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THE OSTEOLOGY OF *MICROGOBIUS SIGNATUS* POEY
(PISCES: GOBIIDAE), WITH COMMENTS
ON OTHER GOBIID FISHES

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THE OSTEOLOGY OF *MICROGOBIUS SIGNATUS* POEY
(PISCES: GOBIIDAE),
WITH COMMENTS ON OTHER GOBIID FISHES

RAY S. BIRDSONG¹

SYNOPSIS: The osteology of *Microgobius signatus* is described in detail and compared with other species of *Microgobius* and with representatives from selected related genera. Osteological evidence supporting the concept of the American seven-spined gobies as a natural assemblage is presented, and the group is formally recognized as the Tribe Gobiosomini of the Family Gobiidae. Osteological characteristics and trends within the gobioids are discussed, and Miller's classification of the group is commented upon.

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INTRODUCTION

In recent years some 20 genera of American Gobiidae with seven spines in the first dorsal fin have been grouped together as the American "seven-spined gobies" (Böhlke and Robins 1968, 1969; Böhlke 1969). The grouping of these more than 100 species has been based primarily on external characteristics; however, my study will show that they may share several distinctive osteological characteristics as well. This new evidence, combined with the circumscribed geographical distribution of the seven-spined gobies, adds weight to their recognition as a natural assemblage.

Böhlke and Robins (1968, 1969) clarified many of the relationships within the central group of American seven-spined gobies (i.e., *Gobiosoma* and its derived genera). They specifically excluded from the central group the genera *Microgobius* and *Bollmannia*, which they believed to be only distantly related to the *Gobiosoma* group, and the genus *Parrella*, which they believed to be a composite and too poorly known to relate. Hoese (1971) differed with some of the generic concepts proposed by Böhlke and Robins, but agreed that *Microgobius*, *Bollmannia*, *Parrella*, and *Palatogobius* do not appear to be closely related to the *Gobiosoma* group. Ginsburg (1939:57) allied *Microgobius* to *Bollmannia* and stated that *Parrella* appeared to be intermediate between the two. More recently, Gilbert (1971: 33) allied a new genus, *Palatogobius*, with *Microgobius* and *Bollmannia*.

This study was undertaken to provide a detailed osteology of a representative American seven-spined goby and to attempt to clarify the relationships between *Microgobius*, *Bollmannia*, *Parrella*, and *Palatogobius* and the *Gobiosoma* group.

ACKNOWLEDGMENTS

I extend thanks to the many people who have rendered assistance during this study. My special thanks goes to C. Richard Robins of the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, for his support and review of the manuscript.

Ernest A. Lachner, Stanley H. Weitzman, and Victor G. Springer, United States National Museum of Natural History, have provided valuable discussion, specimens, and review of the manuscript. Donn E. Rosen and Gareth Nelson, American Museum of Natural History, gave advice on various points of nomenclature. Thomas H. Fraser of the United States National Museum of Natural History provided valuable criticism and suggestions. Other former students at the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, who lent valuable assistance in diverse ways are: William P. Davis, William N. Eschmeyer, Alan R. Emery, Jon C. Staiger, Thomas Devany, David M. Dean, David G. Smith, and Tomio Iwamoto.

Specimens were loaned by James E. Böhlke, The Academy of Natural Sciences, Philadelphia; Charles E. Dawson, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; Carter R. Gilbert, Florida State Museum, University of Florida, Gaines-

ville; Boyd W. Walker, University of California at Los Angeles; Richard H. Rosenblatt, University of California at San Diego; John S. Ramsey, then of the University of Puerto Rico, Mayagüez; Fernando Cervigón, Museo Historia Natural La Salle de la Estación de Investigaciones Marinas de Margarita, Venezuela; John E. Randall, The Bernice P. Bishop Museum, Honolulu; Ralph W. Yerger, Florida State University, Tallahassee; and Giles W. Mead, then of the Museum of Comparative Zoology, Harvard University.

Special thanks go to my wife, Veronica, for her efforts in typing and proofreading several drafts of the manuscript.

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METHODS

Much of the material used in this study was cleared by the trypsin technique of Taylor (1967), and the bones were stained with Alizarin Red-S. Specimens were stored in 100% glycerin. Many specimens were dissected after clearing and staining for more specific examination. Skulls were disarticulated by heating them in a diluted KOH solution. Many additional specimens were radiographed and data on several characters, principally of the axial skeleton, were obtained from these films. Observations and illustrations were made using a Wild M-5 dissecting microscope with camera lucida attachment. The nomenclature of the bones follows that of Springer (1968).

I have devised the following notational procedure to facilitate the discussion of the arrangement and relationships of the spinous dorsal fin pterygiophores with the underlying vertebrae. The notation consists of an initial digit that indicates the interneural space (space between neural spines of the vertebrae) into which the first pterygiophore is inserted (i.e., the starting point of the spinous dorsal fin in relation to the vertebral column). Following the initial digit is a series of numbers in parentheses. Each digit within the parentheses represents an interneural space, and the digit is the number of pterygiophores that insert into that space. All the interneural spaces between the origin of the spinous dorsal fin and the origin of the soft dorsal fin are accounted for in the formula. For example, the notation for *Microgobius signatus* (Fig. 11) is written as 3(221110). Starting with the third interneural space, the pterygiophores are inserted as follows: 2 pterygiophores in space 3, 2 in space 4, 1 in space 5, 1 in space 6, 1 in space 7, and 0 in space 8. The insertion of the first pterygiophore of the soft dorsal fin is implied in the formula; in this example it inserts into space 9.

The condition in which pterygiophores are present without associated spines is noted by an italicized number. For example, the formula for some specimens of *Evermannichthys silus* would be given as 3(122111), indicating that the pterygiophore inserting in interneural space 8 bears no spine. This method of indicating the arrangement of the pterygiophores is not adequate for the description of all conditions found in gobioid fishes, and it will be expanded upon in another study.

MATERIALS EXAMINED

The following list is of selected material. An additional several thousand specimens from over 300 nominal species of gobioid fishes have been examined from cleared and stained material or radiographs, and information has been drawn from these in the preparation of this paper. The standard length is given in parentheses. All material has been cleared and stained except as indicated.

Letter combinations appearing as prefixes to catalog numbers stand for the following museums and institutions: ANSP (Academy of Natural Sciences, Philadelphia); BPBM (Bernice P. Bishop Museum, Honolulu); FSU (Florida State Uni-

versity, Tallahassee); GCRL (Gulf Coast Research Laboratory, Ocean Springs, Mississippi); MCZ (Museum of Comparative Zoology, Harvard University); MHNLS (Museo Historia Natural La Salle de la Estación de Investigaciones Marinas de Margarita, Venezuela); ODU (Old Dominion University, Norfolk, Virginia); SIO (Scripps Institute of Oceanography, La Jolla, California); (SU Stanford University, collections now deposited at the California Academy of Sciences, San Francisco); UCLA (University of California at Los Angeles); UF (Florida State Museum, University of Florida, Gainesville); UMML (University of Miami, Rosenstiel School of Marine Sciences, Miami); UPR (University of Puerto Rico, Institute of Marine Biology, Mayagüez); and USNM (U.S. National Museum of Natural History, Washington, D.C.).

- Microgobius signatus* ANSP 105182, 5 males (40.1-52.0), 7 females (41.0-47.0), Caribbean, Venezuela; MCZ 27130, 8, radiograph, Caribbean, Cuba.
- Microgobius microlepis* UMML 11821, 1 female (28.8), Atlantic, Fla.; UMML 11814, 1 male (32.5), Atlantic, Fla.; UMML 24737, 3(23.3-29.7), radiograph, Atlantic, Fla.; UMML uncat., 22, radiograph, Atlantic, Fla.
- Microgobius gulosus* UMML 8795, 3 males, 3 females (25.4-31.5), 56(20.3-29.7), radiograph, Gulf of Mexico, Fla.
- Microgobius thalassinus* UMML 8808, 2 males (27.2-28.7), 1 female (27.0), Gulf of Mexico, Fla.; USNM 116649, 10, radiograph, Atlantic, N. C.
- Microgobius carri* UMML 7581, 1 male (26.5), Atlantic, Fla.; UMML uncat., 1 male (32.0), 1 female (28.5), Atlantic, Fla.; FSU 18792, 7(34.3-54.8), radiograph, Gulf of Mexico, Fla.
- Microgobius meeki* UPR 2361, 1 male (25.9), Caribbean, Puerto Rico; UPR 2398, 2(14.7, 16.0), Caribbean, Puerto Rico; MHNLS uncat., 1 female (31.8), Caribbean, Venezuela; USNM 49367, 1 male (29.1), holotype, radiograph, Caribbean, Puerto Rico.
- Microgobius emblematicus* USNM uncat., 1 male (36.2), 1 female (36.9), Pacific, Panama; UCLA W54-41, 3, radiograph, Golfo de Nicoya, Mex.; UMML 24746, 10(16.3-26.3), radiograph, Pacific, Panama.
- Microgobius brevispinis* SIO 62-106, 1 male (52.0), 2 females (61.5-62.7), Pacific, Baja Calif.; UMML 23810, 1 (14.9), Pacific, Panama; SIO 62-719, 35(24.5-63.7), radiograph, Pacific, Baja Calif.
- Microgobius tabogensis* USNM uncat., 1 male (33.2), 1 female (37.0), Pacific, Panama; UCLA W52-254, 1 male (39.9), 1 female (39.2), Pacific, Baja Calif.; USNM 81844, 1 female (36.2), radiograph, holotype, Pacific, Panama; SIO 64-84, 9, radiograph, Pacific, Baja Calif.
- Microgobius curtus* UMML 23812, 1 female (36.1), radiograph, Pacific, Panama; UMML 23813, 1 female (39.4), radiograph, Pacific, Panama; UMML 23811, 1 male (39.3), radiograph, Pacific, Panama.
- Microgobius erectus* SIO 64-740, 1 male (36.9), 1 female (36.7), Pacific, Panama; SIO 64-354, 7, radiograph, Pacific, Panama.
- Microgobius cyclolepis* SIO 64-875, 1 male (49.7), 1 female (49.0), 23 specimens radiographed, Pacific, Baja Calif.
- Microgobius miraflorensis* UCLA W52-44, 1 male (36.9), 1 female (31.9), 17 specimens radiographed, Gulf of Calif., Mex.
- Microgobius crocatus* GCRL uncat., No. 1356, 1 male (29.3), 1 female (37.2), Pacific, El Salvador; USNM 202587, 1 male (30.6), radiograph, holotype, Pacific, Panama.
- Aruma histrio* USNM 167583, 2(37.5, 39.6), radiograph, Gulf of Calif.
- Barbulifer antennatus* USNM 202375, 2, radiograph, Caribbean, Barbados.
- Barbulifer pantherinus* USNM 167580, 2(28.9, 33.8), radiograph, Pacific, Mex.
- Bollmannia boqueronensis* UMML uncat., P-751, 1 male (45.0), 1 female (35.2), Atlantic, Venezuela; USNM 49366, 1(70.0), radiograph, holotype, Caribbean, Puerto Rico.

- Bollmannia chlamydes* USNM 93825, 1 male (75.0), radiograph, lectotype, Pacific, Colombia; USNM 41158, 1 female (80.5), radiograph, paralectotype, Pacific, Colombia.
- Bollmannia communis* USNM 119873, 1 (83.2), radiograph, holotype, Gulf of Mexico, La.; USNM 119889, 2, radiograph, paratypes, Gulf of Mexico, Tex.
- Bollmannia litura* UMML 21840, 1 male (47.5), Atlantic, Venezuela; UMML uncat., P-723, 1 male (46.2), 1 female (49.3), Atlantic, Venezuela; USNM 93797, 1 male (39.0), radiograph, holotype, Caribbean, Dominican Republic.
- Bollmannia umbrosa* USNM 107289, 4, radiograph, paratypes, Pacific, Panama.
- Chriolepis benthonis* USNM 47671, 1(31.4), radiograph, holotype, Caribbean, Mex.
- Chriolepis fisheri* SU 37262, 1(18.8), radiograph, holotype, Caribbean, Barbados.
- Chriolepis tagus* USNM 123232, 1(16.4), radiograph, holotype, Pacific, Galapagos.
- Eleotrica cableae* USNM uncat., S. E. P. B. O. P.—HA110, 4(35.6-46.2), radiograph, Pacific, Galapagos.
- Eynpnias aceras* USNM 81835, 1(37.5), radiograph, paratype, Pacific, Panama.
- Eynpnias seminudus* UMML 23457 2(24.3, 26.0), Pacific, Panama.
- Evermannichthys convictor* ANSP 111863, 2(14.8, 15.7), radiograph, paratypes, Atlantic, Bahamas.
- Evermannichthys metzelaari* ANSP 111869, 1(25.2), radiograph, Atlantic, Bahamas.
- Evermannichthys silas* ANSP 111868, 1 male (15.5), paratype, Atlantic, Bahamas; ANSP 111866, 7(14.5-18.9), radiograph, paratypes, Atlantic, Bahamas.
- Evermannichthys spongicola* ANSP 110897, 1(20.0), Atlantic, N. C.
- Gobiosoma bosci* ODU 68-2, 2 males (28.5, 34.1), 2 females (29.0, 29.5), Chesapeake Bay, Va.
- Gobiosoma macrodon* UMML 1612, 2(25.1, 26.2), Atlantic, Fla.
- Gobiosoma nudum* UMML 23454 2(20.0, 22.5), Pacific, Panama.
- Gobiosoma polyporosum* UMML 24452, 1(27.9), radiograph, paratype, Pacific, Panama.
- Gobiosoma puncticulatum* UMML 23472, 1 male (27.3), Pacific, Panama.
- Gobiosoma robustum* UMML 314, 1 male (24.7), 1 female (24.0), Atlantic, Fla.
- Gobulus crescentalis* MCZ uncat., IR-116, 1(21.8), radiograph, Pacific, Panama.
- Gobulus hancocki* USNM 107192, 1(29.0), radiograph, holotype, Pacific, Panama.
- Gobulus myersi* USNM 107283, 1(27.0), radiograph, holotype, Gulf of Mexico, Cape Sable.
- Gymneleotris seminudus* UMML 13663, 2(31.0, 31.6), radiograph, Pacific, Panama.
- Palatogobius paradoxus* UMML 23118, 1 male (26.3), Caribbean, Panama.
- Pariah scotius* ANSP 111861, 2(21.5, 24.4), paratypes, Atlantic, Bahamas; ANSP 111855, 1(16.3), radiograph, holotype, Atlantic, Bahamas; ANSP 111856, 1(10.5), radiograph, paratype, Atlantic, Bahamas; ANSP 111857, 1(18.5), radiograph, paratype, Atlantic, Bahamas; ANSP 111859, 2(17.4, 19.4), radiograph, paratype, Atlantic, Bahamas.
- Parrella fusca* USNM 107295, 1(30.4), radiograph, holotype, Pacific, Panama.
- Parrella macropteryx* UMML uncat., P-723, 1(38.9), Caribbean, Venezuela; UMML 22879, 1, radiograph, Caribbean, Colombia.
- Parrella maxillaris* UMML uncat., Argosy-55, 1 female (23.8), Pacific, Ecuador; USNM 119901, 1, paratype, radiograph, Gulf of Calif.
- Parrella spilopteryx* USNM 107293, 1 male (52.0), radiograph, holotype, Pacific, Panama.
- Psiлотris batrachodes* UMML 9460, 1(10.3), radiograph, paratype, Caribbean, British Honduras.
- Psiлотris celsus* UMML 12926, 1(14.3), radiograph, Atlantic.
- Pycnomma roosevelti* USNM 108139, 1(15.6), radiograph, holotype, Caribbean, Old Providence Is.; USNM 107108, 1(13.9), radiograph, paratype, same locality.
- Pycnomma semisquamatum* SIO 65-273, 4(31.5-34.3), radiograph, Gulf of Calif, Mex.
- Tukugobius carpenteri* USNM 143819, 2 males (40.0-49.0), 2 females (36.9-37.6), Indo-Pacific, Philippine Is.

Varicus bucca USNM 143022, 1(19.2), radiograph, paratype, Caribbean, Cuba.
 ADDITIONAL COMPARATIVE MATERIAL: *Asterropteryx semipunctatus* USNM 161220, Philippine Is.; *Bostrichthys sinensis* USNM 57693, Japan; *Butis gymnopomus* USNM 161177, Borneo; *Chasmichthys dolichognathus* USNM 70754, Japan; *Chloea morarana* USNM 71445, Japan; *Coryphopterus glaucofraenum* ODU uncat., Fla.; *Dormitator maculatus* UMML 5641, Fla.; *Erotelis armiger* UMML uncat., Panama; *Eviota abax* USNM 71405, Japan; *Glossogobius giurus* USNM 99733, Philippine Is.; *Gnatholepis thompsoni* UMML 12668, Fla.; *Gobiodon citrinus* USNM 166998, Egypt; *Gobiomorphus huttoni* ODU uncat., New Zealand; *Gymnogobius macrognathus* USNM 105175, Vladivostok, USSR; *Hypseleotris modestus* USNM 161198, Philippine Is.; *Ioglossus calliurus* UMML 18893, Fla.; *Lophogobius cyprinoides* ODU uncat., Fla.; *Microdesmus floridanus* UMML 20257, Fla.; *Periophthalmus cantonensis* USNM 161015, Philippine Is.; *Ptereleotris heteropterus* BPBM uncat., Hawaii; *Sicydium plumieri* UMML 1867; *Trypauchen vagina* ODU uncat., India; *Typhlogobius californiensis* MCZ 33181, Calif.; *Zonogobius semidoliatus* USNM 160966, Philippine Is.

