

*Tyson belos*, New Genus and Species  
of Western Pacific Fish (Gobiidae,  
Xenisthminae), with Discussions of  
Gobioid Osteology and Classification

VICTOR G. SPRINGER

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## ABSTRACT

Springer, Victor G. *Tyson belos*, New Genus and Species of Western Pacific Fish (Gobiidae, Xenisthminae), with Discussions of Gobioid Osteology and Classification. *Smithsonian Contributions to Zoology*, number 390, 40 pages, 19 figures, 1983.—*Tyson belos* is described, based on specimens from the Great Barrier Reef, Trobriand Islands, and Lau Islands. This diminutive (gravid female 18.8 mm SL), coral-reef species differs conspicuously from all other gobioids in having the following combination of characters: pelvic fins separate, each comprising a single segmented ray and no spine; teeth on vomer; anterior (spinous) dorsal fin lacking. *Tyson* appears to be closely related to *Xenisthmus* Snyder, *Allomicrodesmus* Schultz, and an undescribed genus (and species, reference D.F. Hoese). These genera share at least one synapomorphy within the Gobioidae: ventral lip with free ventral margin extending across dentary symphysis (margin interrupted across symphysis in other gobioids). The subfamily Xenisthminae is recognized on this single character. There are, however, osteological specializations that are known only for *Tyson* and *Xenisthmus* and that are predicted to occur in the other two xenisthmine genera: premaxillary ascending process greatly reduced or absent (if present, lower than anterior maxillary articulating process of premaxilla); ascending processes replaced in position and function by a rostral bone (ossified rostral cartilage); basibranchials 2 to 4 absent. A rostral bone occurs in a few other gobioid genera, but in these the ascending premaxillary processes are well developed, basibranchials 2 to 4 are present, and not all the species in each genus where the rostral bone occurs have a rostral bone, indicating the probability that this bone is a homoplasy in those non-xenisthmine genera where it occurs.

The osteologies of *Tyson* and *Xenisthmus* are described and illustrated. Synapomorphies are provided for the Gobioidae, Rhyacichthyidae, and Gobiidae, and the Rhyacichthyidae is proposed as the sister-group of all other gobioids.

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# *Tyson belos*, New Genus and Species of Western Pacific Fish (Gobiidae, Xenisthminae), with Discussions of Gobioid Osteology and Classification

*Victor G. Springer*

## Introduction

In 1975, Tyson R. Roberts collected a single specimen of a fish from a coral reef in the Trobriand Islands, off eastern New Guinea. He recognized that it was distinctly different from any of which he had knowledge, but he was unable to assign it to a family. He asked my opinion of the specimen's affinities. Although the external anatomy of the specimen did not allow one to assign it with confidence to any infraordinal taxon of fishes, I had the impression that the specimen was a gobioid. To confirm this impression would have required detailed information on the osteology of the specimen, and I was unwilling to sacrifice it for this purpose. Although Roberts generously offered to permit me to describe the species (and genus), I delayed description in the hope that additional specimens would become available. A second specimen, from the Great Barrier Reef, was obtained in 1981 by the Australian Museum, and I then made an osteological preparation of the first specimen. Shortly afterwards, in 1982, I collected two more specimens, from Fiji. It is now possible to confirm my impressions of the gobioid

affinities of the specimens. In addition, a suggestion by Douglass Hoese that the closest relationships of the new species (and genus) might be among those genera considered to be marine eleotridids (Larson and Hoese, 1980) opened up a fertile field of investigation into the family-group taxa of gobioids. I soon found myself immersed in the infamous and unwieldy morass of gobioid systematics, which was not my intention, nor did it fit my research priorities. I decided, therefore, to limit my study and present my findings to date.

In this study I describe the new genus and species, including its osteology and that of its sister genus (*Xenisthmus* Snyder), and assert the probable monophyly of the gobioid subfamily Xenisthminae, which contains only the new genus, *Xenisthmus*, another undescribed genus (reference D.F. Hoese, specimens unavailable to me), and *Allomicrodesmus* Schultz. I also discuss certain osteological characters used or useful in establishing the monophyly of the suborder Gobioidi and some included infrasubordinal groups.

**METHODS.**—Specimens (one each) of *Xenisthmus clarus* and *Tyson belos* and much of the other gobioid skeletal material used in this study were stained for cartilage with alcian blue, cleared with trypsin, and stained for bone with alizarin

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red-s. When I discuss cartilaginous or bony structures, I mean to imply only that the structures stained blue or red (pink), respectively. Some structures, notably fin-ray elements and portions of some skeletal tissues that otherwise stained blue, accepted little or no stain, and most are treated here as if they are bone (these unstained structures accept red stain in other gobioids). On the illustrations, blue-stained structures are indicated by a pattern of hatching; nonstained or red-stained structures are not differentiated; stippling is used sparingly to indicate depth or contours, and in Figure 12 a uniform fine screen was used to indicate depth (otherwise this screen was used for background contrast).

I prepared all the base drawings of the bones, the final renderings of which were executed by P.K. Hollingsworth.

The snout region of a large number of whole specimens of gobioids, including *Xenisthmus* and *Tyson* and particularly genera usually considered to be eleotridids (because they have 6 branchiostegals and separate pelvic fins), was examined to determine if the ventral lip had a complete free ventral margin, and the snout was partially dissected to determine whether premaxillary ascending processes or a rostral bone were present. The osteologies of a number of gobioids have been discussed and illustrated in the literature (not all cited in the present study). I referred to much of this literature for relevant information. Where I encountered apparent discrepancies I attempt to rectify the differences in my discussions. (Birdsong, 1975, also encountered questionable osteological characters in the literature, and I do not, in general, treat those errors that he corrected.)

Established procedures for making segmented dorsal- and anal-fin ray counts on gobioids call for enumerating the posteriormost two dorsal- or anal-fin segmented rays as a single ray. In contrast to the other segmented rays, which have a one-to-one relationship with pterygiophores in these fins, each of these ray pairs is supported by a single pterygiophore, and the two rays of each pair are closely approximate. The posterior member of each pair is often greatly reduced in size;

nevertheless, the structure of each element of each pair is that of a typical segmented ray. In my study I enumerate each element separately.

In referring to the commonly recognized family-group based on *Eleotris* Bloch, I use the family-level adjective "eleotridid." I do not recognize a family group based on *Eleotris*, however, but the adjective is useful when referring to earlier studies that do or when referring to gobioids with the following combination of characters: separate pelvic fins, 6 branchiostegals, fewer than 3 epurals, no rostral bone, free margin of ventral lip not continuous across dentary symphysis. (All these characters, except the number of epurals, are plesiomorphic for gobioids; the number of epurals is plesiomorphic for all non-rhyacichthyid gobioids.)

The following institutional abbreviations are used herein:

- AMNH American Museum of Natural History, New York
- AMS Australian Museum, Sydney (catalog numbers begin with I or IA)
- CAS California Academy of Sciences, San Francisco
- GCRL Gulf Coast Research Laboratory, Ocean Springs, Mississippi
- USNM United States National Museum, the collections of which are housed in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (fish specimens are in the Division of Fishes)

**MATERIALS.**—The osteological descriptions of *Xenisthmus* and *Tyson* are each based on a single specimen (counterstained for bone and cartilage): *Xenisthmus clarus* (Jordan and Seale), USNM 235710, female, 23.6 mm SL (Figure 1); and *Tyson belos*, USNM 229985, female paratype, 18.5 mm SL (Figure 2). Most details of the skeletal anatomy of *X. clarus* were compared for consistency with a counterstained specimen of a different (apparently undescribed) species of *Xenisthmus*: USNM 247387, female, 25.3 mm SL. Differences exhibited by the comparative specimen are reported at appropriate points in the osteological descriptions (one of the prepublication reviewers of this study, D.F. Hoese, checked parts of the osteological description of *Xenisthmus* against a specimen of *X. polyzonatus* (Klunzinger)).

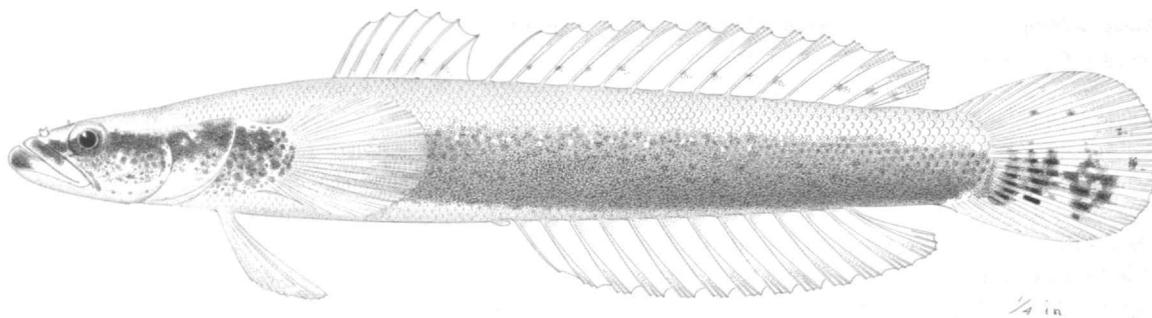


FIGURE 1.—*Xenisthmus clarus* (from Snyder, 1982, pl. 68: fig. 3, *Xenisthmus proriger* [= *X. clarus*]).

Cleared and stained specimens (\* = alizarin only; \*\* = counterstained for cartilage) of other gobioids examined for this study include: *Awaous tajasica* (Lichtenstein), USNM 213491\*; *Butis amboinensis* (Bleeker), USNM 224964\*\*; *Callogobius* species, USNM uncataloged (formerly CAS GVF 1956-28)\*\*; *Calumia godeffroyi* (Günther), USNM 224966\*\*; *Cerdale ionthas* Jordan and Gilbert, GCRL V71:6563\*; *Clarkichthys bilineatus* (Clark), GCRL V71:6019\*; *Eleotris amblyopsis* (Cope), USNM 226200\*\*; *Eviota* species, USNM 224539\*\*; *Gobiomorus dormitor* Lacépède, USNM 79070\*\*; *Gobiosoma homochroma* (Ginsburg), USNM 121937\*; *Gunnellichthys pleurotaenia* Bleeker, GCRL V82:19587\*; *Kraemia bryani* Schultz, USNM 143153\*; *K.* species, AMS I.20978\*; *Microdesmus dipus* Günther, GCRL V69:3610\*; *M. longipinnis* (Weymouth), GCRL V70:4613\*; *Mogurnda mogurnda* (Richardson), USNM 217283\*\*; *Paragunnellichthys seychellensis* Dawson, GCRL V82:19583\*; *Parioglossus taeniatus* Regan, USNM 245268\*\* and AMS I.22138-011\*; *Rhyacichthys aspro* (Valenciennes), AMNH 48695 (complete)\*\* and USNM 247300 (only gill arches and left jaws, suspensorium, and superficial head bones)\*\*; *Valenciennesa strigata* (Broussonet), USNM uncataloged\*.

A complete listing of whole specimens of gobioids examined and partially dissected was not maintained, but those examined included a large number of genera and species, among which were the following: *Bostrychus sinensis* Lacépède, USNM 90325; *Brachyamblyopus urolepsis* (Bleeker), USNM

217307; *Bunaka canarensis* (Day), USNM 164456; *Dormitator maculatus* (Bloch), USNM 192189; *Erotelis* species, USNM 192255; *Gobiomorphus hubbsi* (Stokell), USNM 198507; *Gobiotrichonotus radiocularis* Fowler, USNM 174949; *Heteroleotris nebulofasciatus* (J.L.B. Smith), USNM uncataloged (station no. VGS 69-28); *H. vulgare* (Klunzinger), USNM uncataloged (station no. VGS 69-23); *H. zonatus* (Fowler), USNM 210415; *Leptophilypnus fluviatilis* Meek and Hildebrand, USNM 249722; *Micropercops daybri* Fowler and Bean, USNM 83982; *Ophiocara porocephala* (Valenciennes), USNM 243450; *Oxyeleotris marmorata* (Bleeker), USNM 230328; *Percottus glehni* Dybowski, USNM 77008; *Periophthalmus* species, USNM 249848; *Rhyacichthys aspro*, USNM 247300; *Taenioides limicola* C.L. Smith, USNM 222998; *Tridentiger obscurus* (Temminck and Schlegel), USNM 214523.

I maintain a large and varied collection of cleared and stained specimens of teleost (mostly perciform) fishes that I use to evaluate skeletal characters. Many of these specimens have been listed in earlier studies of mine, and many of these specimens, as well as new additions to the collection, were referred to during the course of the present study.

ACKNOWLEDGMENTS.—Appreciation for the loan of specimens is extended to the following: C.E. Dawson (GCRL), D.F. Hoese (AMS), and D.E. Rosen (AMNH). My colleagues at the Smithsonian Institution, E.A. Lachner and S. Jewett, permitted me to examine skeletal material that they had prepared for use in their own

studies. Helpful discussions (some by mail) were carried on during the course of the work with R.S. Birdsong (Old Dominion University, Norfolk, Virginia), D.F. Hoese, G.D. Johnson (Charleston, South Carolina), E. Murdy (Texas A&M University, College Station, Texas), D.E. Rosen, and S.H. Weitzman. W.F. Smith-Vaniz (Academy of Natural Sciences, Philadelphia) provided information on skeletal characters of several species of Opistognathidae. The manuscript was reviewed critically and substantially improved by suggestions from R.S. Birdsong, R. Winterbottom (Royal Ontario Museum, Ottawa), and D.F. Hoese.

Grants from the Smithsonian Scholarly Studies Program and the Max and Victoria Dreyfus Foundation supported field work in Fiji that resulted in obtaining important material of the new genus and species.

### Family GOBIIDAE

**DIAGNOSIS.**—Gobioid fishes (see "Characters and Classification of the Gobioidae," page 29) with the following synapomorphies: fewer than 3 epurals (3 only in variant specimens); no lateral line on body; no mandibular sensory canal; no more than 3 rows of ctenii on scales (only marginal row may be tooth-like); dorsal end of interhyal articulating with hyomandibula, widely separated from symplectic; large space separating shank of symplectic from preopercle.

#### Subfamily XENISTHMINAE

**DIAGNOSIS.**—Gobiid fishes with free ventral margin of ventral lip extending without interruption across dentary symphysis; premaxillary ascending process greatly reduced or absent (process, if present, lower than anterior maxillary articulating process of premaxilla; Figures 6 and 8b); rostral bone (ossified rostral cartilage, Figure 7) present, completely or almost completely replacing premaxillary ascending processes in position and function; and lacking: basibranchials 2 to 4, hypobranchials 3 (which may be repre-

sented vestigially as cartilaginous fragments), pterosphenioids, and coronomeckelian bones.

All of the above characters, except the absence of the pterosphenioids, appear to be synapomorphies of the Xenisthminae; however, the osteology is unknown for 2 of the 4 genera that I include in the Xenisthminae (based on the presence of an uninterrupted ventral-lip margin; see "Composition" below). The pterosphenioids are absent (homoplasiously?) in some microdesmin gobiids, for instance *Clarkichthys bilineatus*, but present in others, for instance *Paragunnellichthys seychellensis*. In the gobiin *Parioglossus taeniatus*, the pterosphenioids are represented on each side only by tiny fragments of bone and cartilage; the other species of *Parioglossus* examined had moderately well-developed pterosphenioids. It is conceivable that the pterosphenioids are absent in other specimens or species of *Parioglossus*. A rostral bone is present in *Cerdale ionthas* and *Paragunnellichthys seychellensis*, but absent in *Microdesmus dipus*, *Clarkichthys bilineatus*, and *Gunnellichthys pleurotaenia* (all microdesmins). The rostral bone is also present in *Parioglossus taeniatus* (but not in the other species of *Parioglossus* examined), and in a species of *Kraemeria* (but not in *K. bryani*). In all these taxa the ascending premaxillary processes are well developed, and all have basibranchials 2 to 4, hypobranchials 3, and coronomeckelian bones. The possibility exists, nevertheless, that some of these taxa have a sister-group relationship with the Xenisthminae.

The following xenisthmin characters also occur in various non-xenisthmin gobioids: 6 branchiostegals, no postcleithra, no mesopterygoids, pelvic fins not united.

**COMPOSITION.**—*Xenisthmus* Snyder and Tyson, new genus, and probably an undescribed genus and species (based on characters furnished by D.F. Hoese, in litt., 1983), and *Allomicrodesmus* Schultz (monotypic). These four genera possess the uninterrupted free ventral-lip margin.

**REMARKS.**—*Xenisthmus* was first used as the basis of a family-group taxon by Miller (1973:426), who proposed the subfamily Xenisthminae in the Gobiidae to include *Xenisthmus*

alone. None of Miller's diagnostic characters for the subfamily are synapomorphies. Birdsong (1975) questioned Miller's logic in establishing the taxon; with no more information available than that offered by Miller, I would have had to agree with Birdsong's doubts. My reaffirmation of the Xenisthminae stems from the number and extreme distinctiveness of the specializations exhibited by *Xenisthmus* and *Tyson*.

In recognizing the Xenisthminae as a subfamily of the Gobiidae, I am following essentially the gobioid classification scheme given by Miller (1973). Miller recognized only two families in the Gobioidae: Rhyacichthyidae and Gobiidae. Families, such as Microdesmidae, Eleotrididae, Gobioidae, and Kraemeriidae,<sup>1</sup> were either relegated to subfamily status under the Gobiidae or were not recognized. I do not wish to comment on Miller's scheme except to say that I believe that several of his subfamily groups are probably paraphyletic or polyphyletic. In particular, I believe this to be true of the Eleotrididae, which is usually considered to be the primitive sister group of all non-rhyacichthyid gobioids. My main reason for this belief is that there is no synapomorphy that defines the eleotridids.

Schultz (1966), based on inaccurately described characters, initially placed *Allomicrodesmus* in the Microdesmidae. Dawson (1974:409) gave a corrected description of the holotype (and only known specimen) and properly excluded the genus from the Microdesmidae. Dawson was unable to assign *Allomicrodesmus* to a family, but Larson and Hoese (1980) assigned it to the Eleotrididae. *Allomicrodesmus dorotheae* Schultz is known only from the holotype (USNM 113960), from the Marshall Islands, and a specimen from the Great Barrier Reef (AMS I.18740-100). I have examined the latter specimen and find it to be an adult male, 20.0 mm SL (measured from upper-jaw tip; lower jaw protrudes). It is very delicate and slender (greatest depth 1.3 mm). The dorsal fin is single and continuous (the first 2 elements are spines, followed by 32 simple, segmented rays). The anal fin comprises 25 simple elements, the first of which is probably a segmented ray, but I

was unable to satisfy myself of this. There are 3 simple rays in each pelvic fin (I cannot determine if a spine is also present) and the fins are closely approximate at their bases, but not connected by membrane. There are 6 branchiostegals on each side. The gill membranes form a continuous free fold across the isthmus.

