

DEFINITION OF THE SUBORDER BLENNIOIDEI AND ITS INCLUDED FAMILIES (PISCES: PERCIFORMES)

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ABSTRACT

The monophyly of the Blennioidei is hypothesized primarily on the basis of the osteology of five specialized character complexes involving the: dorsal gill arches, pectoral fin and girdle, pelvic fin and girdle, caudal fin, and anal fin. One pair of elements, the pelvises, of one complex appears to differentiate the blennioides from all other perciforms. The lateral surface of each pelvic bone is essentially convex and the two pelvises are united at their anterior and posterior ends, dorsally, and, variously, along their central medial surfaces, thus forming a bean or nut-like pod, which is open ventrally. The Blennioidei comprise six families: Blenniidae, Tripterygiidae, Clinidae, Chaenopsidae, Dactyloscopidae, and Labrisomidae. Monophyly, based on synapomorphies, is hypothesized for each of these families, except the Labrisomidae. The monophyly of the Labrisomidae remains to be hypothesized cladistically. Although new synapomorphies are proposed for some of the other five families, one or more synapomorphies for each of the five has already been recognized in the literature. The phylogenetic relationships of the blennioid families are not hypothesized. The enigmatic families Pterygocephalidae Hubbs (fossil) and Xenocephalidae Kaup, which are occasionally cited as blennioids, are discussed and excluded from the Blennioidei (Xenocephalidae may be a synonym of Dactylopteridae). Some of the characters of the Stichaeoidei are discussed. The stichaeoids, often and unfortunately called "northern blennioids," show closer relationship to the zoarcoids than to the blennioids. To avoid confusion, the common name "northern blennioids" should be avoided; either the common name "stichaeoids" or "spiny worm-fishes" is suggested as a replacement.

In 1975 I presented a talk at the annual meeting of the American Society of Ichthyologists and Herpetologists in which I addressed the composition of the Suborder Blennioidei and the interrelationships of its included families. I did not publish a paper that detailed my concepts because I believed the subject deserved more study before making a formal presentation. Some of my ideas, however, have appeared variously in my publications and have been cited in those of others. Although I still consider the classification of the Blennioidei far from settled, my ideas on the classification of the group are presented here in order that they be available more completely and in one place.

Were this study to be presented according to my original plans, I would discuss the complex history of the classification of the Blennioidei in greater detail than I will here, and I would examine and [attempt to] polarize many more characters of many more taxa than I have so far. And I would never complete the job.

This paper, then, is an opportunistic vehicle to present my ideas in a less than rigorous manner. The reasoning and interpretations of the data are expected to be challenged, but I hope they will stimulate others to develop a more refined blennioid classification. I also hope that I have improved, if only temporarily, on Rosenblatt's (1984: 552) observation that "no satisfactory definition of the Blennioidei has yet been framed."

METHODS

I find it difficult to reconstruct exactly how my *modus operandi* developed and proceeded over the 40 years since I first concentrated study on blennioid fishes. So, I will begin with the present and occasionally interpose the past. In asserting relationships, my thinking is guided, but not corralled, by the phylogenetic paradigm.

I follow tradition in including the blennioids among the order Perciformes, although the monophyly of the Perciformes has not been hypothesized cladistically. The blennioids have been treated as a group by a great number of workers, and the composition of the group has varied almost as greatly among them. Gosline (1968), particularly, and Springer (1968) addressed some of the taxonomic history of the group.

In deciding whether a character, or character complex, is specialized, I base my decisions on character states in perciform fishes generally accepted to be less specialized than blennioids (e.g., percoids). In a real sense, I developed a concept of an archetypical generalized perciform that I used as my outgroup. In doing so, I fully recognize the potential pitfalls of such an approach.

Nomenclature has many important uses, and in the present instance it provides the starting point for my study. If there is a monophyletic Blennioidei, it must include at least a monophyletic Blenniidae. I (Springer, 1968) hypothesized the monophyly (I did not use this wording) of the Blenniidae based on three specializations, one of which, at least, is not reported to occur even homoplastically among other perciforms. This hypothesis has been corroborated by Williams (1990: 6–7), who proposed two additional synapomorphies, neither of which is known to occur homoplastically in other perciforms.

With the Blenniidae as a starting point, I examined a large array of perciform fishes, seeking specializations among them that are shared with the Blenniidae. I concentrated most of my attention on the osteology of these fishes, referring both to the literature and to an extensive array of osteological preparations of perciform and other fishes (for a partial listing see Springer and Freihofer, 1976: 2–3). My conclusions emanate from a weighted group of five specialized character complexes. Those perciforms that share these character complexes with the Blenniidae are blennioids, excluding those fishes that are specialized members of presumed or formally hypothesized monophyletic families whose basal members do not share the five character complexes with the Blenniidae. I recognize that there might be contradictory inferences were the characters subjected to a strict parsimony analysis.

The osteological drawings are based on specimens cleared with trypsin and, for the most part, stained only with alizarin. Cartilage is usually not illustrated. There is very little cartilage in blennioid skeletons, and most of the cartilage that is missing in the illustrations would be present at the anterior ends of the pelvises, between the scapulae and coracoids, and at the ends of the proximal radials of the pectoral fins. I made base drawings of the bones using a Wild M5 microscope with camera lucida. The final drawings were sized, inked, and labeled by T. B. Griswold.

Blennioid Classification since 1975

The most relevant history of the Blennioidei since 1975 is summarized as follows (more details presented in subsequent sections). Springer (in Springer and Freihofer, 1976: 40, and George and Springer, 1980: 4–5) listed the familial taxa that I currently include in the Blennioidei: Blenniidae, Clinidae, Tripterygiidae, Labrisomidae, Chaenopsidae, and Dactyloscopidae. Springer (pers. comm. in Nelson, 1984: 344) presented an abbreviated list of specializations that essentially define the Blennioidei. Eschmeyer (1990) listed all the genera of the Blennioidei and, based on the literature and some advice from me, assigned them among the six families in the suborder.

Springer and Freihofer (1976) discussed a specialization of the enigmatic, monotypic family Pholidichthyidae that might ally it with the blennioids: the pattern of the lateral-line collector nerve. This nerve has been little studied in fishes and the importance of Springer and Freihofer's observation is unknown. Ruck (1976) found a specialization, the septal bone, in the Tripterygiidae, which is otherwise known to occur only in *Pholidichthys* Bleeker. Holleman (1982: 133) referred to Ruck's specialization and first discussed it as a possible synapomorphy for the Tripterygiidae and Pholidichthyidae. Other characters might ally the Pholidichthyidae with other groups of fishes (e.g., fused fifth ceratobranchials; a putative synapomorphy of the Labroidei). Eschmeyer (1990) assigned the Pholidichthyidae to its own suborder, Pholidichthyoidei (first assignment as a suborder).

