the dentary. Branch TH24 passes anteriorly until it reaches the medial edge of the dentary, where it detaches two thin branches, one of which, TH24a (Figs. 8 and 9), passes up the inner side of the dentary and innervates skin near the dorsal edge of the first pore at the anterior end of the mandibular canal. The other thin branch (TH24b; Fig. 9) passes up the external surface of the dentary medial to the anterior end of the canal and innervates skin at the first canal pore. Branch TH24b passes between the medial edge of the dentary and the anterior tendons of the protractor hyoidei (geniohyoideus) muscles, reaching skin on the external surface of the dentary near the symphysis of the lower jaw below the intermandibularis muscle, where it curves toward the midventral line detaching small branches to skin between the anterior ends of the rami of the lower jaw. It then turns posteriorly in skin over the medial edge of the protractor hyoidei and innervates skin. The branches of TH24 going to skin over the anterior end of the dentary canal may be innervating some free lateralis organs. More likely, all the numerous free lateralis organs on the chin between the two dentary rami are supplied by TH25, but this point could not be definitely determined.

Branch TH25, the next most medial of the branches arising from TH21, passes anteromedially and continues between the dentary bone and protractor hyoidei muscle of its side, emerges beneath the skin medial to the anterior tendon of this muscle, and ends in branches which appear to innervate numerous free lateralis organs in this area (Figs. 9 and 17). Branch IO2g2, which corresponds to branch IO2g from the r. mandibularis trigeminus, innervates the intermandibularis and protractor hyoidei muscles and overlying skin. It has already been described under the branches of the r. mandibularis trigeminus.

Branch TH19 of the r. mandibularis facialis remains to be described (Figs. 8 and 10). It probably contains cutaneous fibers of branch IO2g of the r. mandibularis trigeminus, but apparently most of the branches of TH19 are of the communis component for taste buds on the lips and the inside of the anterior end of the lower jaw. On Sihler preparations these communis fibers could be seen to derive from branches of the r. mandibularis facialis internus. Branch TH19 (Fig. 8) continues anteriorly on the ventral surface of Meckel's cartilage some distance and divides into branches TH19a and TH19b. Branch TH19a is shortly joined by branch IO2h containing apparently general cutaneous fibers from the r. mandibularis trigeminus (IO2). The two branches course together to the inner edge of the alveolar region of the dentary, where they divide. An anterior branch, TH19a4, enters the dentary beneath the inner rows of teeth and courses anteriorly towards the symphysis of the lower jaw, supplying teeth and tissue surrounding the teeth. Two posterior branches, TH19a2 and TH19a3 (Fig. 8), course along the inner edge of the alveolar region, branch TH19a2 in bone under the teeth and TH19a3 next to the alveolar region but in mucosa. The latter nerve breaks up into several parallel nerves, one of which, a little posterior to the teeth, drops a little ventrally and innervates an area of the mucosal lining of the inside of the lower jaw. A thin nerve, TH19a1 (Fig. 8), detaches from TH19a and courses forward to an area a little posterior and lateral to the symphysis, where it ends in mucosa that may contain taste buds. Shortly before it breaks up, TH19a1 is joined by part of a long anterior branch, TH19b1 (Fig. 8). Branch TH19b departs from TH19a, continues anteriorly medial to Meckel's cartilage, and divides into TH19b1 and TH19b2. TH19b1 passes anteriorly up to the posterior edge of the intermandibularis muscle where it curves medially and connects to IO2j and TH19a1 by a short branch to each one. The rest of TH19b1 continues medially into the bone of the alveolar region adjacent to the symphysis and could not be followed. TH19b2 curves medially and detaches TH19b3, a thin, long nerve that arches across the tendon of the protractor hyoidei muscle and runs close to the lateral side of the posterior end of the tendon of the opposite side, where it could not be followed further. A similar nerve from the opposite side comes to lie near it. These branches are apparently carrying communis fibers to the floor of the anterior end of the buccal cavity. After detaching TH19b3, the remainder of TH19b2 passes posteriorly as TH19b4 and innervates the mucosa of the buccal cavity. About halfway along its length TH19b1 detaches TH19b1a that curves posterolaterally in the oral membrane of the dentary giving off many fine branches to it.

Ramus Lateralis Accessorius

The ramus lateralis accessorius (RLA), also referred to as the ramus recurrens facialis or simply the recurrent facial nerve, has been described in detail for *Polycentrus* and some other percoids in another paper (Freihofer 1963). Only a summary of its course is given here. The name ramus lateralis accessorius is used in the present paper. The nerve itself has nothing to do with the lateral line innervation. It innervates taste and terminal buds, both of which apparently are basically the same kind of sense organ, the latter being located on the external body surface (Herrick 1899). The nerve fibers of RLA belong to the communis system of nerve components.

The ramus lateralis accessorius in *Polycentrus* consists of two main branches, an orbito-pectoral branch (RLA-OP) that courses to the pectoral, pelvic, and anal fins, and a parieto-dorsal branch (RLA-PD) that courses to the dorsal fin, with some fibers apparently reaching the caudal fin. Both these branches arise intracranially from the geniculate ganglion (Fig. 31).

The orbito-pectoral branch (RLA-OP)

The orbito-pectoral branch of RLA arises from a sizeable bundle of fibers leaving the anterior end of the geniculate ganglion anterior to the facial foramen. The bundle passes through the trigeminal foramen and into and through the extracranial trigemino-facialis complex (Freihofer 1963: figs. 1–4), and then dorsolaterally over the posterior wall of the orbital cavity up to and through the sphenotic bone from which it emerges to lie underneath the last infraorbital bone. RLA-OP courses the overall distance in close proximity or contiguous with the ramus oticus. From under the last infraorbital bone, it passes alongside the anterior end of the pterotic canal as far posteriorly as its midlength, where it passes diagonally under this canal over to its medial side and then rises to the overlying skin, at which point it turns posteriorly and pursues a shallow course beneath the skin, continuing either under the ventral end of the supratemporal canal or between this canal and the posterior end of the pterotic canal, then past the dorsal rami of the ramus supratemporalis vagi and the main branches of the nervus linae lateralis and onto the medial side of the supracleithrum. Crossing this bone, it drops sharply, ventrally down the medial side of the cleithrum onto the first postcleithrum, then alongside the posterior edge of the second postcleithrum, and continues more or less diagonally under skin to near the midventral line, reaching it just posterior to the anus. From this point posteriorly, it courses next to the bases of the anal spines, apparently supplying communis fibers to each branch of a segmental ventral spinal ramus that enters an anal spine or ray.

In its course past the pectoral fin, RLA-OP detaches branches which innervate the pectoral fin (for details see Freihofer 1963). A branch is detached to the pelvic fin as RLA-OP passes this fin.

The parieto-dorsal branch (RLA-PD)

The parieto-dorsal branch of the ramus lateralis accessorius arises by two roots from the large geniculate ganglion which separately pass dorsally around the overlying dorsal lateralis root of the facial nerve and join above it (Fig. 31). RLA-PD passes laterally over to the inside of the cranial wall, encounters the radix profundus and its ganglion, or nearly does, and then rises to the cranial roof beneath the parietal bone, where it is met by the intracranial dorsal vagal ramus, which was identified on serial sections as belonging to the rami cutanei dorsales vagi. This vagal ramus did not actually contact RLA-PD in two Sihler preparations examined but was seen to remain separate from it and to pass anteriorly a short distance to innervate skin. It was sometimes observed on Sihler nerve preparations of several kinds of fishes not to join with RLA-PD nor course with the latter nerve. It seems unlikely that this vagal ramus carries communis fibers as maintained by Herrick (1899).

After passing through the parietal bone, RLA-PD continues laterally across the parietal ridge and to the overlying skin and then posteriorly towards the middorsal line and the dorsal fin. It has similar relations to branches of the dorsal spinal rami innervating the fin spines, rays, and membrane that RLA-OP does for the anal fin. None of the branches of the ramus supratemporalis vagi fuse with RLA-PD as Herrick (1899) found in the atherinid *Menidia*.

It could not be determined by the methods used in this study whether or not any taste buds were innervated by the two main branches of RLA between their cranial exit and the fins or whether there are taste buds in these areas.

Innervation of the Gill Arches

There are four filament-bearing gill arches in *Polycentrus* (Fig. 18, CB1–CB4) and a fifth gill arch which bears no gill filaments and has only one bone supporting it, the fifth ceratobranchial (Fig. 18, CB5). Each of the first four arches has two vertical rows, a medial and a lateral, of gill filaments and a lateral and medial row of gill rakers (Fig. 20, LGR, MGR).

Two pairs of cranial nerves, the glossopharyngeus (IX) and the vagus (X), innervate the five arches and their associated muscles (Fig. 19).

The second or third gill arch exhibits the more complete pattern of branching of a branchial nerve trunk to its gill arch. Typically a branchial nerve trunk divides into two rami, a pretrematic and a posttrematic. The pretrematic ramus of a branchial nerve trunk passes down its gill arch anterior to its gill slit; the posttrematic ramus passes down the succeeding gill arch lying posterior to the same gill slit. For the third gill arch, its pretrematic branchial ramus (Fig. 19, V2PR) innervates the area of the medial row of gill filaments, and its posttrematic ramus (Fig. 19, V2PO) innervates the lateral row of gill filaments of the next posterior gill arch. The glossopharyngeus nerve innervating the first gill arch has a posttrematic ramus (Fig. 19, GLR) passing down the first arch, but the pretrematic ramus (G2) for the glossopharyngeal nerve courses anteriorly onto the palate, where it joins the posterior ramus palatinus. The medial side of the first gill arch and the whole second, third, and fourth gill arches are innervated by vagal branchial trunks one, two, and three, each of which has a pretrematic and posttrematic ramus (see symbols for each arch, Fig. 19). After passing onto a gill arch, posttrematic rami 2, 3, and 4 each gives off a small nerve (shown diagrammatically large in Fig. 19) that passes down the anterior face of a ceratobranchial bone, coursing between the lateral and medial rows of gill rakers, innervating these rakers and the mucous epithelium between them. It is referred to as the gill raker ramus (G6, V1B, V2F). It apparently does not innervate gill filaments. The pretrematic ramus of each branchial arch nerve trunk also has a pharyngeal ramus. Other branches of the pretrematic or posttrematic rami innervate the various gill arch muscles and mucous epithelium on the floor of the gill arches. In *Poly-*

centrus one gill arch muscle, the protractalis pectoralis, is innervated by a branch that comes from the ramus supratemporalis vagi (Fig. 19, PRPE). Branches to the muscles of the gill arches and gill filaments detach from the posttrematic, not from the pretrematic rami.

Nervus Glossopharyngeus

The glossopharyngeal, or ninth pair of cranial nerves, arises by a single root on each side a little below the midlateral extent of the medulla and courses posteroventrally a rather short distance to its cranial exit in the exoccipital bone at the posterodorsal end of the swelling of the otic bulla (Figs. 26, 29). The glossopharyngeal foramen lies directly in front of the vagal foramen but separated from the latter. Shortly beyond its cranial exit, the glossopharyngeus is joined on its ventral surface by the sympathetic trunk. The two course closely bound together anteriorly three-quarters of the way across the otic bulla at which point the petrosal ganglion forms on the glossopharyngeus. A little before or after the petrosal ganglion, some ganglion cells form in what must be the sympathetic part of the compound nerve. The two nerves then separate, the glossopharyngeus continuing anteriorly. At the anterior end of the otic bulla it detaches branch G1 (Fig. 19), which passes anterolaterally and innervates the levator internus II branchial muscle (Fig. 18, LI2). On some Sihler nerve preparations, the glossopharyngeus itself passes through this muscle as it innervates it. The glossopharyngeus next detaches branch G2, the ramus pretrematicus IX, which passes anteriorly and then medially. Upon reaching the proximal head of the first, or suspensory infrapharyngobranchial bone, G2 meets the posterior palatine ramus (PPR, Fig. 19; TH1, Fig. 4) from the truncus hyomandibularis. These two nerves join forming Jacobson's anastomosis, then course anteriorly past the pseudobranch and innervate skin over the posterior end of the palate in the vicinity of the pseudobranch, which is a highly vascularized saclike structure in *Polycentrus*.

The glossopharyngeus, in turning laterally, crosses the anterolateral surface of the levator internus II (LI2; Fig. 18) and passes around the medial and anteroventral surface of the levator externus I (LE1) branchial muscle which it innervates by branch G3 (Fig. 19). The glossopharyngeus (IX; Fig. 19) continues onto the dorsal surface of the first epibranchial bone (EP1; Fig. 18) and laterally along this bone, lying under the bases of a lateral row of gill filaments, this part of the glossopharyngeus being the posttrematic branchial ramus (GLR) of the first gill slit. It continues ventrally onto the ceratobranchial along its posterolateral side under the lateral row of gill filaments. Halfway down the first ceratobranchial, the posttrematic ramus (GLR) detaches a small gill raker branch that passes anteriorly a short distance and which, upon reaching the anterior face of the first gill arch, is joined by a similar gill raker branch (not labeled on Fig. 19) from the pretrematic first vagal branch (not labeled) from the pretrematic first vagal branchial ramus (V1PR). The joined branches (G6; Figs. 19, 20) pass ventrally between the lateral and medial rows of gill rakers innervating them. As the posttrematic ramus of the glossopharyngeus (GLR; Fig. 19) proceeds down the posterolateral side of the ceratobranchial along the bases of the lateral row of gill filaments, a series of very small branches are sequentially detached, each of which passes posteriorly and join together forming a vertical branch, G5 (Fig. 20). Branch G5 weaves in and out between the gill filaments, apparently supplying the muscles of the filaments.

The posttrematic of the glossopharyngeus (GLR) detaches branch G7 (Fig. 19) near the ventral end of the first ceratobranchial; G7 innervates the obliquus ventralis I (OV1) muscle (Fig. 18). The remainder of the posttrematic (GLR, Fig. 19), continues down the lateral face of the first hypobranchial bone and ventrally around its anterior end and up medially and anteriorly to the side of the basihyal bone, along which it courses anteriorly innervating mucosa at the side of the tongue lateral to the basihyal. En route past the first hypobranchial, the glossopharyngeus detaches branch G8 (Fig. 19) for the rectus ventralis I muscle (RV1, Fig. 18). A branch is given off for the mucosa on the floor of the mouth dorsal to the first basibranchial and dorsal hypohyal. The last branch given off runs posterolaterally on the dorsal surface of the dorsal hypohyal towards the first ceratohyal.

Nervus Vagus

The functional components of the nervus vagus, or tenth pair of cranial nerves are (1) visceromotor and communis fibers contained in the pharyngobranchial and intestinal rami; (2) general cutaneous and possibly communis fibers in the rami cutanei dorsales vagi; general cutaneous fibers in the opercular ramus; lateralis and general cutaneous fibers in the supratemporal ramus; and (3) visceromotor fibers in the cardiac ramus. The intestinal and cardiac rami are not considered further. The lateral line nerve of the trunk of the body is considered separately from the vagus. Herrick (1899) found the general cutaneous component to be very small in the vagus of the atherinid *Menidia*, but he found the motor component to be of considerable size, with the communis component by far the largest. Similar relative developments exist in the percoid *Polycentrus*. The cell bodies for the general cutaneous component are located in the jugular ganglion of the vagal nerve; neither this ganglion nor its root was distinguishable from the rest of the ganglion and common root of the vagal nerve in *Polycentrus*.

According to Herrick (1899), fibers of the communis system are of two kinds: fibers that innervate taste buds and fibers that innervate general visceral and mucous surfaces by the simplest free nerve endings. The latter would be comparable to the general cutaneous fibers of external body surfaces.

The root of the vagus arises from the midlateral side of the medulla by four rootlets on dissected specimens, but these appear very close together on serially sectioned specimens and are not distinguishable. The vagal root passes a short distance posteroventrally to its foramen in the exoccipital bone, the foramen for the glossopharyngeal nerve lying a short distance anterior to that for the vagus (Figs. 4, 25, 28–30). Intracranially the nervus vagus is separate from the nervus linae lateralis (NLL). The two nerves pass through the same foramen together, the nervus linae lateralis a little anterior and medial to the nervus vagus.

Intracranial dorsal vagal ramus

Two-thirds along its intracranial course, the nervus vagus detaches a fairly large ramus. This vagal ramus may be equivalent in part to the rami cutanei dorsales vagi of *Menidia*, which rami Herrick (1899) found to arise from the jugular ganglion outside the cranium, not inside as in *Polycentrus*. Part of the rami cutanei dorsales vagi of *Polycentrus* does pass out the cranium as in *Menidia* through the vagal foramen.

The intracranial vagal ramus in *Polycentrus* passes dorsally a short distance from the root of the nervus vagus and detaches a branch about one-third its own size, the extracranial vagal ramus, which passes towards the vagal foramen in the exoccipital bone where the extracranial vagal ramus forms a ganglion just before reaching the foramen. This ganglion is the jugular ganglion of the vagal nerve, the ganglion for general cutaneous sensory neurons. The extracranial vagal ramus (the rami cutanei dorsales vagi, in part) passes through the dorsolateral corner of the vagal foramen between the nervus linae lateralis and the slightly posterior root of the nervus vagus. The extracranial vagal ramus was traced on serial sections almost up to three sizeable fiber bundles lying lateral to the nervus linae lateralis as this nerve leaves the cranium. The extracranial vagal ramus could not be traced beyond this point. The extracranial vagal ramus evidently joins with the three groups of fibers which are evidently lateralis, and together form the ramus supratemporalis vagi. More ganglion cells form in the supratemporal ramus as it moves laterodorsally and anteriorly away from the nervus linae lateralis. The further course of the ramus supratemporalis vagi is described after the intracranial vagal ramus.

One of the three fiber bundles forming the ramus supratemporalis vagi, or part of one of these bundles, must be of motor fibers for the protractalis pectoralis muscle. Another of the bundles is of lateralis fibers for the posttemporal and supratemporal canals. The fiber bundle from the intracranial vagal ramus must be carrying general cutaneous fibers and possibly communis fibers for taste buds, but the methods used in the present study did not permit definite determination of the presence or absence of communis fibers in any of these rami.

Shortly after the intracranial dorsal vagal ramus detaches the extracranial ramus that evidently joins the ramus supratemporalis vagi, the intracranial division forms a sizeable ganglion. The ramus then rises dorsoanteriorly and medially in the cranial cavity up to the parietal bone, through which it passes close to the exit of the ramus lateralis accessorius (RLA-PD) but medial to RLA and about on the same transverse plane with it. Before reaching the parietal, the intracranial dorsal vagal ramus bifurcates. Both branches exit through the parietal, pass transversely across the parietal ridge, and innervate skin on the side of the head dorsal to this ridge. The intracranial vagal ramus exiting through the parietal is missing in *Menidia* (Herrick 1899). It is absent in the atherinid *Atherinops affinis* (Freihofer 1963).

It seems most probable that this intracranial vagal ramus is not carrying communis innervation for taste buds, since RLA which does carry such innervation passes through or close to the area on top of the head served by the intracranial vagal ramus. Nor would it likely be carrying lateralis fibers, since the r. supratemporalis vagi, which carries lateralis fibers, innervates the adjacent area posteriorly, and SORB2 of the supraorbital trunk, also carrying lateralis fibers, innervates the adjacent area anteriorly. If the foregoing statements are correct and the intracranial vagal ramus carries neither lateralis nor communis fibers to the skin, the ramus must be carrying general cutaneous fibers.

Rami cutanei dorsales vagi

The rami cutanei dorsales vagi comprise the general cutaneous bundles of fibers coursing with the nervus vagus (Herrick 1899). Branch r. supr. 2a in *Polycentrus* (Fig. 5) is apparently a cutaneous dorsal branch of the supratemporal vagal ramus and belongs to the rami cutanei dorsales vagi system, but it is described in *Polycentrus* under the ramus supratemporalis vagi.

The intracranial dorsal vagal ramus described above also apparently belongs to the general cutaneous system of branches comprising the rami cutanei dorsales vagi. Although described in *Polycentrus* as a separate ramus, the ramus opercularis vagi (Figs. 11–12, and 19) is apparently general cutaneous in function and also belongs to the rami cutanei dorsales vagi.

Ramus opercularis vagi

The ramus opercularis vagi is associated proximally with the ramus supratemporalis vagi (Fig. 12). In *Polycentrus* the ramus opercularis vagi arises from a thin, elongate ganglion lying outside the cranium and beneath the nervus linae lateralis as this nerve leaves the vagal foramen. The cutaneous root from which the ganglion came could not be observed as a separate entity. Herrick (1899) assigns the r. opercularis vagi to the rami cutanei dorsales vagi. As seen on serial sections, the ramus opercularis vagi is a rather independent entity, although it lies in close proximity to the basal part of both the nervus linae lateralis and the ramus supratemporalis vagi (Fig. 12). The ramus opercularis vagi leaves the side of the ramus supratemporalis vagi near the origin of the latter from the nervus linae lateralis (Fig. 12) and detaches its first branch (PRPE: Fig. 12), which is a visceromotor nerve innervating the nearby protractalis pectoralis muscle lying dorsal to the fourth gill arch. This motor branch is not considered part of, but only associated with, the rami cutanei dorsales vagi. The temporal branch (r. supr. 2a) of the r. supratemporalis vagi may come off as part of the ramus opercularis vagi (Fig. 5) or as a separate branch from the ramus supratemporalis vagi, detaching before the ramus opercularis vagi. The ramus opercularis vagi passes dorsally above the adductor opercularis muscle, across the tip of this muscle, and down its lateral side to the dorsal edge of the opercle, where it penetrates the opercle a little posterior to the hyomandibulo-opercular articulation at about the level of the horizontal thickening of the bone right at the line of insertion of the adductor operculi muscle. Here it divides into three branches, r. op. 1–3 (Fig. 12). Branch r. op. 1 appears to go to the mucosa covering the dorsoposterior side of the posterior wall of the last gill slit. Branch r. op. 2 passes to skin dorsal to the opercle and gives off branch r. op. 2a, which comes close to the terminations of branch TH4AA of the truncus hyomandibularis in the area where a large scale bears a row of free lateralis organs (Fig. 2). These lateralis organs are innervated by TH4AA, not by a branch of r. op. 2a. The rest of r. op. 2a innervates skin on the dorsoposterior lateral side of the opercle (Fig. 11). Branch r. op. 3 innervates most of the medial surface of the opercle down to the subopercle (Fig. 12), where it anastomoses with dorsally coursing branches of TH9C (from the ramus hyoideus) that terminate in the branchiostegal membrane. One dorsal branch of r. op. 3 passes posteriorly and innervates the opercular membrane both dorsal and ventral to the opercular spine. Branch r. op. 3 is the only branch found to extend below the opercle any distance. Where it does extend below the opercle, it enters the branchiostegal membrane and does not appear to course on the subopercle. The innervation to the subopercle is, in part, by several fine branches coming down from a branch of the ramus opercularis vagi that extends horizontally along the line of contact between the opercle and subopercle (Fig. 12) and, in part, by fine branches from the ramus hyoideus coming onto it at the anterior end of the gill cover (Fig. 2).

Ramus supratemporalis vagi

The ramus supratemporalis vagi (Fig. 5) consists mainly of lateralis fibers from the root of the nervus linae lateralis and, to a small extent, of general cutaneous fibers. Most of the cutaneous fibers are apparently carried in branch r. supr. 2a (described below) and also in branch r. supr. 1b (Fig. 5). Communis rami detaching from the r. supratemporalis vagi and from the anteriormost branches of the nervus linae lateralis were observed by Herrick (1899: fig. 3; a. r. VII.1, 2, and 3) to join the ramus lateralis accessorius (RLA) extracranially on the top of the head and nape. No such communis rami were identifiable in *Polycentrus*. The components for the r. supratemporalis vagi in *Polycentrus* are apparently only lateralis and general cutaneous (see also under section on rami cutanei dorsales vagi). Herrick may be wrong in his interpretation of the three rami in *Menidia*.