OSTEOLOGY OF *Microgobius signatus* POEY

HEAD REGION

VOMER (FIGS. 1A, 2, 3).—The toothless vomer (V) is a dorsoventrally flattened bone, anteriorly broadened and posteriorly produced into a narrow process. The posterior process is overlapped by, and closely joined to, the anterior extension of the parasphenoid (PS). The broad, anterior portion of the vomer is completely overlain by the ethmoid cartilage.

MEDIAN ETHMOID (FIGS. 1, 2, 3, 8).—The large complex median ethmoid bone (ME) is dorsally overlapped by the frontals (F) and ventrally joined through cartilage to the parasphenoid (PS). The anterolateral surfaces are synchondrally joined to the respective lateral ethmoids (LE). The anterior face is produced into two transverse shelves to form a deep groove into which the posteromedial portion of the ethmoid cartilage is inserted. On its dorsal surface two small projections serve as points of attachment for the maxillary-ethmoid ligaments (Fig. 8). A thin, bilaminar sheet of bone projects ventrally from the midline of the median ethmoid and forms a partial septum between the orbits anteriorly. The superior and inferior oblique eye muscles originate on the median ethmoid just anterior to the median septum.

LATERAL ETHMOID (FIGS. 1B, 2, 3, 8).—The paired lateral ethmoids (LE), (prefrontals of Starks 1901) are laterally projecting fan-shaped bones that form the major portion of the anterior walls of the orbits. The lateral ethmoid forms a syndesmotic joint with the anterolateral surface of the median ethmoid (ME). Anteromedially, there is a small shelf that articulates with the ethmoid process of the palatine (PAL). At its lateroventral corner the lateral ethmoid articulates with the lacrymal (LAC).

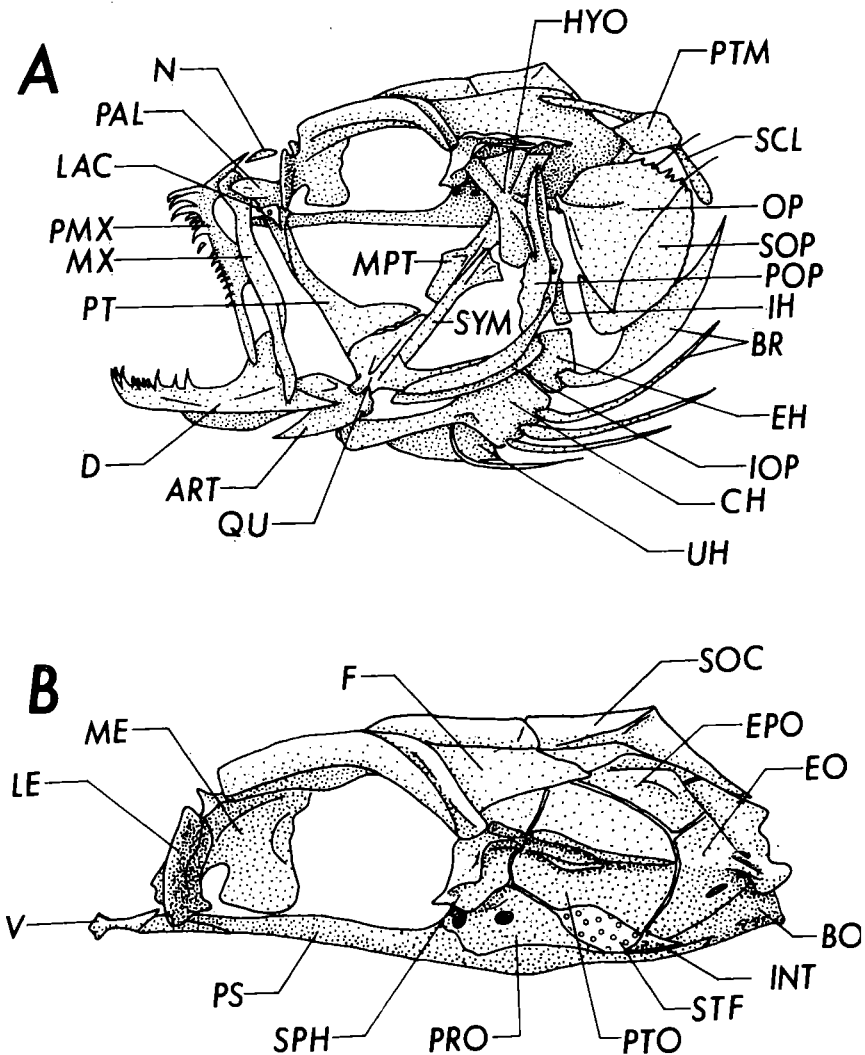


FIGURE 1.—Skull of *Microgobius signatus*. A) articulated skull (lateral view), B) cranium (lateral view).

FRONTAL (FIGS. 1B, 2A, 4).—The frontal bones (F), paired in more generalized gobioids, form a synostosis where they meet along the midline. The fused frontals are narrow between the orbits, but broaden posteriorly to form most of the anterior half of the cranial roof. Each lateral margin bears a deep trough that carries the supraorbital laterosensory canal. Between the orbits the supraorbital troughs lie parallel and share a common wall along the midline. Posteriorly, the troughs

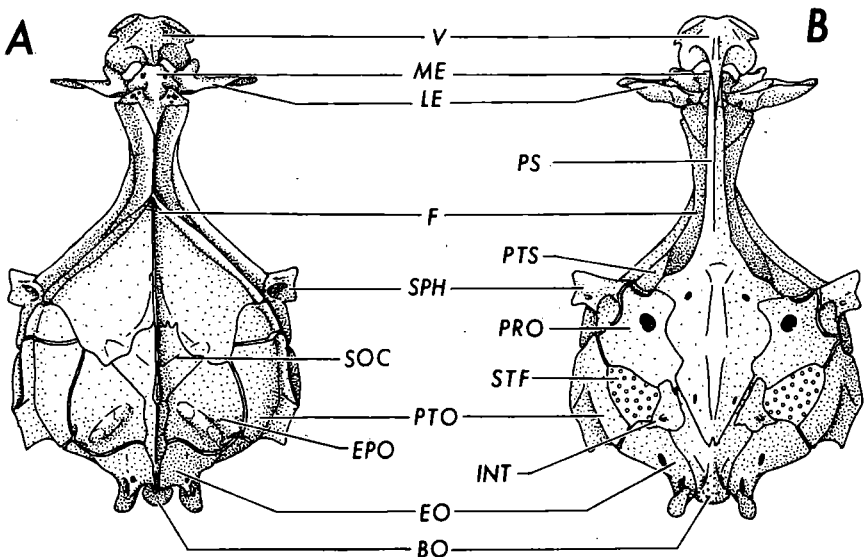


FIGURE 2.—Cranium of *Microgobius signatus*. A) dorsal view, B) ventral view.

diverge in an inverted "Y" shape. Starting at the divergence of the troughs and running posteriad, the frontals form a sagittal crest that is confluent with the sagittal crest of the supraoccipital bone (SOC). The frontal overlaps the median ethmoid (ME) anteriorly and the sphenotic (SPH), pterotic (PTO), epiotic (EPO), and supraoccipital posteriorly. On its ventral surface, near the posterior portion of the orbit, the frontal forms a synarthrosis with the pterosphenic (PTS).

SPHENOTIC (FIGS. 1A-B, 2, 4).—The paired sphenotic bones (SPH) form the posterolateral margins of the orbits. The sphenotic is overlapped by the frontal bone (F) dorsally and synchondrally joined to the pterosphenic (PTS) anteromedially, the prootic (PRO) ventromedially, and the pterotic (PTO) posteriorly. The ventral surface of the sphenotic bears a shallow articular fossa for articulation with the anterior condylar surface of the hyomandibular (HYO). A small foramen pierces the laterally extending wing of the sphenotic. Two shelves of bone along the lateral surface, above and posterior to the wing, form a short trough that houses the anterior portion of the postorbital laterosensory canal (lateral canal of Böhlke and Robins 1968). The trough is continuous with the supraorbital trough of the frontal bone anteriorly and the postorbital trough of the pterotic posteriorly.

PTEROTIC (FIGS. 1A-B, 2, 4).—Each pterotic bone (PTO) forms the posterolateral wall of the cranium. The pterotic is synchondrally joined to the sphenotic (SPH) and prootic (PRO) anteriorly, the epiotic (EPO)

dorsomedially, and the exoccipital (EO) posteriorly. It is slightly overlapped by the frontal (F) at its dorsomedial edge and adjoins the subtemporal fossa (STF) along its ventromedial margin.

Two shelves of bone extend laterally from the pterotic forming a trough continuous with that of the sphenotic and housing the posterior portion of the postorbital laterosensory canal. The two shelves run roughly parallel from the anterior margin to about midway along the bone, where they merge to form a single shelf that continues to the posterior margin of the pterotic. The anteroventral surface of the lower shelf possesses a shallow fossa for the articulation of the posterior condylar surface of the hyomandibular (HYO). The main body of the pterotic (excluding the lateral shelves) is bilaminar with cartilage between the laminae. On its internal surface, parallel to the external shelves, the pterotic takes the form of a bony passage which houses the horizontal semicircular canal. Supratemporal bones are absent.

EPIOTIC (FIGS. 1B, 2A, 5).—The bilaminar epiotic (EPO) bones form a major portion of the posterior cranial roof, occupying not only the epiotic area, but that area usually occupied by the parietals. The parietal bones are apparently absent in all gobioid fishes (Regan 1911, Gregory 1933, Gosline 1955, McAllister 1968).

The epiotic forms a synchondral joint with the pterotic (PTO) laterally, the exoccipital (EO) posteriorly and with its fellow along the cranial midline beneath the supraoccipital (SOC). At the junction of the pterotic, basioccipital (BO), and epiotic, the epiotic bears a small posterolaterally directed process that articulates with the dorsal arm of the posttemporal (PTM). The epiotic is overlapped anteromedially by the frontal (F) and supraoccipital bones.

On the internal surface the epiotic is formed into a short canal that houses the posterior vertical semicircular canal. The location of the canal is evident on the external surface as a broad, posterolaterally oriented ridge.

SUPRAOCCIPITAL (FIGS. 1B, 2A, 3).—The supraoccipital bone (SOC) occupies the posteromedial area of the cranial roof. Along its anterior margin the supraoccipital is rather broadly overlapped by the frontals (F). Along its posterolateral margins it overlaps the epiotics (EPO) and exoccipitals (EO). Along its midline the supraoccipital sends up a sagittal crest that is continuous with the sagittal crest of the frontal bones.

EXOCCIPITAL (FIGS. 1B, 2, 5).—The bilaminar exoccipital bones (EO) form most of the posterior cranial wall and the walls, roof, and floor of the foramen magnum. The exoccipitals are synchondrally joined along

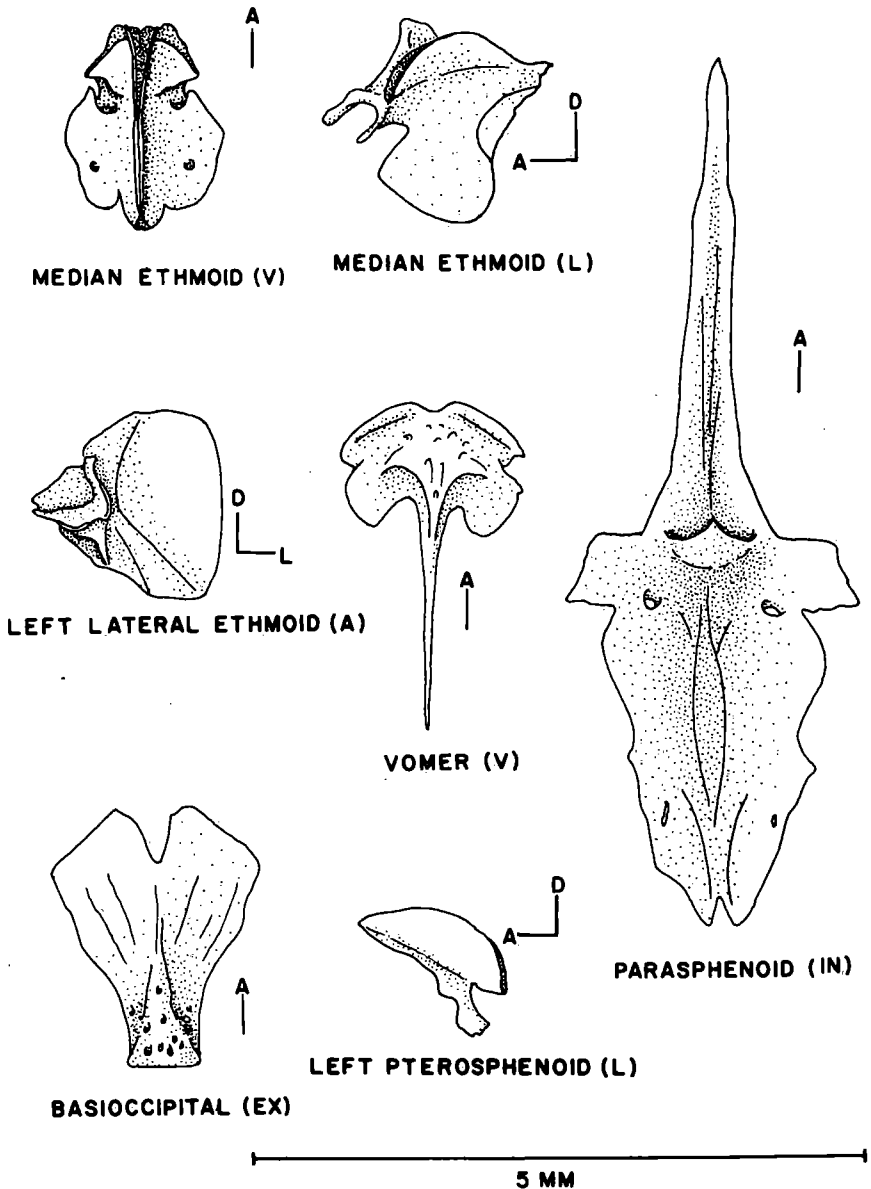


FIGURE 3.—Disarticulated cranial bones of *Microgobius signatus*.

the dorsal midline of the cranium, the joint being overlapped for most of its extent by the supraoccipital (SOC). Ventromedial projections of each exoccipital meet along the midline of the floor of the foramen magnum, thus overlapping the basioccipital and excluding it from par-

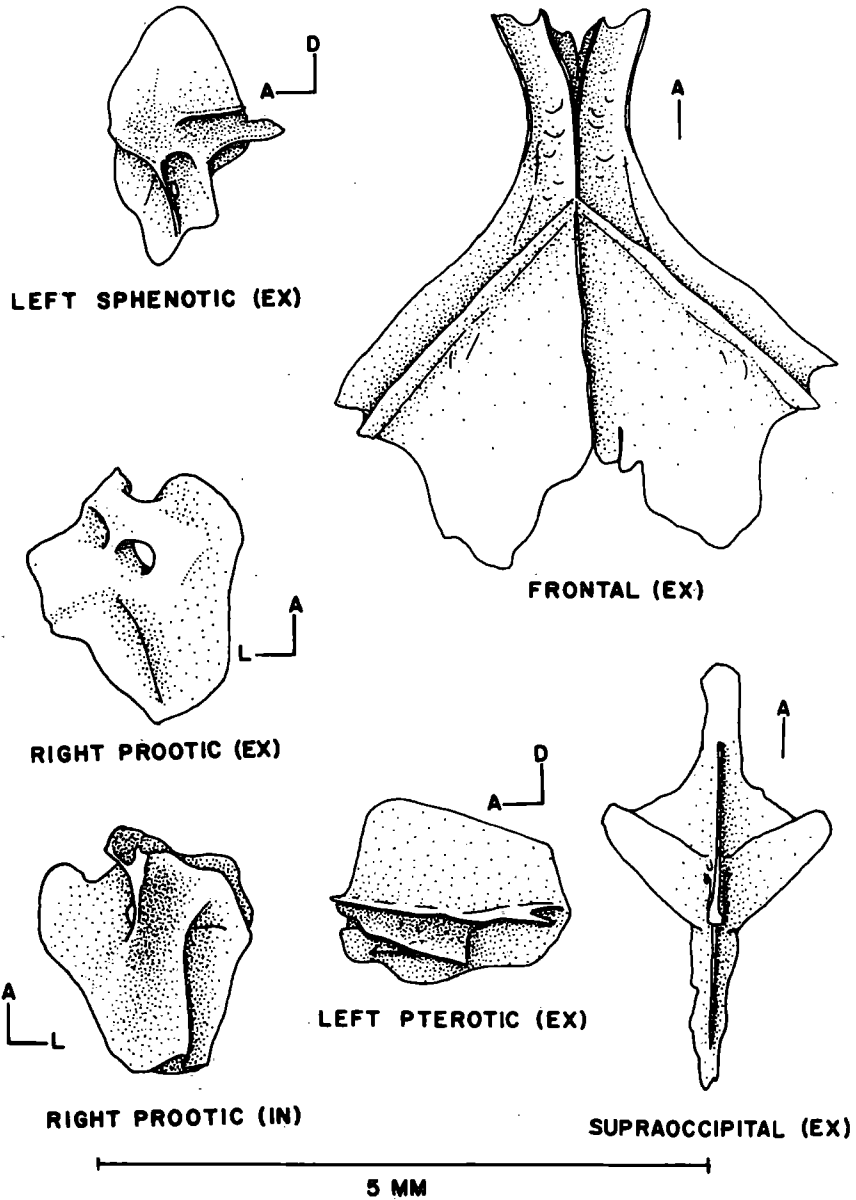


FIGURE 4.—Disarticulated cranial bones of *Microgobius signatus*.

ticipation in the foramen magnum. Along its dorsoanterior margin the exoccipital forms a synchondral joint with the epiotic (EPO); a similar joint is formed with the pterotic (PTO) along the exoccipital lateral margin. The exoccipital appears to form a suture with the basioccipital

along the exoccipital's ventromedial margin. The ventroanterior margin of the exoccipital forms the posterior boundary of the subtemporal fossa (STF). At the anterior extent of the exoccipital-basioccipital joint the exoccipital is narrowly overlapped by the intercalar (INT).