#### **Tyson, new genus**

**DIAGNOSIS.**—A minute fish (less than 20 mm SL) of the subfamily Xenisthminae, lacking: scales, extrascapular bones, lacrimal, gill rakers, an anterior spinous dorsal fin, exoccipital condyles (and, consequently, lateral condyles on the atlas), an uncinat process on epibranchial 1, an interarcual cartilage (Travers, 1981), and infrapharyngobranchials 2 and 4 (including toothplate); and having: 13 + 13 vertebrae, an ossified basibranchial 1, teeth on vomer, fused anterior and posterior ceratohyals, and a single, simple, segmented ray (and no spine) in each pelvic fin (the pelvic-fin formula, 1, alone, is adequate to distinguish *Tyson* from all other gobioids).

Other characters, including many restricted to *Tyson* in the Xenisthminae, are those of the single included species, *Tyson belos*, new species (type-species by original designation and monotypy).

**ETYMOLOGY.**—The generic name is derived from the forename of Tyson R. Roberts, who collected the first specimen and recognized its distinctiveness. Gender, masculine. The stem for formation of family-group and higher level taxa is "tyson."

**COMPARISONS.**—Until more information is available on the other genera of the Xenisthminae, I consider *Tyson* to be most closely related to *Xenisthmus*. In contrast to *Tyson*, *Xenisthmus* has scales, extrascapular bones, a lacrimal, gill rakers, an anterior spinous dorsal fin, exoccipital condyles, an uncinat process on epibranchial 1, an interarcual cartilage, and infrapharyngobranchials 2 and 4 (toothplate), only 10 precaudal vertebrae, a cartilaginous basibranchial 1, an edentate vomer, autogenous anterior and posterior ceratohyals, and pelvic fins I,5. In addition, ex-

cluding the anteriormost anal-fin pterygiophore, *Xenisthmus* has only one dorsal- or anal-fin pterygiophore inserted in each interneural or interhemal space, whereas *Tyson* has 2 or 3. It is possible, however, that *Tyson* is most closely related to *Allomicrodesmus*, which, similar to *Tyson*, has greatly reduced the number of dorsal-fin spines (to 2) and segmented pelvic-fin rays (to 3 in each fin). The undescribed xenisthmine genus is unique among gobioids in having rows of palatine teeth (D.F. Hoese, in litt.).

### *Tyson belos*, new species

#### FIGURE 2

This new species is so distinctive that only a diagnostic description is given here. The description is supplemented by the generic diagnosis presented above and the osteological description (p. 7). Characters of the holotype are indicated by an asterisk.

**HOLOTYPE.**—AMS I.22583-031;  $19.0 \pm 0.5$  mm SL; sex unknown (immature); Australia, Queens-

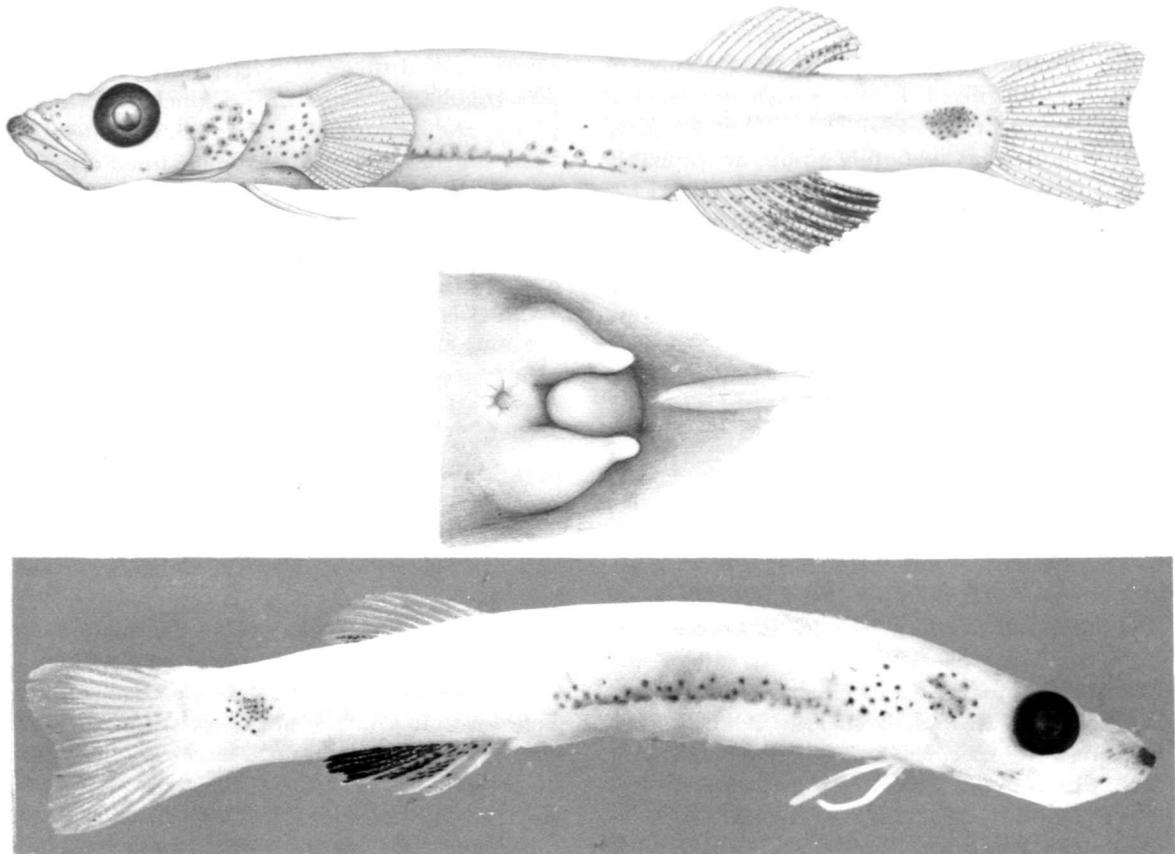


FIGURE 2.—*Tyson belos*, USNM 229985, paratype, female, 18.8 mm SL, Kiriwina Island, Trobriand Islands, Papua-New Guinea (specimen now cleared, stained, and dissected): *top*, left lateral view; *middle*, enlarged ventral view of anus and urogenital papilla (drawings by J.R. Schroeder); *bottom*, right lateral view (photograph by J.F. McKinney).

land, Escape Reef, outer barrier, coral bottom, depth 29 m; coll. 29 Oct 1981 by G. Allen, W. Starck, and T. Ayling.

PARATYPES.—USNM 229985, 18.8 mm SL, ripe female, Papua–New Guinea, Trobriand Islands, west side Kiriwina Island, coral reef, coll. 19 Sep 1975 by T.R. Roberts; specimen now cleared, stained, and dissected. USNM 233515, 12.9 and 16.2 mm SL, sexes unknown, Fiji, Lau Islands, Ono-ilau, outside barrier reef on northwest side of island, depth ~13.7 to ~16.8 m, coll. 1 May 1982 by V.G. Springer et al.

DESCRIPTION.—Dorsal fin I,9 to I,10\* (I,8 to I,9\* if last two rays are counted as one; see Figure 18). Anal fin I,9 to I,10\* (I,8 to I,9\* if last two rays are counted as one). Pectoral fins 17\*, 18, or 21. Pelvic fins not joined, each consisting of a single, unbranched, segmented ray (no spine). Caudal fin emarginate, with 8\* or 9 dorsal procurrent rays; 3 to 5\* simple, segmented dorsal rays; 4\* or 5 branched, segmented dorsal rays; 3\* or 4 branched, segmented ventral rays; 3 to 5\* simple, segmented ventral rays; and 9\* ventral procurrent rays, for a total of 33 or 34\* elements, of which 15 or 17\* are segmented, and of these 7\* to 9 are branched. Vertebrae 13\* + 13\* = 26\*. Branchiostegals 6\*. Scales, gill rakers, sensory pores (except anterior and posterior nostrils) lacking.

Anterior nostril borne on short tube; tube, when depressed, reaches to upper lip; posterior nostril a simple pore just posterior to base of tube of anterior nostril.

Gill openings of holotype and largest paratype extend anteriorly to below level of middle of orbit; in smallest paratypes, to below level of posterior third of orbit.

Color in alcohol: ground color of body pale with few patches of melanophores. Holotype and smallest and largest paratypes each have patch of melanophores on midside of caudal peduncle. Holotype and largest paratype have patches of melanophores posteriorly on dorsal and anal fins. In holotype, dorsal- and anal-fin melanophore patches are extensive, intensive, and occupy approximately same relative area as anal-fin melan-

ophore patch of largest paratype. Dorsal-fin melanophore patch of largest paratype much reduced in area; patch completely absent in two smallest paratypes.

A color transparency photograph (in the USNM collections) taken of the freshly collected holotype is noteworthy mainly for the specimen's exhibiting an irregularly shaped, pinkish spot posteroventrally on the lateral surface of the head, and for a pale rust-colored perfusion about the melanophores on the caudal peduncle. Similar rust-colored areas are also present on the ventrolateral portions of the head and abdomen.

REMARKS.—Although there are only four specimens of *T. belos* available, it appears that there may be geographic variation in fin-ray counts (asterisks indicate counts of holotype). Decision as to whether the differences noted are significant or the result of biased sampling will have to await the availability of more specimens.

Locality	Dorsal fin	Anal fin	Pectoral fins (left/right)
Trobriand Islands	I,10	I,10	21/21
Great Barrier Reef	I,10*	I,10*	17/17*
Lau Islands	I,9	I,9	18/18
	I,9	I,9	18/17

ETYMOLOGY.—The specific name *belos* (arrow), here used as a noun in apposition, is from the Greek and refers to the arrow-like shape of the species.

#### Osteology of *Xenisthmus* and *Tyson*

In the following descriptions, each portion of the skeleton is described first for *Xenisthmus* and then for *Tyson*.

#### CRANIUM

*Xenisthmus* (Figures 3 and 6): All the cranial bones are autogenous, with the possible exception of the pterosphenoids, which are either fused with the sphenotics or absent. The vomer (edentate) and median and lateral ethmoids are well ossified. The lateral ethmoids are separated medially by the ethmoid cartilage, which fills the anterior

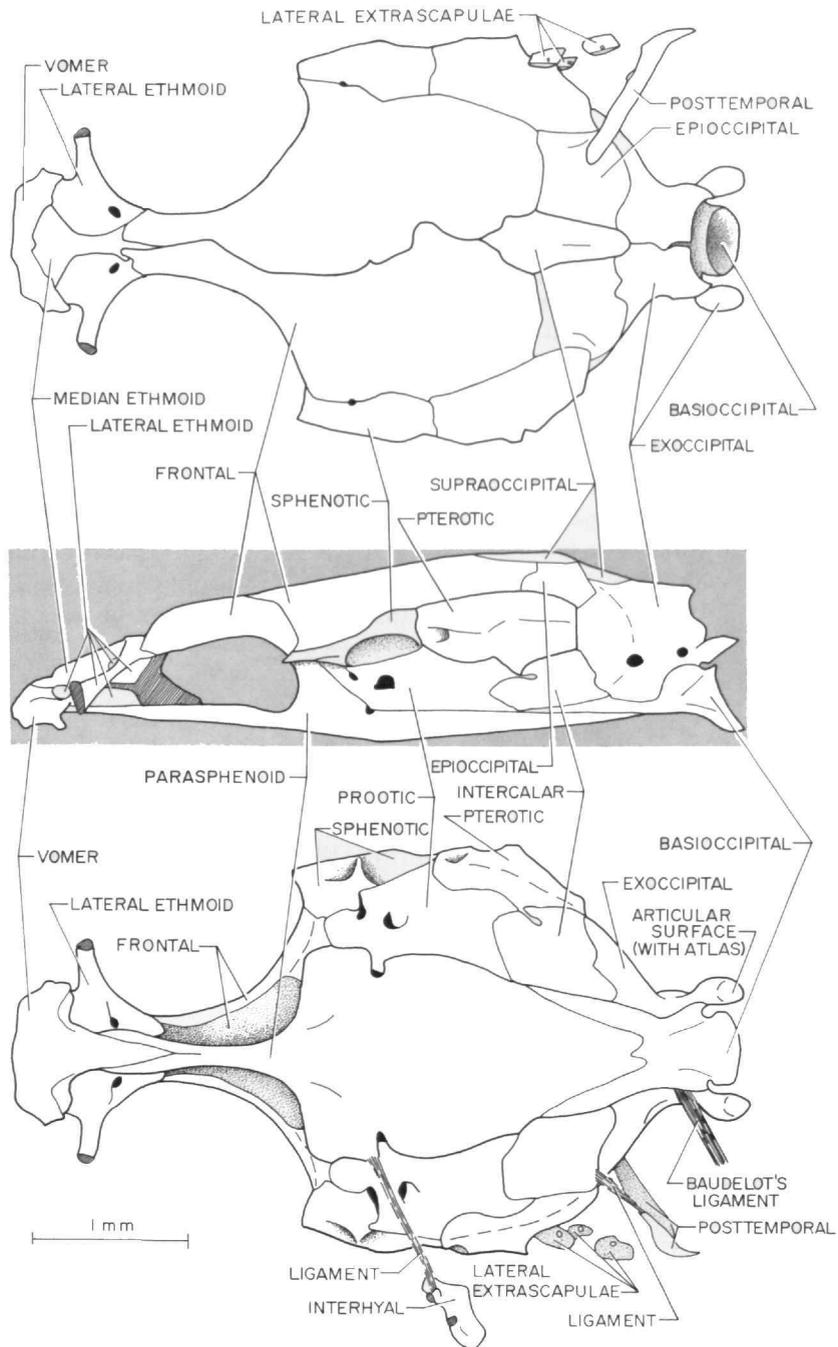


FIGURE 3.—*Xenisthmus clarus*, cranium with some associated bones and ligaments (diagonal hatching represents cartilage): *top*, dorsal view; *middle*, lateral view; *bottom*, ventral view (medial aspect of interhyal illustrated; see also Figure 9).

interorbital region. Each lateral ethmoid bears a strong, cartilaginously tipped, laterally projecting process, to which its respective lacrimal attaches, and each is pierced by a foramen for the olfactory tract.

The frontals are two to three times as long as broad, and they are firmly joined to the ethmoids. Each frontal bears a groove, which is perforated by three minute foramina (not visible in Figure 3), in the supraorbital region, along which the supraorbital canal courses. The groove (and canal) continues along the dorsolateral surfaces of the sphenotic and pterotic. In the postorbital region, each frontal bears a descending wing, which joins its respective sphenotic and prootic, and a parasphenoid ascending wing.

There are no parietals. The epioccipitals are joined along their dorsomedian margins (not visible on external surface of skull) below the supraoccipital, which bears a slight dorsomedian ridge posteriorly. There is no indication of cartilage (blue stain) in the line of junction between the epioccipitals. A flattened area on the posterolateral dorsal surface of each epioccipital serves as the area of attachment for the dorsal arm of its respective posttemporal.

The exoccipitals each bear a lateral condyle that articulates with the lateral condyle on its respective side of the atlas vertebra. The articulating surfaces of the exoccipital condyles are inclined ventroposteriorly. Each exoccipital is pierced by two foramina: the more anterior is the vagal foramen; the more posterior is probably for passage of a spinal nerve. Each exoccipital is excluded from meeting its respective prootic by an interosseous space (subtemporal fossa of Birdsong, 1975) that is bounded by the prootic, pterotic, exoccipital, and basioccipital. Each interosseous space is covered by a large intercalar, which broadly overlaps the four bones surrounding the space. A ligament extending from the ventral arm of each posttemporal attaches to the posterodorsal surface of its respective intercalar close to the junction of the intercalar with the exoccipital. The exoccipitals form the dorsal and lateral walls of the foramen magnum, which is floored by the basioccipital.

The basioccipital articulates with the parasphenoid anteriorly, the centrum of the atlas posteriorly, the exoccipitals dorsally, and the prootics dorsoanteriorly (most of each basioccipital-prootic joint is obscured from view by the overlying intercalar). Each Baudelot's ligament originates on its respective side from a minute process on the posterior midlateral surface of the basioccipital, extends posterolaterad, passing freely through a deep notch in the dorsal end of the cleithrum, and inserts on the posterointernal surface of its respective supracleithrum.

Each prootic articulates with the parasphenoid along the prootic's ventral and anterior margins; with its respective frontal, sphenotic, and pterotic along the prootic's dorsal margin; with its respective intercalar along the prootic's posterior surface; and with the basioccipital along the prootic's posteroventral margin. Each prootic forms only a minute part (ventral rim) of the large sphenotic socket on its respective side that articulates with the dorsoanterior condyle of its respective hyomandibula. (There is a relatively small socket, for reception of the posterodorsal condyle of each hyomandibula, in the anterolateral region of its respective pterotic.) Two large foramina, for passage of the trigemino-facial nerve complex, pierce the wall of each prootic. On each side, ventral to the posterior of these two foramina, is the internal carotid foramen, formed by a notch in the margin of the parasphenoid. Just anterolaterad of each of the internal carotid foramina, there is attached to the parasphenoid, a long, cord-like ligament that extends ventrolaterally and attaches to a process on the medial surface of the respective interhyal (Figure 3).

The prootics lack internal shelves that might form a roof for the posterior myodome. There is, instead, a shallow, anteriorly opening pocket with a thin roof arising from the middorsal surface of the parasphenoid just posterior to the level of the anterior margins of the parasphenoid ascending processes. According to Birdsong (1975: 148, fig. 6B) the medial, inferior, and superior rectus muscles attach in this cavity.

The otoliths were not present, possibly having been lost during preservation and osteological

processing of the specimen. Otoliths are present in the comparative skull, but I did not attempt to extract them.

*Tyson* (Figure 4): Anteriorly there is a single, almost laminar, bone, which appears to comprise fused lateral and median ethmoids, which also appear to be fused to the dorsoanterior surface of the vomer. There is visible on the ventral surface of the cranium, however, a separation of the vomer from the fused ethmoid complex and the parasphenoid. The separation of the dorsoventrally flattened shank of the vomer from the parasphenoid is also visible in a lateral view of the cranium, but no joint can be seen between the vomer and ethmoid complex when the cranium is viewed from in front. An opening for passage of the olfactory tract pierces the complex ethmoid bone on either side.

The vomer bears a single marginal row of nine teeth, comprising four large, recurved canines on each side, separated by a greatly reduced median tooth. These canines are clearly evident when the mouth of an intact specimen is open, and they form the posterior portion of a tooth patch in common with the anterior teeth of the premaxillae.

The anterior ends of the long (over four times longer than broad), paired frontals overlap the ethmoid bone posteriorly. Beginning ventral to the junction of the frontals and ethmoid complex, and extending anteriorly, is the mass of the ethmoid cartilage, which is unstained anteriorly.

