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RAKERS, AND OLFACTORY BULB LOCATION IN
ATHERINIFORM, MUGILID, AND PERCOID FISHES[1]

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INTRODUCTION

The present paper reports on the patterns of trunk lateral line nerves in atheriniform and mugilid fishes and compares the patterns in these fishes with the patterns in percopsiform and percoid fishes and in various lower-placed fishes. The forward position of the olfactory bulb and the presence of gill rakers on the hyoid arch in the mugilid Agonostomus monticola are also described. The significance of the new facts is discussed for mugilid, percoid, and atheriniform classification and relationships.

Lateral line nerves on the trunk have been little utilized in the classification of fishes.[2] This is ironically

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[2]The trunk region of fishes is defined here as that part of the body which lies between the hind end of the cranium and the last caudal vertebra but exclusive of the fins. The term body includes the head, trunk, and fins.

true for atheriniform fishes, many of which have no lateral
line tubed scale row or almost none; yet all of which have
a complex pattern of lateral line trunk nerves. This fact
happens to be of considerable systematic significance. The
primary feature of these patterns is the presence of a
greater or lesser number of ventral segmental lateral line
branches of the main horizontal septum nerve. Until recently
(Freihofer, 1970) the ventral segmental trunk lateralis
branches in fishes had been reported on only once (Handrick,
1901). Numerous kinds of fishes other than atheriniforms
have rather elaborate patterns of these nerves or some modi-
fication of them.

The nerves were studied on specimens prepared by the
Sihler technique of staining nerves in a cleared whole speci-
men (Freihofer, 1966; Fraser & Freihofer, 1971). No serially
sectioned preparations were made. Agonostomus monticola was
examined by dissection of alcoholic specimens.

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EXPLANATION OF TERMS

    The different branches named in the descriptions of the
trunk lateral line nerve patterns are briefly defined as
follows. The horizontal septum nerve, which is the main
trunk lateral line branch of the vagus nerve, courses along
the horizontal septum for the length of the trunk. Dorsal
and ventral segmental rami are branches of the horizontal
septum nerve. They pass dorsally or ventrally in the segment
of the trunk in which they arise. They do not leave that
segment. The ventral segmental rami extend at least halfway
towards the midventral line of the body, usually almost to
it. The dorsal rami usually reach less than halfway to the
middorsal line. The lateral rami, one in each body segment,
are short branches of the horizontal septum lateral line
nerve. They innervate lateralis organs in the tubed lateral
line scales or naked lateralis organs in the skin along the
horizontal septum. If the lateral line scale row lies dorsal
to the horizontal septum, it is these lateral rami that

extend dorsally to innervate the lateral line. For a dorsal-
ly placed lateral line, the rami innervating it usually turn
posteriorly upon reaching the lateral line scale row and
course for a few segments thus overlapping the next few seg-
mental rami. The dorsally placed longitudinal nerve formed
by the dorsal longitudinal rami supplying the lateral line
scale row is called, in this report, a dorsal longitudinal
collector nerve. The dorsal longitudinal collector nerve is
a characteristic of acanthopterygian fishes. It is not
present in fishes placed lower than paracanthopterygians in
the Greenwood et al. classification. Some higher paracanthop-
terygians approach the collector nerve condition. The
collector-like nerve seems to be a significant feature as far
as is presently known. To be distinguished from the dorsal
longitudinal collector nerve is the dorsal longitudinal ramus,
of which two may be present. Each originates from the hori-
zontal septum nerve in the area of the supracleithrum, passes
dorsally some distance before turning posteriorly, and crosses
numerous body segments. The dorsal longitudinal rami con-
trast with the dorsal longitudinal collector nerve in that
each dorsal longitudinal ramus is composed of only one ramus.
In some patterns of trunk lateral line nerves the dorsal,
lateral, and ventral rami of each segment detach from the
horizontal septum nerve as a common ramus which upon reaching
the skin divides into the three segmental rami. This is
true for Umbra, Percopsis, Aphredoderus, and some other forms
examined.
     The following descriptions are preliminary. They are
presented primarily to report on their apparent systematic
significance. In future studies these nerves should be
studied by serially sectioned and stained preparations to
check the end organs of these nerves and to determine whether
or not any branches contain other than lateralis fibers.
Many other genera and families should also be studied. The
systematic significance of the trunk patterns is discussed
for the higher taxonomic categories, but not for the intra-
familial and only partly for the interfamilial categories.

TRUNK LATERAL LINE NERVES IN XENOMUGIL THOBURNI
(Figure 1.)

     The description which follows is made from several speci-
mens of the mugilid Xenomugil thoburni collected at the Gal-
apagos Islands. The trunk lateral line pattern of branching
in Xenomugil consists of five main parts: the midlateral
trunk nerve lying along the horizontal septum; a small first
dorsal longitudinal ramus and a large second dorsal longi-
tudinal ramus; a large ventral branch to the pectoral-pelvic
area; and a large midlateral ventral longitudinal branch.
The two dorsal longitudinal rami come off as a common trunk
from the main lateral line nerve at a point medial to
Baudelot's ligament. The small first dorsal longitudinal
ramus is the most anterior branch and apparently is equiva-
lent to the dorsal longitudinal ramus of most fishes. It

crosses the medial side of the supracleithrum, arches dorsal-
ly nearly to the middorsal line, and then courses posteriorly,
ending in skin a little past the base of the pectoral fin.
The large second dorsal longitudinal ramus emerges from be-
hind the posterior edge of the supracleithrum and passes pos-
teriorly at a level halfway between the horizontal septum and
the dorsal fin. It terminates in skin a little beyond the
end of the spinous first dorsal fin. At the point where the
main trunk lateral line nerve passes medial to the cleithrum,
the large pectoral-pelvic branch arises. The pectoral-pelvic
branch crosses the medial surface of the supracleithrum and
cleithrum and rises to skin along the posterior edge of the
second postcleithrum below the pectoral fin. From here it
follows along the postcleithrum towards the pelvic fin and
terminates in skin a short distance beyond the base of this
fin. En route a sizable branch is detached which innervates
scales over the base of the pectoral fin and scales more an-
teriorly towards the isthmus. En route to the pelvic fin other
branches are given off, innervating scales ventral to the pec-
toral fin and scales between it and the pelvic fin. Five
branches arise on caudal peduncle.

DISTRIBUTION OF PORED LATERALIS SCALES IN XENOMUGIL THOBURNI

     Almost every trunk scale of Xenomugil thoburni has a
small horizontal tube and pore apparently for a lateralis or-
gan. These pored lateralis scales are present even along the
base of the spinous dorsal and anal fins and part-way out on
the caudal fin base. The lateralis tubes on these scales are
tiny compared to the large tubes on the few lateralis scales
on the head. On a few scales in front of and below the pec-
toral fin, either the entire tube or only its posterior half
is vertical. There are fewer tubes in the midlateral area
between the soft dorsal and anal fins. A few scales near the
isthmus each have two tubes.

               TRUNK LATERAL LINE NERVES IN ATHERINOPS AFFINIS
                         (Figure 2.)

     In the atherinid Atherinops affinis, the horizontal sep-
tum lateral line nerve extends from the shoulder girdle to
the base of the caudal fin where it divides, each half pass-
ing obliquely and distally out across the caudal fin rays.
Along its length the horizontal septum nerve gives off dorsal
and ventral segmental rami. There is one dorsal segmental
lateralis ramus for each of the first twelve segments. In
the next 22 segments there are only 3 dorsal segmental rami.
Each of the last 6 segments has a dorsal segmental ramus to
give a total of 21 rami. The first longitudinal dorsal ramus
arches upwards from behind the supracleithrum, reaches almost
to the middorsal line, and extends posteriorly nearly to the
dorsal fin. There are 23 to 26 ventral segmental rami in the
approximately 45 trunk segments. Each ventral segmental

ramus nearly reaches the midventral line. There is an en-
larged ventral pectoral branch, which passes down medial to
the pectoral fin. It comes from behind the pectoral fin
base and innervates lateral line organs ventral to the pec-
toral fin. In some specimens the first two ventral segmen-
tal rami may unite distally and serve the pectoral area. In
a segment lacking a ventral segmental ramus, one of the ven-
tral segmental rami adjacent to that segment divides and sup-
plies the segment. What there is of a tubed scaled lateral
line in Atherinops is described in the next section.

DISTRIBUTION OF TUBED LATERALIS SCALES IN ATHERINOPS AFFINIS
(Figure 3.)

Tubed lateralis scales occurred in the following main
areas on one specimen of Atherinops affinis (number of tubed
scales in parentheses): below and anterior to the pectoral
fin (9); along base of anal fin (6); between base of pectoral
and pelvic fins (12), with none near the horizontal septum;
along base of pelvic fin (6); in area halfway up from mid-
ventral line and between end of anal fin and caudal peduncle
(6); in last seven scales in the row above the midlateral
red muscle band near end of caudal peduncle (3); above the
midlateral red muscle band and just above dorsal edge of
horizontal pectoral fin (6); above the red muscle band and
above the pelvic area (3). Along the red muscle band itself
there is one tubed scale near the cleithrum, one on a verti-
cal above the anterior end of the pelvic fin, and in the
last 21 scales before the base of the caudal fin there are
4 tubed scales and 5 scales with only the pore and no tube;
on the base of caudal fin there are 2 tubed scales along the
midline and one tubed scale above and one below this row of
two scales. There are 2 tubed scales between the end of the
pelvic fin and the front end of the anal fin. These two
scales lie several rows above the row of tubed scales next to
the pelvic and anal fins. In the area between the pelvic
row and the red muscle band there are 3 scattered tubed scales.
All other areas of the trunk are devoid of tubed or pored
scales. A related atherinid, Leuresthes tenuis, shows a
similar distribution of tubed lateralis scales.

TRUNK LATERAL LINE NERVES IN PERCOPSIS TRANSMONTANA
(Figure 4.)