Williams (1990) corroborated Springer's (1968) hypothesized monophyly of the Blenniidae and hypothesized the phylogenetic interrelationships of the tribes within the family (based in part on Smith-Vaniz, 1976). Williams (1990: 8–9) also reported a character relating to the shape of a cartilage on infrapharyngobranchial 3, which he believed was a synapomorphy of the Dactyloscopidae, Chaenopsidae,

Clinidae, and Labrisomidae. Williams (pers. comm.) informed me that his interpretation of the position of this cartilage as an exposed, surface structure in the four families was erroneous. Only the tip of the cartilage is exposed, the remainder forms the internal core of a thin-walled tube of bone, through which the cartilage is visible. In the Blenniidae and Tripterygiidae, only the exposed tip of the cartilage, supported by solid bone, is present. A reformulation of Williams' character may still indicate a synapomorphy of the four families, but the character needs to be reassessed in more than the few nonblenniid taxa he examined (1 clinid, 1 tripterygiid, 2 labrisomids, 3 chaenopsids, 3 dactyloscopids).

Rosen and Patterson (1990), based primarily on Springer (pers. comm., and Springer's osteological preparations) discussed and illustrated the dorsal gill-arch complex of the blennioids (per George and Springer, 1980).

George and Springer (1980) hypothesized the monophyly of the Clinidae, under which they synonymized the Ophiclinidae and Peronedysidae.

Springer (pers. comm. in Holleman, 1982: 133, and pers. comm. in Nelson, 1984: 344) hypothesized the monophyly of the Tripterygiidae based on a single synapomorphy. Hardy (1986: 166) challenged that synapomorphy (I will address the challenge below).

Blot (1984) reported that the monotypic fossil family Pterygocephalidae, originally described and assigned to the Blennioidei by Hubbs (1952), could not be assigned to any extant family of fishes. Blot indicated that *Pterygocephalus* Agassiz might belong near the scorpaenoids, perhaps at the base of a long line leading to the Cephalacanthidae (=Dactylopteridae). On the basis of his pers. comm. with C. Patterson, Blot acknowledged me as correctly having excluded *Pterygocephalus* from the Blennioidei, citing remarks I made to Patterson many years ago after Patterson and I had examined specimens of *Pterygocephalus*.

Stephens (1963) defined the Chaenopsidae, and two of the characters he cited (two infraorbital bones, lack of a lateral line on the body) are apparent synapomorphies of that family. Rosenblatt and Stephens (1978) described a new genus, *Mccoskerichthys*, which they included in the Chaenopsidae, but which has four infraorbital bones, a more primitive condition for one of Stephens' synapomorphies. Hastings and Springer (1990: 97) tentatively hypothesized that *Mccoskerichthys* is the sister group of the Chaenopsidae, that *Stathmonotus* Bean (currently included in the Labrisomidae; Eschmeyer, 1990: 485) is the sister group of *Mccoskerichthys* + the Chaenopsidae, and that *Neoclinus* Girard (also included in the Labrisomidae; Eschmeyer, 1990: 485) may be the sister group of these three taxa (also implied by Stephens, 1963). Hastings and Springer contemplate more study on this arrangement.

There has been little published about the interrelationships of the Dactyloscopidae since George and Springer (1980). Pietsch (1989) followed George and Springer (1980) in excluding the Dactyloscopidae from among its often cited position near the Uranoscopidae.

The Labrisomidae remains undiagnosed as a monophyletic group. Its included taxa and their interrelationships are among the major problems in the intra-subordinal classification of the Blennioidei.

Identification of the Xenocephalidae

Kaup (1858) described *Xenocephalus armatus*, both the genus and species, and the subfamily Xenocephalinae, which recent authors have accorded family status. Nothing definitive has been written about *Xenocephalus* since Kaup, but some

authors have included the family among the blennioids, at least since Jordan (1923) placed it in his Blenniiformes. No one, except Kaup, has reported examining the holotype of *X. armatus*, but it may exist in the collections of the Muséum National d'Histoire Naturelle de Paris (MNHN). Kaup reported that he found the specimen under the name "Grenadier" in the Paris museum, where it had been received from Quoy and Gaimard's "Exp. d'Urville," which probably refers to the 1826–1829 "Astrolabe" expedition (fishes reported by Quoy and Gaimard, 1834). The type locality is New Ireland [eastern Papua New Guinea]. Kaup also reported that he gave a twice [actual] size illustration of the specimen in his "grosse werke," which might indicate that his specimen was small. The illustration, so far as I can tell, was never published, and its disposition is unknown.

At my request, M.-L. Bauchot and M. Desoutter kindly searched for the holotype of *X. armatus* among the MNHN collections and for information on it in the original, unpublished plates and records prepared by Quoy and Gaimard on the "Astrolabe" expedition. They found neither the holotype nor any plates or records referring to it. Based on information in Kaup's description, however, *X. armatus* can be excluded from the blennioids. The following is my translation of Kaup's description, excluding the color pattern.

"The abnormally large head is armed with shields and spines. First dorsal fin missing. Second dorsal fin and anal fin slightly separated from caudal. With truncated head to which the body is joined as an appendage; head and operculum armed. Tiny teeth in both jaws, none on vomer and palatines. Tongue free, thick, almost filling the entire mouth, blunt in front with short tip. Lateral line on the dorsal half of the body and slightly arched [just] following the head. The moderately large eye . . . second dorsal 7, anal 10, pectoral 21, pelvic 5, caudal 20."

The description is incomplete, somewhat ambiguous, and probably contains errors, but the combination of characters approximate those of no known blennioid. The dorsal-, caudal-, and pectoral-fin ray counts are found in no blennioid; the anal-fin ray count, presuming two spines were overlooked, fits only one species of blennioid (*Stanulus seychellensis* Smith).

Among the blennioids, the only forms that might be construed to have shields and spines on the head are the larvae of some Omobranchini (Springer and Gomon, 1975: fig. 3), which are minute and excluded from consideration here because none of the fin-ray counts come close to agreeing with any of those of *Xenocephalus*. My best guess is that *Xenocephalus* is a dactylopterid.