As the r. supratemporalis vagi and nervus linae lateralis move away from each another, a ganglion forms in the ventral part of the r. supratemporalis vagi, and the ramus shortly divides into two main branches: branch r. supr. 1, carrying mainly lateralis fibers innervating lateralis organs in the posttemporal and supratemporal canals, and free lateralis organs in a vertical row of scales above the supratemporal canal, but carrying also some cutaneous fibers for skin dorsal to these canals (Fig. 5); and branch r. supr. 2, carrying lateralis fibers to free lateralis organs in a vertical row anterior to the supratemporal canal (STL; Fig. 17) as well as some cutaneous fibers to skin of the temporal region (Fig. 5).

Branch r. supr. 1, after separating from r. supr. 2, passes straight laterally across the base of the cranium and swings dorsally medial to the cranio-pectoral-girdle muscle, the levator pectoralis, and continues dorsally medial to the supratemporal canal, where it detaches branch r. supr. 1a, which innervates the lateralis organ in the posttemporal canal. From branch r. supr. 1a, a branch passes ventrally (shown extending horizontally in Fig. 7) below the posttemporal canal, where it shortly breaks up in thick skin in front of the dorsal end of the supracleithrum. Also detached medially of the supratemporal canal is r. supr. 1b. It innervates skin located between the anterior, epiotic arm of the posttemporal bone and the posterior end of the supratemporal. The rest of r. supr. 1 detaches r. supr. 1c and r. supr. 1d, each of which innervates a lateralis canal organ in the supratemporal canal. Branch r. supr. 1 then continues in a dorsoanterior curve towards the middorsal line, innervating three scales, each of which bears a row of free lateralis organs that together form a continuous, almost vertical line of organs (Fig. 17).

Branch r. supr. 2a (Fig. 5) is apparently a general cutaneous branch and belongs to the system of branches that Herrick (1899) calls the rami cutanei dorsales vagi. R. supr. 2a passes dorsally medial to the posterior end of the pterotic canal and medial to the anteroventral end of the supratemporal canal where it turns anteriorly, coursing under and innervating skin on the side of the head dorsal to the pterotic in the temporal area of the head. The remainder of r. supr. 2 continues dorsally and detaches another branch that courses towards the temporal area but passes lateral to the levator pectoralis muscle that extends from the posterolateral corner of the cranium back to the proximal end of the opisthotic arm of the posttemporal bone. Branch r. supr. 2 curves dorsoposteriorly and innervates the long vertical row (Fig. 17, STL) of free lateralis organs lying across three consecutive scales anterior to the supratemporal canal. En route r. supr. 2 crosses the orbito-pectoral branch of the ramus lateralis accessorius and runs a short distance anteriorly along RLA-OP.

First vagal branchial trunk

The first vagal branchial trunk, V1, for the second gill arch detaches itself from the pharyngo-intestinal trunk of the vagus (Fig. 19; see symbols for each branchial trunk) shortly after the latter leaves the cranium at the anterior end of the head kidney. It continues anteriorly and then anterolaterally and ventrally, passing medial to the internal and external levator branchial muscles. Medial to these muscles the first vagal branchial trunk detaches V1A (Fig. 19), which innervates the levator externus II muscle (LE2; Fig. 18). Before the detachment of V1A, a ganglion forms on the first branchial trunk. A short distance further, it detaches a second branch (not shown in Fig. 19) to the levator externus II muscle. Before passing around the second levator internus branchial muscle, the first vagal branchial trunk (V1) divides into pretrematic (V1PR) and posttrematic (V1PO) rami. The pretrematic ramus (V1PR) to the first gill arch shortly detaches a pharyngeal ramus, V1P, which passes ventrally directly posterior to the cartilaginous medial process of the first epibranchial bone and continues medially, reaching the mucous epithelium anterior to the second infrapharyngobranchial bone. Continuing anteroventrally from near the base of the pharyngeal ramus (V1P) is branch V1E, here referred to as a gill raker ramus. Branch V1E passes onto the ventral surface of the first epibranchial where it turns posteroventrally between the two rows of gill rakers. Branch V1E meets a second gill raker branch from the first vagal pretrematic ramus at the junction of the first epibranchial and ceratobranchial bones. The reenforced gill raker ramus continues ventrally between the two rows of gill rakers.

The remainder, and larger part, of the first pretrematic vagal branchial ramus (V1PR), passes onto the posteromedial side of the first epibranchial bone at the upper end of the medial row of gill filaments and continues ventrally underneath the filaments, following them onto the ceratobranchial. The first pretrematic ramus detaches the second gill raker branch (described above) at the junction of the epibranchial and ceratobranchial bones of the first gill arch. This ramus passes around the ceratobranchial to its anterior surface and continues in the mucous epithelium between the lateral and medial rows of gill rakers, innervating them and the epithelium to its junction with a similar gill raker branch from the posttrematic ninth nerve (GLR; Fig. 19). The latter branch continues ventrally to the end of the gill raker rows on the first hypobranchial bone. The remainder of the first vagal branchial pretrematic ramus continues under the medial row of gill filaments to its termination on the first hypobranchial.

The posttrematic ramus (V1PO) continues onto the second gill arch, passing onto the posterolateral surface of the second epibranchial bone and underneath the lateral row of gill filaments, and then onto the second ceratobranchial bone where it continues underneath the posterolateral row of gill filaments to the end of the second ceratobranchial. At the junction of the second epi- and ceratobranchials, the posttrematic branch (V1PO) detaches a gill raker branch which passes around to the anterior surface of the second ceratobranchial, down which it continues between the two rows of gill rakers to the end of the second ceratobranchial. The last important branch of the posttrematic ramus is branch V1C, which innervates the obliquus ventralis II (OV2) branchial muscle (Fig. 18). The posttrematic ramus (V1PO) ends after passing between the second cerato- and hypobranchials where it innervates mucous epithelium at the base of the gill arch.

Second vagal branchial trunk

After giving off the first vagal branchial trunk, the rest of the vagus, consisting of the remaining branchial trunks and the ramus intestinalis, passes ventrally and gives off the second vagal branchial trunk which innervates the third gill arch. This trunk passes laterally a short distance and forms the second vagal branchial ganglion. From this ganglion (Fig. 19), the pretrematic and posttrematic rami (V2PR and V2PO) arise and parallel each other for some distance anteriorly. En route to the second gill arch, the second vagal pretrematic ramus (V2PR) detaches the pharyngeal ramus, V2P, which passes medially between the second and third pharyngeal bones, innervating the mucous epithelium and teeth. The rest of the pharyngeal ramus (now labeled V2E) continues as the upper gill raker ramus for the second gill arch onto the anterior surface of the second epibranchial and ventrally down it between the two rows of gill rakers. It then joins the gill raker branch (V1B) from the posttrematic of the first vagal ramus and continues onto the anterior surface of the second ceratobranchial, innervating the two rows of gill rakers and the intervening mucosa. The rest of the second pretrematic ramus (V2PR) passes onto the posteromedial surface of the second epibranchial underneath the medial row of gill filaments, innervating them to the end of the second ceratobranchial.

Just beyond the second smaller ganglion of the second vagal pretrematic ramus, there are two short connections between the two main rami of the second vagal branchial ramus. At the first of these two connections, branch V2A leaves the posttrematic second vagal branchial ramus (V2PO), passes laterally and innervates the levator posterior branchial muscle (LEP). Closely thereafter a larger branch, V2B, detaches from the posttrematic and passes anterolaterally and innervates the large levator externus IV

(LE4) branchial muscle. At the site of the two cross connections, or independently of them and from the second pretrematic branchial ramus, branch V2C detaches and passes anteriorly between the pretrematic and posttrematic second vagal rami. It continues parallel to the latter and above the obliquus dorsalis III muscle (OBD3), detaches a branch (not labeled on Fig. 19) that innervates this muscle and another branch, V2D, that passes anteriorly and innervates the transversus dorsalis II (TD2) branchial muscle.

The second posttrematic vagal ramus (V2PO) continues anteroventrally medial to the large levator externus IV branchial muscle (LE4) and dorsal to the obliquus dorsalis III muscle (OBD3). Then it passes onto the dorsal surface of the third epibranchial and underneath the dorsal end of the lateroposterior row of gill filaments of the third arch and continues underneath the row of filaments to its end at the base of the third ceratobranchial bone. A gill raker branch (V2F) is detached at the joint between the second epi- and ceratobranchials and passes around the arch to its anterior surface where it meets a more dorsal gill raker branch (V3E) from the pretrematic ramus of the fourth vagal branchial trunk. Branch V2F passes ventrally between the two rows of gill rakers, innervating them and intervening mucous epithelium to the end of the third ceratobranchial.

The remainder of the posttrematic ramus (V2PO) of the second vagal branchial trunk, after giving off branch V2F, continues down the third ceratobranchial at its lateroposterior side beneath the bases of the lateral gill filaments to the end of the row. At the base of the third ceratobranchial, the remainder of the posttrematic ramus gives off branches innervating four ventral branchial muscles and then ends in mucous epithelium overlying the hypobranchial and basibranchials of the third arch. The four branches are branch V2J to the third obliquus ventralis muscle (OV3); branch V2H to the rectus ventralis IV (RV4) muscle; a large branch, V2G, to the rectus communis (RCOM) muscle; and a branch (not shown in Fig. 19) to the rectus ventralis V (RV5) muscle.

Third vagal branchial trunk

The third vagal branchial trunk for the fourth gill arch separates proximally from the second vagal branchial trunk, forms a ganglion, passes ventrally a short distance, and detaches branch V3A which drops ventroposteriorly and innervates the retractor dorsalis (RETD) muscle, entering this long muscle anteriorly near its attachment to the third infrapharyngobranchial bone. Next, the third vagal branchial trunk divides into the pretrematic (V3PR) and posttrematic (V3PO) rami, which continue close together anteroventrally towards the fourth epibranchial. The pretrematic ramus (V3PR) passes medial to the levator externus IV muscle (LE4), crosses the dorsal surface of the fourth and third epibranchials, and detaches the pharyngeal ramus, V3P. The pharyngeal ramus passes between the two epibranchials and gives off a medial branch which passes beneath the mucosa towards the third pharyngeal bone, and a lateral branch, V3E, which passes onto the anterior surface on the third epibranchial and then down it between the two rows of gill rakers. The remainder of V3E joins branch V2F at the top of the third ceratobranchial. The pretrematic ramus (V3PR) then continues ventrally down the third epibranchial and ceratobranchial to the end of the latter underneath the medial row of gill filaments.

The posttrematic ramus of the third vagal branchial ramus (V3PO), after departing from the pretrematic ramus, passes ventroanteriorly and gives off a gill raker branch V3B which courses over the proximal end of the fourth ceratobranchial and onto its anterior surface between the two rows of gill rakers for the anterior third of this bone. The rest of the posttrematic passes the joint between the fourth epi- and ceratobranchials, medial to the levator posterior (LEP) muscle. It then crosses the dorsolateral surface of the obliquus posterior muscle (OP) and at the top of the fourth arch detaches branch 3BC which innervates the adductor IV (AA4) branchial muscle. The postrematic then courses down the fourth ceratobranchial underneath the lateral row of gill filaments, near the end of this bone detaching branch 3BD which passes medially and innervates the transversus ventralis IV (TV4) muscle. The end of the posttrematic branch innervates the floor of the pharyngeal cavity at the base of the fourth gill arch. En route down the fourth ceratobranchial, the posttrematic detaches about six short gill raker branches, each of which innervates a series of gill rakers and adjacent mucous epithelium on the anterior surface.

Fourth vagal branchial trunk

After departure of the first three vagal branchial rami, the vagus consists of the intestinal and cardiac rami and the fourth vagal branchial trunk. Only the first three esophageal rami which detach segmentally are illustrated. The intestinal and cardiac rami were not further studied. The ganglion for the fourth vagal branchial trunk forms on the dorsolateral surface of the third ganglion. Near the anterior end of the esophagus, the fourth vagal trunk separates into pretrematic and posttrematic rami, V4PR and V4PO, respectively. The pretrematic (V4PR) ramus passes anteroventrally towards the pharynx where, at the junction of the fourth ceratobranchial and fourth epibranchial, it detaches a small branch (not labeled on Fig. 19) which passes medially under the fourth epibranchial bone, innervating the dorsal extension of the medial row of gill filaments. The rest of the fourth pretrematic ramus continues ventrally about halfway down the fourth ceratobranchial beneath the medial row of gill rakers. Although the gill slit behind the fourth arch is reduced to about half size, the medial row of filaments extends some distance further, but the innervation to it was not detected.

The fourth vagal posttrematic ramus (V4PO) drops ventrally towards the dorsal end of the fifth ceratobranchial bone, passing along the posterior surface of the obliquus posterior muscle (OP), detaching a branch to this muscle (the upper branch of V4B), and another (the lower branch of V4B) to the adductor V (AA5) muscle. Just past the dorsal head of the fifth ceratobranchial, the fourth posttrematic vagal ramus detaches branch V4E, which in turn divides, one part innervating the pharyngoclavicularis internus (PCI) and the other the pharyngoclavicularis externus muscles (PCE). Branch V4D detaches at the same point as V4E and divides; one branch innervates the transversus ventralis IV muscle (TV4) and another branch (not shown) innervates the floor of the pharynx directly posterior to the fifth ceratobranchial. The remainder (V4C) of the fourth posttrematic ramus innervates the teeth and mucous epithelium of the fifth ceratobranchial.

Summary of Gill-Arch Muscle Innervation

Glossopharyngeal nerve innervates:
(1) Levator internus II (LI2) by branch G1
(2) Levator externus I (LE1) by branch G3
(3) Rectus ventralis I (RV1) by branch G8

First vagal branchial ramus innervates:
(1) Levator internus III (LI3) by branch V1A
(2) Obliquus ventralis II (OV2) by branch V1C

Second vagal branchial trunk innervates:
(1) Levator posterior (LEP) by branch V2A
(2) Levator externus IV (LE4) by branch V2B
(3) Obliquus dorsalis III (OBD3) by branch V2C
(4) Transversus dorsalis II (TD2) by branch V2D
(5) Obliquus ventralis III (OV3) by branch V2J
(6) Rectus communis (RCOM) by branch V2G
(7) Rectus ventralis V (nerve supply not shown on Figure 19)
(8) Rectus ventralis IV (RV4) by branch V2H

Third vagal branchial trunk innervates:
(1) Retractor dorsalis (RETD) by branch V3A
(2) Adductor IV (AA4) by branch 3BC
(3) Transversus ventralis IV (TV4) by branch 3BD

Fourth vagal branchial trunk innervates:
(1) Obliquus posterior (OP) by upper branch of V4B
(2) Adductor V (AA5) by lower branch of V4B
(3) Pharyngoclavicularis internus (PCI) by branch V4E
(4) Pharyngoclavicularis externus (PCE) by branch V4E
(5) Transversus ventralis V (TV5) by branch V4D

Ramus opercularis vagi innervates:
(1) Protractalis pectoralis (PRP) by branch PRPE

Lateral Line Nerves of the Trunk

Herrick (1899) did not consider the nervus lineae lateralis to be part of the vagal nerve. He treated it as a separate entity morphologically, since it has a different origin in the medulla oblongata and is physically separate from the vagus nerve, although it has a connection with the vagus by general cutaneous fiber bundles. Some of the latter join the ramus supratemporalis vagi from the vagus. The origin of the lateral line nerve is from the acoustico-lateralis center in the medulla near that of the auditory nerve (Herrick 1899).

The terminology for the trunk lateral line nerves follows Freihofer (1972).

The lateral line of the trunk of most fishes is usually a linear series of scales along the side of the body, each scale having a bony tube or canal opening laterally by a pore onto the surface. A relatively large lateral line canal organ lies about midway inside the tube of each scale. In *Polycentrus* there is only one tubed lateral line scale. It is the first scale after the posttemporal canal. Although there is virtually no scaled or membranous lateral line canal on the trunk in *Polycentrus*, the lateral line nerve on the trunk is well developed. The branches of the lateral line nerve innervate short vertical rows of small, free lateralis organs located on certain scales, the lateralis scales forming longitudinal rows as depicted in Figure 21.

Nervus Linae Lateralis

The nervus linae lateralis (NLL) arises from the brain about halfway down the side of the medulla oblongata and a little anterior to the root of the nervus glossopharyngeus (Figs. 28 and 30). NLL courses posteriorly, almost horizontally, close to the medulla.

As NLL continues posteriorly, it comes to lie lateral to the emerging root of the nervus vagus at the midside of the medulla. The two roots proceed separately lateroposteriorly to their common foramen in the exoccipital bone at the top of the bulge of the wall of the otic bulla, the nervus linae lateralis lying dorsal and lateral to the nervus vagus (Fig. 4). A few ganglion cells form on the dorsal surface of NLL before it passes out through its foramen. More ganglion cells form outside the cranium in the recess between the otic wall of the bulla and the lateral horizontal wall of the exoccipital. Then ganglion cells form a large swelling which continues for some distance as NLL passes posterolaterally through the head kidney. Shortly before leaving the head kidney, the sizeable ramus supratemporalis vagi is detached (Fig. 5), passing dorsally and a little posteriorly towards the medial side of the supratemporal canal. This ramus is described in a preceding section.

Immediately anterior and medial to the supracleithrum, the nervus linae lateralis splits into two large rami, NLL1 and NLL2 (Fig. 21). Ramus NLL2, the dorsal longitudinal "collector" lateral line nerve, passes dorsoposteriorly medial to the shoulder girdle and detaches two branches en route. The larger of these, NLL2a, then gives off a relatively short branch which can be designated the dorsal fin branch. It innervates the vertical row of free lateralis organs on a scale pocket dorsal to the posterior opening of the posttemporal canal (Figs. 17 and 21). The rest of NLL2a curves anterodorsally and then posteriorly, coursing to the anterior end of the dorsal fin where it innervates free lateralis organs on two scale pockets anterior to this fin (Fig. 21). The other branch, NLL2b, innervates the scale pocket directly posterior to the posttemporal canal, which is the only lateral line scale on *Polycentrus*.

The main part of NLL2, the dorsal longitudinal collector lateral line nerve, arches dorsoposteriorly beneath the skin to nearly halfway to the dorsal fin, where it levels off and continues posteriorly gradually dropping ventrally towards NLL1 which it finally overlies at the posterior end of the soft anal fin. En route, NLL2 detaches ten long ramuli which innervate free lateralis organs on ten individual scale pockets along the base of the spinous dorsal fin, and two long ramuli which similarly innervate free lateralis organs on two scale pockets near the base of the soft dorsal fin (Fig. 21). En route it also gives off thirteen shorter ramuli, including NLL2b, twelve of which innervate free lateralis organs on twelve scale pockets that lie horizontally along a line one-third to one-fourth of the way towards the dorsal fin. Ten of these branches occur on the anterior half of the body. The thirteenth ramulus innervates free lateralis organs on a scale pocket a little below NLL2, not far from the caudal peduncle. The main trunk of NLL2 terminates by splitting into two ramuli which supply free lateralis organs on two successive scale pockets anterior to the caudal fin. The branches NLL1 and NLL2 do not rejoin posteriorly.

The other ramus, NLL1, the horizontal septum lateral line nerve of the nervus linae lateralis, continues straight to the caudal fin. En route it detaches three commissural or collector branches, NLL1a, NLL1b, and NLL1c, which join and form the dorsal longitudinal collector lateral line nerve, NLL2. Branch NLL1b detaches a long ramulus which passes dorsally to innervate free lateralis organs on a scale pocket lying directly ventral to the sixth spine of the dorsal fin. The commissural branch NLL1c detaches a ramulus that passes ventrally towards the anterior anal spines where it splits into three branches, each innervating free lateralis organs on a scale pocket directly dorsal to the anal spines. The main trunk, NLL1, next gives off two more ramuli, each innervating a scale pocket and its free organs near the bases of anal spines. The penultimate ventral ramulus divides near the anal fin and innervates the free lateralis organs on three more scale pockets along the base of the fin. Lastly, a ramulus is detached which in turn divides into three more branches which supply free lateralis organs on three scale pockets along the base of the soft anal fin.

The remainder of NLL1 courses posteriorly and bifurcates near the base of the caudal fin. The dorsal fork runs along the bases of the rays of the dorsal half of the fin and detaches a large ramulus which continues in the membrane between the fifth and sixth caudal rays, innervating a long row of about 24 free lateralis organs. The rest of the dorsal fork passes to the skin of the dorsal surface of the caudal peduncle where it innervates, in succession, free lateralis organs on four small scale pockets, one of these branches innervating a scale pocket at the base of the fourth caudal ray. The ventral fork continues in the membrane between the eleventh and twelfth caudal rays, innervating a long line of about 24 free lateralis organs.

DISCUSSION

Free Cephalic Lateralis Organs

Free cephalic lateralis organs (pitorgans) or their derivatives are found in all the classes of jawed fishes. The pitorgans are often rather closely associated with the cephalic lateralis canals. The organs may occur in clusters or lines or in both arrangements on the same fish. In *Polycentrus* they are in clusters at the anterior end of the head and increasingly arranged in lines more posteriorly.

Although considerable information exists on pitlines (see Disler 1971; Stensiö 1947), there is not much information on these organs for perciform fishes. Stensiö (1947) broadly homologizes six pitlines of the cheek and lower jaw in all classes of gnathostome fishes and of amphibians. The purpose here is merely to compare the pitlines of *Polycentrus* with those of some other percoids, with *Menidia*, and with a few lower groups to obtain an idea of the degree of pitline specialization in *Polycentrus*. Simple locational names for various pitlines are used for convenience.

Comparison with Perca fluviatilus

Perca (Disler 1971: fig. 56) has four organs medial to the anterior end of the nasal canal and a longitudinal row of seven or eight organs ventral to the anterior and posterior narial openings. There are three organs in the location of the anterior pitline of *Amia* (Allis 1889: pl. 42, fig. 49) and six organs in the location of the supratemporal row (the posterior pitline of *Amia*). Lastly, *Perca* has a vertical row of about six organs and an opercular row of about eight organs. These pitlines in *Perca* correspond to pitlines in *Polycentrus* having similar location and innervation. *Polycentrus* has more organs at these locations. The main differences between *Perca* and *Polycentrus* are that *Polycentrus* has, in addition to the above lines, well-developed supraorbital, infraorbital, and mandibular pitlines. *Perca* lacks these lines and presumably every organ of each line. *Perca* is a more generalized percoid in its swimming and feeding habits than is *Polycentrus*. These extra cephalic pitlines in *Polycentrus*, together with the development of pitlines on the trunk of the body and the lack of lateral line scales, suggest that the additional pitlines in *Polycentrus* are specializations.

There are indications that the ancestors of percoids may have had a fuller development of the pitline system than do recent species. Numerous beryciforms such as melamphaeids, trachichthyoids, and stephanoberycoids have many free cephalic lateralis organs. Percopsiforms have the system very well developed. So do myctophoids and various other protacanthopterygians, not to mention ostariophysans. Pitlines are well developed in the percoid family Apogonidae, where its elaboration is apparently a specialization rather than a retained ancestral condition. Inspection of nandid genera for pitlines shows that *Nandus* has the system least developed, and the others (*Afronandus*, *Monocirrhus*, and *Polycentropsis*) have it well developed. The lines in nandids have lengthened, but whether a line can be completely lost (not a single free organ present where the line should be) and be redeveloped is uncertain. Both *Polycentrus* and *Apogon* may be examples in which at least some lines redeveloped after having been lost. One would think that as long as the facial and vagal lateralis roots are present, any particular pitline could be completely lost and later reformed. Detailed comparative studies of pitorgans are needed and should prove most interesting.