Posteriorly the exoccipital forms a posteroventrally directed condyle, that articulates with the first vertebral centrum. A lateral bridge of bone runs from the body of the exoccipital to the condyle, thus obscuring the vagal foramen from lateral view. Dorsal to the condyle, a small foramen forms a passageway to the recess housing the vagal foramen. The large glossopharyngeal foramen pierces the ventrolateral wall of the exoccipital anterior to the vagal foramen.

Internally, as viewed through the foramen magnum, the exoccipital bears a thin ventromedially directed strut of bone with an expanded foot that is joined to a dorsally projecting fold of the internal lamina of the basioccipital (BO). The recess formed between the lateral wall of the exoccipital and the strut houses the asteriscus. The asteriscus thus rests on the basioccipital, is medially confined by the exoccipital strut and the fold of the basioccipital, and is laterally confined by the wall of the exoccipital.

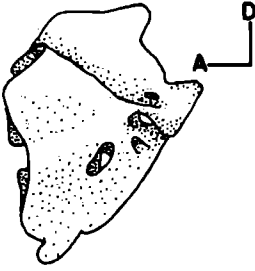
BASIOCCIPITAL (FIGS. 1B, 2, 3).—The basioccipital bone (BO) forms the posteromedial cranial floor. The bone is bilaminar (at least anteriorly) and approximately Y-shaped in ventrodorsal aspect. The arms of the Y project anteriorly, while the stem projects posteriorly as the large circular centrum-like surface articulating with the centrum of the first vertebra. The basioccipital-exoccipital joint was described above.

Along the anterior margin of each arm of the Y the basioccipital forms a synchondral joint with the respective prootic (PRO). Internally, the basioccipital arms form dorsally-projecting and divergent folds of the inner lamina that are continuous with similar folds on the respective prootic bones. Additionally, the anterior portion of the basioccipital is overlapped laterally by the intercalars (INT) and medially by the parasphenoid (PS), thus obscuring the notch between the basioccipital arms and most of the basioccipital-prootic joints from external view.

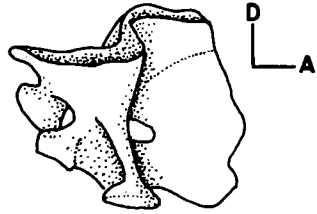
On each posterolateral surface of the articular extension the basioccipital receives a Baudelot's ligament.

INTERCALAR (FIGS. 1B, 2B, 5).—The paired intercalars (INT) are small thin bones applied to the ventral surface of the cranium and separated by (but not touching) the posterior portion of the parasphenoid (PS). Anteriorly the intercalar slightly overlaps the prootic (PRO), and posteriorly it overlaps the exoccipital (EO) and basioccipital (BO). The lateral margin of the intercalar forms the medial boundary of the

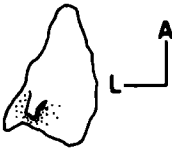
A



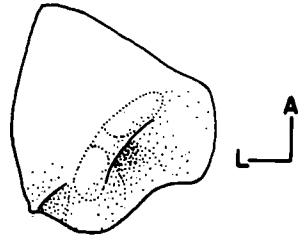
LEFT EXOCCIPITAL (EX)



LEFT EXOCCIPITAL (IN)

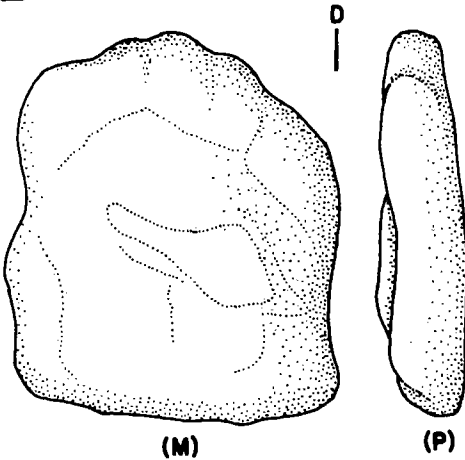


RIGHT INTERCALAR (EX)

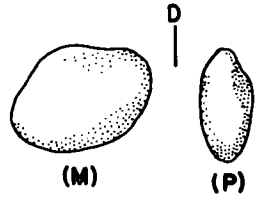


LEFT EPIOTIC (EX)

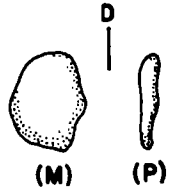
B



SAGITTA



LAPILLUS



ASTERISCUS



FIGURE 5.—A) Disarticulated cranial bones of *Microgobius signatus*, B) Otoliths of *Microgobius brevispinis*.

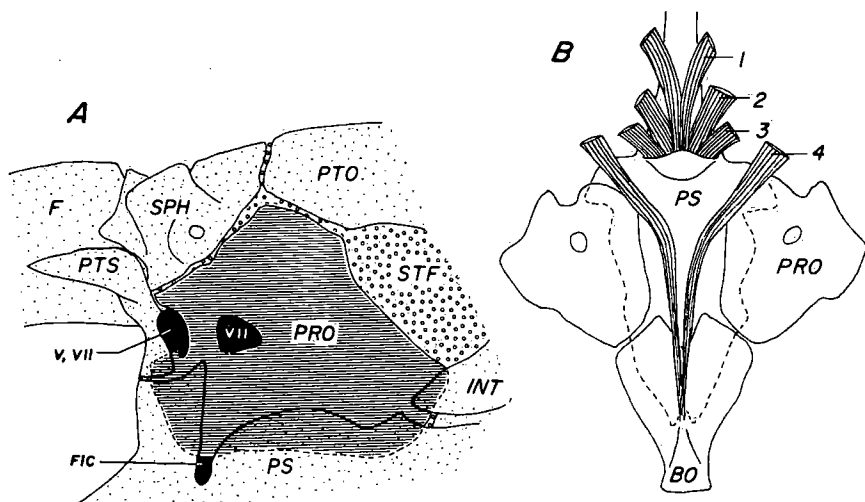


FIGURE 6.—*Microgobius signatus*. A) Left prootic and surrounding bones in ventrolateral view, B) Internal view of parasphenoid and surrounding bones showing the origins of the rectus muscles of the eyes: (1) medial rectus; (2) inferior rectus; (3) superior rectus; (4) lateral rectus.

subtemporal fossa (STF). The intercalar bears no foramen as reported in *Eleotris fuscus* by Freihofner (1970: 253).

Near its posterior margin the intercalar bears a posterolaterally directed process to which the ventral arm of the posttemporal (PTM) (See Fig. 10A) is ligamentously attached.

SUBTEMPORAL FOSSA (FIGS. 1B, 2B).—The paired subtemporal fossae (STF) are large cartilagenous areas of the posterolateral floor of the cranium. Each fossa is bound by the prootic (PRO) anteriorly, exoccipital (EO) posteriorly, intercalar (INT) medially, and the pterotic (PTO) laterally. The large sagitta rests on, and is plainly visible through, the subtemporal fossa.

PROOTIC (FIGS. 1B, 2B, 4, 6).—The paired prootic bones (PRO) form the anterolateral floor of the brain case. Laterally the prootic forms synchondral joints with the sphenotic (SPH) and the pterotic (PTO); posteriorly it forms the anterior margin of the subtemporal fossa (STF) and is overlapped by the intercalar (INT) posteromedially and the parasphenoid (PS) medially.

The anterior margin of the prootic is deeply notched in anteroventral view. This notch forms the ventral and lateral walls of the large anterior trigemino-facial foramen. The dorsal margin of this foramen is formed by the pterosphenoid (PTS), which bridges the notch. The pterosphenoid overlaps the prootic on the medial side of the notch and forms a

synchondral joint with the prootic on the lateral side of the notch. The prootic is also pierced by the large facial foramen, which is just posterior to the trigemino-facial foramen. Both of these foramina open directly into the brain cavity, and there is no formation of a pars jugularis.

The internal lamina of the prootic is formed into a dorsally-projecting fold that is continuous with a similar fold on the basioccipital. The fold serves to laterally bound the utriculus, which lies in a recess on the floor of the prootic.

PTEROSPHEOID (FIGS. 2B, 3, 6).—The paired pterosphenoïd bones (PTS) (dermosphenotic of Miller 1963: 226, alisphenoid of Matsubara and Iwai 1959: 31, and Miller 1973: 399) lie beneath the frontal bones (F) near the posterior ends of the orbits. The pterosphenoïd is composed of a bilaminar, roughly semicircular "body" with a ventromedially projected process. The body of the pterosphenoïd is synchondrally joined to the frontal, sphenotic (SPH) and prootic (PRO) bones. The ventromedial process is synchondrally joined to the parasphenoid (PS) and overlaps a portion of the prootic. The participation of the pterosphenoïd in the formation of the trigemino-facial foramen and its relationship to the prootic have been described above.

PARASPHEOID (FIGS. 1B, 2B, 3, 6).—The parasphenoid (PS) forms much of the medial floor of the skull. Anteriorly the parasphenoid is produced into a narrow process that separates the orbits and, at its anterior extent, overlaps the posterior process of the vomer (V). The parasphenoid overlaps the prootics (PRO) laterally and the basioccipitals (BO) posteriorly. Near the posterior margins of the orbits the parasphenoid is broadened to form laterally projecting wings. Each wing forms a synchondral joint with the ventromedial process of the respective pterosphenoïd (PTS).

Just posterior to the wings, near the lateral margins, the parasphenoid is pierced by two foramina for the passage of the internal carotid arteries. The formation of these foramina is variable, sometimes being formed as openings in the parasphenoid (as illustrated in Figs. 2B and 3) and sometimes as deep notches in the parasphenoid that are laterally bound by the underlying prootics (Fig. 6).

On the internal surface of the parasphenoid, at the level where the bone abruptly broadens, a thin, dorso-anteriorly directed shelf of bone is formed across the midline (Figs. 3 and 6B). The shelf is the point of origin of the medial, superior, and inferior rectus muscles of the eyes. These muscles are dorsally excluded from the brain cavity by a thick membranous sheet. The lateral rectus muscles, unlike the others, enter

the brain cavity and run posteriad along the floor to their point of origin on the basioccipital.

The basisphenoid is absent.

LACRYMAL (FIG. 1A).—The paired lacrymal bones (LAC) are the only remaining vestiges of the infraorbital series. Each thin, triangular lacrymal is loosely joined by a ligament to the ventrolateral corner of its respective lateral ethmoid (LE). A small foramen pierces the lacrymal near the anterodorsal corner.

NASAL (FIG. 1A).—The paired nasal bones (N) lie suspended in connective tissue over the ethmoid region of the skull. Each nasal forms a poorly-ossified roofless trough that is contiguous with the supraorbital trough of its respective frontal bone and houses the anterior extent of the supraorbital laterosensory canal.

OTOLITHS (FIG. 5).—The condition of the material does not permit a detailed description of the otoliths. Those figured are from a closely related species, *Microgobius brevispinis*, and resemble the otoliths of *M. signatus* at least in gross configuration and relative size.

UPPER JAW (FIGS. 1A, 7C-E, 8).—Each *premaxilla* (PMX) bears three processes: (1) an ascending process (ASC PMX), which parallels its fellow along the premaxillary symphysis; (2) a large articular process (AR PMX), which receives the medial head of the maxilla (MX); and (3) a postmaxillary process (PM PMX), which slides under the shaft of the maxilla when the jaws are closed. The premaxillary teeth are situated in two poorly-defined rows; an outer row of 6-8 large recurved caninoid teeth and an inner row of 20-30 smaller caninoid teeth.

Each *maxilla* (MX) is composed of a long thin shaft with two processes at its proximal end: a medial process (M MX) that articulates with the posteroventral surface of the articular process of the premaxilla, and a shorter lateral process (L MX) that bears a recessed lateral surface for articulation with the maxillary process of the palatine (MX PAL). Of some interest is a dorsal slip of the large adductor mandibulae, which inserts midway along the maxillary shaft. Anteriorly this slip is quite discrete, but posteriorly the fibers appear to merge with those of the main body of the adductor mandibulae. This slip of muscle appears similar to the levator maxillae superioris said by Rosen and Patterson (1969) to be characteristic of paracanthopterygian fishes.

The major ligamentous attachments of the upper jaw are described in the legend to Figure 8. In addition, other ligaments connect the posterior tip of the maxilla to (1) the anterolateral face of the dentary, (2) the coronoid process of the dentary, and (3) the posterior tip of the premaxilla.

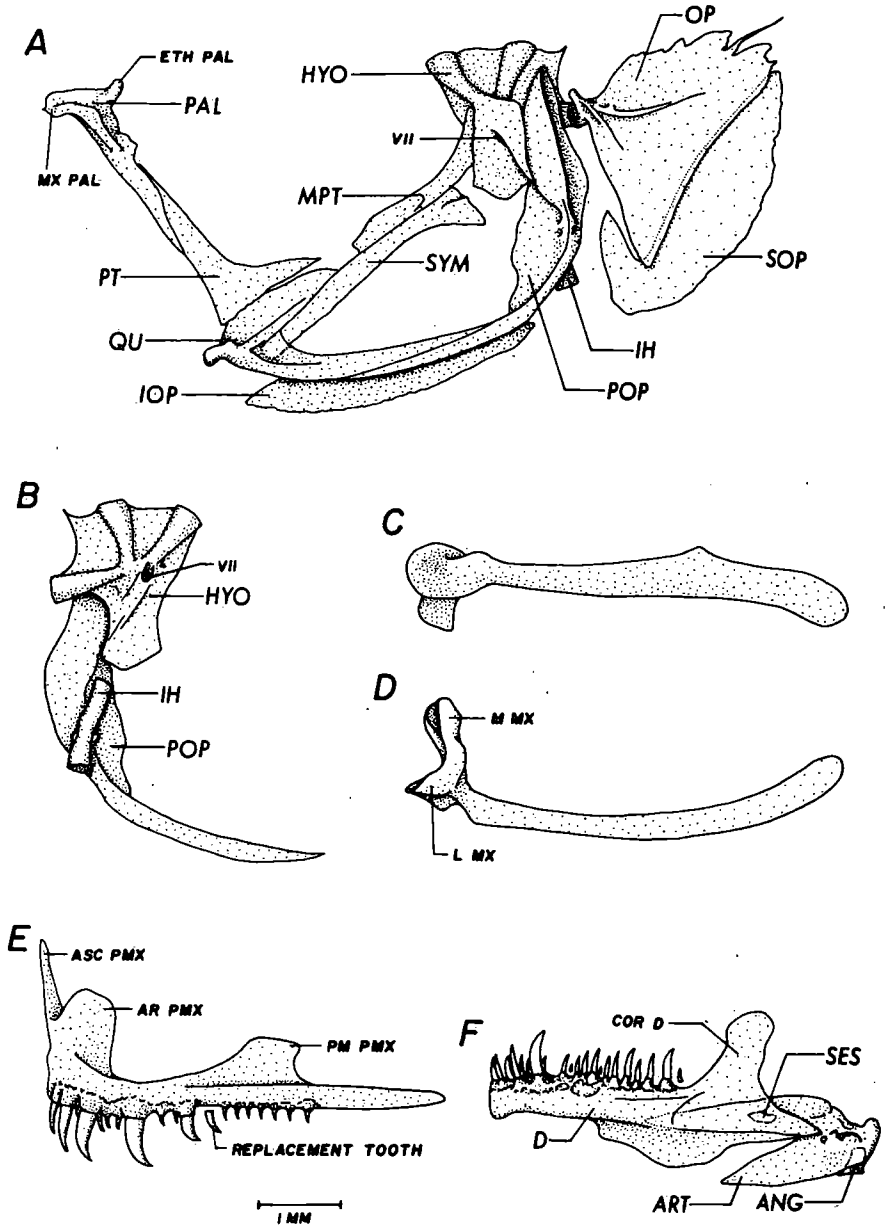


FIGURE 7.—Suspensorium, opercular bones and jaws of *Microgobius signatus*. A) articulated suspensorium and opercular bones (left lateral view), B) medial view of left hyomandibular, interhyal and preopercle, C) left maxilla (lateral view), D) left maxilla (dorsal view), E) left premaxilla, F) left articulated lower jaw bones.