In Percopsis transmontana (= Columbia transmontana)
there are approximately 42 ventral segmental rami of the hori-
zontal septum nerve, one to each trunk segment. Behind the
supracleithrum two branches detach more or less together from
the horizontal septum nerve. One is the dorsal longitudinal
ramus, which almost reaches the origin of the dorsal fin.
The other branch is the first dorsal collector ramus of the
incipient longitudinal collector nerve. It is followed by

three or four other main collector rami for the collector
nerve.   Each collector ramus passes dorsally a short distance
up to the tubed lateral line scale row, which extends the
length of the trunk, and then turns posteriorly and continues
for a number of segments.   Each dorsal collector ramus over-
laps the following collector ramus for several segments.   The
first branch of the first collector ramus is large and passes
ventrally down the posterior edge of the pectoral girdle and
innervates naked lateralis organs in skin ventral and anterior
to the pectoral fin and organs in the skin between the pec-
toral and pelvic fins.   This large branch detaching from the
first collector ramus is an enlarged first ventral segmental
ramus.   It may be joined by the second ventral segmental
ramus in some specimens.   In addition to the ventral segmen-
tal rami, there are also dorsal segmental rami, one to each
segment, and lateral segmental rami, one to each segment.
These three segmental rami, the dorsal, lateral, and ventral,
may all leave the horizontal septum nerve as one common ramus
in each segment.   In the anterior third of the trunk these
common rami detach from the incipient longitudinal collector
nerve, pass to the overlying skin, and divide into the three
rami per segment--the dorsal, lateral, and ventral rami.   The
lateral rami innervate the overlying tubed lateral line
scales.   In the posterior two-thirds of the trunk, a greater
number of common rami detach from the horizontal septum nerve.
Each may have a small connection to the longitudinal collec-
tor nerve.   All that seems to detach from the dwindling in-
cipient longitudinal collector nerve in the posterior half
of the body is a short dorsal ramus in each segment that in-
nervates lateralis organs in the tubed lateral line scale
row.   The longitudinal collector nerve ends on the caudal
peduncle.
     The pattern in Aphredoderus sayanus is much like that in
Percopsis transmontana except that in Aphredoderus both the
tubed lateral line scale row and the dorsal longitudinal col-
lector nerve are more dorsally situated.   In Aphredoderus
the tubed lateral line scale row ends a little past the origin
of the dorsal fin except for a few widely separated tubed
lateral line scales along the remainder of the horizontal
septum.   The dorsal longitudinal collector lateral line nerve
is rudimentary in Percopsis.   A similar but much higher placed
collector nerve is a prominent feature in acanthopterygian
and higher paracanthopterygian fishes.   It has not yet been
found in lower fishes.   The collector nerve pattern is not
present in the atheriniform fishes so far examined nor is it
present in mugilids.   It occurs in sphyraenids and polynemids
but in Sphyraena barracuda it is not much more developed than
in Percopsis.

             LATERAL LINE NERVES IN OTHER ATHERINIFORM FISHES
                         (Figures 5 and 6.)

     In Melanotaenia nigrans (Melanotaeniidae) there is a
large middorsal longitudinal ramus extending halfway between
the horizontal septum and the middorsal line.   It passes up

from behind the cleithrum and ends about midway below the soft dorsal fin. There is no pectoral ventral lateralis ramus. The first ventral segmental ramus lies between the seventh and eighth ribs and is followed by about a dozen longer ventral segmental rami. There are no tubed lateralis scales.

In an exocoetid and a hemiramphid (both unidentified) there is a large pectoral ventral lateralis ramus detached from the main lateralis nerve medial to the cleithrum. It supplies the tubed lateralis scales of the lateral line as the lateral line passes vertically down behind the pectoral fin, and also supplies the extension of the lateral line nearly to the isthmus. There are about 9 subsequent ventral rami, each turning posteriorly near the ventral midline and innervating numerous lateral line scales. In another species of hemiramphid, the enlarged pectoral branch was present, and, beginning about the fifth rib, there was almost one ventral ramus to each segment.

In the cyprinodontid _Profundulus guatamalensis_ there are 2 longitudinal dorsal rami that pass up from behind the cleithrum and course back as far as the middle of the soft dorsal fin. Each detaches separately from the main lateral line nerve. The first segmental ventral ramus begins at the level of pelvic fin origin. There are about 10 subsequent ventral rami. There are no tubed lateralis scales of the lateral line system.

In the oryziatid _Oryzias latipes_ (fig. 5) there are 2 longitudinal dorsal rami coming off together from the main lateral line nerve, a large pectoral ventral lateralis ramus and 4 or 5 succeeding ventral lateralis rami. Three specimens were examined.

In the cyprinodontid _Rivulus milesi_ there is apparently only one dorsal ramus, no pectoral ramus, and no ventral segmental rami. The main horizontal septum nerve appears to give off only a short ramus for each overlying naked lateralis organ or organs.

In the cyprinodontid _Pachypanchax playfairi_ (fig. 6) there are 2 longitudinal dorsal rami coming off together above the cleithrum and about 8 subsequent ventral rami, the first of which lies near the base of the pectoral fin and is the largest. There are no tubed lateralis scales in the lateral line.

TRUNK LATERAL LINE NERVES IN LOWER FISHES

In osmerids (_Spirinchus thaleichthys_) and in clupeids (_Dorosoma petenense_) there is a full development of the lateralis nerves very similar to that in _Percopsis_ and _Atherinops_. In salmonids (_Salmo_ and _Oncorhynchus_) there is a horizontal septum nerve with a short lateral ramus supplying each tubed lateralis scale, but no ventral segmental lateralis rami, only one dorsal longitudinal ramus, and no development of a dorsal longitudinal collector nerve.

The myctophoid _Scopelengys tristis_ has a first dorsal longitudinal ramus extending towards the dorsal fin. From near the base of the first dorsal longitudinal ramus there is

a longitudinal horizontal ramus overlying the horizontal septum nerve and innervating about the first nine segments of the lateral line scale row. There are no ventral lateralis rami from the horizontal septum nerve.

TRUNK LATERAL LINE NERVES IN PERCA FLAVESCENS
(Figure 7.)

In Perca flavescens the lateral line tubed scale row lies about halfway towards the middorsal line and forms a gentle curve from the supracleithrum back to about one-third of the way along the caudal peduncle where it returns to the horizontal septum. The horizontal septum lateral line nerve runs from the supracleithrum back to where it bifurcates at the base of the caudal fin; the dorsal fork passes out to the tip of the caudal fin between the fourth and fifth rays from the midline of the fin; the ventral fork passes out between the third and fourth rays of the ventral lobe. The first dorsal longitudinal ramus reaches nearly to the dorsal fin. In the anterior curved section of the lateral line, the 7 short dorsal rami pass some distance dorsally up to the lateral line where each ramus turns posteriorly and extends along the lateral line supplying from 3 to 10 lateral line scales, the more anterior rami supplying the greater number of scales. These short dorsal longitudinal rami forming the dorsally placed "collector" nerve constitute the characteristic feature of the pattern in Perca. Posterior to the point of return of the tubed lateral line scale row to the horizontal septum on the caudal peduncle each lateral line scale is innervated by a short lateral ramus of the horizontal septum nerve. The pattern in Perca is basically present in approximately 20 acanthopterygian families examined so far. The trunk lateral line nerves of the sparid Spondyliosoma cantharus and the skipjack tuna, Katsuwonus pelamis, have been illustrated by Suckling (1967). Some paracanthopterygians have a similar pattern, for example Gadus (Stannius, 1847) and Otophidium, but no fishes lower than paracanthopterygians are known to have the dorsal longitudinal collector nerve pattern.

RAMUS CANALIS LATERALIS FACIALIS SYSTEM

The ramus canalis lateralis facialis system of nerves consists of branches that in lower fishes usually course lengthwise in the membranous roof of the cephalic lateral line canals (Freihofer, 1970). Most of them arise in the upper cheek region from a branch coming up from the truncus hyomandibularis at a point near the articulation of the opercle with the hyomandibular. The ramus canalis lateralis facialis system is well developed in percopsiforms (reduced or absent in higher paracanthopterygians), well developed in gobioids, present in a simpler state in umbrids and clupeids, present but reduced in beryciforms, and apparently present but still more reduced in some of the most generalized percoids such as acropomatids, scombropids, centropomids and some others; it is well developed in apogonids. The system

is not present and apparently has been lost in atheriniforms. Its absence sets off all of the atheriniforms from most of the other fishes having ventral segmental trunk lateral line nerves.

POSITION OF OLFACTORY BULB IN AGONOSTOMUS AND PERCOPSIS
(Figures 8 and 9.)

Most fishes have the olfactory bulb located at the forebrain. The olfactory bulb is located about two-thirds of the way towards the olfactory organ from the forebrain in Mugil auratus (Holl, 1967). In Agonostomus monticola the olfactory bulb is located at, or nearly at, the olfactory organ and is large. About one-third of the olfactory bulb lies within the concavity of the ethmoid cartilage leading to the very short canal through which the olfactory nerve connects with the olfactory organ. On one specimen examined, the length of the olfactory tract is about one-half the length of the olfactory bulb. The olfactory bulb is about two-thirds the length of both the olfactory lobes and the rest of forebrain lobe. In another specimen of Agonostomus monticola of five inches total length, the distance between the olfactory bulb and olfactory lobe is about six times the length of the olfactory bulb or equal to the length of the forebrain and midbrain. The olfactory bulb in Percopsis omiscomaycus (fig. 9) is also located at or next to the olfactory organ (Freihofer, 1960a; 1960b; Gosline, 1963). In the mugilids Joturus picardi and Valamugil seheli, the olfactory bulb is also at the olfactory organ.

DISCUSSION

Trunk lateral line nerves lend support to the systematic validity of the order Atheriniformes proposed by Rosen (1964). All of the atheriniform fishes examined have ventral segmental trunk lateralis nerves that detach from the main horizontal septum lateral line nerve. These trunk lateralis nerves set apart the atheriniform fishes from the perciform and beryciform fishes which do not have these nerves or a modification of them, but which have instead a dorsally placed "collector-like" longitudinal trunk lateral line nerve formed by branches from the horizontal septum lateral line nerve. The mugilids are an exception to this statement and are discussed below. The ventral segmental trunk lateral line nerves also connect the atheriniform fishes with various lower-placed soft-rayed groups. Comparison of the various patterns of these nerves within the Atheriniformes raises some interesting systematic questions.
The family Atherinidae apparently has the fullest development of the trunk lateralis nerves amongst atheriniform fishes. The other atheriniform groups examined have simpler patterns in that they have fewer ventral branches; Atherinops affinis has 23 to 26 ventral segmental trunk lateralis branches, whereas Oryzias has about 5. In Oryzias there is

an enlarged first ventral branch serving the pectoral and pelvic areas. In the cyprinodont Pachypanchax playfairi there is a smaller pectoral branch. It is followed by 8 ventral rami. In the exocoetids and hemiramphids there is an enlarged pectoral branch and about 9 succeeding ventral branches, each of which in some species turns posteriorly and innervates several lateral line scales. The family Melanotaeniidae has fewer ventral branches than do atherinid fishes judging from one species examined, Melanotaenia nigrans.