The frontals, which bear no sensory canals, extend posteriorly for most of the dorsal surface of the skull, overlapping the anterior end of the supraoccipital, the dorsomedial margins of the fused sphenotic-pterotic complexes, and the anterior ends of the epioccipitals; there are no parietals. Each sphenotic-pterotic complex appears to be a single ossification, with no indication of a line of fusion. Even so, I treat the anterior portion bearing the facet for articulation with the dorsoanterior condyle of the hyomandibula as sphenotic, and the remainder, which bears the facet for articulation with the dorsoposterior condyle of the hyomandibula, as pterotic. The separation of the pterotic portion from the dorsoposterior mar-

gin of the prootic is also unclear, but is marked by a narrow unstained area. I have illustrated (Figure 4) this unstained area as a joint line that is continuous with the joint line between the exoccipital and basioccipital.

On each side of the cranium, in the postero-medial portion of the orbital region, there is a prominent ventrally extending process that is continuous with the sphenotic. Each process represents either a flange of the sphenotic or a fused pterosphenoid (see discussion of prootic, p. 12).

Although the anterior margin of the supraoccipital is reasonably discernible through the transparent frontals, the remaining extent of the supraoccipital and its joints with the epioccipitals are obscured by a granular-appearing area, possibly representing the line of fusion of the supraoccipital with the epioccipitals. (The posterior margin of the supraoccipital as delineated in Figure 4 is even less certain than indicated.) The presumed posteriormost portion of the supraoccipital bears a very short, low, median ridge, which continues posteriorly as the slightly raised joint of the posterodorsally conjoined epioccipitals and the dorsally conjoined exoccipitals.

The relatively small epioccipitals each bear a flattened area dorsally, to which their respective posttemporal is attached. I was unable to determine if the epioccipitals are conjoined synchronally beneath the supraoccipital (Birdsong, 1975, table 1).

The exoccipitals are most noteworthy for lacking condyles for articulation with the atlas (which, consequently, lacks lateral condyles and articulates only with the basioccipital). Each exoccipital is excluded from making contact with its respective prootic by a meeting of the pterotic and basioccipital. The exoccipitals are each pierced by a large vagal foramen; no other foramina are present in these bones. The ligament extending from the posterior end of each posttemporal attaches tightly to a minute process on the midanterolateral surface of its respective exoccipital just posterior to the joint between the exoccipital and pterotic and just below the level of the laterally widest expansion of the pterotic. There are no intercalars. The exoccipitals form the lat-

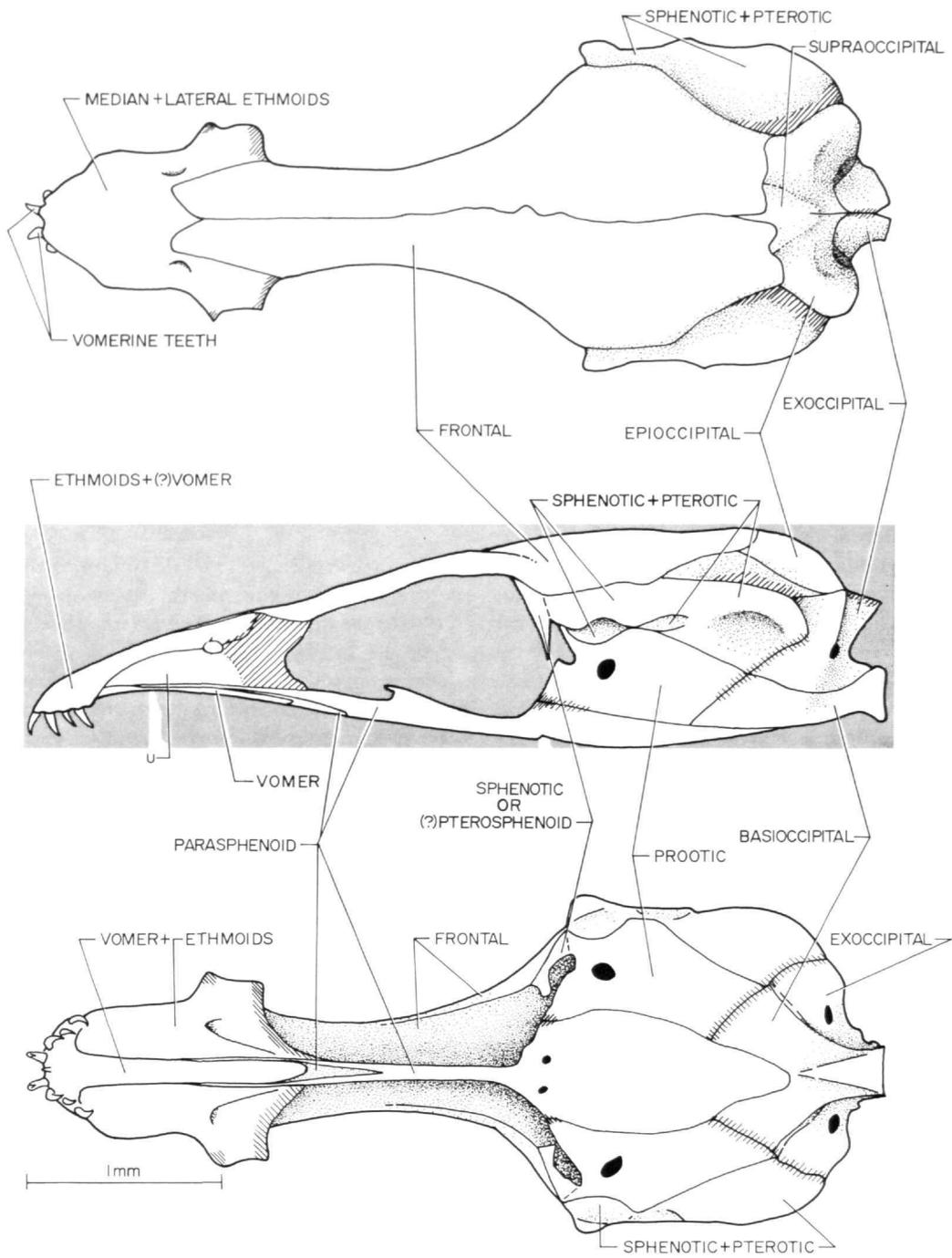


FIGURE 4.—*Tyson belos*, cranium (diagonal hatching represents cartilage): *top*, dorsal view; *middle*, lateral view (U = unstained portion of ethmoid cartilage); *bottom*, ventral view.

eral and dorsal walls of the foramen magnum, which is floored by the basioccipital.

The broadly Y-shaped basioccipital articulates with the atlas posteriorly and accepts the posterior end of the parasphenoid between its anteriorly extending arms, each of which articulates anteriorly with the posterior ends of its respective prootic. Each Baudelot's ligament has a short bifurcation at its proximal end. The anterior branch of the bifurcation attaches to the posterolateral surface of the basioccipital and the posterior branch attaches to a closely adjacent area on the anterolateral margin of the atlas vertebra. The ligament extends posterolaterally and passes freely through a notch in the dorsal process of the cleithrum, then proceeds anteriorly and inserts on the dorsomedial surface of the supracleithrum. Possibly, the bifurcation of Baudelot's ligament and its attachment to both the basioccipital and atlas, rather than only to the basioccipital (as in *Xenisthmus*), is an adaptation for strengthening the connection between the skull and vertebral column, which in other gobioids is shared by three skull bones rather than one.

Each prootic articulates with the parasphenoid along the prootic's ventral margin, with its respective fused sphenotic-pterotic along the prootic's dorsal margin, and impinges slightly (at most) on the ventrolateral margin of the ventrally extending process of the sphenotic in the post-orbital region. Each ventrally extending process appears to form the incomplete anterior border of an opening (anterior passageway for the trigemino-facial nerve complex?) whose posterior border is a notch on the anterior margin of the prootic. In most gobioids with pterosphenoids, each pterosphenoid forms the anterior margin, and the prootic the posterior margin, of the anterior foramen for passage of the trigemino-facial nerve complex. Inasmuch as both foramina for passage of the trigemino-facial nerve complex are contained only in the prootic of *Xenisthmus*, which lacks pterosphenoids, it would appear that the ventrally extending sphenoid processes of *Tyson* represent fused pterosphenoids. Each prootic contains a single complete foramen for passage of the trigemino-facial nerve complex. The prootics

do not bear a shelf on their medial surface, and there is no bony roof over the posterior myodome.

The parasphenoid is perforated by a pair of carotid foramina near the anterior end of its posterior broad portion, and bears a low, median, anteriorly directed hook-like process on the dorsal, interorbital surface of its slender anterior shank, which overlaps the shank of the vomer. There is no bony pocket for reception of the rectus muscles of the eyes in the dorsal surface of the parasphenoid within the cranial vault, as there is in *Xenisthmus*.

The otoliths were not present, possibly having been lost during preservation or osteological processing.

#### JAWS, SUSPENSORIUM, SUPERFICIAL BONES OF HEAD

*Xenisthmus* (Figures 5 and 6; for comparison with the snout region of a relatively unspecialized gobioid see Figure 7): The premaxillae are well-developed bones, each bearing an outer row of large recurved, conical teeth and an inner row of similar but much smaller teeth (in the comparative specimen, the outer row is only slightly larger than the inner teeth, which are scattered over the ventral surface of the premaxillae, but nowhere in more than three rows). Each premaxilla has anterior (articular) and posterior maxillary processes, but lacks an ascending process. The portion of the premaxilla that normally bears an ascending process is reduced to a flattened facet that articulates with a corresponding ventrolateral facet at the end of the median, unpaired, rostral bone, which has functionally replaced the ascending processes of both premaxillae. In the comparative specimen, the ascending processes are represented by facet-bearing knobs, which are, however, lower than the anterior articular processes. The rostral bone, which has a cartilaginous dorsal end, is an ossified rostral cartilage. The rostral bone bears thin anterodorsal and posteroventral flanges on each side. A band-like ligament connects each of the dorsoanterior flanges to the dorsoanterior margin of the palatine bone on its respective side (in other gobioids,

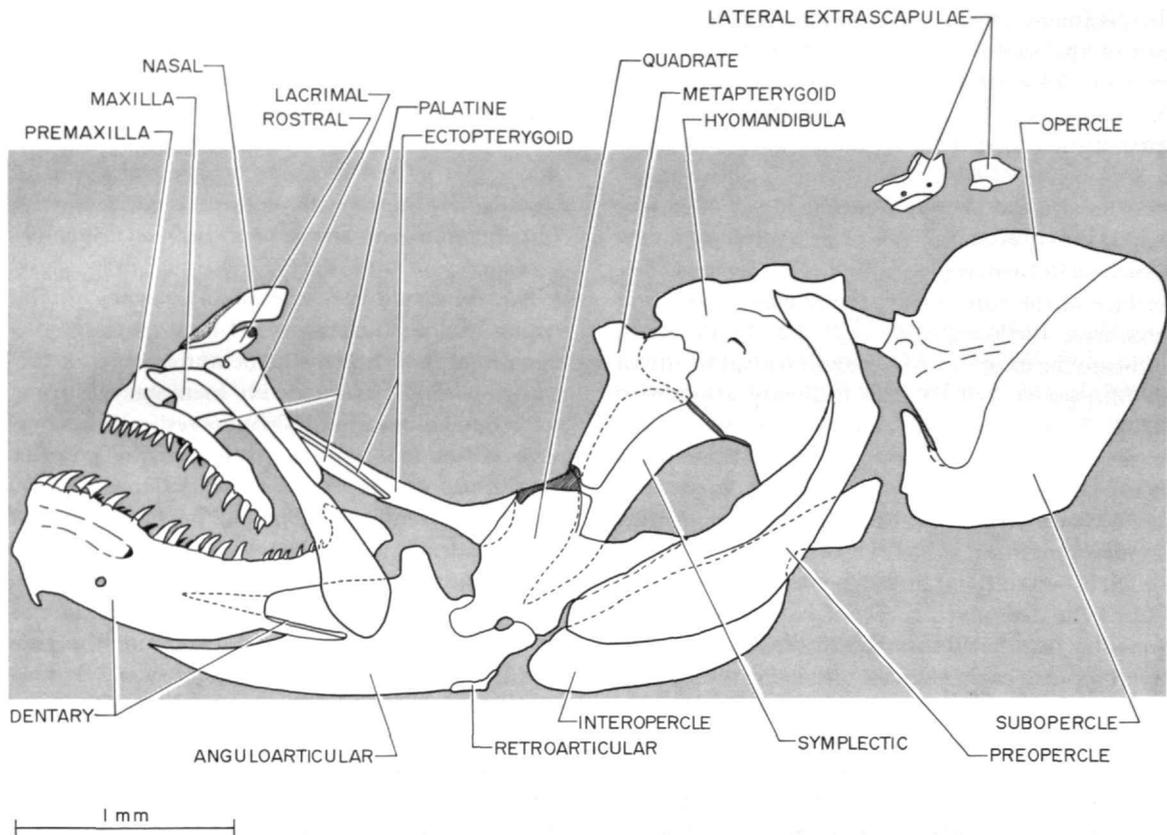


FIGURE 5.—*Xenisthmus clarus*, lateral view of superficial bones, jaws, and suspensorium. (The limits of some bones that are obscured by others are indicated by dashed lines; see Figure 6 for dorsoanterior view of snout region.)

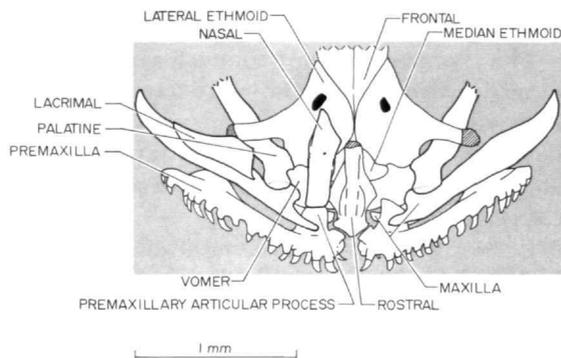


FIGURE 6.—*Xenisthmus clarus*, dorsoanterior view of snout region (frontals and palatines truncated posteriorly; nasal and lacrimal removed from one side; dotted lines indicate margins of maxillary palatine processes obscured by palatines).

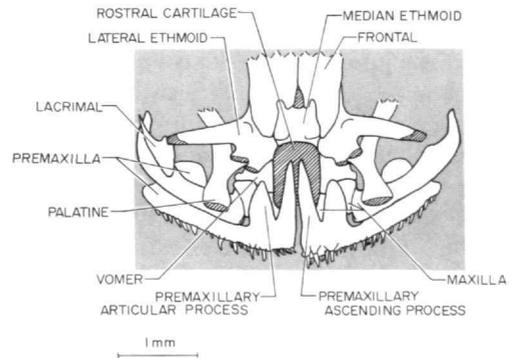


FIGURE 7.—*Eleotris amblyopsis*, dorsoanterior view of snout region (frontals and palatines truncated; lacrimal removed from one side; species lacks nasal bones). Structure of premaxillae and their relation to rostral cartilage represent generalized condition for gobioids.

this ligament attaches the palatine to the dorsal end of the ascending process, thus indicating a shift in "allegiance," but not in function, of the ligament). Another band-like ligament connects each of the posteroventral flanges to the dorsoanterior portion of the palatine process of its respective maxilla. In other gobioids, the same ligament exists, but it is attached to the rostral cartilage, which is, in turn, tightly attached to the posterior surface of the tips of the premaxillary ascending processes. Birdsong (1975:152, fig. 8) does not indicate the existence of a maxillorostral ligament in *Microgobius*, but he does illustrate a ligament labelled "1," which he reports as attaching the base of the premaxillary process to the medial head of the maxilla. There is an unroofed nasal bone on each side of the rostral bone. A small foramen perforates the floor of each nasal bone.

Each maxilla is forked anteriorly where it clasps the articular process of its respective premaxilla. Just dorsal to each maxilla, and laterally overlapping each slightly, is a thin plate-like bone, the lacrimal, which has its strongest attachment with the laterally projecting process of its respective lateral ethmoid. The wall of each lacrimal is pierced by a tiny foramen, but the lacrimals do not appear to bear sensory canals. A suborbital (in agreement with Akihito, 1969) is lacking.

The dentary bones each bear a row of large outer teeth and, anteriorly, two inner rows of much smaller teeth, gradually reducing posteriorly to one inner row (in the comparative specimen the outer teeth are only slightly larger than the inner teeth, which are more or less evenly distributed over the surface of the dentary, but nowhere in more than three rows). The long, club-like maxillodentary ligament on each side inserts in a groove on the anterolateral surface of its respective dentary and connects to the posterior end of its respective maxilla. The anguloarticular on each side inserts into a pocket at the posterior end of its respective dentary. Each long, rod-like Meckel's cartilage extends anteriorly from the endosteal process on the medial surface of its respective anguloarticular to a point in the

hollow end of its respective dentary, just anterior to the level of a foramen that completely perforates the dentary. There is no sensory canal in the mandible. There are no coronomeckelian bones (sesamoid articulars). Each retroarticular is a small bone joined to the ventroposterior end of its respective anguloarticular and is connected by a ligament to the anterior end of its respective interopercle.

The quadrates are the pivotal bones of the suspensorium. Each bears a broad cartilaginous dorsal margin with which the anteroventral, cartilaginous tip of its respective metapterygoid, the posterodorsalmost bony tip of its respective ectopterygoid, and a minute portion of the anterior margin of its respective symplectic articulate. There is a broad groove on the medial surface of each quadrate, to which the ventrolateral surface of its respective symplectic is tightly joined. Each preopercle narrowly overlaps the posterolateral margin of its respective quadrate, and the posterolateral margin of each ectopterygoid is narrowly overlapped by its respective quadrate.

The ectopterygoids are long, rod-like bones, each with a flattened ventrolateral surface along the anterior half of its length. The medial surface of each palatine articulates syndesmotically with a flattened surface of its respective ectopterygoid, but in the anterior region of this joint, the palatine bears a tiny rod of cartilage on its medial surface that participates in the ectopterygoid-palatine articulation.

The symplectics are relatively large. Each forms a synchondral joint with its respective hyomandibula at the symplectic's dorsal end and has a cartilaginous ventral tip on the portion that attaches in the groove on the medial surface of its respective quadrate.

Posteriorly, each metapterygoid broadly overlaps and is tightly joined to the anterolateral surface of its respective symplectic and anterodorsal surface of its respective hyomandibula. Dorsoanteriorly, each metapterygoid is tightly joined to the anterolateral edge of its respective sphenotic.