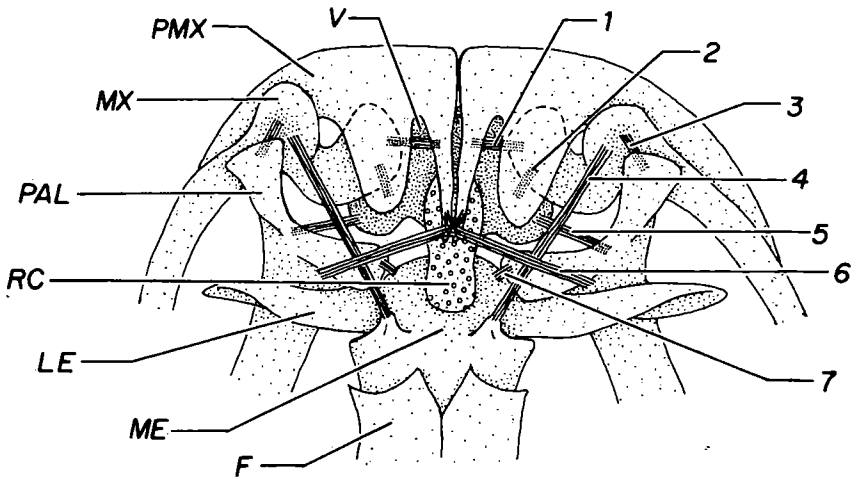


FIGURE 8.—Ligamentous attachments of the upper jaw of *Microgobius signatus* (dorsal view). Stippled lines represent portions of ligaments hidden by bone in the dorsal view. Key to ligamentous attachments: (1) base of ascending process of the premaxilla to medial head of maxilla; (2) articular process of premaxilla to medial head of maxilla; (3) lateral head of maxilla to maxillary process of palatine; (4) articular head of maxilla to dorsal projection of median ethmoid; (5) median head of palatine to postero-lateral corner of vomer; (6) trunk of palatine just below ethmoid process to midline where it joins to its counterpart and to ascending process of premaxilla; (7) ethmoid process of palatine to anterior face of median ethmoid.

LOWER JAW (FIGS 1A, 7F).—The large *dentary* (D) dominates the four bones that form each half of the lower jaw. Anteriorly, it meets its fellow at the mandibular symphysis, and posteromedially it is formed into a deep, tapering pocket that receives the dorsal ramus of the articular (ART). Posteriad, the dentary is dorsally produced into a large coronoid process (COR D), which serves as the primary point of insertion for the massive adductor mandibulae muscles common to gobioid fishes. A large shelf of bone extends ventromedially along the postero-ventral surface of the dentary. The teeth are in two poorly-defined rows; the outer row usually consisting of four enlarged caninoid teeth, and the inner row of 10-15 smaller caninoid teeth in males and 15-25 teeth in females.

Posterodorsally the *articular* bone (ART) bears a saddle-shaped articular surface that receives the articular process of the quadrate (QU). Anteriorly the articular is formed into two rami, the dorsal ramus joining it to the dentary and the ventral ramus extending anteriorly ventral to the dentary. Two small foramina pierce the articular bone just ventral to its articular surface. The slim, cylindrical *Meckel's cartilage* runs longitudinally along the concave medial face of the dorsal ramus of the articular.

Roughly midway along the medial face of the dorsal ramus a small *sesamoid articular* bone (SES) overlaps the Meckel's cartilage.

The small *angular* bone (ANG) is closely applied to the medial face of the articular at the articular's posteroventral corner.

HYOMANDIBULAR AND PALATINE ARCH (FIGS. 1A, 7A-B).—The laterally flattened hyomandibular (HYO) bears three cylindrical struts radiating from near the center of the bone, each capped with a cartilagenous articular surface. The articular terminations of the anterior and posterior dorsally directed struts articulate with the sphenotic (SPH) and pterotic (PTO) respectively. The articular termination of a posteriorly directed strut articulates with the opercle (OP). On its anterior surface the hyomandibular receives the metapterygoid (MPT). The lateral face of the hyomandibular bears a posterolaterally directed flange, thus forming a shallow recess that receives the dorso-anterior face of the preopercle (POP). The medial face of the hyomandibular bears a large foramen, which is the entrance to a short canal that exits on the lateral face just below the flange. The hyomandibular branch of the facial nerve traverses this canal.

The *metapterygoid* (MPT) is laterally expanded along its posterior face, where it is firmly joined to the hyomandibular dorsally and broadly connected to the symplectic (SYM) ventrally. The anterior face is formed into a thin, laterally flattened flange, which is sexually dimorphic in its extent with males showing a greater development than females (compare Fig. 1A, a male, Fig. 7A, a female). At its ventral end the metapterygoid is extended as an unossified cartilage that is firmly bound to the quadrate.

The *symplectic* (SYM) is a rod-shaped bone with a posteriorly projecting, laterally flattened flange on its dorsal end. The anterior face bears a shallow concavity where, dorsally, it receives the metapterygoid and, ventrally, the quadrate (QU). The ventral extremity of the symplectic is ligamentously bound to the medial surface of the posterior arm of the quadrate.

The *quadrate* (QU) is shaped roughly like a V lying on its side. Its anterior extremity, at the apex of the V, is formed into a saddle-shaped process that articulates with the mandible. The dorsal arm of the quadrate is bound posteriorly to the symplectic (SYM), anteriorly to the ectopterygoid (PT), and dorsally to the cartilagenous extension of the metapterygoid (MPT). The long, slender ventral arm of the quadrate is formed into a deep concavity along its ventral surface. This concavity receives the slender, anteroventral extension of the preopercle (POP).

The pterygoid-palatine strut of the suspensorium consists of the palatine (PAL) and a single pterygoid bone. The pterygoid bone, pre-

sumed to be the *ectopterygoid* (PT), cannot be disarticulated even upon boiling in KOH. Posteriorly, the ectopterygoid is bound to the quadrate (QU); anteriorly, it overlaps the descending process of the palatine.

The *palatine* (PAL) is a roughly T-shaped bone composed of a long descending process firmly bound by ligament to the ectopterygoid (PT), and a head formed into a medially projecting ethmoid process (ETH PAL) that articulates with the lateral ethmoid (LE), and an antero-laterally projecting maxillary process that articulates with the articular surface of the lateral process of the maxillary (L MX).

OPERCULAR SERIES (FIGS. 1A, 7A-B).—The *opercle* (OP) is approximately triangular in shape. Anteriorly, it bears a process with a concave anterior face, which articulates with the hyomandibular (HYO). On the medial surface two thickened struts of bone radiate from the base of the articular process, one running posteriorly, the other posteroventrally toward the margin. Posteriorly and ventrally, the opercle slightly overlaps the J-shaped *subopercle* (SOP). The dorsal margin of the opercle and the posterior margin of the subopercle are both poorly ossified, blending into dense membranous connective tissue that gives the bone a ragged appearance in cleared and stained specimens.

The crescent-shaped *preopercle* (POP) bears a deep groove along its dorsoposterior margin. This groove houses the preopercular portion of the laterosensory canal system. Dorsoanteriorly, the preopercle is closely bound by ligament to the hyomandibular (HYO); and ventrally, it extends forward as a slender arm, that inserts into the concaved ventral surface of the ventral arm of the quadrate. Ventral to the hyomandibular, the opercle is anteriorly expanded into a thin shelf. This shelf is well removed from the symplectic (SYM) and bears no symplectic process. Midway along the dorsoventral extent of its medial surface, the preopercle is ligamentously bound to the interhyal.

The thin, blade-like *interopercle* (IOP) lies ventromedial to the preopercle (POP) and quadrate (QU) arms. Anteriorly, the interopercle is ligamentously bound to the angular (ANG); posteriorly, it sends a short ligament to the epihyal (EH) and a longer ligament to the rather distantly removed subopercle (SOP).

HYOID ARCH (FIGS. 7A, 9C-E).—The small cylindrical *interhyal* (IH) serves as the posterior suspensory element of the lower portion of the hyoid arch. On each end it bears a cartilagenous articular cap. Ligaments bind it dorsally to the hyomandibular (HYO) and ventrally to the epihyal (EH). On its lateral surface the interhyal bears a small shelf from which a stout ligament runs to the medial surface of the preopercle (POP).

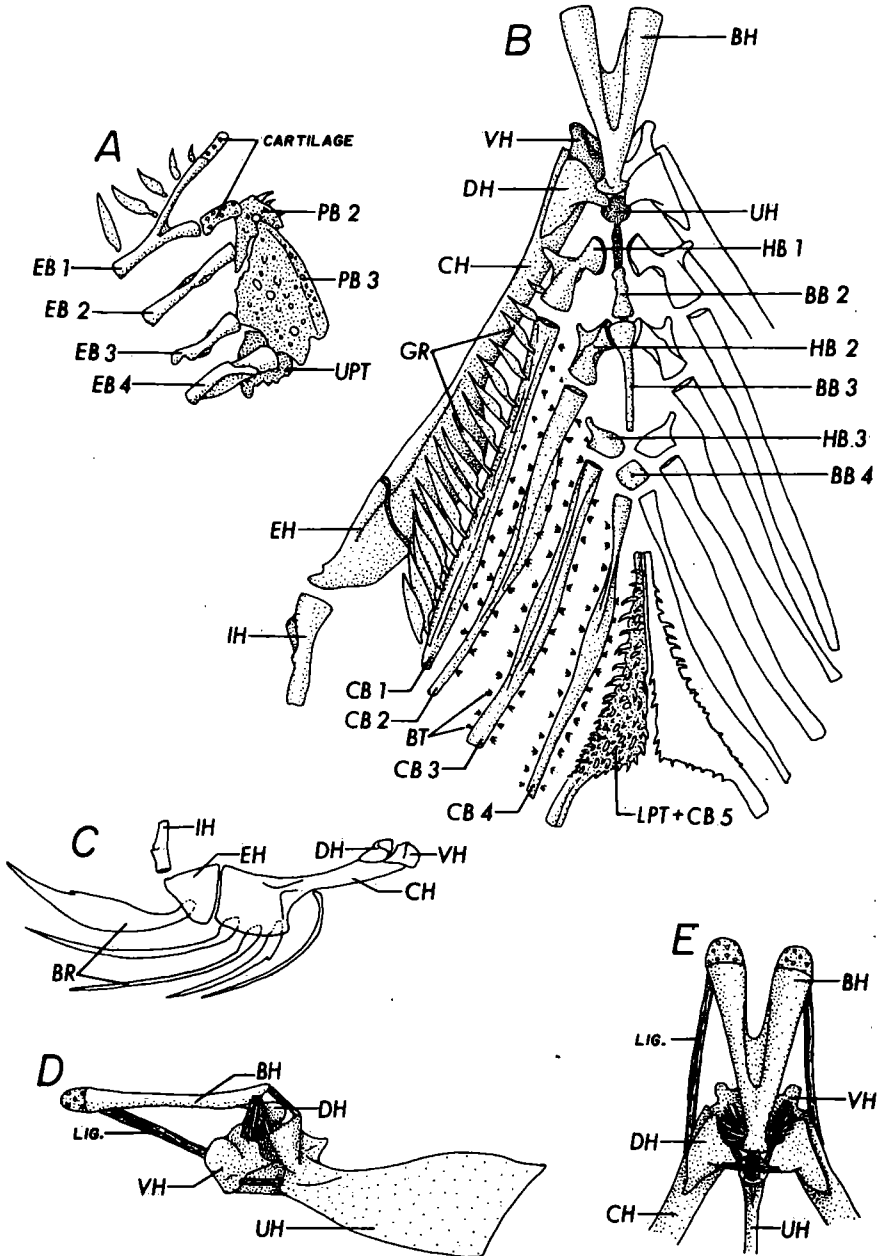


FIGURE 9.—Branchial and hyal bones of *Microgobius signatus*. A) upper branchial bones (left side, dorsal view), B) hyal and lower branchial bones (branchiostegal rays not shown), C) hyal bones (left side, medial view), D) basihyal apparatus (lateral view, left ceratohyal removed), E) basihyal apparatus (dorsal view).

The triangular *epihyal* (EH) bears an articular surface at its postero-dorsal corner where it articulates with the interhyal (IH). Anteriorly, the epihyal is synchondrally joined to the ceratohyal (CH).

In lateral view the *ceratohyal* (CH) is a cleaver-shaped bone, broad posteriorly where it joins the epihyal (EH) and abruptly narrowing roughly midway of its extent to form an anteriorly projecting "handle." Anteriorly, the ceratohyal articulates with the small dorsal and ventral hypohyals (DH and VH). There is no foramen in the ceratohyal.

There are five *branchiostegals* (B1-5). The first, a thin rib-like ray, articulates with the ventral surface of the narrow portion of the ceratohyal (CH). The next three rays are blade like and articulate with the ventrolateral surface of the broad portion of the ceratohyal. The posteriormost branchiostegal is by far the broadest and articulates with the ventrolateral surface of the epihyal (EH).

The roughly bell-shaped *dorsal hypohyal* (DH) is firmly bound to the anterodorsal surface of the ceratohyal (CH). The similarly shaped, but oppositely directed, *ventral hypohyal* (VH) caps the combined dorsal hypohyal-ceratohyal anterior face and forms a synchondral joint with both of these bones. Medially, the ventral hypohyal articulates with its mate.

The *basihyal* (BH) is the anteriormost of the two medially situated unpaired hyal bones. This V-shaped bone is formed of two divergent cylindrical struts, each anteriorly capped with a dome-shaped cartilagenous extension. A thin shelf of bone is formed across the crotch of the basihyal and the posterior tip (base of the V) is laterally expanded. The *urohyal* (UH) is a dorsoventrally broadened, laterally flattened bone lying in the midline just posteroventral to the basihyal. At the anterodorsal corner of the urohyal a cone-shaped knob projects dorsally and receives a large ligament from the posterior tip of the basihyal. Additional ligamentous attachments of the anterior portion of the hyoid arch are shown in Fig. 9D-E. This portion of the hyoid apparatus is interconnected by large amounts of thin sheet-like connective tissue, much of it difficult to discern. The ligamentous attachments illustrated represent only the most well-defined bundles of fibers.

BRANCHIAL ARCHES (FIGS. 9A-B).—The upper pharyngeal bones are represented by epibranchials 1-4 (EB), pharyngobranchials 2-3 (PB) (fused with their respective pharyngeal tooth plates), and pharyngeal tooth plate 4 (UPT). Epibranchial 1 is medially bifid with each arm bearing a cartilagenous extension. Most of the connective tissue suspending the branchial apparatus from the brain case is sheet-like and obscure in my preparations; however, one long well-defined ligamentous bundle can be seen connecting the anterior arm of epibranchial 1 with

the parasphenoid. In Figure 9 the upper and lower pharyngeal bones of the left side have been separated at the articulation of each epibranchial with the posterior tip of its respective ceratobranchial (CB).

The unpaired lower pharyngeal bones consist of *basibranchials* 2-4 (BB). Basibranchial 1 is absent and basibranchial 4 is represented by unossified cartilage.

The paired lower pharyngeal bones are represented on each side by *hypobranchials* 1-3 (HB) and *ceratobranchials* 1-5 (CB) (ceratobranchial 5 is fused with the lower pharyngeal tooth plate). The paired *lower pharyngeal tooth plates* (LPT) are contiguous but unfused along their medial margins.

The first branchial arch bears a row of ossified, blade-like gill rakers along its lateral face. The number of gill rakers (GR) varies somewhat, but typically, there is one on the hypobranchial (HB), about 15-16 on the ceratobranchial (CB), and 4-5 on the epibranchial (EB). Additionally, the medial face of ceratobranchial 1 and the medial and lateral faces of ceratobranchials 2-4 all bear a row of 10-15 patches of very small branchial teeth (BT). The patches, each bearing from three to over a dozen tiny teeth, are suspended in the connective tissue surrounding the ceratobranchials.

PECTORAL GIRDLE AND PAIRED FINS (FIG. 10A).—Each *posttemporal* (PTM) is anteriorly forked to form a dorsal and a ventral process. The processes are ligamentously bound to the epiotic (EPO) and the intercalar (INT), respectively. A blade-like *supracleithrum* (SCL) is ligamentously joined to the posteromedial surface of the posttemporal and to the dorsolateral face of the cleithrum (CL).