Comparison of these ventral segmental trunk lateral line nerves in atheriniform fishes with those in other groups gives an indication of which may be the generalized pattern of these nerves in the atheriniforms. Other groups having these nerves in a pattern similar to that in the Atherinidae are the percopsiforms, osmerids, umbrids, stomiatoids, and clupeids. Judging from comparisons with these groups, it seems most reasonable that the pattern in the Atherinidae is the generalized condition and that the patterns in the exocoetids, hemiramphids,and cyprinodontoids are derived, specialized patterns. On the basis of these lateralis nerves, the Atherinidae, therefore, would be the most generalized atheriniform family and the other atheriniforms may have evolved from an atherinid-like ancestor. Spines in the fins of atheriniforms would then be the generalized condition and fins without spines the advanced condition. The jaws of atherinid fishes appear no more specialized, perhaps less specialized, than those of other families. The same holds for the caudal fin skeleton. These and some other systematic interpretations of atheriniform, mugilid, and sphyrainid fishes differ somewhat from the interpretations in recent papers and are discussed at the end of this report.

The pattern of trunk lateral line nerves suggests what fishes may be the nearest relatives of atheriniforms. As was mentioned above, other groups having a basically similar pattern of trunk lateralis nerves are the percopsiforms, osmerids, umbrids, stomiatoids, and clupeids. The clupeids are morphologically too different to be considered close to the atheriniforms. Stomiatoids evidently are specialized offshoots from an osmerid type ancestor (Weitzman, 1967). The development of the trunk lateral line nerves looks simpler in umbrids than in osmerids, while the ramus canalis lateralis facialis system in umbrids is simpler than that in Percopsis and about as developed as, but somewhat different from, that in osmerids. The percopsiforms not only have a pattern of trunk lateralis nerves more similar to that of the atherinids, but they also have in Aphredoderus (but not in Percopsis) apparently the same basic pattern of the recurrent facial nerve (RLA). Percopsiforms have spines in their fins as do atherinids, whereas osmerids and umbrids lack both spinous fins and RLA. The caudal fin structure of atherinids could feasibly be derived from a percopsid type caudal fin. In reference to atherinid relationships it would be desirable to have hybridization experiments between atherinids and percopsiforms carried further. Those made by Clark Hubbs (1970) between Menidia audens and Aphredoderus sayanus

terminated before gastrulation and so were not deemed suc-
cessful.   Perhaps further attempts using other atherinids
with both Percopsis and Aphredoderus would be successful.
     The myctophoids do not seem as likely to be as close to
the origin of atheriniforms as do the percopsiforms. Mycto-
phoids lack ventral segmental trunk lateral line nerves
judging from Ray (1950) for Lampanyctus leucopsarus and from
a Sihler nerve preparation of Scopelengys tristis. As far as
is known myctophoids also lack the recurrent facial nerve
(RLA). Salmonids (Salmo gairdneri and Oncorhynchus tschawyts-
cha) lack the ventral segmental trunk lateralis nerves, RLA,
and the ramus canalis lateralis facialis system.
     It has been hypothesized (Freihofer, 1970) that the per-
copsiform fishes and the myctophoids have each evolved from
an osmerid-like ancestor. In this connection the interesting
similarity between true smelts and atherinids may be indica-
tive of an actual relationship of atherinids to osmerids by
way of percopsiform-like intermediate ancestors. (In teach-
ing we have had to apologize to students and to ourselves
that the top smelts, Atherinops affinis, family Atherinidae,
are not related to surf smelts, Hypomesus pretiosus, family
Osmeridae. We still may apologize but perhaps now we will
do so with less conviction that the common names are com-
pletely misleading.) Artificial hybridization experiments
between surf smelts and top smelts or some other osmerid-
atherinid combinations should be worth trying (fig. 12).
     Returning to the trunk lateral line system in the Ather-
iniformes, it seems evident from comparing the distribution
of nerves and tubed lateral line scales in Atherinops affinis
(figs. 2 and 3) with the ventrally placed tubed lateral line
scale row in a hemiramphid or exocoetid that the evolutionary
sequence of formation of the ventral exocoetoid lateral line
may have been somewhat as follows. In the generalized hypo-
thetical atherinid ancestor there was a regular midlateral
tubed lateral line scale row and, in addition, naked later-
alis organs scattered over much of the body but most numerous
ventrally and anterodorsally as occurs in Percopsis. These
naked lateralis organs would be innervated by ventral seg-
mental trunk lateralis nerves. A later stage would be forma-
tion of scattered lateral line tubed scales towards the ven-
tral side of the trunk as well as some towards the anteromid-
dorsal line together with the simultaneous beginning of
dissolution of the midlateral lateral line scale row, a stage
approximated in Atherinops affinis. Lastly there would be
the organization of a ventral tubed scaled lateral line from
the initial ventrally scattered tubed lateralis scales and
the disappearance of the anterodorsal incipient lateral line
and the midlateral lateral line. The ventral naked lateralis
organs and the ventral segmental trunk lateralis nerves such
as occur in percopsiform fishes would be a preadaptation to
the formation of such a ventral lateral line scale row. A sim-
ilar but not as advanced ventral lateralis system developed
in some paracanthopterygians. An alternative explanation to
the evolution of the ventral lateral line in exocoetoids is
that the whole midlateral lateral line gradually moved more
ventrally with the nerves that supply each lateral line scale

continually lengthening and keeping up with the lateral line
scales, but this process would not be necessary since the
atherinid ancestors apparently already had long ventral seg-
mental lateral line nerves in the ventral areas. This alter-
native explanation, however, may hold for the part-way
ventral lateral line of many cyprinoid fishes which do not
have ventral segmental lateralis rami reaching almost to the
midventral line.

In comparing trunk lateral lines in Xenomugil (fig. 1)
with those in the Acanthopterygii, Atheriniformes, Paracan-
thopterygii (especially with Percopsis), osmerids, salmonids,
and clupeids, it is seen that the trunk lateral line nerve
pattern of Xenomugil has two major features in common with
patterns in the Atheriniformes, Paracanthopterygii, osmerids,
and clupeids. These features are that there is a first ven-
tral segmental lateralis ramus which is usually enlarged and
serves as a pectoral branch and that there are present one
or more additional ventral lateralis rami. In Xenomugil the
single ventral ramus in addition to the pectoral ventral
ramus extends longitudinally over a number of segments thus
taking the place of a series of individual ventral segmental
rami. In another mugilid from Australia, Myxus elongatus,
there are two ventral rami instead of one in addition to the
pectoral ramus. In Xenomugil the pectoral branch is large
and serves the ventral region back to and for a short dis-
tance past the pelvic fin. Xenomugil also has two dorsal
longitudinal rami as has also Atherinops, Oryzias, and
Pachypanchax. Xenomugil also has pored lateralis scales
over much of the body, a feature which is not found in per-
coidean fishes but which is a lateralis feature similar to
the scattered lateral line scales in atherinids. Thus in
pattern of trunk lateral line nerves, Xenomugil is like the
paracanthopterygians and atheriniforms and unlike the acan-
thopterygians. These basic similarities in the pattern of
trunk lateral line nerves plus the general morphological
similarities mugilids have to atherinoid fishes suggest that
the origin of mugilid fishes might be looked for either in
an atherinomorph or a percopsiform type of fish. There are
several additional morphological features that point more to
the percopsiforms as being closer to ancestors of mugilids.

Agonostomus monticola, a mugilid occurring in fresh water
in Central America has, as described above, the olfactory
bulb located far forward, very close to the olfactory organ
and not at the forebrain, where it is located in most teleosts.
Some species at least of the mugilid genera Joturus and Mugil
also have the olfactory bulb far forward. The only other
teleosts at all close to mugilids that also have it located
at or near the olfactory organ are Percopsis and the gadid
fishes. The olfactory bulb is at the forebrain in Aphre-
doderus.

A fact that by itself is not important is that in
Agonostomus there are small, toothless fleshy structures re-
sembling gill rakers on the hyoid arch (fig. 10). It is sug-
gested here that these structures in Agonostomus monticola
are rudimentary gill rakers. Gill rakers are not present as
far as is known on the hyoid arch of atheriniforms, acanthop-
terygians, or any paracanthopterygians except Percopsis,

which has a series of toothed plates along the hyoid arch
that apparently are the remnants of gill rakers. Neither the
toothed plates nor the rakers are present in Aphredoderus.
Amia calva has hyoid gill rakers and so do a few other lower
fishes. Toothed plates that undoubtedly are remnants from
gill rakers that were once present occur on the hyoid arch of
the beryciform fish, Polymixia lowei, which is another simi-
larity it has to Percopsis. Agonostomus monticola was the
only species among those of several genera of mugilids ex-
amined that had gill raker-like structures on the hyoid arch.
Rather tall and long-based projections tapering to blunt
points are present on the ceratohyal of the maenid Smaris
macrophthalmus. Structures are present on the prominent fold
of skin lying along the edge of the hyoid arch of the hexa-
grammid Hexagrammos decagrammus that strongly resemble the
toothless or nearly toothless gill rakers of the first gill
arch. Generalized scorpaenoids examined such as species of
Sebastes, Helicolenus, Ectreposebastes, and Setarches lack
gill raker-like structures on the hyoid arch. Generalized
percoids examined lack such structures also. It would appear
that the structures noted on the hyoid arch in the percoid
Smaris macrophthalmus and in the scorpaenoid Hexagrammos
decagrammus are independently derived and may not be gill
rakers at all. The structures on the hyoid arch of the mugil-
id Agonostomus monticola may not be rudimentary gill rakers
either but in light of other similarities of mugilids to
atheriniforms and of atheriniforms to percopsiforms, it seems
probable that they are remnants of hyoid arch gill rakers.
Histological study of the structures are needed.

Mugilids have an A_1 jaw muscle that appears to be equiva-
lent to the A_1 of the gadid Microgadus proximus and one that
is similar to but not as developed as the A_1 of percoids.
The caudal fin skeleton of mugilids with its two epurals
could be derivable from that of a percopsiform type. The
mugilid pelvic girdle falls short of being fully thoracic
(Gosline, 1962). The mugilid anal fin is in an interesting
transitional state. It shows a third anal spine developing
with age from an articulated soft ray (Jacot, 1920; Hubbs,
1944). Specimens of Xenomugil thoburni of the same size
(three inches) exhibit the whole range from soft ray to pun-
gent spine for the third anal ray. The first ray of the
second dorsal fin in mugilids is also articulated but shows
considerable fusion towards becoming a spine. Either mugilids
are still in the early stages of development of spines from
soft rays or their spines are changing into soft rays. The
former alternative supports the hypothesis that mugilids are
offshoots from an ancestor that was in the early stages of
evolving spinous fins from soft-rayed fins.

Two other similarities of mugilids with percopsiforms
are worth noting. One is that the cephalic lateralis canals
in Agonostomus and perhaps in most mugilids are covered by
membrane, not by bone, and hence are open as in Percopsis,
osmerids, and paracanthopterygians in general. The open con-
dition in these fishes is apparently the generalized and not
the advanced state. The other similarity is that the lacri-
mal bone is serrated with strong teeth and looks much like
the lacrimal in Aphredoderus and the fossil percopsiform
Sphenocephalus.