Blennioid Specializations

I have been able to find, at most, only one specialization that appears to be restricted unequivocally to the blennioids, as defined here, among the perciform fishes (that is, a specialization that is not duplicated at least homoplastically in a nonblennioid taxon). This specialization relates to the general structure of the pelvises (see character complex 3, below).

My hypothesis of the monophyly of the blennioid fishes, however, is based on five specialized character complexes. Although some blennioid taxa may exhibit more specialized states for some of these character complexes, with one questionable exception (see no. 2 below), no taxon exhibits a less specialized state for any of the complexes or any portion of a complex. In addition to the five complexes, the blennioids share a number of specialized character states (relative to the archetypical perciform) that are distributed more commonly among other perciforms. Finally, the blennioids share several relatively unspecialized perciform

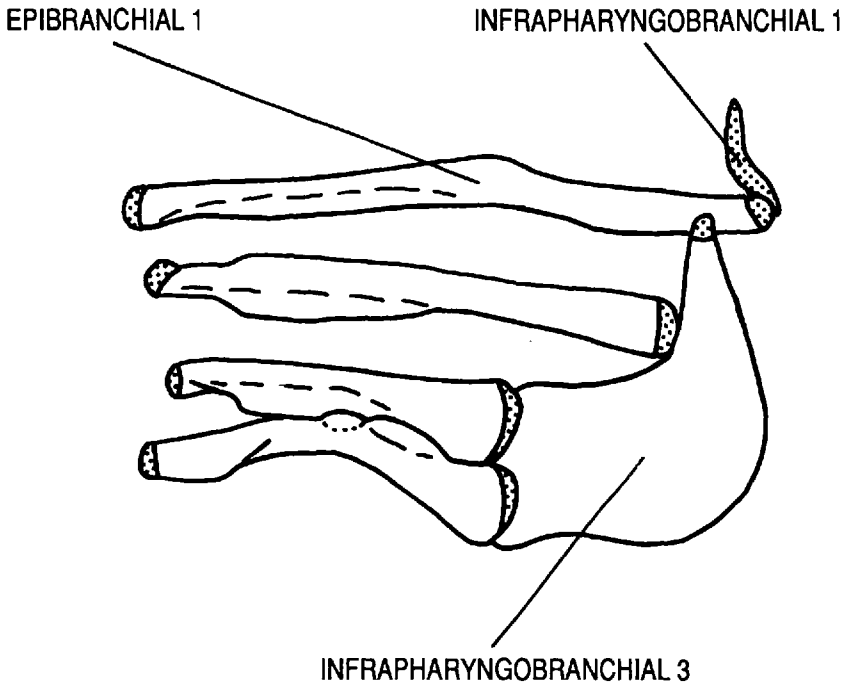


Figure 1. Least specialized state for dorsal gill arches (left side) of a blennioid, based on the labrisomid *Labrisomus bucciferus* (Poey). The only more specialized state differs in lacking infrapharyngobranchial 1 (cartilage indicated by stippling).

character states that may be represented intrafamiliarily by more specialized states. The five specialized character complexes are discussed first, followed by a listing of the other specialized and unspecialized character states.

Specialized Character Complexes

1. Dorsal gill-arch elements (Fig. 1). With rare exception, the 1st infrapharyngobranchial is absent or present primarily as cartilage (present only among some clinids, labrisominids and chaenopsids), and the 2nd and 4th infrapharyngobranchials are absent; the 1st epibranchial lacks an uncinete process and there is no interarcual cartilage.

Rosen and Patterson (1990: fig. 38b) illustrate infrapharyngobranchial 1 as partially ossified in *Chaenopsis alepidota* (Gilbert). In the illustrated specimen, USNM 200391, there is a demarcation between the strictly cartilaginous portions and the portion Rosen and Patterson illustrated as bone; however, the "bony" section is not stained—the specimen was not counterstained for cartilage—as are the bony portions of the other bones they illustrated for that specimen. P. A. Hastings informs me that infrapharyngobranchial 1 is cartilaginous in all labrisomids and chaenopsids he has examined except for one specimen of *Neoclinus blanchardi* Girard (SIO uncat.), in which both are fully ossified, and one specimen of *Hemiemblemaria simulus* Longley and Hildebrand (UMML 15055), in which only one side is ossified. A specimen of the labrisomid, *Labrisomus nuchipinnis* (Quoy and Gaimard), Florida State Museum of Natural History 47331, has a tiny ring of bone at about midlength of the otherwise cartilaginous infrapharyngo-

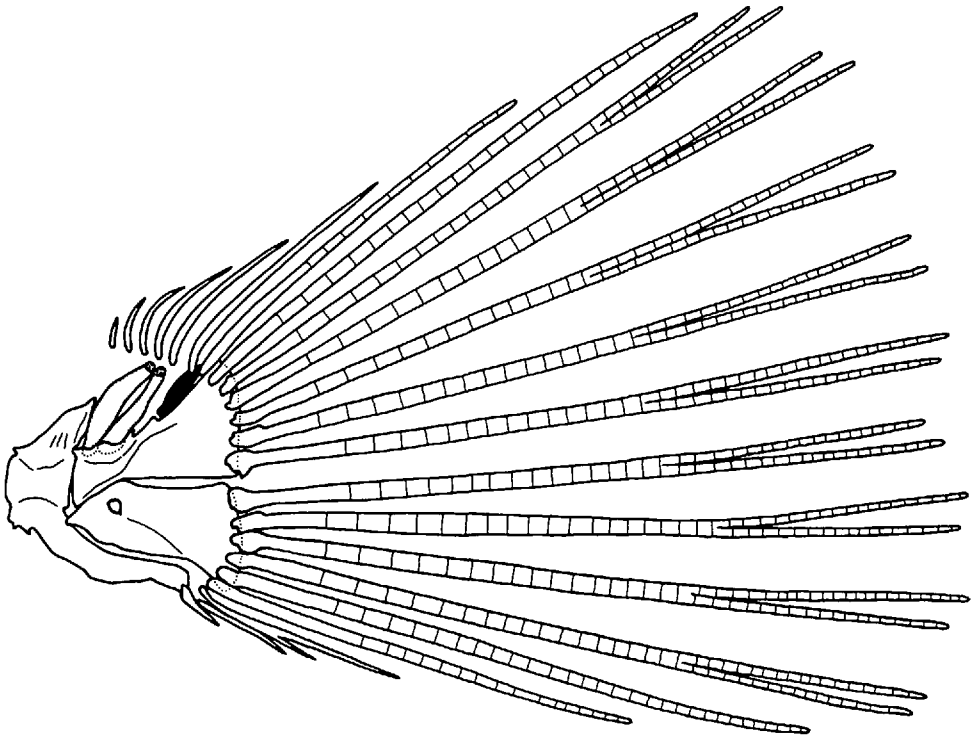


Figure 2. Least specialized state for the caudal-fin complex of a blennioid (excluding number and disposition of procurrent rays), based on the blennioid *Parablennius parvicornis* (Valenciennes) (epurals, with cartilaginous tips, indicated in gray; hypural 5 indicated in black).

branchial 1. These are the only examples of ossification of infrapharyngobranchial 1 in blennioids that I am aware of.