The *cleithrum* (CL) (clavicle of Matsubara and Iwai 1959) is an elongate, crescent-shaped bone, bifid at its dorsal end and articulating with its mate at the ventral end. Posteriorly, along the central third of its extent, the cleithrum bears a deep groove into which the scapular cartilage (SCA) is inserted. Posteroventrally, the cleithrum is produced to form a process, which is synchondrally joined to its respective pelvic bone. The central portion of the lateral surface of the cleithrum bears a pronounced flange from which the relatively large adductor muscle mass originates. Baudelot's ligament is attached to the dorsomedial face of the cleithrum at the crotch of the bifurcation. There are no postcleithra.

The completely unossified *scapula* (SCA) is represented by an elongate cartilage, which is partially concealed in the posterior groove of the cleithrum (CL). Near its dorsal end the scapula is pierced by a large foramen. Ventrally the scapular cartilage joins the coracoid (COR).

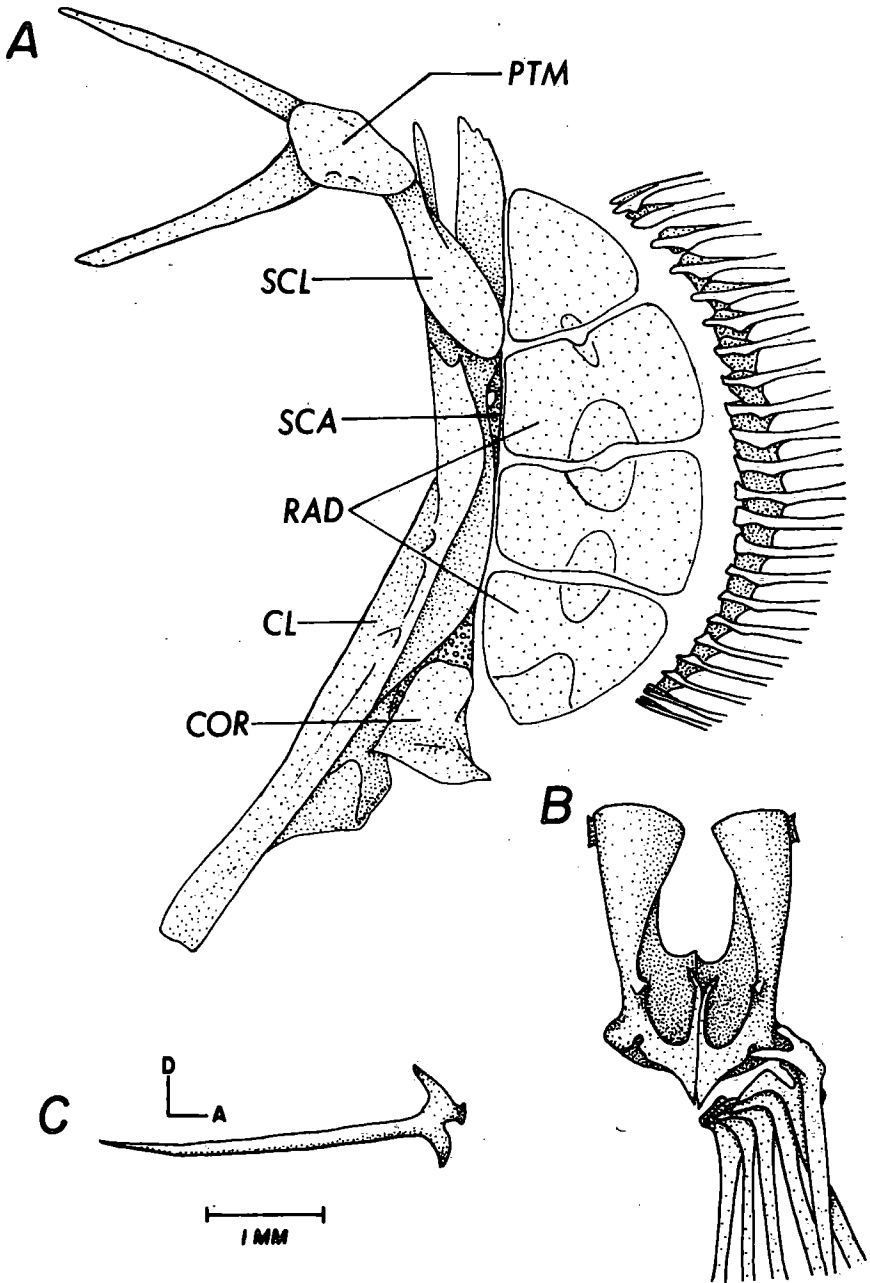


FIGURE 10.—Pectoral and pelvic girdles of *Microgobius signatus*. A) left pectoral girdle, B) pelvic girdle (ventral view, fin elements of right side not shown), C) right pelvic spine (lateral view).

The *coracoid*, a roughly bell-shaped bone in lateral view, also forms a synchondral joint with the posterior surface of the cleithrum.

There are four *radials* (RAD); the dorsal and ventralmost radials are triangular and the two central radials are roughly rectangular in shape. The radial margins are surrounded by cartilage, through which they articulate with each other and with the posterior margin of the girdle. The *pectoral rays*, usually 21-22 in number, insert on the posterior cartilagenous border of the radials. The bases of the pectoral rays, especially the central rays, are bilaterally asymmetric in structure. The medial component of each pectoral ray base bears short dorsal and long ventral flanges, which overlap with the flanges of the adjacent rays.

PELVIC GIRDLE AND FINS (FIGS 10B, C).—In dorsoventral view each *pelvic bone* is formed into a conical anterior projection, which is joined through cartilage with the pelvic process of the cleithrum (CL). Posterodorsally, the conical portion of the pelvis bears a thin medially produced shelf, which forms a symphysis with its mate at the midline. Posteriorly, the pelvic bone is dorsoventrally thickened and, medially, bears a ventro-anteriorly projected ventral process. The finger-like ventral processes of each pelvic bone are contiguous for most of their extent, but diverge near their tips.

Posteriorly, one spine and five rays are attached to the pelvic bone. The base of the pelvic spine bears three medially directed processes. A dorsal and ventral process of the pelvic spine lie over and under, respectively, the posterolateral corner of the pelvic bone. The medial process of the pelvic spine bears an articular surface at its tip and articulates with a posterolateral articular surface on the pelvic bone. The five rays articulate with the pelvic bone by means of cartilage. As in most gobiids the centralmost ray is joined to its opposite by a membrane and the opposing pelvic spines are joined by a membranous frenum.

VERTEBRAL COLUMN AND MEDIAN FINS

VERTEBRAL COLUMN (FIGS. 11, 12).—There are 11 precaudal and 16 caudal vertebrae, including the urostylar elements (US) (erroneously given as 14 + 15 by Jordan and Eigenmann 1886: 514). Caudal vertebrae (excluding the urostyle) are here differentiated from precaudal vertebrae by the absence of pleural ribs (PR) and the presence of a closed haemal arch (HS). This simple distinction is useful for most, but not all gobioids.

All vertebrae, again excluding the urostyle, bear well developed neural spines (NS) and the precaudal vertebrae bear parapophyses

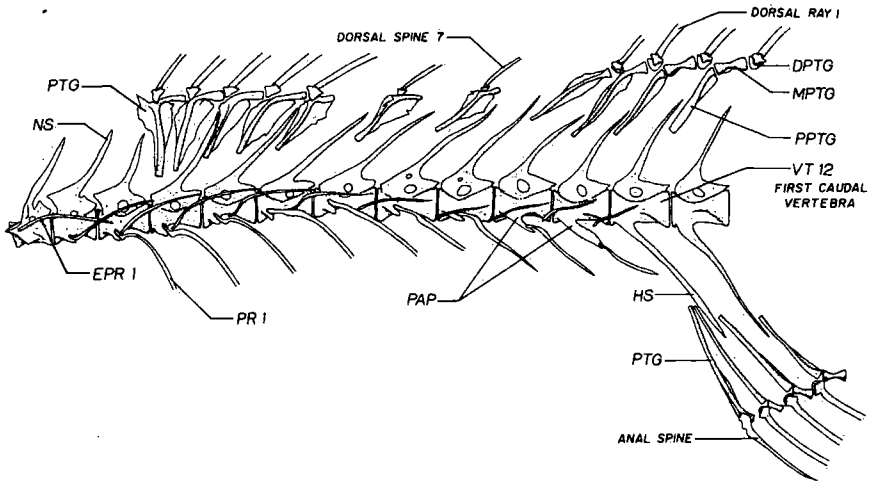


FIGURE 11.—Anterior vertebrae and median fin elements of *Microgobius signatus*.

(PAP) as well. The parapophyses of vertebrae 9-11 are progressively larger than those preceding.

The first two precaudal vertebrae bear only epipleural ribs (EPR), these articulating with parapophyses or their bases. The succeeding precaudal vertebrae (3-11) bear both pleural and epipleural ribs. The pleural ribs articulate with the parapophyses and the epipleural ribs articulate with the pleural ribs. The posterior epipleural ribs become progressively removed from their respective pleural ribs, with those on vertebrae 10 and 11 lying in connective tissue some distance posterior to their associated pleural ribs. Occasionally tiny ossified elements representing epipleural ribs 13 and 14 are found "floating" in connective tissue lateral to the two anteriormost caudal vertebrae.

The first vertebra bears lateral processes, which articulate with the condyles of the exoccipitals. The anterior face of the centrum of the first vertebra is angled slightly posteroventrally for articulation with the basioccipital (BO).

The first vertebra bears well-developed dorsal postzygapophyses. The second vertebra bears both dorsal pre- and postzygapophyses, while the third vertebra has only dorsal prezygapophyses (PZP). The dorsal zygapophyses on all of the succeeding vertebrae are poorly developed (absent on the last 3-4 caudal vertebrae). There are no ventral zygapophyses.

Each of the first 23 vertebrae bears a large foramen through each lateral wall of the neural arch. A second smaller foramen is occasionally present in one or both sides of the neural arch of some vertebrae. In

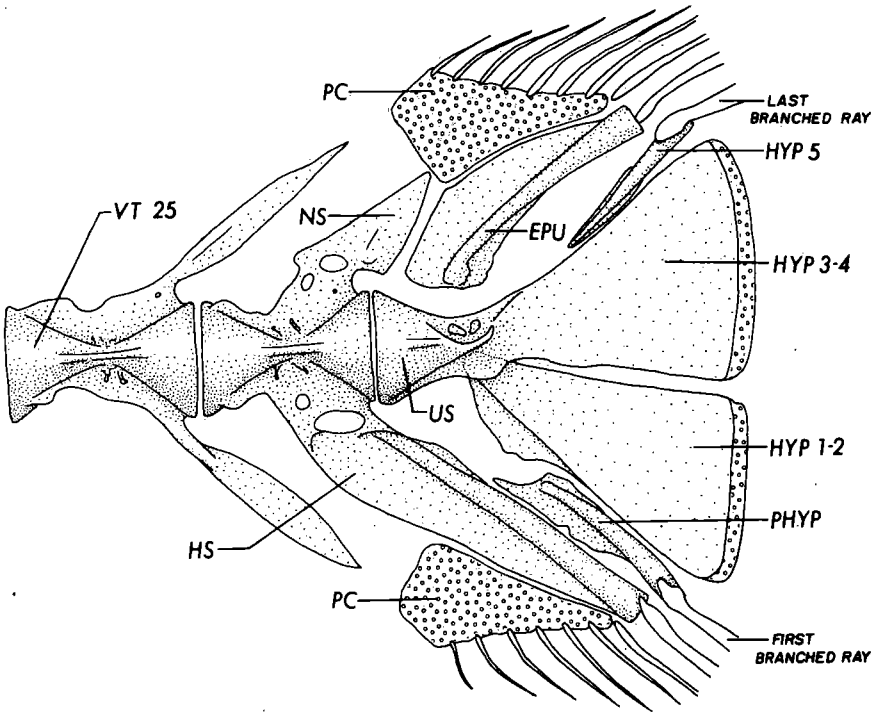


FIGURE 12.—Caudal skeleton of *Microgobius signatus* (median caudal rays not shown).

vertebrae 24 and 25 there is a single small foramen (occasionally absent) on each side of the arch.

The haemal and neural arches of vertebrae 12-22 arise from the anterior half of the centrum. On vertebra 23 the haemal and neural arches arise from a more posterior position near the center (narrow portion) of the centrum. The neural and haemal arches of vertebrae 24-26 arise from the posterior half of the centrum. The neural and haemal spines of vertebra 25 are laterally flattened and blade-like.

Vertebra 26 is somewhat modified for participation in the support of the caudal fin. The neural spine (epural 1 of Johnson 1969: 84) is short and anteroposteriorly expanded. Each lateral wall of the neural arch bears a large foramen and one or two smaller foramina are occasionally present. The haemal spine (hypural 1 of Johnson 1969: 84) is greatly elongated and formed into a cylindrical strut along its posterior margin. Each lateral wall of the haemal arch also is pierced by a large foramen, with one or two smaller foramina of various placement and size being occasionally present. The caudal artery bifurcates posterior to this

haemal spine just below the urostyle. Distally, the haemal spine receives the first segmented (but unbranched) ray.

CAUDAL FIN (FIG. 12).—The urostylar element (US) is composed of a half centrum, which is totally fused with a large fan-shaped element representing hypurals (HYP) 3-4 (hypural 4 of Johnson 1969: 84; hypural 4-5 of Miller 1973: 406). Monod (1968) says the urostylar elements of gobiid caudal fins are composed of the fusion of preural 1 with the urals. This may be correct, though I have no information bearing on the matter.

The parhypural (PHYP) (hypaxial bone of Miller 1963: 231; hypural 1 of Miller 1973: 406; lower splint-like bone of Gosline 1955: 164; hypural 2 of Johnson 1969: 84) is a small bone formed of a cylindrical strut with thin dorsal and ventral flanges. It lies between the last haemal spine and the lower hypural fan.

Hypurals 1 and 2 (hypural 3 of Johnson 1969: 84; hypurals 2-3 of Miller 1973: 406) are fused into a single fan-shaped plate that inserts anteriorly into a recess on the ventroposterior portion of the urostyle near the point of fusion of the urostyle with hypurals 3-4.

Hypural 5 (epaxial bone of Miller 1963: 231; hypural 6 of Miller 1973: 406; upper splint-like bone of Gosline 1955: 164; epural 3 of Johnson 1969: 84), similar in size and shape to the parhypural, lies just above the posterodorsal margin of hypurals 3-4. A single large epural (epural 2 of Johnson 1969: 84) lies above the urostyle just anterior to hypural 5. The epural is formed of a cylindrical strut with a large anterior and small posterior flange.

There are typically 14 branched and segmented caudal rays, which insert on the hypural plate as follows: the first ray (lowermost) on the parhypural, five rays on the cartilagenous posterior margin of hypurals 1-2, seven rays on the cartilagenous posterior margin of hypurals 3-4, and the last ray on hypural 5. Above and below the 14 branched rays there are single segmented unbranched rays inserting on the epural and last haemal spine (HS), respectively. Preceding the segmented rays, both above and below, is a series of 7-8 small segmented procurrent rays, each series inserting along the margin of a large thin sheet of cartilage. These dorsal and ventral procurrent cartilages (PC) are contiguous with the dorsal margin of the epural and ventral margin of the last haemal spine, respectively.

SPINOUS DORSAL FIN (FIG. 11).—The spinous dorsal fins are supported by seven spines, which articulate with seven pterygiophores (PTG). The proximal and medial radials of the spinous dorsal pterygiophores are totally fused, and the distal radial appears to be absent.

The number and arrangement of spinous dorsal pterygiophores is invariable. The first two pterygiophores insert into the third interneural space (space between the neural spines); the third and fourth pterygiophores insert into the fourth interneural space; and the fifth through seventh pterygiophores each insert into their respective interneural space. The sixth and seventh dorsal spines are somewhat more widely spaced than the preceding five spines. There are no predorsal bones.

SECOND DORSAL FIN.—The second dorsal fin (D_2) is composed of one spine and 19-21 soft rays, each supported by a pterygiophore (PTG) except the last two rays, which share the posteriormost pterygiophore. The two anterior D_2 pterygiophores insert into interneural spaces 9 and 10 respectively and have their proximal and medial radials fused. The proximal and medial radials are discrete in all of the remaining D_2 pterygiophores. Each of the D_2 pterygiophores bears a discrete distal radial except the last, which consists of proximal and medial radials only. Each distal radial is composed of a pair of bilateral elements, closely joined to the base of the ray. Soft dorsal pterygiophores 18-20 are inserted into interneural spaces 9-22, with interneural spaces 9-13 typically receiving only a single pterygiophore. The insertion of the remaining pterygiophores into interneural spaces 14-22 displays some individual variation, with each interneural space receiving either one or two pterygiophores; however, the last pterygiophore nearly always inserts into interneural space 22 regardless of the number of pterygiophores present.

