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# Osteology and Classification of the Fishes of the Family Blenniidae

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Frank A. Taylor
*Director, United States National Museum*

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# Contents

# Introduction

The Blenniidae are a family of small, shallow-water, scaleless fishes that are distributed circumglobally, primarily in tropical and subtropical seas, and that comprise about 400 species. The species are basically benthic in habit, though a small group (Nemophidinae) has taken up a somewhat free-swimming habit.

This study is an attempt to define the family Blenniidae osteologically and to identify the major suprageneric groups within the family. The research was undertaken because there is no reasonably comprehensive osteological description available for any species of blenniid, because much of the piecemeal osteological information available on blenniids is misleading, because any sound classification of the suborder Blennioidei will necessitate osteological information on each of the contained families, and because I had a need to elicit information that would be of assistance in my revisionary studies of the blenniid genera.

Gosline (1968) is the latest author to have critically reviewed the higher classification of the perciform fishes and has firmly established the perciform relationships of the blennioids. He differentiated the suborder Blennioidei from the other perciforms primarily on the basis of two characters: pelvic fins anterior in position to pectoral fins; and presence of an exact one-to-one ratio between the vertebrae and the dorsal rays and posterior anal soft rays. All blenniids, with the exception of one monotypic genus, *Plagiotremus*, in which the pelvics are absent, exhibit these two characters.

In the literature discussion that follows I cite only a few of the pertinent papers concerned with the classification of the Blenniidae. Those papers not cited by me are treated by Gosline (1968). A reading of his paper is mandatory for any student of the blennioids.

Hubbs (1952) recognized two superfamilies in the Blennioidei: Zoarcicae (eel or northern blennies) and Blenniicae (tropical blennies). Of the seven characters Hubbs used to distinguish the Blenniicae (in which he included the Blenniidae), two—the number of suborbitals ("circumorbitals" in my study) and the relationship of the ascending wings of the paraspheniod with the descending wings of the frontals—are not acceptable (Springer, 1955, 1956). The remaining five characters, with slight modification, do apply with the exception of individual variant specimens. These characters are: (1) 13 or fewer principal caudal rays; (2) all soft (articulated) fin rays in pelvics, dorsal, and anal fins simple; the other fin rays may be branched, but if so, only twice; (3) dorsal hypurals fused to each other and to urostyle to form chief articulation for upper caudal rays (however, hypural 5 may be separate); (4) pelvics present and seldom degenerate (absent in the monotypic genus *Plagiotremus*); (5) lateral line always simple.

Makushok (1958) reaffirmed the separation of the northern and tropical blennies as proposed by Hubbs, but he split the northern blennies into three superfamilies (Stichaeoidae, Cryptacanthodoidae, Zoarceoidae [I have emended Makushok's spelling of the last two names]), which he did not consider as necessarily being closely related. Makushok also re-evaluated and modified the characters given by Hubbs (1952) to distinguish the northern blennies. In addition, he proposed other characters for separating the northern and tropical blennies: the presence of a basisphenoid and two nostrils on each side of the head in the tropical blennies as opposed to the absence of a basisphenoid and the presence of a single nostril on each side of the head in the northern blennies. The nostril character holds in all the tropical blennies I have seen, but a basisphenoid is lacking in at least one subfamily of that group (Nemophidinae, family Blenniidae). Conclusions based on morphological separation of the two groups of blennies are enforced by geographic separation. As their common names imply, there is very little geographic overlap between the distributions of the Blenniicae and the Zoarcicae (in Hubbs' sense). Where overlap does occur, only a relatively few species of the Blenniicae are involved.

Gosline (1968) recognized five superfamilies in the Blennioidei, the first three and last of which expand the suborder as considered by Hubbs (1952) and Makushok (1958): Notothenioidae, Trachinoidae, Congrogadoidae, Blennioidae (including only the Blenniicae or tropical blennies of Hubbs and Makushok), and Zoarceoidae (in which he included Makushok's three superfamilies of northern blennies and the Bathymasteridae, Zaproridae, and, questionably, the Derepodichthyidae and Scytalinidae). Gosline diagnosed the Blennioidae as follows:

> Head compressed or rounded. Two nostrils on each side. Gill-openings more or less restricted below, the gill membranes attached to one another or to the isthmus. Circumorbital bones usually firmly connected, without a subocular shelf from the second. Medial tabular usually fused to the parietal. Front and rear of suspensorium firmly connected. Prootic usually excluded from the internal orbital border Basisphenoid present.
>
> Pectoral actinosts columnar, longer than scapula and coracoid are broad, the upper pectoral ray articulating with an actinost (except Tripterygiidae). Pelvic fins with two to four soft rays of which the outer are strengthened and the membrane between the rays deeply incised (except such scondarily pelagic forms as *Aspidontus, Runula, Xiphasia*). Dorsal and anal soft rays usually unbranched.

Gosline added another character of which he was not quite so certain: anteriormost anal pterygiophores are attached to the first haemal spine.

All of the above characters, except the presence of a basisphenoid (absent as noted above) and the absence of a subocular shelf (see discussion below on circumorbital bones) are descriptive of the blenniids I have examined.

Gosline closed his discussion of the Blennioidae (Blenniicae in discussion below) by stating that "the relationship of the tropical blennies to any other [perciform] fish group is by no means clear." My study affords no better conclusion.

Hubbs (1952) included three families of living fishes in the Blenniicae: Tripterygiidae, Clinidae, and Blenniidae. I (1955) questioned Hubbs' basis for separating the Clinidae and Blenniidae, redefined the two families, and transferred the subfamily Chaenopsinae from the Blenniidae, in which Hubbs (1953) had placed it, to the Clinidae. Not all my information was accurate, but I still find my general conclusions to have been warranted. Whether the Chaenopsinae deserve to be recognized as a family separate from the Clinidae, as Stephens (1963) proposed, will not be treated here.

I (1966) discussed problems of the interfamilial classification of the families in the Blenniicae and gave characters further separating the Blenniidae from the other included families. My statements in that paper to the effect that all the members of the superfamily might be combined into a single family now appear unwarranted.

Norman (1943) gave the last and, actually, only comprehensive infrafamilial classification of the Blenniidae, including a synopsis of the genera and principal species. He recognized three subfamilies: Ophioblenniinae, Blenniinae, and Salariinae. The Ophioblenniinae have been shown by various workers to be larval stages of various salariin genera, and one genus (*Somersia* Beebe and Tee-Van) included in the Ophioblenniinae by Norman has been shown by me (1959a) to be the juvenile of a species of Clinidae—*Labrisomus nuchipinnis* (Quoy and Gaimard). Norman's Blenniinae includes my Nemophidinae and part of my Blenniinae. Norman's Salariinae I have relegated to the rank of a tribe, which forms the remainder of my Blenniinae. The number of genera now available in the Blenniidae greatly exceeds the number available during Norman's day. A synopsis is therefore given below (without indication of generic synonymies). I have not included a list of the nominal species in each genus as such will not be possible until the genera and species are better known.

The results of my study are presented in the following order: first, a classification of the family Blenniidae to the tribe level, including a list under each tribe or subfamily of the included nominal genera with the type-species and method of type designation. The classification is given first in order that the discussion that follows will be less confusing to the reader. Next follows the osteology of *Entomacrodus nigricans*, which, although not the least specialized blenniid, is generalized enough to be used as a basis for comparison and establishment of an osteological standard for the family. This, in turn, is followed by a general discussion of selected portions of the osteology of the Blenniidae as a whole. Included in the latter discussion are occasional references to characters of species differing notably from *E. nigricans* and usually a general discussion of evolutionary trends for each of the characters in the Blenniidae. Finally, the distinctive characters of the Blenniidae and diagnoses of the subfamilies and tribes are given.

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Much of the comparative blennioid material listed was obtained through the generosity of several colleagues: John S. Stephens, Jr., Mary Louise Penrith, Boyd W. Walker, Richard H. Rosenblatt, Warren C. Freihofer, and Bruce B. Collette.

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## Methods

Much of the material used in this study was cleared and stained by using Taylor's (1967) enzyme method. A few specimens were examined for specific parts by dissection, and some examinations were made on skeletons in the collection of the Division of Fishes, U.S. National Museum (USNM, see material). A large number of specimens were radiographed, and data on various characters, for the most part meristic, were obtained from study of the films.

The drawings were produced by various means. The drawings of *Entomacrodus nigricans* are based on a single specimen, male, 53 mm standard length, from Havana, Cuba, USNM 192195. The various views of the skull (except for the frontal view) were photographed on color film, projected on paper, and those details that it was possible to see were traced off. Further detail was added from examination of the skull with a binocular microscope. The frontal view (fig. 1) of the skull, without facing bones, was drawn by using a camera lucida; the facing bones were added freehand by using the facing bones of the specimen illustrated and by referring to an intact skull of another specimen of the same species. The other drawings of *E. nigricans* and the other species were made by placing the particular bones in a Bausch and Lomb Tri-Simplex micro-projector, outlining the general details of the projection on paper and filling in details from later microscopic examination, or by drawing the parts with the aid of a Wild M–5 microscope and a Wild camera lucida. All the plates and drawings in this paper except figures 13–16 were made by Sharon Lesure; figures 14 and 16 were made by Ann Hoskins and figures 13 and 15 were made by Ann Schreitz. The plates and figures 13 and 16 were labeled by Ann Hoskins; the other figures were labeled by Sharon Lesure.

The drawings of *Aspidontus taeniatus* are based for the most part on a female, 67.5 mm standard length, from Kwajalein, Marshall Islands, USNM 200339; however, after the base drawing was made, the skull accidentally was crushed and it was necessary to use another specimen for some of the details.

All the other species illustrated are based on the single specimens noted in the figure captions.

The description of *Entomacrodus nigricans* is based on the same specimen that was illustrated. Other specimens of this species were examined and no significant differences other than meristic were noted. The illustrated skull was completely disarticulated during the description.

Skulls of other species were completely or partially disarticulated. Cleaning and examination of skulls was done in glycerine and alcohol (some joints are seen better in the latter). Where possible, two or more specimens of each species were examined, but usually the skull of only one was thoroughly cleaned. Only a relatively limited number of characters were recorded for each specimen, although many others were checked, since a complete analysis, as given for *E. nigricans*, was not practical; nevertheless, with the exception of the subfamily Nemophidinae, where more study is warranted, the osteology of *E. nigricans* can serve as a reasonable basis for that of the family.

Considerable material of other perciform families (primarily blennioid) was examined. Examination of this material was cursory and only a few characters were checked on each specimen (for purposes of excluding the species from the Blenniidae): coracoid-cleithrum relationship, dentition, interopercle-epihyal relationship, pectoral radials, and scapula-coracoid relationships. Nonblenniid material is listed in alphabetical order by genus under the appropriate family after the blenniid material list.

The names of the bones follow, in general, those of Starks (1901), with the following exceptions (Stark's name followed by the name herein employed): prefrontal/lateral ethmoid; opisthotic/intercalar; alisphenoid/pterosphenoid; pterygoid/ectopterygoid; glossohyal/basihyal; basihyal/dorsal and ventral hypohyals; preorbital/lachrymal; suborbitals/circumorbitals; supraclavicle/supracleithrum; clavicle/cleithrum; postclavicle/postcleithrum; hypercoracoid/scapula; hypocoracoid/coracoid; actinosts/radials; pelvic bone/pelvis; abdominal vertebrae/precaudal vertebrae; neurapophyses/neural arches; haemapophyses/haemal arches; rib/pleural; interneurals and interhaemals/proximal pterygiophores.

## Material

Material (cleared and stained unless otherwise indicated) of Blenniidae is listed below alphabetically by genus. The identifications to some extent are ad hoc. For most species, specimens to be cleared and stained were selected from large cataloged lots. Thus, usually enough unstained material remains to allow for future reidentification. Most of the generic names employed are those that are found coupled with the specific epithet in recent literature; however, some allocations of species to genera are made herein for the first time. I do not specially signify these new allocations. (While the USNM catalog numbers are correct, the names given here may be different from those given in the catalog records. This is the result of the presently insurmountable task of having material recataloged.) I have attempted to cover a wide range of material, and although the number of generic names used (41) is relatively few, I believe the actual number represented will be significantly greater when the genera and species are better known. I have also drawn upon, but not included in the material lists, information on a large number of noncleared and stained specimens of the same and of many additional species. This information is taken from radiographs of the specimens, the literature, or my own examinations, including dissections.

Measurements are standard lengths in millimeters unless indicated otherwise.

*Alticus saliens* (Forster): USNM 115446, 2 males (42.0–61.9), female (48.3), Tutuila Id., Samoa.

*Andamia heteroptera* (Bleeker): USNM 137769, 2 males (39.7–49.1), female (52.9), Maculabo Id., Philippine Ids.

*Antennablennius velifer* Smith: USNM 200205, 2 males (44.3–59.6), Astola Id., West Pakistan.

*Aspidontus taeniatus* Quoy and Gaimard: USNM 200339, female (67.5), Kwajalein Atoll, Marshall Ids.; USNM 142228, male (90.4), Rongerik Atoll, Marshall Ids.

*Atrosalarias fuscus fuscus* (Rüppell): USNM 199484, female (65.6), Batu Group, Sumatra.

*Atrosalarias fuscus holomelas* (Günther): USNM 174329, male (72.0), Gulf of Carpentaria, Northern Territory, Australia.

*Blennechis filamentosus* Valenciennes: USNM 199432, male (50.1), Anjouan Id., Comoros Ids.

*Blennius canavae* Vinciguerra: USNM 199051, male (37.3), Gulf of Angina, Mediterranean Sea.

*Blennius cristatus* Linnaeus: USNM 192175, male (51.8), 3 females (46.5–47.0), Havana, Cuba.

*Blennius galerita* Linnaeus: USNM 259168–F18, 2 females (49.0–61.0), San Miguel, Azores.

*Blennius gattorugine* Linnaeus: USNM 259168–F3, female (73.7), San Miguel, Azores.

*Blennius marmoreus* Poey: USNM 184257, male (57.2), female (44.6), Madeira Beach, Florida.

*Blennius nicholsi* Tavolga: USNM 201178, male (37.1), female (31.7), Port Sewall, Florida.

*Blennius normani* Poll: USNM 199533, 2 males (56.9–57.2), Gulf of Guinea.

*Blennius ocellaris* Linnaeus: USNM 48387, female (110.7), Italy; USNM 26524 (bone collection), male, complete skeleton, no data.

*Blennius parvicornis* Valenciennes: USNM 259168–F7, 2 females (60.3–90.7), San Miguel, Azores.

*Blennius trigloides* Valenciennes: USNM 259168–F19, 2 females (54.1–61.0), San Miguel, Azores.

*Chasmodes bosquianus* (Lacépède): USNM 199497, 2 males (62.6–66.6), female (32.8), Severn River, Maryland; USNM 201352, 2 males (51.2–59.6), Patuxent River, Maryland; USNM 26523 (bone collection), complete skeleton, no data.

*Cirripectes fuscoguttatus* Strasburg and Schultz: USNM 200612, female (65.7), Marshall Ids.

*Cirripectes jenningsi* Schultz: USNM 200615, 2 males (53.5–56.1), female (62.7), Vostok Id., Pacific Ocean.

*Cirripectes sebae* (Valenciennes): USNM 200605, 2 males (38.4–54.4), female (42.2), Vostok Id., Pacific Ocean.

*Cirripectes variolosus* (Valenciennes): USNM 200614, 2 males (48.0–52.5), female (47.6), Marshall Ids.

*Croaltus bifilum* (Günther): USNM 200207, male (53.2), female (52.6), Astola Id., West Pakistan.

*Cruantus dealmeida* (Smith): USNM 201559, male (32.1), off southwest coast of Sumatra.

*Damania anjouanae* (Fourmanoir): USNM 200552, male (51.0), female (50.6), Grand Comoro Ids.

*Dasson variabilis* (Cantor): USNM 167027, 2 males (57.9–89.5), Ghardaqa, Egypt, Red Sea; USNM 147975, female (75.0), Persian Gulf.

*Ecsenius bicolor* (Day):USNM 201368, male (62.0), female (44.5), One Tree Id., Great Barrier Reef.

*Ecsenius frontalis* (Valenciennes): USNM 200613, female (47.6), Strait of Jubal, Red Sea.

*Ecsenius lividinalis* Chapman and Schultz: USNM 144292, paratype female (30.2), New Georgia, Solomon Ids.

*Ecsenius mandibularis* McCulloch: USNM 201367, male (44.3), female (31.5), One Tree Id., Great Barrier Reef.

*Ecsenius nalolo* Smith: USNM 200602, male (49.0), Red Sea.

*Ecsenius yaeyamaensis* (Aoyagi): USNM 200428, male (38.7), Rabaul, New Britain.

*Enchelyurus* species A: USNM 52248, female (26.7), Samoa; USNM 52251, female (31.3), Samoa.

*Enchelyurus species* B: USNM 137864, male (37.5), female (44.3), Great Tobea Id., Dutch East Indies.

*Enchelyurus kraussi* (Klunzinger): USNM 200609, male (28.4), Mentawei Id., Indonesia.

*Entomacrodus chiostictus* (Jordan and Gilbert): USNM uncataloged, male (ca. 45), no data.

*Entomacrodus cymatobiotus* Schultz and Chapman: USNM 198564, male (39.4), female (35.8), Jarvis Id., Pacific Ocean.

*Entomacrodus decussatus* (Bleeker): USNM 115474, female (41.2), Tutuila Id., Samoa.

*Entomacrodus epalzeocheilus* (Bleeker): USNM 258171–F2, 2 males (55.0–90.0), Seychelles Ids.

*Entomacrodus marmoratus* (Bennett): USNM 142060, 2 females (56.0–58.6), Hawaii.

*Entomacrodus nigricans* Gill: USNM 178738, male (48.5), Bermuda; USNM 192195, male (53.0), 2 females (46.0–48.0), Havana, Cuba; USNM 192201, 2 males (24.4–51.0), female (53.5), Havana, Cuba.

*Entomacrodus rofeni* Springer: USNM 199402, paratype female (37.0), Raroia, Tuamotu Archipelago.

*Entomacrodus stellifer stellifer* (Jordan and Snyder): USNM 132795, female (45.0), Okinawa.

*Entomacrodus stellifer lighti* (Herre): USNM 197976, male (43.7), female (56.8), Hong Kong.

*Entomacrodus striatus* (Quoy and Gaimard): USNM 198655, 2 males (57.6–73.7), Jarvis Id., Pacific Ocean.

*Entomacrodus thalassinus thalassinus* (Jordan and Seale): USNM 142187, male (21.0), female (24.0), Eniwetok, Marshall Ids.

*Entomacrodus vomerinus* (Valenciennes): American Museum of Natural History 3824, 2 females (ca. 59–67), Natal, Brazil.

*Exallias brevis* (Kner): USNM 200544, male (38.5), Vostok Id., Pacific Ocean.

*Glyptoparus delicatulus* Smith: USNM 201417, female (21.6), New Georgia, Solomon Ids.

*Halmablennius lineatus* (Valenciennes): USNM 142193, male (56.1), female (83.4), Bikini, Marshall Ids.; USNM 200206, male (79.4), Astola Id., West Pakistan.

*Halmablennius striatomaculatus* (Kner): USNM 200209, 2 males (37.2–58.6), female (57.3), Nossi Be, Madagascar.

*Hirculops cornifer* (Rüppell): USNM 200030, 2 males (34.0–44.2), female (46.6), Gulf of Suez, Red Sea.

*Hypleurochilus bermudensis* Beebe and Tee-Van: USNM 116805, female (44.8), Tortugas, Florida.

*Hypleurochilus geminatus* (Wood): USNM 116676, 2 males (32.9–49.8), 2 females (28.7–40.4), Beaufort, North Carolina.

*Hypsoblennius gentilis* (Girard): USNM 26515 (bone collection), complete skeleton, San Diego, California.

*Hypsoblennius hentzi* (LeSueur): USNM 156618, male (75.2), Aransas Pass, Texas; USNM 184204, 2 females (35.8–49.5), 2 sex indeterminate (29.5–31.8), Tampa Bay, Florida.

*Istiblennius afilinuchalis* Schultz and Chapman: USNM 200545, male (64.4), female (49.1), Marshall Ids.

*Istiblennius bellus* (Günther): USNM 200610, female (65.3), Nossi Be, Madagascar.

*Istiblennius coronatus* (Günther): USNM 200611, female (56.6), Kwajalein Atoll, Marshall Ids.

*Istiblennius edentulus* (Bloch and Schneider): USNM 200208, male (57.7), female (67.5), Nosse Be, Madagascar.

*Istiblennius periophthalmus* (Valenciennes): USNM 115471, 2 females (49.0–59.6), Swains Id., Pacific Ocean.

*Istiblennius rivulatus* (Rüppell): USNM 200303, 3 males (59.2–84.2), Red Sea.

*Istiblennius zebra* (Vaillant and Sauvage): USNM 200566, male (43.8), female (55.1), Oahu, Hawaii.

*Laiphognathus* species: Stanford University 62088, sex indeterminate (13.9), Goh Kram Id., Gulf of Thailand.

*Lembeichthys celebesensis* Herre: Stanford University 29081, holotype and paratype (55.5 and 54.8), radiographs and gross examination, Lembeh Strait, Celebes.

*Lophalticus kirki* (Günther): USNM 200603, male (61.6), female (42.5), Nossi Be, Madagascar.

*Medusablennius chani* Springer: Stanford University 62057, paratype (14.4), Raroia, Tuamotu Archipelago.

*Meiacanthus* species: USNM 200601, male (37.1), Strait of Jubal, Red Sea.

*Meiacanthus grammistes* (Valenciennes): USNM 201363, male (60.4), One Tree Id., Great Barrier Reef.

*Meiacanthus smithi* Klausewitz: USNM 199422, female (46.2), Malacca Strait.

*Meiacanthus temmincki* (Bleeker): USNM 137832, female (54.3), Philippine Ids.

*Negoscartes guttatus* (Valenciennes): USNM 195702, male (36.2), Dutch East Indies.

*Negoscartes sinuosus* (Snyder): USNM 177144, male (41.6), Hayman Id., Queensland, Australia.

*Omobranchus anolius* (Valenciennes): USNM 197621, 2 females (41.1–41.3), Manly Cove, Sydney, Australia.

*Omobranchus banditus* Smith: USNM 200604, male (50.7), female (39.4), Astola Id., West Pakistan.

*Omobranchus elegans* (Steindachner): USNM 71530, 3 males (45.1–53.4), Misaki, Japan.

*Omobranchus japonicus* (Bleeker): USNM 174330, female (44.6), north of Darwin, Northern Territory, Australia.

*Omobranchus lini* (Herre): Stanford University 29088, paratype female (97.2), Heung Chan, China.

*Omobranchus loxozonus* (Jordan and Starks): USNM 174341, 2 males (53.0–65.6), Groote Eylandt, Northern Territory, Australia.

*Ophioblennius macclurei* (Silvester): USNM 199434, 3 males (34.4–68.6), Puerto Rico.

*Ophioblennius steindachneri* Jordan and Evermann: USNM 26519 (bone collection), complete skeleton, Cape San Lucas, Baja California, Mexico.

*Pereulixia kosiensis* (Regan): USNM 197637, female (100.9), Porte Abril, Mozambique.

*Petroscirtes mitratus* Rüppell: USNM 199433, male (53.7), Madagascar; USNM 200567, female (38.6), Red Sea; USNM 200599, male (51.6), Aldabra Id., Indian Ocean.

*Plagiotremus spilistius* Gill: USNM 21722, holotype, radiograph and gross examination, "Chinese seas."

*Praealticus margaritarius* (Snyder): USNM 115481, male (49.0), female (49.7), Siulagi Pt., Samoa.

*Praealticus tanegasimae* (Jordan and Starks): USNM 123398, male (61.0), female (71.2), Okinawa.

*Rhabdoblennius rhabdotrachelus* (Fowler and Ball): USNM 115609, 2 males (28.5–35.3), female (31.0), Enderbury Id., Phoenix Ids.; USNM 200608, 2 males (29.9–30.5), Tongareva Atoll.

*Runula* species: USNM 200338, male (70.4), Strait of Jubal, Red Sea.

*Runula azalea* Jordan and Bollman: USNM 200392, 3 males (44.4–48.2), Baja California, Mexico; USNM 256392–F6, 2 females (36.9–40.6), Gorgona Id., Columbia.

*Runula laudandus* (Whitley): USNM 201413, female (31.4), Vanikoro Id., Pacific Ocean.

*Runula tapeinosoma* (Bleeker): USNM 195704, male (71.8), female (68.9), Dutch East Indies.

*Salarias fasciatus* (Bloch): USNM 290600, female (36.3), Strait of Jubal, Red Sea.

*Salarias spaldingi* Macleay: USNM 174352, 3 males (61.1–80.6), Yirkalla, Northern Territory, Australia.

*Scartichthys gigas* (Steindachner): USNM 200396, male (42.7), female (40.4), Callao, Peru.

*Stanulus seychellensis* Smith: USNM 142152, 2 males (17.6–19.5), female (19.5), Bikini Atoll, Marshall Islands.

*Stanulus talboti* Springer: USNM 201371, male paratype (35.0), female paratype (33.2), One Tree Island, Great Barrier Reef.

*Xiphasia matsubarai* Okada and Suzuki: USNM 200562, female (224), Pagan Id., Marianas Ids.

*Xiphasia setifer* Swainson: USNM 8293, Hong Kong; USNM 149556, Japan; USNM 192548, Taiwan. One specimen each, radiographs and gross examination.

Undescribed genus (A) and species: USNM 201369, male (32.0), One Tree Id., Great Barrier Reef.

Undescribed genus (B) and species: USNM 197980, male (21.2), Hong Kong.

## Comparative Material

### CHAENOPSIDAE

*Acanthemblemaria crockeri* Beebe and Tee-Van: USNM 201041, 1 specimen, 38.0, Bahia de La Paz, Golfo de California, Mexico.

*Acanthemblemaria exilispinus* Stephens: USNM 201044, 1 specimen, 42.1, Samara Bay, Costa Rica.

*Acanthemblemaria macrospilus* Brock: USNM 201046, 1 specimen, 35.2, Cabo San Lucas, Baja California Sur, Mexico.

*Acanthemblemaria spinosa* Metzelaar: USNM 198278, 4 specimens, 18.9–22.7, Dominica, British West Indies.

*Chaenopsis alepidota* (Gilbert): USNM 200391, 2 specimens, 111.4–114.1 Baja California Norte, Mexico.

*Coralliozetus angelica* (Böhlke and Mead): USNM 201042, 2 specimens, 17.5–24.4, north of Manzanillo, Mexico.

*Coralliozetus boehlkei* Stephens: USNM 201049, 2 specimens, 19.9–22.2, north of Manzanillo, Mexico.

*Coralliozetus micropes* (Beebe and Tee-Van): USNM 201048, 2 specimens, 35.0–38.0, Punta San Guillermo, Baja California, Mexico.

*Ekemblemaria myersi* Stephens: USNM 200399, 3 specimens, 33.3–48.0, Punta Pescadero, Baja California Sur, Mexico.

*Emblemaria hypacanthus* (Jenkins and Evermann): USNM 200398, 3 specimens, 24.5–30.2, Lobos Bay, Golfo de California, Mexico.

*Lucayablennius zingaro* (Böhlke): USNM 258171–F1, 2 specimens, 24.3–26.5, Grand Cayman Island.

*Protemblemaria bicirrus* (Hildebrand): USNM 201047, 1 specimen, 26.7, Golfo de California, Mexico.

*Pseudemblemaria signifer* (Ginsburg): USNM 199622, 2 specimens, 15.2–18.7, Dominica, British West Indies.

### CLINIDAE

*Alloclinus holderi* (Lauderbach): USNM 201164, 2 specimens, 77.8–85.2, Palos Verdes, California.

*Blennioclinus brachycephalus* (Valenciennes): USNM 199572, 2 specimens, 41.9–48.7, Dalebrook, South Africa.

*Blenniomimus cottoides* (Valenciennes): USNM 199568, 2 specimens, 61.8–63.8, Still Bay, South Africa.

*Blennophis anguillaris* (Valenciennes): USNM 199577, 1 specimen, 210.1, Luderitzbucht, South Africa.

*Cancelloxus burrelli* Smith: USNM 199567, 1 specimen, 86.1, Lambert's Bay, South Africa.

*Cirrhibarbus capensis* Valenciennes: USNM 153525, 1 specimen, 96.2, Knysna Estuary, South Africa; USNM 199566, 1 specimen, 56.9, Still Bay, South Africa.

*Clinus perspicillatus* Valenciennes: USNM 201518, 2 specimens, 85.8–87.3, Green's Beach, Tasmania.

*Clinus superciliosus* (Linnaeus): USNM 199565, 2 specimens, 57.5–64.2, False Bay, South Africa.

*Cristiceps flammeus* Jordan and Starks: USNM 71507, 2 specimens, 35.0–43.7, Japan.

*Cryptotrema corallium* Gilbert: USNM 201167, 2 specimens, 24.9–26.5, California.

*Dialommus fuscus* Gilbert: USNM 201165, 3 specimens, 35.7–62.0, Barrington Is., Galapagos Is.

*Exerpes asper* (Jenkins and Evermann): USNM 152013, 2 specimens, 41.0–47.3, Bocochebampo Bay, Golfo de California, Mexico.

*Fucomimus mus* (Gilchrist and Thompson): USNM 199571, 2 specimens, 57.0–60.2, False Bay, South Africa.

*Gibbonsia elegans* (Cooper): USNM 200386, 2 specimens, 64.4–104.2, Isla Guadalupe, Baja California Norte, Mexico.

*Heterostictus rostratus* Girard: USNM 201050, 3 specimens, 118.9–194.0, Newport Bay, California.

*Labrisomus bucciferus* Poey: USNM 82529, 2 specimens, 43.3–51.3, Cabañas Bay, Cuba.

*Labrisomus filamentosus* Springer: USNM 199555, 1 specimen, 56.3, off St. Lucia, British West Indies.

*Labrisomus nuchipinnis* (Quoy and Gaimard): USNM 200304, 6 specimens, 41.8–97.2, Dominica, British West Indies.

*Labrisomus striatus* Hubbs: USNM 201170, 2 specimens, 45.0–60.2, Bahia Santa Inez, Baja California, Mexico.

*Malacoctenus afuerae* (Hildebrand): USNM 200388, 2 specimens, 39.3–53.8, Bahia San Jose del Cabo, Baja California Sur, Mexico.

*Malacoctenus aurolineatus* Smith: USNM 187760, 2 specimens, 35.5–37.5, Serrana Bank, Caribbean Sea.

*Malacoctenus gigas* Springer: USNM 200401, 2 specimens, 75.7–82.9, Puertecitos, Baja California Norte, Golfo de California, Mexico.

*Malacoctenus gilli* (Steindachner): USNM 187764, 2 specimens, 28.0–33.9, Serrana Bank, Caribbean Sea.

*Malacoctenus hubbsi* Springer: USNM 200394, 2 specimens, 60.4–64.0, Bahia Sebastian Vizcaino, Baja California, Mexico.

*Malacoctenus macropus* (Poey): USNM 199562, 1 specimen, 38.8, Virginia Key, Florida.

*Malacoctenus margaritae* (Fowler): USNM 201163, 2 specimens, 43.4–51.0, Isla Santa Inez, Baja California, Mexico.

*Malacoctenus zacae* Springer: USNM 201166, 2 specimens, 44.1–44.2, Isla Cerralbo, Golfo de California, Mexico.

*Mnierpes macrocephalus* (Günther): USNM 201171, 2 specimens, 40.8–41.7, Isla San Jose, Islas Perlas, Panama.

*Muraenoclinus dorsalis* (Bleeker): USNM 93635, 2 specimens, 55.4–56.0, Great Fish Point, South Africa.

*Neoclinus bryope* (Jordan and Snyder): USNM 71529, 3 specimens, 42.7–62.8, Misaki, Sagami Bay, Japan.