The blennioid configuration of the dorsal gill arches otherwise appears to characterize only (all) the Gobiesocidae (Springer and Fraser, 1976; Rosen and Patterson, 1990) and Liparididae (Kido, 1988; Rosen and Patterson, 1990, and pers. observ.; the closely related Cyclopteridae have infrapharyngobranchials 2 and 3), all of which lack infrapharyngobranchial 1, and some highly specialized gobioids (e.g., *Tyson* Springer, 1983) and cottoids (e.g., *Myoxocephalus* Tilesius, Yabe, 1985; Rosen and Patterson, 1990; however, Yabe's fig. 24e shows a short uncinete process dorsally on epibranchial 1 that apparently articulates with infrapharyngobranchial 3).

2. Caudal fin (Fig. 2). The least specialized state for the blennioid caudal fin is as follows: an autogenous ventral hypural plate, which I presume comprises the parhypural and fused hypurals 1 and 2 with no hypurapophysis; a dorsal hypural plate, which I presume comprises fused hypurals 3 and 4, which is, in turn, fused to the urostylar complex; an autogenous hypural 5; uroneurals absent (or indistinguishably fused to complex urostylar centrum); two epurals; fewer than 16 segmented caudal-fin rays, of which fewer than 12 are branched, but rarely more than once (except for the monotypic dactyloscopid genus *Sindoscopus* Dawson, which has the rays branched twice, and at least one of the three species of *Tripterygion* Risso, *T. tripteronotus* (Risso), which has the rays branched several times);

the hemal spine of preural centrum 2 (pu2) and that of pu3 is fused to its respective centrum; the neural spine of pu2 is short.

The adult configuration of the hypural plates and urostylar centrum are present in larval blenniids and tripterygiids, at least (Peters, 1981; Ruck, 1976), and there is, thus, no confirmation for my presumptions of the composition of the plates in these two families. I have seen unidentified dactyloscopid larvae, however, in which the cartilaginous ventral hypural plate exhibits two foramens proximally. These foramens appear to be vestiges of the separations of the plate into the parhypural and hypurals 1 and 2. The posterior of the two foramens closes during ontogeny, but the anterior foramen persists in adults and serves as a passageway for the caudal arteries and veins.

The most frequent intrasubordinal modifications of the caudal fin are: fusion of the ventral hypural plate with the urostylar centrum; loss of hypural 5 (or, doubtfully, fusion with the dorsal hypural plate); loss of one epural (never both); presence of only simple caudal-fin rays; presence of a long neural spine on pu2 (short and long neural spines on pu2 may be present within a single species).

I have not found the least specialized state of the caudal complex of blennioids in any other fishes, although I expect that it occurs homoplastically. A close approximation was reported by Smith-Vaniz and Johnson (1990: fig. 17d) for the specialized plesiopid *Acanthoplesiops psilogaster* Hardy, and a less close approximation was reported by Fraser (1972: pl. 7d) for the specialized apogonid *Gymnapogon annona* Whitley. The caudal skeleton of *A. psilogaster* has three epurals, of which two are fused, but still exhibit a partial separation. It also has a long neural spine on pu2. Ignoring the three epurals, the acanthoclinid configuration does appear as a blennioid variation. Although the elements of the *G. annona* caudal are essentially the same as those of the least specialized blennioid caudal complex, the epurals are much slenderer and more separated from each other than they are in blennioids. Furthermore, the ventral hypural plate of *G. annona* appears to bear an hypurapophysis and the plate only partially contacts the urostylar complex.

Very few fishes appear to manifest any of the more specialized states for the blennioid caudal complex but some that do are: *Chalixodytes* Schultz, Creediidae; *Histrio* Fisher von Waldheim, Antennariidae. Many fishes, however, manifest highly specialized states that might not exclude them from inclusion among the blennioids (e.g., *Pholidichthys*). Numerous other fishes reproduce the blennioid caudal complex, except for incorporating a single, less specialized condition for one component of the complex (e.g., gobiesocid caudals are very similar to those of the blennioids, but the gobiesocids have an autogenous parhypural).

Bannikov (1989) described a new species of fossil fish, which he assigned to the extant clinid genus *Clinnitrachus*, from the Miocene of Romania. Although the description and illustration of the species appears to be that of a clinid, and one character (scales with radii in all fields) is a clinid apomorphy, the purported structure of the caudal fin is not duplicated in any extant blennioid. Bannikov reported that the ventral hypural plate and parhypural are both autogenous. While the ventral hypural plate is autogenous in some modern blennioids, it is not autogenous in any of the many clinids, including *Clinnitrachus*, that I have examined, and the parhypural is never autogenous in any modern blennioid.

In summary, with rare exceptions, one can recognize a blennioid fish based only on the structure of its caudal fin.