There are, therefore, a number of specific morphological features that support the hypothesis that mugilids may have evolved from a percopsiform type of fish.

Another aspect of mugilids is that they are thought to have reached what is broadly called the percoid level of organization. Supporting this view is the fact that mugilids have a pattern of the recurrent facial nerve (RLA) like that of Serranus which has one of the main percoid patterns of RLA. According to Rosen (1964) mugilids, sphyraenids, and polynemids have their jaw skeleton, jaw musculature, and caudal fin, as well as almost all other structural complexes usually studied, constructed much like they are in percoids. This may be correct, but what the new facts reported here for mugilids indicate is that the percoid developments are associated with other structural states that are prepercoidean and some that specifically are percopsiform.

Sphyraenids and polynemids still need more study. The polynemid pattern of the recurrent facial nerve is not a Serranus pattern as reported earlier from dissection of a preserved specimen (Freihofer, 1960). New work (unpublished) on polynemids shows these fishes to have a pattern of the recurrent facial nerve much like that in scorpaenids. The scorpaenid pattern is most similar to the Serranus pattern as is also the pattern in polynemids. The polynemids also have a percoid or acanthopterygian pattern of trunk lateral line nerves. On this evidence polynemids would be further removed from the old percesocine affinities they have often been given. There is at present insufficient evidence of similarity of polynemids to other percoid families to place them in close relationship to any family of these fishes. The pattern of RLA if it is any yardstick of affinity would indicate that polynemids stand in the basal complex of early perciform evolution somewhere near the scorpaenoid line. Reflecting this possibility, the polynemids may be placed as a suborder before the Percoidei but with the notation that they apparently did not give rise to other percoids.

A similar problem exists with sphyraenids. They differ from atheriniform fishes in many structural complexes (Rosen, 1964) but they also have two important indications of a prepercoidean ancestry. One is the trunk lateral line pattern and the other is the pattern of the recurrent facial nerve (RLA). In Sphyraena barracuda the "collector" nerve is rudimentary. It lies very close to the horizontal septum lateral line nerve, and it is short, so short that it barely reaches beyond the tip of the pectoral fin before it returns to the horizontal septum. There are only two dorsal rami forming it. In percoids the collector nerve returns to the horizontal septum on the caudal peduncle. It also lies much more dorsally in percoids and has numerous dorsal rami composing it. The short and low condition of the longitudinal collector nerve may well not be the result of the elongate body form of barracudas. The trunk lateral line nerves in Sphyraena look suspiciously like they are partially in a prepercoid pattern.

In pattern of RLA, Sphyraena resembles Aphredoderus and Atherinops affinis. In these fishes RLA emerges from the

cranium through the parietal bone or from under its posterior
edge and courses back under the skin to the dorsal fin.   In
these fishes there is a dipping down of RLA towards the ver-
tebral column in the area of the pectoral fin.   It is at this
point or at the posterior end of the cranium that there are
apparent nerve fiber connections of RLA with crossing dorsal
rami of the occipitospinal or first spinal nerves.   Fibers
from RLA presumably could be distributed to the pectoral area
via the ventral rami of the spinal nerves in these fishes.
The nerve fiber connections of RLA with the spinal rami need
confirmation by special stain preparations showing the fiber
tracts.

The pattern of RLA appears to be basically the same in
Aphredoderus, atherinids, and sphyraenids and different from
patterns in other fishes so far examined.   If the details of
the fiber relations of RLA with the dorsal rami are correctly
interpreted here, then this similarity in RLA and in trunk
lateral line pattern would be of basic systematic importance
in setting up a relationship between these fishes.

The condition of the first ray of the second dorsal fin
in the Sphyraenidae may also indicate that sphyraenids are
descendants of fishes which were in the early stages of de-
veloping spines in their fins.   In sphyraenids the first ray
of the second dorsal fin has fused to the point of having lost
its articulations but not to the point of having lost its bi-
laterally double structure (Hubbs, 1944).   The two dorsal
fins are also widely separate in the sphyraenids as they are
in some other seemingly generalized early spiny-rayed fishes
(e.g., percopsiforms, atherinids, phallosthethoids, mugilids,
acropomatids, and apogonids).

The several features discussed for sphyraenids give
cause for questioning the present systematic placement of
barracudas (Greenwood et al., 1966) as a suborder of perciform
fishes presumably derived from a generalized percoid ancestor
of a hypothetical sea bass type as implied in Regan's (1913)
classification of percoid fishes.   An alternative view is
that sphyraenids, similarly to mugilids, have branched off
early from a percopsiform-like ancestor and attained some
percoid-like developments but did not reach a generalized
percoid level and are not percoid derivatives.   A reasonable
position for the barracudas for the present is as a suborder
placed before the suborder Percoidei and separate from the
Mugiloidei.

The possibility exists that similarities between some of
the atheriniform groups is the result of convergence and does
not indicate phylogenetic relationships.   It seems far more
likely that similarities between these fishes are due to
natural relationships.   There has not been any good demonstra-
tion of convergence in them.   Unless there is good anatomi-
cal evidence of convergence, the safer procedure is to accept
the similarities until convincing evidence of convergence is
available.   Otherwise one can be wrong for the right reasons.

If the superorder Atherinomorpha (Greenwood et al.,
1966) was proposed mainly on the basis of spines in the ather-
iniforms having been evolved independently from the spines in
other acanthopterygians, then the rank of superorder for the

atheriniforms should be abandoned. No reasons were given
for its creation. There is little or no evidence that the
nonspinous atheriniform fishes are the most generalized.
There is good evidence for the fact that spines in fins were
the generalized atheriniform condition and that spines were
present in the fins of their forebears.

The atheriniform fishes can be depicted as follows for
the three systems of nerves described and discussed in the
preceding sections. The ventral segmental trunk lateralis
nerves are well developed in the generalized forms such as
the Atherinidae, but are reduced in number of ventral rami in
more specialized forms. There is no evidence of a dorsal
longitudinal collector-like lateral line nerve. The recur-
rent facial nerves are present in atherinoids and exocoetoids
and are absent, presumably through loss, in cyprinodontoids,
the pattern of RLA present being most similar to that in
Aphredoderus. The ramus canalis lateralis facialis system
is apparently absent or not recognizable in atheriniforms.

The following changes in atheriniform and mugilid clas-
sification are recommended: that the atheriniforms be placed
in the superorder Acanthopterygii; that the basal family in
the order be the Atherinidae of the suborder Atherinoidei;
that the suborders Exocoetoidei and Cyprinodontoidei be con-
sidered as derivatives of an atherinid-like ancestral stock;
that the atheriniforms be shown in a phylogenetic classifi-
cation as descended from percopsiform ancestors; that the
mugilids be placed first as a suborder in the perciforms with
the notations that they did not give rise to other percoids
and that they are apparently atheriniform relatives but per-
copsiform derivatives as are possibly also the perciforms
and beryciforms.

Figure 11 shows the proposed systematic scheme for the
hypothetical origins and relationships of percopsiforms,
atheriniforms, perciforms, beryciforms, and paracanthop-
terygians.

Lastly, by way of summary, the broader systematic inter-
pretations discussed in the preceding pages are compared
with the interpretations of the most recent authors working
on atheriniform classification (see Gosline, 1962, 1963, 1968,
and 1971; Rosen, 1962, 1964; Greenwood et al., 1966; Rosen
and Patterson, 1969). A point of major difference between
the views of these workers and the views given in the present
paper concerns the origin of the atheriniform fishes. Rosen
(1964) postulated that the precursor of the atheriniforms may
have been basically of a hemiramphid form with an incipient
tendency to develop spinous rays but without a spinous or an-
terior dorsal fin. The view in the present paper is that the
precursor was basically of an atherinid form with a spinous
anterior dorsal fin. Rosen (1964) specifically argued against
any connection of atheriniforms with percopsiforms. Gosline
most recently (1971) thought that the origin of the cyprino-
donts was at about the percopsiform level of organization.
Such an origin may be correct, but the view expressed in the
present paper is that the cyprinodontoid fishes have evolved
from an atherinoid-like ancestor which in turn was derived
from a percopsiform-like ancestor. Anatomical studies by

Rosen (1964), and by the author in the present paper and hy-
bridization experiments by Clark Hubbs (1970) support the
hypothesis that cyprinodontoids have closer relationships to
atherinids than they do to percopsiforms. Gosline (1962)
pointed out similarities between cyprinodontoids and ather-
inids that would seem to indicate relationship, but then he
wrote that the similarities between these two groups could be
the result of adaptations to a common mode of life. He con-
cluded that the two groups were convergently alike and not
phylogenetically related. Little is known about the "mode
of life" of any of these fishes. Besides, the two groups
could have similar "modes of life" and be phylogenetically
related. Rosen (1964) concluded that cyprinodontoids and
atherinoids were part of a phylogenetically natural group in-
cluding also the phallostethoids, exocoetoids, scomberesocoids,
and adrianichthyoids. Evidence from particular groups of
nerves presented in the present paper supports Rosen's inter-
pretations. The nerve evidence does not support the placing
of the Atherinidae together with the Mugilidae, Sphyraenidae,
and Polynemidae as a suborder in the Perciformes as advocated
by Gosline (1971). The views presented in the present paper
agree with Gosline's consideration of the Mugilidae as an
early percoid-like group with a relationship to the Atherini-
dae and the placing of the Mugilidae as a suborder at the be-
ginning of the Perciformes. The further views advocated in
the present paper are that the Mugilidae is the lone family
in that suborder and that the relationships of the Mugilidae
to the Atherinidae are as two separate lines stemming from a
percopsiform-like ancestor. These points bear on Rosen's
conclusion (Rosen, 1964, p. 260) that mugilids, sphyraenids,
and polynemids are not separable from the Perciformes. The
nerve evidence supports the view that mugilids have an an-
cestral, lineal relationship to percopsiforms and a collat-
eral relationship with atheriniforms. Mugilids, therefore,
in a sense would be partially separable from perciforms. The
nerve evidence also supports the view that sphyraenids may have
a percopsiform or atheriniform relationship and that they
never were full percoids and were not derived from percoids.
Sphyraenids also would be in a sense partially separable from
perciforms. It has been suggested in the present study that,
although mugilids are percoids of a type, traces of their
ancestry are still apparent, an ancestry that is percopsi-
form and not beryciform. If a percopsiform ancestry is cor-
rect for mugilids, the most interesting new possibility is
that the same ancestry may also hold for the most generalized
percoids. The success of hybridization experiments (Clark
Hubbs, 1970) between the pirateperch, Aphredoderus sayanus,
and darters (family Percidae) seems to be significant sup-
port of such an ancestry.