Comparison with Menidia

Herrick describes for *Menidia* some twigs of a branch (SO. 14; Herrick 1899:pl. 2, fig. 3) of the r. ophthalmicus superficialis facialis that supply free lateralis organs (g, h, and i) lying between the dorsal margin of the anterior narial opening and the anterior end of the nasal canal. These organs correspond to a cluster of organs in the same location in *Polycentrus*, but the innervation is different in *Polycentrus*, being from the r. buccalis facialis of the infraorbital trunk.

If Herrick is correct, *Menidia* stands alone among teleosts, as far as I can determine, in its innervation of these snout organs. Examination of Sihler preparations of representatives of 85 families did not show any species with free lateralis organs in this area innervated from the supraorbital trunk. Herrick found other pit organs on the snout of *Menidia* to be innervated from the infraorbital trunk. These include three organs (a, b, and c; Herrick 1899:pl. 2, fig. 3) lying between the anterior and posterior nostrils and three more organs on top of the anterior end of the snout medial to the anterior nostril, one organ lying quite far medially. These pitorgans correspond in position and innervation to similar clusters of pitorgans in *Polycentrus*.

In *Menidia* there are pitorgans lying below the orbit in the area of the missing part of the infraorbital canal that are innervated by the r. buccalis facialis. They presumably represent the modified canal neuromasts from the missing canal segment. In *Polycentrus* there is an infraorbital row containing many more pitorgans than in *Menidia* which are innervated by the r. buccalis, but in *Polycentrus* the canal and canal bones are still present, although there is only one canal neuromast in the fused second, third, and fourth infraorbital bones. The interesting question is, Do these pitorgans along the edge of these infraorbitals represent modified canal neuromasts or do they represent a proliferation of pitorgans that were never canal neuromasts but which formed or proliferated as the canal neuromasts disappeared? The implication by other authors seems to be that they presumably are modified canal neuromasts.

Menidia also has one pitorgan at the dorsoanterior corner of the opercle and four at the ventroanterior corner, much as in *Polycentrus* (Fig. 2, branches TH4AA for the opercle, and TH9B02 for the subopercle; and Fig. 15), innervated by branches of the r. opercularis facialis. *Menidia* apparently has a reduced cheek pitline (either the vertical or horizontal cheek line of *Amia*; see Allis 1889: fig. 42) innervated by branch M.VII 1 (Herrick 1899: fig. 3) supplying only one pitorgan, which is all Herrick found. The same branch, M.VII 1 of the r. mandibularis externus facialis, also innervates four organs over the horizontal arm of the preopercular canal and another organ at the base of the third pore of the preopercular canal. These four organs plus one organ more anteriorly correspond to the mandibular pitline of *Amia* (Allis 1889: fig. 42) and to a similar line of organs in *Polycentrus* (Fig. 17).

Herrick shows no pitorgans associated with the supratemporal canal in *Menidia*, whereas *Polycentrus* has a lower line (STL; Fig. 17) and a higher line (two scales above the supratemporal canal, each bearing a row of pitorgans) innervated by the r. supratemporalis vagi.

Comparison with cyprinids

Pitlines are well developed in *Phoxinus* (Manigk 1934: fig. 1). A number of lines correspond in position and innervation to those in *Polycentrus*. A seemingly important difference in *Phoxinus* that is not found in *Polycentrus* and not noted in other fishes is the presence of lateralis fibers in the r. mandibularis trigeminus. These fibers supply pitorgans located in *Phoxinus* at the anteroventral corner of the cheek above the mandibular canal. In other fishes, organs in this location would be innervated by the r. buccalis accessorius. These pitorgans in *Phoxinus* could not be homologous with part of the postmaxillary or supramaxillary lines of Stensiö (1947). Another unusual innervation occurs in *Phoxinus* for pitorgans lying just in front of the vertical arm of the preopercle and along its horizontal arm (Manigk 1934: fig. 1). These pitorgans in *Phoxinus* are supplied by branches of the r. hyoideus. The same pitorgans and innervation occurs in *Parasilurus* (Atoda 1936). In *Polycentrus* the preopercular pitline is supplied by branches of the r. mandibularis externus facialis. It would seem most probable that the pitorgans in this location in *Phoxinus* are an independent development. They would not appear to be homologous with any of the six pitlines of Stensiö. Another difference in *Phoxinus* is that pitorgans on the uppermost cheek region ventral to the pterotic canal are supplied by the ramus oticus. *Polycentrus* lacks these pitorgans.

Comparison with esocoids

Esocids and umbrids have numerous cephalic pitlines (Nelson 1972), some of which lie in gaps in the cephalic canal system. Three of the pitlines of *Polycentrus* are compared with pitlines in corresponding places in esocoids. The lines are the subnasal, infraorbital, and supraorbital. In *Polycentrus* the infraorbital and subnasal pitlines (Fig. 17) are innervated by branches of the r. buccalis facialis of the infraorbital trunk (Fig. 1, branches 3b, 3c, IO2fg, and a vertical branch of IO1d2 that goes to pitorgans below the posterior nostril) and by one branch (TH10A; Fig. 2) from the r. buccalis accessorius, which supplies pitorgans at the posterior end of the infraorbital pitline. Nerve fibers of the r. buccalis facialis come from the dorsal lateralis root of the facial nerve (Fig. 31) and course in the infraorbital trunk. The innervation for these three pitlines in umbrids and esocids is quite different from that in *Polycentrus*. Sihler nerve preparations of *Esox vermiculatus* and *Umbra pygmaea* show that these pitlines are all innervated by a branch of the r. buccalis accessorius facialis which detaches from the truncus hyomandibularis high up on the side of the cheek. The lateralis fibers constituting the r. bucc. acc. fac. belong to the ventral lateralis root of the facialis. Another pitline, the supraorbital, is innervated in *Polycentrus* by the r. ophthalmicus superficialis facialis, the fibers of which belong to the dorsal lateralis root of the facial nerve, whereas in esocids and umbrids these pitorgans are innervated by fibers derived from the ventral lateralis root of the facial nerve. They course in the supraorbital branch of the r. bucc. acc. fac. These three cephalic pitlines of esocoids, therefore, are not homologous with pitlines in corresponding positions in *Polycentrus* or with corresponding pitlines in numerous acanthopterygians.

Nelson (1972: 16) states that for esocoids in which a segment of a cephalic canal has been eliminated, the canal neuromasts may be modified into superficial pitorgans. As far as I have been able to determine, branches of the r. bucc. acc. fac., which innervate these pitorgans in esocoids, never innervate canal neuromasts. These branches appear to belong to a special pitline system represented in part at least by the ramus canalis lateralis facialis system seen well developed in *Lampanyctus* (Freihofer 1970; Ray 1950) and to which the r. bucc. acc. fac. belongs. It would seem worthwhile to entertain the thought that all pitorgans are innervated by a system of lateralis nerve fibers distinct from that which innervates canal neuromasts. The main difference between the two classes of lateralis fibers, if there are two classes, may be that lateralis fibers innervating canal neuromasts can induce bone formation, whereas lateralis fibers innervating pitorgans cannot. It would make sense to keep the "power" of bone induction in one system of fibers.

The esocoids appear to be an exception to the general statement made by Nelson (1972) that pitlines are not useful in higher category classification. The innervation of pitlines in esocoids may be particularly useful for this purpose.

Comparison with Amia

Polycentrus has several pitlines that have the same location and innervation as in *Amia*. These are the vertical pitline of the cheek (Allis 1889: pl. 42, fig. 49), the supratemporal (extrascapular), the mandibular, and probably the anterior pitline. *Polycentrus* lacks the middle pitline (innervated by the glossopharyngeus nerve in *Amia*), the gular pitline, and the horizontal pitline of *Amia*. Pitlines present in *Polycentrus* that are absent in *Amia* are the supraorbital, infraorbital, chin, narial, opercular, subopercular, and preopercular pitlines. The interesting question is still unanswered of whether or not the narial pitlines of *Polycentrus* and other fishes correspond to modified canal neuromasts that resulted from the loss of ethmoidal and antorbital canals presumably present in the ancestors of teleosts.

Cephalic Lateralis Canals and Neuromasts

The cephalic lateralis canals and their organs for *Polycentrus* are shown in Figures 1, 2, 3, 5, 10, and 17. The number of neuromasts for each cephalic canal-bearing bone is given in Table 1 for *Polycentrus*, several other perciforms, *Menidia*, *Gadus*, and *Amia*.

The head canals of *Polycentrus* are all enclosed in bone. There are four separate infraorbitals including the lachrymal and the dermosphenotic (shown missing in all nandids by Liem 1970: fig. 3). Judging from *Perca*, *Kuhlia* (Table

TABLE 1. THE NUMBER OF CANAL NEUROMASTS IN EACH CEPHALIC CANAL-BEARING BONE.[3,7]

Name of Canal	*Polycentrus*[4]	*Amia*	*Roccus*	*Paralabrax*	*Kuhlia*	*Perca*	*Archoplites*	*Scomber*	*Gadus*	*Menidia*[5]
Nasal	1	3	1	1	1	1	1	3	2	1
Frontal	4	3	4	4	4	4	4	4	3	5
Ethmoidal	–	2	–	–	–	–	–	–	–	–
Antorbital	–	4	–	–	–	–	–	–	–	–
Lachrymal	4	2	4	4	4	4	3	4	5	2
2nd Infra[2]	1	1	1	1	1[6]	1	1	1	1	3
3rd Infra[2]	–	1	1	1	2	1	1	1	1	–
4th Infra[2]	–	1	1	1	–	1	2	1	1	–
5th Infra[2]	1	1	1	1	1	1	1	2	1	–
6th Infra[2]	1[1]	1	1[1]	1[1]	1	1	1[1]	1[1]	1	–
7th Infra[2]	–	1[1]	–	–	1[1]	1[1]	–	–	1[1]	1[1]
Pterotic	2	3	2	2	2	2	2	3	1	1
Supratemporal	2	4	3	3	3	4	3	3	3	3
Posttemporal	1	1	1	1	1	1	1 or 2	1	1	1
Preopercle	7	6	6	6	6	6	6	3	5	5
Articular	1	3	1	1	1	1	1	1	1	1
Dentary	4	7	4	3	4	6	4	4	6	6

[1] This last infraorbital is the dermosphenotic.

[2] Infra = infraorbital

[3] It is assumed that the primitive number of infraorbitals in percoids is seven, counting the lachrymal as the first.

[4] In *Polycentrus* the second, third, and fourth infraorbitals may have fused and also the fifth and sixth.

[5] The primitive number of infraorbitals for atherinids is uncertain. The second infraorbital consists of two bones (*Pranasus* and *Melanotaenia*). There is plenty of space between the second infraorbital and the dermosphenotic for two or three missing bones. Herrick (1899) shows for *M. beryllina* eight large free lateralis organs in place of the missing infraorbitals.

[6] The third and fourth infraorbitals have apparently fused as indicated by the presence of two canal neuromasts in the third infraorbital.

[7] The species examined are *A. calva*, *P. clathratus*, *K. rupestris*, *Perca flavescens*, *Archoplites interruptus*, *S. japonicus*, and *M. beryllina*. Two specimens were examined of *Polycentrus* and *Kuhlia* but only one for each of the other species.

1), and *Lobotes*, the generalized number of infraorbitals for percoids appears to be seven (counting the lachrymal as the first), but judging from *Roccus* and *Paralabrax*, it appears to be six. In Table 1 it is assumed that seven is the primitive number of infraorbitals for percoids. *Polycentrus* is specialized compared with *Roccus*, *Perca*, *Kuhlia*, *Archoplites*, and *Paralabrax* in apparently having infraorbitals 2, 3, and 4 as well as 5 and 6 fused, and in having only one canal organ in each compound bone. In *Nandus* (Liem 1970: fig. 20) the second infraorbital is missing, but the dermosphenotic is present. *Afronandus* (Liem 1970: fig. 18) has only the lachrymal, the other infraorbitals having disappeared. It would be particularly interesting to study the infraorbitals of *Nandus* and the other nandid species for the varying conditions of the canal bones, their neuromasts, and the pitorgans associated with the infraorbitals. Some understanding might be gotten of the presumed evolution of pitorgans from modified canal organs, freed when their canals disappeared. Characteristics of the infraorbitals should be useful in nandid taxonomy.

Polycentrus is also specialized in having one less organ in the supratemporal, one more in the preopercle, and one less in the pterotic than do the above percoids. *Archoplites* appears more specialized than *Roccus* and *Polycentrus* in having one less organ in the lachrymal and one more organ in the fourth infraorbital. *Polycentrus*, therefore, is a little more specialized in the cephalic canals and their neuromasts compared to some generalized serranids and centrarchids.

Polycentrus differs from the five other percoids in the innervation of the two pterotic canal neuromasts. Both of its neuromasts are innervated by the ramus oticus, whereas in *Roccus*, *Kuhlia*, *Paralabrax*, *Archoplites*, and *Perca* the second organ is innervated by the r. supratemporalis vagi. *Polycentrus* appears to be specialized over the other percoids in the pterotic canal organs.

Compared with the head canals of *Scomber* (see Allis 1903) and *Gadus* (see Cole 1898), those in *Polycentrus* are more generalized in several respects. Instead of the single nasal canal organ present in *Polycentrus* and many other percoids and perciforms (in fact in most spiny-rayed fishes), *Scomber* has three and *Gadus* two organs in this canal. Study of the innervation of the nasal canal organs in *Scomber* and *Gadus* is necessary for understanding the significance of these differences in number of nasal organs.

In *Scomber* the anteriormost organ is innervated from the infraorbital trunk (by the r. buccalis facialis), which fact suggests fusion of a prenasal ossicle onto the nasal, a feat which is very rare in teleosts, if not unique. Out of more than 90 families of teleosts examined, the Scombridae is the only one found so far with this evident condition. The other two nasal canal organs are innervated from the supraorbital trunk and are evidently derived from an original single organ. The two rear nasal canal organs in *Rastrelliger kanagurta* are very close together and are innervated by a branch that divides just before reaching the two organs, which suggests the original single organ has divided.

The nasal canal bone of *Gadus* has an even more interesting history than has the nasal bone of *Scomber*. Study of the innervation of the frontal and nasal canal organs in Sihler preparations of *Microgadus* and *Merluccius* (Gadidae), *Physiculus* (Moridae), and *Malacocephalus* (Macrouridae) indicates that the anteriormost frontal canal organ has migrated forwards over the floor of the frontal canal and onto the rear of the floor of the nasal canal, the original nasal canal organ having moved onto the anterior half of the nasal canal. Examination of the nasal and frontal canals in many families of paracanthopterygian and acanthopterygian fishes for the number of canal organs in these bones reveals that there is always one organ in the nasal and four in the frontal in all families examined except in the gadoids, ophidioids, and the beryciform *Stephanoberyx*. Cole's figure of *Gadus* (Cole 1898:pl. 22, fig. 2) shows two nasal and three frontal canal organs located in the posterior half of the frontal, the anterior half of the frontal being empty of organs. The ophidioids that were examined (*Brotula*, *Lepophidium*, *Dicrolene*, and *Chilara*) agree with the gadoids in the number of organs in the nasal and frontal, their innervation, and the lack of organs in the anterior half of the frontal. Zoarcids have one nasal and three frontal canal organs. Though the ophidioids and gadoids share a very unusual and rather surprising specialization of the nasal bone, it is not unique to them. *Stephanoberyx*, as already mentioned, also has it. The nasal bone in the three groups is always spacious and curved rather steeply downward around the anterior end of the olfactory organ. The original nasal canal neuromast is located in the anterior half of the canal about at the ventral bend in the canal. Both nasal canal neuromasts have migrated anteriorly, the original nasal neuromast into the front end of the canal and the posterior neuromast into the rear of the canal. Stimuli for the nasal canal organs apparently come from a ventral direction. Though this condition of the nasal canal is rare, it is the result of processes that could plausibly happen more than once in teleosts. It surely has occurred independently in *Stephanoberyx*. Whether it has or not in the gadoids and ophidioids remains to be seen.

Compared with other spiny-rayed fishes examined, the nasal canal and its bone in *Polycentrus* is in a generalized state, having only one canal neuromast and almost no membranous extension anteriorly. The nasal canal of some percoids has an anterior membranous extension of greater or lesser extent, and sometimes there is a canal neuromast in it. In the latter instance, the membranous walls are thickened (formed of secondary cartilage from the dermis) and may have the shape of a small infraorbital canal bone. Examples are found in some lutjanids and pomadasyids. There may be one prenasal bone with a canal neuromast, as in the Toxotidae, or there may be two separate prenasals, one membranous and one bony (Carangidae), or both bony and separate (Coryphaenidae), or both bony and fused but separate from the nasal (Rachycentridae and Echeneidae). These percoids with two prenasals (no other percoids having two have been found) appear to share the same specialization and very likely form a natural, related group. *Nematistius* also was found to have a small, partially ossified prenasal canal unit with a neuromast. The Sciaenidae and Polynemidae have a complex prenasal membranous canal development containing neuromasts. All of the additional prenasal canal units, whether membranous or ossified, are innervated from the infraorbital trunk.

The nasal canal of berycoids, compared with that of *Polycentrus*, other percoids, and, in fact, with that seen in all other Sihler-prepared specimens and in all published accounts, is strikingly different and specialized. The character consists of two (or one) secondary canal neuromasts in addition to the single original (primary) neuromast. The secondary neuromasts lie very close to the anterior edge of the floor of the nasal canal, one organ near each lateral corner of the canal, and are innervated from the infraorbital trunk. The original nasal canal neuromast lies near the midlength of the canal and is innervated from the supraorbital trunk.

The berycoids all have this character (at least one species of each family examined), but the stephanoberycoids, including melamphaeids and gibberichthyids, do not. Polymixiids have what appears to be an earlier development of the berycoid condition. In *Polymixia* there are three free lateralis organs in a membranous canal that passes across but just outside of the entrance to the nasal canal. This membranous canal is connected across the tip of the snout with a similar canal on the other side of the head. Another lateralis organ lies at the midpoint of the crossing canal. The stephanoberycoids have what appears to be a still more generalized condition in that there is a row of free lateralis organs in the skin across the tip of the snout in place of the membranous canal of *Polymixia* and a somewhat enlarged free lateralis organ in the skin just outside each lateral corner of the opening in the nasal canal in place of the canal organ inside the nasal canal near each corner in berycoids.

The mode of formation of the secondary nasal canal organs of berycoids is what makes this nasal canal specialization especially different from that in other fishes. In berycoids free lateralis organs close to the nasal canal opening have apparently been simply engulfed by the bony nasal canal without first being formed in a prenasal ossicle. In carangids, rachycentrids, echeneids, coryphaenids, and other groups, the prenasal ossicle or ossicles do not fuse onto the nasal bone. In *Scomber* a prenasal ossicle undoubtedly has fused onto the nasal bone. In berycoids there are no indications of such fusion; the one or two added canal neuromasts lie very close to the anterior edge of the nasal bone, there is no pore marking a fusion, and there is no bend or irregularity indicating a junction of two bones.

It appears that in the berycoids we have an example, surely very rare, of two free transverse organs (reduced to one organ in some berycoids) being, in effect, "captured" (engulfed) by a nasal canal bone! The berycoid nasal canal bone specialization would seemingly remove the berycoids from being considered the ancestral source of percoids. The same statement may hold for the stephanoberycoids which have what appears to be an earlier stage of the polymixiid condition. This character state in beryciforms will be presented in a separate paper.

It may be added that beryciforms have other specializations of the cephalic lateralis system. In stephanoberycoids the supratemporal canal is actually in communication with the nasal canal and the frontal canal via a large lateralis chamber lying in the interorbital area over the frontals. In melamphaeids the lachrymal canal is in communication with the nasal canal. These developments are rare or unique in teleosts.

In summary, two generalizations might be made about the innervation of the snout region for teleosts from conditions observed in *Polycentrus* and Sihler nerve preparations of representatives of 85 families. The lateralis innervation of the supraorbital trunk ends with the nasal canal bone. Any pitorgan development on the snout will be innervated from the infraorbital trunk. Any new canal and canal neuromasts beyond the anterior end of the nasal canal will also be innervated from the infraorbital trunk. A similar generalization applies to the general cutaneous innervation of the supraorbital trunk. In most of the fishes observed, it ended about at the anterior end of the nasal bone or a little beyond it. Only in the atherinomorphs and holocentrids did it extend significantly further, going to the upper jaw as a large nerve.

Innervation of the Upper Jaw

In *Polycentrus* the upper jaw is supplied with general cutaneous innervation by the inferior ramulus of the ramus maxillaris trigeminus (IO3; Fig. 1) and with gustatory innervation by the anterior ramus of the palatine nerve (Fig. 1). No other nerves go to the upper jaw, not even from the supraorbital trunk, which itself is something of a surprise if the upper jaw is considered a part of the snout. *Polycentrus* is representative of most teleosts in innervation of the upper jaw. One exception is *Menidia* (Herrick 1899; fig. 3, the yellow branch to the upper jaw). In *Menidia* the supraorbital trunk is continued out to the tip of the upper jaw, supplying it rather heavily with general cutaneous innervation. The nerve is large, as seen on Sihler nerve preparations of various atherinomorphs. Of 85 families, only the seven atherinomorph families examined and the Holocentridae had the premaxillary extension of the supraorbital trunk. In the Holocentridae the functional component is, presumably, also general cutaneous.

Cheek Muscle Innervation

The pattern of innervation of the cheek muscle in *Polycentrus* (Fig. 6) reflects the partial subdivision of the adductor mandibulae into three parts called A_1, A_2, and A_3 (Fig. 22), branches IO2c and IO2d innervating A_1, branch IO2e innervating A_2, and the hatched parts of IO2 innervating A_3. The pattern in *Polycentrus* is generalized for percoids. In fact, most of the other percoids examined had more distinctive patterns of innervation of the cheek muscle than does *Polycentrus*, each being a little different from the others. The sciaenids were especially distinct, the $A_1\beta$ muscle in some species being developed as fully as the $A_1\beta$ in percopsiforms, including its pattern of innervation. Atherinomorphs (7 families examined) have an innervation pattern distinct from that of all other families studied except gasterosteids in which it is the same. Much can be learned of systematic interest from the cheek muscles by study of the pattern of innervation within the muscle. Results of a study of the $A_1\beta$ muscle are being prepared for a separate paper.

Correct Name for Ramus Lateralis Accessorius

Herrick (1899: fig. 3) describes three ramuli from the r. lateralis vagi which join the r. recurrens facialis to form the r. lateralis accessorius facialis (RLA). These ramuli join RLA on the posterior part of the head above the pharyngeal area and on the anterior part of the trunk. Herrick indirectly derives these ramuli from a small bundle of fibers (about 20) which detach from the root of n. glossopharyngeus, this small bundle joining intracranially the root of the ramus lateralis vagi (r. lat. vagi). The fibers are of small to medium diameter, considerably smaller than lateralis fibers to canal neuromasts, according to Herrick, but larger than average communis fibers. Herrick could not trace these medium-small fibers from the glossopharyngeus through the ganglion of the r. lat. vagi. He assumed that fibers of the same size observed leaving the other side of the ganglion were the same as the ones observed entering it, that is, that they were from the 20 fibers from the glossopharyngeus. He rather confidently identifies the three ramuli from the r. lat. vagi which appear to join RLA as being derived from the small bundle of fibers from the root of the glossopharyngeus. He furthermore assigns them to the communis system. Herrick's reasons, others in addition to those just given, are not very convincing. The use of the name ramus lateralis accessorius, therefore, really rests upon the fact that this nerve is made up of gustatory fibers from both the facialis and vagus (or glossopharyngeus) nerves.