3. Pelvic fins and pelvises (Figs. 3–8). The pelvic-fin ray bases (not illustrated) are positioned well anterior to a vertical through the anteriormost pectoral-fin ray base; each fin comprises an embedded, nonpungent spine and fewer than 5

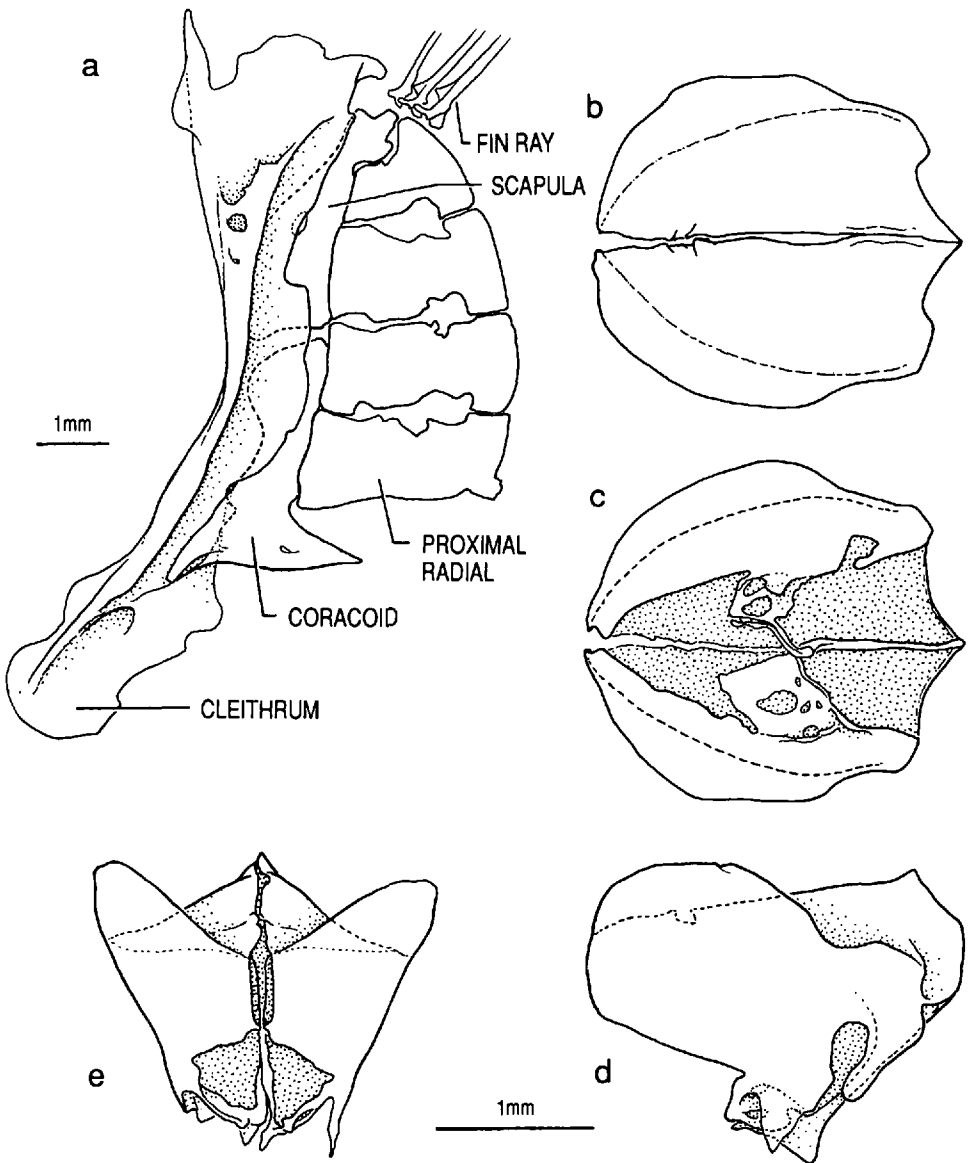


Figure 3. Pectoral and pelvic girdles of a tripterygiid, *Tripterygion tripteronotus*, USNM 276290, 56 mm SL: *a*, left-side lateral view of pectoral girdle with bases of dorsalmost pectoral-fin rays indicated; *b-e*, dorsal, ventral, lateral, and frontal views of pelvises.

(2–4) simple segmented rays (one species of the blenniid genus *Plagiotremus* Gill lacks pelvic fins; 4 rays only in some blenniids and one labrisominid *Calliclinus geniguttatus* (Valenciennes)); the lateral surface of each pelvis is essentially convex and the two pelvises are united dorsally and at their anterior and posterior ends and, variously, along central, slender, weak, anteriorly extending medial processes (processes absent in dactyloscopids and some chaenopsids). The joined pelvises thus form a somewhat bean- or nut-like pod, which is open ventrally, and has a dorsally extending flange anteriorly on each side (at least some tripterygiids also

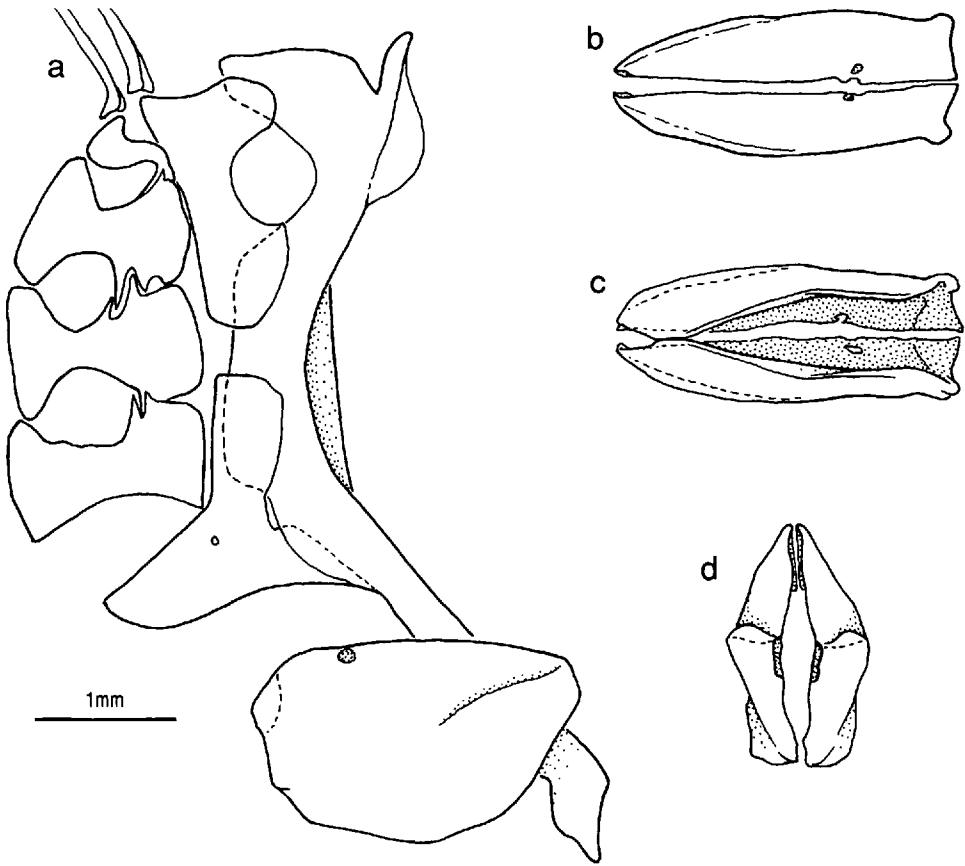


Figure 4. Pectoral and pelvic girdles of a dactyloscopid, *Dactylagnus mundus*, USNM 270365, 40 mm SL: *a*, left-side internal view of pectoral girdle with right-side pelvis and bases of dorsal-most pectoral-fin rays indicated (for labels see Fig. 3); *b-d*, dorsal, ventral, and frontal views of pelvises (note: the illustrated specimen is a juvenile in which the dorsal margins of the pelvises have not yet made contact and the lateral flange-like processes that contact the cleithra are incompletely formed).