Each hyomandibula bears three convex con-

dyles, each of which articulates (anterior to posterior) with a socket in its respective sphenotic, pterotic, and opercle. There is a thin, raised flange on the lateral surface of each hyomandibula, to which is tightly and conformably joined a thin, raised flange on its respective preopercle. The preopercular sensory canal courses ventrally along the posterior surface of the groove formed by the compound flange. Anteroventrally, on the medial surface of each hyomandibula, is a broad cartilaginous area. Posterodorsal to this area is the axil formed by the junction of the posterior convex condyle of the hyomandibula with the body of the hyomandibula. The medial surface of the preopercle lies lateral to this axillar area, and the dorsal end of the interhyal is ligamentously attached to this surface well dorsal to the cartilaginous ventral end of the hyomandibula. There may also be weak membranous attachments of the interhyal to the hyomandibula in the axillar area, but I was unable to ascertain such with certainty. The ventral end of each interhyal joins the posterodorsal edge of its respective posterior ceratohyal. This joint forms a lateral bulge, which is accommodated by a deep rounded indentation in the ventral margin of the adjacent interopercle. Each interopercle is attached by ligament at its posterior tip to the ventroanterior margin of its respective subopercle.

The lateral extrascapulae (supratemporals of Akihito, 1971) are contained in the skin dorsal to the opercles. There are two, unroofed, lateral extrascapulae on the left side and three on the right (three on the left and two on the right in the comparative specimen). Akihito (1971) reported that *Xenisthmus clarus* has two extrascapulae on each side, concluding that the anterior and median extrascapulae on each side, which are present in some gobioids, are fused. The presence of three extrascapulae on one side and two on the other in each of my specimens supports Akihito's conclusion; however, in one specimen it is the median and anterior elements that are fused, and in the other specimen, the median and posterior elements. Radiographs of several specimens of

*Xenisthmus* indicate that the presence of three or two extrascapulae on one or both sides are both common conditions. In the osteological preparations, the floor of each of the three extrascapulae is pierced by a tiny foramen; the fused anterior plus median extrascapulae of the opposite side is pierced by two foramina, and the remaining extrascapula, by one foramen. Akihito (1971, figs. 1B, 2H) diagrammed the laterosensory canals and pores of *X. clarus*.

*Tyson* (Figure 8): The premaxillae are slender bones bearing an outer row of small, fine, caniniform teeth, with an incomplete second, inner, row of much larger canine teeth restricted to the anterior ends of the premaxillae. The largest tooth on each premaxilla is adjacent to the symphysis. The premaxillae lack any vestige of ascending processes, but each has anterior (articular) and posterior maxillary processes. The anterior ends of the premaxillae are slightly separated at the symphysis, forming a space into which inserts a narrow process (not visible in Figure 8) at the ventroanterior end of the rostral bone. Each premaxilla articulates with the long, anteriorly forked maxilla on its respective side at the premaxilla's articular process, which is clasped by the maxillary fork. This articulation, together with the same articulation on the opposite side of the head, joins the ventrolateral end of the median rostral bone, which functionally acts as a pair of long premaxillary ascending processes, riding over the dorsoanterior surface of the cranium. A pair of ligaments inserts on the lateral margin of each side of the rostral bone: one ligament of each pair attaches the lower third of the margin to the medial surface of the lateral fork at the anterior end of the maxilla, and the other attaches the middle of the margin to the dorsomedial process of the palatine. There is a process, which bears a cartilaginous cap, on the medial surface of each maxilla just posterior to the base of the maxillary fork.

Each dentary bone bears a single row of large, recurved, canine teeth, the largest of which is just posterolateral to the anteriormost tooth (near dentary symphysis), and just above the anterior

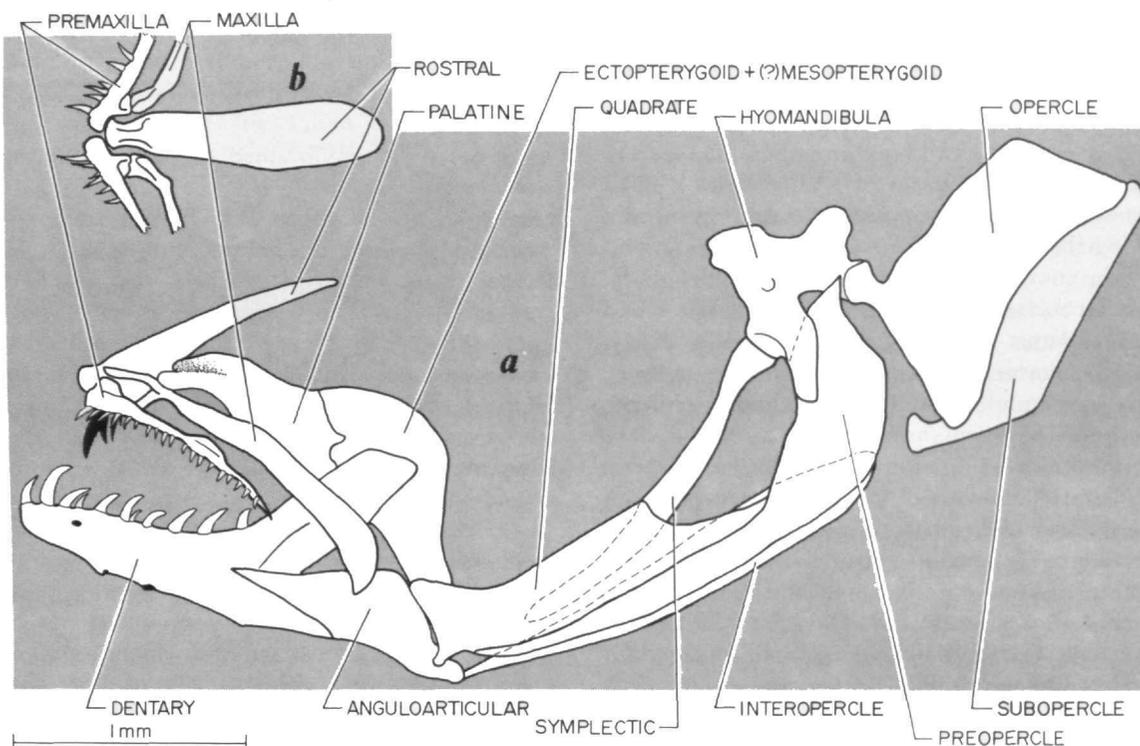


FIGURE 8.—*Tyson belos*, superficial bones, jaws, and suspensorium: *a*, lateral view (limits of some bones that are obscured by others are indicated by dashed lines); *b*, dorsal view of rostral bone showing relationships with anterior ends of premaxillae and maxillae.

attachment of the long, large maxillodentary ligament, which connects the posterior end of the maxilla to the anterolateral surface (which is not grooved) of the dentary. Each dentary bears two or three small foramina, one anterolaterally and one or two along the midventral edge of the bone. As there is no mandibular sensory canal, these foramina are probably for passage of nerves and/or blood vessels. Each Meckel's cartilage is long and slender and extends for most of the length of its respective dentary, continuing posteriorly to its origin on the anguloarticular bone, whose anterior process inserts into a shallow pocket at the dentary's posterior end. There are no coronomeckelian or retroarticular bones, although the latter are probably fused indistinguishably to the anguloarticulars. A short, strong ligament attaches the ventralmost edge of the quadrate

articulating process of each anguloarticular to the anterior end of its respective interopercle.

Each palatine is a laminar bone with a two-tipped process at its anterior end. The ventral of the two tips bears a cartilaginous cap (not shown in Figure 8) and overlaps the lateral surface of the base of the lateral fork of its respective maxilla. The dorsal tip is the attachment point for a ligament that inserts on the midlateral margin of the rostral bone. The posterior end of each palatine broadly overlaps, on its respective side, the anterolateral surface of what appears to be a fusion of the ectopterygoid and mesopterygoid bones. As many gobioids, including *Xenisthmus*, either lack mesopterygoids or have them greatly reduced, it is possible that *Tyson* has no mesopterygoids and that the ectopterygoids and palatines have become broadly expanded relative to their

shape in other gobioids. The ventrolateral surface of each ectopterygoid is joined to the dorsomedial surface of its respective quadrate.

Each quadrate is unusually long and shaped like a scimitar (blade tip directed posterodorsally) with a ledge coursing along its posterolateral margin. The dorsal margin of the ventroanteriorly extending arm of its respective preopercle is tightly bound (fused?) to the ledge. On its medial surface, each quadrate attaches to the ventral half of its respective symplectic. The symplectics are long, rod-like bones, and ellipsoid in cross-section. The posterodorsal end of each symplectic is tightly attached (fused?) to a process on the ventroanterior margin of its respective hyomandibula. There is a broad gap between the symplectic and the preopercle, which is joined near its dorsal end to the ventral arm of the hyomandibula. There is no sensory canal in the preopercle.

Each interopercle, which is almost entirely internal to its respective preopercle, is long and flat, except for a relatively heavy, cup-like process on its posteromedial surface. A knob-like process on the ventrolateral surface of the posterior end of the respective posterior ceratohyal articulates with the cup-like process. Each interopercle is well separated from the ventroanterior process of its respective subopercle and is attached to that process only weakly. The interhyals are tiny and completely ossified dorsally, and each is well separated from its respective symplectic. Each interhyal is ligamentously attached at its dorsal end just dorsal to the ventral end of the medial surface of its respective hyomandibula and to the medial surface of its respective preopercle. Ventrally, each interhyal is attached to a dorsolateral process at the posterior end of its respective posterior ceratohyal.

Each opercle bears a strong, concave dorsoanterior condyle that articulates with the posterior condyle of its respective hyomandibula, and the opercle overlaps and is tightly connected to the dorsolateral surface of its respective subopercle.

Each hyomandibula has two convex condyles dorsally and one posteriorly. The dorsoanterior

condyle articulates with a socket formed completely by the sphenotic (no contribution from the prootic); the dorsoposterior condyle articulates with a socket formed by the pterotic; and the posterior articulates with a socket formed by the opercle.

There are no metapterygoid, lacrimal, suborbital, nasal, or lateral extrascapular bones.

#### HYOID ARCH

*Xenisthmus* (Figure 9): Each side of the ventroanterior end of the urohyal is connected by a short, strong ligament to a large process on the anteromedial surface of the hypohyal on its respective side. The dorsal and ventral hypohyals on each side are fused. (In the comparative specimen, autogenous dorsal and ventral hypohyals are present and the urohyal is attached to the ventral pair.) The dorsoanterior surface of the urohyal is directly beneath and slightly anterior to the median, cartilaginous basibranchial 1 (Figure 11).

Each anterior and posterior ceratohyal pair is joined in a synarthrosis. Each anterior ceratohyal bears a cartilaginous tip ventroanteriorly where the anterior ceratohyal is capped by its respective hypohyal. Each hypohyal (dorsal hypohyal in comparative specimen) bears a rounded dorso-medial process that joins one of the two concave surfaces at the posterior end of the basihyal. Somewhat lateral to the medialmost surface of each hypohyal rounded process is a small area of cartilage. The posterior, deeper portion of each hyoid arch, formed by the anterior and posterior ceratohyals on each side, is concave on its medial surface. Each anterior ceratohyal bears five branchiostegals, the two anteriormost, which are attached to the ventral side of the slender, anterior portion of the anterior ceratohyal, are the smallest; the next three branchiostegals are attached laterally on the expanded portion of the anterior ceratohyal, and the anteriormost of these is the largest of all the branchiostegals. The posteriormost branchiostegal is attached to the posterior surface of the posterior ceratohyal. The ventral

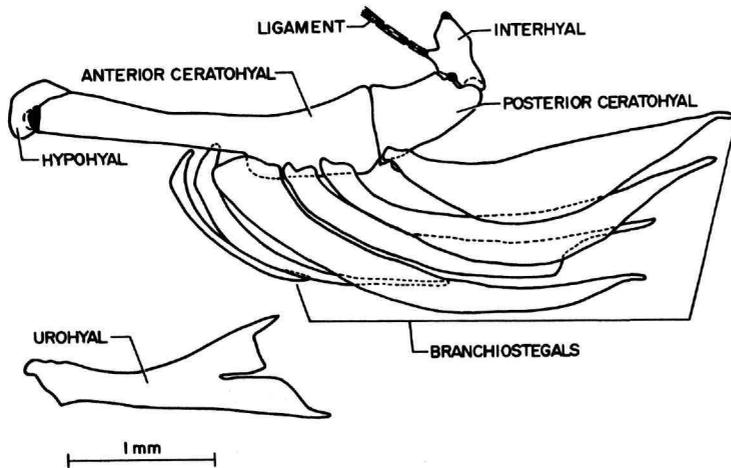


FIGURE 9.—*Xenisthmus clarus*, lateral view of urohyal and left hyoid arch, rotated  $\sim 45^\circ$  clockwise about long axis (the limits of some bones that are obscured by others are indicated by dashed lines; two small areas of cartilage on the interhyal and one at the anterior end of the anterior ceratohyal are indicated by diagonal hatching; ligament attaching to interhyal extends to parasphenoid, Figure 3).

end of each interhyal is syndesmotically joined to the dorsoposterior end of its respective posterior ceratohyal. Each interhyal bears a cartilaginously tipped dorsal process, a cartilaginously tipped ventroanterior process (which articulates with the posterior ceratohyal), and a prominent midanteromedial process from which a strong cord-like ligament extends to the parasphenoid (Figure 3).

*Tyson* (Figure 10): The dorsoanterior surface of the urohyal is tightly joined to the ventral surface of the ossified basibranchial 1 (Figure 13). There is a single hypohyal on each side (each probably representing a fusion of the dorsal and ventral hypohyals of each side), and a single ceratohyal on each side (each representing a fusion of the anterior and posterior ceratohyals of each side). Of the 6 branchiostegals on each side, the 2 smallest are attached to the narrow anterior process of their respective ceratohyal, and the remaining four to the broad posterior process. Each interhyal is attached on its ventromedial surface to a process on the dorsolateral surface of the posterior portion of its respective ceratohyal. There is a tiny area of cartilage on the medial surface of the interhyal at its point of attachment to the ceratohyal. The presence of a ligament extending from the interhyal to the parasphenoid was not noticed (and was probably not present), but may have been removed early in the dissection before I became aware of the existence of

such a ligament in *Xenisthmus*. The right ceratohyal exhibits an incomplete ventral separation, with cartilage present between the attachment of the fourth and fifth posteriormost branchiostegals. This separation is probably a landmark for separation of the anterior and posterior ceratohyals that are normally present in fishes.

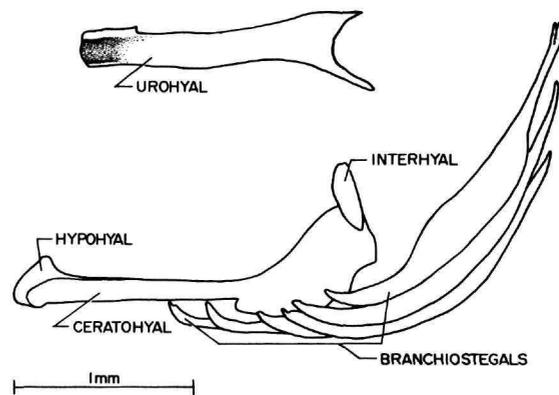


FIGURE 10.—*Tyson belos*, lateral view of urohyal (isolated) and left hyoid arch, rotated  $\sim 45^\circ$  clockwise about long axis.

#### BRANCHIAL APPARATUS

*Xenisthmus* (Figure 11; for comparison with a relatively unspecialized gobioid branchial apparatus, see Figure 12): The basihyal is a relatively thin, dorsally concave, ventrally convex bone that

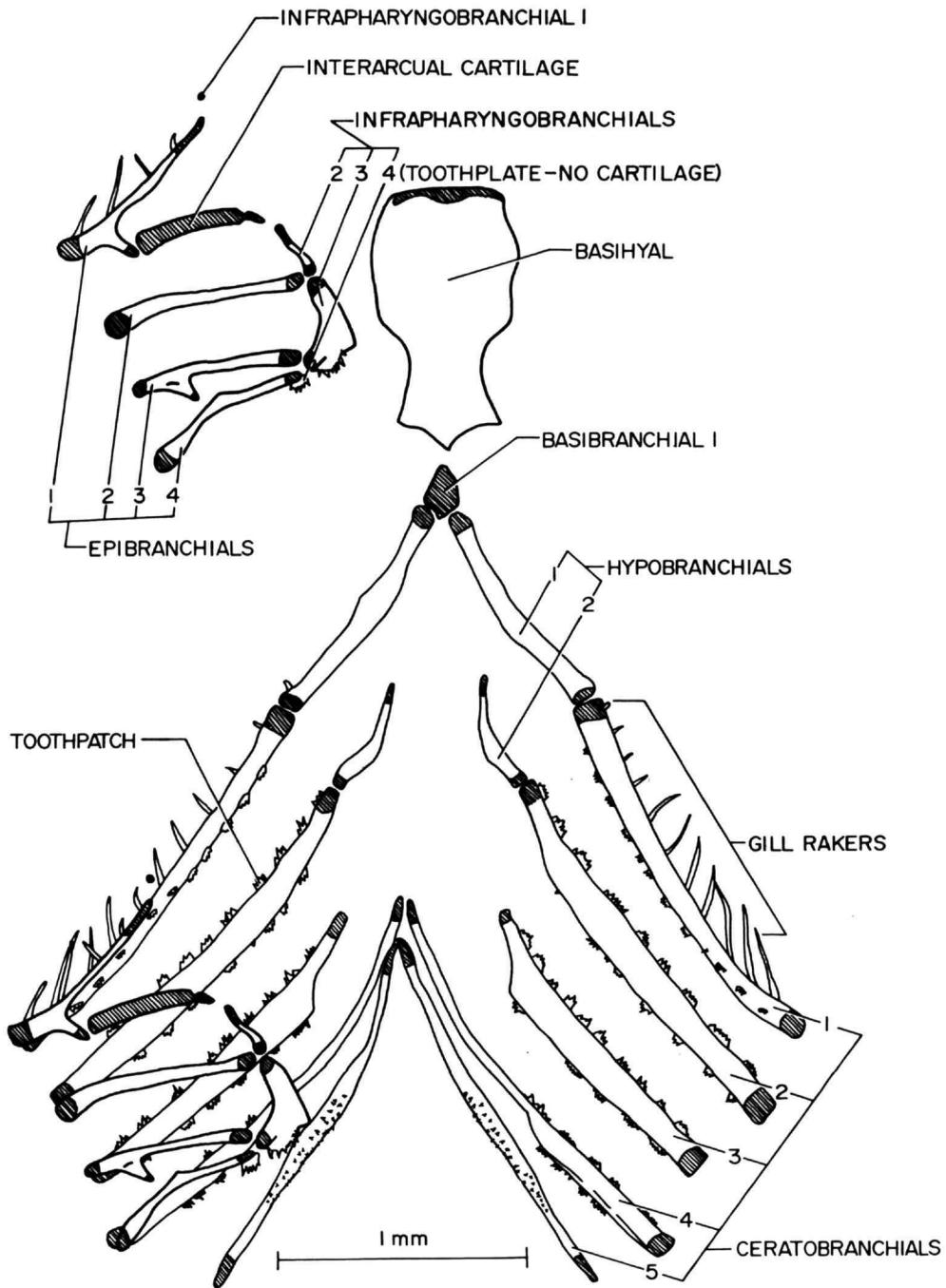


FIGURE 11.—*Xenisthmus clarus*, dorsal view of gill arches and basihyal (right-side dorsal elements removed; left-side dorsal elements illustrated both in place and separately; arches spread slightly for clarity).