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ADDENDUM

Partial list of material examined. The letters SU or CAS before a catalogue number indicate the specimens are from the fish collection of Stanford University or of the California Academy of Sciences. The Stanford collection was recently (1971) removed to the California Academy of Sciences.

Agonostomus monticola, SU 37434. Gorgona Island, Colombia.

Atherinops affinis. Not catalogued. San Francisco Bay, California.

Melanotaenia nigrans, CAS 14411. Aquarium specimens, no data.

Myxus elongatus, CAS 14406. Dee Why Lagoon, near Sydney, Australia.

Oryzias latipes, CAS 14408. Aquarium specimen, no data.

Percopsis transmontana, not catalogued. Marys River, near Wren, Oregon.

Rivulus milesi, CAS 14412.

Sphyraena barracuda, not catalogued. Miami, Florida, 1967.

Xenomugil thoburni, CAS 14407. Galapagos Islands.
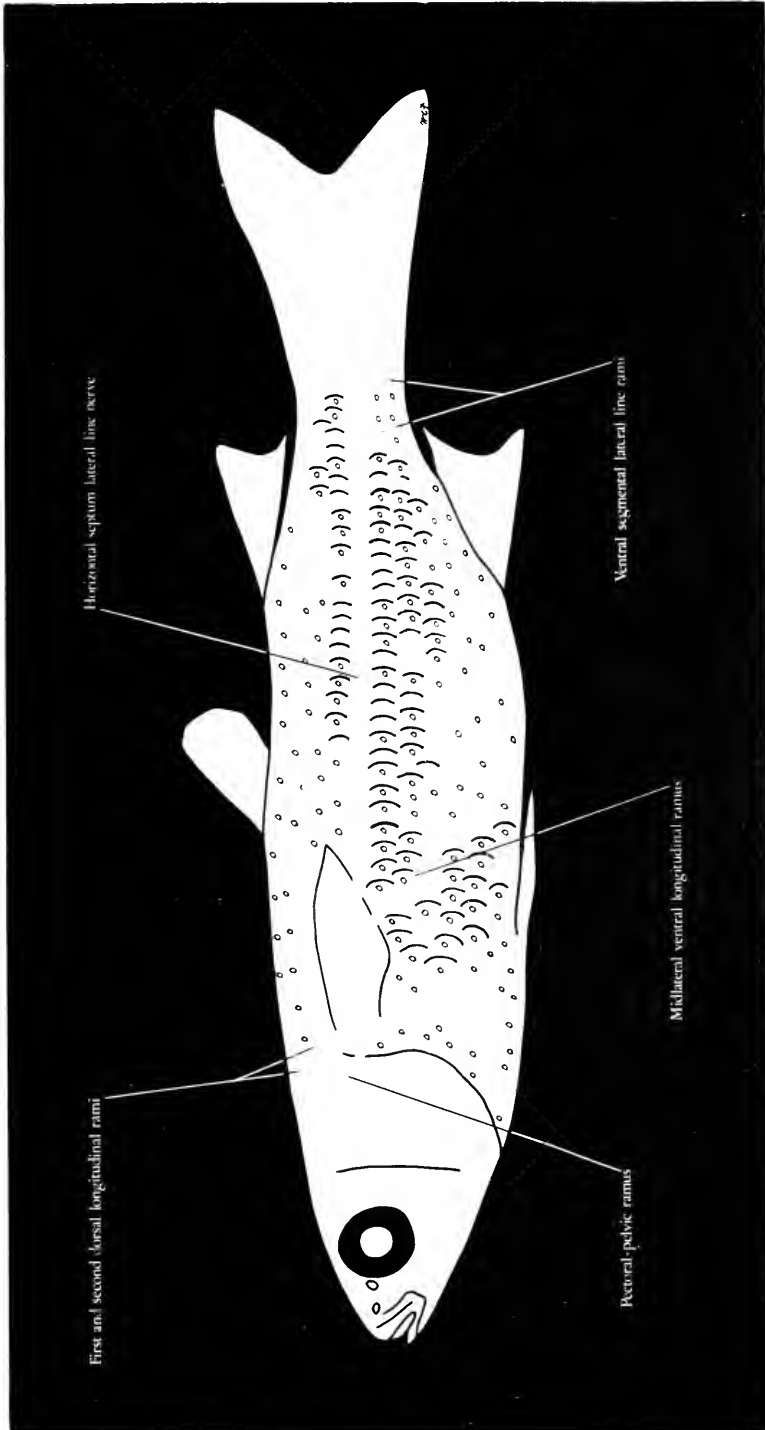