In *Polycentrus* no such ramuli from the r. lat. vagi were observed to join the recurrent facial ramus. In *Polycentrus* there is an intracranial vagal ramus that passes up to the parietal bone, and on some specimens it passes out of the cranium through the same foramen as does RLA, but on other specimens it passes through its own foramen close to that for RLA. In the latter specimens it was observed to pass to overlying skin and to skin lying anterior to its cranial exit. As far as could be determined from serial sections of *Polycentrus*, it was seen to be an intracranial part of the rami cutanei dorsales vagi. It would be carrying general cutaneous innervation to the top of the head. *Menidia* lacks this intracranial vagal ramus. Herrick equates the three extracranial ramuli from the r. lat. vagi of *Menidia* with this vagal ramus that is present in many other fishes (see Freihofer 1963 for examples). It may be equivalent as Herrick thought, but what seems quite doubtful from Herrick's discussion of these three ramuli is that they are of the communis component and that they join RLA and presumably course some distance with it. On a Sihler nerve preparation of the atherinid *Atherinops affinis*, no ramuli from the r. lat. vagi were observed to anastomose with RLA. *Atherinops* also lacks an intracranial vagal ramus to the parietal. These three ramuli of *Menidia* and the intracranial vagal ramus of *Polycentrus* and other fishes need more study. If they prove not to be communis, that is, if there is no vagal communis contribution to the formation of RLA, there would be reason for changing the name of RLA to simply that of the ramus recurrens facialis, in recognition of its purely facial communis composition. The facial part of RLA is much larger than is the vagal in apparently all teleosts having RLA. One disadvantage of using the name RLA is that it implies that the nerve is an accessory lateral line nerve of the acoustico-lateralis system, which it is not. The term RLA should stand until the question of the contribution of the vagal communis is resolved.

Trunk Lateral Line Nerves

The pattern of the trunk lateral line nerves of *Polycentrus* (Fig. 21) is especially interesting because it shows some ventral and dorsal segmental lateral line branches which previously have been known only in various lower, non-acanthopterygian fishes and in a less-developed state in zoarcids, gobiids, and mugilids (Freihofer 1970, 1972). There is one basic difference between the *Polycentrus* pattern and that of other fishes having ventral segmental lateral line nerves. In *Polycentrus* as well as in the other 20 or so percoid families that have been examined, there is a dorsal longitudinal collector lateral line nerve. Other perciformes examined have this collector also, but the zoarcids, gobiids, and mugilids do not have it. The atherinomorphs all lack it, as do other groups examined that are classified lower than the acanthopterygians and paracanthopterygians. Some of the paracanthopterygian fishes develop a dorsal longitudinal collector lateral line nerve at least towards the distal end of the dorsal longitudinal ramus. The ventral segmental lateral line branches in *Polycentrus*, of which there are five, are a secondary development on a basic percoid pattern and is apparently associated with the specialized swimming habits of *Polycentrus*. It would be interesting to see the lateral line nerves of nandids more generalized than *Polycentrus*, especially *Nandus*. It would take very carefully preserved specimens to provide the information, but the distribution of free lateralis organs on the head and trunk of all nandid genera should be determined. The results should have systematic significance for nandid classification.

Polycentrus is a secretive fish which stalks its prey by an extremely slow forward movement made by the beating of its transparent soft dorsal and anal fins, its mode of forward progress, its coloration, and its body shape resembling a drifting dead leaf. When startled or after attacking a prey fish, *Polycentrus* can move quite rapidly backwards from its position near the surface to its retreat near the bottom in a hole or pot. The head and trunk lateral line system may reflect specializations for such swimming behavior. The lateralis organs of the trunk are all free or naked organs borne on scales, a series of about eight organs on each such scale, the lateralis-bearing scales being arranged in rows following the main contours of the trunk (Fig. 21). The lateral line on the head is also specialized in that there are large neuromasts in the head lateralis canals as well as free organs arranged as shown in Fig. 21.

The distribution of free lateralis organs on the trunk of *Polycentrus* illustrates to what degree lateralis organs can migrate and their nerves follow them. The question arises for the zoarcids, gobioids, and mugilids as to whether these groups have lost all traces of the basic percoid pattern or whether they ever had them.

The large number (20 to 25) of free lateralis organs on the inside of the chin between the anterior ends of the dentaries is interesting in that a similar aggregation was observed on various other percoids. It is apparently an important location for receiving lateralis stimuli, which in *Polycentrus* may serve a prey-locating function.

An External-Internal Lateral Line Canal Nerve Relationship

Worthy of special note is a branching relationship observed on a number of ramuli going to individual neuromasts of the head canals (see branches to second and third pores of lachrymal canal, Fig. 1, and SORB 4, SORB 11, and SORB 11a, Fig. 3). A similar relationship was also observed for lateral line scales on the trunk of various fishes. In this relationship a neuromast ramulus detaches from a main nerve ramus and courses alone towards its canal neuromast, but before reaching its canal neuromast, the ramulus itself detaches a branch which curves away and passes some distance to skin or membrane around an adjacent canal pore. In some instances, on Sihler nerve preparations this branch to the membrane around the pore ended in branchlets that resembled in appearance those that elsewhere were known to be innervating free lateralis organs. Such organs occur in the skin along the supraorbital and infraorbital canals (Fig. 17) and elsewhere. If the ramulus were carrying only general cutaneous innervation, it would seem as practical, a distribution to have such fibers course in other rami that carry the main cutaneous innervation.

The arrangement of a canal neuromast ramulus closely associated with a ramulus innervating free lateralis organs in the skin would allow for the reception of differences between lateralis stimuli inside and outside the canals for each such location. Its development in *Polycentrus* is no doubt associated with this fish's very slow swimming habits, but it was observed also in other fishes, even for the trunk lateral line scales. Herrick (1899) briefly described a few of these branches on the head of *Menidia* but did not comment on them.

Radix Profundus

The complex relationships of the radix profundus with the oculomotor nerve and trigeminal sympathetic ganglion in *Polycentrus* (Fig. 14) are quite similar to those of the perciform *Uranoscopus* (Young 1931: text-fig. 8). There is a difference in *Menidia* that may be significant systematically. Herrick (1899) found that a recognizable intracranial profundus root and ganglion are missing in this atherinid. Since the ciliary nerves are present in *Menidia*, the root and ganglion of the profundus must be present also, but apparently they are fused with the trigeminal root and ganglion, a condition which may be representative for atherinomorphs.

A Stretch-Receptor Nerve to Base of Maxillary Tendon

Especially interesting is a branch (IO2f1; Figs. 6 and 10) of the r. mandibularis trigeminus which ends in a dense ramification of nerve fibers in the tendinous mucosa on the inside of the mouth, the innervation being directly in front of the anterior edge of the quadrate near the articulation head of this bone. This tendinous membrane fans out towards the ventral end of the maxillary tendon. Branch IO2f1 may innervate stretch-receptor organs in this membrane. A similar branch was observed on a number of other kinds of fishes. It was a large branch in a goatfish, *Parupeneus porphyreus*. A similar branch occurs in *Menidia*, but Herrick (1899) did not suggest any stretch-receptor innervation for it. It should be of interest to functional anatomists studying jaw mechanisms.

Simplifying Cranial Nerve Studies

The fifth, seventh, ninth, and tenth cranial nerves are the most complex in their branching and number of nerve components, and for these reasons they hold the most interest for systematists. Of these four cranial nerves, the fifth and seventh rank above the ninth and tenth. Broader taxonomic coverage can be had by concentrating only on the fifth and seventh nerves, or by restricting the study even further to a certain trunk, ramus, or even to only a single larger branch of a ramus. The nerve chosen should be an integral unit, complete in itself, and not parts of two nerves or character complexes.

It is also best to chose only one nerve component in a nerve trunk or ramus rather than include all components with all their branches. For example, one of the character complexes selected for comparison with *Polycentrus* was the lateralis component in the supraorbital trunk. Only the nasal and frontal bones were included. These seemed to form a natural morphological unit for this component in this nerve trunk.

For practical purposes comparative studies can be made directly from Sihler nerve preparations without recourse to serial-section techniques and involved neurological research. Prior grounding in the important nerve references employing functional component analysis is, of course, essential. A brief listing of the most important of the longer studies is given in the "Introduction." There are huge gaps in the taxonomic coverage in the nerve literature. The gaps can be filled effectively by a reference collection of Sihler nerve preparations.

The nerve components of the various trunks, rami, and smaller branches can be worked out with relative assurance in most instances by study of Sihler nerve preparations and dissections of preserved specimens. The dissections should expose the roots and ganglia of the trigeminus, facialis, glossopharyngeus, and vagus nerves. The motor and lateralis components are not difficult to determine because their end organs are relatively large. Since free lateralis organs may be lost in the handling and preparation of specimens, the distribution of these organs should be plotted from freshly and carefully preserved specimens (Fig. 17). Such a drawing is useful in helping assign terminal branches in a particular area of a Sihler preparation to the lateralis component. The gustatory component is difficult to determine unless the fibers course more or less as independent nerves for most of their length. Taste (terminal) buds located on the external body surface are too small to be seen except microscopically. Most of the gustatory system will be represented by the distinctive branches of the recurrent facial and palatine nerves. Dissection of the geniculate ganglion should disclose the presence of larger bundles of gustatory fibers leaving this ganglion and entering the supra- and infraorbital trunks, but since these fibers disappear into the branches of these trunks, appropriate microtechnique methods are necessary for determining their distribution. For most systematic purposes gustatory fibers entering these two trunks can be ignored. For practical purposes the last component, the general cutaneous, is what remains after the other three components have been determined. In fishes, general cutaneous fibers terminate in free nerve endings in the skin or in special tactile elaborations of skin, such as cirri and other skin flaps, or in barbels or barbel-like structures.

After determination of the functional components at the periphery of the nerves, the presence of a component can be shown diagrammatically in drawings by a distinctive symbol, the fiber bundles of each branch being brought together as they course centrally towards the cranial roots and ganglia and to the brain. An example in which these simplified approaches were taken in a systematic study is that by Springer and Freihofer (1976).

Short cuts such as those suggested above are necessary if nerves are to be used in the classification of fishes. Basic, descriptive neurological studies are still needed on numerous groups. It may fall to the lot of some systematists to do them. Neurologists have seemingly turned to other tasks.

SUMMARY

1. The courses of the trigeminus, facialis, glossopharyngeus, and vagus cranial nerves of a percoid fish, *Polycentrus schomburgkii*, are described in detail, and the functional components of the nerves determined as far as possible with the methods used. The closest groups with which *Polycentrus* could be compared in published accounts were *Scomber* (Scombridae) and *Menidia* (Atherinidae). Comparisons were also made from Sihler preparations of numerous groups (representatives of 85 families available) for selected nerves.

2. Nothing unusual was noted in the olfactory (I), optic (II), oculomotor (III), trochlear (IV), or abducens (VI), nerves.

3. The radix profundus in *Polycentrus* has the same relationships to the Gasserian ganglion, trigeminal sympathetic ganglion, ciliary ganglion, and oculomotor nerves as it has in *Uranoscopus*, as far as could be determined.

4. *Polycentrus* was compared with five percoids (*Roccus*, *Kuhlia*, *Perca*, *Paralabrax*, and *Archoplites*) and several other groups of fishes for cephalic canal neuromasts and with additional groups for cephalic free lateralis organs (pitorgans).

5. *Polycentrus* is more specialized than the above percoids, both in number of pitlines and in their size.

6. A pitline corresponding to the vertical pitline of *Amia* is present and innervated from the truncus hyomandibularis by the ramus buccalis accessorius. The posterior end of the infraorbital pitline is also innervated by a branch of the r. buccalis accessorius, which represents a specialization since the infraorbital pitline is usually innervated from the infraorbital trunk by the r. buccalis. This posterior part of the infraorbital pitline may represent the horizontal pitline of *Amia* that has moved up to the edge of the infraorbital.

7. Some pitlines of some fishes may not be homologous with corresponding pitlines of other fishes. Esocoids are an example. At least three pitlines in *Polycentrus* (the infraorbital, subnasal, and supraorbital) are not homologous with pitlines in the same location in esocoids. These three pitlines in esocoids are all innervated by the r. buccalis accessorius from the tr. hyomandibularis, whereas in *Polycentrus* the first two are innervated from the infraorbital trunk by the r. buccalis and the last pitline (the supraorbital) is innervated from the supraorbital trunk.

8. Reflecting perhaps the greater development of the infraorbital pitline is a specialization of the infraorbital canal-bearing bones, a first step towards degeneration of the infraorbital canals; the second, third, and fourth infraorbitals are fused and there is only one canal neuromast in the compound bone. In other respects the cephalic lateralis canal-bearing bones are a little more specialized (one less neuromast in the supratemporal and one more in the preopercular canals) than in *Roccus*, *Paralabrax*, *Archoplites*, and *Kuhlia*.

9. Various clusters and lines of cephalic pitorgans should be useful in nandid taxonomy.

10. The innervation of the snout in fishes is an important area for comparison in systematic studies. The snout in teleosts is innervated from

two sources: the supraorbital and infraorbital trunks. In *Polycentrus* the supraorbital trunk supplies one canal lateralis organ of the nasal canal, and the infraorbital trunk innervates apparently all of the free lateralis organs on the snout dorsomedial and ventral to the nasal bone. In some fishes there are important differences in this generalized condition seen in *Polycentrus*. If there are further developments of the lateralis system on the snout, such as an extension anteriorly of the nasal canal, they are innervated by the infraorbital trunk. Innervation of the nasal canal organ or organs should be determined in systematic studies because two (or three) lateralis organs in the nasal canal may indicate a fusion of the nasal canal bone (with one or two canal organs) and a prenasal canal (with one canal organ), the latter being innervated by the infraorbital trunk, or it may have other significance. An example of a group having a nasal and two prenasals (the anterior one membranous and the posterior one bony) is the Carangidae. Other percoids having two prenasals with features indicating a shared, derived specialization with the Carangidae are the Coryphaenidae (two bony prenasals, each separate and free from the nasal), Rachycentridae (two bony prenasals fused but free from nasal), and Echeneidae (same as Rachycentridae). Some other percoids having other specializations of an anterior extension of the nasal canal are the Sciaenidae and Polynemidae (both with deep, complicated membranous extensions); Toxotidae (a broad, bony prenasal); and Lutjanidae (one membranous prenasal). The Scombridae is so far unique in having a bony prenasal fused to the nasal.

11. Compared with *Polycentrus*, other percoids, and all teleosts examined, the berycoids have a quite different specialization of the nasal canal. It consists of one or two nasal canal secondary neuromasts located close to the anterior edge of the floor of the canal and innervated from the infraorbital trunk. *Polymixia* exhibits a stage that could be antecedent to that of berycoids. Stephanoberycoids have what may be the most generalized condition for beryciforms. It appears that in berycoids free lateralis organs lying close in front of the opening of the nasal canal were directly incorporated into the anterior end of the nasal canal without the prior formation of a prenasal ossicle that subsequently fused onto the nasal canal bone. The "capture" or engulfing mode of formation would be rare, if not unique. In any event, the nasal canal specialization appears basic in berycoids. It indicates that neither stephanoberycoids, polymixioids, nor berycoids are the ancestral source of perciforms. There are other striking specializations of the cephalic lateralis canal system of beryciforms.

12. The gadoids and ophidioids have a shared specialization of the nasal canal in which the anteriormost frontal canal neuromast has migrated into the nasal canal, giving that canal two neuromasts and the frontal canal only three, the usual number being four for almost all acanthopterygians examined. *Stephanoberyx* also has this specialization but not *Gibberichthys*. The zoarcids have only three frontal canal neuromasts, but only one nasal canal neuromast.

13. The general cutaneous component of the supraorbital trunk in *Polycentrus* ends on the snout posterior to the upper jaw, which is where it ends in most teleosts. In all atherinomorph fishes examined, it continues anteriorly as a large nerve onto the upper jaw. The only other group also found having a similar large extension onto the snout is the Holocentridae. The premaxillary extension of the supraorbital trunk carries general cutaneous fibers in atherinomorphs. The functional component is not yet known for holocentrids, but it probably is general cutaneous.

14. The pattern of branching of the ramuli from the ramus mandibularis trigeminus into the adductor mandibulae muscles of the cheek in *Polycentrus* consists of two ramuli leaving the ramus mandibularis trigeminus close together. Their ramifications in the subdivisions of the cheek muscle mass reflect the structure of the muscle. The pattern of nerve branching in the adductor mandibulae muscle can be important in understanding the subdivisions of this muscle, such as the origin of the $A_1\beta$ muscle. It also may have systematic significance. An example was discovered in comparing the pattern of *Polycentrus* with that of the atherinid *Menidia*. The atherinomorphs as a group have a nerve pattern to the cheek muscle different from that of all other fishes examined except for the gasterosteids.

15. The recurrent facial ramus (RLA) is present in one of the basic percoid patterns (referred to as the *Serranus* pattern), characterized by an orbito-pectoral and a parieto-dorsal branch.

16. There are few or no lateralis fibers in the ramus hyoideus.

17. There are apparently few or no communis fibers in the ramus mandibularis trigeminus and r. maxillaris trigeminus.

18. The anterior ramus palatinus joins the r. maxillaris trigeminus on the upper jaw. Some groups of fishes lack this anastomosis (atherinomorphs being one).

19. There is a Jacobson's anastomosis.

20. The ramus mandibularis internus facialis is present.

21. A nerve possibly functioning mainly as an innervation for stretch receptors in the membrane and tendons associated with the base of the maxillary tendon was observed in *Polycentrus* and some other percoids.

22. A double type of cephalic canal lateralis innervation was observed on *Polycentrus* and some other acanthopterygians. It consists of two branches detaching from a single lateralis branch that innervates a canal neuromast: one of the two canal branches innervates the canal neuromast, and the rest of the canal branch passes to the membrane around the adjacent canal pore, the membrane at least sometimes observed to bear free lateralis organs.

23. There is an intracranial vagal ramus which in *Polycentrus* is a branch of the ramus cutanei dorsales vagi. This intracranial vagal ramus does not course with the recurrent facial ramus. It does not contribute to the latter ramus. No vagal branch was seen to contribute to the recurrent facial nerve on the nape. The question of the intracranial ramus being of general cutaneous or communis component should be studied in other fishes. If the intracranial vagal ramus does not contribute communis fibers to the recurrent facial nerve, then the name of ramus lateralis accessorius should not be used and the name of recurrent facial nerve be used in its stead for the entire course of the nerve.

24. The trunk lateral line nerves show a basic acanthopterygian pattern of a so-called dorsal, longitudinal collector lateral line nerve. In addition there are a number of dorsal and ventral segmental branches which innervate three rows of scales bearing free lateralis organs (pitorgans): a row along the base of the dorsal fin; a row halfway between the dorsal fin and the horizontal septum; and a row along the base of the anal fin. There are two rows of free organs on the caudal fin: one on its upper lobe and one on its lower lobe. There is only one regular tubed lateral line scale, the first one. Each of these separate rows of free organs on a scale may represent a canal neuromast that has migrated towards the base of a fin and subdivided into about eight smaller free organs; or each row of free organs on a scale may represent multiplication of a single pitorgan originally associated with each tubed lateral line scale. Such pitorgans were observed, one per lateral line scale, on some lateral line scales of other fishes. It was not observed on the single tubed scale of *Polycentrus*. It is not known which of the possible origins is correct for the development of such free lateralis organs, either on the head or on the trunk of the body.

25. Some interesting systematic problems on the higher category classification of certain groups of fishes were disclosed in the comparative studies made between *Polycentrus* and groups represented in the nerve literature and from Sihler nerve preparations.

26. For systematic purposes the most useful cranial nerves to study are the fifth, seventh, ninth, and tenth, with the fifth and seventh being the most useful, if a choice has to be made. These cranial nerves are the most complex and offer the most characters.

27. From a consideration of the usefulness that nerves apparently have for studies on the classification of fishes and the great gaps there are in the taxonomic coverage of the nerve literature for fishes, it is apparent that at least one basic descriptive study of the cranial nerves of a representative of each order is definitely needed. This research should be carried out by systematists. Morphologists are no longer interested in descriptive nerve studies.

28. Making the preceding recommendations much more feasible is the Sihler technique for staining nerves in a cleared, intact specimen.

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Literature Cited

Allis, Edward Phelps, Jr. 1889. The anatomy and development of the lateral line system in *Amia calva*. J. Morphol. 2(3): 463–568, 10 text-figs. + pls. 30–42 (49 figs.).

———. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. J. Morphol. 12(3): 487–808, pls. 20–38 (64 figs.).

———. 1903. The skull, and the cranial and first spinal muscles and nerves in *Scomber scomber*. J. Morphol. 18: 45–329, 1 text-fig., pls. 3–12.

———. 1910. The cranial anatomy of the mail-cheeked fishes. Zoologica (Stuttgart), 57: iii + 219, 8 pls.

Atoda, K. 1936. The innervation of the cranial nerves of the catfish: *Parasilurus asotus* L. Sci. Rep. Tohoku Univ., Sendai 11(4): 91–113.

Baudelot, Emile. 1883. Recherches sur le système nerveux des poissons. Paris. 178 pp., 10 pls.

Cole, Frank J. 1898. Observations on the structure and morphology of the cranial nerves and lateral sense organs of fishes; with special reference to the genus *Gadus*. Trans. Linn. Soc. Lond., ser. 2, Zool. 17(5): 17–221, pls. 21–23.

Cuvier, Georges L. C. F. D., and Achille Valenciennes. 1828. Histoire naturale des poissons, 1. Paris. xvi + 573 pp.

Disler, N. N. 1971 [1960]. Lateral line sense organs and their importance in fish behavior. Academy of Sciences of the U.S.S.R., Severtsov Institute of Animal Morphology. (Transl. from Russian by H. Mills and M. Yariv. Israel Program for Scientific Translations, Ltd. 328 pp., 57 figs.)

Fraser, Thomas H., and W. C. Freihofer. 1971. Trypsin modification for Sihler technique of staining nerves for systematic studies of fishes. Copeia 1971(3): 574–576, 1 fig.

Freihofer, Warren C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull. 8(2): 79–189, 29 figs.

———. 1966. The Sihler technique of staining nerves for systematic study especially of fishes. Copeia 1966(3): 470–475, 2 figs.

———. 1970. Some nerve patterns and their systematic significance in paracanthopterygian, salmoniform, gobioid, and apogonid fishes. Proc. Calif. Acad. Sci., ser. 4, 38(12): 215–264, 20 figs.

———. 1972. Trunk lateral line nerves, hyoid arch gill rakers, and olfactory bulb location in atheriniform, mugilid, and percoid fishes. Occas. Pap. Calif. Acad. Sci. 95: 31 pp., 12 figs.

———, Leonard J. V. Compagno, and William Rogers. 1977. Additional notes on the use of the Sihler technique of staining nerves of small, whole specimens of fishes and other vertebrates. Copeia 1977(3): 587–588.

Gilmore, R. G., Jr. 1972. The cephalic nerve pattern and lateral line system of *Hyporhamphus unifasciatus* and *Strongylura marina* (Pisces: Exocoetidae, Belonidae). Master's Thesis. University of West Florida. 35 pp., 7 text-figs.

Greenwood, P. Humphry, Donn E. Rosen, Stanley H. Weitzman, and George S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131(4): 339–456, text-figs. 1–9, pls. 21–23, charts 1–32.

Gupta, O. P. 1972. On the origin and innervation of the cranial and spinal nerves along with the autonomic nervous system of the Indian Gar-fish, *Xenentodon cancila* (Ham.). Anat. Anz. 131: 39–50, 4 figs.

Hennig, Willi. 1966. Phylogenetic systematics. (Transl. by D. Dwight Davis and Rainer Zangerl.) University of Illinois Press. 263 pp., 69 figs.