attaches to the hypohyals at its posterior end and bears a cartilaginous margin anteriorly. The basihyal is slightly removed anteriorly from the small cartilaginous basibranchial 1, which is at-

tached posteriorly to the anterior, cartilaginous ends of the hypobranchials 1. There are no other basibranchials present, either as cartilage or bone. Of the hypobranchials, only 1 and 2 are present

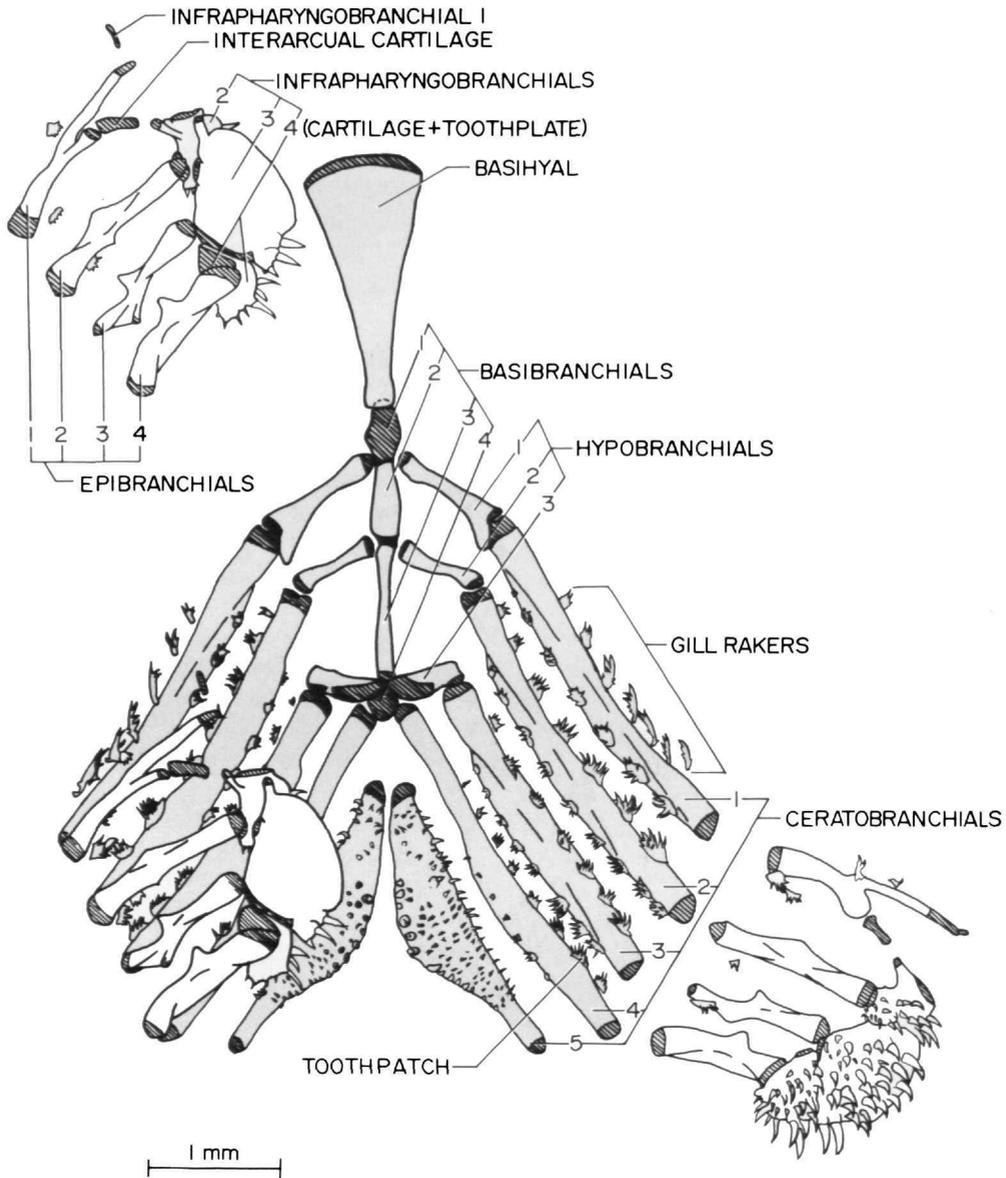


FIGURE 12.—*Eleotris amblyopsis*, dorsal view of gill arches and basihyal (right-side dorsal elements removed and illustrated from ventral aspect; left-side dorsal elements illustrated both in place and separately). Structure represents generalized condition for gobioids.

(a small piece of cartilage, representing a vestigial hypobranchial 3, is present on each side in the comparative specimen). The hypobranchials 2 are widely separated at their anterior ends. Ceratobranchials 1–5 are present. Slender gill rakers (without teeth) are present on the anterior margins of ceratobranchials 1 and epibranchials 1, and a single, small gill raker is present posteriorly on the left hypobranchial 1, but not on the right, or on either of the hypobranchials 1 of the comparative specimen. The posterior margins of ceratobranchials 1 and both margins of ceratobranchials 2 to 4 bear small, autogenous toothpatches. The slender ceratobranchials 5 bear scattered fine teeth on their dorsal surfaces. Epibranchials 1 to 4 are present, and all are ossified. Epibranchials 1 and 3 each bear a cartilaginously tipped uncinat process; that of each epibranchial 1 articulates with the interarcual cartilage on its respective side. Each epibranchial 4 articulates dorsally with a tiny toothpatch, representing the only indication of its respective infrapharyngobranchial 4. There is a tiny piece of cartilage that is loosely attached, and well separated from, the dorsalmost tip of epibranchial 1. This tiny cartilage represents a vestigial infrapharyngobranchial 1. The infrapharyngobranchials 2 are each reduced in size to a small, cartilaginously tipped edentate rod, positioned entirely anterior to its respective infrapharyngobranchial 3, whose ventral surface is covered by a patch of fine teeth (the right infrapharyngobranchial 2 of the comparative specimen bears a single tooth posteroventrally; the left is edentate).

*Tyson* (Figure 13): The basihyal is a relatively long, dorsally flattened, ventrally rounded bone with a cartilaginous tip anteriorly. The basihyal articulates at its posterior end with the anterior end of the relatively large basibranchial 1, and ventroposteriorly on each side with the dorsal surface of each hypohyal. Basibranchial 1 is ossified (unusual for a gobioid) and is the only basibranchial present, either as cartilage or bone. The dorsoanterior surface of the long urohyal is tightly bound to the rounded ventral surface of basibranchial 1. Of the hypobranchials, only 1 and 2 are

present. The anterior ends of the hypobranchials 1 articulate in depressions at the posterior end of basibranchial 1. The anterior ends of the hypobranchials 2 articulate together. Ceratobranchials 1 to 5 are present and each 5 bears a single row of small teeth. Each pair of ceratobranchials 4 and 5 articulate together at their anteriormost tips. Epibranchials 1 to 4 are present, but the epibranchials 1 are present only as club-shaped cartilages and they and the epibranchials 4 each lack an uncinat process. There are no interarcual cartilages. The infrapharyngobranchials 1 are present as small cartilaginous rods, each attached to the dorsal end of its respective epibranchial 1. The infrapharyngobranchials 2 appear to be absent, or each is fused to its respective infrapharyngobranchial 3. Each infrapharyngobranchial 3 bears a patch of teeth ventrally and two cartilaginous processes laterally. Epibranchial 2, of each side, articulates at its dorsal end with the anterior cartilaginous process of its respective infrapharyngobranchial 3, and, similarly, the dorsal ends of epibranchials 3 and 4 articulate with the posterior cartilaginous process. Each epibranchial 3 lacks a posterior cartilaginously tipped process for articulation with its respective epibranchial 4. The infrapharyngobranchials 4 and associated toothplates are absent, although conceivably fused to the infrapharyngobranchials 3. There are no gill rakers or toothpatches, other than those already mentioned, on any of the arches.

#### PECTORAL AND PELVIC FINS AND GIRDLES

*Xenisthmus* (Figures 14 and 15): The paired cleithra are joined at their ventral ends, between which is a small, autogenous, wedge-shaped cartilage (ventral intercleithral cartilage). Postero-dorsal to the ventral end of each cleithrum is a posteriorly projecting process. The pelvic intercleithral cartilage (an unpaired, median structure) forms a bridge between the processes.

Each pelvis is a complex bone consisting of a medial, anteriorly acute, somewhat triangular portion with two elongate processes. One is cone-like with a cartilaginous core that attaches to the

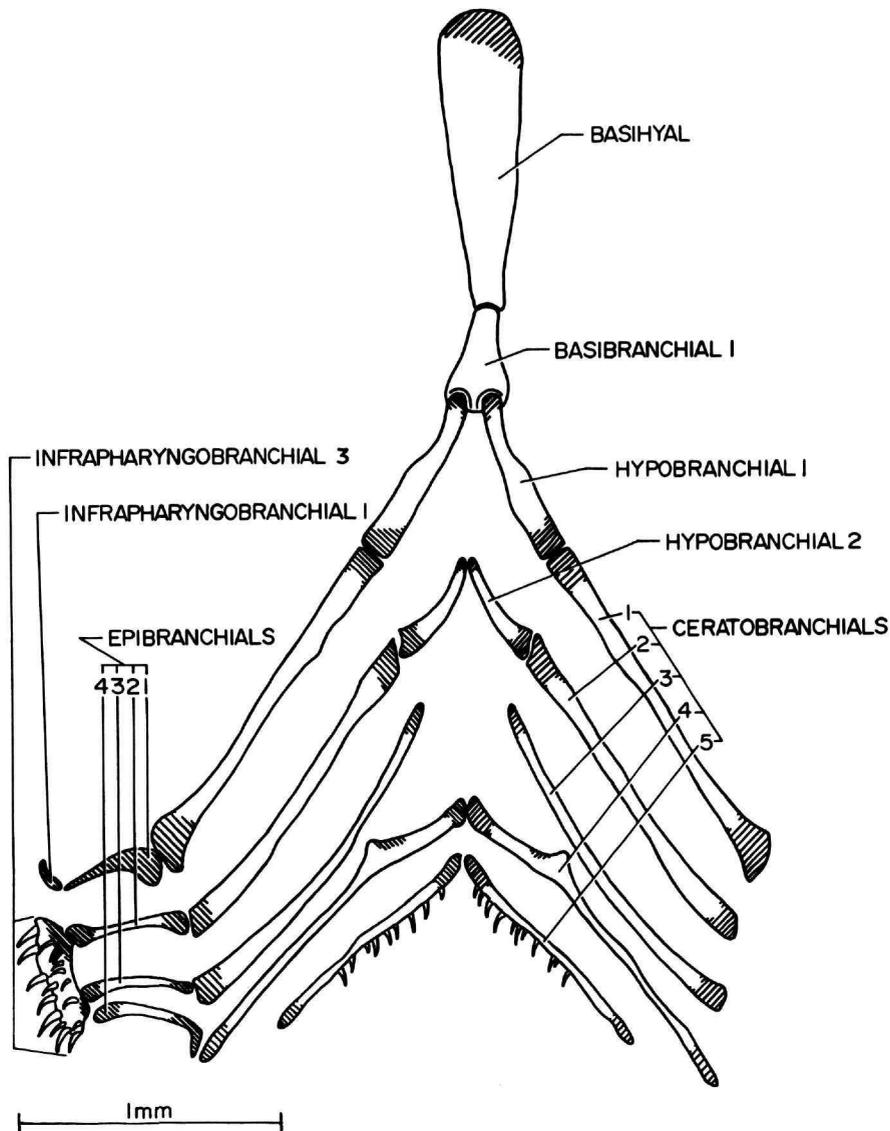


FIGURE 13.—*Tyson belos*, dorsal view of gill arches and basihyal (left-side dorsal elements rotated laterally as a unit, right-side dorsal elements removed, arches spread slightly for clarity).

pelvic intercleithral cartilage (the cartilage of both structures is probably continuous, but that of the pelvis is only faintly blue-stained, whereas the pelvic intercleithral cartilage is deeply blue-stained); the other is a slender, laminar, anteriorly projecting process that is membranously at-

tached to the cone-like process for most of its length, but is continuous at its base with the cone-like process. The dorsomedial margin of the triangular process is closely joined to its fellow on the opposite side. The anterior, conjoined ends of the triangular processes are attached by tough

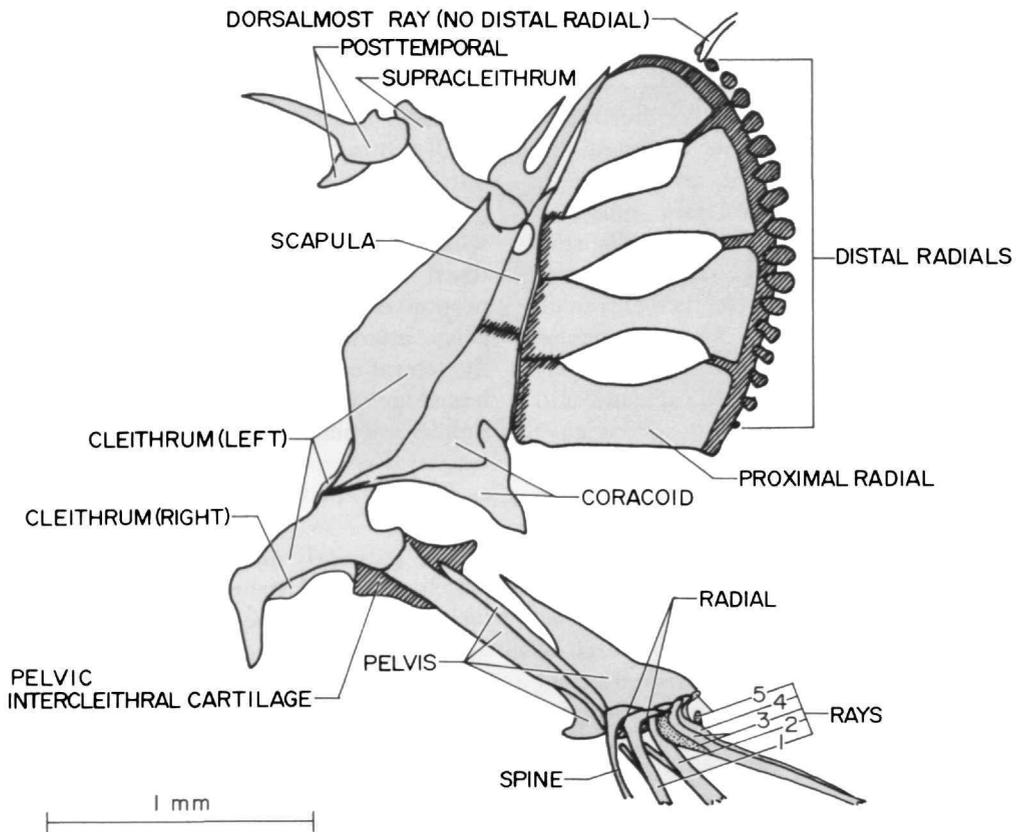


FIGURE 14.—*Xenisthmus clarus*, lateral view of pectoral- and pelvic-fin girdles and supports (only dorsalmost pectoral-fin ray indicated; pelvic-fin elements truncated; see also Figure 15).

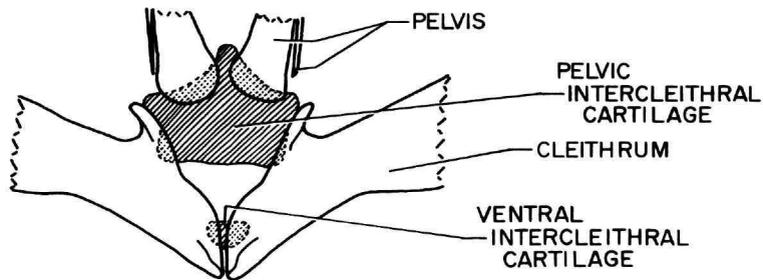


FIGURE 15.—*Xenisthmus clarus*, ventral view of ventral portion of cleithra and anterior portion of pelvises (anterior is oriented toward bottom of page).

membrane to a short, midposterior process on the pelvic intercleithral cartilage. Each of the triangular processes gives rise to a slender, medial, ventroanteriorly directed process (not illustrated) that is also closely bound to its fellow on the opposite side. A relatively large cartilage (pelvic radial) is attached to the ventrolateral margin of each of the triangular pelvic processes. The split bases of the pelvic-fin spine and 5 segmented rays on each side straddle their respective radial. Based on the pelvic girdle of *Tyson*, it appears that the entire pelvic girdle (both sides together) forms initially as a single block of cartilage, and the intercleithral cartilage and two cartilaginous radials (one on each side) are all the cartilage that remains after the girdle ossifies. (The intercleithral cartilage and radials do not appear to ossify in gobioids, except possibly in very large specimens of large species.)

The posttemporals connect the pectoral girdles to the skull by way of the supracleithra, each of which is joined anteriorly to the posteromedial surface of its respective posttemporal and posteriorly to a notch in the dorsolateral surface of its respective cleithrum. Each supracleithrum is also connected with the base of the skull on its respective side by the Baudelot's ligament of that side, which passes freely through a deep notch in the dorsal end of its respective cleithrum. There are no postcleithra present. (Birdsong, 1975:170, incorrectly indicated that dorsal postcleithra are present in *Xenisthmus*, but on his page 183 correctly noted that, according to Miller, 1973, the *Xenisthminae* lacked dorsal postcleithra.)

The scapula and coracoid on each side are synchondrally joined along a horizontal line of deeply stained cartilage; the remainder of the scapula is ossified; the scapular foramen is surrounded by bone. Except for the narrow synchondral joint with the scapula, each coracoid consists of a dorsal, faintly pink-stained portion and a ventral, sharply defined, darker pink portion that includes the posteriorly projecting coracoid process. The proximal and distal ends of the proximal radials are cartilaginous, as are the distal radials in their entirety. Every pectoral-fin ray (17 each side), except the dorsalmost one on each side,

embraces a separate distal radial; the dorsalmost has no distal radial.

*Tyson* (Figure 16): The paired cleithra are joined at their ventral ends, between which is a small ventral intercleithral cartilage. Posterodorsal to the ventral ends, and joining them, is the pelvis, a median block of cartilage (staining darkest in its dorsalmost and ventralmost portions) with a foramen medially. The anterior portion of the pelvis is the homologue of the pelvic intercleithral cartilage in *Xenisthmus*, and the lateral edge on each side of the pelvis is the homologue of a pelvic radial. A long, unstained, simple, segmented ray articulates with the ventrolateral edge (radial portion) of the pelvis on each side. There are no other elements in the pelvic fin.