*Neoclinus uninotatus* Hubbs: USNM 201172, 1 specimen, 146.0, El Segundo, Los Angeles County, California.

*Ophiclinops varius* (McCulloch and Waite): USNM 201459, 1 specimen, 30.0, Green's Beach, Tasmania.

*Ophiclinus aethiops* McCulloch and Waite: USNM 201465, 1 specimen, 123.4, Green's Beach, Tasmania.

*Ophiclinus greeni* Scott: USNM 201460, 1 specimen, 76.9, Green's Beach, Tasmania.

*Ophthalmolophus acuminatus* (Valenciennes): USNM 199579, 2 specimens, 75.1–76.4, Port Nolloth, South Africa.

*Ophthalmolophus agilis* (Smith): USNM 199576, 2 specimens, 51.6–74.8, Port Nolloth, South Africa.

*Ophthalmolophus venustris* (Gilchrist and Thompson): USNM 199573, 1 specimen, 78.7, Sea Point, South Africa.

*Paraclinus fasciatus* (Steindachner): USNM 199563, 2 specimens, 34.8–35.7, Virginia Key, Florida.

*Paraclinus marmoratus* (Steindachner): USNM 62754, 1 specimen, 56.6, Knight's Key, Florida.

*Pavoclinus heterodon* (Valenciennes): USNM 199569, 2 specimens, 73.5–91.7, South Africa.

*Pavoclinus pavo* (Gilchrist and Thompson): USNM 199575, 2 specimens, 50.0–51.1, East London, South Africa.

*Petraites brevicristatus* (Gilchrist and Thompson): USNM 199578, 1 specimen, 50.9, False Bay, South Africa.

*Petraites phillipi* (Lucas): USNM 201519, 2 specimens, 56.3–75.5, Green's Beach, Tasmania.

*Stathmonotus gymnodermis* Springer: USNM 198273, 2 specimens, 29.2–29.3, Dominica, British West Indies.

*Stathmonotus sinuscalifornici* (Chabanaud): USNM 201162, 2 specimens, 26.7–33.2, Isla Ildefonso, Golfo de California, Mexico.

*Starksia cremnobates* (Gilbert): USNM 201169, 6 specimens, 20.0–34.2, Las Tetas de Cabra, Golfo de California, Mexico.

*Starksia fasciata* (Longley): USNM 198267, 3 specimens, 16.5–16.9, Dominica, British West Indies.

*Starksia nanodes* Böhlke and Springer: USNM 200305, 2 specimens, 14.7–15.4, Dominica, British West Indies.

*Xenopoclinus leprosus* Smith: USNM 199570, 65.5–68.3, Lambert's Bay, South Africa.

### TRIPTERYGIIDAE

Undescribed genus and species: USNM 200393, 2 specimens, 33.6–40.7, Isla San Jose, Baja California Sur, Mexico.

*Axoclinus* species: USNM 200389, 2 specimens, 42.1–50.3, Bahia Los Angeles, Baja California, Mexico.

*Axoclinus carminalis* (Jordan and Gilbert): USNM uncataloged, 3 specimens, ca. 25–32, Mazatlan, Mexico.

*Enneanectes boehlkei* Rosenblatt; USNM 199564, 2 specimens, 13.8–17.0, Dominica, British West Indies.

*Enneanectes* species: USNM 200397, 4 specimens, 23.3–38.4, Isla San Jose, Baja California Sur, Mexico.

### ACANTHOCLINIDAE

*Acanthoclinus* species: USNM 200546, 1 specimen, ca. 55, Wellington, New Zealand.

### STICHAEIDAE

*Ulvaria subbifurcata* (Storer): USNM 201949, 2 specimens, 81.6–114.5, Nahant, Massachusetts.

### DACTYLOSCOPIDAE

*Dactylagnus mundus* Gill: USNM 200385, 2 specimens, 88.7–92.3, Baja California Norte, Mexico.

### ALABESIDAE

*Alabes rufus* (Macleay): USNM 201415, 1 specimen, 60.0 total length, Kangaroo Island, South Australia.

### TRACHINIDAE

*Trachinus draco* Linnaeus: USNM 201573, 3 specimens, 38.6–106.5, St. George Bay, Lebanon.

### KUHLIIDAE

*Kuhlia sandvicensis* Steindachner: USNM 115006, 1 specimen, 174.7, Hull Island, Phoenix Islands, partial dissection of alcohol-preserved specimen.

### POMACENTRIDAE

*Abudefduf abdominalis* (Quoy and Gaimard): USNM 6941, 1 specimen, 64.8, Honolulu, Hawaii, partial dissection of alcohol-preserved specimen.

## Classification of the Family BLENNIIDAE

- Subfamily Blenniinae
  - Tribe Blenniini
  - Tribe Omobranchini
  - Tribe Salariini
- Subfamily Nemophidinae

## Nominal Genera of the Tribe Blenniini

*Adonis* Gronow, 1854, Catalogue of fish . . . in British Museum, p. 93 (type-species: *A. pavonius* Gronow, 1854, =*Blennius ocellaris* Linnaeus, 1758, by subsequent designation, in parentheses, of Jordan and Evermann, 1905, Bull. U.S. Fish Comm., vol. 23, p. 496).

*Aidablennius* Whitley, 1947, Australian Zool., vol. 11, no. 2, p. 150 (type-species: *Blennius sphynx* Valenciennes, *in* Cuvier and Valenciennes, 1836, by original designation).

*Blenniolus* Jordan and Evermann, 1898, U.S. Nat. Mus. Bull. 47, pt. 3, p. 2390 (type-species: *Blennius brevipinnis* Günther, 1861, by monotypy).

*Blennitrachus* (also *Blenitrachus*) Swainson, 1839, Natural history of fishes, amphibians, and reptiles, vol. 2, pp. 78, 182, and 274 (type-species: *Pholis quadrifasciatus* Wood, 1825, = *Blennius bosquianus* Lacépède, 1800, by subsequent designation, in parentheses, of Jordan and Evermann, 1898, U.S. Nat. Mus. Bull. 47, pt. 3, p. 2391).

*Blennius* Linnaeus, 1758, Systema Naturae, 10th ed., p. 256 (type-species: *B. ocellaris* Linnaeus, 1758, by subsequent designation of Jordan and Gilbert, 1882, U.S. Nat. Mus. Bull. 16, p. 759; the type-species has often and incorrectly been cited as *B. galerita* Linnaeus).

*Chaleroderma* Norman, 1943, Ann. Mag. Nat. Hist., ser. 11, vol. 10, p. 803 (type-species: *Blennius capito* Valenciennes, *in* Cuvier and Valenciennes, 1836, by original designation and monotypy).

*Chasmodes* Valenciennes, *in* Cuvier and Valenciennes, 1836. Histoire naturelle des poissons, vol. 11, p. 295 (type-species: *Blennius bosquianus* Lacépède, 1800, by subsequent designation of Jordan and Gilbert, 1882, U.S. Nat. Mus. Bull. 16, p. 756).

*Coryphoblennius* Norman, 1943, Ann. Mag. Nat. Hist., ser. 11, vol. 10, p. 802 (type-species: *Blennius galerita* Linnaeus, 1758, by original designation and monotypy).

*Dubiblennius* Whitley, 1930, Mem. Queensland Mus., vol. 10, no. 1, p. 20 (type-species: *Blennius tonganus* Jordan and Seale, 1906, by original designation and monotypy).

*Homesthes* Gilbert, *in* Jordan and Evermann, 1898. U.S. Nat. Mus. Bull. 47, pt. 3, p. 2394 (type-species: *H. caulopus* Gilbert *in* Jordan and Evermann, 1898, by original designation, in parentheses, and monotypy).

*Hypleurochilus* Gill, 1861, Proc. Acad. Nat. Sci. Philadelphia, vol. 13, suppl., p. 44 (type-species: *Blennius multifilis* Girard, 1858, =*Blennius geminatus* Wood, 1825, by subsequent designation of Gill, 1861, Proc. Acad. Nat. Sci. Philadelphia, vol. 13, p. 168).

*Hypsoblenniops* Schultz, 1943, Journ. Washington Acad. Sci., vol. 32, no. 5, p. 153 (type-species: *H. rickettsi* Schultz, 1942, =*Blennius gentilis* Girard, 1854, by original designation and monotypy).

*Hypsoblennius* Gill, 1861, Proc. Acad. Nat. Sci. Philadelphia, vol. 13, suppl., p. 44 (type-species: *Blennius hentzi* LeSueur, 1825, by monotypy).

*Ichthyocoris* Bonaparte, 1833, Iconografia della fauna italica . . ., vol. 3, introd. p. 8 (type-species: *Salarias varus* Risso, 1826, =*Blennius fluviatilis* Asso, 1801, by subsequent designation of Jordan, 1917, Genera of fishes, pt. 1, p. 142).

*Isesthes* Jordan and Gilbert, 1882, U.S. Nat. Mus. Bull. 16, p. 757 (type-species: *Blennius gentilis* Girard, 1854, by original designation).

*Lipophrys* Gill, 1896. American Nat., vol. 30, p. 498 (type-species: *Blennius pholis* Linnaeus, 1758, by original designation and monotypy).

*Lupinoblennius* Herre, 1942, Stanford Univ. Publ., Univ. Ser., Biol. Sci., vol. 7, no. 2, p. 302 (type-species: *L. dispar* Herre, 1942, by original designation and monotypy).

*Medusablennius* Springer, 1966, Copeia, no. 1, p. 56 (type-species: *M. chani* Springer, 1966, by original designation and monotypy).

*Parablennius* Ribeiro, 1915, Arch. Nac. Rio de Janeiro, vol. 17, Blenniidae, p. 3 (type-species: *Blennius pilicornis* Cuvier, 1829, by monotypy).

*Pholis* Cuvier, 1817, Regne animal, vol. 2, p. 251 (type-species: *Blennius pholis* Linnaeus, 1758, by tautonymy; a junior homonym of *Pholis* Gronow, *in* Scopoli, 1787, Pholididae).

*Pictiblennius* Whitley, 1930, Mem. Queenland Mus., vol. 10, pt. 1, p. 19 (type-species: *Blennius intermedius* Ogilby, 1915, by original designation).

*Queriblennius* Whitley, 1933, Rec. Australian Mus., vol. 19, p. 93 (type-species: *Blennius gaudichaudi* Whitley, 1933, by original designation and monotypy).

*Runulops* Ogilby, 1910, Proc. Roy. Soc. Queensland, vol. 23, p. 55 (type-species: *Blennechis fasciatus* Jenyns, 1842, =*Blennius sordidus* Bennett, 1828, by subsequent designation of Jordan, 1920, Genera of fishes, pt. 4, p. 536, as "orthotype"; by Norman, 1943, Ann. Mag. Nat. Hist., ser. 11, vol. 10, p. 802, as "type").

*Salaria* Forskål, 1775, Descriptiones animalium . . ., pp. x and 22 (type-species: *Blennius salaria* Valenciennes, *in* Cuvier and Valenciennes, 1836, Histoire naturelle des poissons, vol. 11, p. 248, by subsequent monotypy and tautonymy).

*Scartella* Jordan, 1886, Proc. U.S. Nat. Mus., vol. 9, p. 50 (type-species: *Blennius microstomus* Poey, 1861, =*Blennius cristatus* Linnaeus, 1758, by monotypy).

*Semablennius* Fowler, 1954, Notulae naturae, no. 265, p. 1 (type-species: *S. gallowayi* Fowler, November 1954, =*Blennius nicholsi* Tavolga, May 1954, by original designation and monotypy).

*Spinoblennius* Herre, 1935, Field Mus. Nat. Hist., Zool. Ser., vol. 18, no. 12, p. 435 (type-species: *S. spiniger* Herre, 1935, =*Blennius brevipinnis* Günther, 1861, by original designation and monotypy).

*Zeablennius* Whitley, 1930, Mem. Queensland Mus., vol. 10, no. 1, p. 20 (type-species: *Blennius laticlavius* Griffin, 1926, by original designation and monotypy).

## Nominal Genera of the Tribe Omobranchini

*Cruantus* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no 14, p. 234 (type-species: *Omobranchus dealmeida* Smith, 1949, by original designation).

*Cyneichthys* Ogilby, 1910, Proc. Roy. Soc. Queensland, vol. 23, p. 55 (type-species: *Blennechis anolius* Valenciennes, *in* Cuvier and Valenciennes, 1836, by original designation, in parentheses, and monotypy).

*Graviceps* Fowler, 1903, Proc. Acad. Nat. Sci. Philadelphia, vol. 55, p. 170 (type-species: *Petroscirtes elegans* Steindachner, 1877, by original designation and monotypy).

*Laiphognathus* Smith, 1956, Mem. Mus. Castro, 1955, no. 3, p. 23 (type-species: *L. multimaculatus* Smith, 1956, by original designation and monotypy).

*Omobranchus* Ehrenberg, *in* Cuvier and Valenciennes, 1836, Histoire Naturelle des poissons, vol. 11, p. 287; first appearance in synonymy but subsequently validated by Swainson, 1839, Natural history of fishes, amphibians, and reptiles, vol. 2, p. 274, (type-species: *O. fasciolatus* Ehrenberg, *in* Cuvier and Valenciennes, 1836, by monotypy).

*Pauloscirtes* Whitley, 1935, Rec. S. Australian Mus., vol. 5, no. 3, p. 351, (type-species: *Petroscirtes obliquus* Garman, 1903, by original designation and monotypy).

*Poroalticus* Fowler, 1931, Proc. Acad. Nat. Sci. Philadelphia, vol. 83, p. 403 (type-species: *P. sewalli* Fowler, 1931, =*Petroskirtes japonicus* Bleeker, 1869, by original designation and monotypy).

## Nominal Genera of the Tribe Salariini

*Alticops* Smith, 1948, Ann. Mag. Nat. Hist., ser. 11, vol. 14, p. 340 (type-species: *Salarias periophthalmus* Valenciennes, *in* Cuvier and Valennciennes, 1836 by original designation).

*Alticus* Commerson, *in* Lacépède, 1800, Histoire naturelle des poissons, vol. 2, p. 479 (type-species: *A. saltatorius* Commerson *in* Lacépède, 1800, =*Blennius saliens* Forster, 1788, by monotypy). Note: Both Commerson's genus and species were described in synonymy in Lacépède's treatment of *Blennius saliens* and would not be available under the International Rules of Zoological Nomenclature. *Alticus* is a widely accepted genus and it seems best to conserve it.

*Andamia* Blyth, 1858 Journ. Asia. Soc. Bengal, vol. 27, no. 3, p. 270 (type-species: *A. expansa* Blyth, 1858, =*Salarias heteropterus* Bleeker, 1857, by monotypy).

*Antennablennius* Fowler, 1931. Proc. Acad. Nat. Sci. Philadelphia, vol. 83, p. 245 (type-species: *Blennius hypenetes* Klunzinger, 1871, by original designation and monotypy).

*Atrosalarias* Whitley, 1933, Rec. Australian Mus., vol. 19, p. 93 (type-species: *Salarias phaiosoma* Bleeker, 1855, =*Salarias fuscus* Rüppell, 1835, by original designation).

*Basilisciscartes* Fowler, 1939, Notulae naturae, no. 26, p. 2 (type-species: *Blennius saliens* Forster, 1788, by original designation and monotypy).

*Blenniella* Reid, 1943, Journ. Washington Acad. Sci., vol. 33, no. 12, p. 383 (type-species: *B. rhessodon* Reid, 1943, =*Salarias gibbifrons* Quoy and Gaimard, 1824, by original designation and monotypy).

*Blennophis* Valenciennes, *in* Webb and Berthelot, 1843, Iles Canaries, Poissons, p. 60 (type-species: *B. webbi* Valenciennes *in* Webb and Berthelot, 1843, =*Salarias atlanticus* Valenciennes, *in* Cuvier and Valenciennes, 1836, by monotypy; a junior homonym of *Blennophis* Swainson, 1839, Clinidae).

*Cirripectes* (also *Cirripectus*) Swainson, 1839, Natural history of fishes, amphibians, and reptiles, vol. 2, pp. 79, 80, 182, 275 (type-species: *Salarias variolosus* Valenciennes, *in* Cuvier and Valenciennes, 1836, by monotypy).

*Crenalticus* Whitley, 1930, Mem. Queensland Mus., vol. 10, no. 1, p. 21 (type-species: *Salarias crenulatus pallidus* Whitley, 1930, =*Salarias sinuosus* Snyder, 1908, by original designation).

*Croaltus* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 247 (type-species: *Blennius bifilum* Günther, 1861, by original designation and monotypy).

*Cynoscartes* Norman, 1943, Ann. Mag. Nat. Hist., ser. 11, vol. 10, p. 31 (type-species: *Salarias atlanticus* Valenciennes, *in* Cuvier and Valenciennes, 1836, by original designation and monotypy).

*Damania* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 239 (type-species: *Andamia anjouanae* Fourmanoir, 1954, by original designation).

*Ecsenius* McCulloch, 1923, Rec. Australian Mus., vol. 14, no. 2, p. 121 (type-species: *E. mandibularis* McCulloch, 1923, by original designation and monotypy).

*Entomacrodus* Gill, 1859, Proc. Acad. Nat. Sci. Philadelphia, vol. 11, p. 168 (type-species: *E. nigricans* Gill, 1859, by monotypy).

*Erpichthys* Swainson, 1839, Natural history of fishes, amphibians, and reptiles, vol. 2, p. 275 (type-species: *Salarias quadripennis* Cuvier, 1817, =*Blennius* *fasciatus* Bloch, 1786, by subsequent designation of Jordan, 1919, Genera of fishes, pt. 2, p. 202, as "logotype"; a junior objective synonym of *Salarias* Cuvier, 1817).

*Exallias* Jordan and Evermann, 1905, U.S. Bur. Fish., Bull. 23, pt. 1, p. 503 (type-species: *Salarias brevis* Kner, 1868, by original designation and monotypy).

*Fallacirripectes* Schultz and Chapman, 1960, U.S. Nat. Mus, Bull. 202, vol. 2, p. 362 (type-species *F. minutus* Schultz and Chapman, 1960, =*Stanulus seychellensis* Smith, 1959, by original designation).

*Giffordella* Fowler, 1932, Proc. U.S. Nat. Mus., vol. 80, no. 6, p. 14 (type-species: *G. corneliae* Fowler, 1932, by original designation and monotypy).

*Gloriella* Schultz, 1941, Copeia, 1941, no. 1, p. 17 (type-species: *Cirripectes caninus* Herre, 1936, =*Salarias brevis* Kner, 1868, by original designation and monotypy).

*Glyptoparus* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 249 (type-species: *G. delicatulus* Smith, 1959, by original designation and monotypy).

*Halmablennius* Smith, 1948, Ann. Mag. Nat. Hist., ser. 11, vol. 14, p. 340 (type-species: *Salarias unicolor* Rüppell, 1835, by original designation).

*Hepatoscartes* Fowler, 1944, Acad. Nat. Sci. Philadelphia Monogr., no. 6, p. 230 (type-species: *H. umbrifasciatus* Fowler, 1944, =*Ophioblennius steindachneri* Jordan and Evermann, 1896, by original designation and monotypy).

*Hirculops* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 247 (type-species: *Blennius cornifer* Rüppell, 1829, by original designation and monotypy).

*Istiblennius* Whitley, 1943, Australian Zool., vol. 10, pt. 2, p. 185 (type-species: *Salarias muelleri* Klunzinger, 1880, by original designation and monotypy).

*Labroblennius* Borodin, 1928, Bull. Vanderbilt Oceanogr. Mus., vol. 1, no. 1, p. 31 (type-species: *L. nicholsi* Borodin, 1928, =*Ophioblennius steindachneri* Jordan and Evermann, 1896, by monotypy).

*Leoblennius* Reid, 1943, Journ. Washington Acad. Sci., vol. 33, no. 12, p. 282 (type-species: *L. schultzi* Reid, 1943, =*Salarias brevis* Kner, 1868, by original designation and monotypy).

*Litanchus* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 247 (type-species: *Antennablennius* (*Litanchus*) *velifer* Smith, 1959, by original designation).

*Lophalticus* Smith, 1957, Ann. Mag. Nat. Hist., ser. 12, vol. 9, p. 889 (type-species: *Salarias kirki* Günther, 1868, by original designation and monotypy).

*Negoscartes* Whitley, 1930, Mem. Queensland Mus., vol. 10, no. 1, p. 20 (type-species: *Salarias irroratus* Alleyne and Macleay, 1877, by original designation and monotypy).

*Nixiblennius* Whitley, 1930, Mem. Queensland Mus., vol. 10, no. 1, p. 20 (type-species: *Blennius snowi* Fowler, 1928, by original designation and monotypy).

*Ophioblennius* Gill, 1860, Proc. Acad. Nat. Sci. Philadephia vol. 12, p. 103 (a substitute name for *Blennophis* Valenciennes, *in* Webb and Berthelot, 1843, taking the same type-species: *Blennophis webbi* Valenciennes, *in* Webb and Berthelot, 1843).

*Pereulixia* Smith, 1959, Rhodes Univ. Ichthyol. Bull., no. 14, p. 238 (type-species: *Salarias kosiensis* Regan, 1908, by original designation and monotypy).

*Pescadorichthys* Tomiyama, 1955, Japanese Journ, Ichthyol., vol. 4, nos. 1–3, p. 8 (type-species: *Salarias namiyeh* Jordan and Evermann, 1903, by original designation and monotypy).

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## Nominal Genera of the Subfamily Nemophidinae

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## Osteology of *Entomacrodus nigricans*

### Head Region

MEDIAN ETHMOID (fig. 1).—The median ethmoid has a flat anterior face and is paddle-shaped, tapering dorsally. The dorsalmost margins of the bone are bounded laterally by the anteroventralmost extensions of each frontal; most of the remaining margins are bounded by the lateral ethmoids; the ventrolateralmost margins impinge on the vomer. The posterior face of the ethmoid forms the anterior surface of a large cupshaped cavity at the internal anterior end of the skull (anterior myodome). The lateral margins of the cavity are bounded by thickened mesial projections of the lateral ethmoids, and the ventral margin is bounded by the dorsal surface of the vomer. Ventrally the median ethmoid joins the small plugshaped ethmoid cartilage, which inserts in a deep depression in the anterior surface of the vomer.

LATERAL ETHMOID (figs. 1–4, 7).—Each lateral ethmoid joins dorsally and externally the anterolateral surface of its respective frontal, ventrally the ethmoid, and posteroventrally and mesially the lateral ethmoid of the opposite side. Anteriorly the lateral ethmoids are fanshaped, each with a large foramen for the olfactory tract opening close to the surface joining the frontal. The ventral surface of the lateralmost extension of each lateral ethmoid forms a syndesmotic joint with the broad dorsal surface of its respective lachrymal (first circumorbital). Ventrally and mesially there is an enlarged condyle on each lateral ethmoid that articulates with the dorsomesial surface of its respective palatine bone. This connection is a diarthrosis (see Thiele, 1963, for *Blennius*).

There is a thin, median, cartilaginous, and membranous interorbital septum that attaches to the posterior surface of the lateral ethmoids, the anteroventral surface of the frontals, the anterodorsal surface of the parasphenoid, and includes the anterior end (belophram, see p. 43) of the basisphenoid.

Vomer (figs. 1, 2, 4).—Viewed dorsally or ventrally the vomer is a T-shaped bone with the cross arm (head) of the T anterior. Ventrally the head of the vomer bears a row of conical teeth. Dorsally each side of the vomerine head bears thin, ascending, irregular processes that join with the lateral ethmoids. The processes surround a median depression in the vomer that contains the ethmoid cartilage. For most of its length the posterior process of the vomer is overlapped on either side by thin anteriorly extending blades of the parasphenoid.

Parasphenoid (figs. 1, 2, 4).—The median, ventrally keeled parasphenoid externally overlaps each side of the vomer anteriorly. On each side, at about its midlength, the parasphenoid gives rise to broad ascending processes, each of which meets its respective frontal dorsally, impinges slightly on the lateral margin of the basisphenoid and broadly on the ventral external surface of its respective pterosphenoid and the anteroventral portion of its respective prootic. Posterior to the ascending processes on each side, the parasphenoid joins its respective prootic for most of the prootic's ventral margin. The posterior end of the parasphenoid is joined and overlapped on either side by the median basioccipital.

On each side, somewhat posterior to the anterior end of the parasphenoid and extending just anterior to the origin of each ascending process, the parasphenoid bears dorsally a narrow ventrolaterally directed shelf. This shelf, as well as the remaining ventrolateral surface of the parasphenoid on each side, gives rise to a broad sheet of connective tissue that attaches to the mesopterygoid and metapterygoid.

Basioccipital (figs. 2–5).—The basioccipital is roughly rectangular in ventral (and dorsal) aspect. There is a deep, slender notch in the median anterior portion of the bone. Anteroventrally and medianly the basioccipital is overlapped by the parasphenoid and appears roughly V-shaped in ventral aspect. The posterior portion of the basioccipital is thickened and expanded into a large circular condyle, which articulates with the centrum of the first vertebra. Dorsoposterolaterally on each side, the basioccipital joins the ventral surface of each exoccipital. Dorso-anteriorly the basioccipital joins the posteroventral surface of the prootic. The dorsoposterior surface of the basioccipital forms the floor of the foramen magnum.

Frontal (figs. 1–4).—The frontals are relatively long and large bones each consisting of a narrow, anterior arched portion and a posterior broad portion. They are joined to each other for their entire length. Along the longitudinal midline of the dorsal surface of the skull they narrowly and irregularly overlap each other; posteriorly their median edges are raised dorsally and form a low, thin crest, highest at its posterior end. The crest terminates at the large mid-dorsal opening of the supratemporal branch of the laterosensory canal system (the external, cutaneous openings, pores—termed "predorsal commissural pores" by Springer, 1967b—are extensions of this single opening).

The dorsoposteriormost portion of the crest of each frontal impinges on its respective side on the lateral surface of the raised, anterior extension of the supraoccipital (not visible externally).

The dorsoposterior end of each frontal lies under the dorso-anterior end of its respective parietal but may form a pocket into which the end of the parietal inserts. At the externally visible anteriormost extension of its respective parietal, each frontal abruptly passes external to the ventroanterior portion of the parietal and continues ventrally external to the dorso-anterior end of its respective pterotic, the dorso-anterior end of its respective sphenotic, and the dorsoposterior end of its respective pterosphenoid.

Each frontal has a lateroventral descending wing, the ventral portion of which meets and lies internal to the dorsoposterior portion of the ascending wing of the parasphenoid on its respective side, but external to the dorso-anterior portion of its respective pterosphenoid.

The sensory canal (supraorbital) in the frontal extends through the anterior arch of the frontal and along the lateral margin of the bone. The anterior opening of the canal is continuous with the dorsal opening of the sensory canal of the nasal bone. At a point just anterior to where the arched and broad portions of the frontal meet (above the orbits), each frontal is pierced medially by a foramen that leads to its sensory canal, thus forming a common connection between the two supraorbital canals. This common connection also opens to the surface of the skull by a foramen between the frontals (half the margin of this foramen formed by each frontal). There are several openings to the supraorbital canal in the region above the orbit. The most posterior of these openings is at the junction with the dorsal opening of the infraorbital canal in the fifth circumorbital (dermosphenotic) bone. The supratemporal canal continues posteriorly from the orbital region and joins the pterotic canal (the latter canal is contained partially in the sphenotic).

Parietal (figs. 1, 3, 5).—The parietals contact each other only for a very short distance, at the dorsal midline of the skull just anterior to the large dorsomedian opening of the supratemporal canal of the laterosensory system. Along most of their median borders the parietals are separated from each other by the frontals anteriorly and by the supraoccipital posteriorly. Just anterior to its posterior end, each parietal bears a raised crest through which the supratemporal canal passes (there are three external openings to this canal in each parietal). Dorsally each parietal crest curves anteriorly and is continuous with the anteriorly extending dorsal crest of the parietal's respective frontal. Just before the parietal crest curves anteriorly it also joins a raised portion of the supraoccipital that forms the posteriormost border of the large dorsomedian opening of the supratemporal canal of the laterosensory system. The crest of each parietal is continuous ventrolaterally with the crest of its respective pterotic. The posterolateralmost end of each parietal crest forms the anterior border of an external opening of the supratemporal canal. The posterior border of each opening is formed by its respective epiotic (anterior margin of the raised process that articulates with the posttemporal). The canal in each parietal crest is continuous with the canal in the mesially extending arm of its respective lateral extrascapular. There are no median extrascapulars.

Each parietal contacts its respective pterotic laterally. Posterolaterally each parietal fits into a deep groove between the bladelike and pyramidally shaped portions of its respective pterotic. The portion of the parietal continuing anteriorly from the groove is overlapped externally by the bladelike portion of the pterotic alone. Ventrolaterally each parietal overlaps the dorsoposteriormost extension of its respective sphenotic.

On the internal surface of the parietal is a shallow groove continuous ventrally with a similar groove in the sphenotic. The anterior vertical semicircular canal of the ear lies in this groove.

Pterotic (figs. 1–5).—Each pterotic is an irregularly shaped bone with a heavy-bodied and roughly pyramidally shaped, hollow, posterior section (forming the posterodorsolateral corner of the skull) and a long, thin, bladelike anterior section. The internal perimeter of the pyramidal section is a roughly ringlike jointing surface that lies internal to, and is separated by a deep groove from, the dorsally lying bladelike section. Sandwiched in the groove between these two pterotic portions is the posterolateral region of the parietal. The parietal extends anteriorly beyond the level of the groove and lies under the pterotic bladelike portion.

The ringlike jointing surface of each pterotic's pyramidal section joins its respective sphenotic dorso-anteriorly, prootic ventroanteriorly, exoccipital ventroposteriorly, and epiotic dorsoposteriorly. Some portion of the synchondral joints with each of these four bones, except the sphenotic, is visible on the external surface of the skull. Dorso-anteriorly, each pterotic overlaps its respective frontal (but the anteriormost tip of the pterotic passes under the frontal), overlaps portions of the dorsal and posterolateral surfaces of its respective sphenotic, and is overlapped ventrolaterally by its respective intercalar (a portion of the intercalar may also insert in a pocket on the pterotic external surface).

The posterior end of each pterotic's bladelike portion is raised dorsally into a thin crest that is continuous with a crest formed by its respective parietal. Just ventrolateral to the pterotic crest is the fossa in which the posterior dorsal condyle of the hyomandibular articulates. Extending posterolaterally from the fossa is the expanded pterotic "spine." A ridge on the ventral side of the spine is continuous with a ridge on the surface of the intercalar. A broad ligament arises from the ridge (both portions) and attaches to the dorsoanterior surface of the cleithrum. The ventral arm of the posttemporal is attached by a short ligament to the area where the ridges of the pterotic and intercalar meet. A slender dorsal projection of the proximal portion of the pterotic spine exists posterior to, and slightly separated from, the lateral end of the raised crest of the pterotic's blade-like portion, thus forming a U-shaped groove. A branch of the laterosensory canal passes through this groove to the preopercle. The ⅂-shaped lateral extrascapular at its anterolateral angle has an opening that faces the internal margin of the groove. The internally directed arm of the ⅂-shaped extrascapular lies against the posterior surface of the pterotic crest. The posteriorly directed arm of the extrascapular lies on top of the pterotic's thickened pyramidal portion, and obscures the pterotic-epiotic joint in this region.

Anteriorly, on the internal surface of the pterotic blade, there is a broad, shallow groove for the pterotic canal of the laterosensory system (the internal wall of the groove is formed by the sphenotic). The groove becomes a tube in the bladelike portion at about the midlength of the blade and continues posteriorly, opening externally just posteroventral to the lateral end of the pterotic crest. The pterotic canal here continues into the anterolateral opening of the lateral extrascapular. Internally, the pterotic's pyramidal portion contains a U-shaped canal that surrounds the horizontal semicircular canal of the ear.