have weak ventrally extending flanges). In anterior view the joined pelvises look like a kind of nun's hat (Figs. 3e, 4d, 5f, 6e, 7f, 8e).

A similar complex is not found among other perciforms, in most of which the pelvises, although joined in some forms, are rod-like, elongate-triangular, or depressed-ovoid in form. The position, shape, and association of the blennioid pelvises probably are adequate for determining that a fish is a blennioid.

4. Anal-fin ray elements. The anal fin comprises fewer than three (0–2) non-pungent spines and only simple segmented rays.

Cottoids, gobiesocids, bembropids, creediids, leptoscopids, and hoplichthyids are among the few perciforms exhibiting anal-fin ray elements similar to those of blennioids.

5. Pectoral fins and girdle (Figs. 3–8). Some or all of the four proximal pectoral-fin radials are longer than deep, and longer than the horizontal width of the scapula or coracoid; some or all of the rays are unbranched, and when branched rays are present, there are unbranched rays both above and below the branched rays; bases of the two hemitrichs of the dorsal-most pectoral-fin ray not particularly differentiated from bases of hemitrichs of next-to-dorsalmost ray; ventroanteriorly

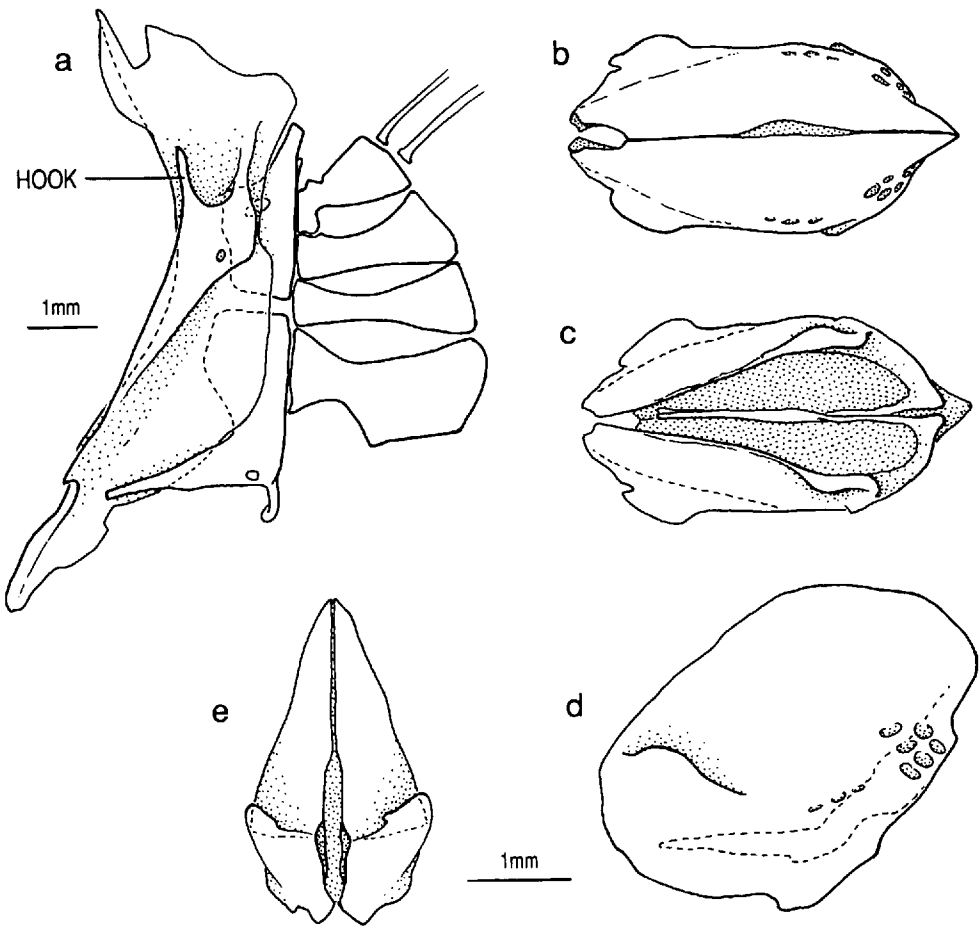


Figure 5. Pectoral and pelvic girdles of a clinid, *Gibbonsia elegans*, USNM 200386, 64 mm SL: *a*, left-side lateral view of pectoral girdle with bases of dorsalmost pectoral-fin rays indicated (for labels see Fig. 3); *b–e*, dorsal, ventral, lateral, and frontal views of pelvises.

extending process of coracoid, when present, shorter than dorsal portion of coracoid; ventroposterior corner of coracoid forms a distinctly demarcated, posteriorly or ventromedially directed process that is well removed ventrally from the proximal radials (does not subtend, or almost subtend the ventralmost proximal radial). Depending on the taxon, the process may be broadly triangular and acute (least specialized state—occurs in tripterygiids and dactyloscopids, at least), or blunt, spike-like, with the spike tip variously hooked or otherwise developed (other blennioids).