Herrick, C. Judson. 1897. The cranial nerve components of teleosts. Anat. Anz. 13(16): 425–431.

———. 1898. Experiments with the Weigert method. J. Comp. Neurol. 8: XXVII to XLIV.

———. 1899. The cranial and first spinal nerves of *Menidia*; a contribution upon the nerve components of the bony fishes. J. Comp. Neurol. 9: 153–455, pls. 14–20.

———. 1900. A contribution upon the cranial nerves of the codfish. J. Comp. Neurol. 10: 265–316, pls. 21–22.

———. 1901. The cranial nerves and cutaneous sense organs of the North American siluroid fishes. J. Comp. Neurol. 11: 177–249, pls. 14–17.

———. 1903. The doctrine of nerve components and some of its applications. J. Comp. Neurol. 13: 301–312.

Hollister, Gloria. 1934. Clearing and dyeing fish for bone study. Zoologica (N.Y.): 12(10): 89–101.

Laurent, P., and S. Dunel. 1966. Recherches sur l'innervation de la pseudobranchie des téléostéens [in French, English summary]. Arch. Anat. Microsc. Morphol. Exp. 55: 633–656, 9 figs.

Leach, E. H. 1946. Curtis' substitute for van Gieson's stain. Stain Technol. 21: 107–110.

Liem, Karel. 1970. Comparative functional anatomy of the Nandidae (Pisces: Teleostei). Fieldiana: Zool. 56: 1–166, 66 figs.

Maheshwari, S. C. 1965. The cranial nerves of *Mastacembelus armatus* (Lacépède). Jpn. J. Ichthyol. 12(3/6): 89–98, 4 figs.

Manigk, Wolfgang. 1934. Der Trigemino-Facialiskomplex und die Innervation der Kopfseitenorgane der Elritze (*Phoxinus laevis*). Z. Morphol. Oekol. Tiere 28: 64–106, 16 figs.

Mithel, Manorama. 1964a. The cranial nerves of the sisorid catfish *Bagarius bagarius*. Copeia 1964(4): 673–678, 2 figs.

———. 1964b. The cranial nerves of *Mystus seenghala* (Sykes). Agra Univ. J. Res. 13(1): 67–78, 7 figs.

Narawane, D. D. 1965. Studies on the skeleton, musculature and distribution of nerves in the caudal peduncle and fins of *Heteropneustes fossilis* Bloch. (Physostomi-Siluridae). J. Univ. Bombay 33(5): 64–75, 7 figs.

Nelson, Gareth J. 1972. Cephalic sensory canals, pitlines, and the classification of esocoid fishes, with notes on galaxiids and other teleosts. Am. Mus. Novit. 2492: 49 pp., 23 figs.

Norris, Henry Waldo. 1925. Observations upon the peripheral distribution of the cranial nerves of certain fishes (*Amia*, *Lepidosteus*, *Polyodon*, *Scaphirhynchus*, and *Acipenser*). J. Comp. Neurol. 39: 345–432, 12 text-figs., 7 pls. (figs. 13–19).

———, and Sally P. Hughes. 1920. The cranial, occipital, and anterior spinal nerves of the dogfish, *Squalus acanthias*. J. Comp. Neurol. 31(5): 293–402, 53 figs.

Pancratz, D. S. 1930. The cranial nerve components in the toadfish (*Opsanus tau*). J. Comp. Neurol. 50(3): 247–286, 2 pls.

Pinkus, Felix. 1894. Die Hirnnerven des *Protopterus annectens*. Morphol. Arbeit. (Jena) 4: 275–346, 7 pls.

Ray, Dixie Lee. 1950. The peripheral nervous system of *Lampanyctus leucopsarus*. J. Morphol. 87(1): 61–178, pls. 1–17.

Rosen, Donn E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bull. Am. Mus. Nat. Hist. 127(5): 217–268, figs. 1–23, pls. 14–15.

———. 1973. Interrelationships of higher euteleostean fishes, pp. 397–513, 129 figs., 4 tables. *In*, Greenwood, P. Humphry, R. S. Miles, and Colin Patterson. Interrelationships of fishes, Supplement no. 1 to Zool. J. Linn. Soc. 53: 536 pp.

———, AND COLIN PATTERSON. 1969. The structure and relationships of the paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141(3): 357–474, figs. 1–74, pls. 52–78, tables 1–8.

SAXENA, P. K. 1966. Cranial nerves of the common catfish, *Clarias batrachus* (Linn.). Jpn. J. Ichthyol. 14(1/3): 91–98, pls. 8–12.

———. 1967. The cranial nerves of the mud eel, *Amphibnous cuchia* (Ham.). Acta Anat. 68: 306–320, 3 figs. [Summaries in French and German]

———. 1969a. The cranial nerves of *Nandus nandus* (Ham.) and *Xenentodon cancila* (Ham.). Anat. Anz. 124(2): 142–155, 3 figs.

———. 1969b. The cranial nerves of *Notopterus notopterus* (Pallas). Anat. Anz. 124(2): 198–209, 3 figs.

———, AND RAKESH K. RASTOGI. 1968. The cranial nerves of the flat-fish, *Cynoglossus bilineatus* (Lac.). Annot. Zool. Jpn. 41(2): 70–76, 4 figs.

SHELDON, R. E. 1914. Paraffine-Weigert methods for the staining of nervous tissue, with some new modifications. Folia Neurobiologica 8(1): 1–28.

SPRINGER, VICTOR G., AND WARREN C. FREIHOFER. 1976. Study of the monotypic fish family Pholidichthyidae (Perciformes). Smithson. Contrib. Zool. 216: iv + 43 pp., 23 text-figs.

STANNIUS, HERMANN. 1849. Das peripherische Nervensystem die Fische, anatomisch und physiologisch Untersucht. Rostock. 156 pp., 5 pls.

STENSIÖ, E. A. 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. K. Sven. Vetenskapsakad. Handl., ser. 3, 24(3): 195 pp., 38 figs.

VASISHT, H. S., AND I. B. S. UBEROI. 1965. Anatomy of *Mystus seenghala* (Sykes). IV. Nervous system. Res. Bull. Panjab Univ. (new ser.) 16(1–II): 61–85.

WILLIAMS, T. W. 1943. A technique for the gross differential staining of peripheral nerves in cleared vertebrate tissue. Anat. Rec. 86: 189–194, 1 pl.

WINTERBOTTOM, RICHARD. 1974a. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Phila. 125(12): 225–317, 56 figs.

———. 1974b. The familial phylogeny of the tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology. Smithson. Contrib. Zool. 155: iv + 201, 185 figs.

YOUNG, J. Z. 1931. On the autonomic nervous system of the teleostean fish *Uranoscopus scaber*. Q. J. Microsc. Sci. (new ser.) 74: 491–535, 12 text-figs.

Abbreviations for Figures

A_1, A_2, A_3—divisions of the adductor mandibulae muscle.
AA4, AA5—m. adductores 4,5.
ADD OP—m. adductor operculi.
AAP2—m. adductor arcus palatini anterior portion.
AD HYO—m. adductor hyomandibularis.
ADD OP—m. adductor opercularis.
AN—anterior narial opening.
Anasto w—anastomoses with.
AWB1,2,3—divisions of the mentalis muscle.
BB1, BB2, BB3—basibranchials 1, 2, 3.
br—branch.
br & vis tr of vag—branchial and visceral trunks of nervus vagus.
CB1 to CB5—ceratobranchials 1, 2, 3, 4, 5.
CIR—a circular, roundish bundle of muscle on top of m. transversus dorsalis.
Cor 1 to Cor 6—branches of ramus ophthalmicus trigeminus to cornea.
EM—longitudinal orientation of medial fibers of the sphincter oesophagi.
EP1 to EP4—epibranchial bones 1 to 4.
fac—facialis.
FR COM—frontal commissure of supraorbital canal.
G—nervus glossopharyngeus (n. IX).
G1—branch of m. glossopharyngeus to m levator internus 2.
G2—ramus pretrematicus IX.
G3—branch of IXth to m levator externus 1.
G5—branch of IXth to muscles of gill filaments.
G6—branch of IXth to gill rakers.
G7—branch of IXth to m. obliquus ventralis 1.
G8—branch of IXth to m. rectus ventralis 1.
GAM—area of attachment of some gill arch muscles.
GANG IX—petrosal ganglion of IXth cranial nerve.
GG4—ganglion of 4th vagal branchial ramus.
GLR—ramus posttrematicus of IX.
H AB—m. hyoidei abductores.
H AD—m. hyoidei adductores.
HB1 to HB3—hypobranchial bones 1 to 3.
INFO1, 4—canal neuromasts 1 and 4 of infraorbital canal.
IO1 to IO1f1b.—branches of ramus buccalis facialis to lateralis organs (or to skin of cheek; these branches actually belong to the r. maxillaris inferioris trigeminus).
IO2 to IO2f—branches of ramus mandibularis trigeminus.
IO2a—ramus opercularis trigeminus.
IO2c, IO2d, IO2e—to adductor mandibulae muscle of cheek.
IO2f, IO2f1, 2, 3—to tendinous mucosa near ventral end of maxillary tendon and adjacent skin.
IO2f4, a, b—to skin over articular and lip pad at posterior end of lower jaw.
IO2f5 thru IO2f5e—to skin over articular, interopercle, angular, anterior end of preopercle and bases of anterior branchiostegal rays.
IO2f6 thru IO2f9—to skin over ventral surfaces of articular and dentary bones.
IO2g, IO2g2, IO2g2a—ramulus mandibularis internus trigeminus (IO2g) and branches to m. protractor hyoidei and adjacent skin and mucosa (IO2g2) and m. intermandibularis (IO2g2a).
IO2h thru IO2j—branches of ramulus mandibularis trigeminus externus (IO2h) to lower lips, labial cartilage, teeth, and skin near symphysis of lower jaw.
IO3 and IO3a to IO3d—ramus maxillaris inferioris trigeminus and its branches.
IX—nervus glossopharyngeus.
LL pore 1, 2, 3, 4—lateral line canal pores 1 to 4 of dentary.
LE1, LE2, LE4—m. levator externus 1, 2, 4.
LEP—m. levator posterior.
LGR—lateral row of gill rakers.
LI1 to LI3—m. levator internus 1, 2, 3.
Lig 1—palatomaxillary ligament.
Lig 4—palatopalatine ligament connecting palatine of each side across ascending process of premaxillary.
m—muscle.
MGR—medial row of gill rakers.
MP1 to MP10—lateralis organs 1 through 10 of mandibulo-preopercular canal.
MTC—patch of free lateralis organs between anterior ends of dentaries.
NLL—nervus linae lateralis vagi and some of its branches.
NLL1—horizontal septum lateral line nerve of nervus linae lateralis.
NLL1 V1—1st ventral branch of NLL1.
NLL2 to NLL2b—the longitudinal collector lateral line nerve (NLL2) and some of its branches.
OBD3—m. obliquus dorsalis 3.
OP—m. obliquus posterior.
OV1 to OV3—m. obliquus ventralis 1 to 3.
P2—branch of r. palatinus.

PCI—m. pharyngoclavicularis internus.
PCE—m. pharyngoclavicularis externus.
PCL—vertical row of free lateralis organs in front of preopercle.
PH1 to PH3—infrapharyngo-branchials 1 to 3.
PIV—pharyngo-intestinal trunk of nervus vagus.
PN—posterior narial opening.
PO1—1st lateralis organ of postorbital section of cephalic lateralis canal system.
PPR—posterior palatine ramus.
PR HY—m. protractor hyoidei.
PRP—m. protractalis pectoralis.
PRPE—branch of ramus opercularis vagi to m. protractor pectoralis.
PT1—lateralis organ of posttemporal canal.
QTAW—quadrate tendon of mentalis muscle.
r—ramus.
RCOM—m. rectus communis.
r com v—ramus communicans from Gasserian ganglion to truncus hyomandibularis.
RETD—m. retractor dorsalis.
r hyo—ramus hyoideus
RIN—r. intestinalis and r. cardiacus vagi.
RLA-OP—orbito-pectoral branch of ramus lateralis accessorius (recurrent facial nerve).
RLA–PD—parieto-dorsal branch of ramus lateralis accessorius.
r mand fac—r. mandibularis facialis.
r mand ext fac—ramus mandibularis externus facialis.
r mand int fac—ramus mandibularis internus facialis.
r mand trig (IO2)—ramus mandibularis trigeminus.
r op 1 thru r op 3b—branches of ramus opercularis vagi to skin and mucosa of opercle and part of subopercle.
r oper fac—ramus opercularis facialis.
r op sup fac—ramus opercularis superficialis facialis.
r oph sup fac—ramus ophthalmicus superficialis facialis.
r ophth sup tri—ramus ophthalmicus superficialis trigeminus.
r oper vagi—ramus opercularis vagi.
R SUPR 1 to R SUPR 1d—branches of lateralis portion of ramus supratemporalis vagi with some general cutaneous fibers.
R SUPR 2 and R SUPR 2a—portion of ramus supratemporalis vagi containing in part the rami cutanei dorsalis vagi.
RSV—ramus supratemporalis vagi.
RV1, RV4, RV5—m. rectus ventralis 1, 4, and 5.
SIR—esophageal ramus of 4th vagal branchial ramus.
SO1 to SO5—canal neuromasts 1 through 5 of supraorbital canal.
SORB 2 to SORB2b—branches of truncus supraorbitalis to meninges, skin, and free lateralis organs above orbit.
SORB3—joins RLA-PD intracranially.
SORB4—branch of ramus ophthalmicus superficialis facialis.
SORB5—branch of r. ophth. sup. trigeminus to skin dorsal to orbit.
SORB6 to SORB7A—branches of r. ophth. sup. trigeminus to skin of snout.
SORB8 and SORB9—branches of r. oph. sup. facialis to 1st and 2nd supraorbital canal organs of frontal bone.
SORB10, SORB11–11a—branches of r. oph. sup. trigeminus to skin and free lateralis organs near nasal canal and to lateralis organ of nasal canal.
ST1—dorsalmost lateralis organ of supratemporal canal.
STL—vertical line of free lateralis organs in front of supratemporal canal.
SYM TR—sympathetic trunk.
T—tendon.
TA1, TA3—tendons of A_1 and A_3 divisions of m. adductor mandibulae.
TAWβ^3 + TA2—tendon of A_2 and of AWβ^3 divisions of mentalis muscle.
TD1, TD2—m. transversus dorsalis 1 and 2.
TH—truncus hyomandibularis.
TH1—posterior palatine ramus.
TH2, TH3—anterior and posterior parts of ramus opercularis profundus facialis.
TH4—ramus opercularis superficialis facialis.
TH4AA, TH4BB, TH4BB1, TH4BB2—branches of r. oper. sup. fac. innervating lateralis organs on opercle and subopercle.
TH5—to canal organ #11 of mand.-preopercular canal.
TH6—to skin between opercle and interopercle.
TH7—anastomoses with cutaneous branch from IO1c.
TH8—to canal organ #10 of mand.-preopercular canal.
TH9, TH9A, TH9B, TH9B1a–1e, TH9B0, TH9B02–05, TH9C, TH9C2, TH9D–TH9F, TH10, TH10A–TH10B4, TH11—ramus hyoideus and its branches.

TH12—ramus mandibularis internus.
TH12A–TH12C—to mucosa of anterior part of palate and to ectopterygoid teeth.
TH13, TH13A–B, TH14–15—branches of ramus hyoideus.
TH16—branch of ramus hyoideus anastomosing with IO2f.
TH17–TH17a, TH18—lateralis branches of r. mand. fac. to mand. preopercular canal.
TH18a—branch of combined r. mand. tri. & r. mand. fac. to mucosa on medial side of dentary.
TH19, TH19a–TH19a4, TH19b–TH19b4, TH19b 4a—branches of combined r. mand. tri. and r. mand. fac. to skin, taste buds, gums of teeth, and mucosa of anterior part of lower jaw.
TH20—lateralis branch of r. mand. facialis to mandibulo-preopercular canal.
TH20a–TH20c—to skin on ventral surface of dentary.
TH21, TH21a, TH22—lateralis and cutaneous branches of combined r. mand. tri. & r. mand. fac. to mandibulo-preopercular canal and to skin.
TH23, TH23a–b, TH24, TH24a, TH24b, TH25—lateralis and cutaneous branches of combined r. mand. tri & r. mand. fac.
tr—truncus.
TS1—canal neuromast of first (and only) truncus lateral line scale.
TV4, TV5—m. transversus ventralis of the fourth and fifth branchial arches, respectively.
V1—1st vagal branchial ramus. V1 is the prefix to all branches of this first ramus.
V1A—branch of 1st branchial ramus to levator externus 2.
V1B—branch of 1st vagal posttrematic branchial ramus to gill rakers.
V1C—to m. obliquus ventralis 2.
V1E—to 1st epibranchial gill rakers.
V1P—pharyngeal ramus of 1st vagal pretrematic branchial ramus.
V1PO—1st vagal posttrematic branchial ramus.
V1PR—1st vagal pretrematic branchial ramus.
V2A—branch of 2nd vagal posttrematic branchial ramus to m. levator posterior.
V2B—branch of 2nd vagal posttrematic branchial ramus to m. levator externus 4.
V2C—branch of 2nd vagal pretrematic branchial ramus to m. obliquus dorsalis III and m. transversus dorsalis 2.
V2D—branch of 2nd vagal pretrematic branchial ramus to m. transversus dorsalis 2.
V2E—branch of V2P to ceratobranchial gill rakers.
V2F—branch of 2nd posttrematic vagal branchial ramus to gill rakers.
V2G—branch of 2nd posttrematic vagal branchial ramus to m. rectus communis.
V2H—branch of 2nd posttrematic vagal branchial ramus to m. rectus ventralis 4.
V2J—branch of 2nd vagal branchial posttrematic ramus to m. obliquus ventralis 3.
V2P—pharyngeal ramus of 2nd vagal pretrematic ramus.
V2PO—second vagal posttrematic branchial ramus.
V2PR—2nd vagal pretrematic branchial ramus.
V3A—branch of 3rd vagal branchial ramus to m. retractor dorsalis.
V3B—branch of 3rd vagal branchial posttrematic dorsalis ramus to gill rakers.
V3E—gill raker branch of pharyngeal ramus of 3rd vagal branchial ramus.
V3P—pharyngeal ramus of 3rd vagal branchial ramus.
V3PO—3rd vagal posttrematic branchial ramus.
V3PR—3rd vagal pretrematic branchial ramus.
V4A—to mucosa of roof of posterior end of pharynx.
V4B—branch of 4th vagal posttrematic branchial ramus to m. obliquus posterior and adductor 5.
V4C—branch of V4PO to teeth and mucosa of 5th ceratobranchial.
V4D—branch of V4PO to m. transversus ventralis IV.
V4E—branch of V4PO to pharyngoclavicularis externus and internus muscles.
V4PO—4th vagal posttrematic branchial ramus.
V4PR—4th vagal pretrematic branchial ramus.
X—nervus vagus.
1a to 1h—branches of ramus maxillaris trigeminus (coursing in ramus buccalis facialis) to skin over cheek and part of preopercle.
3b to 3g—branches of ramus buccalis innervating free lateralis organs on orbitals and lachrymal.
3 BC—branch of 3rd vagal posttrematic branchial ramus to m. adductores 4.
3 BD—branch of 3rd vagal posttrematic branchial ramus to m. transversus ventralis 4.

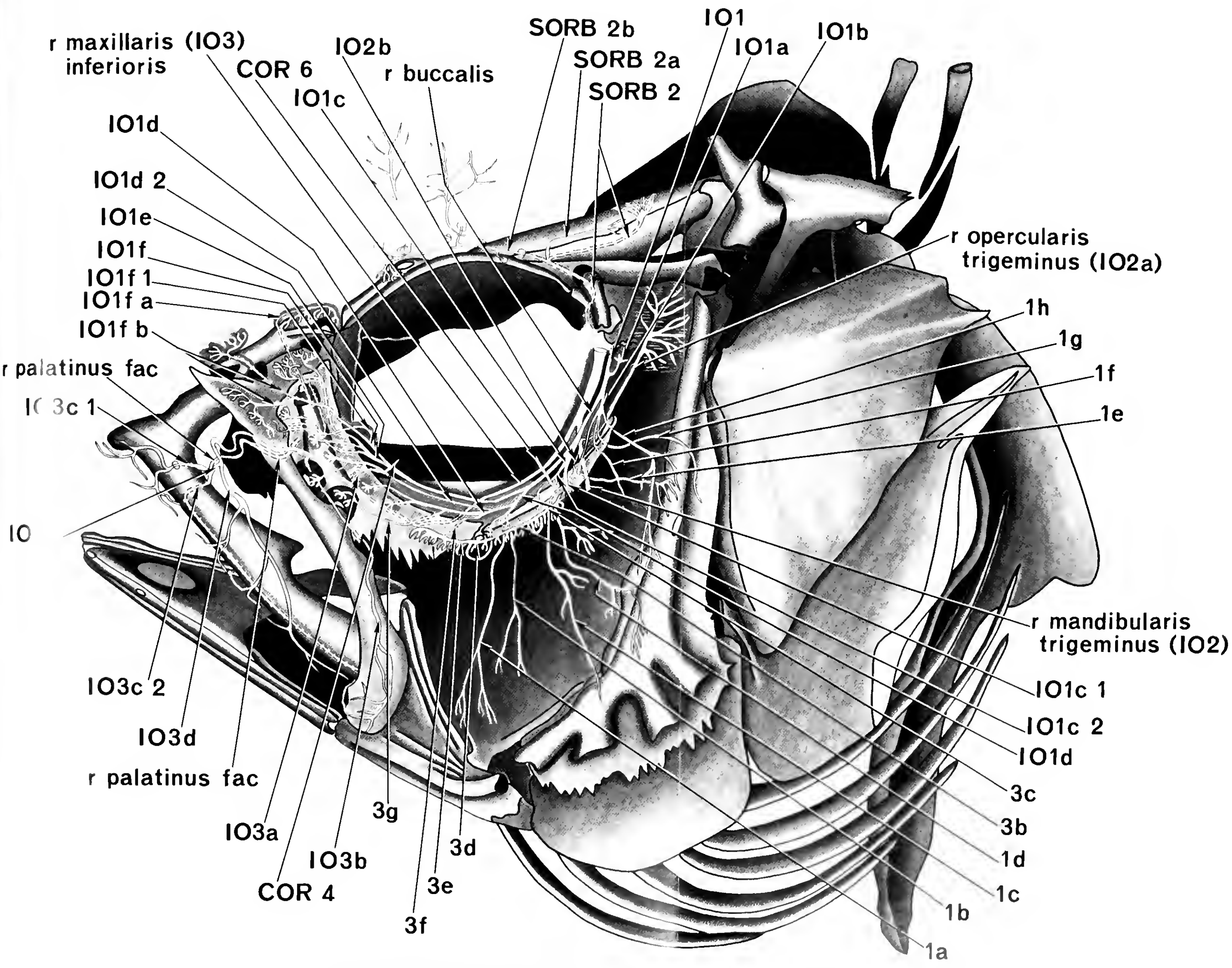


FIGURE 1. *Polycentrus schomburgkii*. Lateral view of branches of infraorbital trunk to snout and suborbital regions. See text and list of abbreviations.