The anteriorly flattened posttemporals each attach to the flattened dorsolateral surface of their respective epioccipital. The plane of each posttemporal gradually twists posteriorly and the bone becomes flattened in the vertical plane, where it joins the anterolateral surface of its respective supracleithrum. The posttemporals lack an ossified ventral arm, and the cleithra have no notch in their lateral surface as they do in *Xenisthmus*. The ventral posttemporal arm is represented by a long ligament that attaches to a process on the exoccipital. The scapula and coracoid of each side are represented by an undifferentiated, mostly cartilaginous plate (scapulo-coracoid) attached to the medial side of its respective cleithrum. The pink-stained (bony) portion of the scapulo-coracoid is restricted to the coracoid portion of the plate. The scapular foramen is complete (surrounded by cartilage). The proximal pectoral-fin radials are represented on each side by a cartilaginous plate with four large, oblong openings. Each of the tiny, cartilaginous distal radials is embraced by the two halves of an unstained, simple, segmented ray, and every ray is associated with its own distal radial (rays omitted in Figure 16). There are no postcleithra.

#### VERTEBRAE AND UNPAIRED FINS

*Xenisthmus* (Figure 17): The vertebral column comprises 26 vertebrae: 10 precaudal (8th and

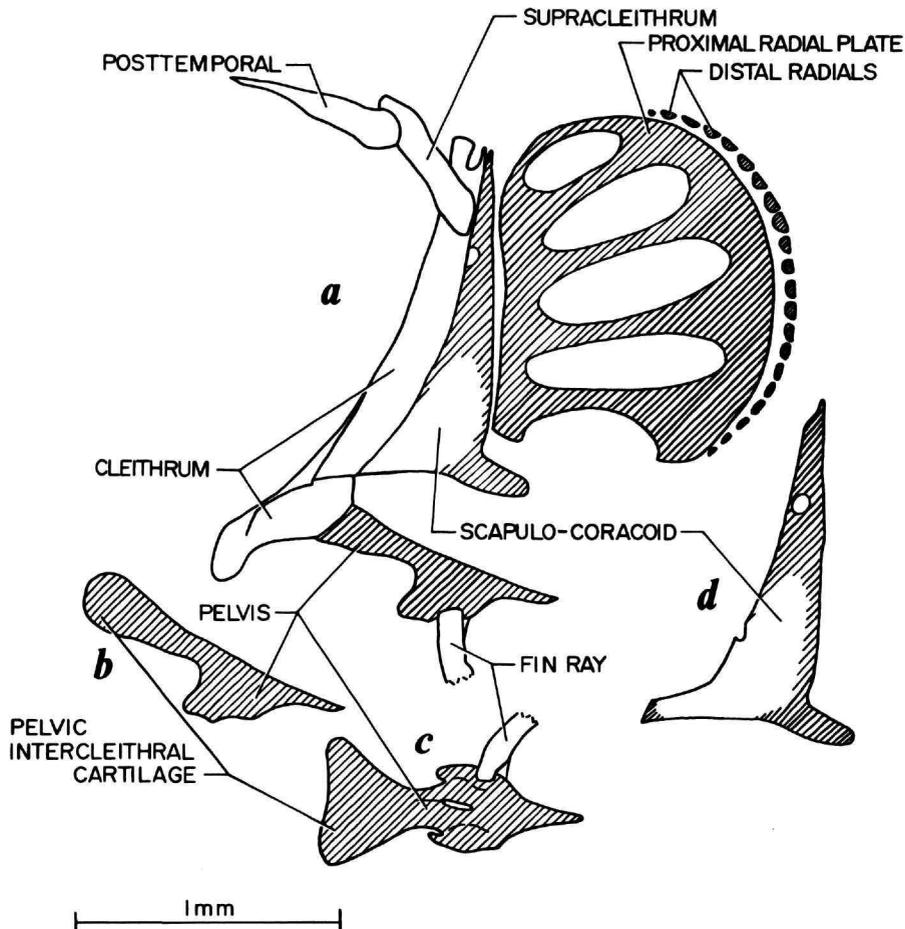


FIGURE 16.—*Tyson belos*, pectoral- and pelvic-fin girdles and supports: *a*, lateral view (pectoral-fin rays not shown; pelvic-fin ray truncated); *b*, lateral view of isolated pelvis; *c*, ventral view of pelvis (left fin ray removed, right truncated; oblong area in center of pelvis is a foramen); *d*, lateral view of isolated scapulo-coracoid (circular area in scapular portion is scapular foramen).

9th abnormal, almost completely fused; normal in comparative specimen) and 16 caudal (the 10 + 16 count is consistent in all of a number of *Xenisthmus* specimens examined by radiography). None of the precaudal vertebrae has a complete hemal arch. The anteriormost vertebra (atlas) bears a condyle on either side for articulation with the exoccipitals. The first hemal spine defines the first caudal vertebra. Epipleural ribs are associated with the anteriormost 16 vertebrae (each side), and pleural ribs with the 3rd to 10th

(each side). The penultimate vertebra (Pu2) bears a relatively high neural spine and a long hemal spine that participates in the caudal-fin structure. There is an arched, elongate groove on each side at the base of the hemal spine.

The posteriormost vertebral centrum (comprising fused ural centra and preural centrum 1) has hypurals 1 to 4 fused to it. Hypural 5 is autogenous, as are the parhypural and the 2 epurals, and all 4 of these elements have cartilaginous distal tips (as does the hemal spine of Pu2). There

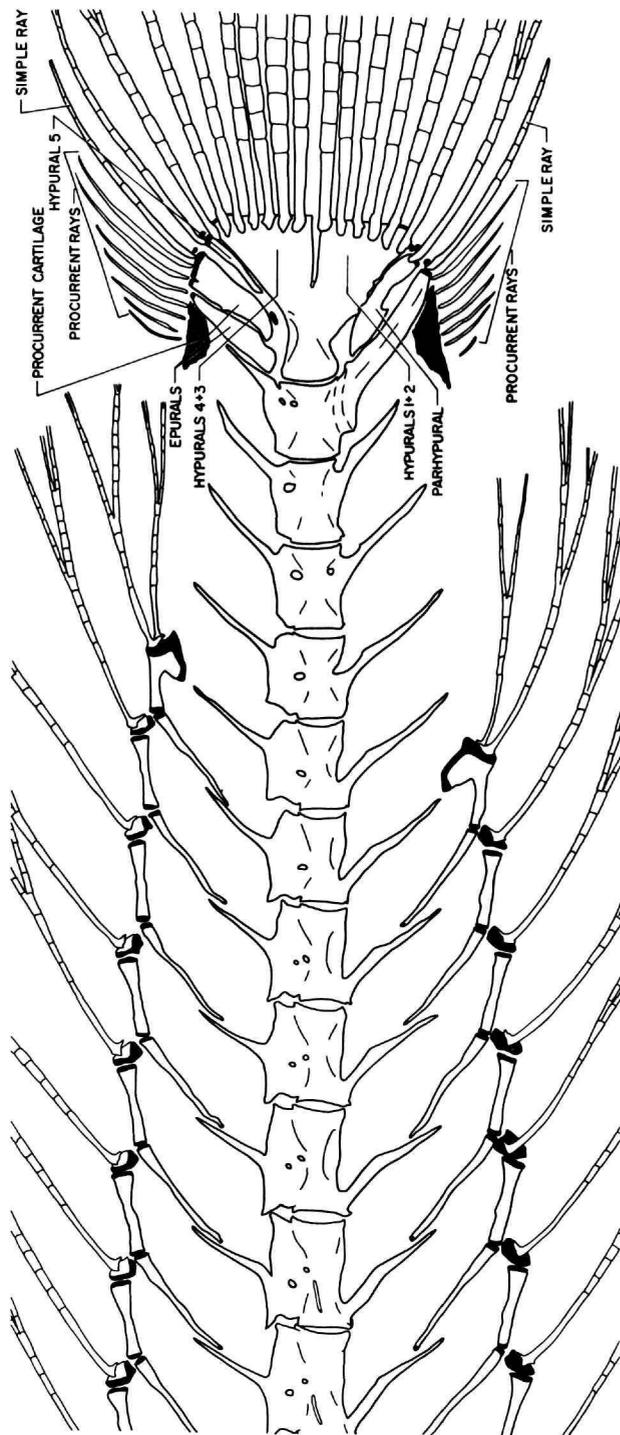
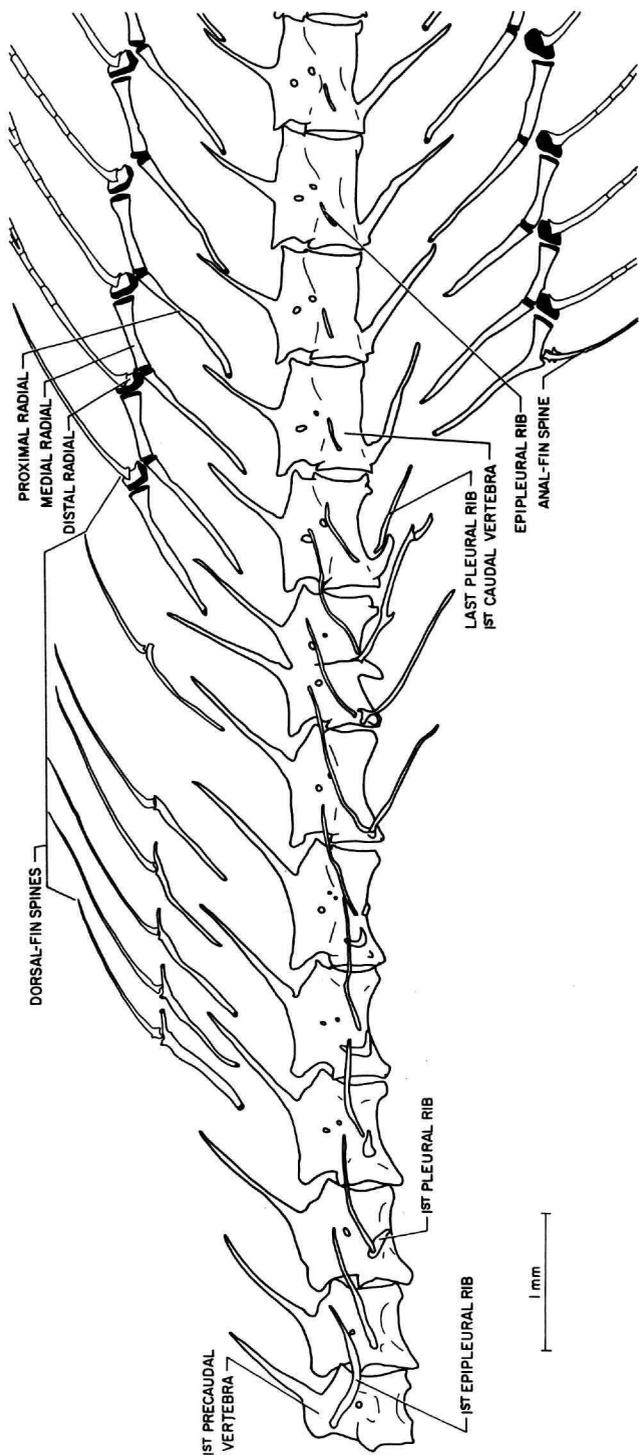


FIGURE 17 (above).—*Xenisthmus clarus*, vertebrae and unpaired fins (most segmented rays are truncated; note aberrant fusion of 8th and 9th precaudal centra).

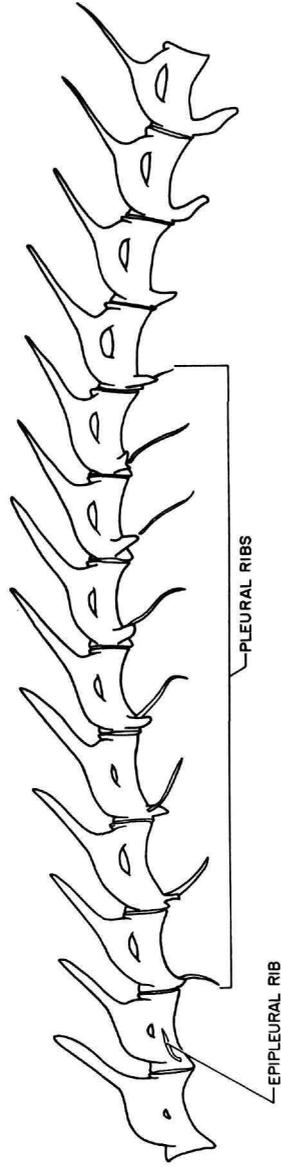
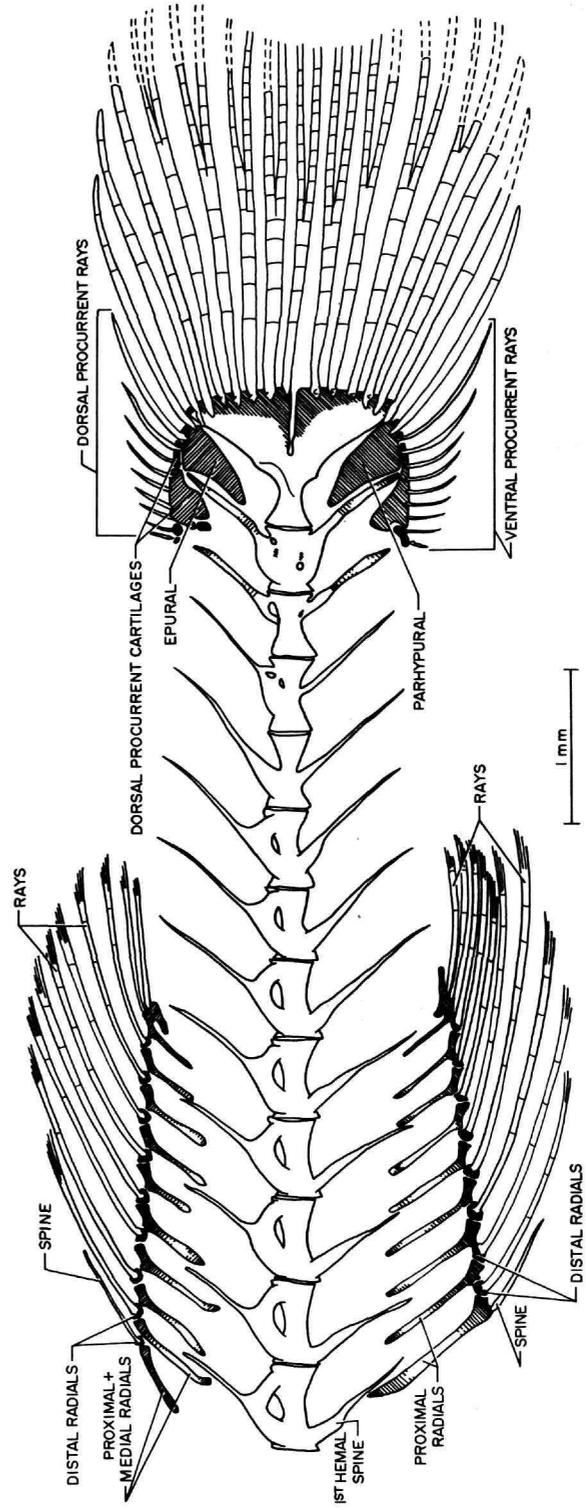


FIGURE 18 (below).—*Tyson bellos*, vertebrae and unpaired fins.



are no autogenous uroneurals, but a small piece of cartilage occurs in the area below the posterior epural, which may represent a vestige of a uroneural (not labelled in Figure 17; the cartilage is also present in the comparative specimen; autogenous, ossified uroneurals are unknown in gobioids). There is a large dorsal and a large ventral procurrent cartilage (occupying, respectively, the interneural and interhemal spaces between Pu2 and Pu3), posterior to each of which are 2 (dorsal) or 3 (ventral) small cartilages.

There are 7 dorsal and 7 ventral procurrent rays (unsegmented), 1 dorsal and 1 ventral segmented, unbranched (simple) ray, and 8 dorsal and 7 ventral branched rays, for a total of 31 caudal-fin elements (32 in the comparative specimen, which has an additional ventral procurrent ray).

The first dorsal fin consists of 6 spines, whose pterygiophores have the formula (Birdsong, 1975:137): 3(2,2,1,1,0), which is consistent in all of several specimens that were examined radiographically. Each of the pterygiophores has a cartilaginous ventral tip. The second dorsal fin consists of a spine and 13 segmented rays, all rays branched (12 to 14 rays, varying with the species; D.F. Hoese, in litt.). Each of the second dorsal-fin elements, except the spine and posteriormost two rays, is associated with its own tripartite pterygiophore (proximal + medial + distal radials; the distal radials are largely cartilaginous and do not appear to be differentiated into bilateral halves). The spine of the second dorsal fin is associated with a bipartite pterygiophore, the proximal portion of which possibly consists of fused proximal + medial radials. The posteriormost two rays are associated with a single pterygiophore consisting of a single proximal radial and a complex, hatchet-shaped distal radial of uncertain composition.

The anal fin consists of a spine and 12 branched, segmented rays, and each of these elements except the anteriormost 2 and posteriormost 2 is associated with its own tripartite pterygiophore, similar to those in the dorsal fin. The spine lacks its own pterygiophore and is supported by the fused proximal + medial radial of the an-

teriormost segmented ray. The pterygiophore supporting the posteriormost 2 rays is similar to that of the dorsal fin. All the second dorsal-fin and all but the 2 anteriormost anal-fin pterygiophores insert into separate interneural or interhemal spaces.

*Tyson* (Figure 18): The vertebral column comprises 26 vertebrae: 13 precaudal and 13 caudal. Only the posteriormost two precaudal vertebrae have complete hemal arches (but no hemal spines). The first hemal spine defines the first caudal vertebra. The atlas does not bear lateral condyles for articulation with the exoccipitals, which also lack condyles. The only epipleural ribs are attached to the second precaudal vertebra, somewhat dorsal to the ventroanterior margin of the centrum on each side. Pleural ribs occur on the third to tenth precaudal vertebrae. Pu2 has a long neural and a long hemal spine.

The posteriormost vertebral centrum is similar in structure to that of *Xenisthmus*. An autogenous hypural 5 is absent. A large cartilaginous parhypural and comparable, single epural are present. There is no "uroneural" cartilage (see *Xenisthmus*). There are several accessory (procurrent) cartilages distal to the parhypural and epural, and in the interneural and interhemal spaces between Pu2 and Pu3.

None of the procurrent rays and segmented caudal-fin rays are stained. There are 9 dorsal and 9 ventral procurrent rays, 3 dorsal and 3 ventral simple, segmented rays, and 5 dorsal and 4 ventral branched rays in the caudal fin, for a total of 33 caudal-fin elements.