SPHENOTIC (figs. 1–4).—Each somewhat paddle-shaped sphenotic gives rise on its posteroventrolateral border to the upper half of a cupshaped articulating surface (fossa) for the dorsal anterior condyle of its respective hyomandibular (the lower half of the articular surface for the hyomandibular is formed by the prootic). A longitudinal ridge on each sphenotic external surface gives rise to a ventrolateral process (the sphenotic spine) just dorsoposterior to the level of the anterior hyomandibular condyle.

Externally, most of the dorsal portion of each sphenotic is overlapped by the internal surface of the bladelike portion of its respective pterotic, the ventral margin of which rests in a longitudinal sphenotic groove that passes just internal to the sphenotic spine. The supratemporal canal joins the pterotic canal, which passes over the sphenotic's anterolateral surface in the region overlapped by the pterotic (the outer wall surrounding the canal is formed by the pterotic). The extreme dorsoposterior extension of each sphenotic is overlapped by its respective parietal. The slender anterior extension of each sphenotic overlaps the dorsal external surface of its respective pterosphenoid and is overlapped by its respective frontal. A ridge on the internal surface of each sphenotic forms a synchondral joint with the dorsoposterior margin of its respective pterosphenoid. At its posterior end, each sphenotic forms a synchondral joint with its respective pterotic; at its ventroposterior margin, a synchrondral joint with its respective prootic.

A broad, shallow groove on the internal posterior end of each sphenotic is continuous with a similar groove on its respective parietal. Part of the anterior vertical semicircular canal of the ear lies in this groove.

A narrow canal passes diagonally through each sphenotic. The anterior opening of the canal is on the ventro-antero-internal margin of the sphenotic's broad portion just dorsal to the articulating surface for the hyomandibular. The posterior opening of the canal is in a groove just mesial to the posterior margin of the sphenotic spine (just external to the groove on the sphenotic inner surface for the tube of the anterior vertical semicircular canal). Although the nerves were not investigated, it is probable that the n. ramus oticus passes through this canal.

Pterosphenoid (figs. 2, 4).—Ventrally, each thin, internally concave pterosphenoid lies internal to the dorsoposterior portion of its respective ascending wing of the parasphenoid and posteriorly internal to the anterior portion of its respective sphenotic. The ventroposterior margin of the pterosphenoid forms a synchondral joint with the internal dorso-anterior margin of the prootic, while an anteriorly extending projection of this prootic margin is external to the posterior margin of the pterosphenoid. The dorsoposterior margin of each pterosphenoid forms a synchondral joint with its respective sphenotic along a ridge on the internal surface of the sphenotic.

Basisphenoid (fig. 2).—Viewed dorsally, the median basisphenoid appears Y-shaped with the broad arms ("meningost"—see discussion under sphenoid region, p. 43) of the Y oriented posterolaterally and the slender, pointed shank directed anteriorly. There is a foramen present just anterior to the angle of junction of the arms of the Y (not present in all specimens). The shank extends into the interorbital septum, where it bends sharply ventrally and just fails to reach the dorsal surface of the parasphenoid. The distolateral margin of each basisphenoid arm forms an overlapping, irregular joint with the ventralmost internal surface of its respective pterosphenoid, thus sandwiching this narrow pterosphenotic portion between the basisphenoid and ascending process of the parasphenoid. For a short distance ventral to its joint with the pterosphenoid, the ventral surface of the distal margin of each basisphenoid arm rests on an internally projecting surface of its respective ascending wing of the parasphenoid.

The posterior muscles of each eye pass beneath the basisphenoid and extend along the floor of the cranium (dorsal surfaces of the shank of the parasphenoid and basioccipital) and terminate just anterior to the ventral margin of the foramen magnum. Other than the roof formed by the basisphenoid anteriorly, the muscles are not roofed by bone (the roof of the posterior myodome is membranous for most of its length).

Prootic (figs. 1, 2, 4).—Each complex prootic joins the parasphenoid along the grooved prootic ventral and ventroposterior margins; joins its respective sphenotic along the prootic dorsal margin, its respective pterotic along the prootic dorsoposterior margin, its respective exoccipital along the prootic ventroposterior margin, and the basioccipital for a short distance at the prootic's internal ventroposteriormost margin. Dorso-anteriorly, each prootic overlaps the posterior margin of its respective pterosphenoid and forms a joint with the pterosphenoid's posterior margin along the prootic's internal dorso-anterior margin. On the dorsoposterior external surface, each prootic is overlapped by its respective intercalar. Variably, a shallow pocket may be present on the external surface of the prootic into which a narrow portion of the edge of the intercalar may insert. On its external surface each prootic bears a bridge that ends dorsally at the ventral portion of a fossa in which the anterior condyle of the hyomandibular articulates (the dorsal portion of the fossa is formed by the sphenotic). Internal to the bridge is a hollow with a large opening to the interior of the cranium. A second smaller opening exists at the posteroventral origin of the bridge. The trigemino-facial complex of nerves passes through these foramina. At the external anteroventral point of junction of each prootic with the parasphenoid is an opening (carotid foramen) to an anteriorly extending canal, the walls of which are formed by the parasphenoid and prootic.

Internally each prootic is divided by a thin arching ridge into a large anterior and a small posterior section. Ventrally each section is concave. Dorsally the anterior section is a wall pierced by the two openings in the region of the bridge. The posterior upper section is concave and separated by a narrow convexity from the lower concavity. The anterior ventral concavity surrounds a portion of the brain. The posterior ventral concavity is actually half of a larger concavity formed with the exoccipital (partly floored by the basioccipital) against which the sagitta lies. (The convex mesial surface of the sagitta surrounded by the sacculus projects into the cranial cavity and rests against, or close to, the brain.) The tiny lapillus is situated just dorsal to the sagitta in the ventroposterior portion of the posterodorsal prootic concavity. (The asteriscus is just posterior to the sagitta and rests against the wall of the exoccipital.) The otoliths, in their membranous sacs, project into the cranial cavity and are not separated by bone or cartilage from the brain. The otoliths are illustrated in figure 6. The membranous tube of the anterior semicircular canal lies along the posterior surface of the arching ridge, which divides the prootic into anterior and posterior portions. This ridge continues dorsally beyond the prootic and becomes a concavity on the internal surfaces of the sphenotic and parietal, conforming to the membranous tube of the anterior semicircular canal.

Epiotic (figs. 2–5).—Each epiotic is a domeshaped bone with a raised, large, flattened, external process that articulates with the ventral surface of the dorsal arm of its respective supratemporal. The anterior end of this process lies closely adjacent to the parietal crest and forms a roof over the mesial arm of the ˥-shaped lateral extrascapular. The process indents anteromedially and forms the posterior border of a dorsal opening to the supratemporal laterosensory canal (the anterior border formed by the parietal crest). The internal perimeter of each epiotic dome, similarly shaped to that of the pterotic internal perimeter, is ringlike and forms synchondral joints with its respective exoccipital ventroposteriorly, pterotic anteriorly, and the supraoccipital dorsoposteriorly. Anteriorly the external epiotic surface contacts its respective parietal's ventropostero-internal margin. An arched groove on the internal epiotic surface continues as a tube through the bone through which passes the posterior vertical semicircular canal of the ear.

Externally each epiotic is posteriorly overlapped by a portion of the supraoccipital.

Exoccipital (figs. 2–5).—Externally each exoccipital contacts its respective prootic anteriorly and anteroventrally, its pterotic and epiotic dorsally, the supraoccipital dorso-anteromesially, the opposite basioccipital dorsoposteromesially, overlaps the parasphenoid ventromesially and joins the first vertebra ventroposteriorly. It is externally overlapped by its respective intercalar medio-anteriorly. (Variably a shallow pocket may be present on the external surface of the exoccipital into which a portion of the intercalar's posterior margin may insert.)

Ventrally, on its internal surface, each exoccipital has a ventroanteriorly extending laminar projection, which joins the basioccipital on the projection's ventral margin—the main wall of the exoccipital also joins the basioccipital on the exoccipital's ventral margin; thus, a shallow anteriorly open pocket in the exoccipital, floored by the basioccipital, is formed. Internal and for the most part anterior to the projection is the posterior portion of the concavity, formed with the posteroventral portion of the prootic. The posterior portion of the sagitta rests dorsally internal to this concavity. A secondary, circular concavity exists posteriorly in this exoccipital concavity and is mostly dorsal to the level of the laminar projection. The lapillus rests partly over the anterior portion of the secondary concavity. It seems probable, because of the shape and size of the two concavities, that in life the sagitta and lapillus fitted neatly into these concavities; the laminar projection would then act as a retaining device covering the inner surfaces of the ventroposterior end of the sagitta and the ventral end of the lapillus. These otoliths and the sacculus and utriculus probably were displaced slightly in preservation and subsequent clearing and staining.

Both dorsal and posterior to the level of the just-discussed concavities of each exoccipital, there are two ridges, in line but extending in different planes, on the internal surface of the exoccipital. The pterotic's ventral margin and the prootic's postero-internal margins join the ventro-anterior ridge, and the epiotic's ventroposterior margin joins the long dorsoposterior ridge. The pterotic and epiotic form a joint that is perpendicular to the level of the two exoccipital ridges and dorsal to the narrow space separating the ridges. Ventral to the area of separation of the two exoccipital ridges is a relatively large and deep concavity. In the area of this concavity the membranous horizontal and posterior vertical semicircular canals of the ear join. The horizontal canal passes through a tube of bone extending somewhat dorso-anteriorly from the concavity. The walls of this tube are formed by the exoccipital and pterotic posteriorly and the pterotic alone anteriorly. The vertical canal passes through a tube of bone extending somewhat dorsally from the concavity. The walls of this tube are formed by the exoccipital and epiotic ventrally and the epiotic alone dorsally.

Ventroposteriorly, each exoccipital forms a coneshaped condyle, which is joined to the centrum of the first vertebra. On the ventral external surface of each exoccipital slightly anterior to the condyle, there is an opening to a canal (vagal foramen) that passes through the exoccipital and enters the cranial cavity just ventral to the large concavity discussed above. The external opening of the canal is shielded anteriorly by a ventrally raised portion of the exoccipital.

The exoccipitals contribute the major portion of the walls surrounding the foramen magnum. The remainder of the wall, the midfloor, is formed by the basioccipital.

Intercalar (figs. 1, 2, 4, 5).—Each intercalar is a thin, irregularly shaped bone with a median ridge externally. Each bone overlaps its respective prootic, exoccipital, and pterotic, and portions of the intercalar's irregular margin may insert into shallow pockets in these three bones. A broad ligament, continuous on the pterotic spine, extends from the ridge of each intercalar to the anterodorsal surface of its respective cleithrum. A short ligament from the area where the ridge of the intercalar meets that of the pterotic spine extends to the anterior end of the ventral arm of the posttemporal.

Supraoccipital (figs. 2, 3, 5).—The supraoccipital forms the dorsoposterior cap of the skull. The dorsoposterior convex portion (concave on its internal surface) of the supraoccipital joins each exoccipital and epiotic along the dorsomesial margins of those bones. Thin laminar extensions of the convex portion overlap the epiotics externally (thus covering the epiotic-supraoccipital joint). A narrow, median, dorso-anterior raised extension of the supraoccipital convex portion forms the posterior border of the large dorsomedian opening to the supratemporal canal of the laterosensory system. The lateral margins of the raised extension contact the parietal crest in the region of the dorsomedian opening. Anterior to the raised extension is a broad notch that allows passage of the supratemporal canal. Anterior to the notch the supraoccipital is raised again, as a bladelike extension. The posterior edge of the blade forms the median anterior margin of the dorsomedian opening to the supratemporal canal. Ventrally the blade expands laterally on either side as a thin flange. The dorsomesial portions of each parietal and the dorsoposterior portions of each frontal rest on top of the flange on its respective side.

Circumorbital bones (figs. 1, 3, 7).—There are five circumorbital bones on each side in *Entomacrodus.* The anteriormost (lachrymal) is much larger than the others. The lachrymal is broad dorsally where it is tightly joined to the ventrolateral surface of the lateral ethmoid. Anteriorly, the lachrymal is deep and concave. The end of the lateral arm of the palatine lies internal to the concavity. The third circumorbital is expanded mesially into a narrow subocular shelf that overlaps the second and fourth circumorbitals. The dorsal end of the fifth circumorbital attaches to the frontal. The fifth circumorbital is presumably the dermosphenotic. Each circumorbital bears, or participates in forming, external openings to the infraorbital sensory canal. The anterior termination of the infraorbital canal is in the lachrymal, where the canal exits at three main openings: one dorso-anteriorly and two lateroventrally.

Sclerotic bones.—Each eye is bounded anteriorly and posteriorly by a pair of separated, concave, sclerotic bones (not illustrated).

Nasal bones (figs. 1, 3, 7).—The nasals are separated, elongate, tubular bones with dorsal and ventral lateral projections. A laterosensory canal extends the length of each nasal and is continuous dorsally with the supraorbital canal of the respective frontal. An external opening in the head skin, just lateral to the anterior end of each frontal, also leads to the nasal canal where the canal continues from the nasal to the frontal. A second opening just below the dorsal end of the nasal leads to an external opening adjacent to the posterior nostril. The opening at the ventral end of each nasal exits externally as a pore before each anterior nostril. The nasal capsule on each side is between the two lateral nasal projections and is supported mesially by the broad flange that comprises the ventral projection.

Opercular series (fig. 7).—The opercle is a thin, flat bone, except for a thickened, anteriorly concave articulating surface at its dorso-anterior end that articulates with the hyomandibular. Ventrally the opercle inserts in a groove in the thin, flat subopercle. Dorso-anteriorly the subopercle lies ventral to the opercle's posterior margin. A slender extension of the dorsal end of the subopercle projects for a short distance beyond the dorsal level of the opercle. The interopercle is a short, bladelike bone that is well removed from the subopercle. The interopercle is internal to the preopercle and is not visible when the head is viewed laterally. The interopercle's anterior end is attached by a ligament to the angular. The interopercle's posterior end is thickened and ligamentously attached to the posterior end of the epihyal, where the epihyal joins the interhyal. No portion of the interopercle is posterior to the posterior end of the epihyal. Ligaments also extend from the interopercle's posterior end to the subopercle's ventral end.

The preopercle is a crescent-shaped bone with a sensory canal (preoperculomandibular) extending its entire length. The dorsal extension of the canal continues into an opening of the L-shaped lateral extrascapular at the anterolateral angle of the lateral extrascapular. The ventral extension of the canal enters the articular. There are five lateral, external openings to the sensory canal in the preopercle. Dorsally the preopercle is external to the dorsoposterior portion of the hyomandibular. Somewhat below its dorsal end, the preopercle lies partially internal to a ventral extension of the hyomandibular. Anteroventrally the preopercle fits closely into a groove on the quadrate's posterior margin.

UPPER JAW (figs. 1, 7).—The premaxillaries are thin bones each consisting of a ventral, ventrally concave, elongate portion (the body of the premaxillary) and a slender, bladelike ascending process. Each ascending process and respective concave portion is a single bone, though only weakly joined. (Greenwood et al.; 1966, misquoted Thiele, 1965, in stating that the blenniid premaxillary ascending process was separate from the remainder of the premaxillary.) Each ascending process arises from two points, anterior and posterior, on the body of its respective premaxillary. There are openings through the body of the premaxillary just lateral and mesial to the base of each ascending process. The two premaxillaries are not in close contact but are separated by a relatively broad area of connective tissue. The ascending processes extend dorsally to a point between the ventral ends of the nasal bones. A small sphere of cartilage (rostral, but not to be confused with the rostral cartilage of the more primitive fishes) attaches to the posterodorsal ends of the ascending processes. The dorsolateral surface of each premaxillary bears a number of fine, short bony spurs. The dorsal portion of the body of each premaxillary (the "premaxillary crest" of Norman, 1943) lies external to the bases of the majority of the premaxillary teeth on its respective side. The basal portions of the functional premaxillary teeth (the teeth numbering about 180) are arranged in a linear close-set series and are loosely suspended in a continuous band of connective tissue attached to the ventral surface of the premaxillaries. The teeth and connective tissue collectively are called herein the "premaxillary dental plate." None of the teeth are in direct contact with the bone of the premaxillary. The lateral ends of the dental plate extend beyond the lateral end of the premaxillary on each side. Dorsal to the functional (ventralmost) series of teeth and imbedded in the connective tissue, there are about 10 interrupted horizontal series of replacement teeth. The replacement teeth are formed less completely than the main series and decrease in relative development from the ventralmost to the dorsalmost series. The functional teeth are laterally compressed and broadly based (in lateral aspect) with slender, blunt, recurved tips.

The heavy-bodied maxillaries lie closely adjacent and dorsal to the premaxillaries, and anteriorly, mesial to the palatines and lachrymals. The maxillaries are complex bones each consisting of a broad, posteriorly extending shank (somewhat concave ventrally, with a large foramen posteriorly, which is not visible in the illustration) and an anterior expanded portion. Each anterior portion is concave ventrally with a blunt, rounded protuberance extending dorsally, another longer protuberance extending anteriorly, a cupshaped depression in the bone between the protuberances, and an anteromesially arising, laterally recurved hook. A portion of the lateral arm of each palatine bone passes over its respective maxillary and is held in position by both connective tissue and the laterally recurved hook of the maxillary. The concavity below the anteriorly extending protuberance of each maxillary saddles its respective premaxillary just lateral and posterior to the premaxillary ascending process. Connective tissue arising from all its surfaces variously attaches each maxillary with its respective premaxillary, palatine, and lachrymal. A ligament extends from the anteriorly extending protuberance of each maxillary to the midmesial margin of its respective nasal bone.

A slender ligament from the anteromesial surface of each maxillary extends dorsoposteriorly and joins with a broad ligament arising from the dorsal margin of its respective articular; together they broadly attach to the cranium along the area from about the sphenotic spine to the parietal crest.

Lower jaw (figs. 1, 7).—The ventro-anterior portion of each articular inserts into the posterior end of its respective dentary. At the posterior end of each articular there is a broad concave articulating surface for its respective quadrate. A small angular clasps each articular at the latter's ventroposterior end. Each angular is connected by a ligament to the anterior end of its respective interopercle. A small sesamoid articular (not illustrated) is attached in a conforming concave depression on the midanteromesial surface of each articular. Immediately ventral to each sesamoid articular is the greatly reduced endosteal process (not illustrated) of each articular, more deeply stained than the remainder of the articular. A greatly reduced Meckel's cartilage is continuous with the anterior end of each endosteal process and sesamoid articular. This cartilage extends anteriorly for a short distance into the dentary, terminating at about the level of the base of the dentary's recurved canine tooth.

Just lateral and dorsal to the area clasped by the angular, there is an opening to the sensory canal (preoperculomandibular) that passes ventromesially through the articular and exits on the ventromesial surface. The canal then passes into an opening in the dentary on the mesial surface of the latter's ventroposteriormost end. The canal immediately divides and exits through a large opening at the dentary's ventrolateralmost corner and another opening just anterior to the latter opening, but on the ventral margin of the dentary.

The dentaries are concave anteriorly for reception of the bilaterally continuous dentary dental plate, which bears about 140 functional teeth. These teeth are similar to those of the premaxillary dental plate and are loosely attached in a band of connective tissue. The teeth of the dental plate do not directly contact the bone of the dentary. There are about seven interrupted horizontal series of replacement teeth embedded in the connective tissue of the dental plate ventroposterior to the functional series of teeth. In addition to the teeth of the dental plate, each dentary bears a large recurved canine implanted on the bone dorsolaterally. There is a large fossa, open posteriorly, in the dentary beneath each of these canines. Completely contained in each of these fossae, there is another (replacement?) canine tooth. The contained canine was not found in any of the other specimens of *E. nigricans* examined.

A large posterior pocket in each dentary allows for insertion of the anterior portion of its respective articular. A circular opening to the pocket is present posterolaterally in each dentary. There are several fine, short spurs on the anteromesial surface of each dentary.

Hyomandibular and palatine arch (figs. 1, 3, 7).—Each hyomandibular bears two condylar surfaces dorsally. The anterior articulates with a fossa formed by the sphenotic and prootic and the posterior articulates with a fossa in the pterotic. On the internal surface of each hyomandibular between and just below the condylar surfaces, there is a small opening that leads into a ventrally extending canal (for the n. truncus hyomandibularis) that exits on the external surface of the hyomandibular near its ventro-anterior margin. Dorsoposteriorly on each hyomandibular, there is a third condylar surface that articulates with the opercle. The dorsal end of each preopercle lies just external to this condyle on its respective hyomandibular. A posteroventrally directed blade of each hyomandibular overlaps its respective preopercle dorso-anteriorly. The anteroventral portion of each hyomandibular is thickened into a supporting rod that is capped with cartilage and is attached ligamentously to the cartilaginous dorsal ends of its respective symplectic and interhyal. The dorso-anterior end of each hyomandibular overlaps and is attached to the dorsal end of its respective metapterygoid. The anterior margin of each hyomandibular is broadly attached ligamentously to the posterior margin of its respective metapterygoid.

Each broadly crescentic symplectic attaches along its ventral third to its respective quadrate in a groove on the quadrate's inner surface.

Each palatine bone consists of a ventroposterior shank and an anterodorsolaterally extending arched arm. The mesial surface of each palatine shank closely joins the ventrolateral surface of its respective ectopterygoid. The posteriormost end of the shank attaches in a notch near the ectopterygoid's posterior end. The mesial surface of the anterodorsolaterally extending arm of each palatine is connected loosely to the antero-external surface of its respective maxillary. A laterally directed, recurved, hooklike process of each maxillary clasps the arched arm of its respective palatine somewhat dorsal to the ventral end of the palatine arm. The palatine arm and the end of the maxillary hook are visible just anterior to the anterior marginal concavity of the lachrymal. On the dorsal surface of the proximalmost portion of the palatine arm, there is a slightly concave surface that articulates with the condylar surface of its respective lateral ethmoid.

The anteromesial end of each palatine is attached strongly to the ventromesial surface of its respective lateral ethmoid and to the dorsoposterior surface of the head of the vomer on its respective side.

Each ectopterygoid is joined along its anteroventral margin to its respective palatine and along its anterodorsal margin to its respective mesopterygoid. Posteromesially each ectopterygoid is joined to the anteromesial surface of its respective quadrate. The ventroposterior edge of the ectopterygoid rests in a shallow groove on the quadrate's anteroventral surface. The ectopterygoid at its posterior quarter inserts in a groove on the quadrate's anteroventral margin.

Each mesopterygoid attaches at its anteriormost end to its respective palatine, along the mesopterygoid ventral margin to its respective ectopterygoid, and at its posteroventromesial surface to its respective quadrate. The posterior margin of each mesopterygoid is attached to its respective metapterygoid by connective tissue.

Each quadrate is a fanshaped bone with a midvental process that articulates with its respective articular. Each quadrate has a groove anteroventrally and another ventromesially that clasp its respective ectopterygoid. A groove on the posteromesial surface of each quadrate attaches to its respective symplectic. Each quadrate bears a strengthened posterodorsal articulating surface that terminates in cartilage and is attached ligamentously to the cartilaginous end of its respective metapterygoid. The postero-internal surface of each quadrate is joined closely to its respective preopercle on the latter's anteroventral surface. A shallow pocket extends along the ventrolateral margin of each quadrate.

HYOID ARCH (fig. 8).—Each dorsal and ventral hypohyal forms an interdigitating joint with its respective ceratohyal. The upper external portion of each dorsal hypohyal is thin and laminar. Anteriorly the laminar portion thickens and curves broadly internally encompassing a ſ-shaped depression, the floor of which forms the roof of a cupshaped depression that is bounded ventrolaterally by the ventral hypohyal. The upper lateral projection of each side of the unpaired, medianly positioned urohyal firmly attaches to the ventral portion of this depression on its respective side. The ventrolateral projection of each side of the urohyal overlaps and attaches to the ventrolateral surface of its respective ventral basihyal. The saddle-like depression thus formed between the projections on either side of the urohyal strongly interlocks the ventral hypohyals.

Each epihyal and ceratohyal join by an interdigitating joint. Each ceratohyal bears two deep notches ventroposteriorly in each of which a branchiostegal (first and second branchiostegals) is attached. The third and fourth branchiostegals attach to the lateral surface of the posterior end of the ceratohyal; the fifth and sixth branchiostegals attach to the lateral surface in the area of the interdigitating joint between the ceratohyal and epihyal. The anteroventral surface of the interhyal connects to the dorsoposterior surface of the epihyal. The posterior end of the interopercle attaches to the epihyal just anterior to the attachment of the interhyal. Strands of connective tissue extend from the posterior surface of the urohyal to the ventral junction of the two cleithra.

Branchial arches (fig. 9).—The branchial arches are suspended from the ventral side of the cranium. The first arch is connected ligamentously to the cranium by the first epibranchial. The epibranchials of the second, third, and fourth arches of each side are attached on their respective side to a single tooth bearing upper pharyngeal bone (probably representing the second through fourth pharyngobranchials), which is in turn suspended from the cranium. The fifth arch is represented by a single tooth bearing lower pharyngeal bone (fifth ceratobranchial). A broad ligament attaches the anterodorsal end of the lower pharyngeal to the dorsoposterior surface of the fourth ceratobranchial. The first and second hypobranchials of each side attach between the first and second and the second and third basibranchials, respectively. The third hypobranchial of each side is directed anteriorly and attached by a ligament from its anterior end to the flattened ventral surface of its respective second hypobranchial. At its posterolateral end, each third hypobranchial is attached to the distal end of its respective third ceratobranchial. A flattened plate of cartilage is situated between, and attached ligamentously to, the posteromesial ends of the third hypobranchials of both sides. This same cartilage also attaches to the distal ends of the fourth ceratobranchial and lower pharyngeal bone of each side. Each of the first four arches bears a double row of short, slender gill-rakers (not illustrated) anteriorly and a double row of long, slender, bony gill filament supports posteriorly (not illustrated). The fifth arches (lower pharyngeals) each bear a row of gill-rakers anteriorly, but no gill filament supports.

Outline of the laterosensory system.—The anteriormost opening of the laterosensory system on each side is through the ventral end of the respective nasal bone. The canal extends the length of each nasal and enters the anterior end of each nasal's respective frontal. The canal of each frontal (supraorbital) joins the other through an internal opening in the median wall of each frontal in the region above the orbits and, at this junction, exits to the surface of the skull by a common opening formed between the frontals. Each supraorbital canal then passes dorsolaterally along its respective frontal. There are several openings to each supraorbital canal in the region over the orbit. At the dorsoposterior end of the orbit, each canal sends a branch (infraorbital) through its respective circumorbital bones, with openings to the canal in some bones and between each pair of bones. Each supraorbital canal extends posteriorly and joins its respective pterotic canal (at its entrance into the pterotic an anterior extension of the sphenotic shares with the pterotic in surrounding the pterotic canal). Each pterotic canal exits at the posterior end of its respective pterotic where it divides into two branches. One branch passes laterally and enters the preopercle, becoming the preoperculomandibular canal. The preoperculomandibular canal extends along the length of the preopercle (with five external openings) and enters the articular, almost immediately passing into the dentary and again exiting almost immediately from two openings in the posterior end of the dentary. The other branch from the pterotic canal enters the lateral extrascapular and there divides into two branches. One branch extends dorsomesially (supratemporal canal) through the posterior end of the parietal (with several external openings), continues to the supraoccipital, where it exits as the dorsomedian opening of the skull and joins the supratemporal canal from the opposite side of the skull. The second branch passes from the lateral extrascapular into the posttemporal and then into the supracleithrum. From the supracleithrum the canal enters the skin of the side and continues as the lateral line canal. Periodically along the lateral line, there are small tubular ossifications that presumably surround the neuromasts. The lateral line is continuous to an area below the anterior portion of the soft dorsal fin; thence it continues as isolated bipored tubes, ending well anterior to the caudal peduncle.

## Vertebral Column and Unpaired Fins

FIGURES 10, 11

There are 34 vertebrae (range for the species: 33–35; up to 36 in other species of *Entomacrodus*). The centra are amphicoelous, constricted midlaterally, lack lateral longitudinal struts, and bear a canal for the notochord. The first three centra are of about equal length and shorter than the remaining centra, which are roughly equal in length. The anterior end of the first centrum articulates with the basioccipital. There is a neural spine present on all but the first two and last centra. The neural arches of the first two vertebrae are complete (fused above). The neurapophyses (neural prezygapophyses) of the first vertebra are enlarged, directed dorsally, and articulate with the exoccipital condyles. The first recognizable neural postzygapophyses are on the fifth vertebra. The centra of the first three vertebrae bear posteriorly directed processes ventrally that overlap the next succeeding centrum. These processes are not serially homologous with the neural or haemal pre- or postzygapophyses. The third through sixth vertebrae bear concave parapophyses that articulate with the heads of the first through fourth pleural ribs on each side. The parapophyses are unmodified on the seventh and eighth vertebrae and articulate on their mesial surface with the fifth and sixth pleural ribs on each side. The ninth and tenth vertebrae bear parapophysial stays (Makushok, 1958) connecting the parapophyses, which articulate respectively with the seventh and eighth ribs on each side. The eleventh vertebra (first caudal vertebra) bears the first haemal spine and the ninth (terminal) pair of pleural ribs, which articulate with the haemal arch. All the caudal vertebrae except the hypural bear distinct haemal spines. The first epipleurals are attached to the neural arch of the first vertebra. The succeeding epipleurals are attached gradually more ventrally on the succeeding vertebrae. The second pair of epipleurals are attached to the neural arch of the second vertebra; the third through eighth are attached to their respective pleural ribs on the third through eighth vertebrae, and the ninth through thirteenth (terminal) are attached to the lateral surface of the nonautogenous parapophyses of their respective haemal arches on the ninth through thirteenth vertebrae. The first recognizable haemal prezygapophysis appears on the twelfth vertebra; and the first noticeable haemal postzygapophysis, on the ninth vertebra.

The neural and haemal spines of the antepenultimate and penultimate vertebrae are nonautogenous. The haemal spine of the penultimate vertebra is modified for participation in support of the ventral procurrent rays of the caudal fin; the neural spine is reduced (absent?) and does not participate in support of the fin. There are eight unsegmented, unpaired, dorsal procurrent caudal rays, and seven unsegmented, unpaired, ventral procurrent caudal rays. (Of six other specimens examined, all had eight dorsal procurrent caudal rays; five had seven and one had eight ventral procurrent caudal rays.) There are 13 segmented rays in the caudal fin, the middle nine of which are branched (once). There are two epurals that attach anteriorly in a median groove on the dorsal surface of the urostylar portion of the fused dorsal hypural plate ("hypurals 3 and 4," using the terminology of Nybelin, 1963) and urostyle. If uroneurals are present, their identity has been completely lost through fusion. The minimal hypural (Makushok, 1958; an "epural" in Springer, 1966; "hypural 5," Nybelin, 1963) is attached posterodorsally to the fused dorsal hypural plate. The minimal hypural is attached to the posteriormost dorsal procurrent caudal ray and shares with the fused dorsal hypural plate in support of the dorsalmost segmented caudal ray. (This condition exists in all the other species of *Entomacrodus* examined except *E. stellifer* and *E. rofeni*, where the minimal hypural appears to support only the procurrent caudal ray.) Five branched caudal rays also attach to the fused hypural plate. There is one ventral hypural plate bearing four branched and two unbranched caudal rays. This plate attaches (but is autogenous) proximally to the urostylar portion of the fused dorsal hypural plate and urostyle. The ventral hypural plate probably consists of a haemal spine and hypurals 1 and 2; it lacks the posterolaterally directed phlange for the attachment of part of the flexor caudalis ventralis superficialis muscle (Greene and Greene, 1914) found in many perciforms and lower teleosts (Gosline, 1960, 1961). This is not surprising in view of the fact that *Entomacrodus* is a benthic genus that probably does not use the caudal fin as much for propulsion as do free swimming fishes. An opening on either side of the ventral hypural plate is the point at which the caudal artery bifurcates and the two portions exit. According to Nybelin (1963), the last preural (precaudal) vertebra is the last vertebra anterior to the bifurcation of the caudal artery.