Other perciforms have pectoral-fin supports similar to those of blennioids, e.g., certain specialized pseudamine apogonids. The longest radial of cirrhitids (cheilodactylids not examined) is about the same length as the coracoid, which has a spike-like process similar to that of the blennioids. The cirrhitid coracoid has an additional, laterally projecting spike at its ventroposterior end that is not found in the blennioids, and the prominent scapular and coracoid foramens of the cirrhitids are much larger and more prominent than those of the blennioids. The proximal radials of gobioids are often longer than the scapula or coracoid, and

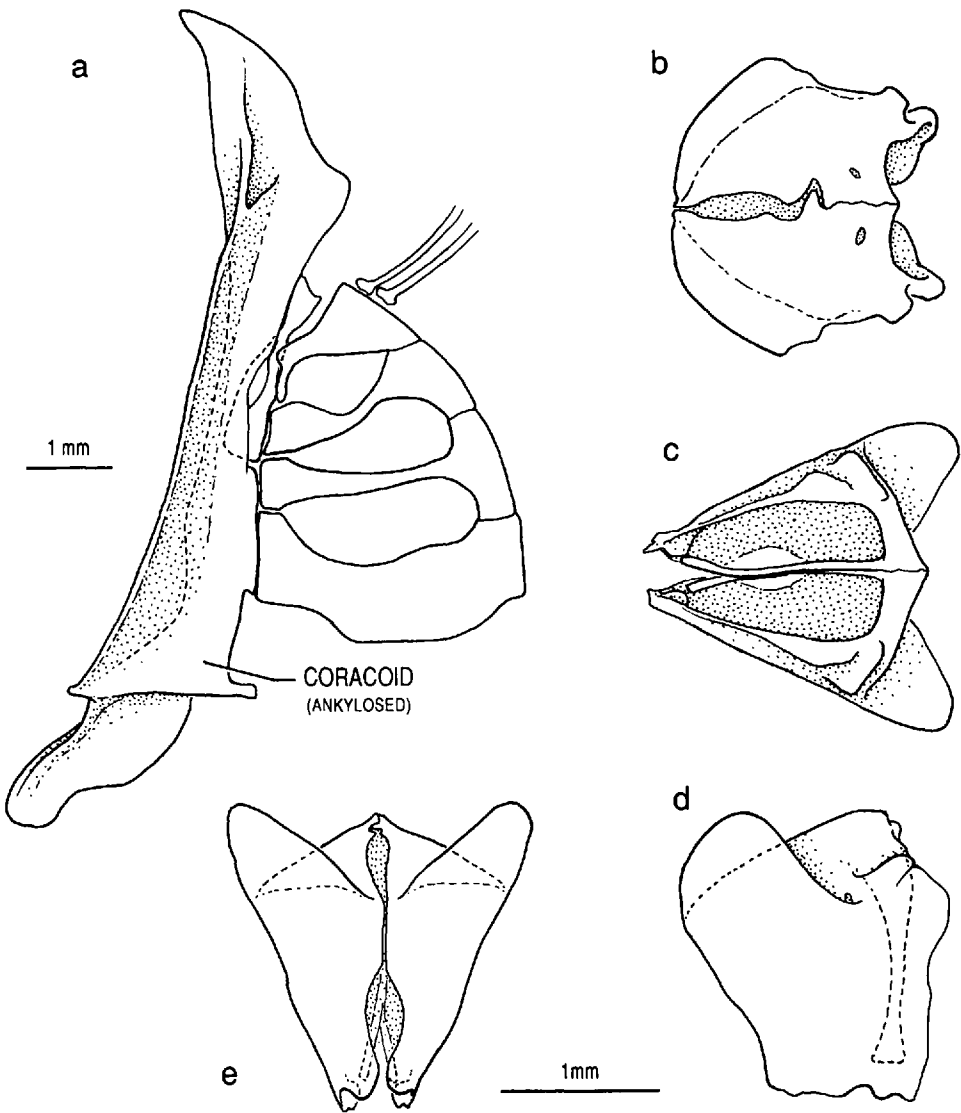


Figure 6. Pectoral and pelvic girdles of a blenniid, *Parablennius marmoreus*, Florida Museum of Natural History 11021, 53 mm SL: *a*, left-side lateral view of pectoral girdle with bases of dorsalmost pectoral-fin rays indicated (note coracoid is ankylosed to cleithrum; for labels see Fig. 3); *b-e*, dorsal, off-ventral, lateral, and frontal views of pelvises.

the coracoid of some gobioids, particularly eleotridids and xenisthmids bears a ventroposterior process similar to that of blennioids (Springer, 1983: figs. 14, 16, 1988: fig. 7).

Perhaps not so obvious, is the similarity of the state of the coracoid in a serranid, such as *Variola louti* (Forsskål), to that of a blennioid, such as *Tripterygion tripteronotus*. In *V. louti*, the coracoid has an elongate anteroventrally extending process and a triangular posteriorly extending process somewhat ventral to the ventralmost proximal pectoral-fin radial. If the anteroventrally extending process