FIGURE 1. The trunk lateral line nerves of Xenomugil thoburni (family Mugilidae). See text for description. Diagrammatic. Open circles indicate pores of lateral line scales.
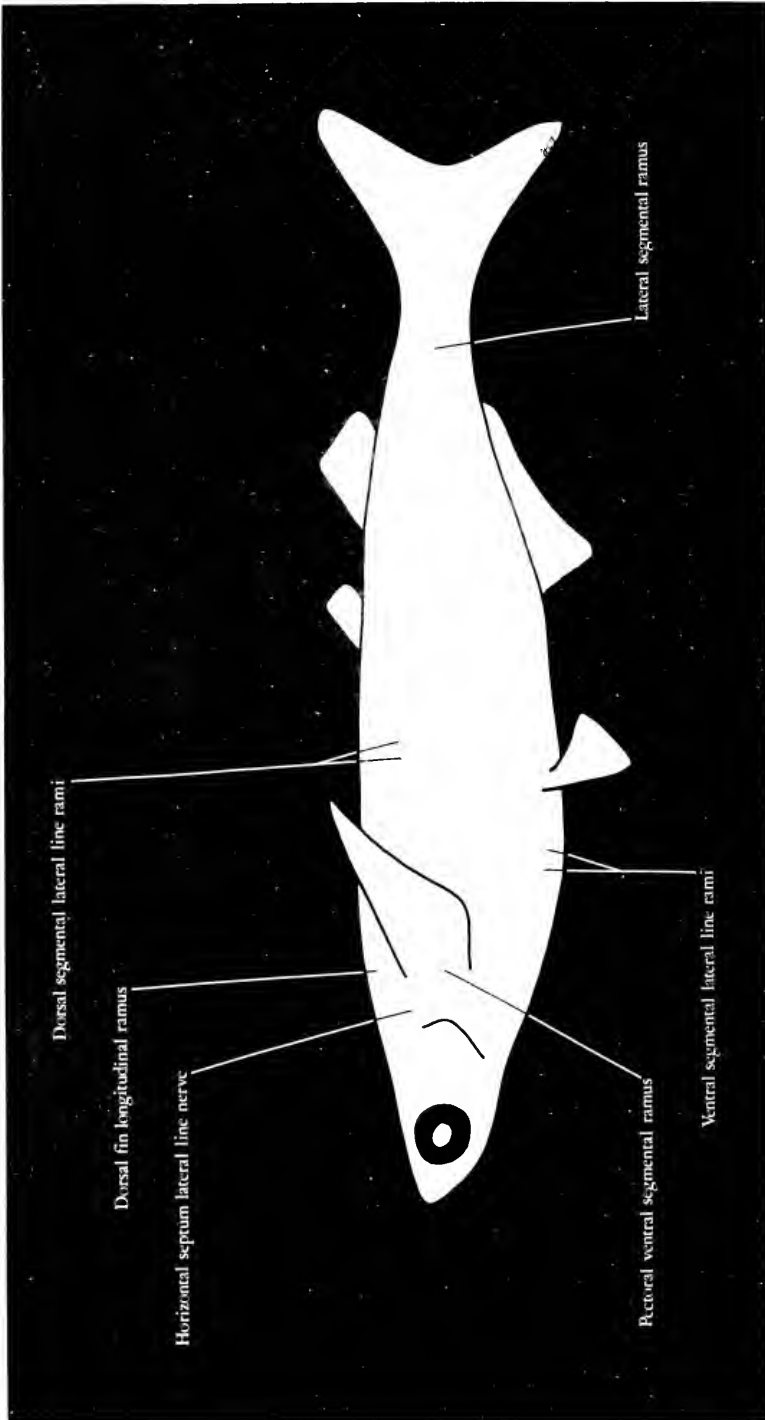
FIGURE 2. The trunk lateral line nerves of Atherinops affinis (family Atherinidae). See text for description. Diagrammatic.
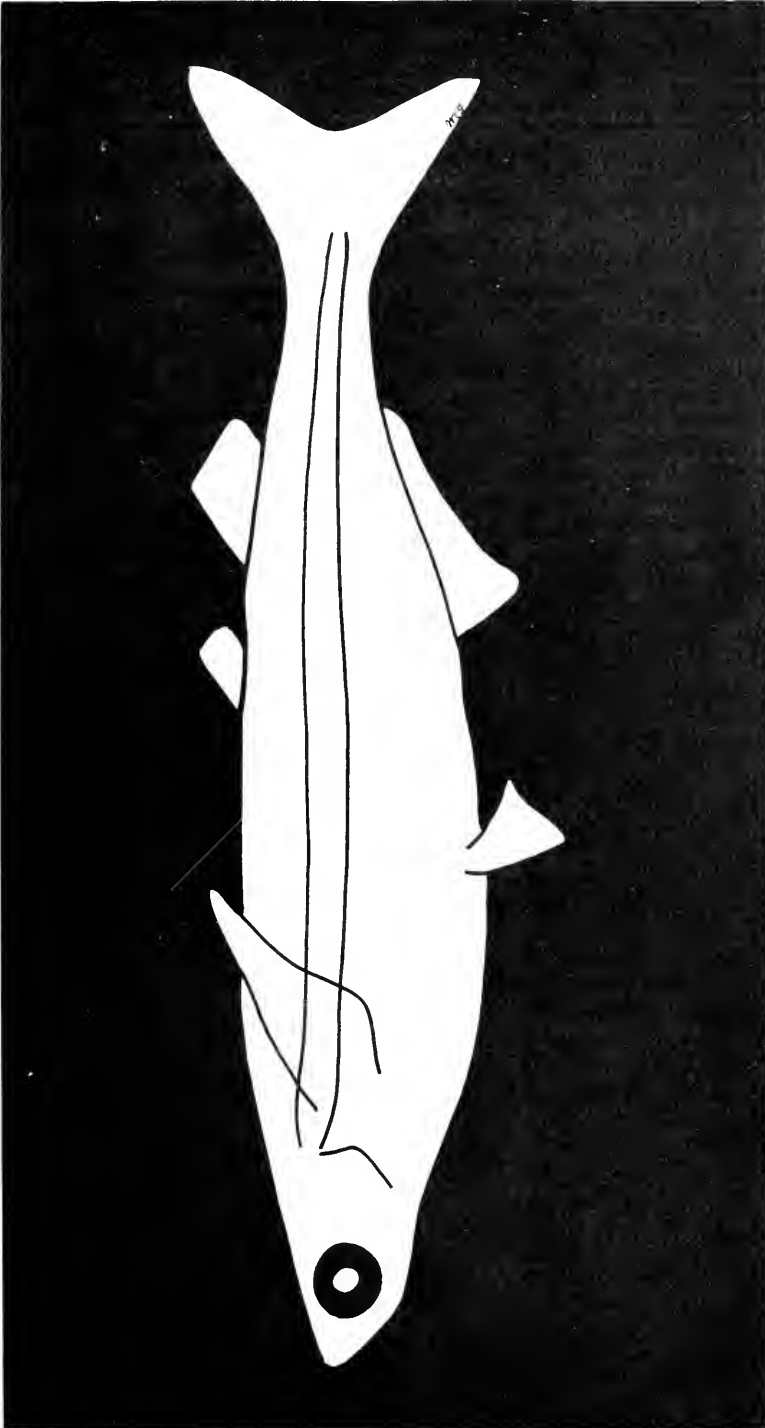
FIGURE 3. Distribution of tubed lateralis scales of Atherinops affinis (family Atherinidae), illustrating a hypothetical intermediate stage in evolution of ventral lateral line of flying fishes, half-beaks, and belonids. Tubed lateralis scales increase in number ventrally; dorsally more tubed scales are reduced, some only to pores indicated by dots.
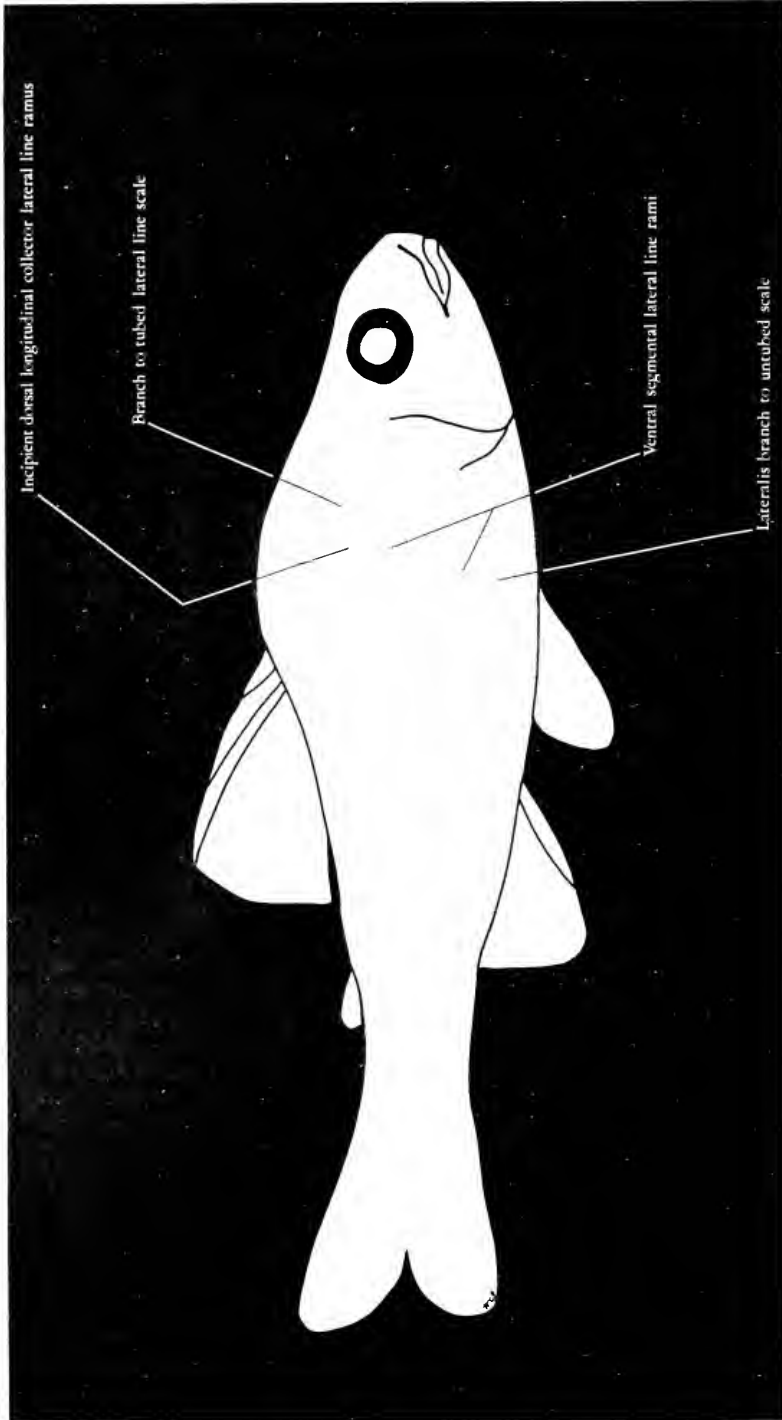
FIGURE 4. The trunk lateral line nerves of Percopsis transmontana (family Percopsidae). See text for description. Diagrammatic.
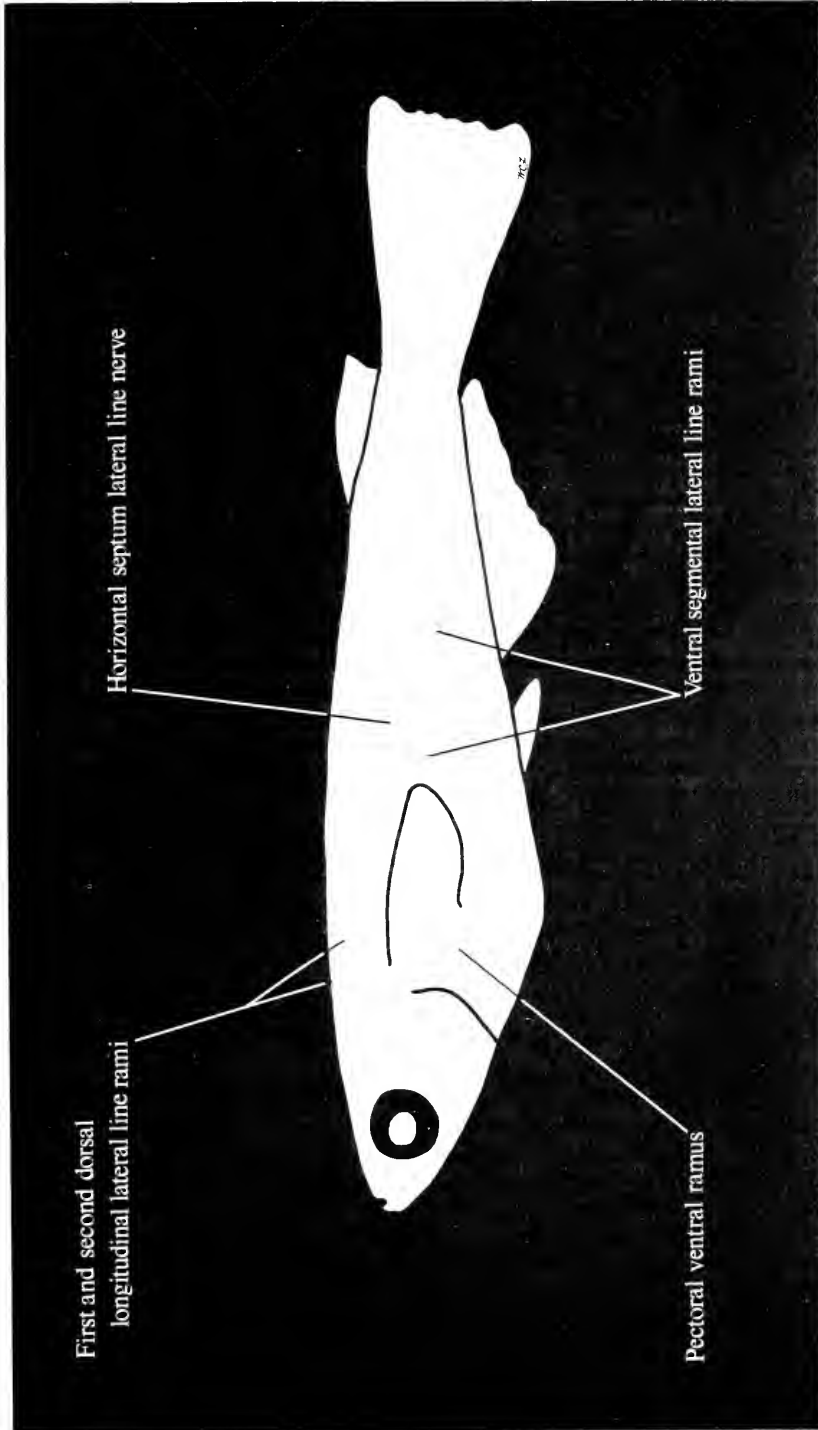
FIGURE 5. The trunk lateral line nerves of Oryzias latipes (family Oryziatidae). See text for description. Diagrammatic.