There are 13 spines and 15 rays (range for the species: 13–16; for the genus: 13–18) in the dorsal fin. Each spine except the terminal one is attached, usually by a ring joint, to its own pterygiophore. The thirteenth spine is much reduced and is attached to the same pterygiophore (proximal) that supports the first dorsal ray. It would appear that the spines (in blenniids) have been shifted one pterygiophore posteriorly in their pterygiophore relationships and that the thirteenth spine has become attached to a ray-supporting proximal pterygiophore. The shape of the ray-supporting pterygiophores is different in appearance from the spine-supporting pterygiophores and, thus, favors such an assumption. Also, the first spine-supporting pterygiophore is larger than the others and possibly consists of a fusion of the first two pterygiophores. (This condition is common in tropical blennioids, and some malformed specimens of the generally considered more primitive Clinidae actually exhibit two pterygiophores: together equal in size and shape to the normal single first ptergiophore, instead of one; in such specimens the first spine is attached to the second pterygiophore.) The possibility cannot be excluded, however, that the first dorsal spine's pterygiophore has been lost.

The dorsal segmented rays are bilaterally paired structures, and each except the terminal is attached to a bilaterally paired distal pterygiophore, which in turn is attached anteriorly to the expanded distal end of the unpaired proximal pterygiophore just anterior and attached posteriorly to a subterminal prominence of the proximal pterygiophore just posterior. The terminal dorsal ray lacks a distal pterygiophore and is directly attached to the distal end of the terminal proximal pterygiophore. Each spine-bearing pterygiophore and each proximal pterygiophore is attached to a separate neural spine.

There are two anal spines and 17 segmented rays (range for the species: 14–18; for the genus: 14–20). Each ray is a bilaterally paired structure. The first spine is attached to its own pterygiophore but the second spine is attached to the proximal pterygiophore supporting the first distal pterygiophore and its associated first ray. It may be that, similar to the condition in the dorsal fin, the first spine-bearing pterygiophore has been lost and the first spine is attached to the second pterygiophore and the second spine has been shifted onto the proximal pterygiophore of the first ray. The spine-bearing pterygiophore is different in appearance from the ray-bearing proximal pterygiophores. Each segmented ray except the last two is supported by an unpaired distal pterygiophore, which is attached in turn anteriorly to the expanded distal end of the proximal pterygiophore just anterior, and attached posteriorly to a subterminal process on the proximal pterygiophore just posterior. The terminal two anal rays lack distal pterygiophores, and both are attached to the distal end of the terminal proximal pterygiophore. In some specimens of *E. nigricans* (and other species of *Entomacrodus*) the terminal two proximal pterygiophores each support a single ray and in this condition only the last ray lacks a distal pterygiophore.

The two pterygiophores supporting the first and second anal spines are attached to the posterior surface of the first haemal spine. The remaining proximal pterygiophores are attached each to a separate haemal spine.

### Pectoral and Pelvic Girdles and Fins

FIGURE 12

Each posttemporal is dorsoventrally forked and has a tube for a sensory canal passing through the bone between the forks. The sensory canal from the posteriorly directed arm of each lateral extrascapular passes into the canal of its respective posttemporal. The dorsal fork of each posttemporal articulates anteriorly with a process on its respective epiotic. The anterior end of the lower fork attaches by a short ligament to the area of junction of the continuous ridge formed by its respective intercalar and pterotic. The sensory canal passes from each posttemporal into a short tube in its respective supraclieththrum at the antero-internal surface of the supracleithrum, where the supercleithrum attaches to its posttemporal. This surface is modified to form a confluent joint with the supracleithrum. For most of its length the internal surface of each supracleithrum is attached to the dorso-external surface of its respective cleithrum. The supracleithral canal is very short and enters the skin of the side where the canal continues as the lateral line canal. The lateral line canal is continuous in its dorsal portion and bears several very short, spaced, ossified tubes (not illustrated). The canal descends to the midside posterior to the level of the appressed pectoral rays and becomes a series of disconnected bony tubes (not illustrated), which terminate below the level of the anterodorsal rays.

Each cleithrum is a large, roughly cresentic bone with the open end of the arc anterior. The dorsal end of each cleithrum is expanded as an anteriorly extending projection that is attached by ligaments to the rear end of the skull. The ventro-anterior end of each cleithrum is joined to the same portion of the cleithrum of the opposite side, and these together are attached by strands of connective tissue to the median urohyal.

There are two slender postcleithra on each side. The dorsal end of the upper postcleithrum on each side is flattened, and its external surface is attached loosely to the dorsoposteriormost internal surface of its respective cleithrum, and its internal surface is attached similarly to the external distalmost end of the first epipleural on its respective side. The lower postcleithrum on each side is attached at its dorsalmost end to the anteroventral end of its respective upper postcleithrum. The two postcleithra on each side are more or less in line with the pleural ribs, and it would seem that they function as a pleural rib protecting the viscera.

Subdorsally on the external surface of each cleithrum, there are adjacent large and small openings; the large opening exits almost immediately ventral into a large excavation. The small opening leads into a canal that extends through most of the arc of its respective cleithrum and exits just internal to the anterior edge of its respective pelvis. The canal broadens into a large sinus at the level of the coracoid. On the anterior concave surface of each cleithrum at this same level, there are several foramina that enter the sinus. Dorsally just below the large and small openings in each cleithrum, most specimens bear two foramina, each on a different cleithral surface, which pierce the cleithrum and, thus, interrupt the canal into which the smaller opening leads. Uncommonly, one of these foramina is absent.

Each scapula is a small bone applied closely to the internal dorsoposterior surface of its respective cleithrum. A small rodlike portion of each scapula (the dorsalmost portion of the scapula) overlaps its respective cleithrum externally. The tip of this projection stains darkly and seems to lie in a band of cartilage and ligament extending to and along the distal ends of the pectoral radials. There is a small raised process dorsally on each scapula (internal surface) from which a ligament extends to the dorsal midmargin of the respective dorsalmost pectoral radial. The latter process bears an opening at its base that leads into a canal opening into the relatively large median scapular foramen. Along the midposterior margin of each scapula are two enlarged condyles, one above the other. The upper of these processes articulates with the proximal end of the dorsalmost pectoral radial, and the lower articulates with the proximal end of the second to dorsalmost radial. The ventral end of the scapula is joined synchondrally to the dorsal end of the coracoid. The coracoid has become fused completely with the cleithrum with little or no evidence of a joint. It is represented by a darkly staining synchondral joint with the scapular (above) a long raised condyle on the posterior margin of the cleithrum, which synchondrally joins the proximal ends of the lower two pectoral radials on its respective side, and a mesially projecting spikelike process (the "postcoracoid process" of Swinnerton, 1905), which appears to arise ventrally from the cleithrum. Ligaments extend from the process to the ventral surface of the lowermost pectoral radial.

There are four pectoral radials on each side. The uppermost on each side is shortest, fanshaped distally, and attached to the upper four pectoral rays; the next lower radial bears a long, slender shank and an expanded distal end that attaches to the fifth and sixth pectoral rays from the dorsalmost radial. The next lower radial is the longest, with a slightly broader head and more expanded base than the previous radial, and attaches to the seventh through ninth pectoral rays from the dorsalmost. This radial attaches proximally to both the scapula and coracoid. The ventralmost radial is hourglass shaped with a well-developed ventral phlange. The distal end of the ventralmost radial attaches to the tenth through fourteenth rays from the dorsalmost. The proximal end of the lowermost radial attaches to the coracoid condyle.

The pectoral rays join the radials through cartilage and other connective tissue. The bases of both halves of each ray are expanded, and in the lower half of each fin these expansions gradually take the form of dorsally extending processes that overlap the next ray dorsal.

Each pelvis is a laterally convex (concave inner surface) bone with a thin, external, dorsoposteriorly extending triangular phlange, a thicker internally extending dorsoposterior roof, and a thin, slender internal blade arising from the ventral end of the roof and extending to the anterior end of the pelvis (projection free at anterior end). Each pelvis is closely attached to its respective cleithrum just dorsal to the cleithral symphysis along the pelvis external and anterior surface. Together the two pelvises form a relatively short "pod" that fits snugly in the angle formed by the anteroventral junction of the two cleithra.

Each pelvis is attached strongly to the other along the internal margin of the pelvic roof and the anteriorly extending projection. Anteriorly, the roof joint surfaces are appressed to each other; posteriorly, the joint surfaces are interdigitating. Between the anterior and posterior portions of the roof joint each surface indents and forms half of the margin of a medial opening. Anteromedially, immediately below the roof joint, the surface of each pelvis indents to form half of the margin of another, larger opening. Just posterior to this latter opening in each pelvis, there are one or two slitlike foramina. Ventral to these foramina a small, thin-walled, anteriorly opening pocket is formed in each pelvis. At the posterior external corner of each pelvis, there is an irregular depression into which the forked base of the respective pelvic fin spine is attached. A thickened process extends internally from the internal face of each depression. The base of the second through fourth pelvic fin rays, each a bilaterally paired structure, attach on each side to their respective pelvis along a line extending internal to the depression. The first pelvic fin ray base attaches to the pelvic fin spine just above the spine base. Each pelvic fin spine has a forked base that attaches to the pelvis. The dorsoposterior arm of each fork gives rise to two separated processes. Slightly distal of its midpoint each spine abruptly narrows. A broadened portion proximal to this narrowing is the area of attachment of a broad ligament. Each half of the bases of the first two pelvic fin rays bears externally directed processes; the third and fourth ray bases are unmodified.

## General Discussion of Blenniid Osteology

ETHMOID REGION.—The position of the median ethmoid in relation to the dorsal aspect of the skull is a relatively constant feature within groups of the Blenniidae. In the Blenniini, Omobranchini, and Nemophidinae the median ethmoid is the anteriormost bone of the skull and is visible when the skull is viewed dorsally (pls. 2, 4, 6, 8). The median ethmoid in these groups seems to function as a brace to withstand pressure from the upper jaw; it is associated with a strengthening of the ascending processes of the premaxillaries and a carnivorous habit. In contrast, the Salariini have some portion of the wings of the lateral ethmoids anterior to the median ethmoid (the median ethmoid forms the posterior border of a depression bounded laterally by the lateral ethmoids) and the median ethmoid is not visible (fig. 3, pl. 10) when the skull is viewed dorsally. This condition reaches the extreme in some species of *Ecsenius* (pl. 10), wherein the lateral ethmoids almost encapsulate the median ethmoid and the dorsal end of the latter may be forced back into the orbital region. The condition in *Ecsenius* appears to be the result of extreme shortening of the parasphenoid, with an associated ventroposteriorly curving of the lateral ethmoids to compensate for the shortening. In *Andamia*, the only exception in the Salariini examined, the median ethmoid is the most anterior skull bone and is obvious when the skull is viewed dorsally (pl. 11). The condition in *Andamia* appears to have developed as a result of a depression of the frontals in the orbital region.

The relative size of the median ethmoid is much smaller in the Salariini than in the other blenniids, and this reduction is associated with the extreme weakening of the ascending processes of the premaxillaries and the peculiar nature of the teeth, which in turn are associated with a primarily herbivorous, grazing habit.

In the Blenniinae, as in many perciforms, there is a sphere of cartilage (rostral cartilage) attached to the posterior edges of the distal ends of the ascending processes of the premaxillaries. This cartilage was not seen in the Nemophidinae. The purpose of this cartilage is not clear, but in blenniids it seems to serve as a cushion between the ascending processes and the median ethmoid. In some species of a few genera, an endochondral ossification develops in the rostral cartilage. Such an ossification has not been described for other perciform fishes, but for the cyprinoids Harrington (1955) proposed the name "kinethmoid" for a bone in relatively the same position as the blenniid rostral ossification (since previous names for the cyprinoid kinethmoid, particularly "rostral," have been applied to other bones, their usage might result in confusion). The kinethmoid of the cyprinoids functions in the mechanism for protrusion of the premaxillaries, but since the premaxillaries of blenniids are not protrusible, the function must be different. Although it is not at all certain that the cyprinoid kinethmoid is homologous with the rostral ossification of blenniids, I am provisionally appropriating the name "kinethmoid" for use in the blenniids. Harrington used the name to denote a movable bone in the ethmoid region, and, in the sense of a movably attached bone, the name can be applied also to blenniids.

Those blenniids that were found to have a kinethmoid were the Blenniini: *Blennius marmoreus, B. cristatus* (pl. 1), *B. canevae, B. parvicornis, B. gattorugine, Hypleurochilus geminatus, H. bermudensis, Medusablennius chani;* Omobranchini: *Enchelyurus kraussi* (fig. 13), *E.* species A, *E.* species B; and Salariini: *Stanulus talboti* (of the two specimens examined, the male did and the female did not have a kinethmoid; whether this is a case of sexual dimorphism or of exceptional occurrence, or absence, is not known).

The presence or absence of teeth on the vomer has been used as a generic character in blenniids. Until Smith's (1959) description of *Pereulixia, Lophalticus,* and *Hirculops*—all with vomerine teeth—only *Entomacrodus* was reported as having vomerine teeth. I (1967b) found that, although vomerine teeth are characteristic of *Entomacrodus*, occasional individuals of some species will lack them. (No replacement teeth were seen developing on the vomer, and it is possible that all individuals of a given species of *Entomacrodus* may have them initially, but, if lost accidentally, they are not replaced.) In addition to the above genera, I find that some species of *Blennius, Rhabdoblennius, Praealticus, Stanulus,* and an undescribed genus near *Rhabdoblennius* also have vomerine teeth. In *Stanulus, S. talboti* has the teeth while *S. seychellensis* does not. The holotype of *Rhabdoblennius rhabdotrachelus* lacks vomerine teeth, but all other specimens of the species that I have seen have them. None of the Omobranchini or Nemophidinae are known definitely to have vomerine teeth; however, Sze-Chung (1957) described a species with vomerine teeth, *Lembeichthys furcocaudalis,* that appears to be almost identical with *Plagiotremus spilistius.* The holotype and only known specimen of the latter species does not have vomerine teeth. Vomerine teeth are typically blunt and short and hidden by the velum of the upper jaw. Their function is not known.

SPHENOID REGION.—According to Chabanaud (1936), the basisphenoid of the higher teleosts is the result of the fusion of two ossifications. One, called "meningoste" by Chabanaud, is formed in the dura mater, and the other, called "belophragme," is formed in the interorbital septum; I have anglicized these words below. Chabanaud concluded that the teleostean basisphenoid is not homologous with that of higher vertebrates and, thus, he proposed the name "propitual" for the bone. I accept Chabanaud's findings but have conserved the name "basisphenoid" because of its widespread usage in ichthyology. Most ichthyologists have overlooked Chabanaud's study.

In the Blenniinae a basisphenoid is present in all species. In the Nemophidinae the basisphenoid is absent. In the Blenniini and Salariini the basisphenoid is complete (both belophram and meningost portions are present and fused except in the single specimen of *Blennius canevae* examined, where the meningost and belophram are separate). In the Omobranchini the basisphenoid is complete in *Laiphognathus*, *Cruantus*, *Omobranchus loxozonus*, and *O. elegans*. The belophram is not fused with the meningost in *O. anolius* and is absent in the other species of *Omobranchus* and *Enchelyurus*. The tendency to reduce the basisphenoid in the Omobranchini, as well as other characters (see especially "Jaws and Dentition" below), seems to place this group near the evolutionary line that gave rise to the Nemophidinae.

In the Nemophidinae, *Aspidontus*, *Blennechis*, *Petroscirtes*, and *Runula* have a structure that superficially resembles a basisphenoid in shape and position. This structure is formed by the junction of a mesially extending outgrowth of the anterior margin of the pterosphenoid of each side. These outgrowths meet at the entrance to the braincase and form a tightly interdigitating joint with each other. I term this formation "pseudobasisphenoid" since I first believed it to be a basisphenoid. In addition, each of the pterosphenoids of *Runula* also have a second, more dorsal, mesially extending outgrowth that fails to meet its opposite. The latter outgrowths are visible in plate 8, bottom. The other genera of the Nemophidinae exhibit the second outgrowths to a much lesser degree than *Runula*—or not at all. In *Meiacanthus*, *Dasson*, and *Xiphasia*, the more ventral outgrowths were present but failed to meet. In *Meiacanthus* and *Dasson* at least, the outgrowths were joined ligamentously. The pseudobasisphenoid forms the anterior roof of the otherwise membranous roofed posterior myodome.

*Rhabdoblennius* (Salariini) is unique among the material examined not only in having a complete basisphenoid but also in having mesial outgrowths of the pterosphenoids that meet dorsal to the basisphenoid These outgrowths are comparable in position to the nonmeeting dorsal outgrowths of the pterosphenoids of the Nemophidinae. An undescribed genus near *Rhabdoblennius* has the mesial outgrowths, but these fail to meet.

In a previous paper I (1966) noted that in the blenniids the ascending wings of the parasphenoid reach the descending wings of the frontals and, thus, exclude the pterosphenoids from the orbital region. In most of the blenniids this does seem to be the case; however, there are several exceptions, some of which seem to be variations exhibited by individual specimens. I have examined specimens of *Blennius cristatus*, *B. canariensis*, *Hypleurochilus geminatus*, *Scartichthys gigas*, and an undescribed genus related to *Rhabdoblennius* in which the pterosphenoid of one or both sides separates the parasphenoid wings from the frontals. In addition, Thiele (1963) reported this condition for *Blennius gattorugine,* but this was not true for my specimen. In the Nemophidinae the ascending wings of the parasphenoid may reach the descending wings of the frontals, while at the same time the pterosphenoids, which are internal to these structures, may extend beyond the common margin of these wings and enter, somewhat, the orbital region, where the bone can be seen when the skull is viewed laterally (e.g., pl. 8, center and bottom). In *Runula,* the pterosphenoids typically separate the frontal from the parasphenoid (the illustrated specimen of *R. azalea,* pl. 8, is exceptional). The character, therefore, is not entirely satisfactory for separating blenniids and clinids, although it does indicate a strong trend.

In all the Blenniini and Salariini the pterosphenoid is visible when the skull is viewed laterally. In the Omobranchini the pterosphenoid has become greatly reduced and is a very thin bone closely applied to the inner surface of the frontal and sphenotic; it is excluded from view when the skull is viewed laterally. In the Omobranchini the pterosphenoid can be missed easily unless a careful dissection and disarticulation is made. In the Nemophidinae the pterosphenoid is usually in view when the skull is viewed laterally, but in *Meiacanthus* and *Petroscirtes* the pterosphenoids are not visible when the skull is so viewed, except that a portion may be visible through the foramen through which the V–VII complex of cranial nerves pass.

In *Meiacanthus* there is a unique, continuous ridge formed on the external surface of the ascending wing of the parasphenoid and prootic. The posterior edge of the metapterygoid is attached strongly to this ridge. This attachment greatly increases the immobility of the palatine arch.

Circumorbital bones.—The number of circumorbital bones in blenniids varies from two to five and is frequently diagnostic for genera. In the Blenniini, *Medusablennius* has two circumorbitals (Springer, 1966), the other genera have five (I, 1955, erroneously reported four circumorbitals in *Hypleurochilus geminatus*). In the Omobranchini, *Enchelyurus* has three circumorbitals (fig. 13), *Cruantus* has four, and *Laiphognathus* and *Omobranchus* have five (pl. 3). In the salariini all the genera have five circumorbitals except *Ecsenius* (pl. 9) and an undescribed genus, which have four. (I, 1955, erroneously reported that *Entomacrodus textilis* and *Scartichthys atlanticus*=*Ophioblennius atlanticus* had four.) One specimen of *Enchelyurus* species and one of *Andamia heteroptera* each had four circumorbitals on one side and the normal number for the species on the other. In the Nemophidinae the genera all have four circumorbitals (pls. 5, 7) except *Meiacanthus,* which has three.

Smith and Bailey (1962) reported that most teleosts, including the basal percoids, have six circumorbitals. The blenniids and most of the other members of the Blenniicae have five circumorbitals, thus indicating specialization for this character.

The dorsoposteriormost circumorbital (dermosphenotic) of blenniids is the most reduced of the series and frequently is completely overlapped laterally and excluded from view by the next, more ventral circumorbital.

The presence or absence of a subocular shelf in most blenniids is a matter of subjective decision. The structure ranges from not, or only slightly, present to clearly present and well developed (*Stanulus seychellensis*). Gosline (1968) believed that only *Trachinus* and the congrogadoids among the blennioids had a subocular shelf.

JAWS AND DENTITION.—Norman (1943) in splitting off two subfamilies of the Blenniidae (Blenniinae and Salariinae) used the nature of the jaws and teeth as primary characters. Most workers, including myself, have followed Norman's classification. While the jaws and dentition are the most important characters for separating the Salariini as a taxonomic group, considerably more detail than was used by Norman is necessary to explain them. During my study I have been able to elaborate somewhat on the matter, but more data, primarily histological, are needed on the structure and the relationships of the teeth to the jaws before a full meaning of the characters can be analyzed.

In the Blenniini a canine, rarely two, is present on each premaxillary and each dentary of most species (absent from both jaws in *Chasmodes* and *Hypsoblennius*). The canines range from not enlarged (some species of *Blennius*) to greatly enlarged (*Hypleurochilus*), and there may or may not be a diastema between the premaxillary comblike teeth and the canines; there is no diastema on the dentary. The dentary canines are slightly larger than the premaxillary canines. The comblike teeth number 14 to 56 on the premaxillaries (combined count of both sides) and 15 to 64 on the dentaries (combined count of both sides). Usually the upper jaw has more teeth than the lower, but there is some variation within species. The number of teeth increases significantly with growth in most species. I (1959b, 1967a) have noted this for *Chasmodes bosquianus* and *Hypsoblennius sordidus*, and Randall (1966) has noted it for *Hypleurochilus aequipinnis*. The teeth are firmly attached to the jaw bones, but, even so, they are still slightly movable.

In the Blenniini the replacement teeth develop within the jawbone, which is essentially a bony capsule surrounding a mass of connective tissue. The advanced replacement teeth appear within the jawbone with their tips protruding through foramina (pl. 1).

The ascending processes of the premaxillaries (described in detail by Thiele, 1963, for *Blennius ocellaris, B. sanguinolentus* and *B. gattorugine*) usually are based weakly on the body of the premaxillary in the Blenniini, but in *Blennius ocellaris* and *B. normani* they are based strongly. The latter two species are unique in the genus *Blennius* in that the distal ends of the ascending processes abut against the ventral end of the median ethmoid. In the other species of *Blennius* the processes ride over or in front of the median ethmoid. *Blennius ocellaris* and *B. normani* are also the only two species of Blenniini in which the dentaries are joined together by a suturing joint. It is for these reasons that I believe the genus *Blennius* should be restricted to *B. ocellaris*, type-species, and to *B. normani*. To restrict them, however, would be to leave a number of species presently assigned to *Blennius* without a generic name. Until a revision of the genus is made, I recommend maintaining the status quo. Norman (1943), without giving reasons, restricted his subgenus *Blennius* to *B. ocellaris; B. normani* was not described at that time. The tips of the premaxillary ascending processes in *Hypleurochilus* and, to a lesser degree, *Hypsoblennius* also abut against the median ethmoid.

*Chasmodes bosquianus* is unique in the Blenniini (and Blenniidae) in having a greatly elongated maxillary and, consequently, a very large gape. Its near relative, *C. saburrae*, is normal in these respects.

In the Omobranchini there is always a canine on each premaxillary and dentary, infrequently two. (Immature females of *Omobranchus herklotsi* (Herre) have normal omobranchinine canines in both jaws, but adult females of this species have no canines. This loss of canines is accompanied by a marked increase in the size of the gape and an anterior, broad rounding of the lower jaw, a type of sexual dimorphism that is unique in the Blenniidae.) The upper canines are much smaller than the greatly enlarged, recurved lower canines in *Omobranchus* (pl. 3) and *Cruantus*, slightly smaller in *Enchelyurus* and *Laiphognathus*, and are separated by a diastema from the comblike teeth. Depending on the species, the comblike teeth number from 14 to 30 for each pair of premaxillaries and dentaries. The number of teeth in the upper and lower jaws is about equal for any specimen, with a slight tendency for the lower jaw to have more teeth in some species. The small amount of data I have available indicates that the number of comblike teeth increases with standard length, but I hazard the guess that only rarely would the number ever reach 40 in either jaw. The teeth are attached rather firmly to the jaw bone but are slightly movable. The capsule-like nature of the jaws and the development and appearance of the replacement teeth are similar to that described for the Blenniini. The ascending process of each premaxillary is based rather strongly on the body of the premaxillary in adults, somewhat weakly in the young. In *Omobranchus elegans* the dorsal end of the ascending process of the premaxillary abuts against the median ethmoid, similar to the condition found in some Blenniini. The dentaries of all species, with the possible exception of *Omobranchus herklotsi*, are joined medially by a suturing joint.

In the Salariini (this discussion excludes mention of larval stages) there is a canine, rarely two (for exceptions, see below), present on each dentary of most species. The presence or absence of canines and their relative size is sometimes sexually dependent (in such instances, the males have them and the females do not, or those of the males are larger). When present, the canines are well separated from the comblike teeth, except the anterior pair in *Ecsenius* (see p. 49). The canines may be relatively large and pointed as in some species of *Entomacrodus* or quite reduced and blunted as in some species of *Ecsenius* and *Glyptoparus*. The premaxillaries never bear canines. One species of *Ecsenius*, *E. mandibularis*, has a linear series of up to eight canines on each dentary, all about equal in size, and in *Glyptoparus* as many as three canines are commonly present on each dentary.

The number of comblike teeth on both premaxillaries in the Salariini number from 30 in an undescribed genus to about 250 in *Cirripectes jenningsi*. The number of comblike teeth on both dentaries ranges from 22 in *Hirculops* to 147 in *Atrosalarias*. There is a relatively sharp break in the number of upper jaw teeth between a small group of genera related to *Rhabdoblennius*, in which group the numbers rarely exceed 50 (79 in an undescribed genus), and those of the majority of the genera, wherein the numbers exceed 100. These differences are associated, for the most part, with certain changes in the structure of the premaxillaries. Usually the number of teeth in the upper jaw greatly exceeds the number in the lower jaw and may be as much as three times as great (*Ecsenius*). The only information as to whether number of teeth increases with increase in standard length in the Salariini was reported by Springer and Smith-Vaniz (1968) for *Atrosalarias*, in which there was a highly significant correllation between upper or lower jaw teeth and standard length.

Norman (1943) described the premaxillaries of the Salariini as forming a bony crest for reception of the upper lip. He described the teeth, except in *Rhabdoblennius*, as being movable. The bony crest is not as Norman described it, and the movability of the teeth is dependent to some extent on the number of teeth in the jaws. In those species with relatively few teeth in the upper jaw (and/or lower jaw) the teeth are proportionately stronger, and the connective tissue holds them more tightly to the jaw. In all the genera with large numbers of teeth as well as in *Croaltus*, *Antennablennius*, *Rhabdoblennius*, *Glyptoparus*, and two undescribed genera, which have small numbers of upper jaw teeth, the premaxillaries have become relatively thin, arched, platelike bones (fig. 7, pl. 9) unlike the bony capsule found in the other blenniids. The comblike teeth of the genera with high numbers of teeth are suspended loosely in a thick band of connective tissue that is attached to the premaxillary; the bases of the teeth make no contact with the bone of the premaxillary. In the listed genera (*Croaltus*, etc.) there is much less connective tissue, and it is possible that the teeth in these genera do make slight contact with the bone of the premaxillaries. Compared with the Bleniini and Omobranchini, the premaxillaries of the Salariini have become greatly excavated anteriorly, and so the bony capsule is open. There are no longer foramina in the bone for the replacement teeth, and these teeth rest in bands imbedded in the connective tissue (fig. 1, pl. 9). The crestlike formation of the body of the premaxillary lies dorsal to the bases of the functional teeth (and replacement teeth), but it has nothing to do with reception of the upper lip as Norman proposed. In *Hirculops* an intermediate condition exists in the premaxillaries, which are partially excavated medially but retain the blenniinine form laterally, with foramina through which the replacement teeth appear.

Among the Salariini, the dentaries of *Croaltus*, *Antennablennius*, *Rhabdoblennius*, and *Hirculops* are blenniininelike (bony capsule), with the functional teeth based on the jawbone and with the advanced replacement teeth making their appearance through foramina. The dentaries of the other genera are similar to the premaxillaries in that they are excavated and have the teeth loosely attached in a thick band of connective tissue; however, in *Ecsenius* (pl. 9) the lateralmost comblike tooth on each dentary is slightly broader (in frontal view) and more robust than the teeth more medial in position. This contrasts strongly with all other blenniids in which the lateralmost comblike tooth is the smallest and weakest. In addition, the lateralmost tooth of *Ecsenius* may be enlarged and canine-like as well as firmly attached to the bone of the jaw, whereas the other teeth are weakly attached. The lateralmost canine-like tooth of *Ecsenius* is well separated from the small, blunt canine (or canines) present posteriorly on the dentary.

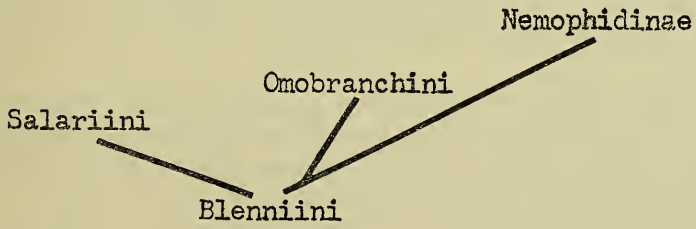
The ascending process of the premaxillary of the Salariini is based very weakly on the body of the premaxillary and easily is broken at the base in dissection. The dentaries are joined by an even, nonsuturing joint, similar to that of most blenniinines.

Because there are Salariini with jaws similar to, or intermediate in nature between, those of the Blenniini and most specialized Salariini, one can postulate derivation of the Salariini from the Blenniini. There is also a case to be made for combining the two tribes. The small area of overlap, however accompained by a conceptual practicality (most ichthyologists have a concept of the blenniinine and salariinine dentitions), leads me to maintain the separation.

The Nemophidinae always have one, sometimes two, greatly enlarged, recurved canines posteriorly on each dentary. The genus *Meiacanthus* is unique among all fishes in having the dentary canines with a deep groove running along the anterior surface. Just posterior to the base of the canine in each dentary is a depression in the bone. A gland fits into this depression and extends anteriorly into the base of the groove in the canine. There is no information on the use or venomosity of the canine and gland. Tomiyama (1956) noted the presence of grooved canines in *M. kamoharai*. Varying with the genus, there are none to two canines, smaller than the dentary canines, posteriorly on each premaxillary. The premaxillary canine is separated by a diastema from the comblike teeth. The comblike teeth number from 16 to 42 in the upper jaw and from 16 to 78 in the lower jaw. Depending on the genus, the upper comblike teeth may equal or slightly exceed in number those in the lower jaw (*Aspidontus*, *Blennechis*, *Dasson*, *Xiphasia*, *Plagiotremus*), may be slightly fewer in number than those in the lower jaw (*Meiacanthus*, *Petroscirtes*, *Xiphasia*, *Lembeichthys*), or may be greatly exceeded by those in the lower jaw (*Runula*). I have no data on whether tooth number increases with standard length. The teeth vary from being weakly to strongly attached to the jaw bones, but the teeth are always at least slightly movable. The capsule-like nature of the jaws and their relationship to the replacement teeth is similar to that of the Blenniini and Omobranchini. The ascending process of the premaxillary is considerably reduced, strongly based on the body of the premaxillary, and is no longer a seemingly separate structure as it superficially appears to be in the Blenniinae. The dentaries of the Nemophidinae join medially by a suturing joint.