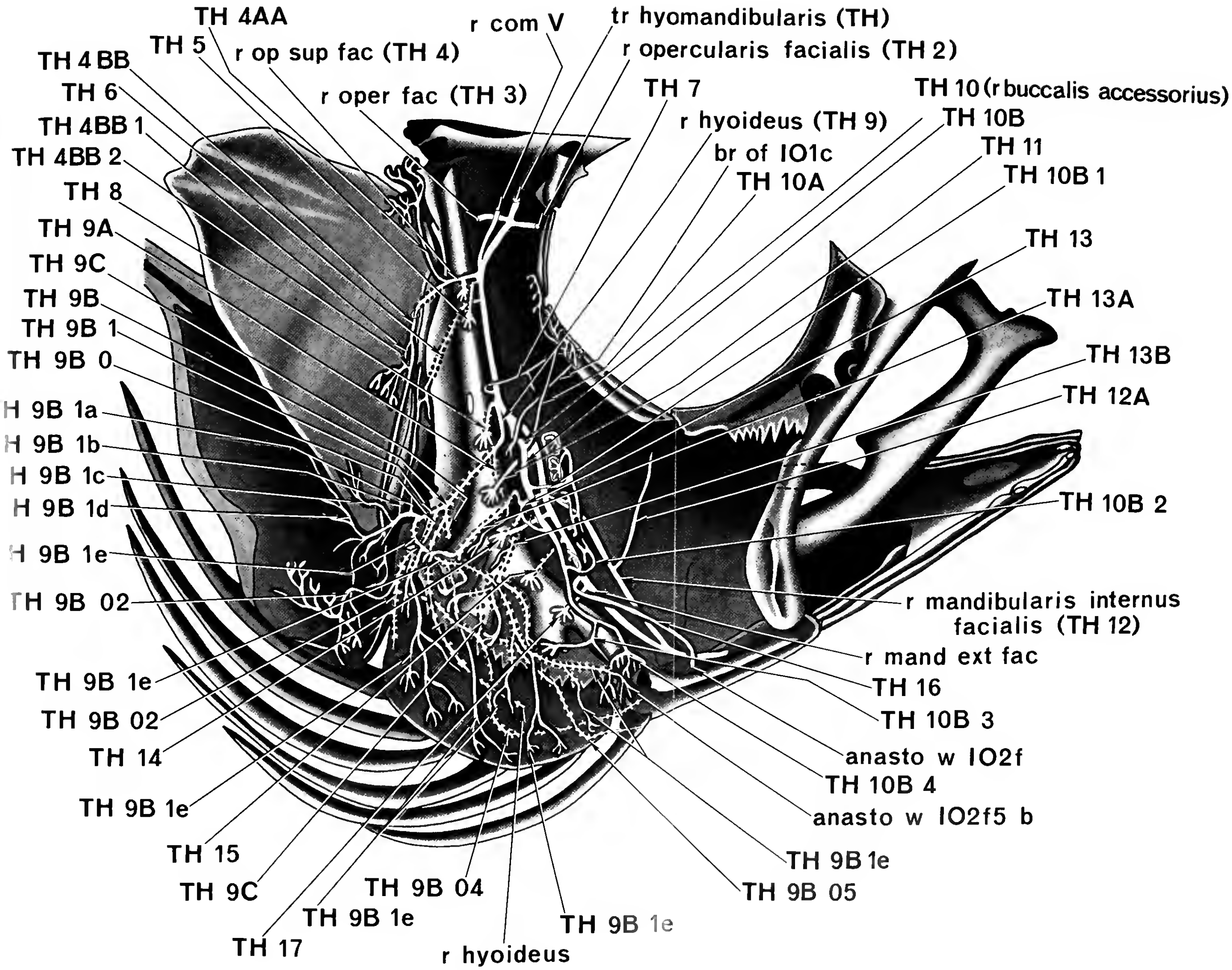


FIGURE 2. *Polycentrus schomburgkii*. Lateral view of branches of truncus hyomandibularis.

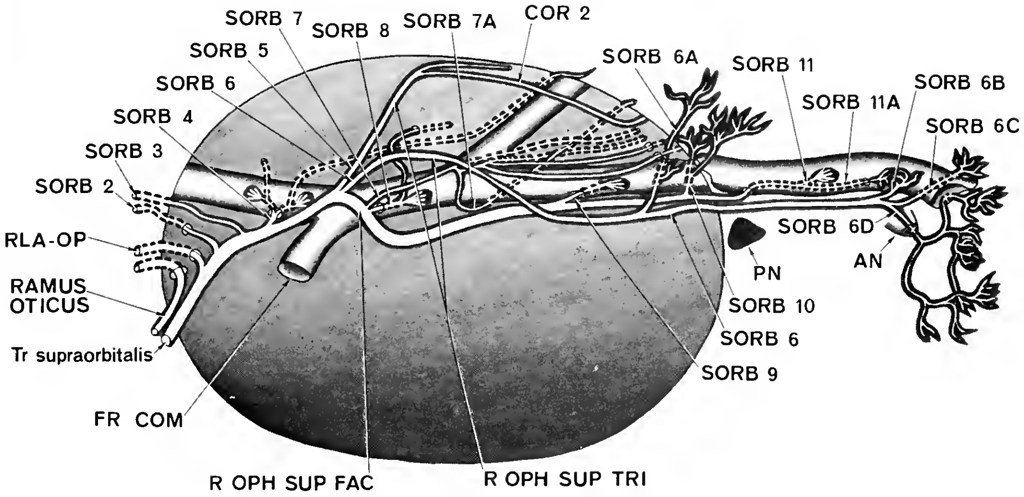


FIGURE 3. *Polycentrus schomburgkii*. Oblique view of supraorbital trunk looking towards roof of orbital cavity.

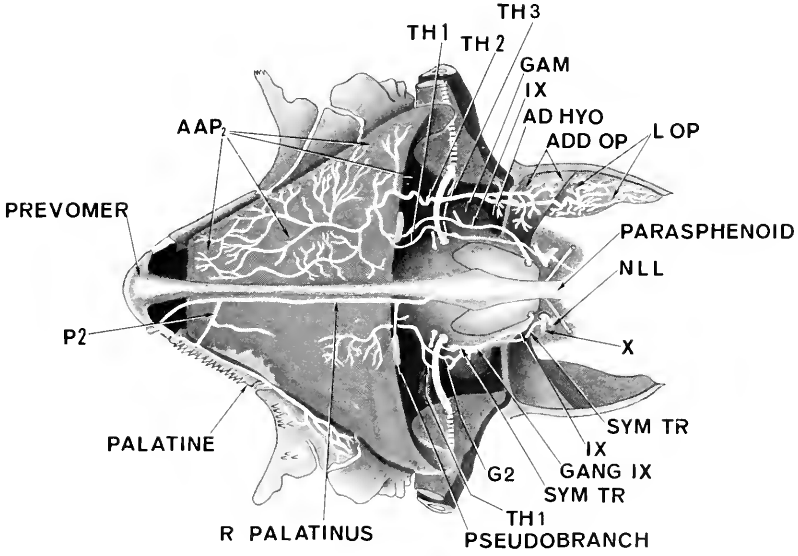


FIGURE 4. *Polycentrus schomburgkii*. View looking dorsally showing branches of truncus hyomandibularis and glossopharyngeal nerves to palate and posterior floor of cranial area.

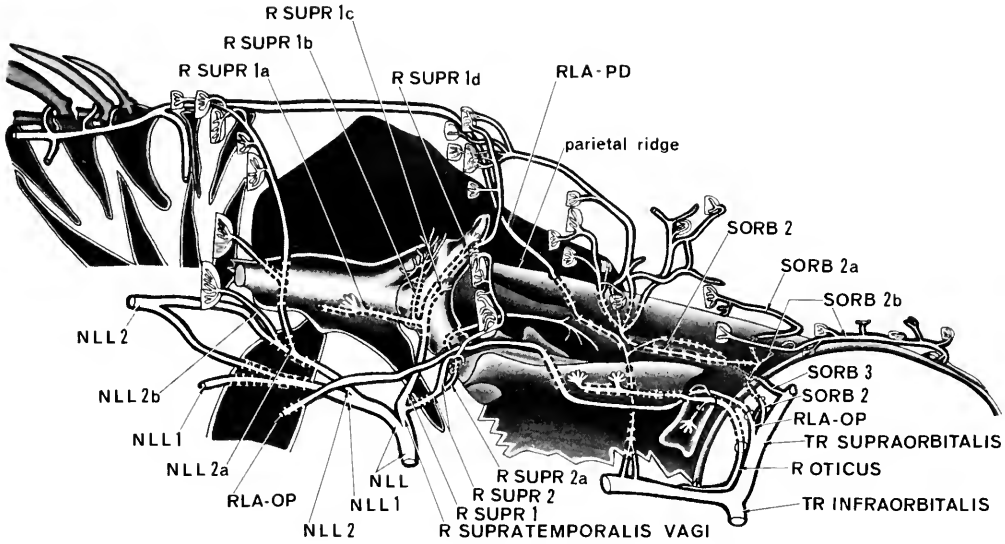


FIGURE 5. *Polycentrus schomburgkii*. Lateral view of main divisions and some branches of supraorbital trunk, lateral line nerves and supratemporal ramus of vagus nerve to dorsoposterior side of head.

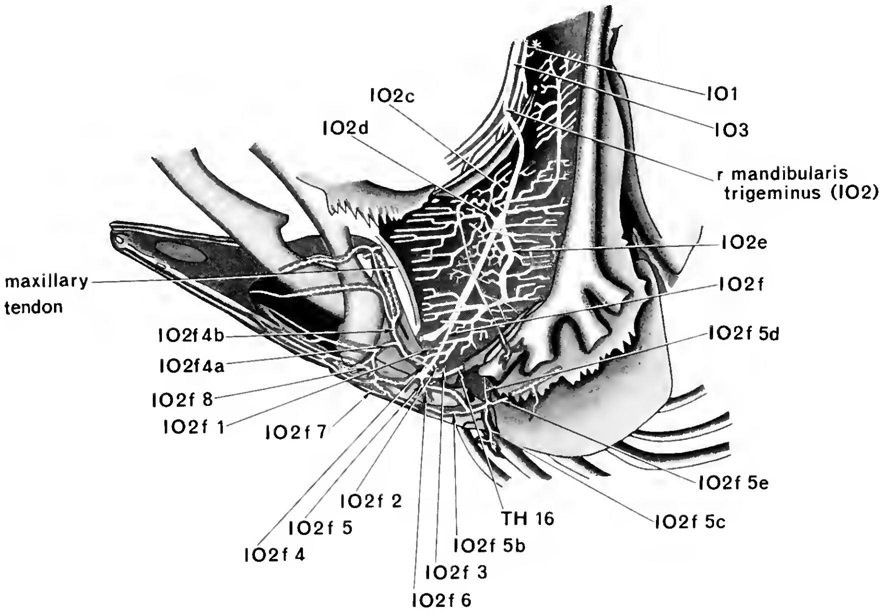


FIGURE 6. *Polycentrus schomburgkii*. Lateral view of cheek area showing pattern of innervation to adductor arcus palatini and adductor mandibulae muscles.

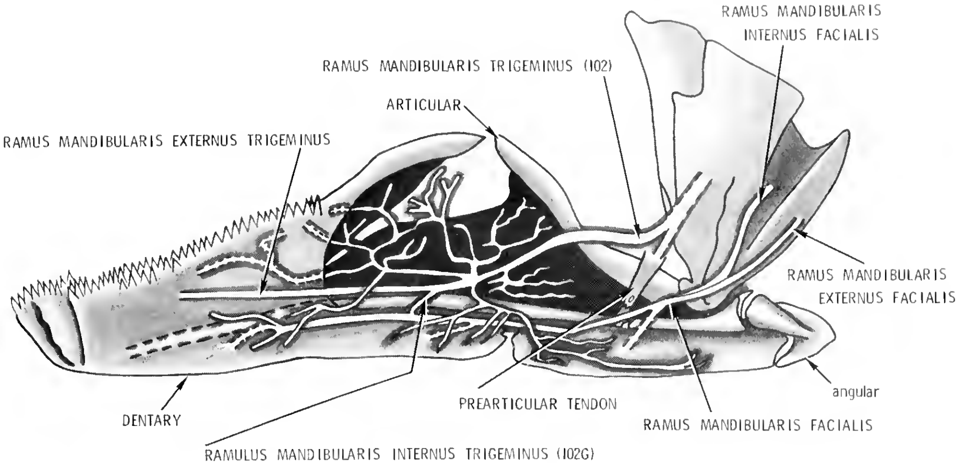


FIGURE 7. *Polycentrus schomburgkii*. Medial view of lower jaw showing innervation to mentalis division of adductor mandibulae muscle.

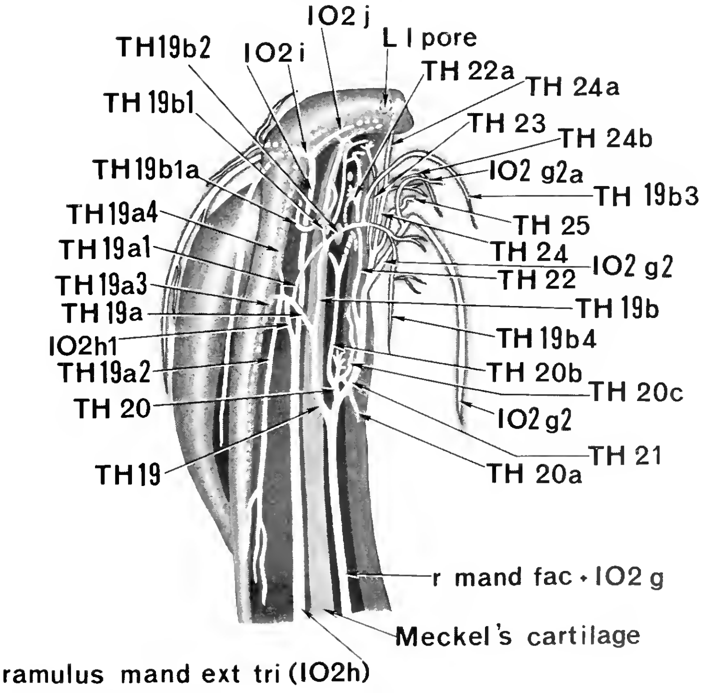


FIGURE 8. *Polycentrus schomburgkii*. Dorsal view of branches of ramus mandibularis trigeminus and of r. mand. facialis to anterior half of lower jaw.

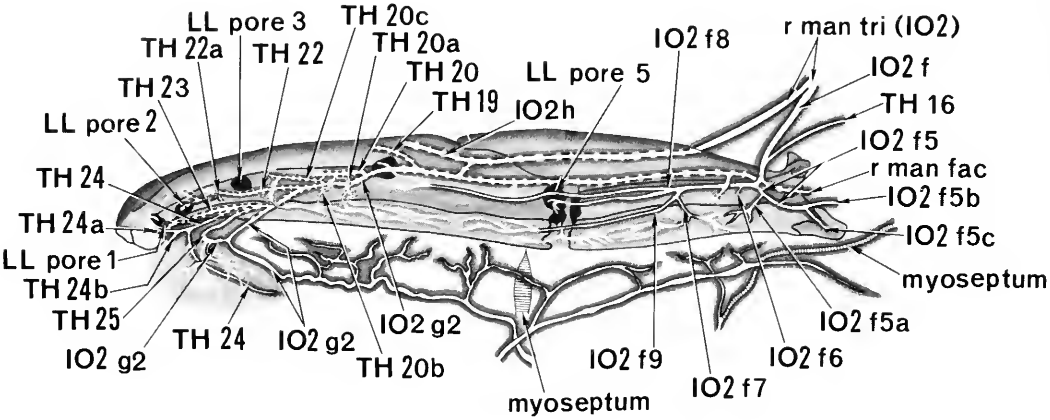


FIGURE 9. *Polycentrus schomburgkii*. Ventral view of branches of ramus mandibularis trigeminus and r. mand. facialis to lower jaw.

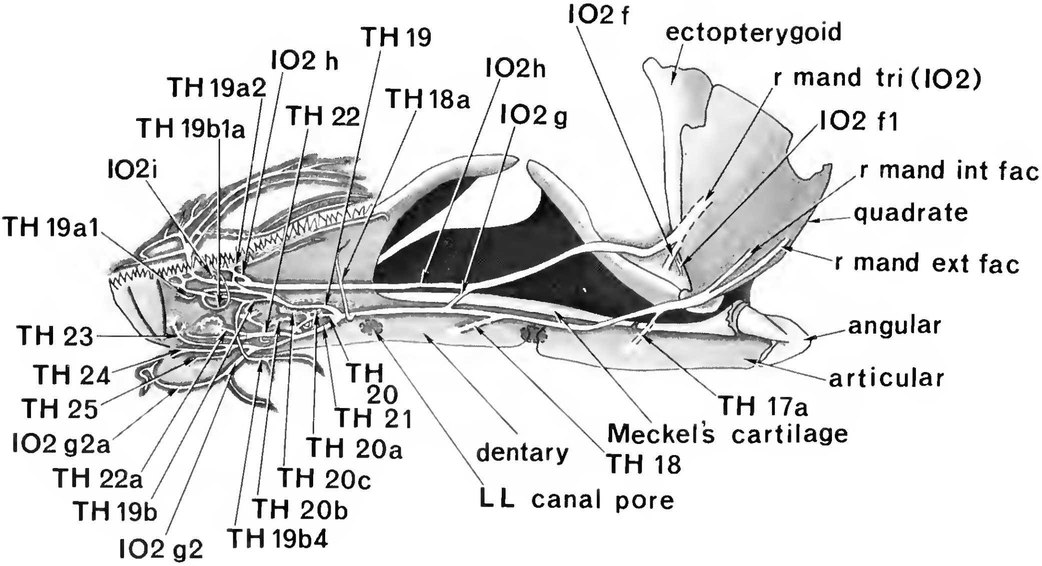
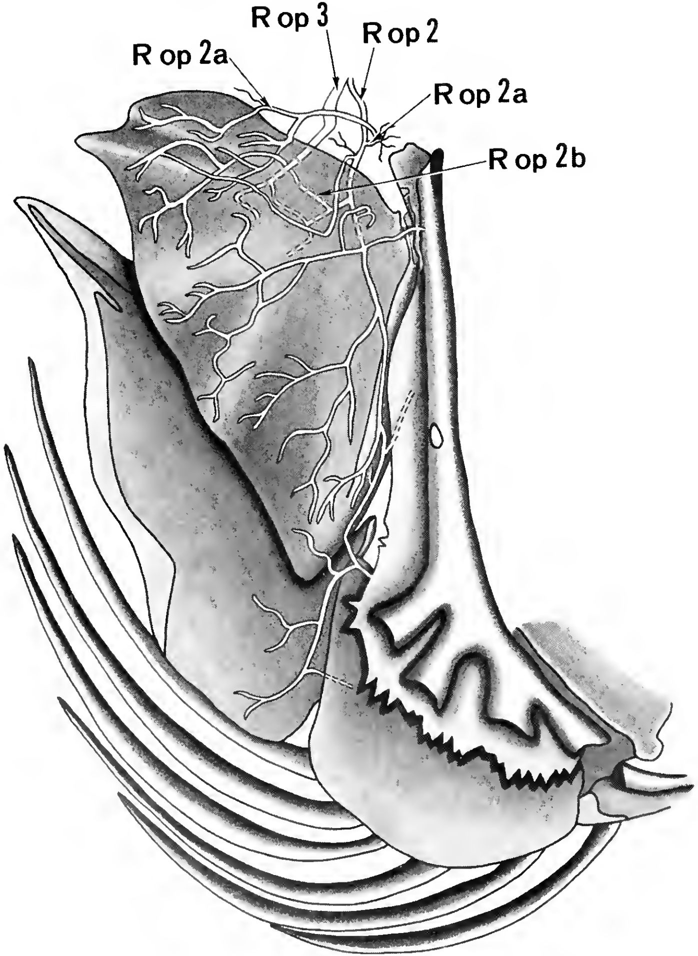


FIGURE 10. *Polycentrus schomburgkii*. Medial view of lower jaw showing some innervation of dentary region.



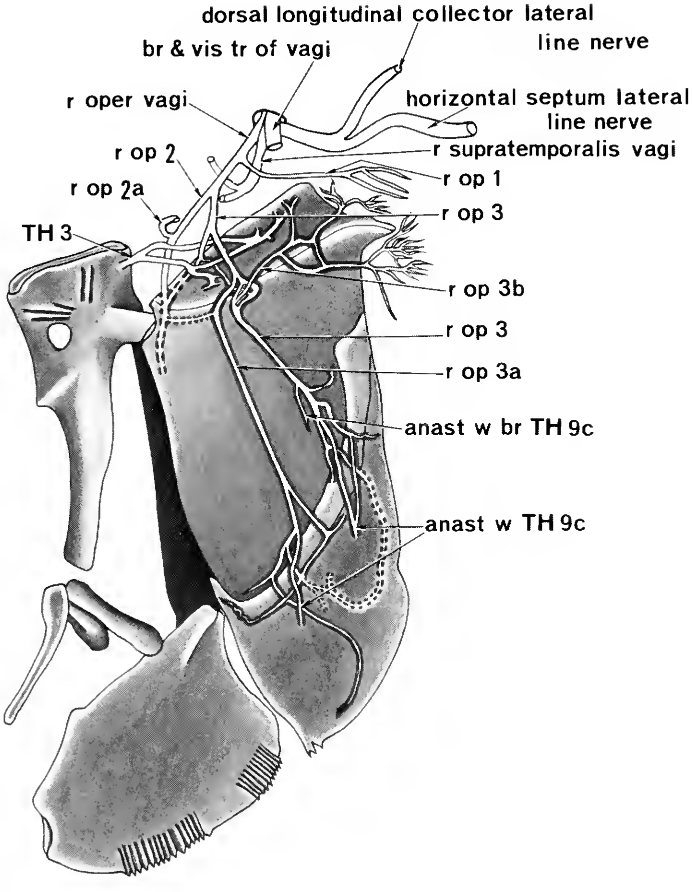


FIGURE 11 (Left). *Polycentrus schomburgkii*. Lateral view of opercular bones showing branches of ramus opercularis vagi to lateral surface of opercle.

FIGURE 12 (Right). *Polycentrus schomburgkii*. Medial view of opercular bones showing some branches of ramus opercularis vagi.

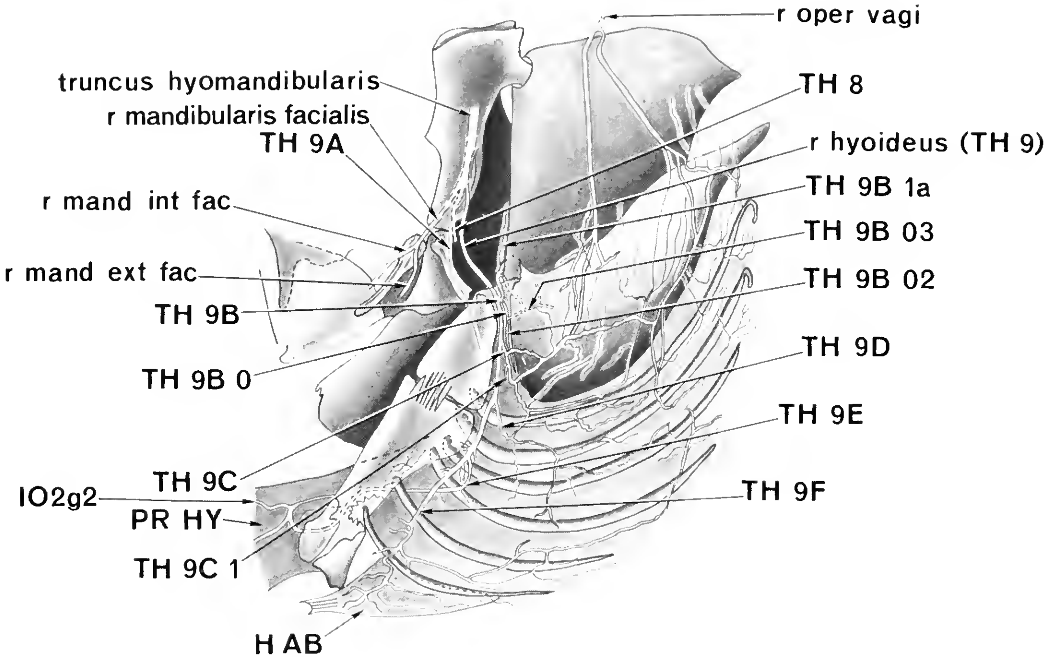


FIGURE 13. *Polycentrus schomburgkii*. Medial view of hyoid arch and opercular bones showing distribution of ramus hyoideus.