ANAL FIN.—The anal fin is composed of one spine and 20-22 soft rays supported by 19-21 pterygiophores (PTG). The first anal pterygiophore has its proximal and medial radials fused and supports both the anal spine and the first soft ray. Each of the succeeding pterygiophores supports a single ray, except the last which supports the two final rays. The second through penultimate pterygiophores are each composed of a proximal (PPTG), medial (MPTG), and distal radial (DPTG). The distal portion is apparently absent in the last pterygiophore. The insertion of the first two anal pterygiophores is invariably anterior to the first haemal spine. The insertion of the remaining pterygiophores shows similar variation to those of the soft dorsal fin, but typically insert into the first 12 interhaemal spaces with either one or two pterygiophores per space.

DISCUSSION

The search for the relationships of *Microgobius* within the genera of seven-spined gobies has been a quest of limited reward. Before dis-

TABLE 1.—OSTEOLOGICAL CHARACTERISTICS OF THE GOBIOIDEI.

- Parietals, basisphenoid, and orbitosphenoid absent.
 Epiotic forming a synchondral joint with mate beneath the supraoccipital.
 Intercalar reduced (lost in some species).
 Infraorbital, except lacrymal, absent in most species (one reported present in 2 species of eleotrids by Akihito 1969 and in *Rhyacichthys* by Miller 1973).
 Supratemporals absent in most species (reported present in 6 species of eleotrids by Akihito 1971).
 Wide separation of the symplectic from the preopercle.
 Preopercle attached to quadrate and hyomandibular thus forming a third strut of the suspensorium.
 Symplectic dominates the symplectic-metapterygoid strut of the suspensorium in most species.
 Mesopterygoid reduced or absent.
 Interhyal ligamentously attached to preopercle.
 Branchiostegal rays 4 to 7 (usually 5).
 First basibranchial absent, fourth basibranchial present as cartilage.
 Baudelot's ligament present.
 Dorsal postcleithrum absent in all groups except the eleotrids.
 Ventral postcleithrum reduced or absent in many species.
 Scapula reduced in most species (cartilagenous in many).
 Pectoral radials 3 to 4 (usually 4).
 Vertebral number usually 25 to 27; however, may exceed 60 in some species.
 Superneurals absent.
 Number and arrangement of spinous dorsal pterygiophores highly stable within most species, usually 6 to 7.
 Penultimate vertebra with a short expanded neural spine and an elongated and expanded haemal spine.
 Procurrent caudal rays supported by cartilagenous plates in most species.
 Epurals number 1 to 3, usually 1 to 2.
 Hypurals 3 and 4 fused to each other and to the urostyle.
 Hypurals 1 and 2 fused to each other in all species and to the urostyle in some groups.
 Parhypural and hypural 5 greatly reduced.

cussing the osteological evidence bearing on the subject, a more general discussion of gobioid osteology seems in order. Miller (1973) offers a valuable discussion of the major features of gobioid osteology, including the available fossil data and a review of gobioid classification. My attempt here is to add to Miller's discussion and, on some points, offer a different point of view.

Though gobioids are easily defined by osteological characters (see Table 1), they are remarkably similar in gross osteology. The distinguishing features mostly involve the loss, fusion, or reduction of bone. Compared to most other teleosts, the gobioids have a highly simplified skeletal structure. The simplified skeleton, combined with the gross similarity of the species, makes evolutionary trends difficult to discern and greatly complicates the task of sorting out convergent characters. In spite of their great proliferation and the variety of habitats they exploit, the majority of gobioids remain rather generalized, benthic fishes. This is not to say that osteological evidence will contribute little

to the unraveling of gobioid phylogeny. On the contrary, there appear to be many useful osteological characters; however, the problems mentioned, together with the difficulty encountered in selecting representative material from the vast array of species, will make progress slow.

Table 1 is an attempt to set forth some of the osteological trends within the gobioids. No taxon above the generic level has been adequately studied and these trends are tentative at best. The generalized character states given are those found in the monotypic family Rhyacichthyidae and among the Eleotrididae. These two groups show less loss and fusion of bone than do other groups of gobioids and on this basis appear to be the most generalized.

The tentative list of gobioid osteological characteristics appearing here is drawn from the literature and from my own observations. In the ensuing discussion I shall briefly elaborate on the occurrence and lability of some of these characters and attempt to reconcile my observations with those of other workers.

CRANIUM.—Gosline (1955: 163) states that the alisphenoid (= pterosphenoid) is unknown in gobioid fishes. Pterosphenoid bones have been reported in *Mistichthys* (TeWinkle 1935), *Periophthalmus* (Lele and Kulkarni 1938), *Kraemeria* (Matsubara and Iwai 1959), *Lebetus* (Miller 1963) and in *Rhyacichthys* (Miller 1973). *Microgobius*, *Bollmannia*, *Parrella*, and *Gobiosoma* all possess well-developed pterosphenoid bones, as do all other gobioids that I have examined for this character.

Regan (1911: 729) describes the epiotics as being separated by the supraoccipital in gobioids. Gosline (1955: 163) described a similar situation in all of the genera he examined except *Kelloggella*, *Kraemeria*, and *Microdesmus*. In *Microgobius* and other American seven-spined genera, each epiotic forms a synchondral joint with its mate beneath the supraoccipital. Examination of representatives from *Erotelis*, *Chasmichthys*, *Eviota*, *Ptereleotris*, *Lophogobius*, *Gnatholepis*, and *Coryphopterus* reveals a condition similar to that found in *Microgobius*, and indicates the meeting of the epiotics beneath the supraoccipital is at least common and perhaps typical in gobioids.

The development of a shallow shelf-like myodome on the parasphenoid (as described in *M. signatus*) for the attachment of the medial, inferior, and superior rectus muscles appears to be an advanced feature in gobioids. A similar structure has been observed in such advanced but diverse genera as *Ptereleotris*, *Periophthalmus*, *Bollmannia*, *Parrella*, and others. The parasphenoid shelf is lacking in those eleotrids examined for the structure (i.e., *Eleotris pisonis*, *E. amblyopsis*, *Bostrichthys*

sinensis, and *Gobiomorphus huttoni*). Dissection of *Eleotris amblyopsis* shows the rectus muscles to originate separately along the parasphenoid in the anteroposterior order of medial, inferior, superior, and lateral muscles. Unlike the condition in *Microgobius*, the lateral rectus muscle penetrates the brain cavity only for a short distance and originates on the parasphenoid near the carotid foramen.

SUSPENSORIUM.—Gosline (1955: 160) and Miller (1973) have commented upon the unusual nature of the gobioid suspensorium, the most notable feature being the formation of a posterior strut composed of the quadrate and preopercle, which is widely removed from the symplectic-metapterygoid strut. Additionally, there is a tendency in many species for the symplectic to dominate the symplectic-metapterygoid strut with the metapterygoid sometimes reduced to a small fragment (e.g., *Mistichthys luzonensis* [TeWinkel 1935]). Matsubara and Iwai (1959: 30) failed to find a symplectic bone in *Kraemeria sexradiata*, though Gosline (1955: 161) has indicated a rather large symplectic in *K. samoensis*. I suspect that the description of the metapterygoid by Matsubara and Iwai (1959: 29, 32) actually is of the combined metapterygoid and symplectic bones.

Miller (1973) placed special importance on the development of an anteroventral process ("bridge") of the metapterygoid that overlaps the quadrate and the development of a symplectic process on the preopercle (see Fig. 14) in defining subfamilies in his classification of gobioids. My observations show both of these characters to display considerable lability and suggest the strong possibility of several convergent losses or developments of these features in gobioids. Within the American seven-spined gobies the occurrence of a quadrate process is distributed in relation to other characters in such a way as to suggest that the feature has either been independently lost in several lineages or developed *de novo* within the group. Furthermore, some species (e.g., *Periophthalmus cantonensis*) display considerable intraspecific variability in the development of a quadrate process.

The symplectic process shows similar variability, appearing in at least some species of each of Miller's subfamilies with the exception of the Kraemeriinae. In at least one species, *Microgobius cyclolepis* (Fig. 13), the symplectic process displays sexually dimorphic development.

The pterygoid-palatine strut of gobioids is characterized by the reduction or loss of the mesopterygoid bone (Gosline 1955: 160). Akihito (1969) found a mesopterygoid to be present only in 17 species (all eleotrids) among the 106 gobioid species he examined. Even among the eleotrids the mesopterygoid is lost in some lineages (e.g., *Erotelis* and *Gobiomorphus*).

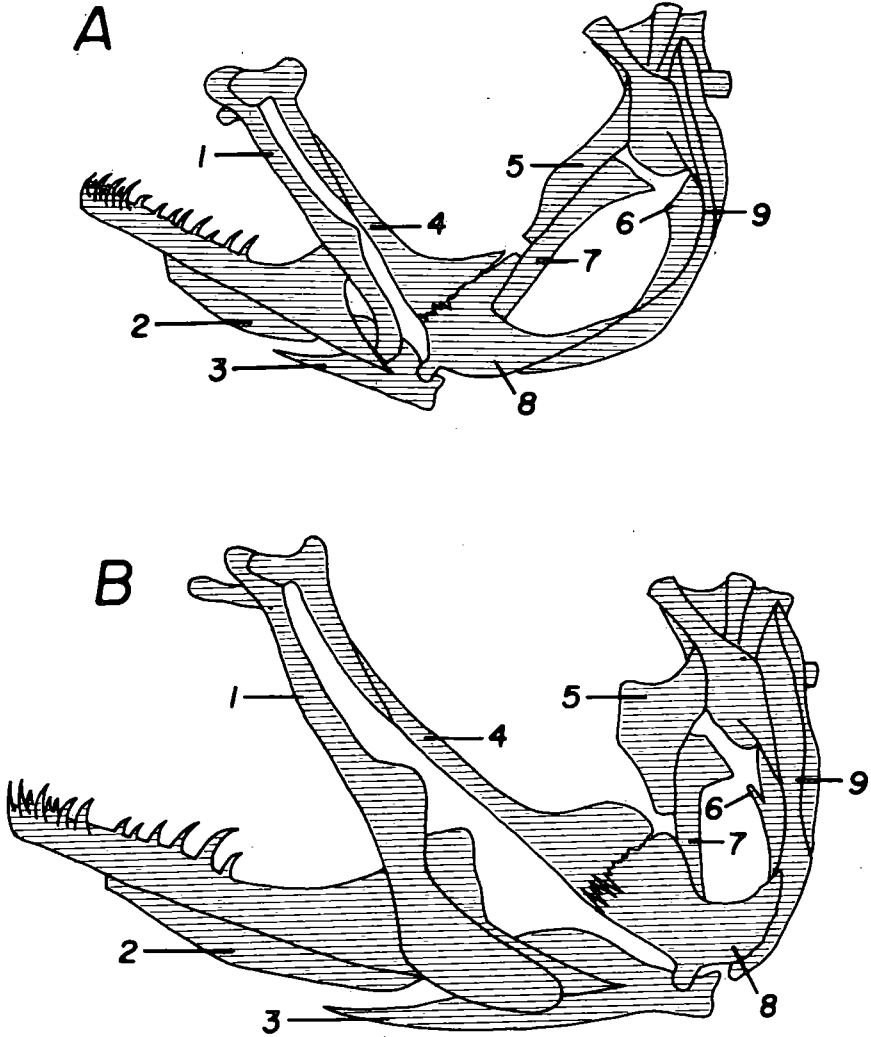


FIGURE 13.—Selected bones of the jaw and suspensorium of *Microgobius cyclolepis* showing sexual dimorphism. A) female, 49.3 mm SL, B) male, 50.4 mm SL. Key to numbers: (1) maxilla; (2) dentary; (3) articular; (4) ectopterygoid; (5) metapterygoid; (6) symplectic process of preopercle; (7) symplectic; (8) quadrate; (9) preopercle.

HYOID ARCH.—Gosline (1955: 161) called attention to several characteristic features of the hyoid arch and branchiostegal ray configuration in gobioids. The main variation from the condition described in *Microgobius* is found in *Rhyacichthys* and in the eleotrids, which possess an additional branchiostegal on the narrow portion of the ceratohyal.

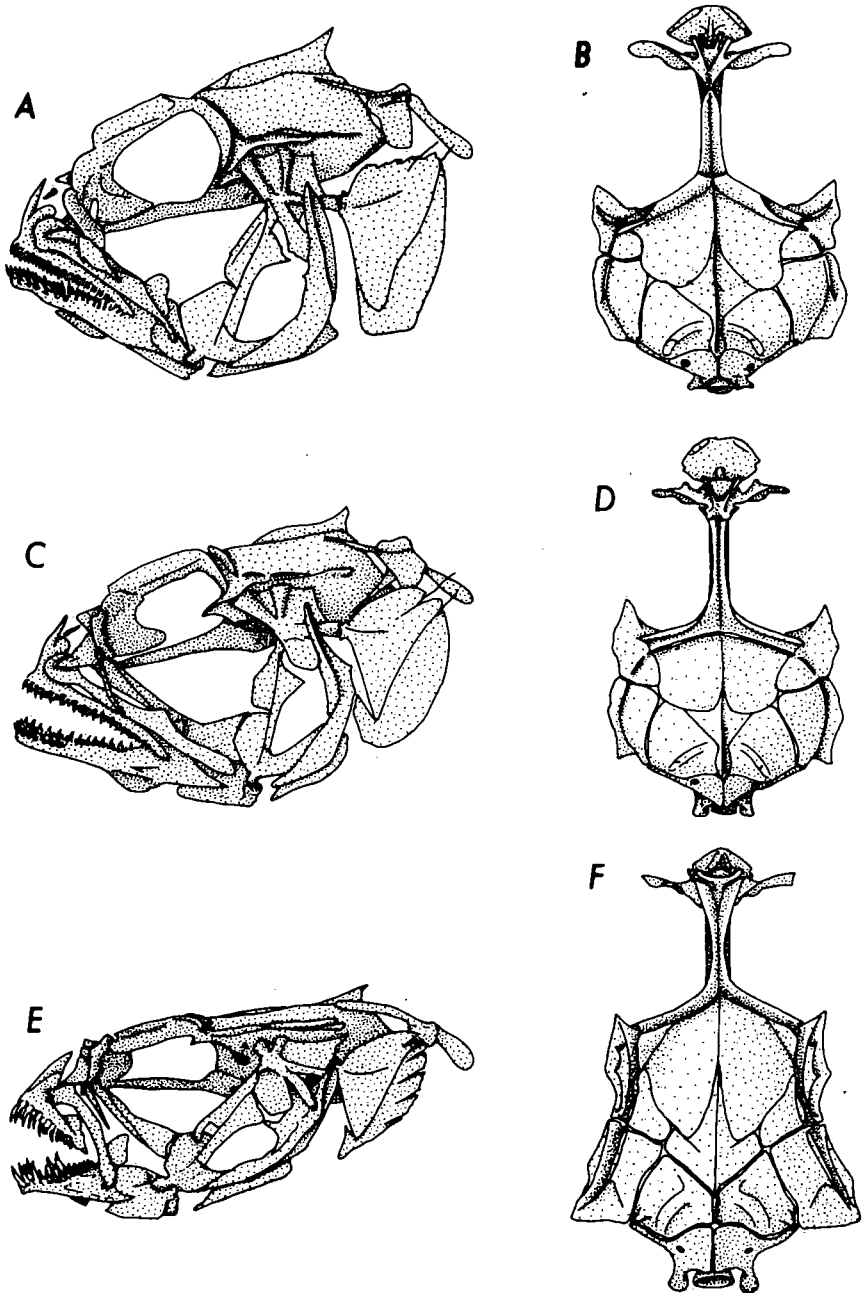


FIGURE 14.—Articulated skull (branchial bones removed) and cranium (dorsal view) of representative Gobiosomini. A, B) *Bollmannia boqueronensis*; C, D) *Parrella macropteryx*; E, F) *Gobiosoma bosci*.

The fossil gobioid family Pirskeniidae, from the Upper Oligocene of Bohemia, is said by Miller (1973) to possess six or seven branchiostegals.

An additional unusual feature, the attachment of the interhyal to the preopercle, has received little attention in the literature. This feature, described for *Microgobius signatus*, has been found in all species examined, including such diverse groups as *Ioglossus*, *Periophthalmus*, *Sicydium*, *Erotelis*, *Butis*, *Coryphopterus*, and *Gnatholepis*, and may be characteristic of gobioids in general.

The absence of the first basibranchial also appears to be typical of gobioids. The anteriormost basibranchial described by Matsubara and Iwai (1959: 30) in *Kraemeria sexradiata* appears to be the urohyal. Miller's description of the basibranchials 1-3 in *Rhyacichthys* appears to be of basibranchials 2-4.

Takagi (1950) attempted to arrange Japanese gobies into a phylogenetic sequence based upon the shape of the basihyal. The basihyal bones of gobioids vary from a long narrow shape (e.g., *Ptereleotris*) to a spatulate shape (e.g., *Bollmannia*) or a bifid shape (e.g., *Parrella*). The spatulate and bifid basihyals appear easily derived one from the other. Virtually nothing is known of the functional aspects of the various types of basihyals in gobioids and it seems likely that a great deal of parallelism may have taken place.