The jaws and dentition appear to be the major features from which clues are to be found for the evolutionary paths followed within the Blenniidae. The other families of the Blenniicae, generally considered less specialized than the Blenniidae, as well as many of the perciforms usually considered more primitive, have moderately well-developed premaxillary ascending processes, teeth implanted on the bones of the jaws, no specialized posterior canines, and dentaries that are joined by an even, nonsuturing joint. In these respects, the jaws and dentition of some of the Blenniini would be considered the least specialized of the Blenniidae. Within the Blenniini, two species, *Blennius ocellaris* and *B. normani*, have reduced the size of the premaxillary ascending processes while strengthening them; they have the lower jaws joined by a suturing joint and have moderately developed upper and lower canines. These two species are somewhat intermediate between the Omobranchini and other Blenniini and are probably similar to the stock that gave rise to the Omobranchini (specializations of the Omobranchini differentiating them from the Blenniini—and Nemophidinae are the spur on the interopercle, the reduction of the pterosphenoid, and the pelvic fins with I,2 rays). The jaws and dentition of the Omobranchini (reduced and strengthened premaxillary ascending processes, sutured lower jaws, enlarged canines in both jaws) are markedly similar to the jaws and dentition of the Nemophidinae, which differ from those of the Omobranchini mainly in having further reduced and strengthened the premaxillary ascending processes and in having further enlarged or otherwise modified the dentary canines. The highly restricted gill opening of the Nemophidinae is found in most members of the Omobranchini and may be additional evidence for a common ancestor. That the Nemophidinae are more specialized than the Omobranchini and other Blenniinae is indicated by their loss of the basisphenoid and intercalar.

As mentioned above, there are genera of the Salariini with jaws and dentition intermediate between the Blenniini and most specialized Salariini. The Salariini are obvious offshoots of the Blenniini or the group that gave rise to the Blenniini. A hypothetical phylogenetic tree for the four suprageneric taxa that I recognize in the Blenniidae can be constructed as follows (in doing this, I am fully congnizant of the inherent problems of basing such a tree on the living members of a group):



Other skull bones.—Prootics: In many perciforms each prootic possesses a ventral, mesially extending ledge that joins the ledge from the opposite prootic to form a roof, with the basisphenoid (meningost portion), over the anterior portion of the posterior myodome. A prootic roof was found only in *Blennius cristatus* and *B. galerita*.

Roofing Bones: Two genera, *Enchelyurus* (fig. 13) and *Runula* (pl. 8) are distinct in the Blenniidae in having the frontals fused (synostosis) into a single bone, with little or no evidence of a joint line between them. It is possible that *Xiphasia*, *Plagiotremus*, and *Lembeichthys*, which are closely related to *Runula*, also may have the frontals fused. Fusion of the frontal has been reported also in, and as diagnostic of, the Anarhichadidae (Barsukov, 1959) of the northern blennioid superfamily Zoarceoidae (*of* Gosline, 1968). *Runula* further is peculiar in the Blenniidae in that the nasals, median ethmoid, and lateral ethmoids have become fused to the fronatls, effectively forming a strong, solid block of bone anteriorly on the skull. The external joint lines of these bones are evident since the synostosis has taken place internally only.

There is a tendency among the Nemophidinae for ornamentation of the skull bones, particularly the frontals. The ornamentation ranges from tiny, shallow depressions in *Runula* (pl. 8) to large, deep holes in *Aspidontus* (pl. 6). The excavations are filled with connective tissue. The reason for this ornamentation is not clear although it may be a response to the free-swimming habit of these fishes: a method of decreasing the weight of the bone.

Typically in the Blenniidae, the parietals meet only at a point just anterior to the median, predorsal pore of the supratemporal canal. The parietals are otherwise separated by the supraoccipital and frontals. In *Aspidontus* (pl. 6), *Blennechis*, *Dasson*, and *Petroscirtes*, the parietals meet for a relatively greater distance and the pore opening is either anterior to or between the parietals, In some species, *Andamia heteroptera* (pl. 11), for example, the supraoccipital completely separates the parietals, and the pore opens through the supraoccipital alone. Frequently in juvenile blenniids the parietals fail to meet, so that the circumstance in *Andamia* may be the result of neoteny. In a number of Salariini and Omobranchini the meeting of the parietals on the dorsal skull surface isolates an anterior island of the supraoccipital from the main body of the supraoccipital (pl. 4, upper; 10, upper).

Bony crests, formed by the midline meeting of the frontals and parietals of each side and along the posterior margins of the parietals and pterotics, are absent in juveniles, appearing gradually with the increase in size of the individuals of many species.

Lateral Extrascapulars: In the blenniids the only pair of extrascapulars present is the lateral extrascapular pair. These are present in all genera except *Ecsenius* (pl. 10), *Petroscirtes*, and one of two specimens of *Dasson*, wherein there has been a synostosis of the extrascapulars with the pterotics, and *Runula* (pl. 8), wherein the synostosis has been with the parietals, with complete loss of any indication of a joint line. In many blenniids the lateral extrascapulars may become encapsulated secondarily and lost from view in large specimens of a particular species when the pterotic-parietal crests, together with the epiotic facet for articulation with the posttemporal, close over them.

Intercalar: The intercalars are present in all the Blenniinae and absent in all the Petroscirtinae except *Dasson*.

Vertebral column.—The number of vertebrae in blenniids varies from 29 (rarely 28) in *Stanulus* to 134 in *Xiphasia.* Only in some genera of the Nemophidinae does the number of vertebrae exceed 45. The number of precaudal vertebrae—i.e., anterior to the first vertebra with a well-developed haemal spine; most often the transition from precaudal to caudal vertebrae is abrupt, from no haemal spine to a well-developed one—ranges from 9 to 12 in the Blenniinae and from 11 to 16 in the Nemophidinae. By far the most common number is 10 (secondarily 11) in the Blenniinae and 13–16 in the Nemophidinae. A variation of plus or minus one precaudal vertebra from the modal number is a rarity for a specimen of any species of the Blenniinae and is only slightly more common in the Nemophidinae.

The precaudal vertebrae bearing parapophysial stays (always those vertebrae just anterior to the first caudal vertebra) varies from none to three in the Blenniinae and to five in the Nemophidinae. A variation of plus or minus one from the modal number is common for any specimen of a given species.

In the Blenniinae, except the Omobranchini, the neural arch of the first vertebra, with rare individual variants, is complete, but lacks a neural spine. The first well-developed neural spine usually appears on the third vertebra (on the fourth vertebra in the single specimen of *Istiblennius coronatus* examined). Infrequently there is a low, weak neural spine on the second, and less commonly on the first, vertebra. In the Omobranchini a well-developed neural spine frequently occurs on the second vertebra. In the Nemophidinae the two sides of the first and/or second neural arch fail to meet dorsally in *Runula, Dasson, Blennechis,* and *Aspidontus.* The first well-developed neural spine may be on the second or third vertebra.

In the Blenniinae, except the Omobranchini, many species and genera possess a well-developed process (not labeled in fig. 11) on each side of the base of the neural arches of the third, fourth, or fifth vertebra (just the first two or all three of these vertebrae). Strong ligaments extend from these processes to the proximal ends of the associated epipleurals. In the Omobranchini, the processes are always present and occur on the neural arches of the second or third to fifth through tenth vertebrae, depending on genus and species. In the Nemophidinae, except *Xiphasia,* where apparently they are absent, the processes exist on the neural arches of the third to fifth through tenth vertebrae. The processes in all blenniids are sometimes not noticeable in small or young specimens.

In all the blenniids there is a tendency for the parapophyses of the middle precaudal vertebrae to develop into winglike processes that overlap and attach ligamentously to the next vertebra anteriorly. This development reaches its extreme in *Xiphasia,* where in many respects they superficially resemble the condition in the fossil elopoid *Lamino-*

*spondylus transversus* (Springer, 1957), the only nonblenniid reported to possess such an arrangement.

The number of epipleurals ranges from eight or nine in *Xiphasia* to 31 or 32 in *Lophalticus*. The number is fairly variable within genera, but only slightly so within a species, wherein a variation of four epipleurals is uncommon. In blenniids the differentiation between the anterior two epipleurals and the pleurals is not always clear. In *Ecsenius*, uniquely, the first two epipleurals articulate with well-developed cuplike parapophyses similar to, although smaller than, those with which the pleurals of the third and fourth vertebrae articulate. These epipleurals appear, serially at least, to be typical ribs (in percoids the pleurals are usually considered to begin on the third vertebra, the epipleurals on the first—Gosline, pers. comm.). The third through fifth epipleurals of *Ecsenius* also are modified uniquely in that they develop a flattened process ventrally where they articulate with the pleurals. Above this process the epipleural bends up toward the neural arch process to which it is ligamentously attached (the bend is apparently an ossification of the attaching ligament and is not differentiated from the remainder of the epipleural). Variably there is a slight, irregular extension arising from the epipleurals above the flattened process mentioned above (apparently an ossification in the vertical transverse septum). The third epipleural on each side of one of the specimens of *Stanulus seychellensis* also had a dorsal fork that appeared to be an ossification of a portion of the ligament attaching the epipleural to the neural arch process.

In the Blenniinae the pleurals extend from the third to the ninth through twelfth vertebrae, depending on the species. There is occasionally a variation of one vertebra as to which vertebra the last pleural attaches. The terminal pleurals may be on the terminal precaudal vertebra or on the first caudal vertebra, usually constant within a species. In the Nemophidinae the pleurals extend from the third or fourth (rarely the fourth) vertebra to the twelth through sixteenth vertebra. The last pleural may be on the penultimate or ultimate precaudal vertebra, or on the first caudal vertebra. There seems to be relatively more intraspecific variation in the position of the terminal ribs with regard to which vertebra they attach than is found in the Blenniinae.

CAUDAL FIN.—Gosline (1961) defined the most primitive perciform caudal skeleton as follows:

> (a) 15 branched caudal rays; (b) 3 epurals; (c) 2 independent uroneural ossifications (each uroneural is actually a paired element); (d) urostyle with a single ossification; (e) 6 independent hypurals; and (5) haemal arches of the two vertebrae ahead of the urostylar vertebra separate from their centra, i.e., autogenous.

Gosline (pers. comm.) has accepted Nybelin's (1963) modification of the terminology used by Gosline (1961), and so the ventralmost of

Gosline's six hypurals is considered a haemal spine and there remain only five independent hypurals.

In establishing a basal blennioid (suborder Blennioidei) stock, Gosline (1968) believes that the Acanthoclinidae or Opisthognathidae are the most primitive members. Figure 14 is an illustration of the caudal fin of *Acanthoclinus* species from New Zealand. This caudal fin, while considerably advanced over the most primitive perciform caudal, serves as a basis for interpretation of the blenniid caudal. The caudal of *Acanthoclinus* has: 14 branched caudal rays; three epurals; no independent uroneural ossifications (these apparently are fused to the urostyle); a single urostyle ossification to which is fused an indistinguishable hypural plate probably consisting of hypurals 3 and 4; an independent hypural 5 dorsal to the fused hypural plate and urostyle; an independent fused ventral hypural plate consisting probably of a haemal spine and hypurals 1 and 2 (in addition, this plate exhibits the hooklike process on the haemal spine portion that is common in primitive perciforms and to which the flexor caudalis ventralis superficialis muscle attaches); and the haemal arches of the two vertebrae ahead of the urostylar vertebra fused to their centra. The blenniid caudal is considerably more specialized than that of *Acanthoclinus*. Differences are, for the most part, the result of more fusions and the loss of some elements.

The caudal fin of the Blenniinae is typically rounded with the longest rays on the ventral half of the fin. *Atrosalarias*, *Ecsenius* (both Salariini), and *Omobranchus* (Omobranchini) are exceptions in that the adults may have the upper and lower rays greatly produced and the tips of the other rays may extend beyond the margin of the inter-radial membrane. The caudal of the Nemophidinae is shaped similar to that of the Blenniinae, but many of the species have the caudal rays produced as in the three genera listed above.

The number of segmented caudal fin rays in blenniids varies from 10 (*Xiphasia* and rarely *Atrosalarias*) to 15 in *Omobranchus lini* (the range in *O. lini* is from 13 to 15 with no sharp mode). The usual number of segmented rays is 11 in the Nemophidinae and 13 in the Blenniinae, but some genera or species of the latter have different counts: *Chasmodes*, 11 to 12; *Ecsenius bicolor* and *Praealticus margaritatus*, 14; *Andamia*, *Damania*, *Alticus* and *Lophalticus*, 12; *Atrosalarias*, 10 to 14, usually 12 or 13 (rays unbranched in all these taxa). A variation of one ray from the modal number in specimens of any species is not uncommon. The caudal rays may all be simple (all Nemophidinae, all Omobranchini except individual variants with one or two branched rays, *Medusablennius chani* of the Blenniini, and many genera of the Salariini, listed above) or some may be branched (most Blenniini and Salariini). The caudal rays are never branched more than once. In species with branched caudal rays, the uppermost and lowermost one or two segmented rays are never branched. When branched rays are present they most often number nine; some species have fewer, but only individual variants of any species will have as many as 10. In species with an uneven number of segmented caudal rays there is always one more ray attached on the upper hypural plate than to the lower.

The number of dorsal procurrent rays varies from two (*Xiphasia*) to 10 (*Stanulus seychellensis*), but rarely exceeds eight. The ventral procurrent rays vary from one (*Xiphasia*) to 10 (*Stanulus seychellensis*), but rarely exceeds eight. Usually there is one more dorsal procurrent ray than there are ventral procurrent rays in any specimen.

The four basic types of caudal fin in blenniids are illustrated in figure 15. The main variations from these four types are: whether the caudal rays are all simple or include some branched rays, whether the ventral hypural plate is autogenous or fused to the urostylar vertebra (the latter condition occurs only in *Enchelyurus*, *Laiphognathus*, and *Xiphasia*), or whether the two epurals are fused together (only in the single specimen of *Glyptoparus*, which may be exceptional).

In all blennids the anteriormost epural (a neural arch; see caudal of *Acanthoclinus*, figure 14) is always fused to its (the penultimate) vertebra and there are never more than two epurals, never less than one. (This is also true of all the comparative material of the superfamily Blenniicae examined except the clinid *Blenniomimus cottoides*, which has three epurals. The northern blennioids usually have three epurals.) Also in blenniids, the haemal arches of the penultimate and antepenultimate vertebrae are always fused to their respective centra. The hooklike process for attachment of the flexor caudalis ventralis inferioris muscle is absent; this process is a marker for the haemal spine portion of the ventral hypural plate (Gosline, 1960, 1961).

The most primitive blenniid caudal is that in figure 15A (see also fig. 10). This type caudal consists of two epurals, an autogenous minimal hypural (hypural 5), a fused hypural plate and urostyle (probably consisting of the urostyle, hypurals 3 and 4, and two uroneurals), an autogenous ventral hypural plate (probably consisting of hypurals 1 and 2 and a haemal spine), and nine branched caudal rays. This type caudal fin is found in most species of the Salariini (which are the most specialized in dentition of the blenniids) and some species of the Blenniini (*Medusablennius chani*, most species of *Blennius*). There is a tendency for the minimal hypural to be decreased in size in the Salariini and, based on the shape of the fused urostyle and upper hypural plate, the minimal hypural would appear to be lost, rather than fused, in those genera of Salariini and other blenniid taxa that have no obvious minimal hypural. The other types of blenniid caudals are considered specialized. The caudal illustrated in figure 15B is found in *Hypleurochilus* (Blenniini), *Omobranchus lini*, and *O. anolius* (Omobranchini, but with simple rays only). *Laiphognathus* (Omobranchini) may also have the caudal type figured in figure 15B (fin was damaged), but the lower hypural plate is fused to the upper and the rays are not branched. The caudal in figure 15C is found in *Negoscartes*, *Salarias fasciatus*, *Astrosalarias* (Salariini, the last-mentioned genus with simple rays), *Enchelyurus* (Omobranchini, but with simple rays and the ventral hypural plate fused to the urostyle), and occasional specimens of *Meiacanthus*, *Runula*, and *Petroscirtes* (Nemophidinae, but all as variants only). The caudal illustrated in figure 15D is found in all other Nemophidinae (except the ventral hypural plate is fused to the urostyle in *Xiphasia*), *Hypsoblennius*, *Blennius nicholsi*, *Chasmodes bosquianus* (Blenniini, but with branched caudal rays), *Omobranchus loxozonus*, *O. elegans*, and *O. banditus* (Omobranchini). The latter type caudal appears to be the most specialized of the blenniids.

It is probable that the various types of blenniid caudals, except the least specialized, have arisen several times within the various suprageneric taxa, but trends are evident. As postulated on the basis of jaws and dentition (q.v.), the Nemophidinae are derived either from the Omobranchini or from a group that gave rise to the Omobranchini. This is supported somewhat by the caudal type (fig. 15D) found in some *Omobranchus* species and the Nemophidinae (including the fact that these two groups share in having only simple caudal rays). That the Omobranchini are derived from the Blenniini is supported perhaps by the fact that some species of each group have the type caudals illustrated in figures 15B and C. The Salariini were postulated as being derived from the Blenniini, and the most primitive type blenniid caudal is found only in these two groups.

DORSAL FIN.—The dorsal fin of all blenniids is composed of flexible spines and segmented rays. The number of spines varies from four (three in variant individuals) in some species of *Meiacanthus* to 17 in *Lophalticus*. The most frequent numbers of spines encountered are 11 to 13. The number of spines is relatively constant for a genus (*Meiacanthus* with three to 10 and *Xiphasia* with 11 to 14 are noteworthy exceptions) or species but may vary plus or minus one spine.

In many genera of the Blenniini and Salariini there is a tendency to reduce the size of the posteriormost spine, and in some species the spine is noticeable only in osteological preparations or on radiographs. The reduction of the terminal spine seems to have developed independently in many genera and is therefore of little significance in determining relationships. The dorsal fin membrane usually is incised at the level of the reduced spine (one notable exception: *Ophioblennius*).

The number of segmented rays varies from 10 in *Stanulus* to 119 in *Xiphasia*, with most genera having fewer than 25. With the exceptions of *Stanulus* and *Pereulixia* there are always more rays than spines. Usually the rayed portion of the dorsal fin is higher than the spinous portion, but in *Blennechis filamentosus*, *Blennius ocellaris*, *Blennius normani*, and males of *Blennius nicholsi* and *Omobranchus lini*, the lengths of the anterior dorsal spines greatly exceed those of the rays, and in some species of *Ecsenius* the posterior dorsal spines may exceed the lengths of the rays. There are no gaps in the dorsal fin that would indicate the dropping out of a spine (or its associated proximal pterygiophore) as is common in the Clinidae. The terminal spine and the first ray are always articulated with the same proximal pterygiophore. This feature is of value in making dorsal element counts from radiographs of damaged specimens.

The rays, except for the posteriormost, each articulate with small, bilaterally paired distal pterygiophores, which in turn articulate with an unpaired proximal pterygiophore that may embody the medial pterygiophore of more primitive teleosts. The posteriormost ray may lack the paired distal pterygiophore. The presence or absence of the terminal distal pterygiophore is fairly constant within a species or certain groups of species, but much more data are required to determine the significance, if any, of this condition. In general, the Nemophidinae, Omobranchini, and Blenniini tend to have the terminal distal pterygiophore; the condition in the Salariini is variable.

Anal fin.—The anal fin invariably has two spines with the unusual intraspecific variant having one or three. The first spine in females usually is reduced and frequently is noticeable only in osteological preparations or on radiographs. The segmented anal rays vary in number from 11 in *Stanulus* to 119 in *Xiphasia*, with most genera having fewer than 25. The number of segmented anal rays usually exceeds the number of segmented dorsal rays by one or two, but may equal them or be as many as 11 fewer in number (*Meiacanthus*). The anal spines are attached only to proximal pterygiophores. The second anal spine and the first segmented ray are attached to the same pterygiophore. The rays, except for the posteriormost, articulate with paired distal pterygiophores, which in turn articulate with proximal pterygiophores that may embody the medial pterygiophore of more primitive teleosts. The presence or absence of the terminal distalpterygiophores is correllated closely with its presence or absence in the dorsal fin (q.v.).

In some genera and some species of the Salariini (*Entomacrodus*, *Stanulus*, *Istiblennius*, *Ophioblennius*, *Scartichthys*, *Exallias*, *Pereulixia*, *Halmablennius*), the terminal proximal anal pterygiophore typically supports two rays, the posterior of the two much reduced in size. I (1967) discussed this condition in detail for *Entomacrodus* and now believe the condition is evidence of phyletic relationship because subjectively I had grouped together the genera in which the condition occurs before I knew the range of its occurrence.

The anal rays are usually shorter than the dorsal rays, but in some species of *Salarias* the anterior anal rays are greatly produced and much longer than any of the dorsal rays.

Pectoral girdle and fins.—The pectoral girdle of blenniids is most notable for the reduction in size and synostosis of the coracoid with the cleithrum. The scapula also is reduced beyond what one ordinarily finds in perciforms, but it is never fused with the cleithrum. In most blenniids the scapular foramen is bounded entirely by the scapula, but in some genera and species, notably most Nemophidinae, *Ecsenius*, and some species of *Omobranchus* and *Blennius*, the anterior border of the scapular foramen is incomplete and is bordered by the cleithrum.

In all blenniid genera except *Enchelyurus* (Omobranchini), *Alticus*, *Andamia*, *Damania*, *Lophalticus*, and *Praealticus* (Salariini) there are two normally formed postcleithra on each side. In the listed genera the postcleithra appear as one to three small, well-separated ossifications in the connective tissue of the skin in what would have been their normal position if they had been formed normally. The dorsalmost postcleithral element may or may not be in contact with the cleithrum. It is interesting to note that the salariinine genera listed usually have been considered, primarily on intuitive grounds, to be related (as indicated also by their names). The peculiar nature of the postcleithra tends to confirm previous opinion.

In the Blenniinae the supracleithrum is similar to that described for *Entomacrodus nigricans* in its relationship to the posttemporal; however, in the Nemophidinae the supracleithrum has become much extended anteriorly and the posttemporal has become much reduced. The supracleithrum of the Nemophidinae has a close connection with the epiotic not found in the Blenniinae. It appears that in the Nemophidinae the postcleithrum has taken over the function of the posttemporal. In the Nemophidinae and Omobranchini the supracleithrum never bears a sensory canal, but such a canal is variably present, depending on the genus, in the Blenniini and Salariini.

The posttemporal is forked in all Blenniinae and unforked in the Nemophidinae (with the exception of one of the two specimens of *Aspidontus taeniatus* examined, where it gives a slight indication of forking). The lower arm of the posttemporal of the Blenniinae is attached variably by a ligament to the intercalar (usually at a point near the junction of the intercalar and pterotic spine) or to the posterior surface of the pterotic spine. There is variation within a genus in this respect; for instance, in all the species of *Entomacrodus* exaamined, except those of the *striatus* species group (Springer 1967b) the attachment is similar to that described for *E. nigricans*. In the *striatus* species group the attachment is to the pterotic. In the Nemophidinae there does not seem to be a ligament in the position of the ventral arm of the post-temporal. The presence or absence of an intercalar or its relative size appears to be independent of whether the posttemporal is forked or whether it attaches to the intercalar or pterotic.

The number of pectoral rays in blenniids varies from 11 to 18, with 11 and 18 rays as uncommon intraspecific variants (counts of 17 and 18 rays are known only for *Atrosalarias*). The most frequently encountered modal numbers of rays for any species are 13 to 15. The modal number of rays appears to be fairly constant within most genera (some notable exceptions: *Ecsenius*, *Enchelyurus*, and *Blennius*). The rays are unbranched, except that some large specimens of particular species may show a slight forking at the tips of one or two rays.

The number of pectoral radials is invariably four, but the relationship of radials to scapula and coracoid is variable. The relationships range from two radials articulating with the scapula, one with both the scapula and coracoid (at the scapulo-coracoid joint), and one with the coracoid (or radial formula 2–1–1, in some species of Blenniini and Omobranchini), to one radial articulating with the scapula and three with the coracoid (1–0–3, in *Ecsenius*, *Aspidontus*, and *Blennechis*). The most common relationship is that of two radials articulating with the scapula and two with the coracoid (2–0–2), which occurs in most Salariini. The relationships grade into each other somewhat because one radial may articulate with the cartilaginous scapulo-coracoid joint area (which may be a relatively broad area, rather than one that has the osseous portions of the two bones impinging).

Regan (1913) indicated that the most generalized perciforms had a 2–1–1 radial formula. A perusal of Starks' (1930) paper on the pectoral girdle as well as my own dissections of *Kuhlia sandvicensis* (3–0–1, Kuhlidae) and *Abudefduf abdominalis* (3–1–0, Pomacentridae), both of which are less specialized than blenniids—at least in caudal structure (Gosline, 1961)—indicates that most of the generally considered less-specialized perciforms do have a radial formula of 3–1–0 or 2–1–1. All chaenopsids, tripterygiids, and clinids (except *Mnierpes* and some species of *Labrisomus*, *Malacoctenus*, and *Ophiclinus*—all clinids—with radial formulas of 3–0–1), which are less specialized than blenniids, have a radial formula of 2–1–1. If the meager evidence presented herein is indicative of evolutionary trends in the perciforms—and I think it is—then the primitive perciform had three radials attached to the scapula and one probably in the area between the scapula and coracoid. The path followed has been to move the radials ventrally off the scapula and gradually set them on the coracoid. Thus, the 2–1–1 radial formula is the most primitive for blenniids; and the 1–0–3 formula, the most specialized. As noted above, in blenniids, the 2–1–1 formula occurs only in the Blenniini and Omobranchini. As discussed under dentition, jaws, and caudal structure, the Blenniini appear to contain the most primitive blenniids; the Omobranchini are considered to be derived from them.

Pelvic fins.—Each blenniid pelvic fin comprises a spine (visible only in osteological preparations) and two to four simple, segmented rays, except in the nemophidinid genera *Plagiotremus* and *Lembeichthys*, each monotypic. *Plagiotremus* lacks pelvic fins or girdle entirely. *Lembeichthys* has greatly reduced pelvic fins that may comprise a spine and only a single ray (material for clearing and staining was unavailable). All the blenniids except some of the Nemophidinae have well-developed pelvics. Reduced or otherwise abnormally formed pelvics are found commonly in individual specimens of many of the genera of the Nemophidinae. Such reduction or malformation is probably the result of the group's having become free-swimming; the pelvics no longer function as a pedestal for support as it does in the other blenniids, which are benthic inhabitants, and, thus, there is no selective advantage in having pelvic fins.

Nemophidinae with normal pelvics have a fin formula of I,3. In the Blenniinae the Blenniini usually have I,3 (secondarily I,4) pelvic rays; the Omobranchini have I,2 pelvic rays; and the Salariini have I,2 to I,4 pelvic rays. A variation of plus or minus one ray from the modal number for any species is found commonly only in the Blenniini.

It would appear that a pelvic fin ray count of I,4 would be the most primitive for blenniids inasmuch as it most closely approximates the I,5 condition of the less specialized perciforms. However, none of the other, usually considered less specialized, families of the Blenniicae have pelvic fins with more than I,3 rays (most have I,3), and only a relatively few species of the Blenniidae have I,4 rays. While it is conceiveable that these blenniid species have retained a more primitive number of pelvic rays, I think it more probable that they have added a ray to the basic I,3 blennioid pelvic condition. In *Hypleurochilus geminatus*, a relatively specialized member of the Blenniini, the pelvic count is strongly modal at I,3, but individuals with I,4 rays are not rare. It seems that the addition or subtraction of a pelvic ray in blenniids would not be a developmentally difficult process.

## Distinctive Characters of the BLENNIIDAE

The family Blenniidae can be distinguished from all other blennioids on the basis of any one of at least three characters, the first of which is the most easily described: the coracoid is reduced and fused (synostosis) to the cleithrum. Usually there is no remnant of a joint line between these two bones. All other blennioids have an unreduced and distinctly separate coracoid.

The second character concerns the relationship of the interopercle with the epihyal and subopercle. I (1966) briefly discussed this as a family character and Thiele (1963, pp. 386–387; fig. 28) described the relationship in some detail for three species of *Blennius*. The posterior end of the interopercle and the ventral end of the interhyal form a ligamentous, tight connection with a prominence on the posterolateral surface of the epihyal. In all blenniids except the Omobranchini, which comprises only a few species, the posterior end of the interopercle is anterior (even though only slightly) to the posterior end of the epihyal (fig. 16A). In the Omobranchini the condition is essentially the same except that there has developed, probably secondarily, a posteriorly projecting spur on the ventroposterior end of the interopercle (fig. 16B).

The blenniid interopercle is greatly reduced and is internal to the ventral portion of the preopercle (no portion of the interopercle and subopercle are in bony contact although they are ligamentously attached). The interopercle is not normally visible when the skull is viewed laterally. The reduced nature and peculiar relationships of the interopercle probably caused Pinto (1959) to report that the interopercle was absent in blenniids. In the nonblenniid blennioids except *Chaenopsis*, the interopercle overlaps and extends posterior to the posterior end of the epihyal, and the interopercle is usually apparent when the skull is viewed laterally. In *Chaenopsis* the posterior end of the epihyal has been raised considerably, relative to its anterior end. The interopercle has retained its normal position and is not joined closely to the epihyal; the posterior end of the interopercle is well below and anterior to the level of the posterior end of the epihyal. In no case, however, is there a duplication in any of the nonblenniid blennioids of either of the two interopercle-epihyal relationships found in the blenniids.

The third character lies in the nature of the dentition. Anteriorly on the dentaries and premaxillaries, the blenniids (adults) have a single row of evenly aligned, close-set (no space between teeth distally) comblike teeth. Normally there are no functional teeth, villiform or otherwise, behind the anterior row in either jaw. Posteriorly on the dentary or premaxillary, straight or recurved canines may be present. The canines may be greatly enlarged or scarcely larger, more pointed or more blunt, than the comblike teeth. Teeth are never present on the palatines and are present on the vomer of only a relatively few species. In contrast to the blenniids, the other blennioids have the teeth in the jaws relatively separated from each other. There is usually more than one row of functional teeth in each jaw, usually consisting of villiform teeth behind a large outer row. There are no enlarged or separated canines posteriorly in the jaws, and teeth are frequently present on the vomer and palatines. In addition, some nonblenniids have platelike crushing teeth.

Several characters descriptive of the blenniids serve to separate the blenniids from one or more of the other blennioid families. These are: the low number of spines in the dorsal fin (3–17, usually less than 14); the presence of only flexible, nonpungent spines; the ratio of spines to rays in the dorsal fin (with rare exception, more rays than spines); the nonprotractile premaxillaries; the short ascending premaxillary process (shorter than the body of the premaxillary); the usual meeting of the descending processes of the frontals with the ascending processes of the parasphenoid to exclude the pterosphenoids and prootics from the orbits (at least pterosphenoids of other Blenniicae enter the orbits); the lack of scales; the presence of pelvic fins (in all but one species); the lack of a pectoral ray articulating directly with the scapula (the presence of a pectoral ray articulating with the scapula is diagnostic of the Tripterygiidae within the superfamily Blenniicae); and the absence of branched pectoral rays.

## Diagnoses of the Subfamilies and Tribes

Subfamily Blenniinae (characters given in the diagnoses of the tribes are not all given in the subfamily diagnoses).—Basisphenoid present; intercalar present; ascending process of premaxillary weakly to strongly based on body of premaxillary; dentaries united by even nonsuturing or suturing joint; dentaries and premaxillaries with or without enlarged canine posteriorly; vomer with or without teeth; frontals not ornamented; circumorbitals 2–5 (most genera with 5); posttemporal with well-developed, ventrally extending arm; supracleithrum articulating anteriorly with posttemporal; last dorsal spine normal to vestigial; dorsal fin with or without a notch between spinous and rayed portions; segmented dorsal fin rays 10–26 (usually less than 24); 0–2 proximal dorsal fin pterygiophores dorsal to supra-occipital; segmented caudal rays 10 to 15 (usually 12 to 14); caudal fin with or without branched rays; pelvic rays I,2–I,4; vertebrae 28–44; 9–12 precaudal vertebrae; neural arch of first and second vertebrae complete (closed dorsally, except in aberrant individuals); posteriormost pleural on vertebra 9–12; minimal hypural (hypural 5) present or absent; 2 epurals (infrequently 1); gill opening ranging from restricted to above level of pectoral base to unrestricted; adults essentially benthic.