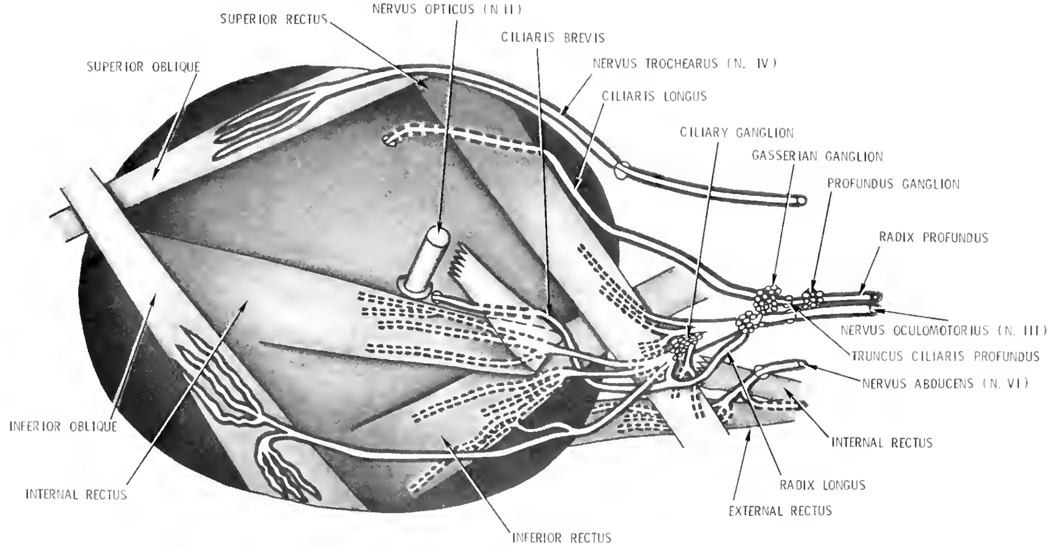


FIGURE 14. *Polycentrus schomburgkii*. Medial view of eyeball and eye muscles showing distribution of cranial nerves III, IV, and VI, and ramus profundus.

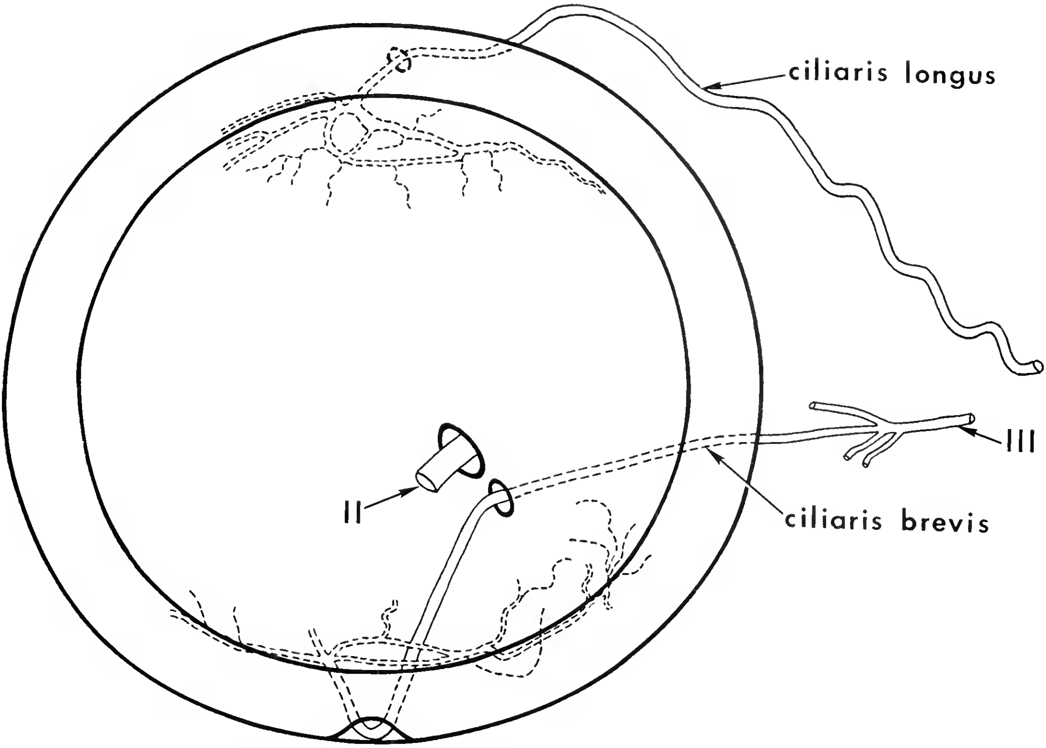


FIGURE 15. *Polycentrus schomburgkii*. Medial view of eyeball showing branches of ciliaris longus and ciliaris brevis of radix profundus.

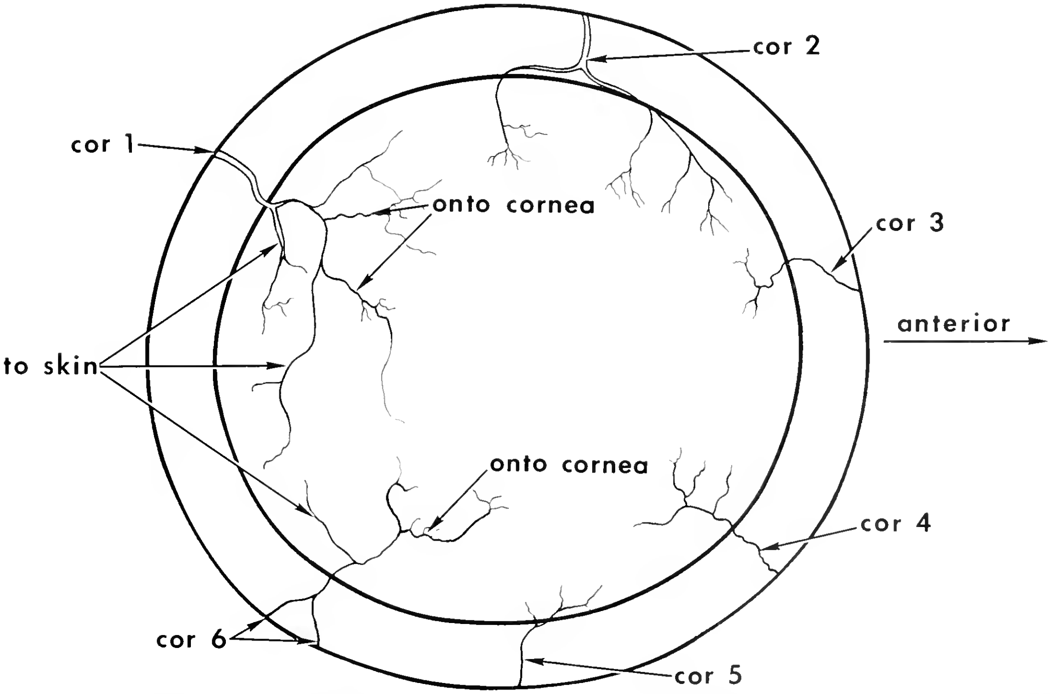


FIGURE 16. *Polycentrus schomburgkii*. Lateral view of eyeball showing branches of supraorbital and infraorbital trunks innervating skin and cornea.

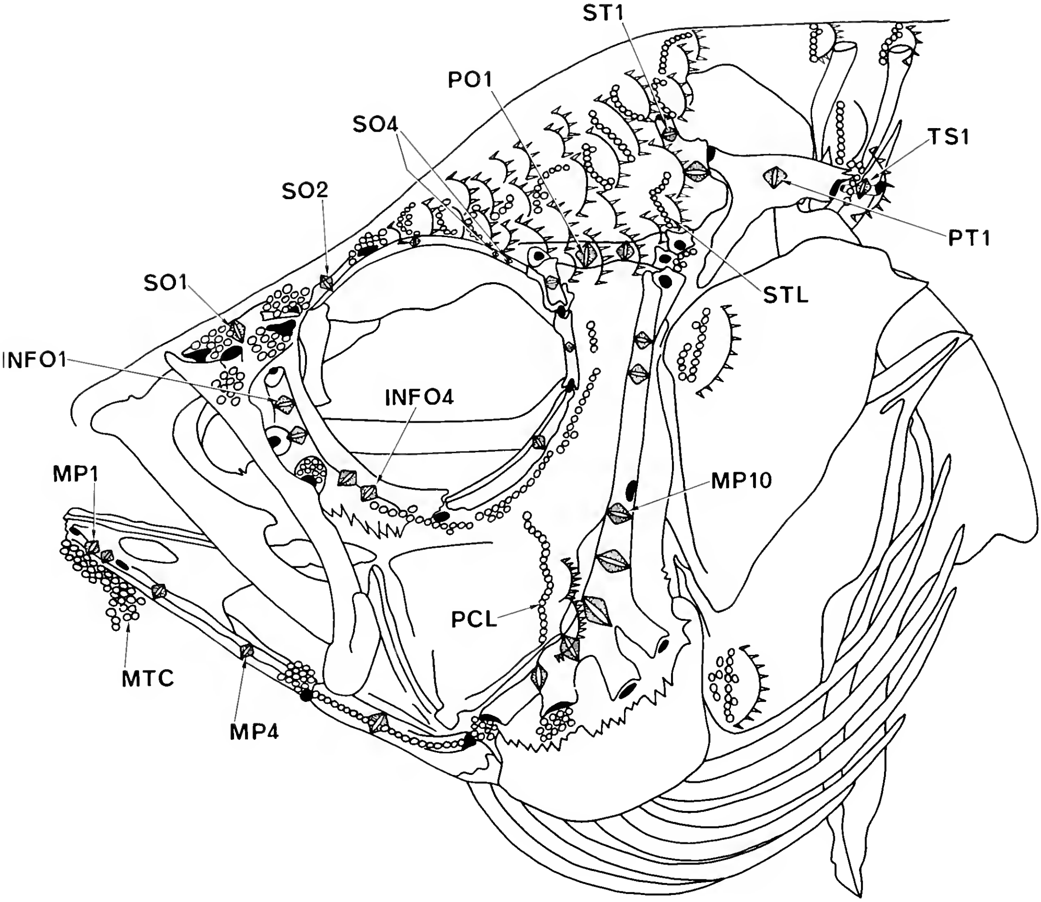


FIGURE 17. *Polycentrus schomburgkii*. Lateral view of head showing distribution of free lateralis organs (open circles), canal neuromasts (paired triangles), and canal pores (black circles).

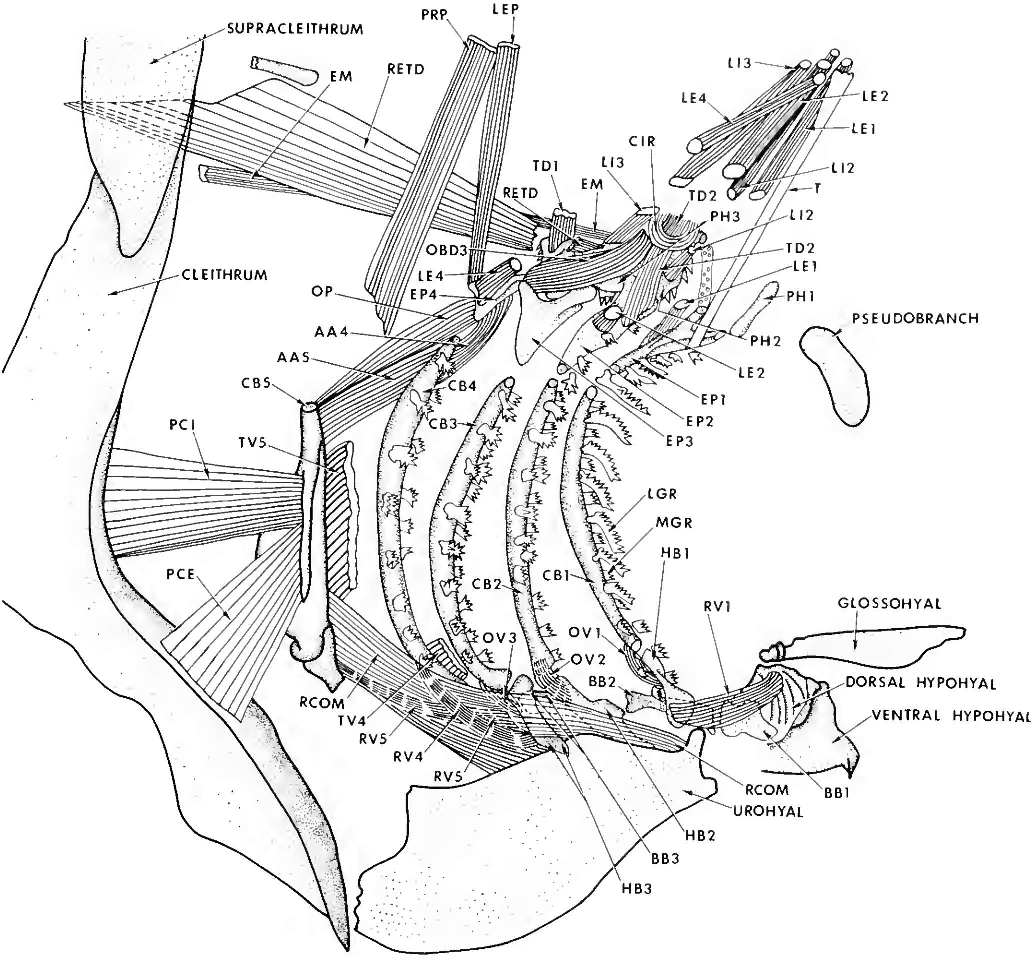


FIGURE 18. *Polycentrus schomburgkii*. Lateral view of gill arches and pectoral girdle showing associated gill arch muscles. Anterior to right.

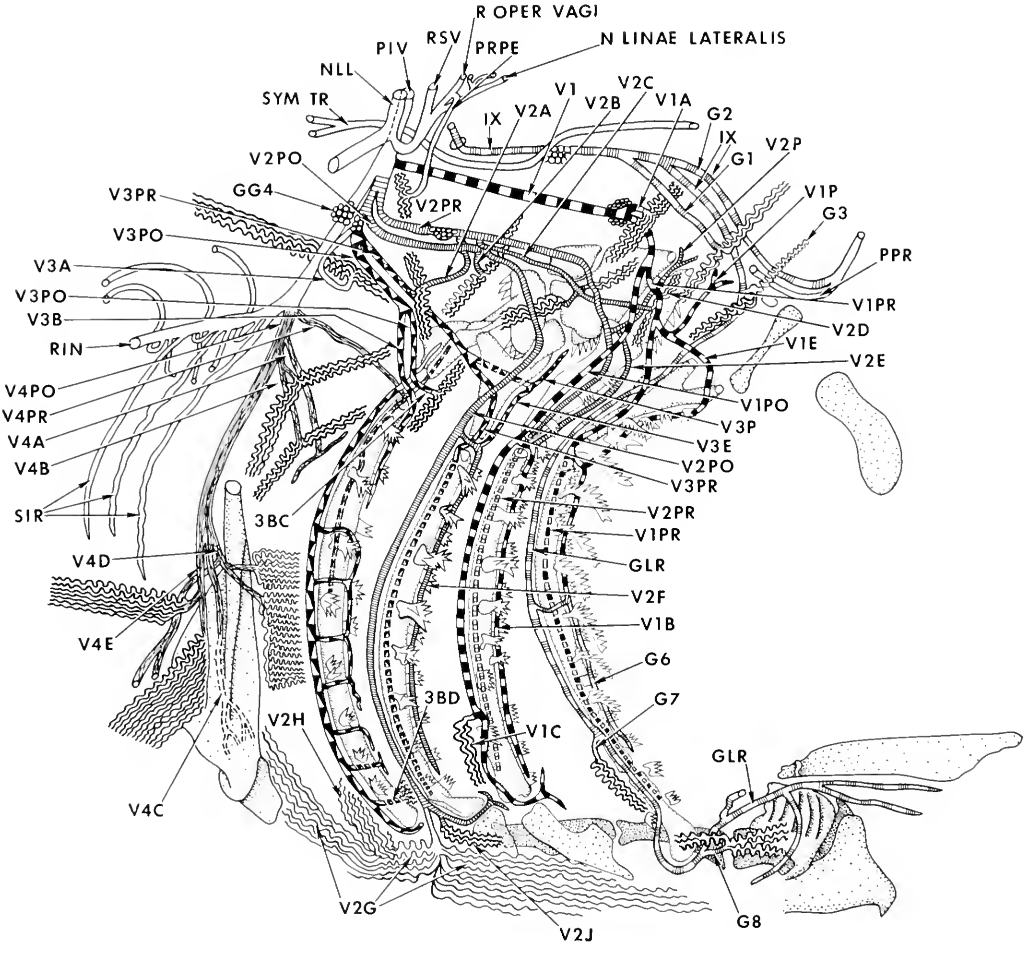


FIGURE 19. *Polycentrus schomburgkii*. Lateral view of gill arches showing innervation.

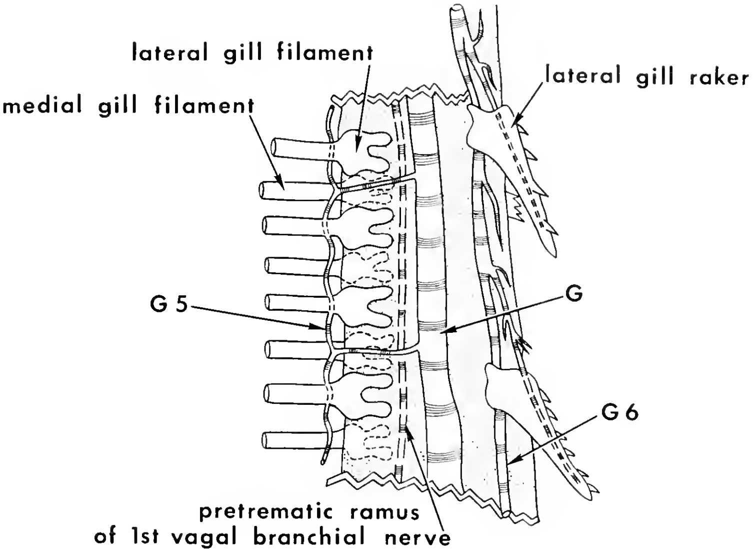


FIGURE 20. *Polycentrus schomburgkii*. Lateral view of ceratobranchial section of first gill arch showing details of innervation of branches of glossopharyngeal nerve.

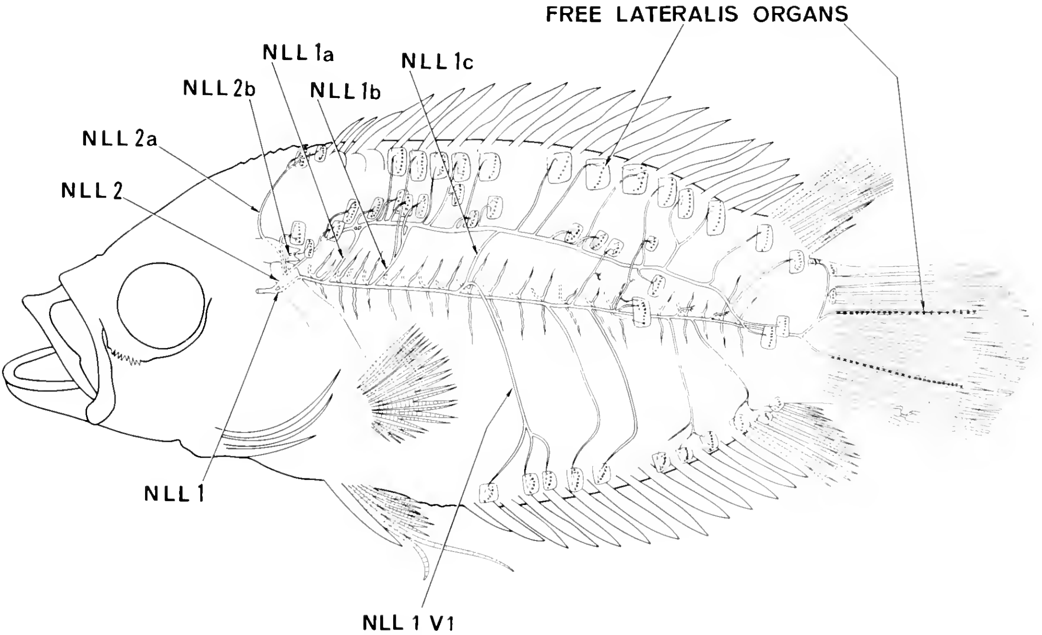


FIGURE 21. *Polycentrus schomburgkii*. Lateral view showing trunk lateral line nerves.

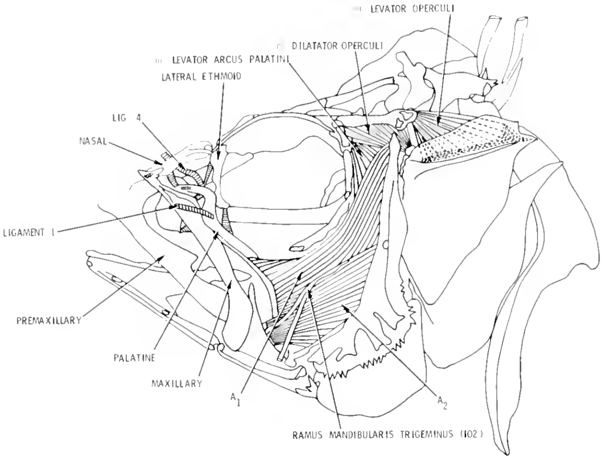


FIGURE 22. *Polycentrus schomburgkii*. Lateral view of head showing opercular and superficial cheek muscles and jaw ligaments.

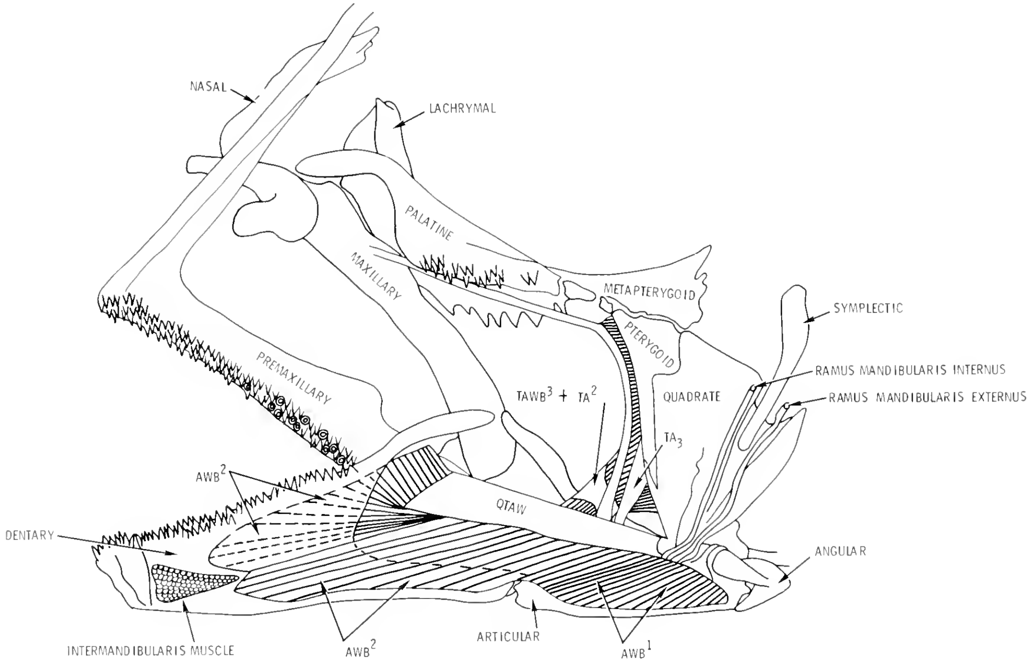


FIGURE 23. *Polycentrus schomburgkii*. Medial view of jaws and associated bones showing tendons of jaw muscles and mentalis (A_w) muscle.