None of the dorsal- and anal-fin rays are stained. The radials of both fins are cartilaginous, except for portions of some of the proximal radials, which are unstained. There is no anterior spinous dorsal fin. The posterior dorsal fin consists of a spinous ray and 10 simple, segmented rays (the anteriormost 1 and posteriormost 2 rays lack segmentations but consist of bilateral halves typical of segmented rays). Each element, except the 2 posteriormost rays, is associated with its own proximal and distal radials (the proximal radial probably also embodies a medial radial). The last 2 dorsal-fin rays are born on a complex proximal

radial. The structure of the anal fin is similar to that of the dorsal fin except that the spine lacks both distal and proximal radials and articulates with the proximal (proximal + medial?) radial of the first segmented ray. All of the anal-fin rays are segmented. In contrast to *Xenisthmus*, and except for the first 2 anal-fin pterygiophores, the dorsal- and anal-fin pterygiophores are inserted 2 or 3 pterygiophores per interneural or interhemal space.

### Characters and Classification of the Gobioidei

The gobioids have not been evaluated cladistically in the literature. It is my intent here to contribute toward such an evaluation.

To establish the monophyly of the suborder Gobioidei, it is first necessary to select an outgroup as a basis for comparison. The gobioids are usually considered to belong to the order Perciformes, and although the monophyly of the Perciformes has not been established and is doubtful, indeed (however, see Rosen and Parenti, 1981:19–20, where three characters discussed would place the gobioids in their Percomorpha), I accept its monophyly for the purpose of discussion, and I accept its composition as proposed by Gosline (1968). A sister group for the Gobioidei has not been proposed, and I will not propose one formally here.<sup>2</sup> The main outgroup for my discussion is, therefore, the Perciformes less the Gobioidei. I also use the preperciform order Beryciformes (Zehren, 1979) as a secondary outgroup. Obviously, I have examined only a fraction of the numerous supraspecific taxa contained in the Perciformes, Beryciformes, and Gobioidei, but I have studied a large number of them over the past 30 years and have examined the literature on many others. In any event, the propositions I will introduce are subject to falsification, or corroboration, and hopefully will lead to a better understanding of the gobioids.

The Gobioidei was defined in its essentials by Regan (1911), and elaborated on most substantively and recently by Gosline (1955), Miller (1973), and Birdsong (1975). Hoese (1976) recognized six families in the Gobioidei: Rhyac-

ichthyidae, Pirskeniidae (fossil), Eleotrididae (in which he included *Xenisthmus*), Gobiidae, Microdesmidae, and Kraemeriidae. I propose that the Gobioidei comprises, with one exception, those taxa treated as gobioids by these authors. Miller (1973) included the Pholidichthyidae among the gobioids. The Pholidichthyidae is a monotypic family of uncertain, possibly blennioid or zoarceoid, relationships (Springer and Freihof, 1976) that does not share, even as homoplasies, any of the four gobioid synapomorphies that I will propose. It also does not exhibit any of a number of other specializations present, apparently, in all gobioids, that are not clearly gobioid synapomorphies.

The most complete attempt to characterize the gobioids is that by Birdsong (1975, table 1), who proposed approximately 30 skeletal characters to define the group. In the following section, I will first discuss the four gobioid synapomorphies (the first of which was also noted by Birdsong), and follow this by a discussion of the most important of Birdsong's characters (stated, for the most part, as he gave them).

Of the four gobioid synapomorphies, number 1 was proposed by Regan (1911) and the others have not been proposed previously. The first three synapomorphies appear to be unequivocal, but it is possible that the hypothesized fourth synapomorphy is represented in a more specialized state in certain nongobioids that possibly could be related to the gobioids.

1. Parietals absent. As far as I have been able to determine, all other perciform fishes have parietals. Among nonperciforms, parietals are absent in, at least, all tetraodontiforms (Tyler, 1980:30) and some cyprinodontoids (Parenti, 1981).

2. Pelvic intercleithral cartilage present (Figure 15). I have not found a pelvic intercleithral cartilage in any other perciform or nonperciform taxon. It is probable that the pelvic intercleithral cartilage is lost in the gobioid genus *Expedito* Snyder, which appears to lack a pelvic girdle altogether (Birdsong, 1975).

3. Dorsal end of interhyal fails to meet dorsal end of symplectic. In many preperciforms and

most, if not all, nongobioid perciforms, the cartilaginous dorsal ends of the symplectic and interhyal meet and articulate as a unit with the relatively slender ventral process of the hyomandibula (Figure 19 *top*). Additionally, the dorsal end of the interhyal, and sometimes that of the symplectic, usually impinges on the medial surface of the preopercle. All gobioids are specialized for this character complex. The most plesiomorphic configuration for this character complex among the gobioids appears to be present only in *Rhyacichthys* (Figure 19 *middle*), which differs from the generalized perciform configuration in having the interhyal displaced ventrally and articulating only with the preopercle. The remaining gobioids appear to be more specialized for the character complex (Figure 19 *bottom*, most generalized gobioid configuration): the ventral process of the hyomandibula has become quite broad and the dorsal ends of the interhyal and symplectic have become widely separated. The dorsal end of the interhyal maintains a close connection with the ventral process of the hyomandibula (and in this respect is less specialized than *Rhyacichthys*) and may or may not be attached ligamentously to the preopercle as well.

4. Basibranchial 1 cartilaginous. The primitive state for basibranchial 1 in perciforms is for this structure to be well ossified. For further discussion of this character, see character 16 and, particularly, note 6 (page 37).

5. Orbitosphenoid absent. I confirm this character, which is a synapomorphy of the Perciformes.

6. Basisphenoid absent. The basisphenoid is absent also in various other perciforms (zoarceoids, stichaeoids, and gobiesocids, at least), and may prove useful in establishing the sister group of the gobioids.

7. Intercalar reduced (lost in some species). The intercalar is well developed in many gobioids (for instance, see Figure 3), including *Rhyacichthys*, which appears to be the most generalized gobioid. (Miller's (1973) figure 3b, shows a very large opisthotic (= intercalar) in the ventral view of the skull of *Rhyacichthys*. The intercalar is inexplicably missing in the lateral view, Miller's figure 3c, of

the same skull.) A well-developed intercalar is common to many perciforms and preperciforms, and will probably be of little use for establishing gobioid interrelationships.

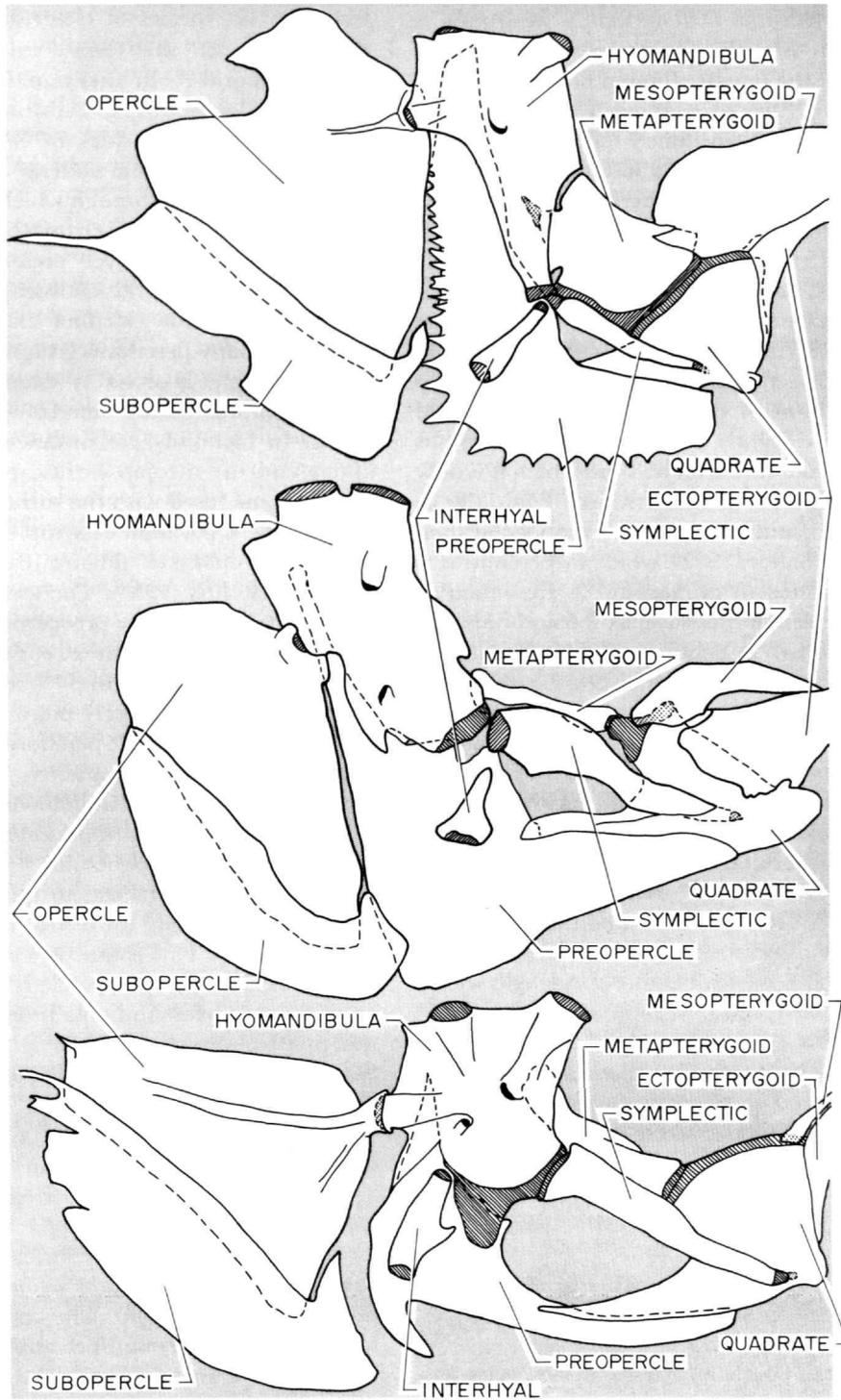
8. Infraorbital, except lacrimal, absent in most species; one reported present in two species of eleotridids by Akihito (1969) and in *Rhyacichthys* by Miller (1973). I would restate this character as follows: infraorbitals represented only by lacrimal and, in *Rhyacichthys* only, one other.<sup>3</sup> (The lacrimal is most correctly termed "infraorbital 1," but for convenience of discussion "lacrimal" is used in my study.)

Birdsong's statement of this character contains some confusion, not of his own making. Akihito's (1969) "suborbital" is not a bone of the infraorbital series (sometimes termed circumorbital or suborbital series), which includes the lacrimal (termed "praeorbital" by Regan, 1911). Akihito reported the "suborbital" in two genera (*Bostrichthys*, = *Bostrychus*, and *Oxyeleotris*) of eleotridids in which it occurs irregularly (D.F. Hoese, in litt., states that this bone is also present in two other eleotridid genera, *Micropercops* Fowler and Bean and *Sineleotris* Herre). I have examined Akihito's suborbital and find that it is an ossification of the anteroventral portion of the membrane lining the orbital cavity. I believe that the bone is a specialization confined to certain eleotridid genera (not present in all specimens of a given species). In order to avoid confusion with other bones in the orbital region, I suggest that the term "intraorbital" be applied to it. Intraorbital has not been used previously for any bone in the orbital region.

Miller (1973) used the term "prefrontal" to

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FIGURE 19.—Medial views of suspensorial region (interopercles removed) to illustrate relationship of hyomandibula, interhyal, and symplectic. *Top*, *Centropomus* species (USNM 114415; Centropomidae; representative of generalized condition for perciform fishes); *middle*, *Rhyacichthys aspro* (representative of most generalized condition for gobioids; disconnection of interhyal from hyomandibula is probably an autapomorphy); *bottom*, *Eleotris amblyopsis* (representative of generalized condition for nonrhyacichthyid gobioids). The limits of bones that are obscured by others are indicated by dashed lines.



denote the lacrimal of *Rhyacichthys*. Prefrontal is a term often used also for the lateral ethmoid or a portion of the lateral ethmoid of dermal origin (Harrington, 1955:287). When I first examined the lacrimal in an unstained specimen of *Rhyacichthys*, I thought it was an antorbital, a dermal bone that is attached to the lateral ethmoid, is dorsal and/or anterior to the lacrimal, and often participates in support of the nasal capsule.<sup>4</sup> The bone in *Rhyacichthys* that Miller termed "suborbital" appears to be infraorbital 2 or 3, which is not present in other gobioids (although D.F. Hoese, in litt., thinks it may be represented by the intraorbital of eleotridids). The additional infraorbital is tightly connected by ligamentous tissue to the lateral ethmoid, from which it is only slightly separated (I misidentified it initially as the lacrimal), and it bears a broad subocular shelf (Smith and Bailey, 1962), which in perciforms is usually confined to infraorbital 3. Inasmuch as generalized perciforms have six infraorbitals, the reduction to two in gobioids must be considered to be a specialization. It is not possible to decide if this specialization is a gobioid synapomorphy, because families such as the gobiesocids, callionymids, or batrachoidids, in which the only infraorbital present is the lacrimal, may have arisen with the gobioids from a common ancestor having only two infraorbitals.

Among the "orbital" bones of *Rhyacichthys*, Miller (1973, fig. 2a, b) indicated the presence of a single scleral ossification in each eye of *Rhyacichthys*, which presence I confirm. A single scleral ossification occurs also in some eleotridids (D.F. Hoese, in litt.), but other gobioids, including eleotridids, I have examined have only a circular ribbon of scleral cartilage in each eye. Perciform fishes commonly have two scleral ossifications in each eye, and although I have not searched widely among the perciforms, I have seen a single scleral ossification only in callionymids. The value of a scleral ossification, particularly the presence of only one in each eye, for basing gobioid intra- and/or interrelationships, is, perhaps, worthy of further investigation.

9. Supratemporals absent in most species (re-

ported in six species of eleotridids by Akihito, 1971). I prefer the term "extrascapulae" to "supratemporals." In addition to Akihito's six species, Miller (1973, fig. 2a,b) indicates one extrascapula (on each side) in *Rhyacichthys*. The gobioid extrascapulae are lateral in position. Median extrascapulae, through which the supratemporal commissural branch of the laterosensory canal passes, are primitively present in perciforms (in addition to lateral extrascapulae) but are absent in gobioids. Median extrascapulae are lacking in many perciform groups, and the value of this character is probably secondary to the loss of the supratemporal commissural canal in gobioids. In blenniids, for instance, the canal remains and the median extrascapulae appear to have become fused with the surface of the skull.

10. Wide separation of symplectic from preopercle. This character (Figure 19 *bottom*) was first noted by Gosline (1955). The wide separation of the symplectic from the preopercle appears to be descriptive of all gobioids except the most generalized, *Rhyacichthys* (Figure 19 *middle*) in which the two bones are scarcely more separated, if at all, than they are in some perciforms (for instance, Figure 19 *top*). As a character, the symplectic-preopercle relationship in gobioids is useful only as an indication that *Rhyacichthys* is the sister group of all the other gobioids.

11. Preopercle attached to quadrate and hyomandibula, forming third strut of suspensorium in most species. This character was first noted by Gosline (1955). The preopercle is attached to the quadrate and hyomandibula in many perciforms and preperciforms, and the arrangement of these bones, as such, has little bearing on gobioid interrelationships.

12. Symplectic dominates symplectic-metapterygoid strut of suspensorium of most species. The symplectic of gobioids, in contrast to most perciforms, is usually a larger bone than the metapterygoid and usually forms a stronger link between the quadrate and hyomandibula than does the metapterygoid. The condition appears to be characteristic of unspecialized gobioids, but its status as a synapomorphy is confused by the

absence of the metapterygoid in such groups as the gobiesocids, callionymids, and draconettids (Gosline, 1970, fig. 1; Springer and Fraser, 1976). According to D.F. Hoese (in litt.), "specialized gobiids often have a very expanded metapterygoid," a condition that would appear to be unspecialized.

13. Mesopterygoid reduced or absent. Miller (1973:408) reports, and I confirm (Figure 19 *middle*), that the mesopterygoid in *Rhyacichthys* is well developed, in contrast to its state in other gobioids that have a mesopterygoid. The reduction in size or loss of the mesopterygoid may be a basis for establishing intragobioid, but not intersubordinal, relationships. Among the gobioids, the mesopterygoid is present only in *Rhyacichthys* and most eleotridids (D.F. Hoese, in litt.).

14. Interhyal ligamentously attached to preopercle. I have not made an extensive survey of the relationship between the interhyal and preopercle in nongobioid perciforms. In gobioids the lateral surface of the interhyal is completely or almost completely appressed against the medial surface of the preopercle, and determination of the nature of the interhyal-preopercle attachment is difficult. The eleotridids I examined did not appear to have a ligamentous attachment to the preopercle, although Birdsong (1975) reported such an attachment for *Butis*, which I also examined. I found a ligamentous attachment apparent in *Rhyacichthys*, *Xenisthmus*, *Tyson*, and the gobiid *Valenciennesia strigata*, indicating that such an attachment is probably plesiomorphic for gobioids. Determination of whether it is a gobioid synapomorphy will require extensive study of nongobioid perciforms, but may prove important.

15. Branchiostegal rays 4 to 7. Seven branchiostegals (on each side) is a common number for perciforms and probably represents the primitive number for the group. Among gobioids, 7 branchiostegals have been reported only for: 1 of 12 specimens of the eleotridid *Odontobutis obscura* (Temminck and Schlegel) (Akihito, 1969:105); the monotypic Milyeringidae (McAllister, 1968:147; referred to the synonymy of the Eleotrididae by D.F. Hoese, pers. comm.; specimens

of *Milyeringa* Whitley were unavailable to me, but, D.F. Hoese informed me that all 4 of the specimens he examined had only 6 branchiostegals); and 2 fossil species (Obrhelová, 1961):<sup>5</sup> *Pirskeniuss diatomaceus* Obrhelová (Pirskeniidae) and *Lepidocottus papyraceus* (Agassiz) (Gobiidae?). *Rhyacichthys*, xenisthmids, and the eleotridids have 6 branchiostegals; all remaining gobioids have 4 or 5 (I have not found 4 in my material, but Akihito (1969:106), reported 4 in one of 10 specimens of the gobiid *Periophthalmus cantonensis* (Osbeck)). Six branchiostegals is a number that occurs frequently also in nongobioid perciforms. It is doubtful that the primitive number of branchiostegals (7, or 6 if, as I think probable, 7 represents a gain) in gobioids will provide much help in basing gobioid interrelationships.