PECTORAL GIRDLE.—The most pronounced divergence of the pectoral girdle from the condition seen in *Microgobius signatus* is that described in *Kraemeria samoensis* (Gosline 1955: 163) and *K. sexradiata* (Matsubara and Iwai 1959: 31). These species lack the ventral arm of the posttemporal and have only three ossified radials. The reduction or absence of the ventral arm of the posttemporal has also been reported for *Kelloggella oligolepis* (Gosline 1955: 163) and *Microdesmus dipus* (Dawson 1968: 520).

Some confusion exists concerning the absence of scapula and coracoid bones in many gobioids. Akihito (1963, 1967) has shown the degree of ossification of the scapula in gobioids to be variable. The scapula is listed as "absent" (determined by Alizarin Red staining, but perhaps present as cartilage) in 34 of 106 species examined by Akihito (1969). Likewise, Gosline (1955: 164) states that the scapula is absent in *Gobiodon* and *Awaous*, and both scapula and coracoid are missing in *Microdesmus*, *Ptereleotris*, *Kelloggella*, and *Kraemeria*; and Miller (1973) refers to the absence of the scapula in several gobioid lines. As in *Microgobius signatus*, the scapula is unossified in many gobioids; however, all of the cleared and stained specimens examined by me, including representatives of *Gobiodon*, *Microdesmus*, and *Ptereleotris*, have at least a cartilagenous scapula, and all possess an ossified coracoid. In *Periophthalmus* the

scapula appears to be completely fused to the cleithrum (Lele and Kulkarni 1939: 130).

Akihito (1969) has shown the widespread occurrence of ventral postcleithra in gobioids (74 of 106 species examined). Among the American seven-spined gobies, a ventral postcleithrum is known to occur only in *Bollmannia* and *Palatogobius*. The development of ventral postcleithra is quite variable in gobioids, sometimes intraspecifically so, and its systematic importance seems limited.

Dorsal postcleithra appear to be present only among eleotrids and in *Xenisthmus* and *Gobiomorphus*, two genera showing a mix of eleotrid and gobiid features.

PELVIC GIRDLE.—Several groups of gobioids show tendencies toward the reduction or loss of the pelvic fins (e.g., trypauchenids and microdesmids). This tendency is most apparent among elongate, burrowing forms and reaches its extreme in *Expedio parvulus*, which appears, from radiographic observation, to have lost the entire pelvic girdle.

VERTEBRAL COLUMN AND MEDIAN FINS.—Several characters of systematic importance are present in the vertebral column and median fins of gobioids, however, a detailed discussion of these is in preparation, so my comments here are limited to a few selected features.

The caudal structure of *Microgobius* appears to be rather characteristic of gobioids of general. The large amount of consolidation and simplification characterizing the gobioid caudal skeleton makes interpretation difficult. The fusion of the lower hypural to the urostyle and hypurals 3-4, as seen in *Gobiosoma* and derivative genera, is apparently an uncommon feature (only reported in *Kraemeria* and *Kelloggella* [Gosline 1955]), as is the loss of the parhypural and hypural 5 (reported in *Periophthalmus barbarus* [Lele and Kulkarni 1939]).

Gobioids vary from one to three in number of epurals, with only *Rhyacichthys* known to have three epurals and the vast majority of gobioids possessing either one or two. Miller (1973) utilized the number of epurals as a fundamental character in separating several of his subfamilies of Gobiidae. The number of epurals appears to exhibit some lability, and the character should be used with caution in defining groups above the generic level. Virtually all of the intermediate conditions between two discrete epurals and a single fused epural are found in gobioids. Eleotrids and some gobiids possess two epurals, each with a cylindrical strut running through it. Other species have two contiguous epurals, with only the posteriormost containing a strut. In this latter condition the two epurals, when considered as a unit, closely resemble the single epural shown in Fig. 12 for *Microgobius signatus*. Some species of the genus *Gobionellus* that appear to represent natural as-

semblages of closely related forms show interspecific variation in epural number (Carter R. Gilbert, pers. comm.). Additionally, two species of gobiids, *Tamanka siitensis* and *Rhinogobius hadropterus*, are known to be variable in epural number and display conditions ranging from two discrete epurals to partial or total fusion into a single unit. Reduction in epural number has probably occurred independently several times in gobioids. Even in some of the more primitive forms, such as *Gobio-morphus huttoni*, the epurals are firmly fused into one unit while retaining the two struts typical of eleotrids.

The gobioids show a considerable range of vertebral number (25 to 60+); however, there is a great intraspecific stability in most groups. Groups showing significant variation in vertebral number are nearly always burrowing or hole dwelling in habit and frequently elongate in form. Elongation of the body has been accomplished by the elongation of the vertebrae in some (e.g., *Taenioides*, *Gobioides*, and *Trypauchen*) and by the addition of vertebrae in others (e.g., microdesmids).

The majority of gobioids possess pleural and epipleural ribs as described for *Microgobius*; however, two different specializations have been noted. In some elongate burrowing forms (e.g., *Inu*) the ribs are greatly reduced in size, and in others (e.g., *Expedio* and *Leucopsarion*) the ribs are apparently absent. A second specialization, noted only in *Periophthalmus*, is a tendency for the epipleural ribs to fuse with the pleural ribs. These two specializations appear to have rather obvious functional significance: in the burrowing forms the reduction of ribs promotes body flexibility, and in *Periophthalmus* the fusion provides increased support for the viceral cage during terrestrial forays.

Among the numerous minor specializations of the median fins, only two will receive comment here, and again burrowing species and "terrestrial" species are involved. In many burrowing groups (e.g., *Chloea*, *Clevelandia*, *Clariger*, *Typhlogobius*, *Inu*, and others) the spinous dorsal fin is greatly reduced in both size and number of elements. Frequently the pterygiophores are retained without the spines. In at least some species of the genera *Expedio*, *Luciogobius*, *Leucopsarion*, and *Inu* no vestige of the spinous dorsal fin remains. The reduction in the spinous dorsal fin may be attributable to a decrease in the swimming and signal function in burrowing species.

The specialization of the spinous dorsal fin of the periophthalmids, a "terrestrial" group, involves the addition of spines to the dorsal fin without the addition of supporting pterygiophores. The periophthalmids utilize the erect dorsal fin as a signal during terrestrial activity, and the accessory spines would appear to give needed support to the fin membrane in an air environment.

COMPARISON OF *M. signatus* WITH OTHER SPECIES OF *Microgobius*.—The species of *Microgobius* are remarkably similar in their osteological features, and few trends within the genus can be discerned.

Microgobius carri diverges most from the condition described for *M. signatus* by the absence of a median frontal crest, a narrower, though still bifid, basihyal, and in having a larger lacrymal bone. Based on trends seen in gobioids in general, all of these characteristics of *M. carri* appear to be primitive. *M. carri* further differs in having a relatively large mouth in both sexes and a laterally expanded and trifurcated tip of the neural spine on the third vertebra. In these two features *M. carri* appears to be advanced over other members of the genus; however, the trends in these characters are obscure. Several species (*M. brevispinis*, *M. miraflorensis*, *M. cyclolepis*, and the males of *M. microlepis*) show some lateral expansion of the second and third neural spines, but none approach the condition seen in *M. carri*.

All species of *Microgobius*, except *M. signatus*, show small to large differences in mouth size between the sexes, the mouth of the male being larger. In *M. carri* the mouth of the females is also large, though smaller than the male's, and displays many of the attendant osteological features only seen in the males of other species. The sexual dimorphism of the mouth is reflected in several bones of the jaws and suspensorium and becomes increasingly pronounced in larger, more mature individuals. In all species of the genus, including *M. signatus*, the males show a greater development of the anterior flange of the metapterygoid.

Sexual dimorphism of mouth size is most pronounced in *M. gulosus*, *M. miraflorensis*, *M. crocatus*, and *M. cyclolepis* (Fig. 13 A, B). The following list of osteological differences seen in mature males of *M. cyclolepis* when compared to females of equal size illustrates the modifications of jaw and suspensorium bones attendant with the increase in mouth size. These same differences may be seen when small-mouth species (e.g., *M. signatus*) are compared to large-mouth species (e.g., *M. carri*).

Dentary—longer with greater development of ventral shelf and coronoid process.

Articular—longer and stouter dorsal and ventral rami.

Premaxilla—longer shaft.

Maxilla—longer and stouter shaft with an expanded and posteriorly produced distal tip (distal tip in females is anteriorly recurved).

Ectopterygoid—longer shaft with an expanded base more firmly sutured to the quadrate.

Quadrate—articular process more ventrally oriented so that dorsal and ventral arms are oriented anteriorly and posteriorly, re-

spectively; dorsal arm lengthened; ventral arm dorsally expanded and shortened.

Symplectic—shorter and more vertically oriented.

Metapterygoid—shorter, more vertically oriented and anteriorly expanded as a thin flange.

Preopercle—anteroventral extension shorter, giving preopercle a more vertical orientation; development of a symplectic process (this feature seen only in *M. cyclolepis*).

In general, the bones of the jaws and the anterior strut of the suspensorium in males are lengthened, whereas the posterior bones of the suspensorium are shortened and more vertically oriented. All of these features are necessitated by the increase in mouth size without a corresponding isometric increase in the length of the skull.

COMPARISON OF *Microgobius* WITH RELATED GENERA OF AMERICAN SEVEN-SPINED GOBIES. (FIG 14).—I have not attempted to examine each of the genera in detail. The genera *Bollmannia* and *Parrella*, allied with *Microgobius* by Ginsburg (1939: 37), were most closely examined. *Palatogobius*, allied to *Microgobius* by Gilbert (1971: 33); *Gobiosoma*, the large genus indicated to be the basal group for most of the American seven-spined genera by Böhlke and Robins (1969); and the divergent genera *Evermannichthys* and *Pariah* were compared with *Microgobius*, based on limited cleared and stained material and radiographs. The genera *Chriolepis*, *Psilotris*, *Varicus*, *Gobulus*, *Pycnomma*, *Gymneleotris*, *Eleotrica*, *Barbulifer*, *Enypnias*, and *Aruma* were examined only from radiographs; and *Nes*, *Risor*, and *Ginsburgellus* were not examined.

Table 3 shows a comparison of *Microgobius*, *Bollmannia*, *Parrella*, *Palatogobius*, and *Gobiosoma* for 15 osteological characters. *Gobiosoma* is used in this discussion as defined by Böhlke and Robins (1968: 53) and not according to the more limited definition of Hoese (1971, unpublished dissertation).

Böhlke and Robins (1968, 1969) suggested that 15 of the 20 American seven-spined genera were derived from *Gobiosoma*, excluding only *Microgobius*, *Bollmannia*, *Parrella*, and the subsequently described *Palatogobius* (these four genera will be referred to hereafter as the *Microgobius* group). Hoese (unpublished dissertation), though differing with the generic concepts and relationships within the *Gobiosoma* group as proposed by Böhlke and Robins, agrees that the *Microgobius* group does not appear to be closely related to the *Gobiosoma* group.

The *Gobiosoma* group is distinctive in having hypurals 1-2 fused with hypurals 3-4 and the urostyle, a feature that is both rare and specialized in gobioids. Examination of this feature in representatives from

TABLE 2.—OSTEOLOGICAL TRENDS WITHIN THE COBIOIDEI.

Character	Generalized condition	Most frequent condition	Most specialized condition
1 Frontal bones	No median crest; not fused; broad between the orbits	No median crest; fused; narrow between the orbits	Formed into median crest; fused; narrow between the orbits
2 Median ethmoid	No formation of interocular septum	Interocular septum present	Interocular septum present
3 Teeth on vomer	Present	Absent	Secondarily developed ?
4 Parasphenoid	No transverse shelf for attachment of rectus muscles	Transverse shelf for attachment of rectus muscles	Transverse shelf for attachment of rectus muscles
5 Intercalar	Well developed	Moderately developed	Absent
6 Cephalia sensory canals	Supported by open troughs	Supported by open troughs	Enclosed in bony tubes
7 Lacrymal	Well developed	Moderately developed	Poorly developed (unossified)
8 Infraorbital bones	1 present in a few species	Absent	Absent

TABLE 2 (CONTINUED)

Character	Generalized condition	Most frequent condition	Most specialized condition
9 Supratemporal bones	2-3 present in a few species	Absent	Absent
10 Preopercle	Well developed symplectic process	Variable	No symplectic process
11 Mesopterygoid	Present	Absent	Absent
12 Metapterygoid	Broad, overlapping quadrate	Variable	Narrow, greatly reduced and widely separated from quadrate
13 Basihyal	Spatulate	Variable	Narrow or bifid
14 Epihyal	Sutured to ceratohyal ¹	Not sutured to ceratohyal	Not sutured to ceratohyal
15 Branchiostegal rays	6-7	5	4 (according to Takagi, unpublished, M.S.)
16 Posttemporal bone	Well developed dorsal and ventral arms	Well developed dorsal and ventral arms	Ventral arm unossified or absent (?)
17 Dorsal postcleithrum	Present	Absent	Absent
18 Ventral postcleithrum	Present	Present	Absent
19 Scapula	Well ossified, enclosing scapular foramen	Partly ossified, not enclosing scapular foramen	Unossified or apparently fused to cleithrum in some

TABLE 2 (CONTINUED)

Character	Generalized condition	Most frequent condition	Most specialized condition
20 Pectoral radials (Ossified)	4	4	3
21 Position of pelvic spine	In line with pelvic rays	In advance of pelvic rays	In advance of pelvic rays
22 Number of pelvic rays	5	5	0
23 Vertebral number	25-33	25-37	60+
24 Epipleural ribs	Articulating with pleural ribs	Articulating with pleural ribs	Fused to pleural ribs or absent
25 Pleural ribs	Present on all precaudal vertebrae except the first two	Present on all precaudal vertebrae except the first two	Absent
26 Spinous dorsal pterygiophores	Number of pterygiophores equals number of spines	Number of pterygiophores equals number of spines	Accessory spines developed without pterygiophores or spines lost with pterygiophores retained
27 Epurals	2-3	1-2	1
28 Hypurals 1-2	Articulate with urostyle	Articulate with urostyle	Fused to urostyle
29 Parhypural and hypural 5	Small, with a cylindrical core	Small, with a cylindrical core	Minute, without a cylindrical core; apparently absent in some

¹ Seen only in large individuals

TABLE 3.—COMPARISON OF *MICROGOBIUS* WITH SOME RELATED GENERA IN SELECTED OSTEOLOGICAL CHARACTERS.

Character	<i>Microgobius</i>	<i>Bollmannia</i>	<i>Parrella</i>	<i>Palatogobius</i> ¹	<i>Gobiosoma</i>
Bony support of supraorbital sensory canal	Canal supported by an open trough	Portions of canal enclosed in bony tube (S) ²	Canal supported by an open trough	Canal supported by an open trough	Variable, open troughs in some species, enclosed in bony tube in others (S)
Position of frontal bones in relation to median ethmoid	Overlaps median ethmoid	Barely reach median ethmoid (S)	Overlaps median ethmoid	Overlaps median ethmoid	Overlaps median ethmoid
Transverse crest on frontal bones	Present	Present as part of bony tube	Present, but reduced	Present, but greatly reduced	Present, sometimes as part of bony tube
Sagittal crest on frontal bones	Present (S)	Present (S)	Absent	Absent	Absent
Basihyal shape	Bifid (S)	Spatulate	Bifid (S)	Narrow	Spatulate
Teeth on vomer	Absent	Absent	Absent	Present (at least in holotype)	Absent

TABLE 3 (CONTINUED)

Character	<i>Microgobius</i>	<i>Bollmannia</i>	<i>Parrella</i>	<i>Palatogobius</i> ¹	<i>Gobiosoma</i>
Process on metapterygoid overlapping quadrate	Absent (S) ²	Absent (S)	Absent (S)	Absent (metapterygoid greatly reduced) (S)	Present
Symplectic process on preopercle	Slightly developed to absent (S)	Slightly developed to absent (S)	Absent (S)	Present	Present
Ossified nasal bones	Present	Present	Present	Absent (S)	Absent in some species (S)
Lateral shelves on posttemporal	Absent (S)	Present (two shelves)	Present (one shelf)	Present (one shelf)	One shelf present, but reduced
Sphenotic shape	Short	Short	Short	Short	Elongate in some (S)
Ventral postcleithrum	Absent (S)	Present	Absent (S)	Present	Absent (S)
Hypurals 1-2 fused to hypurals 3-4. and to urostyle	No	No	No	No	Yes (S)
Shape of brain case in dorsal view	Circular	Circular	Circular	Circular	Elongate
Fused frontal bones	Yes (S) ²	Yes (S)	Yes ? (S)	No	Yes (S)

¹ This genus is known only from the holotype and two other specimens that differ from the holotype in lacking vomerine teeth. The possibility exists that the non-type specimen examined in this study is not conspecific with the holotype.

² (S) = those character states that appear to be specialized.

4 subgenera of *Gobiosoma* and 9 derived genera showed the only exception to the fused condition of the caudal to be in *Gobiosoma polyporosum* (= *G. etheostoma* according to Hoese, unpublished dissertation). On the basis of other characters, Dawson (1969: 514) suggested this species to be one of the most primitive members of *Gobiosoma*.