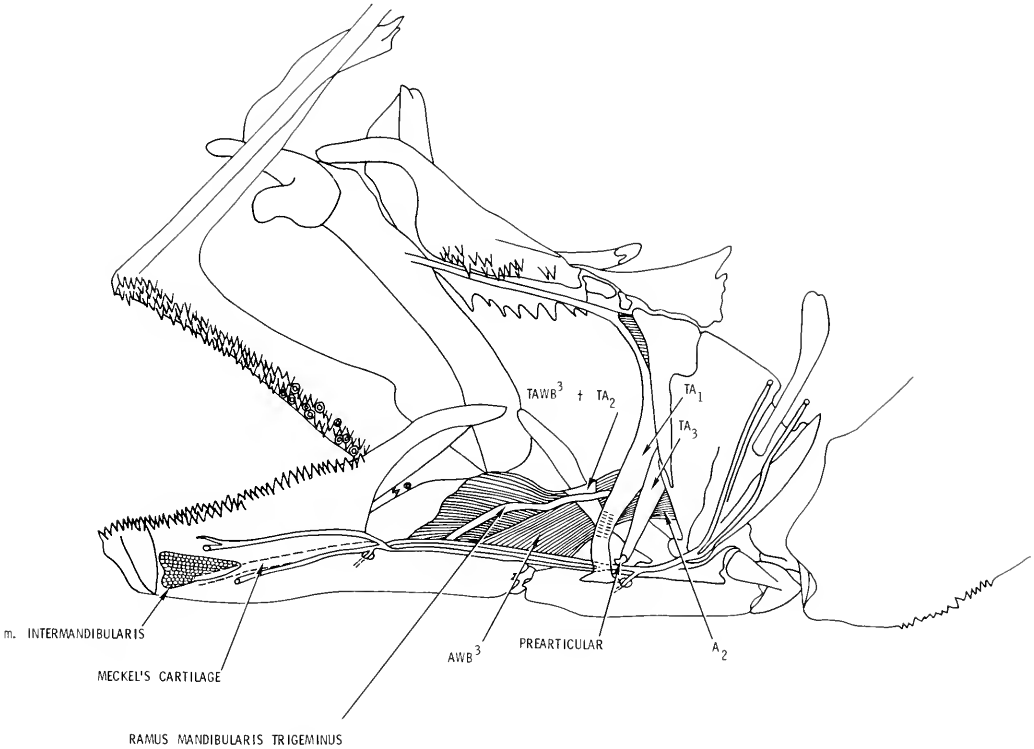


FIGURE 24. *Polycentrus schomburgkii*. Medial view of jaws showing insertion of adductor mandibulae muscles and tendons.

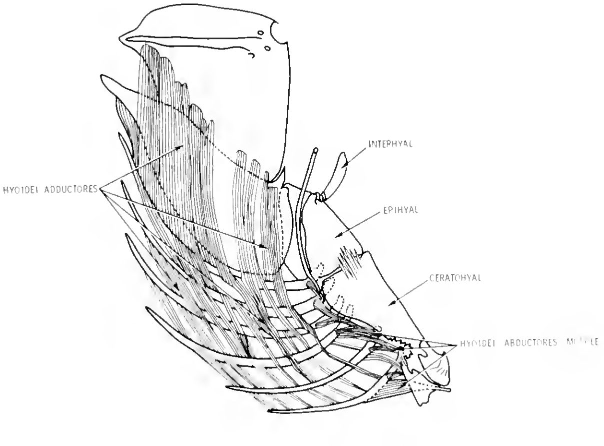


FIGURE 25. *Polycentrus schomburgkii*. Medial view of opercle and hyoid arch showing hyohyoideus muscle.

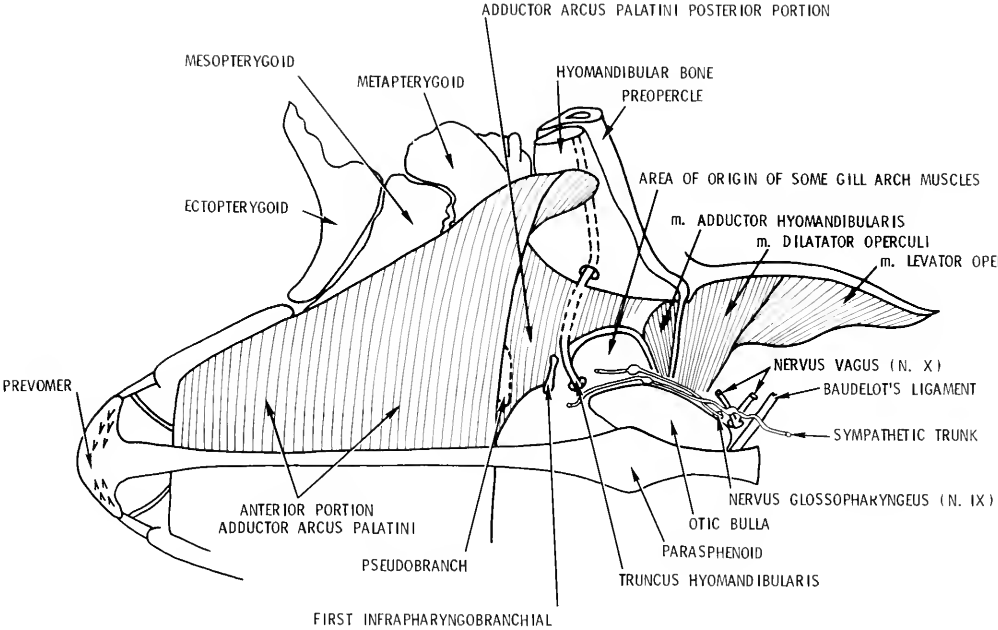


FIGURE 26. *Polycentrus schomburgkii*. Ventral view of palate and rear of cranium showing muscles of palate, hyomandibular, and opercle.

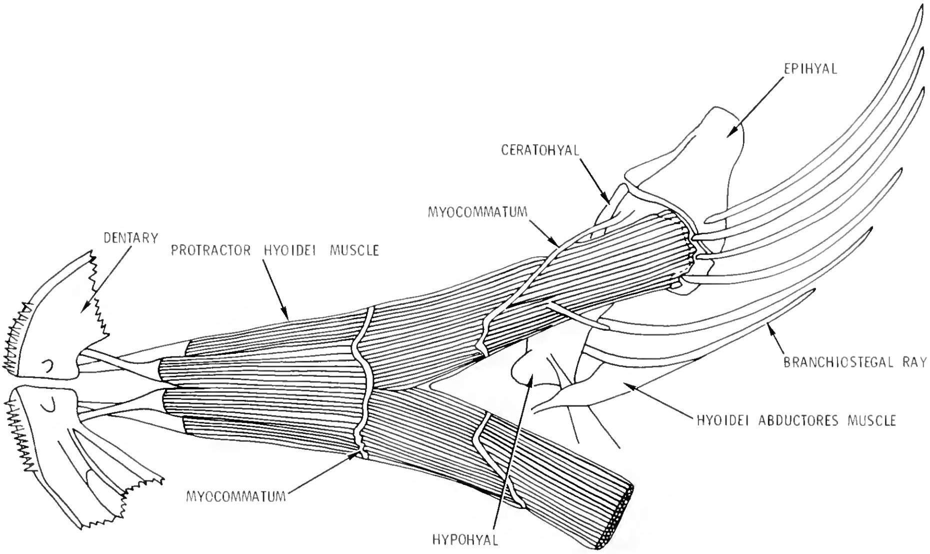


FIGURE 27. *Polycentrus schomburgkii*. Ventral view of protractor hyoidei muscle, tip of lower jaw, and part of hyoid arch.

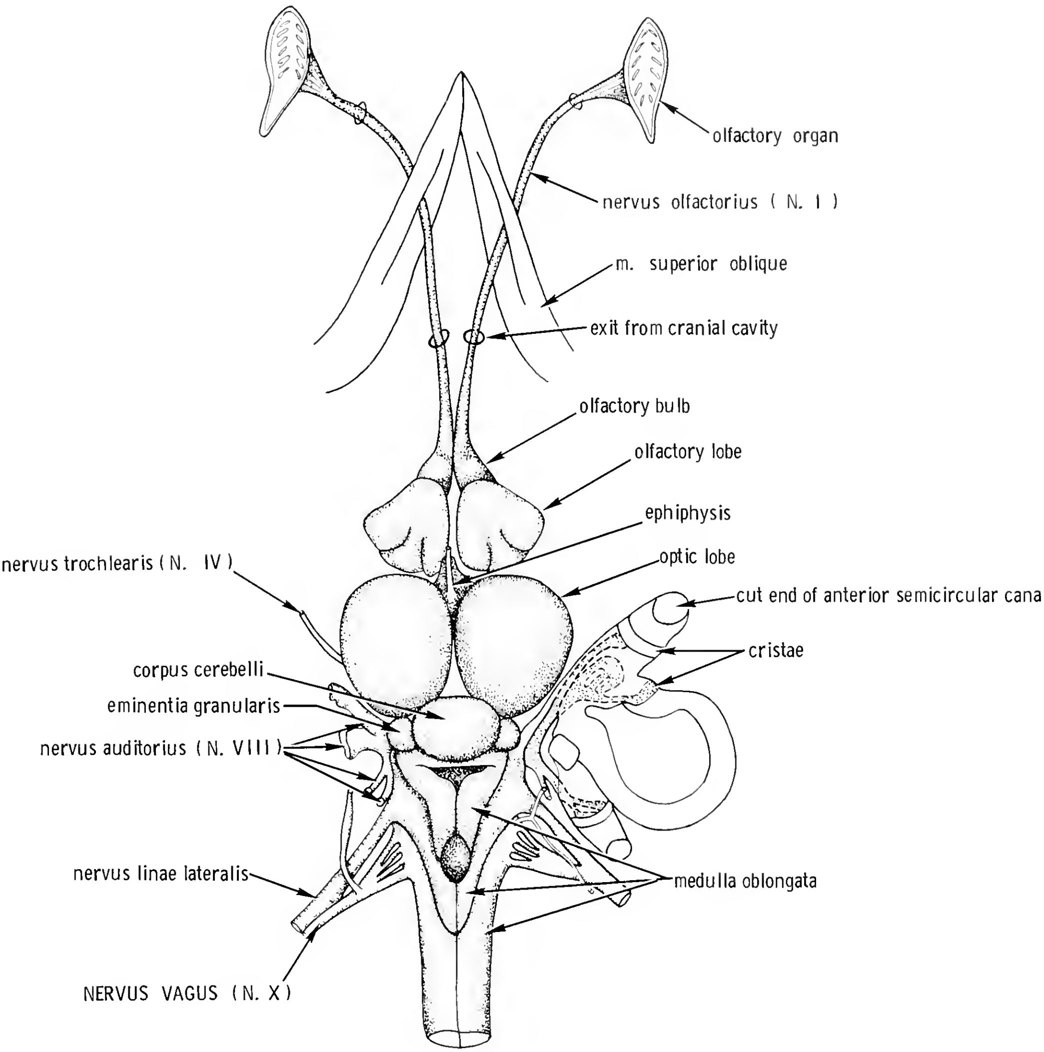


FIGURE 28. *Polycentrus schomburgkii*. Dorsal view of brain and nerve roots.

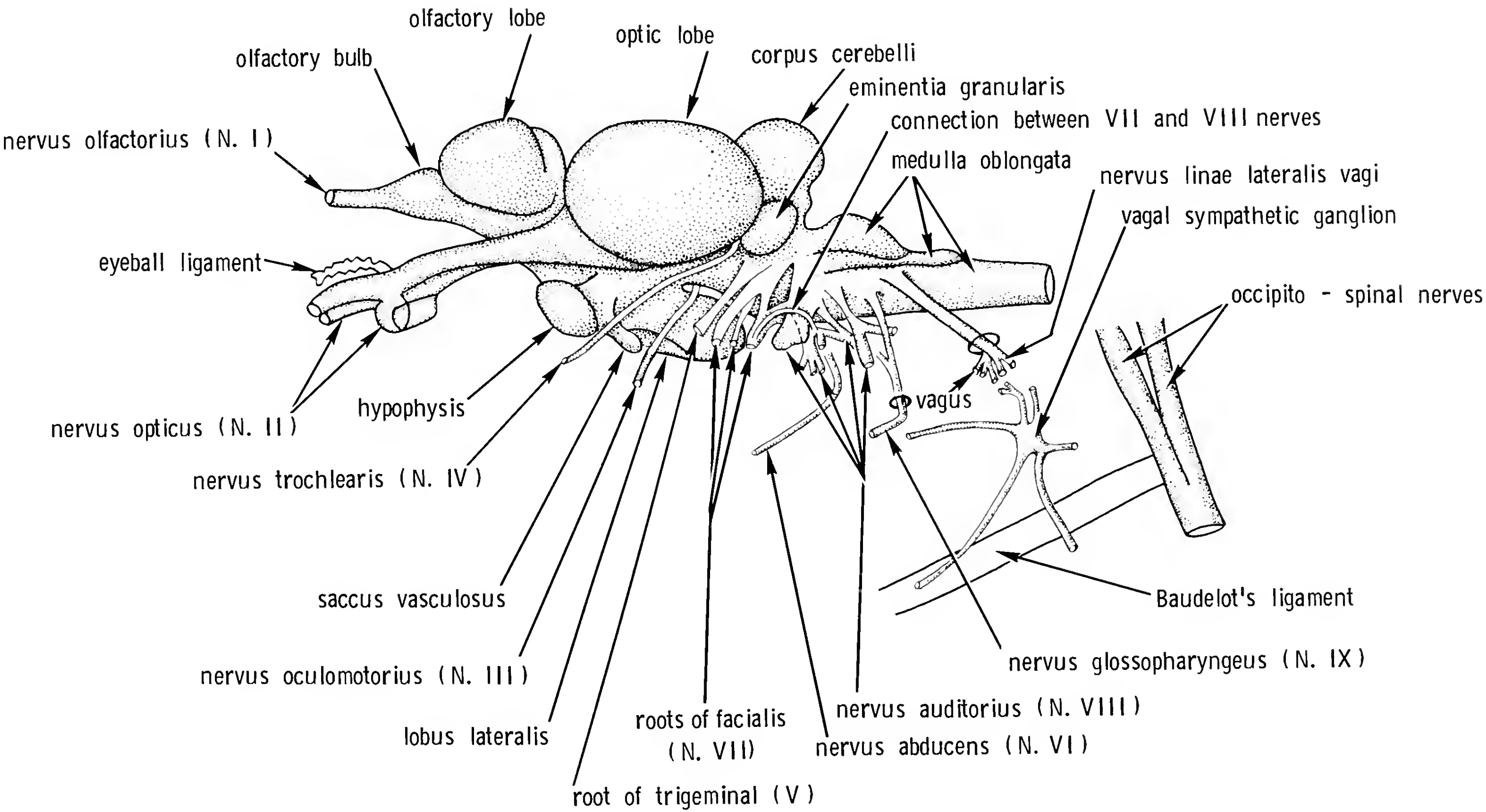


FIGURE 29. *Polycentrus schomburgkii*. Lateral view of brain and nerve roots.

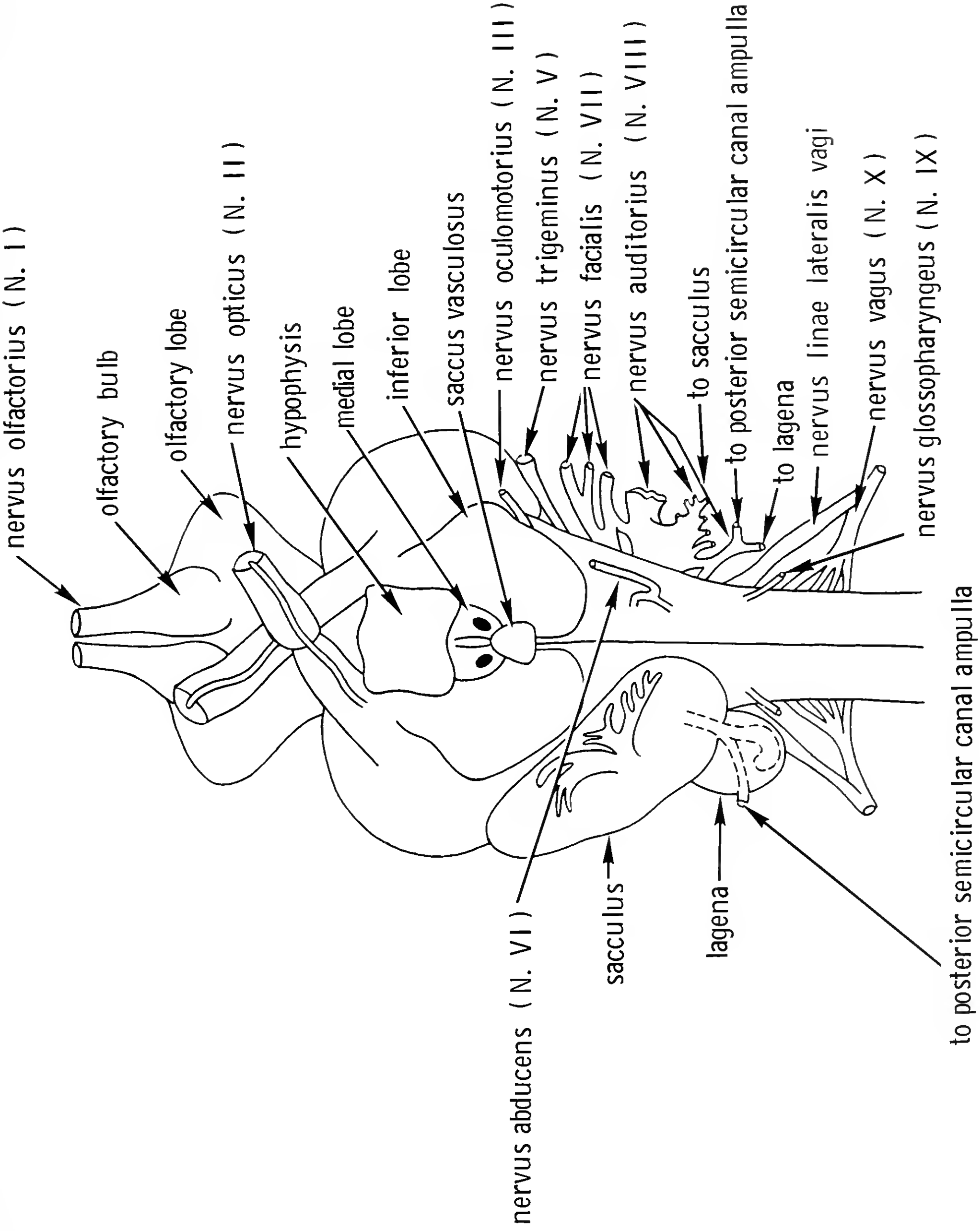


FIGURE 30. *Polycentrus schomburgkii.* Ventral view of brain and nerve roots.

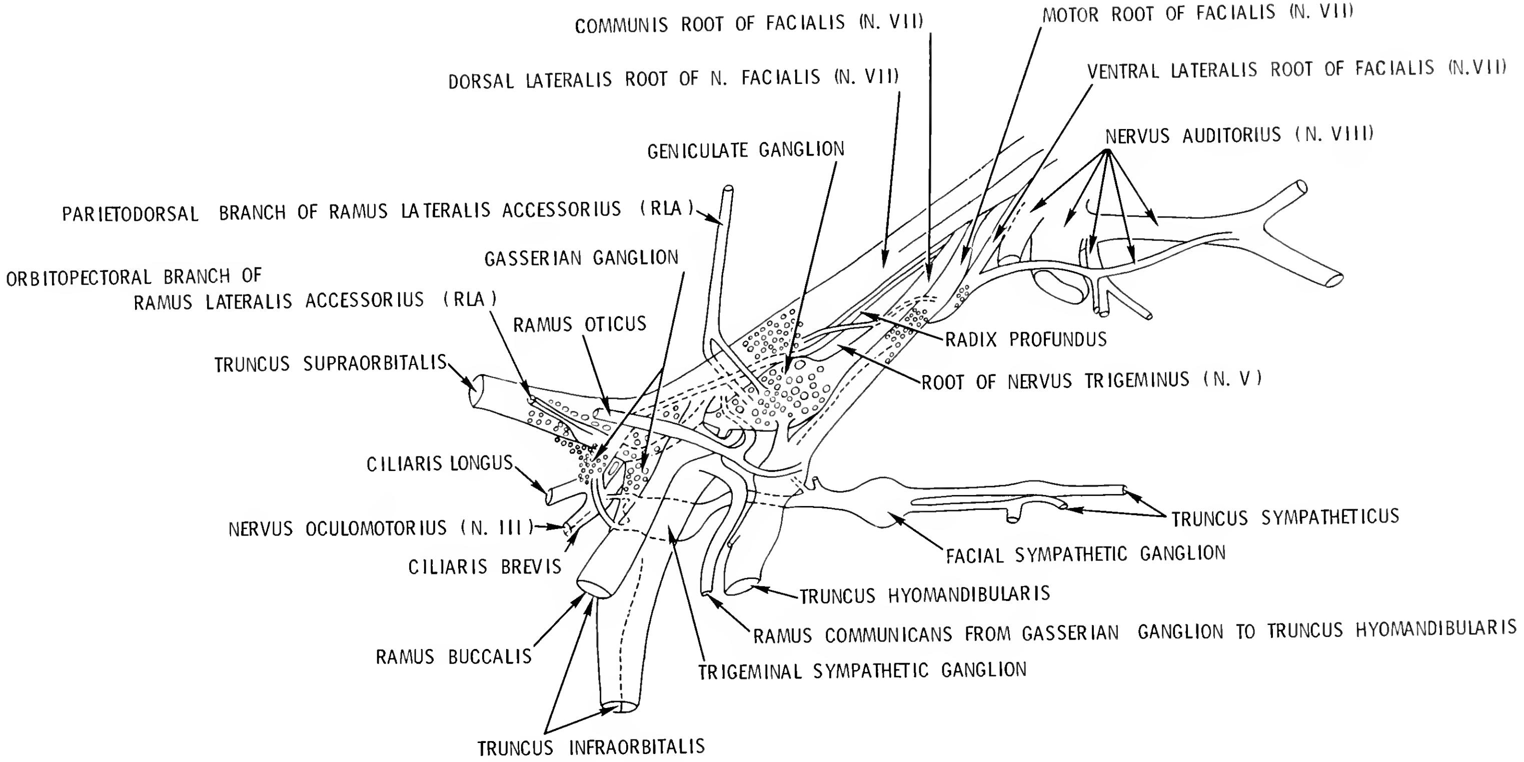


FIGURE 31. *Polycentrus schomburgkii*. Left lateral view of nerve roots and ganglia of trigemino-facialis complex. Drawn from a dissection. Gasserian ganglion cells shown as small circles at bases of supraorbital and infraorbital trunks.