Tribe Blenniini (type-genus *Blennius* Linnaeus): Interopercle without posteroventral spur; pterosphenoid visible when skull is viewed laterally; dorsal fin with or without a notch between spinous and rayed portions; dorsal fin rays 13–24; last anal pterygiophore supporting a single ray; pelvic rays I,3–I,4; 6–10 branched rays in caudal fin (except all rays simple in *Medusablennius chani*); gill opening usually extending ventrally to or below level of midbase of pectoral; premaxillaries and dentaries strong, not excavated; bases of comblike teeth of dentaries and premaxillaries joined closely and tightly to bone; replacement teeth developing internally in hollow of each premaxillary and dentary (developing replacement teeth completely surrounded by bone of jaws); posterior canines present or absent on dentaries and premaxillaries, enlarged or normal relative to comblike teeth; teeth on premaxillaries fewer than 60; ascending process of premaxillary weakly to strongly based on body of premaxillary; dentaries united by even, nonsuturing joint (except *Blennius ocellaris* and *B. normani*), circumorbitals 5 (2 in *Medusablennius chani*); supracleithrum with or without tube for sensory canal.

Tribe Omobranchini, new tribe (type-genus: *Omobranchus* Ehrenburg): Interopercle with ventroposterior spur extending posteriorly beyond posterior margin of epihyal; pterosphenoid not visible when skull is viewed laterally; dorsal fin without a notch between spinous and rayed portions; dorsal fin rays 17–26; last anal pterygiophore supporting a single ray; pelvic rays I,2; caudal rays unbranched (rare individuals with 1 or 2 rays branched); gill opening usually restricted to area above level of dorsalmost pectoral ray base; premaxillaries and dentaries strong, not excavated; bases of comblike teeth of premaxillaries and dentaries joined closely and tightly to bone; replacement teeth developing internally in hollow of premaxillaries and dentaries (developing replacement teeth completely surrounded by bone of jaws); posterior canines present on dentaries and premaxillaries (except adult females of *Omobranchus herklotsi*), enlarged relative to comblike teeth; teeth on premaxillaries fewer than 40; ascending process of premaxillary strongly based on body of premaxillary; dentaries united by suturing joint; circumorbitals 3–5; supracleithrum without tube for sensory canal.

Tribe Salariini (type-genus *Salarias* Cuvier): Interopercle without ventroposterior spur; pterosphenoid visible when skull is viewed laterally; dorsal fin with or without a notch between spinous and rayed portions; dorsal fin rays 10–24; last anal pterygiophore supporting 1 or 2 rays; pelvic rays I,2–I,4 (most genera I,3 or I,4); caudal rays branched or unbranched (branched in most genera); gill opening extending ventrally to below level of ventral pectoral base; premaxillaries and dentaries weak to moderately strong; one or both moderately to greatly excavated; bases of comblike teeth of premaxillaries and dentaries usually not closely and tightly joined to bone (usually loosely suspended in thick band of connective tissue); replacement teeth developing in excavated area of premaxillaries and dentaries (not completely surrounded by bone of jaws); posterior canines present or absent on dentaries (enlarged or normal relative to comblike teeth), absent on premaxillaries; teeth on premaxillaries 30–250 (more than 100 in most genera); ascending process of premaxillary weakly based on body of premaxillary; dentaries united by even, nonsuturing joint; circumorbitals 5 (4 in two genera); supracleithrum with or without tube for sensory canal.

SUBFAMILY NEMOPHIDINAE.—Basisphenoid absent; intercalar absent (except *Dasson*); pterosphenoid visible or not visible when skull is viewed laterally; ascending process of premaxillary arising broadly and firmly from body of premaxillary; dentaries united by suturing joint (except possibly *Runula laudandus*); premaxillaries and dentaries strong, not excavated; bases of comblike teeth of dentaries and premaxillaries closely and loosely to tightly joined to bone; replacement teeth developing internally in hollow of premaxillaries and dentaries (developing replacement teeth completely surrounded by bone of jaws); dentary with greatly enlarged canine posteriorly; vomer without teeth (except possibly *Plagiotremus spilistius*); frontals with or without dense ornamentation (consisting of small to large depressions); circumorbitals 3 or 4; posttemporal without ventrally extending arm; supracleithrum articulating anteriorly with epiotic and post-temporal; supracleithrum without tube for sensory canal; last dorsal spine normal; dorsal fin without a notch between spinous and rayed portions; segmented dorsal fin rays 15–119 (more than 24 in most genera); 1–4 proximal dorsal fin pterygiophores dorsal to supraoccipital; last anal pterygiophore supporting a single ray; segmented caudal rays 10–11; caudal fin without branched rays; pelvic rays, when not deformed (a common occurrence in some genera), I,3 (no pelvics in *Plagiotremus spilistius*); vertebrae 31–134; precaudal vertebrae 11–16; first and/or second neural arch usually incomplete (open above); posteriormost pleural on vertebra 12–16; minimal hypural (hypural 5) absent; 1 epural (infrequently 2); gill opening usually restricted to small opening dorsal to level of pectoral base; adults free-swimming during much of their activity.

Norman (1943) used two characters not included above to distinguish those genera I include in the Nemophidinae from the other blenniids: the fact that the interorbital width is greater than the orbital diameter; and the nature of the relationship of the premaxillaries, median ethmoid, nasals, "praeorbitals" and "postorbitals." The first character does separate some genera of the Nemophidinae from those of the Blenniinae, all of which have the interorbital width much less than the orbital diameter; but *Meiacanthus* and *Blennechis* of the Nemophidine have the interorbital width much narrower than the orbital diameter, and so the character does not hold. The second character was not described clearly by Norman, and I am unable to evaluate it. I did not notice, however, any consistent differences between the snout regions in the two subfamilies that I recognize.

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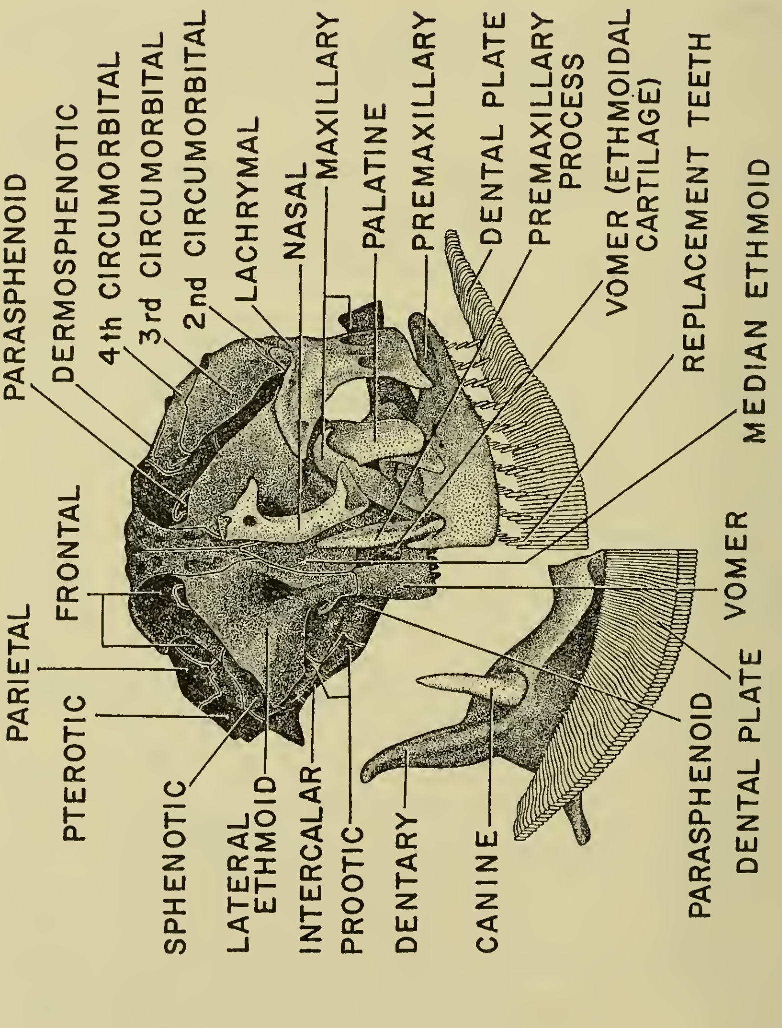


Figure 1.—*Entomacrodus nigricans*, anterior view of skull showing one of each of the bilaterally paired attaching bones.

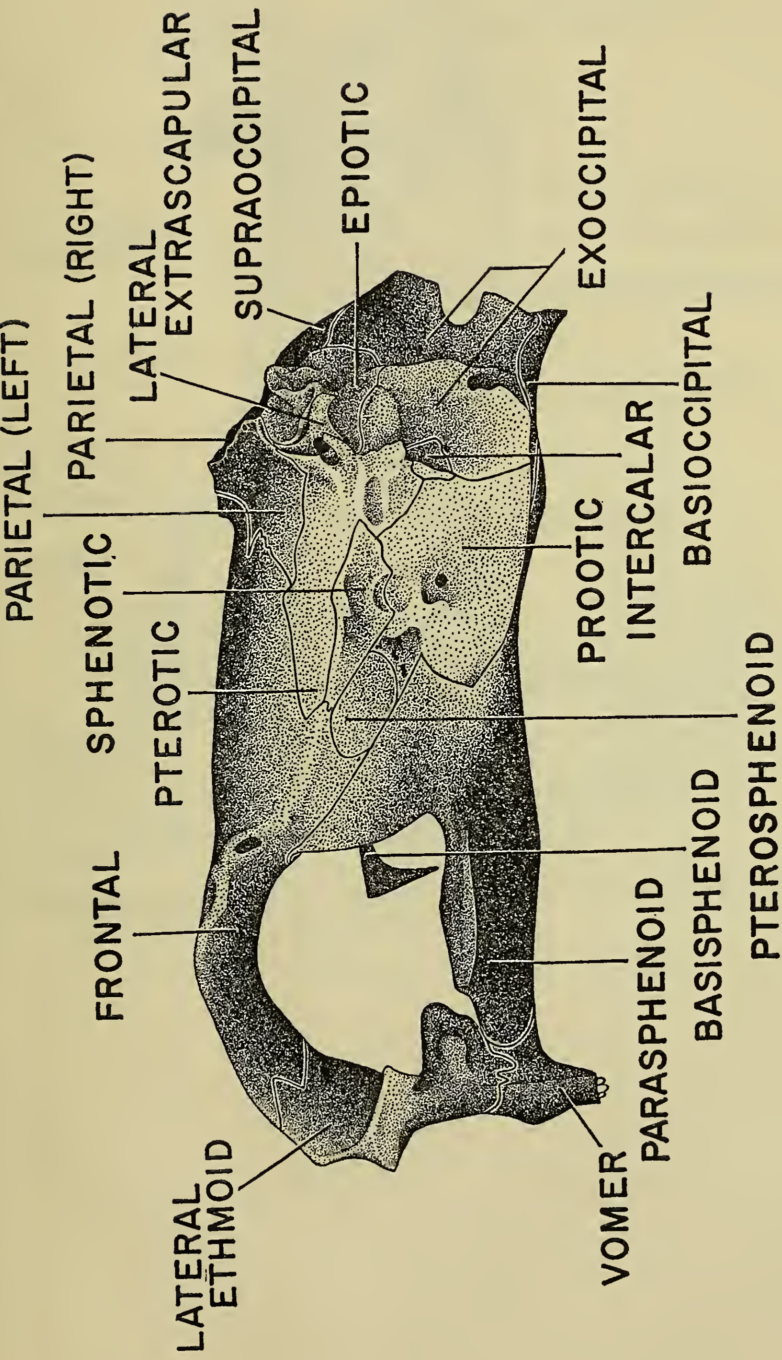


Figure 2.—*Entomacrodus nigricans*, lateral view of cranium.

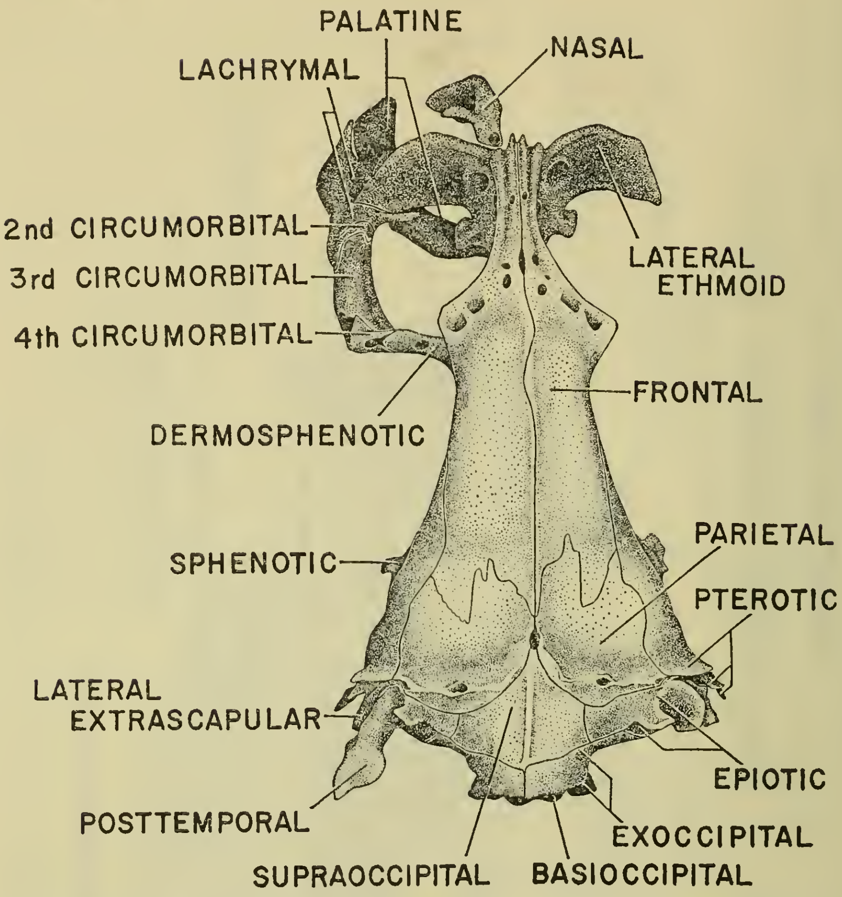


Figure 3.—*Entomacrodus nigricans*, dorsal view of cranium showing some of the attached bones in place.

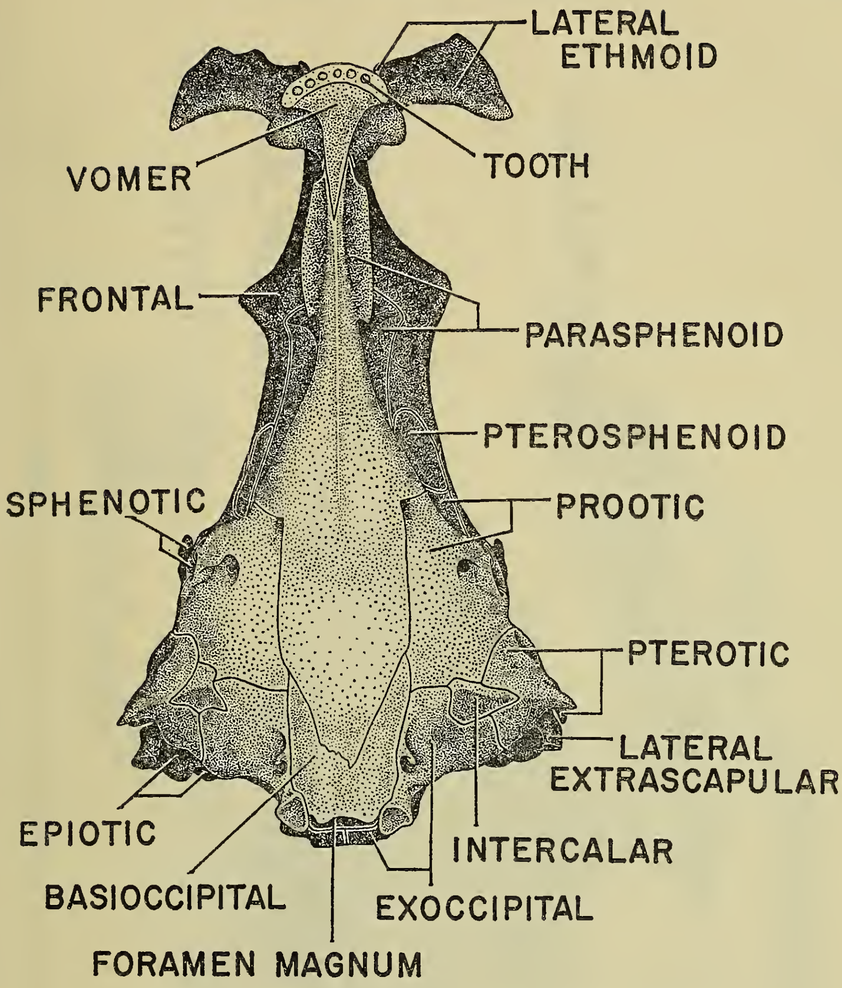


FIGURE 4.—*Entomacrodus nigricans*, ventral view of cranium.

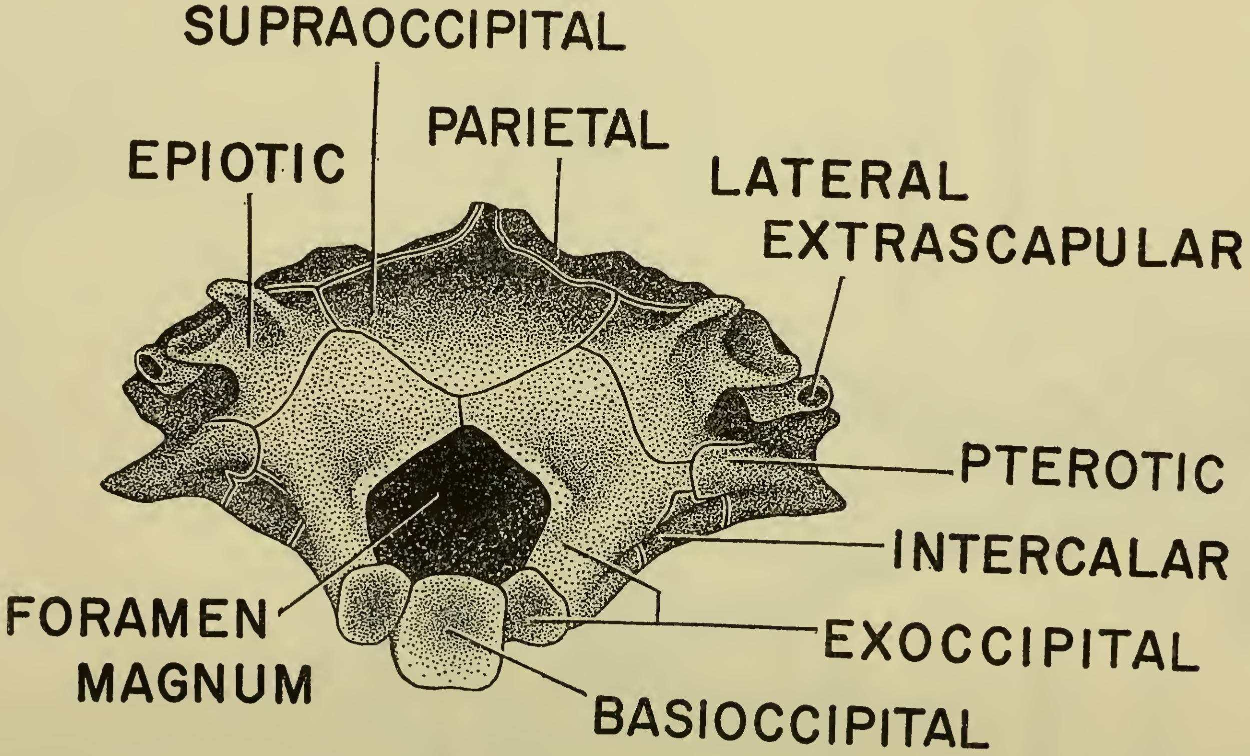


Figure 5.—*Entomacrodus nigricans*, posterior end of cranium.

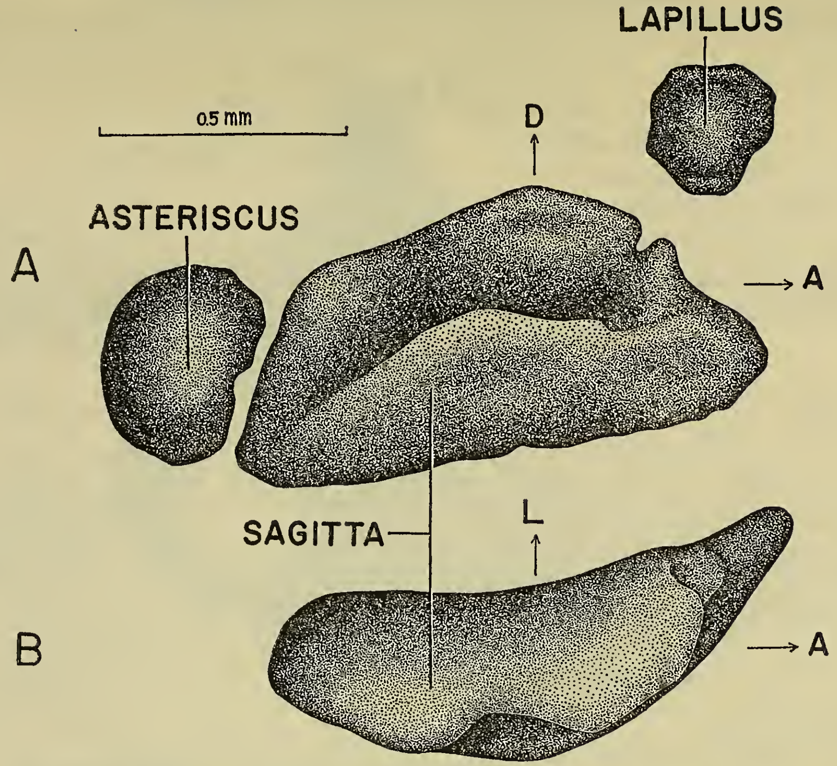


FIGURE 6.—*Entomacrodus nigricans*, otoliths of left side: A, medial view; B, dorsal view. (Directional arrows: A, anterior; D, dorsal; L, lateral.)

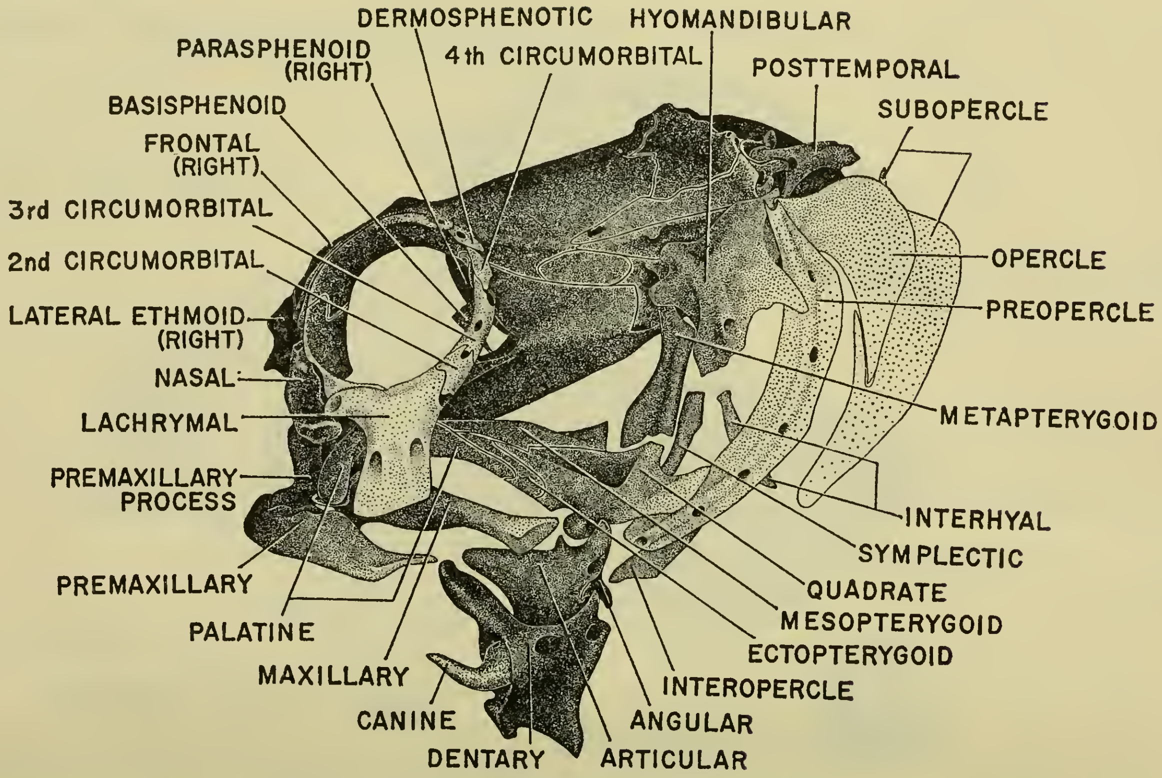


FIGURE 7.—*Entomacrodus nigricans*, lateral view of skull, posterior end tilted slightly away from viewer, lower jaw pivoted ventrally and laterally more than possible in life (teeth, other than canine, not illustrated).

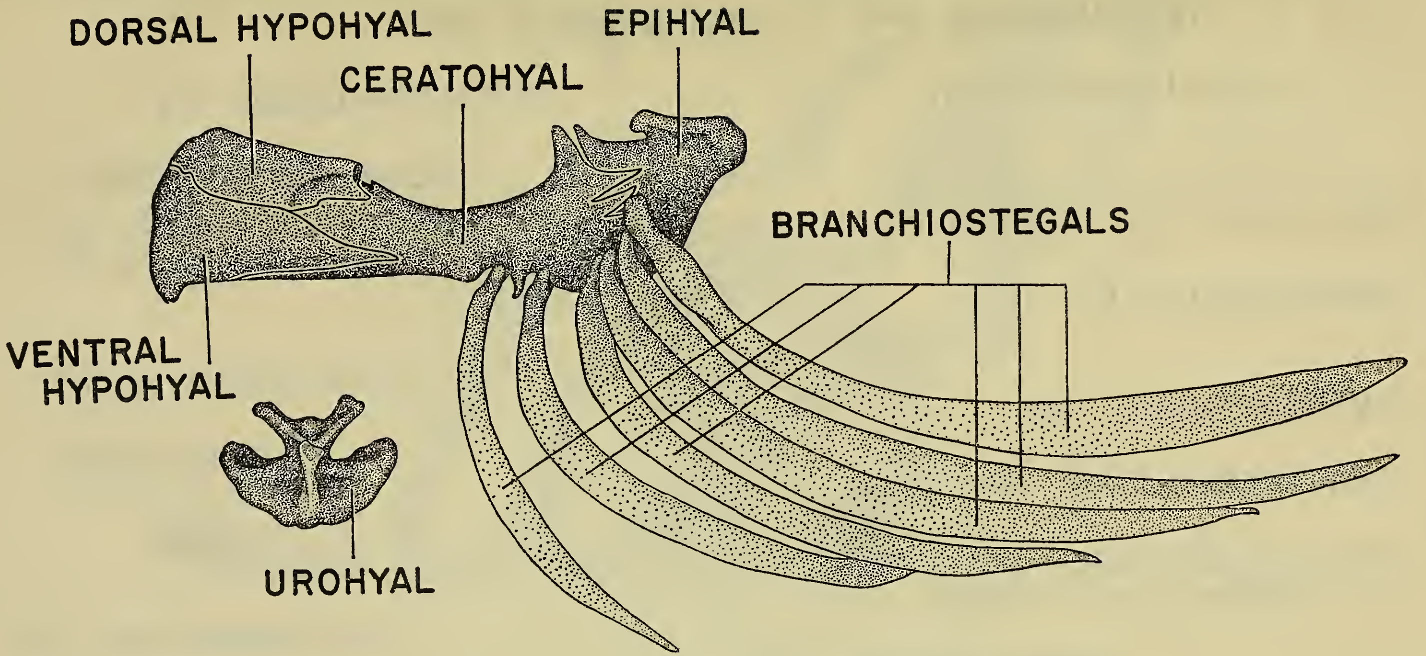


FIGURE 8.—*Entomacrodus nigricans*, lateral view of left hyoid arch and frontal view of urohyal.