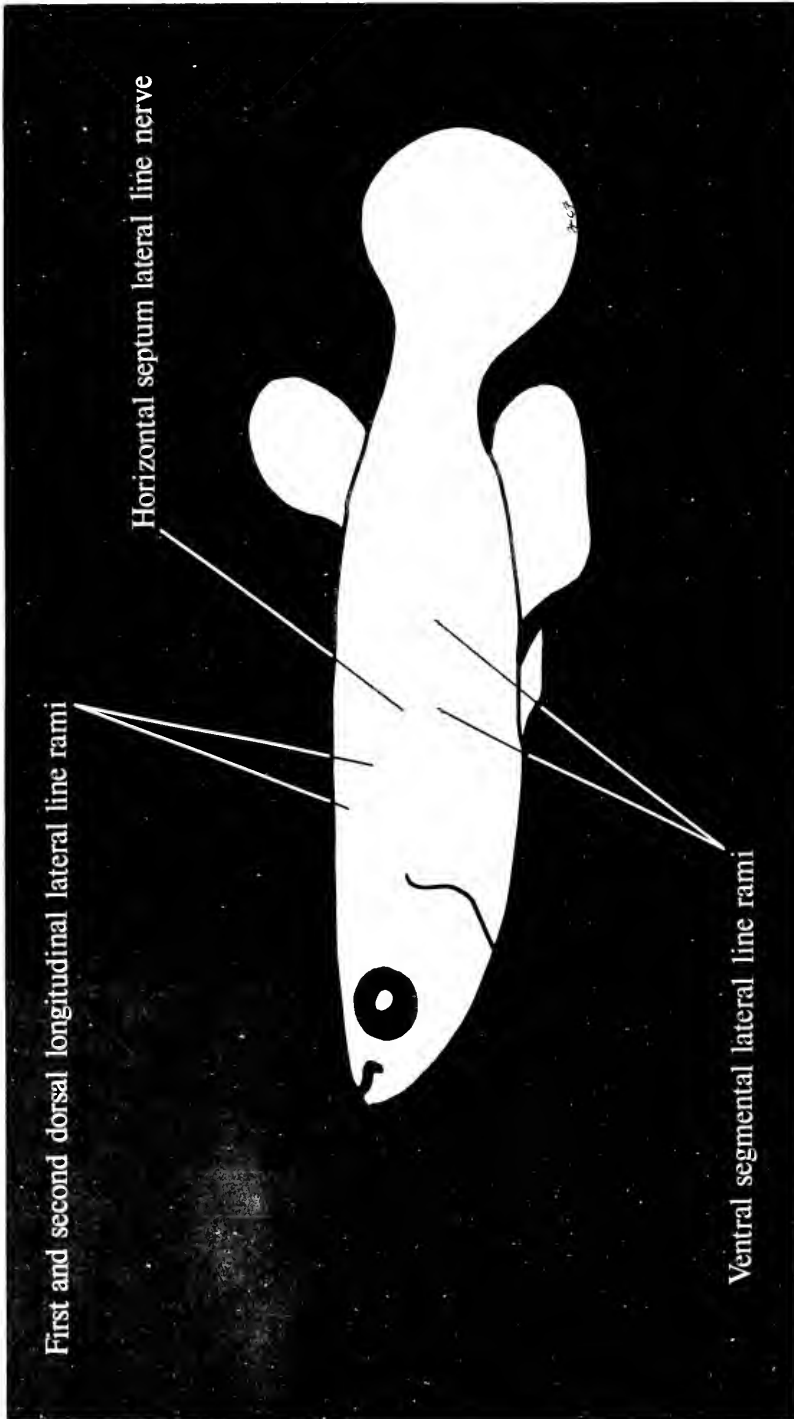
FIGURE 6. The trunk lateral line nerves of Pachypanchax playfairi (family Cyprinodontidae). See text for description. Diagrammatic.
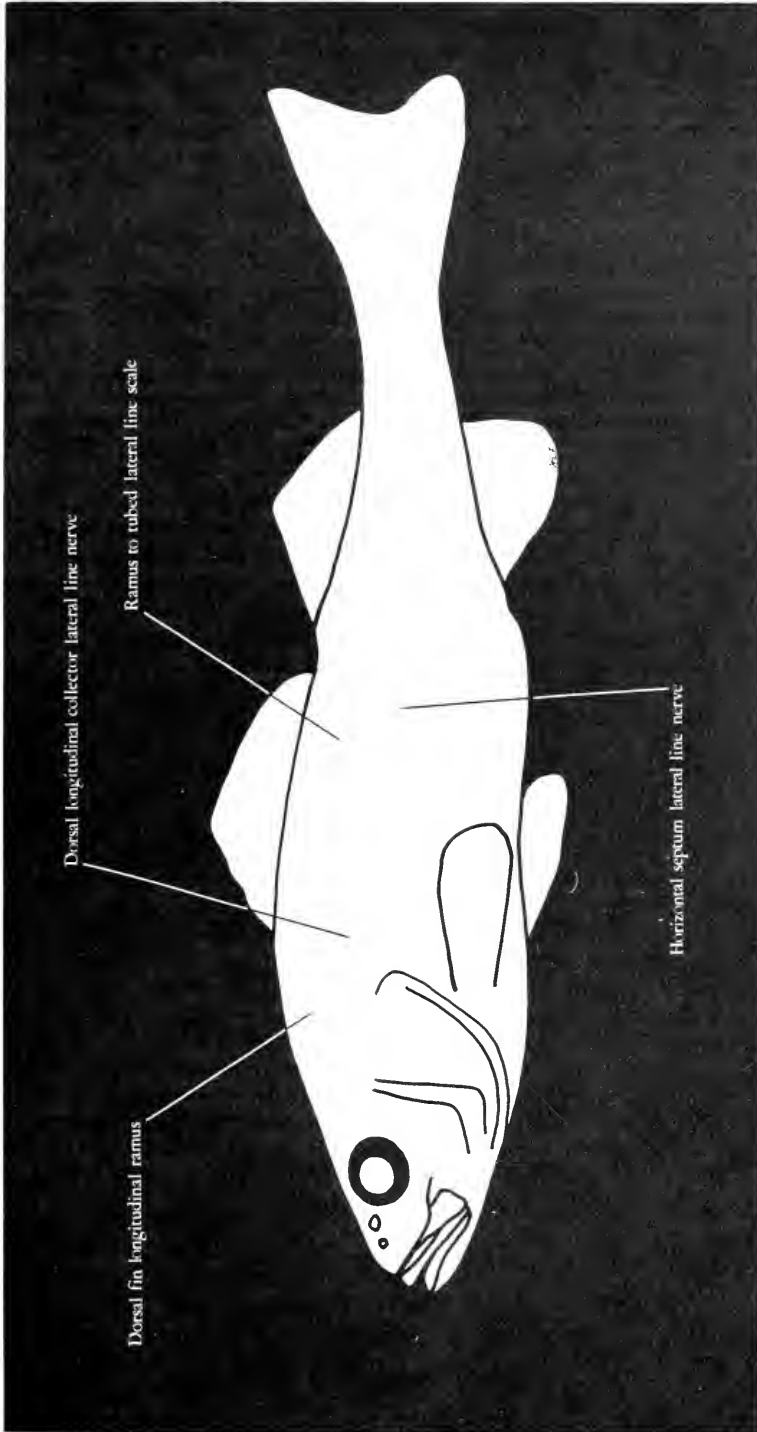
FIGURE 7. The trunk lateral line nerves of Perca flavescens (family Percidae). See text for description. Diagrammatic.
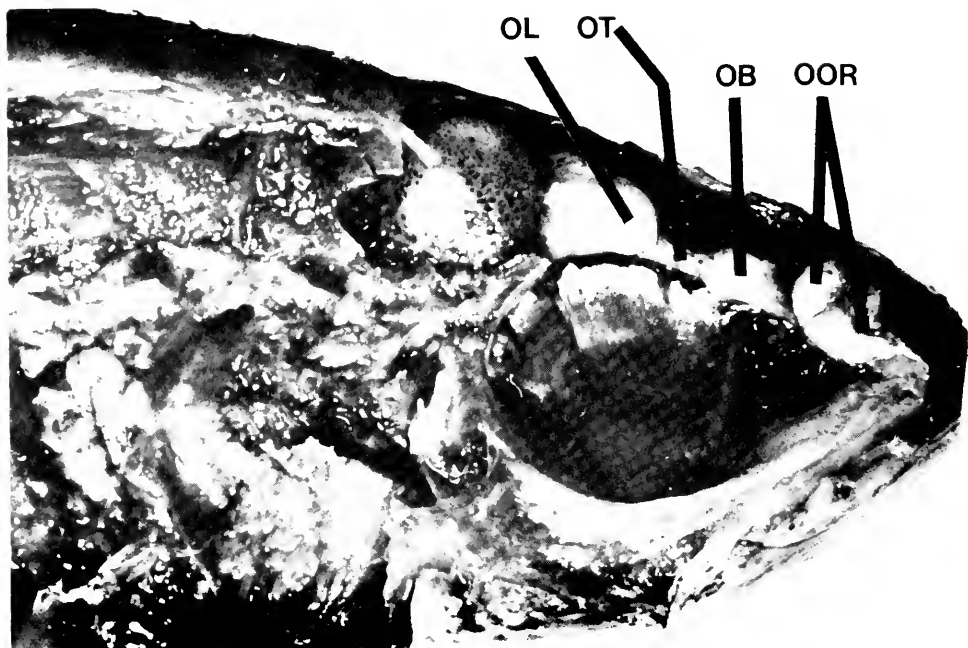
FIGURE 8.   The position of the olfactory bulb in the mugilid Agonostomus monticola. OB, olfactory bulb; OL, olfactory lobe of forebrain; OOr, olfactory organ; OT, olfactory tract.
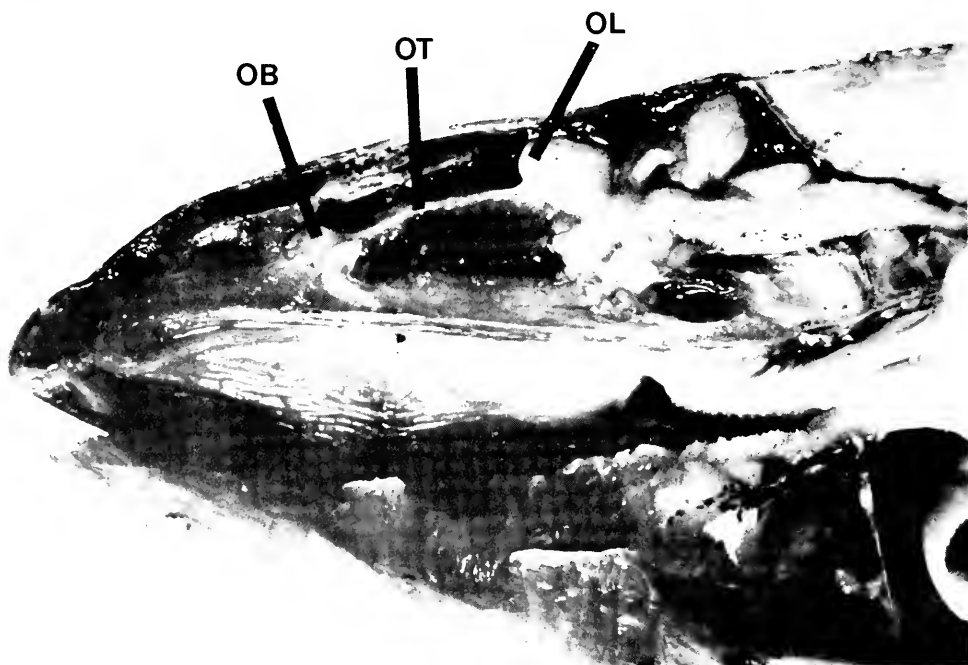
FIGURE 9.   The position of the olfactory bulb in Percopsis omiscomaycus. OB, olfactory bulb; OL, olfactory lobe of forebrain; OT, olfactory tract.
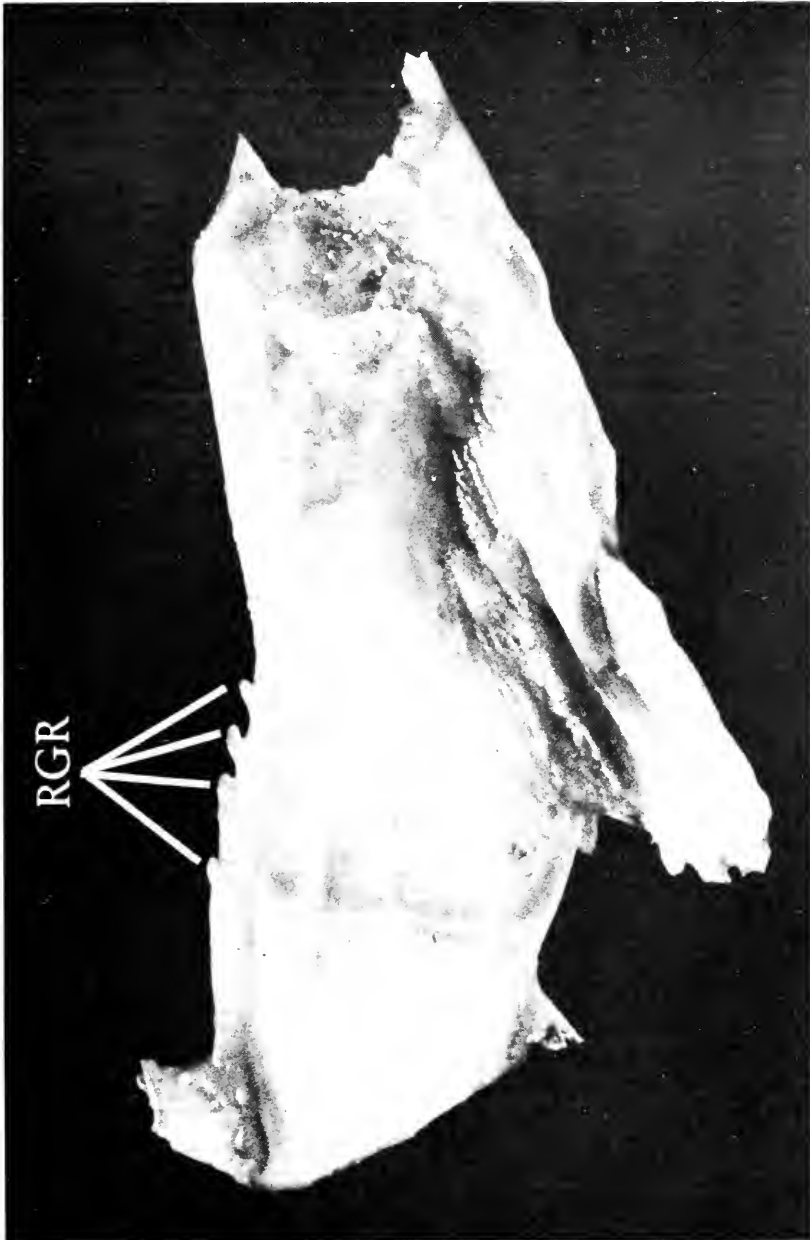
FIGURE 10. Sideview of ceratohyal and epihyal portion
of left hyoid arch of Agonostomus monticola; anterior to right.
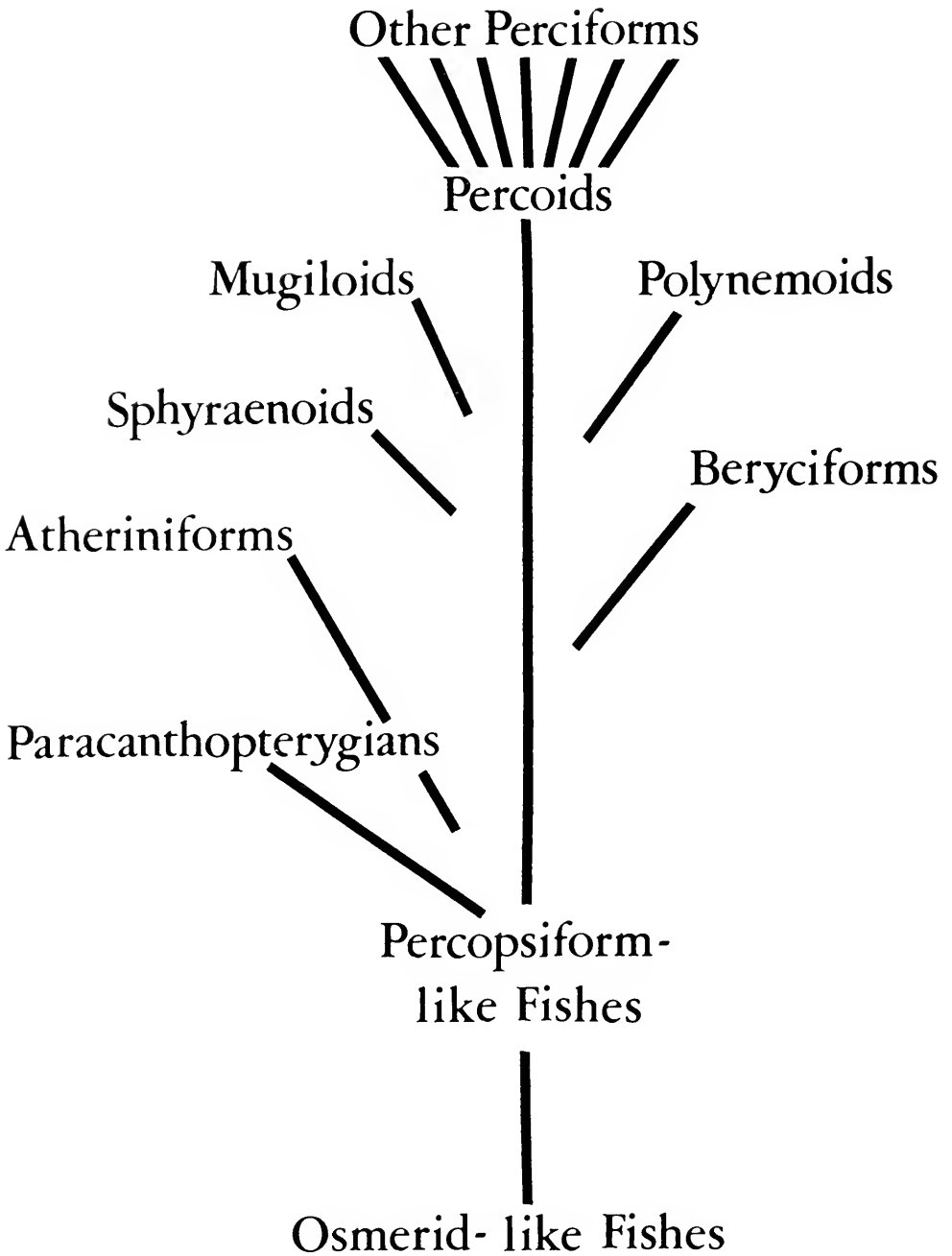RGR, rudimentary gill rakers.