The absence of the fused caudal condition in the *Microgobius* group suggests a more primitive origin for these genera and essentially excludes any of the *Gobiosoma* lineages from their ancestry. Conversely, specializations (?) occurring in *Microgobius*, *Bollmannia*, *Parrella*, and *Palatogobius* appear to exclude each of these genera from the ancestry of each other (see Table 3).

Understanding of relationships is greatly impaired by the difficulty of discerning specialized trends in small groups such as these being considered, and by the lack of understanding of the lability of most of the characters. Since many of the osteological character states here compared represent seemingly minor modifications, it is by no means certain that the trends within the American seven-spined gobies follow the apparent trends seen in gobioids in general. For example, fusion of the frontal bones appears to be a common, though specialized, condition in gobioids; however, in many small gobioids separate frontal bones appear to be correlated with an overall reduction in ossification and in these groups the separate frontals may represent a specialized condition. Likewise, the vomerine teeth of *Palatogobius* may be a *de novo* development. In the absence of strong contrary evidence, however, those character states appearing to be generalized within gobioids are assumed to be generalized within the American seven-spined gobies.

Of the 15 osteological characters compared in Table 3, *Palatogobius* possesses fewer specializations (2) than any of the other American seven-spined genera examined, and also shares the fewest specialized features with the other genera. Specialized features are distributed among the other genera as follows: *Microgobius* (7), *Bollmannia* (6), *Parrella* (5), and *Gobiosoma* (6). On the basis of shared specialized osteological features, the closest relation appears to be between *Microgobius* and *Parrella* with five shared specializations, followed by *Microgobius* and *Bollmannia* with four, and *Bollmannia* and *Parrella* with three. *Microgobius*, *Parrella*, and *Bollmannia* each share three specializations, though not the same three features, with the *Gobiosoma* group and one specialization with *Palatogobius*. From this evidence it appears that *Microgobius*, *Parrella*, and *Bollmannia* are more closely related to each other than to the *Gobiosoma* group, and *Palatogobius* is possibly more primitive than any of these groups and somewhat removed from them phylogenetically.

VALIDITY OF THE AMERICAN SEVEN-SPINED GOBY GROUP.—All of the American seven-spined goby genera examined (except *Evermannichthys* and *Pariah*, discussed separately below) share the following osteological features: 11 precaudal vertebrae; 16 or 17 caudal vertebrae; a spinous dorsal fin formula of 3(221110); an unossified scapula; and the insertion of the first two anal pterygiophores anterior to the first haemal spine. They further share, along with many other gobioids, those character states given as the "most frequent condition" in Table 2 for the characters numbered, 2, 4, 5, 7, 8, 9, 11, 14, 15, 16, 17, 20, 21, 22, 23, 24, 25, 26, 27, and 29.

The most convincing evidence for considering the American seven-spined gobies a natural assemblage is the shared features of 11+16–17 vertebrae and the 3(221110) pterygiophore pattern. Vertebral number and pterygiophore pattern are extremely stable characters within many groups of gobioids. For example, in the examination of radiographs of over 250 specimens of *Microgobius* only five specimens varied from the typical condition in these two characters. Furthermore, the combination of 11+16 vertebrae and 3(221110) pterygiophore pattern is virtually unique to the American seven-spined group.

In the examination of dorsal fin characteristics and vertebral number of over 400 species of gobioids from around the world, only one species from outside the Americas has been found with a pterygiophore pattern of 3(221110). This species, *Tukugobius carpenteri* from the Philippines, also possesses 11 precaudal vertebrae, a vertebral number uncommon in other than the American seven-spined genera. The pterygiophore number and arrangement in *T. carpenteri* is constant, though in many specimens the last D₁ spine is absent. The occurrence of two epurals in *T. carpenteri* is the only gross osteological characteristic distinguishing it from the American seven-spined genera. The importance of two epurals versus one epural is difficult to assess at this time, and the relationship of *T. carpenteri* to the American seven-spined gobies must remain in question.

The genera *Evermannichthys* and *Pariah*, allied with the seven-spined genus *Risor* by Böhlke and Robins (1969: 14) and Böhlke (1969: 3), differ from the seven-spined genera in having 12–15 precaudal vertebrae, 17–20 caudal vertebrae, and either a variable number of dorsal spines (3–7 in *Evermannichthys*) or 8 dorsal spines (in *Pariah*). Examination of limited material of *Pariah* (7 specimens) reveals a constant D₁ formula of 3(2211110) and 12+17 vertebrae. This condition differs from that of the seven-spined genera only in the addition of one precaudal vertebra and its associated pterygiophore and spine.

Evermannichthys shows considerable inter- and intraspecific variation

in pterygiophore pattern, number of dorsal spines, and number of vertebrae. *E. metzelaari* varies from 3 to 7 in number of dorsal spines (Böhlke and Robins 1969). My examination of a single specimen showed a D_1 formula of 4(21111101) and 15+20 vertebrae. In 2 specimens of *E. convictor* the D_1 formulae were 4(211110) with 13+17 vertebrae and 3(2111110) with 13+18 vertebrae. In 7 specimens of *E. silus*, two were 3(121110) with 12+17 vertebrae, three were 3(1211110) with 13+17 vertebrae, one was 3(1211101) with 13+17 vertebrae, and one was 3(122111) with 12+17 vertebrae. The extreme variability of these characters in *Evermannichthys* makes interpretation difficult, and consequently adds little information to the validity of their placement with the seven-spined genera. Böhlke and Robins (1969: 13) have pointed out that *Risor*, *Pariah*, and *Evermannichthys*, all sponge dwelling gobies, seem to form a natural progression from the *Gobiosoma* (*Tigrigobius*) line, with *Evermannichthys* being the most highly specialized for this mode of life. These two genera also share with *Gobiosoma* and its derivatives the feature of having hypurals 1-2 fused to hypurals 3-4 and the urostyle. It is perhaps significant that these reductions in the number of dorsal spines and/or increases in variability in the spinous dorsal fin and an increase in vertebral number are similar to the modifications seen in other genera of hole dwelling or burrowing gobies (e.g., *Chloea*, *Clevelandia*, *Clariger*, *Typhlogobius*, *Luciogobius*, *Ilypnus*, *Inu*, and others). Considering all of the evidence, it appears that *Evermannichthys* and *Pariah* are indeed properly placed with the *Gobiosoma* group of American seven-spined gobies.

Recently, Miller and Tortonese (1968: 355) have suggested an alignment of the six-spined Mediterranean gobiid *Odondebuena balearica* with the American seven-spined genera based upon similarities in squamation and sensory pore and free neuromast patterns. I have not examined *Odondebuena*, but its six-spined condition, combined with the present difficulty of interpreting the phylogenetic significance of sensory pore and neuromast patterns in gobioids, leaves the alignment of this genus with the American seven-spined gobies in doubt.

Nominal gobioid families are presently poorly defined, some poorly conceived, and all in a considerable state of systematic disorder. Considerable caution is therefore dictated in the erection of new taxa above the species level. The American seven-spined gobies, however, do appear to be a natural assemblage of species, defined by those characters given in this discussion, and worthy of more formal designation. The American seven-spined gobiids are here designated as the tribe Gobiosomini of the family Gobiidae, containing the genera given below. Recognition of the group at the tribal level is conservative, though somewhat arbitrary,

and provides a less cumbersome reference than does "American seven-spined gobies."

FAMILY GOBIDAE

GOBIOSOMINI, new tribe

<i>Gobiosoma</i> Girard 1858	<i>Varicus</i> Robins and Böhlke 1961
<i>Nes</i> Ginsburg 1933	<i>Chriolepis</i> Gilbert 1892
<i>Aruma</i> Ginsburg 1933	<i>Risor</i> Ginsburg 1933
<i>Eleotrica</i> Ginsburg 1933	<i>Evermannichthys</i> Metzelaar 1919
<i>Pycnomma</i> Rutter 1904	<i>Pariah</i> Böhlke 1969
<i>Gymneleotris</i> Bleeker 1874	<i>Ginsburgellus</i> Böhlke and Robins 1968
<i>Enypnias</i> Jordan and Evermann 1898	<i>Microgobius</i> Poey 1876
<i>Barbulifer</i> Eigenmann and Eigenmann 1888	<i>Parrella</i> Ginsburg 1939
<i>Gobulus</i> Ginsburg 1933	<i>Bollmannia</i> Jordan 1890
<i>Psilotris</i> Ginsburg 1953	<i>Palatogobius</i> Gilbert 1971

ADDITIONAL COMMENTS ON MILLER'S CLASSIFICATION OF GOBIOIDS.— In establishing the Tribe Gobiosomini it seems appropriate to discuss the recent classification of gobioids proposed by Miller (1973). Miller's classification is as follows:

Family Rhyacichthyidae, monotypic

Family Gobiidae, 2,000 ± species

Subfamily Eleotrinae, 40 genera

Subfamily Pirskenaia, monotypic (fossil)

Subfamily Xenisthminae, monotypic

Subfamily Gobionellinae, 20 genera

Subfamily Tridentigerinae, 2 genera

Subfamily Gobiinae, 200 (?) genera

Subfamily Kraemeriinae, 4 genera

Miller further divides the Gobiinae into six tribes. Though the tribes were not defined, it is apparent that the Tribe Gobiosomini, as here conceived, constitutes a part of Miller's Tribe Gobiini.

The placement of all gobioids (except *Rhyacichthys*) into one family appears to lack a great deal in utility and mask the diversity of the group. Further, Miller's justification for this lumping seems faulty. He implies that the classificational hierarchy of the teleosts dictates that gobioids be placed in only two families, but I find as much diversity of form and habit among the gobioids as there is among the percoids, a group divided into 71 families by Greenwood *et al.* (1966). Miller also reasons that "on the basis of presumed geological age, we may equate the entire suborder Gobioidi with a subfamily of insecta, and view the gobiid subfamilies as tribes" I see no utility in attempting to equate higher taxa of fishes with taxa of insects. If this reasoning is

followed, I presume we must then equate the Teleostei with the carabid beetles, the two groups being of approximately the same size, geological age and ecological diversity; and reduce the teleosts to a single family!

My primary concern with Miller's classification is more basic than the assignment of taxonomic level, however, and is directed toward the definition of the groups and the implied phylogeny. The following characters were used by Miller in defining the groups: (1) number of epurals; (2) number of branchiostegals; (3) presence of mesopterygoid; (4) presence of an upper postcleithrum; (5) presence of a scapula; (6) presence of supratemporals; (7) nature and extent of the metapterygoid connection to the quadrate; (8) connection of the preoperculum to the symplectic; (9) number of pectoral radials; (10) fusion of the hypurals; (11) position of the anteriormost supraorbital (oculoscapular) sensory canal pore; and (12) number of preopercular sensory canal pores.

The occurrence and lability of most of these characters have been commented upon in the preceding discussion. Characters 11 and 12 (above), features of the cephalic sensory canal system, require comment here. Character 11 is difficult to evaluate in the form used by Miller. Essentially, it involves two character states, the anterior pore being situated either before the anterior nostril or behind the anterior nostril. I have no information on the lability of this feature, but the assignment of a character state is as much dependent upon the position of the anterior nostril as upon the position of the pore, thus rendering the character ambiguous at best. The number of preopercular canal pores (character 12 above) is an especially labile feature in gobioids. Though there is a general tendency for eleotrids to have more preopercular pores (given as "up to 5" by Miller), the vast majority of gobioids possess either 2, 3, or none, with abundant evidence that reduction of the preopercular pores has occurred numerous times within gobioids.

Though no list of species examined is given, it is apparent that a portion of the problems with Miller's classification stems from being based on a relatively small sample of the gobioids. I can think of no other explanation for his tendency to place intermediate forms into separate subfamilies (e.g., Xenithminae and Tridentigerinae). Other intermediate forms exist that would appear to be as worthy of subfamilial status as these two. For example, the Xenithminae differ from the Eleotrinae by the loss of the upper postcleithrum and the mesopterygoid. *Gobiomorphus* would then seem to be worthy of subfamily recognition since it differs from the Eleotrinae by the loss of the mesopterygoid and the fusion of the epurals, and from the Xenithminae by the fusion of the epurals and the loss of the supratemporals.

Other forms, such as *Chasmichthys dolichognathus*, with two epurals,

a symplectic process on the preoperculum (as in the Tridentigerinae), and a broad metapterygoid connection to the quadrate (as in the Eleotrinae) yield problems, as does *Luciogobius guttatus* with two epurals and a quadrate process on the metapterygoid (as in the Tridentigerinae), but without a symplectic process on the preoperculum (as in the Gobionellinae and some Gobiinae). I have little doubt that a broader survey of gobioids would further erode the concept of several of Miller's subfamilies. Miller says (p. 420) that "since none of these groups [subfamilies of Gobiidae] possesses all the primitive characters occurring within the family, traditional raising of the Eleotrinae, or any of the other subfamilies, to separate family rank would involve arbitrary division of the series on merely one of several skeletal criteria." However, this has obviously not been applied in his erection of subfamilies.

Miller's reliance on the retention or loss of a few primitive, simple, and probably somewhat labile osteological features in his classification appears to greatly influence his view of gobioid evolution. The following passage (p. 420) is Miller's most concise statement of his view of gobiid phylogeny: "Despite a gradually increased skeletal specialization through these gobiid subfamilies, there seems little evidence that one is very much older than any other as a separate line, and they must therefore rank equally in a system intended to demonstrate phylogeny. Their disparity in structure and extent of specialization thus may be interpreted as reflecting differences in rate of evolution since their origin as separate phyletic lines in a period of explosive radiation from early gobiid stock." I find Miller's phyletic "sunburst" most unsatisfying and optimistically believe that further evidence will reveal a more cladistic picture of gobioid evolution.

Though it may seem appropriate for this criticism of Miller's classification to be accompanied by an alternative proposal, I have resisted this temptation. Less than one percent of the described species have received detailed osteological examination. New information is being obtained at an increasing rate, and it appears to me prudent to live a while longer with the imperfect classification that exists.

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KEY TO ABBREVIATIONS

ANG—angular	MX PAL—maxillary process of palatine
AR PMX—articular process of premaxilla	N—nasal
ART—articular	NA—neural arch
ASC PMX—ascending process of premaxilla	NC—neural canal
BB—basibranchial	NS—neural spine
BH—basihyal	OP—opercle
BO—basioccipital	PAL—palatine
BR—branchiostegal	PAP—parapophysis
BTP—branchial tooth patch	PB—pharyngobranchial
C—centrum	PC—procurrent cartilage
CB—ceratobranchial	PHYP—parhypural
CH—ceratohyal	PM PMX—postmaxillary process of premaxilla
CL—cleithrum	PMX—premaxilla
COR—coracoid	POP—preopercle
COR D—coronoid process of dentary	PPTC—proximal radial
D—dentary	PR—pleural rib
DH—dorsal hypohyal	PRO—prootic
DPTG—distal radial	PS—parasphenoid
EB—epibranchial	PT—ectopterygoid
EH—epihyal	PTG—pterygiophore
EO—exoccipital	PTM—posttemporal
EPO—epiotic	PTO—pterotic
EPR—epipleural rib	PTS—pterosphenoid
EPU—epural	PZF—prezygapophysis
ETH PAL—ethmoid process of palatine	QU—quadrate
F—frontal	RAD—pectoral radials
FIC—foramen for internal carotid artery	RC—rostral cartilage
GR—gillraker	SCA—scapular cartilage
HB—hypobranchial	SCL—supracleithrum
HS—haemal spine	SES—sesamoid articular
HYO—hyomandibular	SOC—supraoccipital
HYP—hypural	SOP—subopercle
IH—interhyal	SPH—sphenotic
INT—intercalar	STF—subtemporal fossa
IOP—interopercle	SYM—symplectic
L MX—lateral head of maxilla	UH—urohyal
LAC—lacrymal	UPT—upper pharyngeal tooth plate
LE—lateral ethmoid	US—urostyle
LPT—lower pharyngeal tooth plate	V—vomer
M MX—medial head of maxilla	VH—ventral hypohyal
ME—medial ethmoid	VT—vertebra
MPT—metapterygoid	V—foramen for trigeminal nerve
MPTG—medial radial	VII—foramen for facial nerve
MX—maxilla	

ABBREVIATIONS USED AS ORIENTATION GUIDES:

A, anterior; D, dorsal; L, lateral; M, medial; P, posterior; V, ventral; EX, exterior; IN, interior.

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MSS must be submitted in duplicate (please no onionskin) and satisfy the following minimal requirements: They should be typewritten, double-spaced (*especially* tables, figure captions, and "Literature Cited"), on one side of numbered sheets of standard (8-1/2 x 11 in.) bond paper, with at least one-inch margins all around. Tables (which should be unruled) and figure legends should be typed on separate sheets. All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All illustrations should have a cover sheet. All lettering will be medium weight, san-serif type (e.g., Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lowercase letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm. high. The maximum size for illustration is 8-5/8 x 14 in. (twice typepage size); illustrations should not be less than typepage width (4-5/16 in.). Designate the top of each illustration and identify on the back with soft pencil by author's name, MS title, and figure number.

Manuscripts and all editorial matters should be addressed to:

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