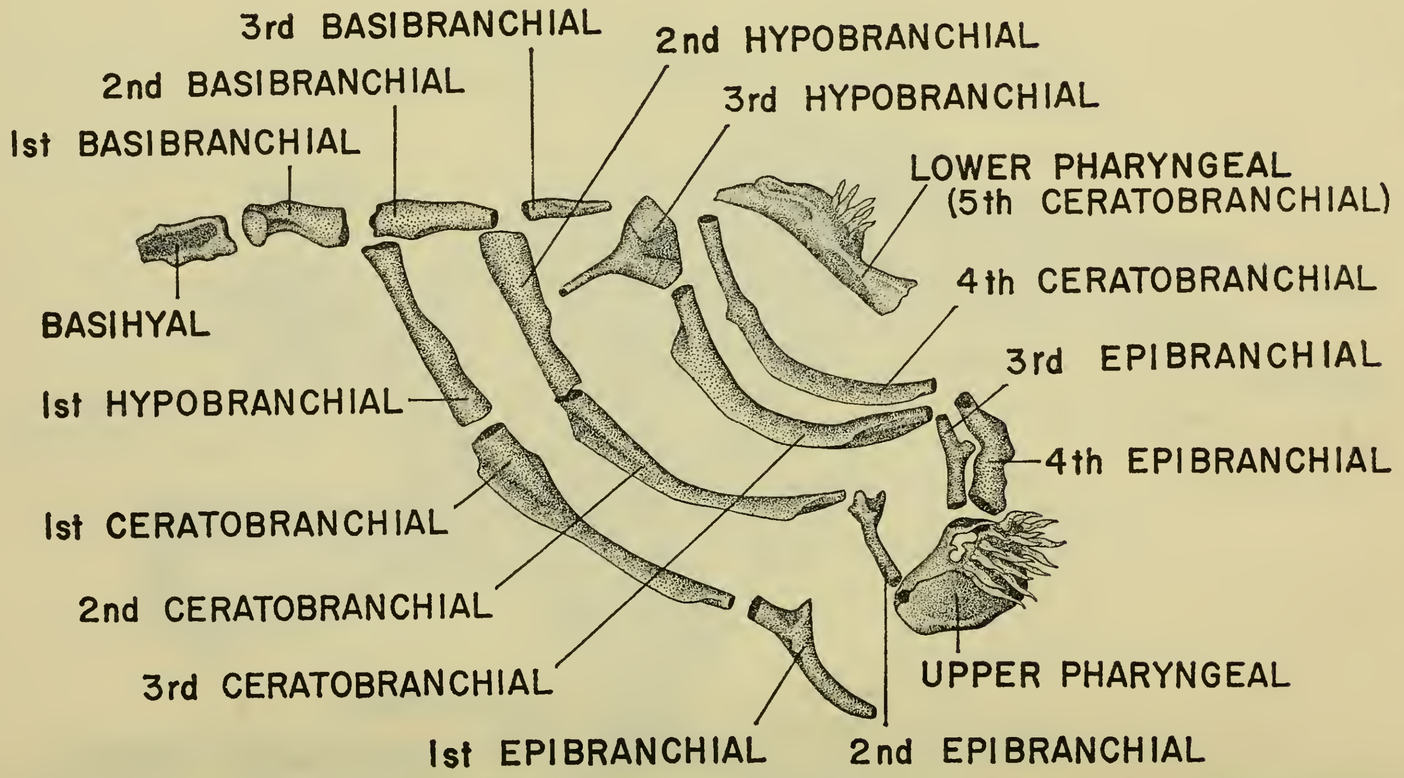
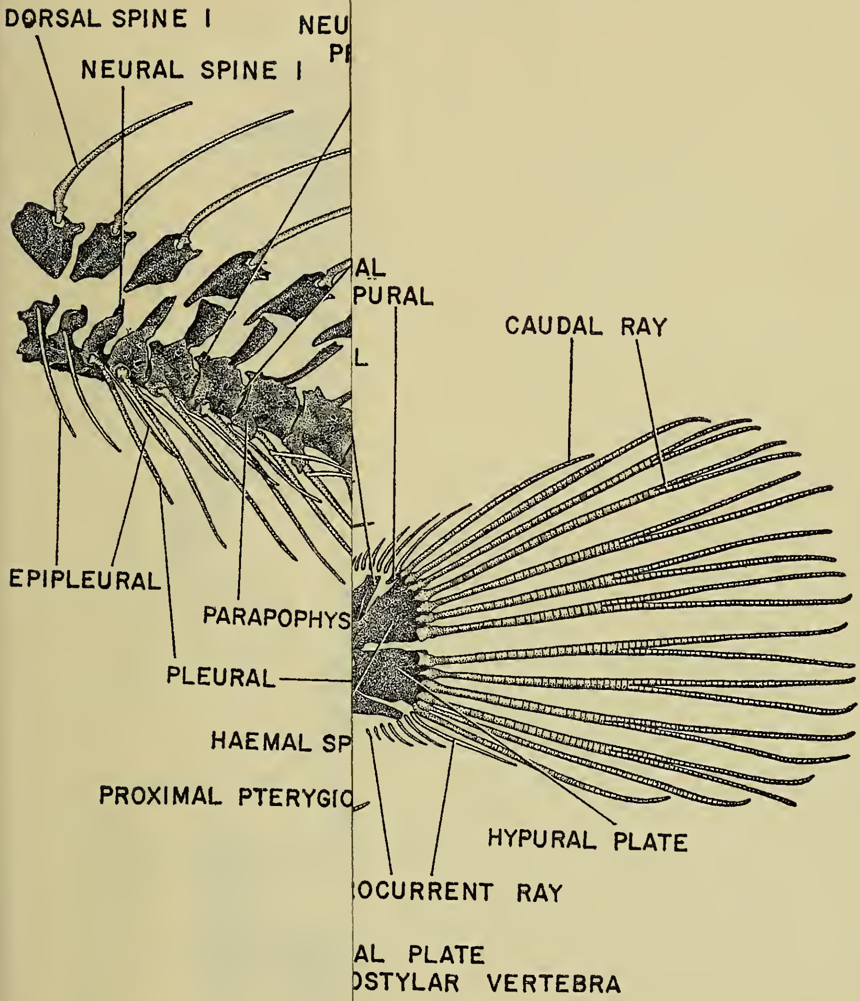


FIGURE 9.—*Entomacrodus nigricans*, basibranchials and left gill arches, dorsal view (except epibranchials and upper pharyngeal turned back so that ventral surface of upper pharyngeal visible; gill-rakers omitted).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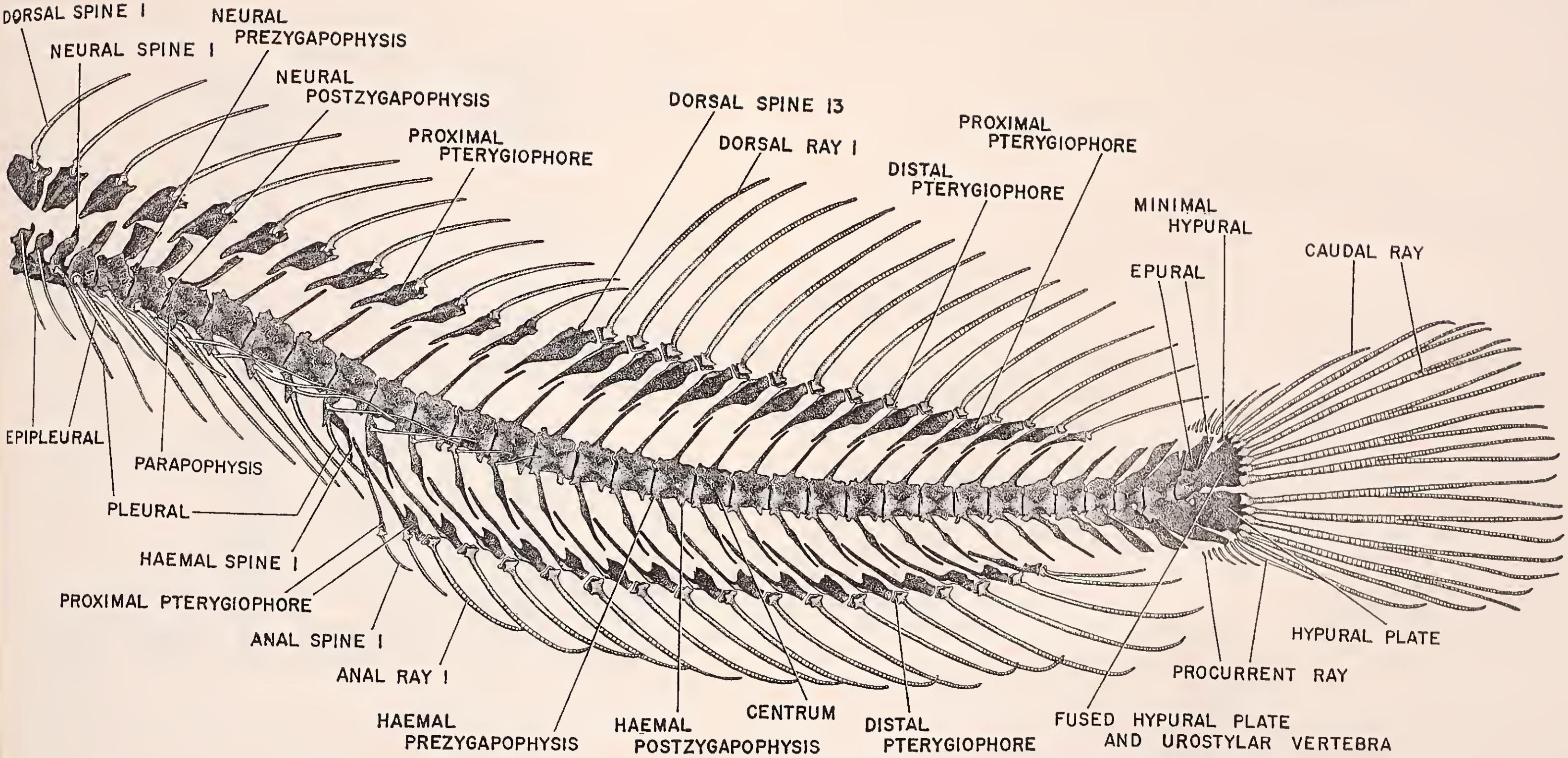


FIGURE 10.—*Entomacrodus nigricans*, axial skeleton and unpaired fins (anterior six epipleurals pivoted ventrally for purposes of clarity).

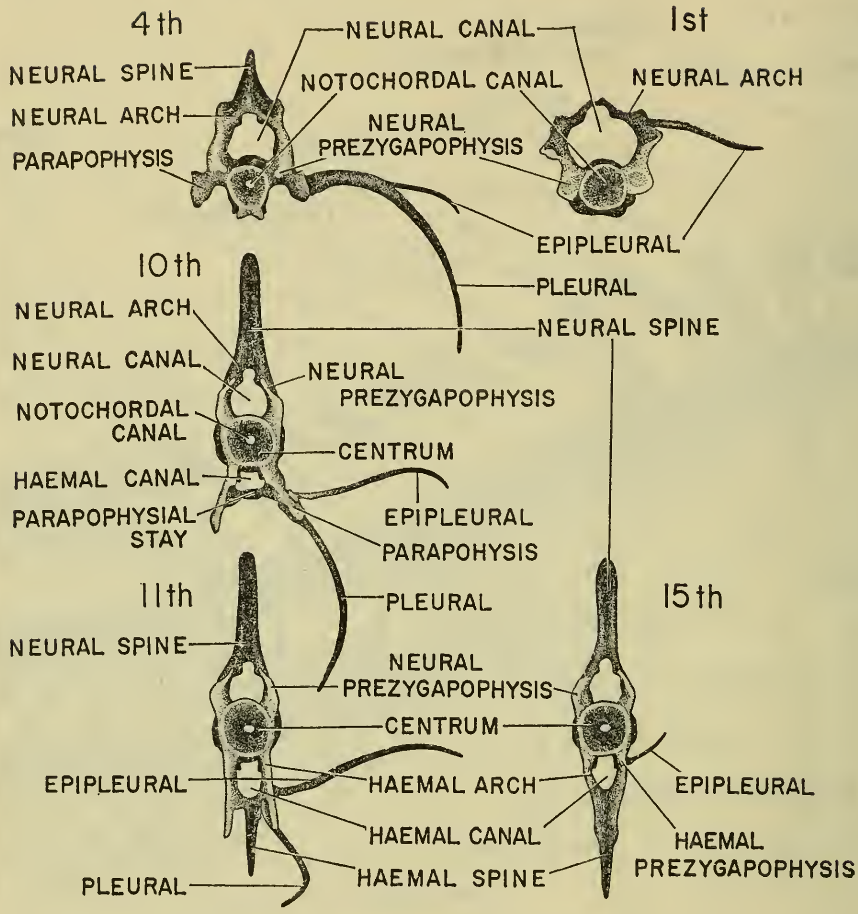


FIGURE 11.—*Entomacrodus nigricans*, anterior views of selected vertebrae.

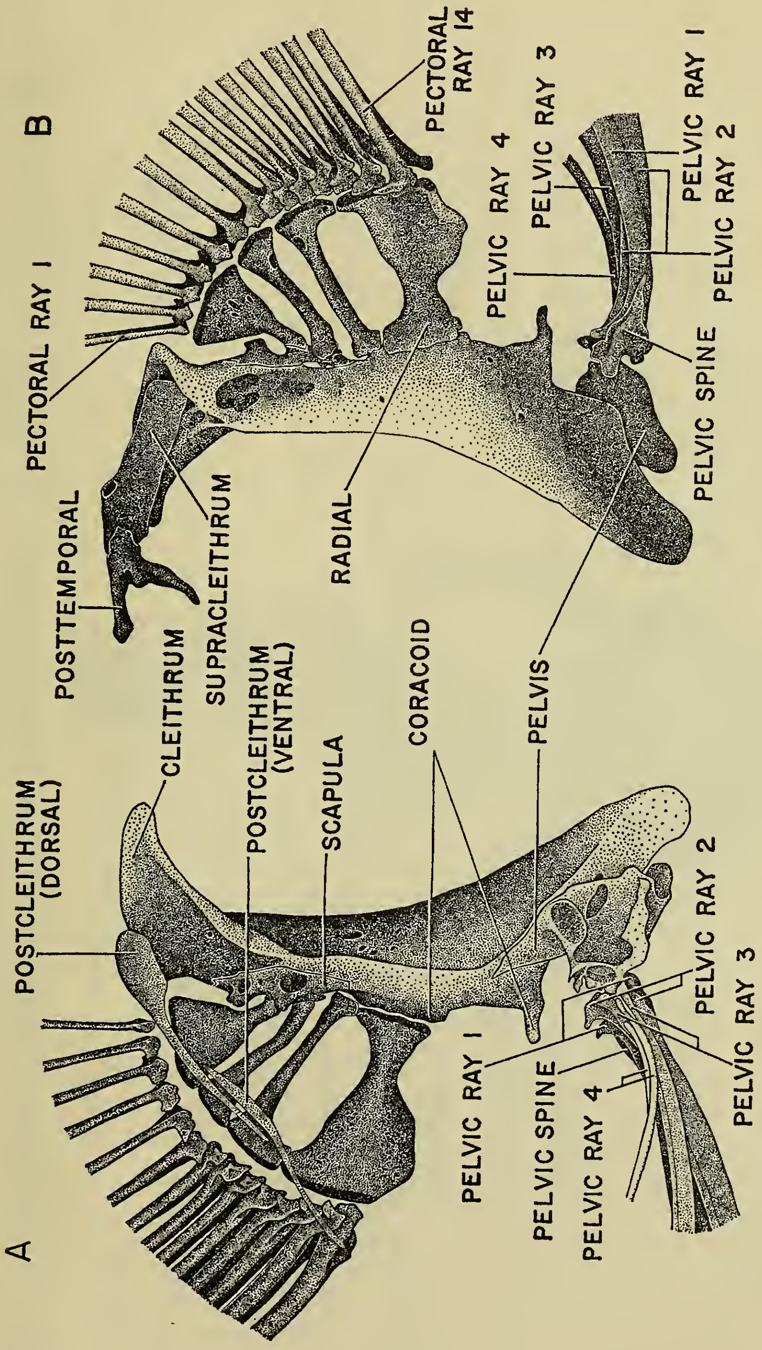


Figure 12.—*Entomacrodus nigricans*, pectoral and pelvic girdles and fins: A, internal view; B, lateral view.

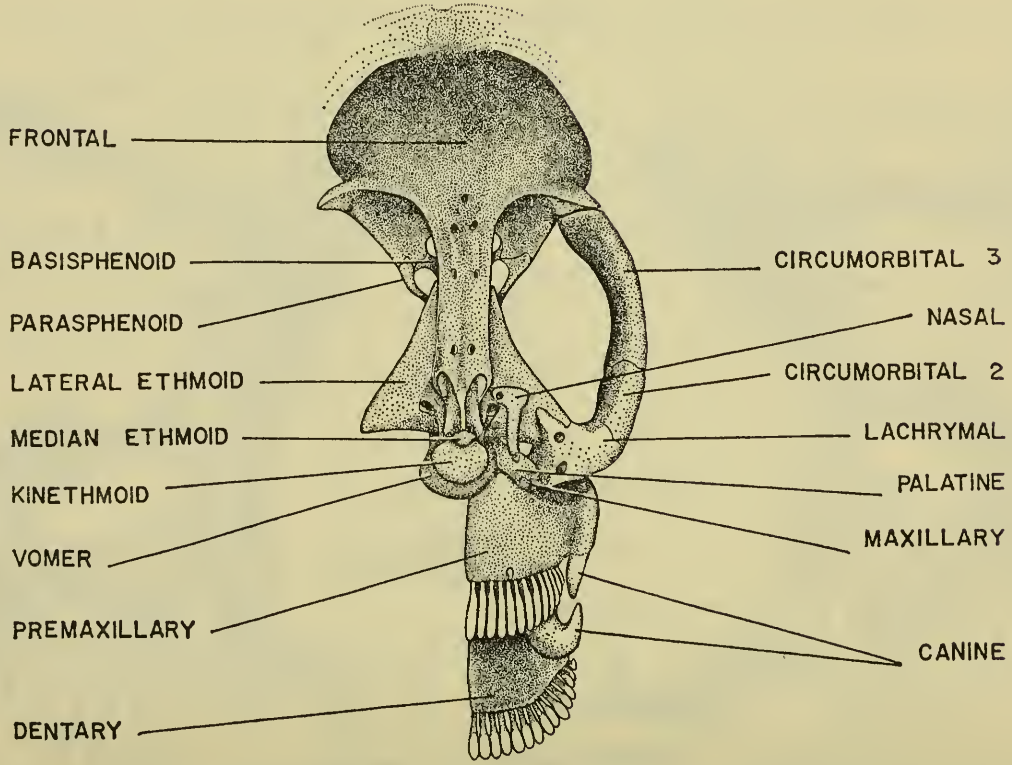


Figure 13.—*Enchelyurus kraussi*, USNM 200609, male, 28.4 mm standard length, anterior view of skull (axis of skull raised posteriorly relative to anterior end).

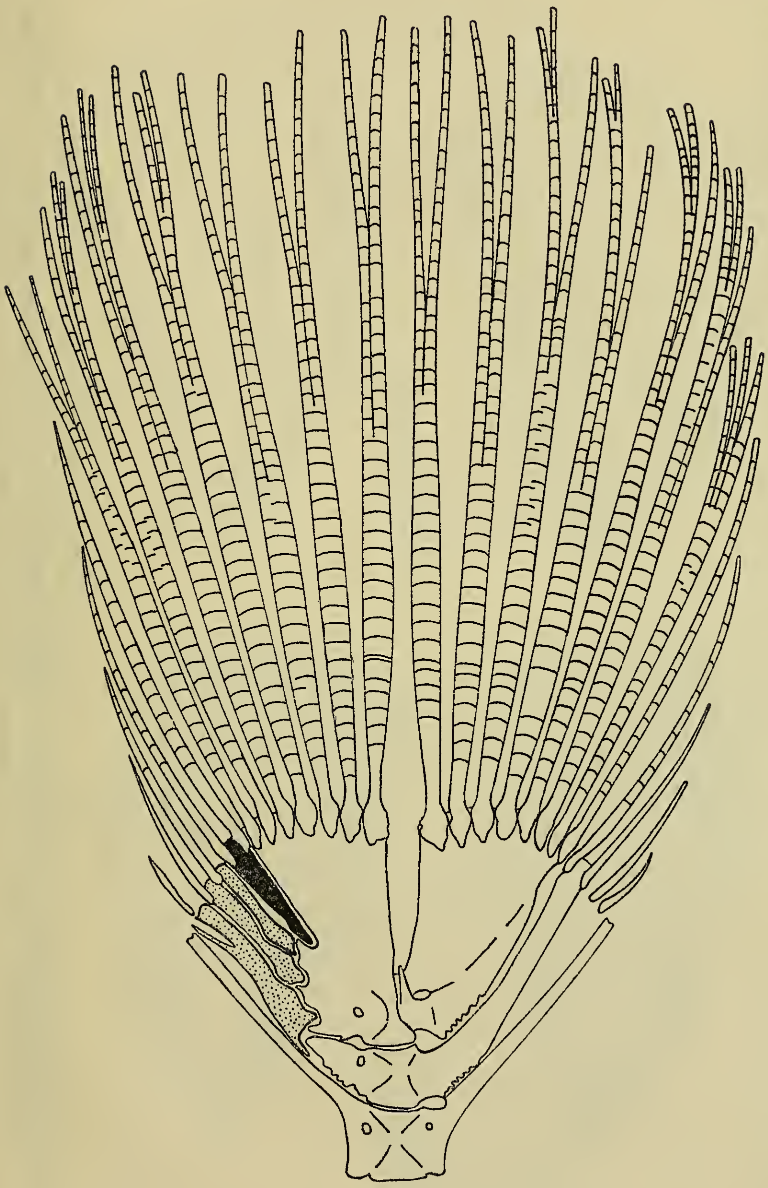


FIGURE 14.—*Acanthoclinus* species USNM 200546, ca. 55 mm standard length, caudal fin (epurals stippled, hypural 5 solid black).

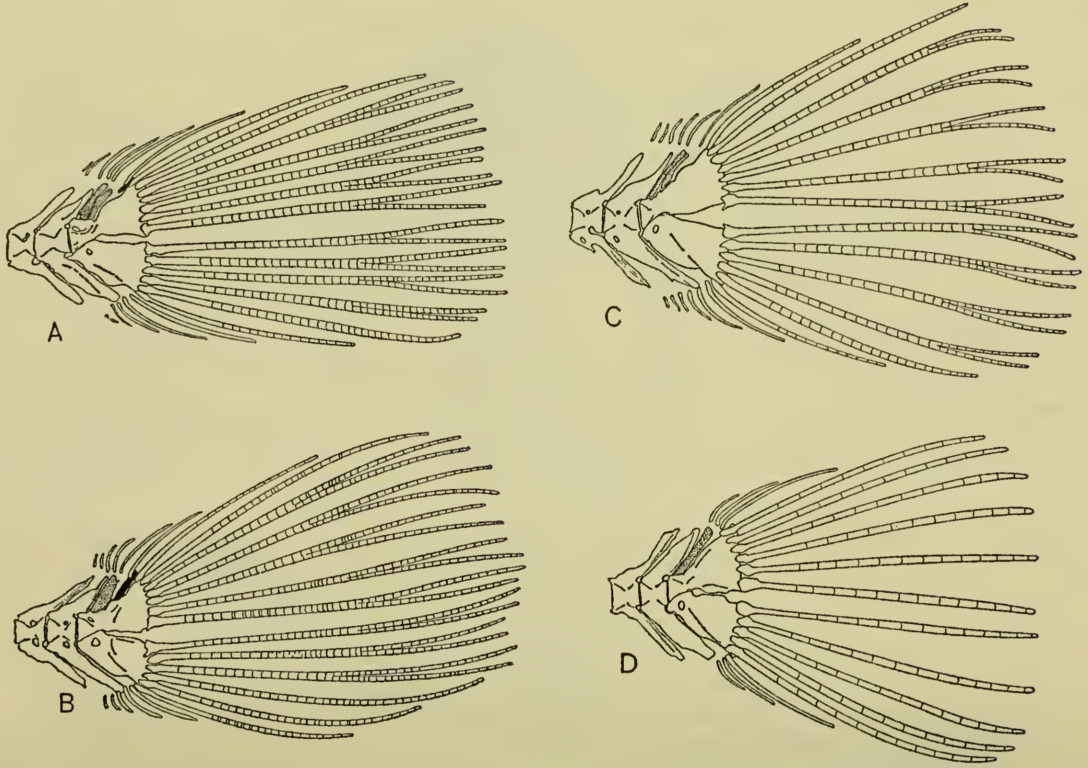


Figure 15.—Caudal fin types of blenniids: A, *Blennius trigloides*, USNM 259168 F–19; B, *Hypleurochilus geminatus*, USNM 116676; C, *Negoscartes guttatus*, USNM 195702; D, *Blennechis filamentosus*, USNM 199432. (Epurals stippled, hypural 5 solid black.)

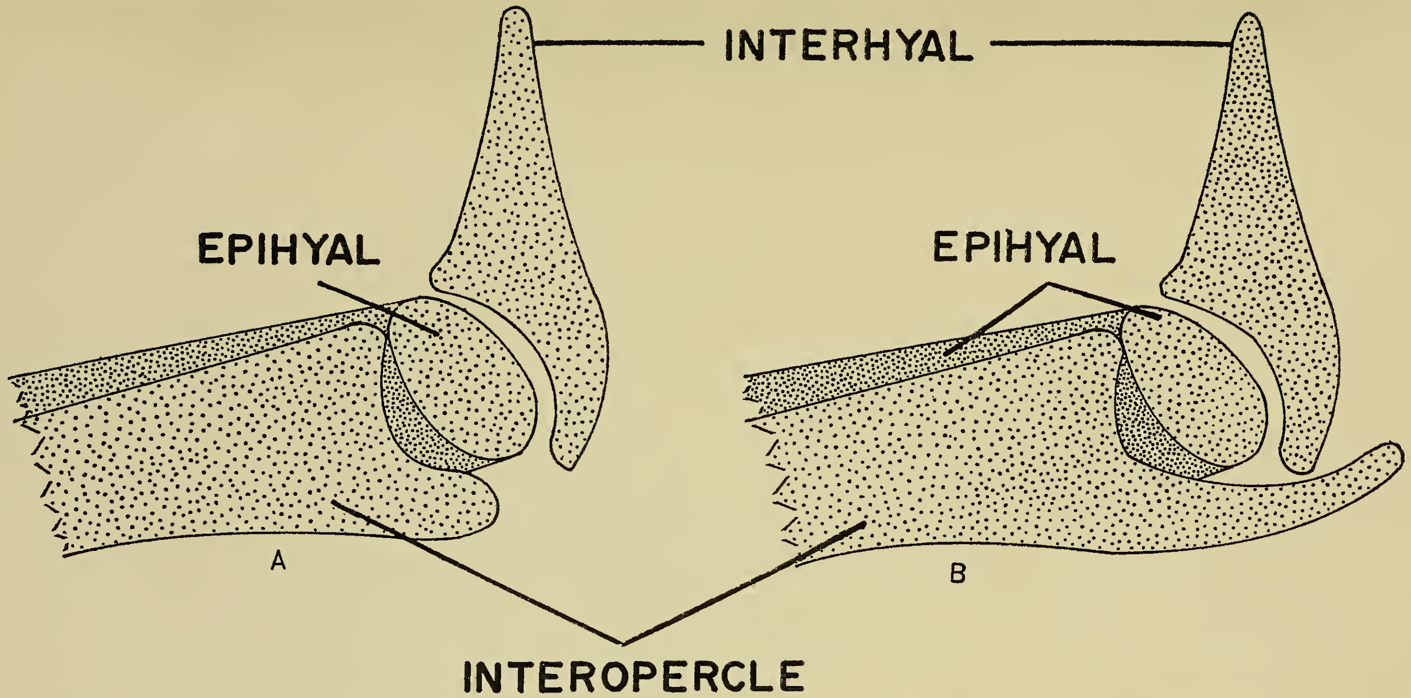
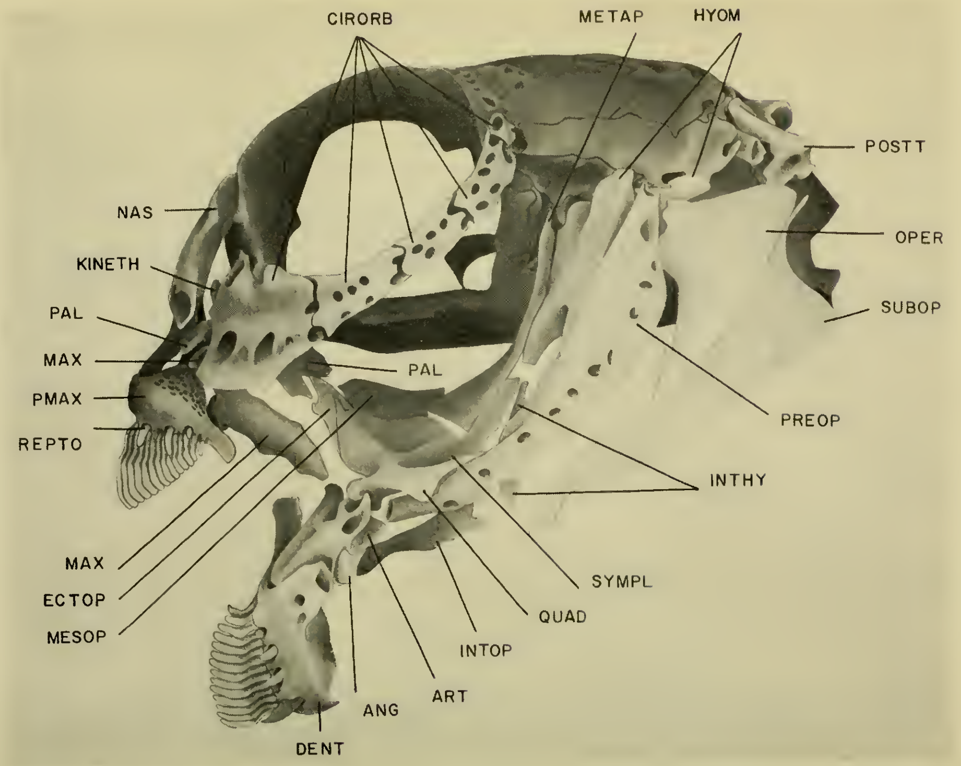


FIGURE 16.—Diagrammatic illustrations of the two types of interopercle-interhyal-epihyal relationships found in blenniid fishes, lateral views: A, all blenniids except tribe Omobranchini; B, tribe Omobranchini.