16. First basibranchial absent. With possibly only one exception (*Kraemeria*), this character applies to no gobioid I know of. Basibranchial 1 appears to be present in all gobioids, but it is usually present only as cartilage. Hence, basibranchial 1 is probably overlooked in specimens that have not been counterstained for cartilage.<sup>6</sup> As an ossified basibranchial 1 is common to preperciforms and perciforms, the nonossified basibranchial 1 of gobioids is a specialization and may be a synapomorphy; however, the reductive nature of the basibranchial 1 character is confused by the fact that some forms, such as the Gobiesocidae, lack basibranchial 1 altogether (Springer and Fraser, 1976). Among the gobioids, basibranchial 1 is known to be ossified only in *Tyson*, possibly *Kraemeria* (as originally reported by Matsubara and Iwai, 1959, but questioned by Birdsong, 1975), and occasionally, perhaps, in *Rhyacichthys*. In my specimen of *Kraemeria*, basibranchial 1 appears to be a knob of bone, the ventral surface of which is attached, or weakly fused, to the anterodorsal process of the urohyal; a conspicuous joint is present between the two bones. In two other specimens of *Kraemeria* (one of which I have not seen; information provided by D.E. Rosen), it is not possible to decide if the knob of bone is basibranchial 1 or part of the urohyal. Perhaps of relevance here is that the

urohyal is tightly attached to basibranchial 1 in *Tyson*, and a fusion between the two structures might occur occasionally under such a condition. In gobioids with a cartilaginous basibranchial 1, the dorsal process of the urohyal is often closely applied to the ventral surface of the basibranchial, but the two elements can be readily separated. I consider the ossified basibranchials 1 of *Tyson* and *Kraemeria* to be homoplasies.

17. Fourth basibranchial present as cartilage. This is the generalized condition of basibranchial 4 in most, if not all, perciforms and preperciforms (Zehren, 1979:57) and is of little use for establishing gobioid interrelationships. *Tyson* and *Xenisthmus* are specialized in lacking basibranchial 4 altogether.

18. Baudelot's ligament present. This ligament is also present in a wide variety of perciforms and preperciforms (Zehren, 1979:53); hence, it is of little use for establishing gobioid interrelationships.

19. Dorsal postcleithrum absent in all groups except eleotridids. The dorsal postcleithrum is present in *Rhyacichthys* (Miller, 1973, fig. 6a,b), which some earlier authors placed in the Eleotrididae, and some eleotridids, but not in gobiids (sensu Miller, 1973). The presence of the dorsal and ventral postcleithra by perciforms is a primitive character found also in preperciforms (Zehren, 1979:69). What is specialized about the postcleithra in those gobioids that have retained either or both of them is that the two bones are reduced in size and are never connected when both are present, as they normally are in nongobioids. The postcleithra of perciforms have not been surveyed, and the usefulness of postcleithral characters for basing gobioid interrelationships is unknown.

20. Scapula reduced in most species. The scapula is fairly well developed in *Rhyacichthys*, at least, and the character as stated is of little use for basing gobioid interrelationships. Akihito (1969) noted a trend toward lack of ossification of the scapula in gobioids generally considered to be more specialized.

21. Supraneurals [= predorsal bones] absent.

The presence of two predorsal bones appears to be plesiomorphic for perciforms (Smith and Bailey, 1961). However, G.D. Johnson (pers. comm.) considers three predorsal bones to be the primitive state). Therefore, the absence of predorsal bones in gobioids is a specialization. Many perciforms besides gobioids lack predorsal bones, and the character is of questionable value for establishing gobioid interrelationships.

There is much confusion surrounding the interpretation of the bones referred to as supraneurals or predorsals. Birdsong (1975:163) referred to these bones as "predorsal bones" and (p. 164) "supraneurals" (sic). Zehren (1979:61-62), who referred to Weitzman (1962, figs. 16 and 17), defined predorsals as bones that "resemble the proximal radials of the dorsal fin, with which they are serially homologous" (implying that these bones had lost their associated fin-ray elements). He defined supraneurals as "detached neural spines." However, it is clear from Weitzman's discussion (1962:40-41) that Weitzman's supraneurals are the homologues of Zehren's predorsals. Gobioids lack both predorsals and supraneurals, using Zehren's terminology. An autogenous neural spine at the anterior end of the vertebral column is a condition found in relatively unspecialized perciforms and preperciforms (hence, gobioids are specialized for this character, but so are many other perciforms).

22. Penultimate vertebra [Pu2] with a short expanded neural spine and an elongated and expanded hemal spine. This is the primitive condition of Pu2 for perciforms and many preperciforms. What is specialized about the gobioid Pu2 (and Pu3) is the fusion of the hemal spine of Pu2 (and Pu3) with its respective centrum. Fusion of the hemal spines of Pu2 and Pu3 with the respective centrum of each occurs widely among perciforms, particularly benthic forms, and has probably occurred homoplasiously.

23. Procurent caudal rays supported by cartilaginous plates in most species. This is another widely distributed character, occurring in a variety of relatively unspecialized perciforms (e.g., percichthyids, apogonids) and preperciforms. In

some perciforms (for instance, serranids) only the ventral plate is present. I have not noted any perciforms in which only the dorsal plate is present.

Other gobioid character states given by Birdsong (1975, table 1) pertain to numbers of pectoral-fin radials, vertebrae, spinous dorsal-fin pterygiophores, and structure of the complex urophore (last vertebra). All of the characters are descriptive of gobioids, but are either primitive for the perciforms or difficult to defend as gobioid synapomorphies, and I will not pursue them further.

Two additional characters (24, 25), not treated by Birdsong, the procurrent spur (Johnson, 1975), and the ventral intercleithral cartilage (Figure 15) deserve comment.

24. The procurrent spur, which is found in preperciforms and various perciforms, is absent in gobioids, and possibly represents a specialized state (Johnson did not indicate character polarity). The absence of the spur is also characteristic of many benthic, nongobioid perciforms, such as blennioids, but may occur in free-swimming nongobioids, such as lutjanids. As such, the loss of the spur, if a specialization, may have occurred independently many times.

25. All gobioids appear to have a ventral intercleithral cartilage, which I predict will be shown to be a gobioid synapomorphy. This cartilage is also present in some pempheridids (*Parapriacanthus ransonetti* Steindachner, at least, but absent in *Pempheris* Cuvier), batrachoidids (D.E. Rosen, pers. comm.), and, perhaps (based on dissection of specimens not stained for cartilage), stichaeids, bathymasterids, notothenoids, and cheimarrichthyids.

In the preceding discussion, I have alluded to the primitive nature of several of the gobioid characters as they occur in *Rhyacichthys*. Miller (1973) first noted *Rhyacichthys*' basal position among the gobioids. In the following discussion, I treat the plesiomorphic characters unique to *Rhyacichthys* among the gobioids.

1. Lacrimal and one other infraorbital bone present (only lacrimal present in other gobioids);

see discussion above under character 8.

2. Three epurals (1 or 2 in other gobioids, but occasionally 3 or 1 in species normally having 2 epurals; D.F. Hoese, in litt.).

3. Lateral line present on midrow of body scales (absent in other gobioids). In addition, and not previously reported, *Rhyacichthys* possesses a short lateral-line scale row both just above and just below the midrow lateral line. The dorsal and ventral lateral lines commence at the caudal-fin base and extend posteriorly onto the caudal fin. They appear very much as they do in *Lates* Cuvier and Valenciennes (Centropomidae) (Greenwood, 1976, fig. 28a). Greenwood considered the triple lateral line of *Lates* to be a synapomorphy of *Lates*, as he thought this character had not been reported in any other percoid. Rivas (1966, key), however, used the presence or absence of "accessory lateral lines on the caudal fin" to distinguish species groups in *Lutjanus* Bloch (Lutjanidae). The accessory lateral lines of *Lutjanus* are similar in appearance to those of *Rhyacichthys* and *Lates*. Besides these three genera, accessory caudal lateral lines also occur in *Neoscorpis* Smith (Scorpididae), *Morone* Mitchill (Percichthyidae) (G.D. Johnson, pers. comm.), and some Percidae (Collette and Bănărescu, 1977). The presence of accessory lateral lines in these families probably indicates that the character is primitive for the perciforms, or some subgroup of the perciforms that includes, at least, percoids and gobioids.

4. Major branches of lateral-line canals present and well developed on head (Miller, 1973, fig. 10). In other gobioids, the head canals are, variously, incomplete and missing. For instance, only *Rhyacichthys* among the gobioids has a mandibular sensory canal, which is a common perciform and preperciform character.

5. Dorsal ends of symplectic and interhyal almost adjacent (Figure 19 *middle*). The two ends are well separated in other gobioids (Figure 19 *bottom*); see gobioid synapomorphic character 3 above.

6. Large gap between preopercle and symplectic not present; see character 10 (p. 32).

7. Scales with multiseriate ctenii. This character was first noted by Miller (1973), who described it in detail (gobioid scales appear to be specialized in that only the posteriormost, peripheral ctenii may be teeth-like; the others are cuboidal). Although a few other gobioids may exhibit two or three rows of ctenii, by far the majority have none or only one row, and only *Rhyacichthys* has more than three. Multiseriate ctenii occur commonly in other perciforms.

8. Mesopterygoid well developed; see character 13 (p. 33).

9. Caudal fin emarginate. This is the primitive condition for preperciforms and perciforms. In almost all gobioids, the caudal fin is rounded or lanceolate, but a few genera, such as *Rhyacichthys*, *Ptereleotris* Gill, *Tyson*, and the juveniles of various others, have emarginate caudal fins.

In addition to these characters *Rhyacichthys* shares with other gobioids the most primitive state for numerous other characters (including, but not limited to, the tripartite structure of the dorsal- and anal-fin pterygiophores, and general configuration of the hyoid and gill arches.

Miller (1973) provides a comprehensive discussion of other characters in *Rhyacichthys* and their status relative to other perciforms. In spite of Miller's and my contributions, I believe that a detailed osteological description of *Rhyacichthys* is needed (in part, to resolve conflicts between his and my findings). Such a description might best be based on specimens of 50–75 mm SL, in order that advanced ossification or other ontogenetic changes not obscure significant characters. *Rhyacichthys* is probably the gobioid most important for determining the interrelationships of the gobioids.

The only family besides the Gobiidae that Miller (1973) recognized in the Gobioidae is the Rhyacichthyidae. I believe that Miller was more impressed by the primitive characters of *Rhyacichthys* than by its specializations (I confess to the same bias). It is difficult to provide a list of synapomorphies for *Rhyacichthys*; however, the relatively tiny, ventrally directed mouth with broad patches of villiform teeth, the absence of coronomeckelian bones (associated with the anguloarti-

culars primitively), the greatly thickened and muscular pelvic fins and ventral pectoral-fin rays, and the disconnection of the dorsal end of the interhyal from the hyomandibula are obvious specializations not present in the generally considered primitive perch-like perciforms or generally considered primitive non-rhyacichthyid gobioids such as the eleotrids.

I do not doubt that the Rhyacichthyidae will stand as a family and that Miller's Gobiidae will be found to comprise several groups worthy of family recognition, but I have little more to offer on the subject than that the Xenisthminae will probably constitute one of them.

### Notes

<sup>1</sup> Steindachner (July 1906) described *Kraemeria*, which he placed in the family Trichonotidae. Jordan and Seale (December 1906) described *Vitreola*, which they placed in the Gobiidae (Eleotrinae). Regan (1908) described *Psammichthys*, which he placed in the Trichonotidae. Fowler (1928) first, and correctly, proposed that these three genera are synonyms and that *Kraemeria* is the senior name. Fowler included *Kraemeria* in the Trichonotidae. Regan (1911) first proposed the family Psammichthyidae (not designated as a new family, however) for *Psammichthys* alone. Jordan (1923) continued this allocation, at the same time placing *Vitreola* in the Gobiidae, and *Kraemeria* in the Trichonotidae. Whitley (1935) probably assumed that because *Kraemeria* is a senior synonym of *Psammichthys* that the family Psammichthyidae was invalid. Whitley (1935) erected the Kraemeriidae (not designated as a new family or replacement name, however) in which he included the Psammichthyidae as a junior synonym. Article 23 (d)(i) of the *International Code of Zoological Nomenclature* (1964) states: "A family-group taxon formed by the union of two or more taxa of that group takes the oldest valid family-group name among those of its components . . ." Psammichthyidae has priority over Kraemeriidae; however, Article 23(d)(ii) states: "If a zoologist observes that strict application of the Law of Priority to two or more synonymous family-group names would upset general usage, he is to request the Commission to decide which name is to be accepted for the Official List of Family-Group Names in Zoology." The inference here is that the Commission will decide in favor of general usage. There is little question that Kraemeriidae is the most-used of the two taxa in question, and it appears frequently in the literature. As far as I can discern, Psammichthyidae, a more or less cumbersome name, has rarely been used as a senior synonym since Whitley proposed Kraemeriidae. I do not intend to request the Commission to decide the issue of the proper family-group name for the taxon represented by the two names in ques-

tion. There are two reasons for this. Foremost is the fact that I consider the infrasubordinal classification of the Gobioidae to be in a tenuous state presently. With the possible exceptions of the Rhyacichthyidae, Gobiidae, and Xenisthminae, as proposed herein, monophyletic family-groups have not been proposed in the suborder, and there is a good possibility that when they are, a family-group taxon for *Kraemeria* may not be needed. The second reason for not requesting a decision from the Commission is that that body more often than not fails to act or delays action inordinately, thus inhibiting nomenclatural progress. In keeping with the spirit of the *Code*, I recommend that those desirous of using a family-group name for the group in question, use Kraemeriidae.

<sup>2</sup> Rosen and Parenti (1981) treated the classification and intrarelationships of the atherinomorph fishes. Among the included families is the Phallostethidae, which possibly exhibits a close relationship with the gobioids. I have no direct experience with the phallostethids and base my remarks on information in the literature.

Unlike Rosen and Parenti's Division 1 atherinomorphs (in which they include the phallostethids), but like the gobioids, the phallostethids are specialized in lacking parietals and a basisphenoid, and having the pelvic-fin elements, when present, closely associated with the cleithra (Roberts, 1971). Like other Division 1 atherinomorphs but unlike the gobioids, the phallostethids are specialized in having the rostral bone (cartilage in other atherinomorphs) decoupled from the premaxillae, in having a different arrangement of ligaments in the snout region, and in lacking infrapharyngobranchial 4 (which is lacking in *Tyson*, however). Other characters given by Rosen and Parenti to define the atherinomorphs variously apply to, or have not been investigated in, gobioids. Determining whether the phallostethids are more closely related to the gobioids than to Division 1, or other, atherinomorphs, will require more study, but the possibility of such a relationship should be considered.

<sup>3</sup> Obrhelová (1961) reported that the lacrimal was absent in the fossil gobioid family Pirskeniidae. As the lacrimal is a small, thin, loosely attached, superficial bone in most gobioids, its loss during fossilization might be expected.

<sup>4</sup> Although I have not seen the "lacrimal" defined as such, the term, as applied in the literature on teleosts, refers to a bone that articulates with the usually cartilaginously tipped, transverse process of the lateral ethmoid. In most fishes, but not gobioids, the lacrimal is a canal-bearing bone. See Gosline (1961:25-31) and Weitzman (1962:28-31) for discussion of the antorbital, and Weitzman (1962:28, footnote 7) for discussion of names of various series of bones in the orbital region.

<sup>5</sup> Obrhelová (1961) gives contradictory information on the number of branchiostegals in her new, monotypic family Pirskeniidae. On page 108 she states, in the diagnosis of the family, that the Pirskeniidae have 6 or 7 branchiostegals,

gives the generic composition of the family as, "Gattungen: *Pirskenius* n. g.," as if to indicate more than one genus was to be included (but none were), and states in the diagnosis of the genus that *Pirskenius* has 6 or 7 branchiostegals. On page 110, in a comparison of *Pirskenius* with *Lepidocottus aries* (Agassiz), which has 5 branchiostegals, she reports only that *Pirskenius* has 7 branchiostegals; and on pages 152-155 she describes the positions of these branchiostegals on the epihyal and ceratohyal (= anterior and posterior ceratohyals). Finally, on pages 178-179 (table 21) she records only 7 branchiostegals for each of the 10 specimens of *Pirskenius* for which branchiostegal counts are given (she had an additional 20 specimens, but gives no data on these). The confusion about the number of branchiostegals in *Pirskenius* may have resulted from Obrhelová's belief (1961:111) that the closest [related] species to the monotypic *Pirskenius* is the fossil *Lepidocottus papyraceus* (Agassiz), "bei welcher L. Agassiz die Anwesenheit von 6-7 radii branchiostegi anführt, wie es bei der von uns beschriebenen Gattung der Fall ist." She, additionally, leaves open the possibility that *L. papyraceus* might be the same species as her *Pirskenius diatomaceus*. In short, I believe Obrhelová diagnosed the Pirskeniidae and *Pirskenius* as having 6 or 7 branchiostegals because during preparation of her study she considered including *L. papyraceus* in that family and genus, but having changed her mind, neglected to correct the diagnoses.

<sup>6</sup> Lack of cartilage stain is probably the reason Miller (1973) and Birdsong (1975) missed basibranchial 1 in their material. Miller's illustration (fig. 5g) of the basibranchials of *Rhyacichthys* has basibranchial 2 labelled as basibranchial 1, basibranchial 3 labelled as basibranchial 2, and does not illustrate basibranchial 4 (which is cartilaginous and cuboid in my specimen). Instead he shows a separate, elongate bone, which he labels as basibranchial 3, in the position of basibranchial 4. This last-named structure appears to be the posterior end of basibranchial 3, which in gobioids extends posteriorly ventral to basibranchial 4, which is invariably a cuboidal structure (Figure 12) filling most of the area outlined by the anterior ends of the ceratobranchials 4 and the medial ends of the hypobranchials 3. Miller indicates that this piece of basibranchial 3 is ossified and disconnected from the main body of basibranchial 3 (his 2). I cannot explain this discrepancy between my specimen and his, which is about 40 mm SL shorter than the larger of the two specimens of *Rhyacichthys* I examined, and which would be expected to be less well ossified. Miller shows a gap between the anterior end of basibranchial 2 (his 1) and the basihyal. In my specimen, this gap is filled dorsally by connective tissue and ventrally by the small, cartilaginous basibranchial 1, which extends almost directly ventral from the ventrally directed anterior end of basibranchial 2. The anteriormost tip of basibranchial 1 in my specimen is stained faintly pinkish, indicating that a slight amount of ossification has occurred. The dorsal surface of the urohyal lies directly beneath the ventral surface of basibranchial 1 and is at-

tached to it by tough connective tissue. D.F. Hoese informed me that basibranchial 1 is completely ossified in his 110 mm SL specimen of *Rhyacichthys*. I would like to observe this for myself, but in view of the partial ossification of basibranchial

1 in my specimen, it is possible that variation in the degree of ossification of this element occurs. If this is so, the fourth synapomorphy I gave for the Gobioidae would have to be amended to: tendency for basibranchial 1 to fail to ossify.

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