FIGURE 11. A proposed systematic scheme of hypothetical origins and relationships of percopsiforms, atheriniforms, perciforms, beryciforms, and paracanthopterygians.
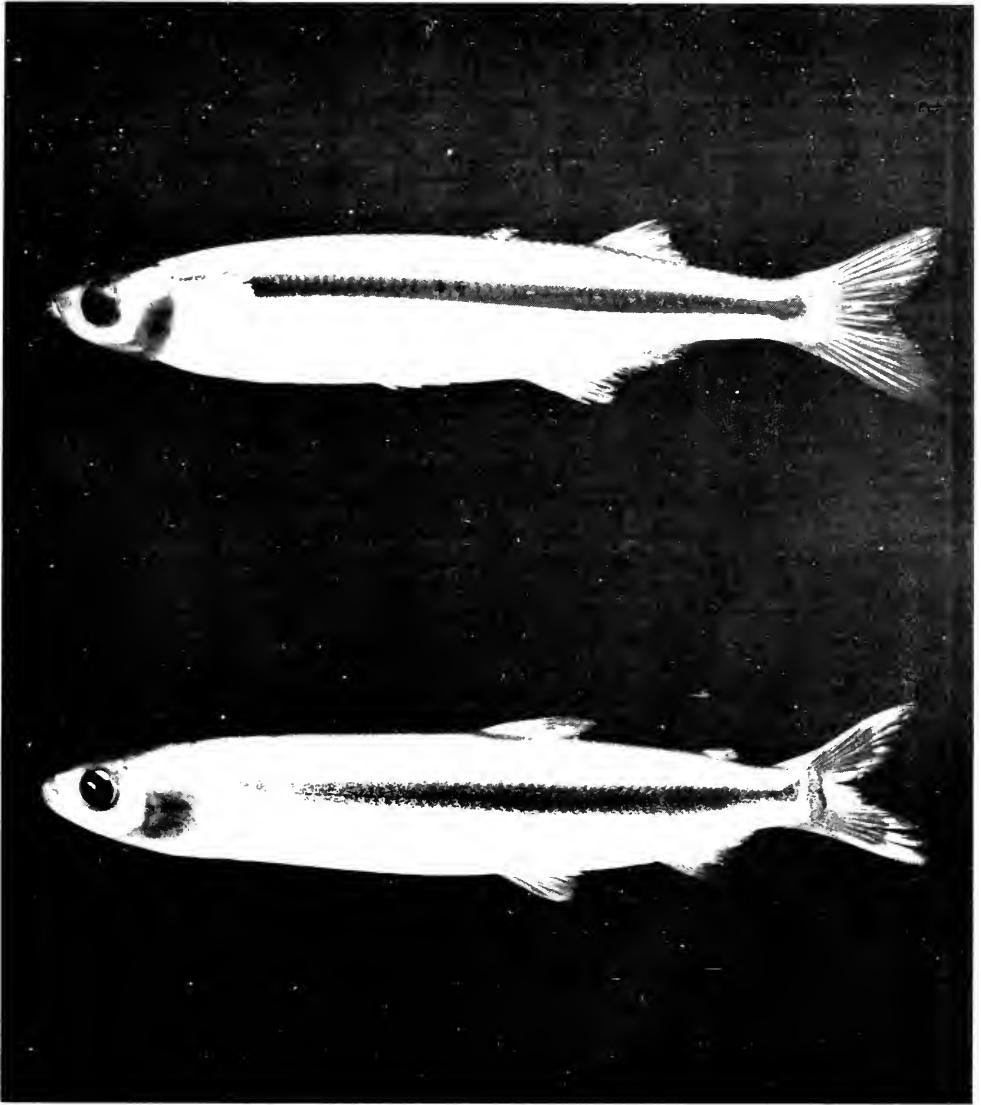
FIGURE 12.   Representatives of two superficially similar families not previously considered related but which may have an indirect relationship. Upper fish is <u>Atherinops</u> <u>affinis</u>, the top "smelt" of family Atherinidae or <u>silversides</u>; lower fish is <u>Hypomesus</u> <u>pretiosus</u>, the surf smelt of family Osmeridae or true smelts.