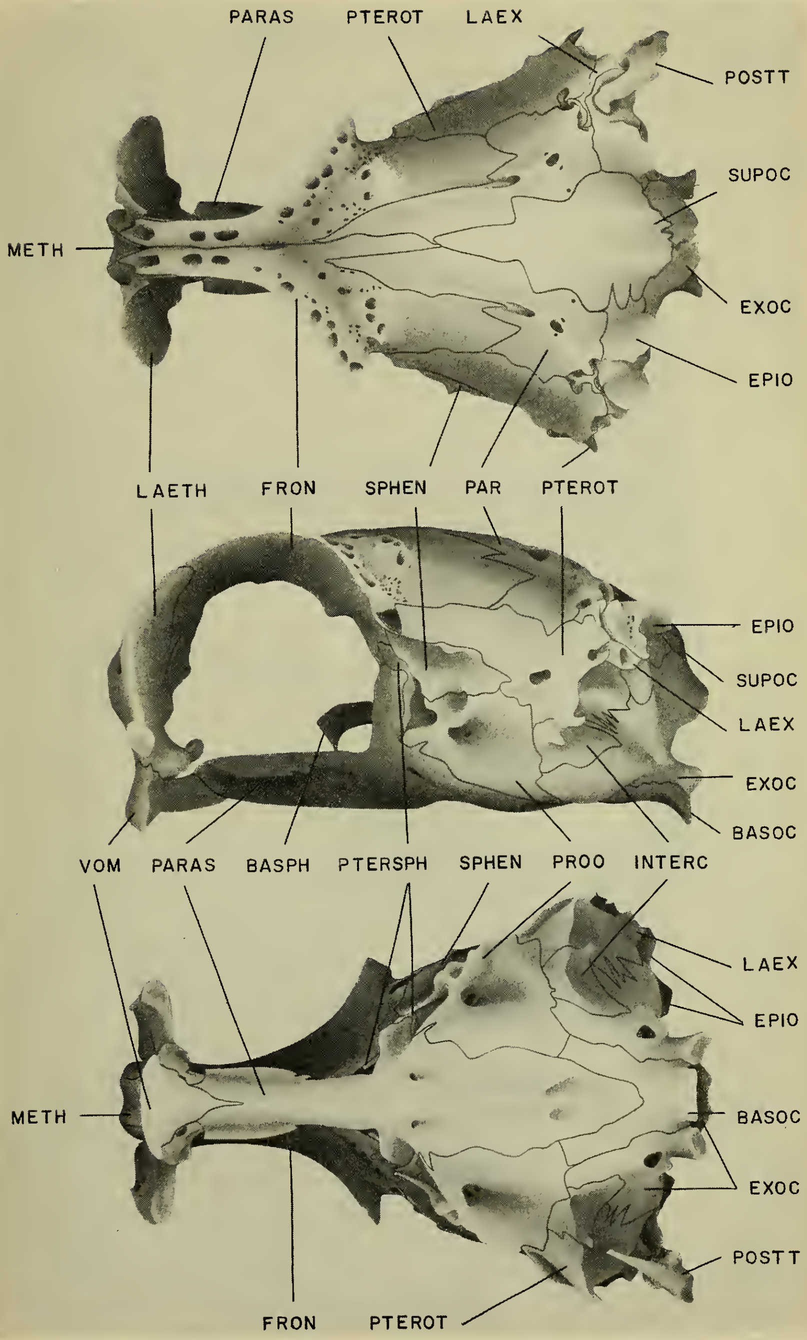
# PLATES

## Abbreviations Used on Plates

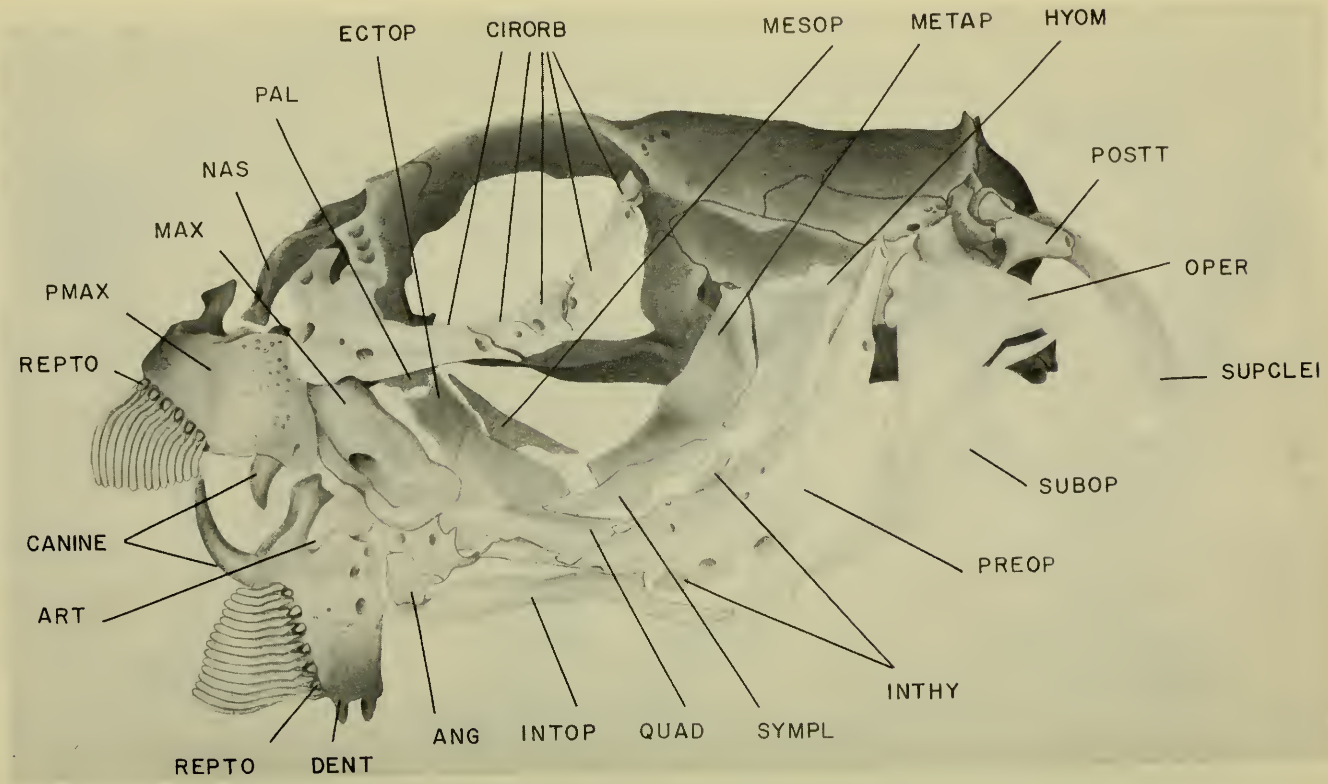
ANG—angular
ART—articular
BASOC—basioccipital
BASPH—basiphenoid
CANINE—canine
CIRORB—circumorbitals
DENPL—dental plate
DENT—dentary
ECTOP—ectopterygoid
EPIO—epiotic
EXOC—exoccipital
FRON—frontal
HYOM—hyomandibular
INTERC—intercalar
INTHY—interhyal
INTOP—interopercle
KINETH—kinethmoid
LAETH—lateral ethmoid
LAEX—lateral extrascapular
MAX—maxillary
METH—median ethmoid
MESOP—mesopterygoid
METAP—metapterygoid
NAS—nasal
OPER—opercle
PAL—palatine
PAR—parietal
PARAS—parasphenoid
PMAX—premaxillary
POSTT—posttemporal
PREOP—preopercle
PROO—prootic
PTEROT—pterotic
PTERSPH—pterosphenoid
QUAD—quadrate
REPTO—replacement tooth
SPHEN—sphenotic
SUBOP—subopercle
SUPCLEI—supracleithrum
SUPOC—supraoccipital
SYMPL—symplectic
VOM—vomer



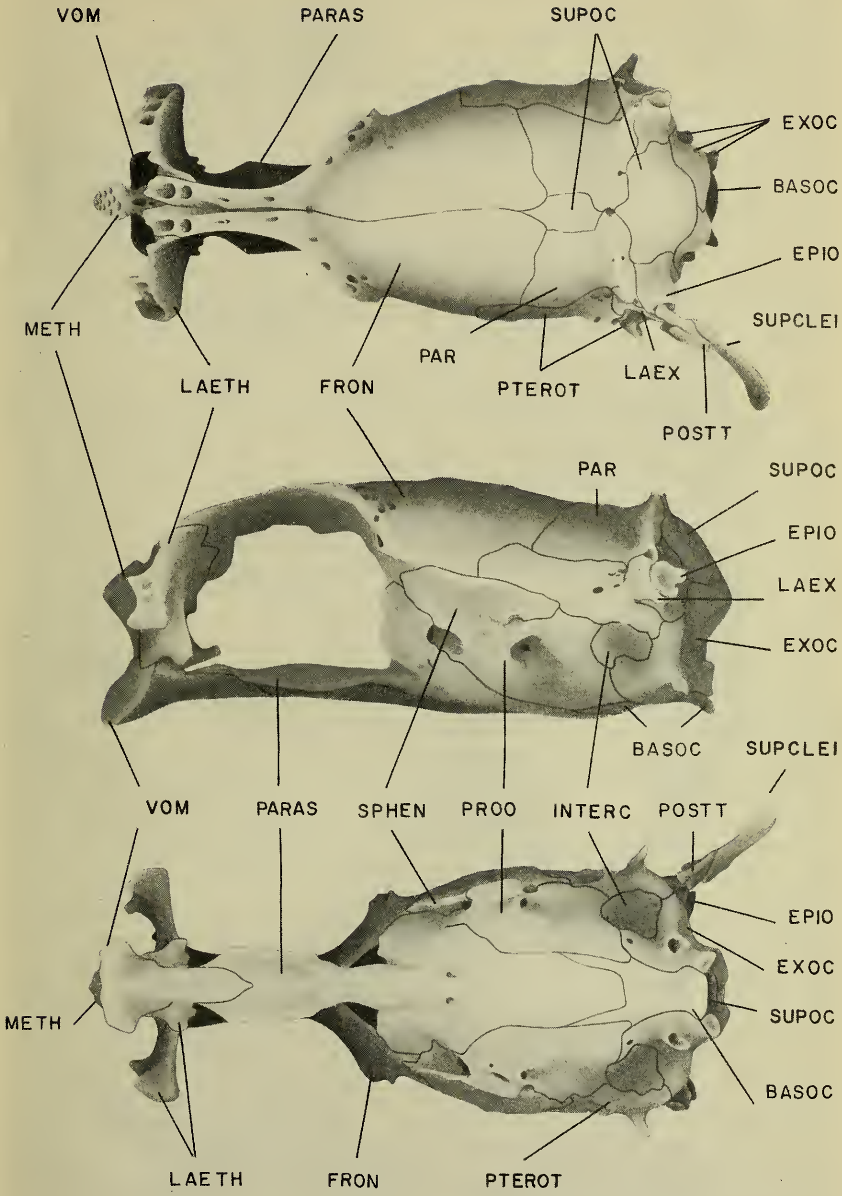
*Blennius cristatus*, USNM 192175, female, 46.5 mm standard length, lateral view of skull with lower jaw pivoted ventrally more than possible in life.



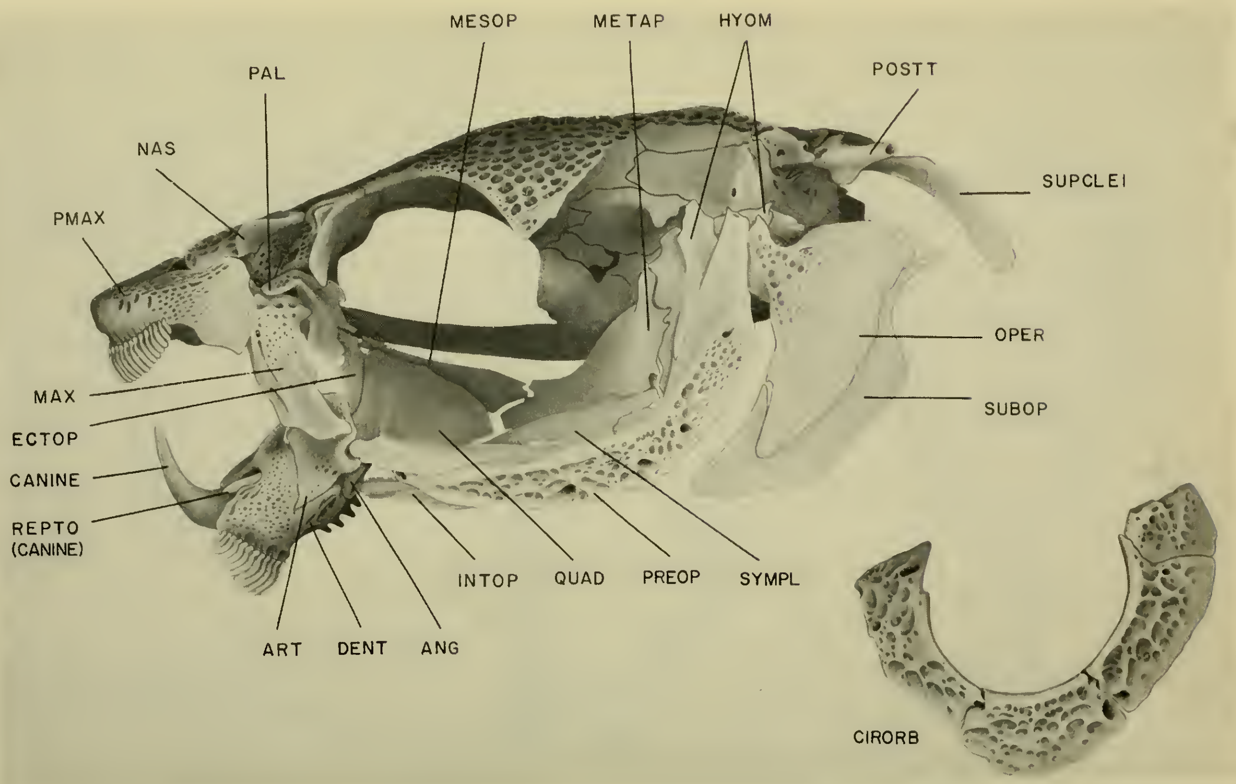
*Blennius cristatus,* USNM 192175, female 46.5 mm standard length, cranium: top, dorsal view; center, lateral view; bottom, ventral view.



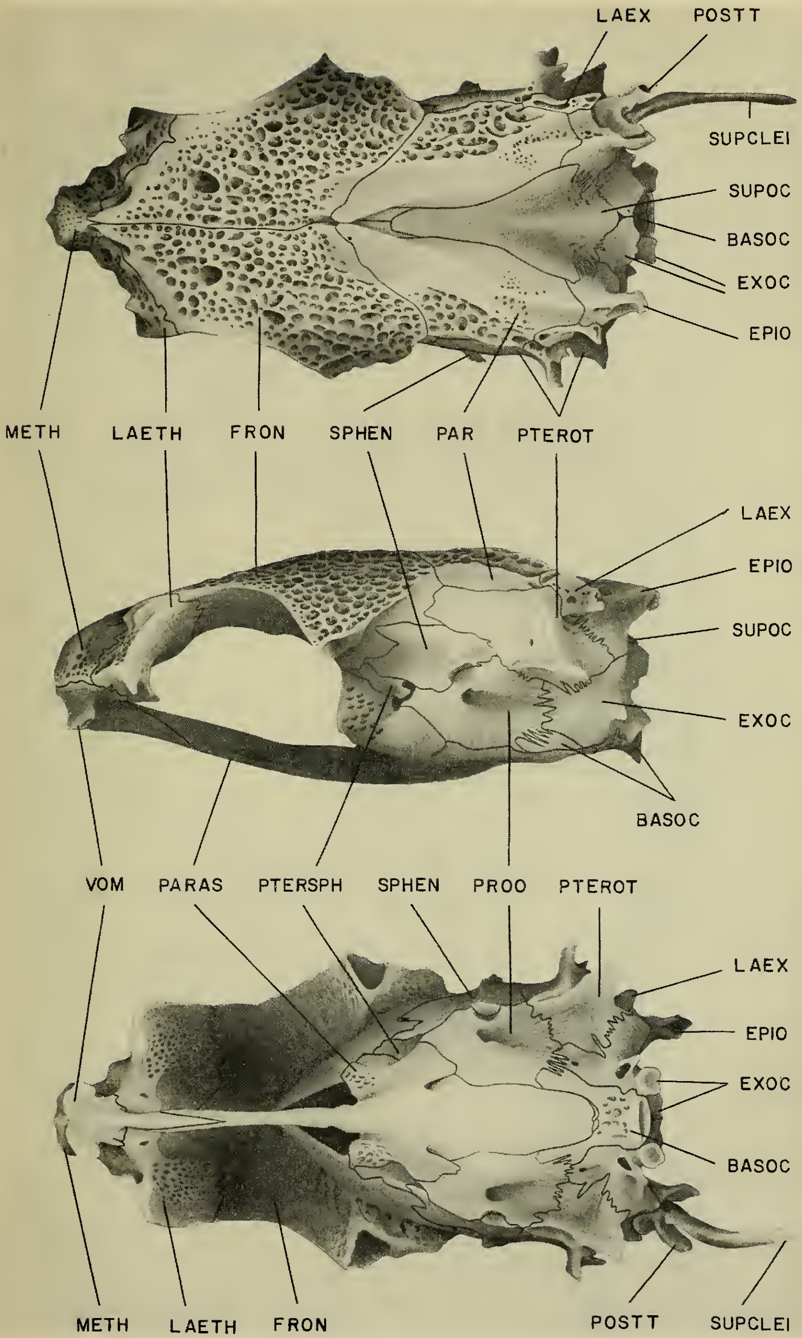
*Omobranchus japonicus*, USNM 174330, female, 44.6 mm standard length, lateral view of skull.



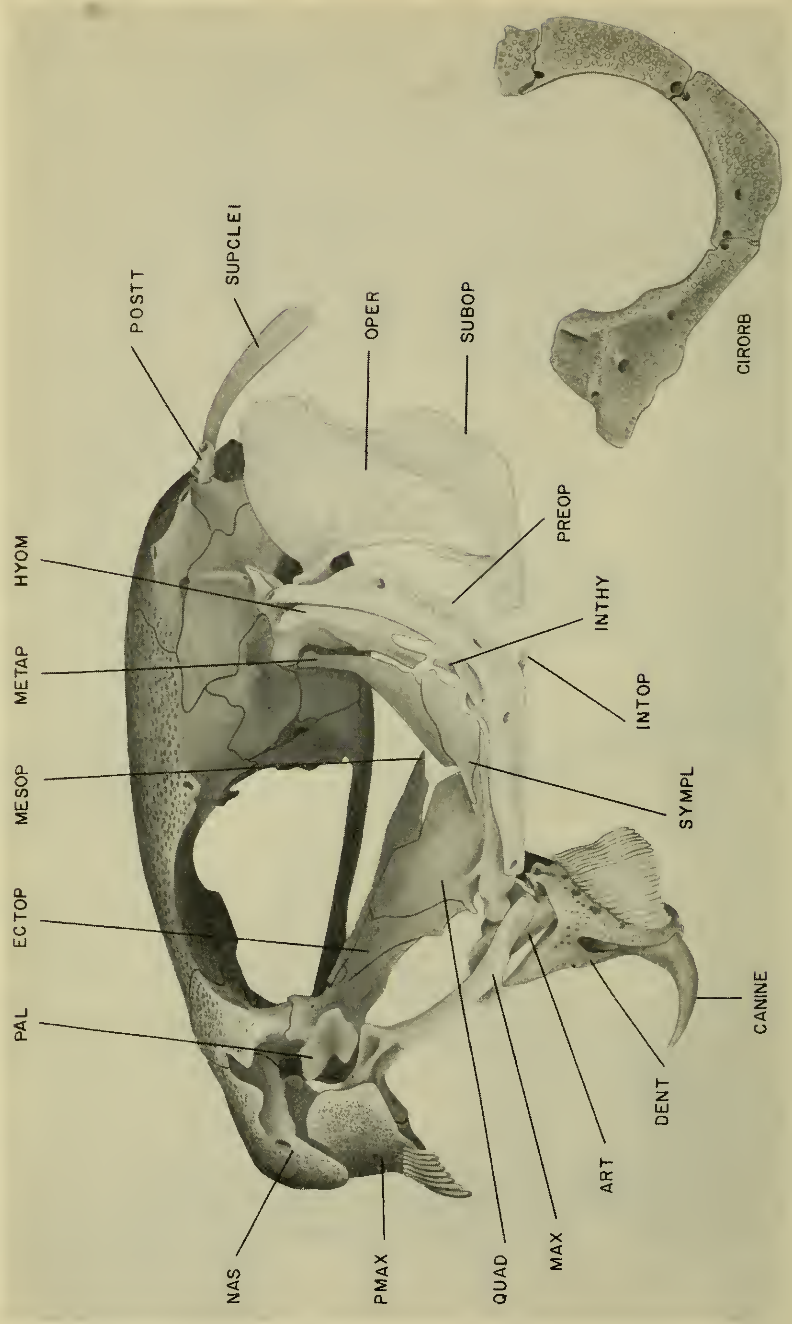
*Omobranchus japonicus*, USNM 174330, female, 44.6 mm standard length, cranium: top, dorsal view; center, lateral view; bottom, ventral view.



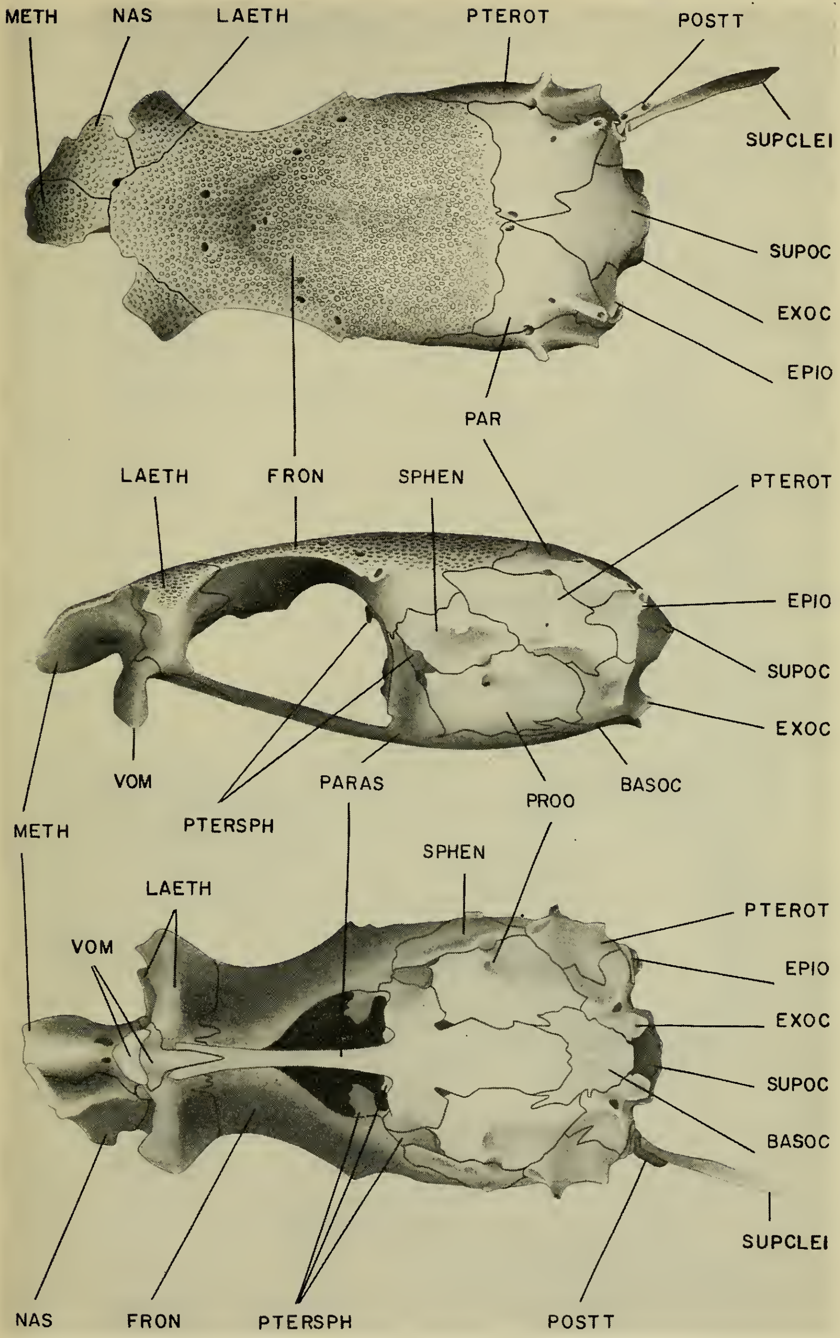
*Aspidontus taeniatus*, USNM 200339, female, 67.5 mm standard length, lateral view of skull with circumorbital bones removed.



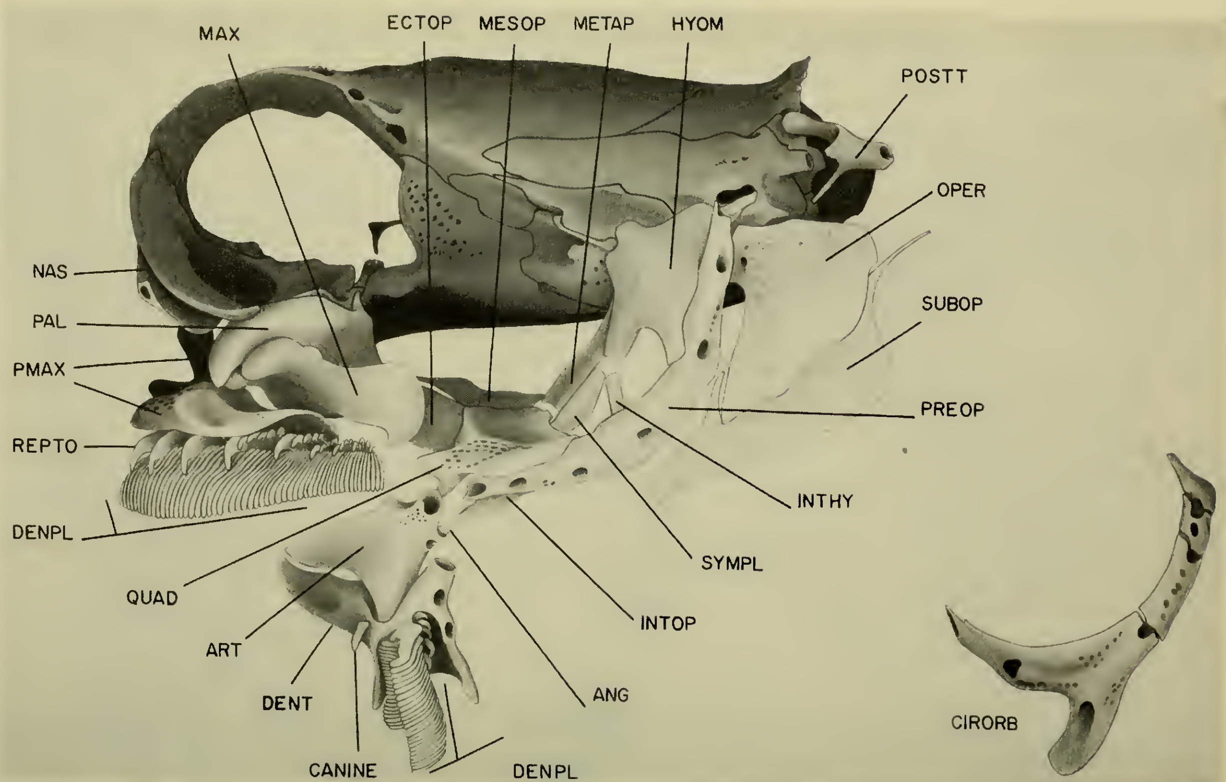
*Aspidontus taeniatus*, USNM 200339, female, 67.5 mm standard length, cranium: top dorsal view; center, lateral view; bottom, ventral view.



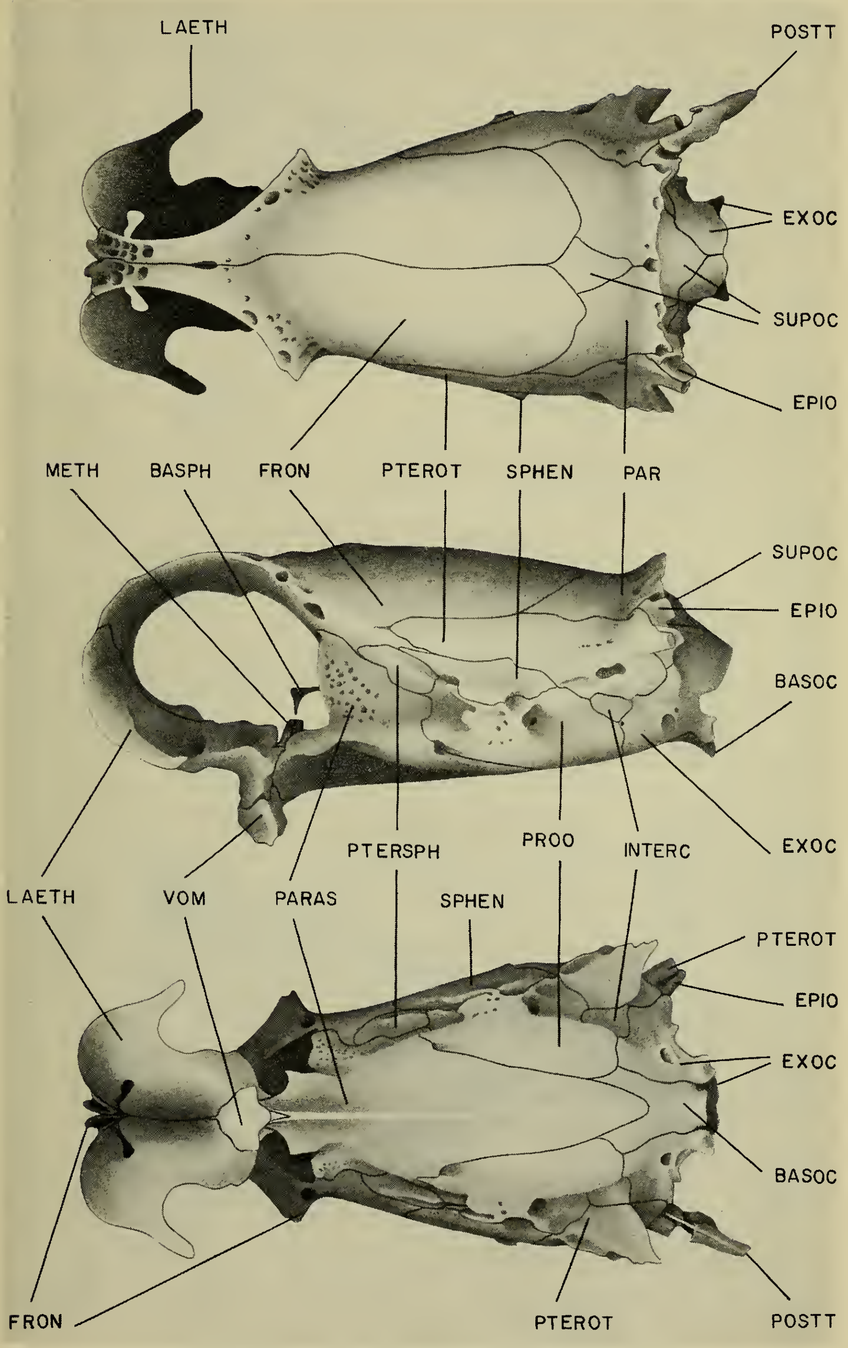
*Runula azalea*, USNM 200392, male, 47.3 mm standard length, lateral view of skull with circumorbital bones removed.



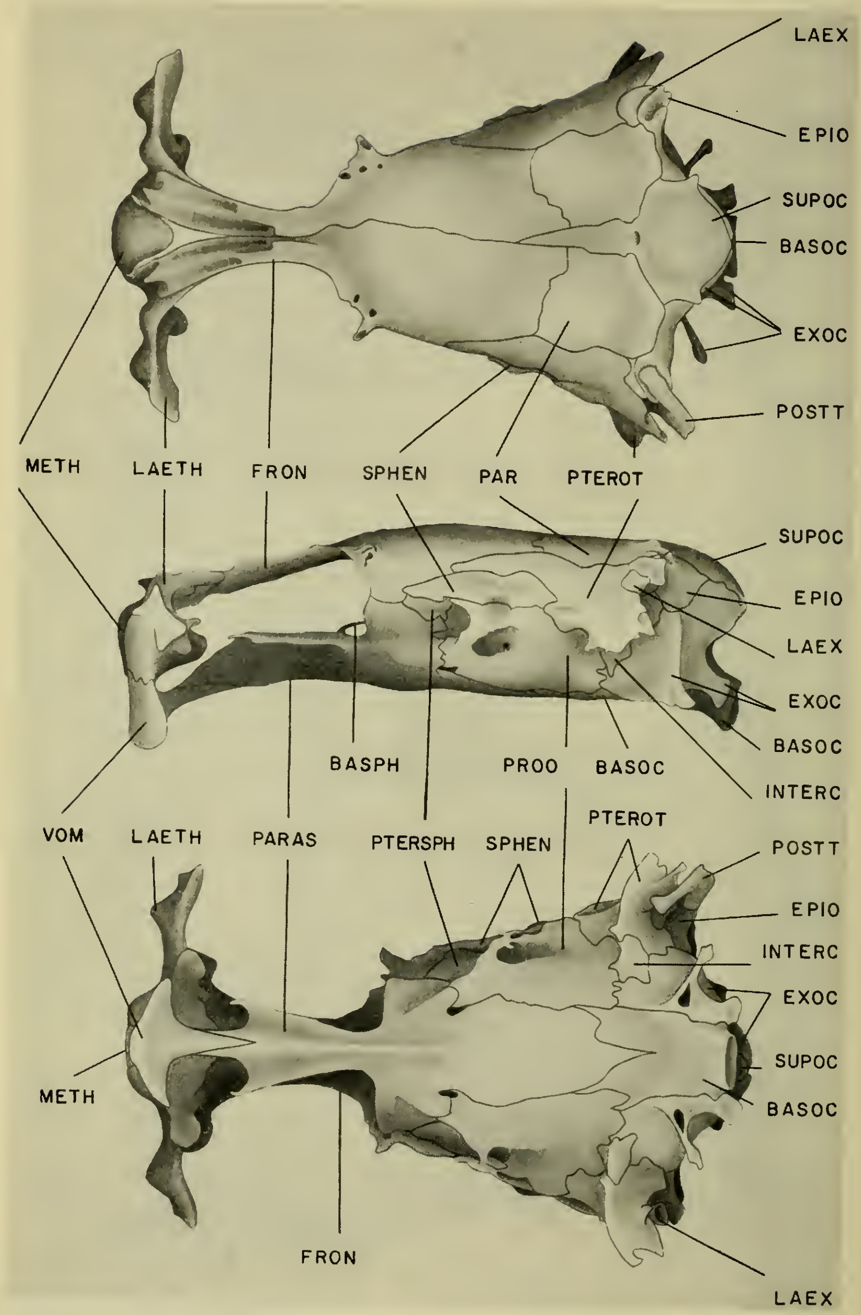
*Runula azalea*, USNM 200392, male, 47.3 mm standard length, cranium: top, dorsal view; center, lateral view; bottom, ventral view.



*Ecsenius nalolo*, USNM 200428, male, 49.0 mm standard length, lateral view of skull with circumorbital bones removed and lower jaw pivoted ventrally more than possible in life.



*Ecsenius nalolo*, USNM 200428, male, 49.0 mm standard length, cranium: top, dorsal view; center, lateral view; bottom, ventral view.



*Andamia heteroptera*, USNM 137769, female, 52.9 mm standard length, cranium: top, dorsal view; center, lateral view; bottom, ventral view.