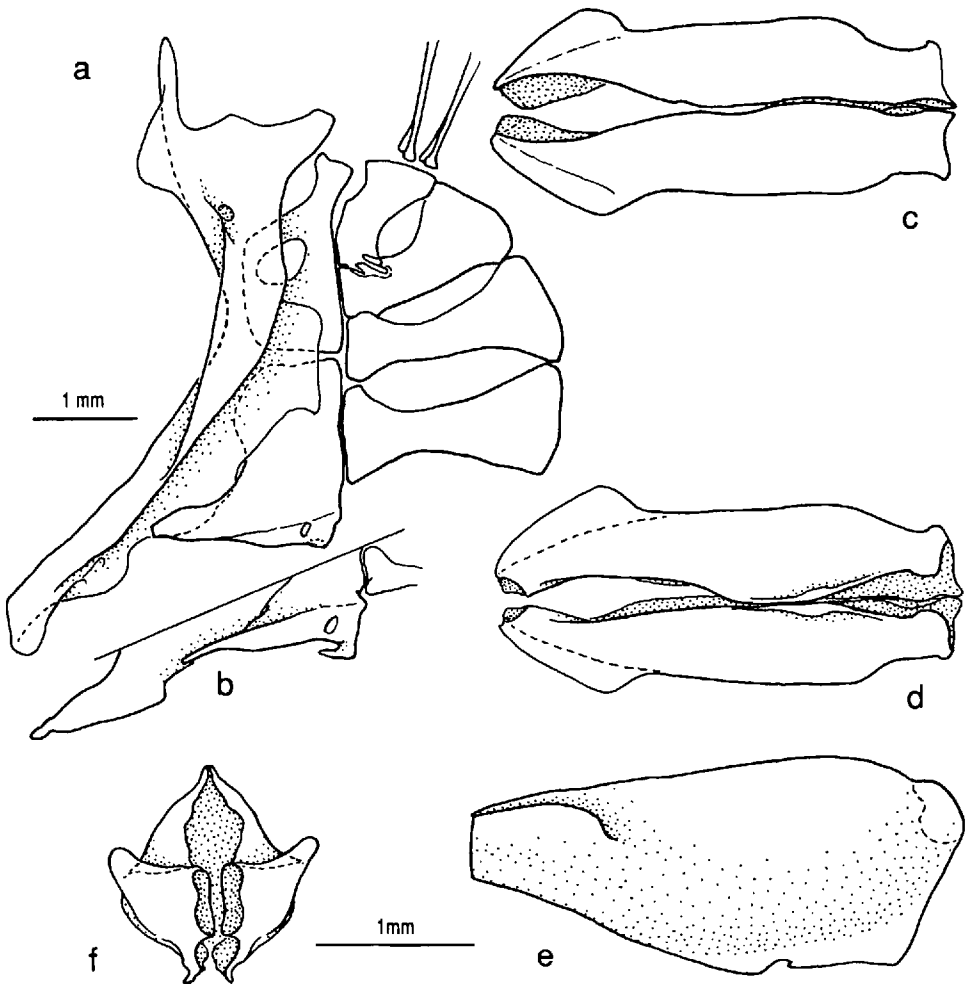


Figure 7. Pectoral and pelvic girdles of a chaenopsid, *Ekemblemaria myersi*, USNM 200399, 48 mm SL: *a*, left-side lateral view of pectoral girdle with bases of dorsalmost pectoral-fin rays indicated (for labels see Fig. 3); *b*, off-ventral view of cleithrum, coracoid, and ventralmost proximal radial to show structure of ventroposterior coracoid process; *c-f*, dorsal, ventral, lateral, and frontal views of pelvises.

were shortened considerably, the state of the coracoid would be similar to that of *T. tripteronotus*.

Some More Commonly Distributed Specializations

6. Dorsal- and anal-fin pterygiophore-vertebral relationship. The pterygiophores in these fins bear an essentially one-to-one relationship with the vertebrae. The main variation occurs anteriorly in each fin. In the dorsal fin the anteriormost pterygiophores may be crowded or displaced over the head dorsally, and thus difficult to associate with a particular vertebra. In the anal fin the anteriormost pterygiophores may be crowded and two or three may appear to be associated primarily with the hemal spine of the first caudal vertebra. Many perciforms

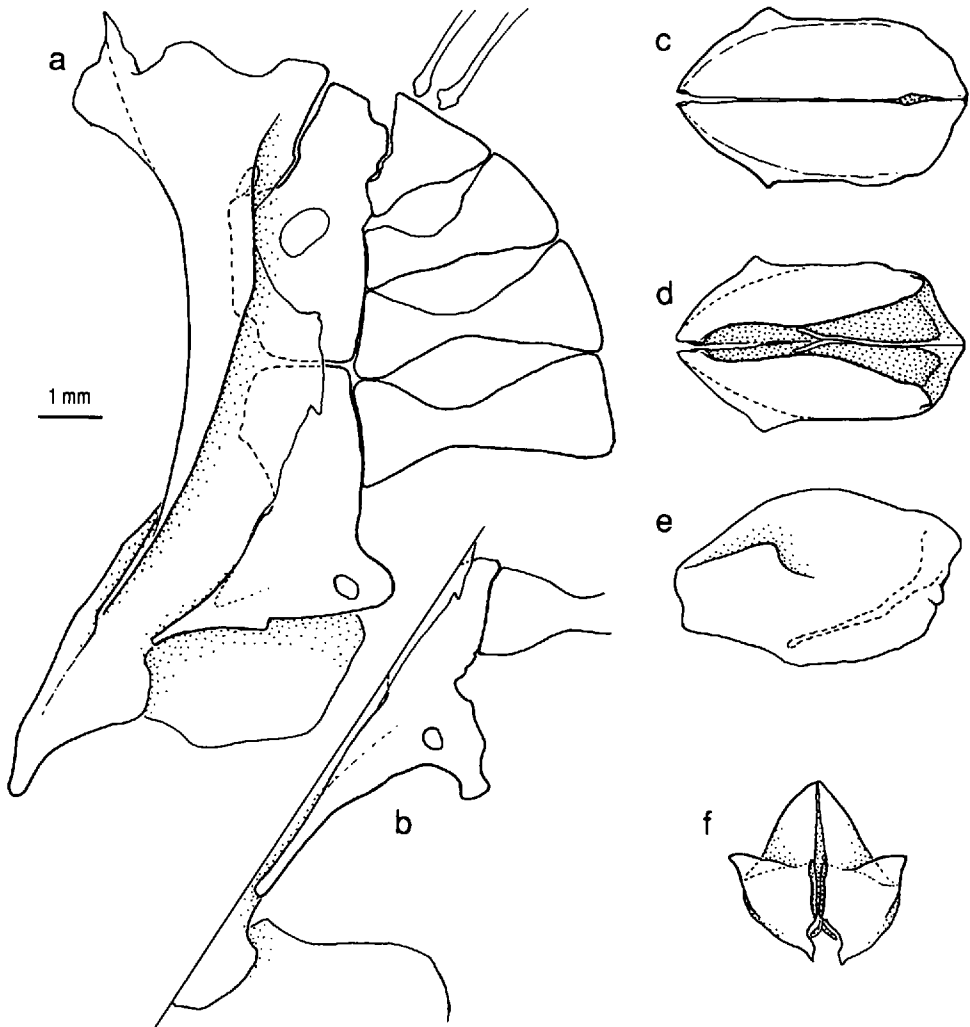


Figure 8. Pectoral and pelvic girdles of a labrisomid, *Alloclinus holderi*, USNM 201164, 78 mm SL: *a*, left-side lateral view of pectoral girdle with left pelvis and bases of dorsalmost pectoral-fin rays indicated (for labels see Fig. 3); *b*, off-ventral view of left pelvis, cleithrum, coracoid, and ventralmost proximal radial to show structure of ventroposterior coracoid process; *c-f*, dorsal, ventral, lateral, and frontal views of pelvises.

exhibit such one-to-one relationships, but preperciforms and many generally considered less specialized perciforms do not.

7. Dorsal- and anal-fin pterygiophore structure. The pterygiophores associated with the dorsal- and anal-fin spines each consist of a single element, which probably represents fused proximal and middle radials, and, perhaps, fused distal radials of the preceding pterygiophore as well (Mooi, 1993). Each pterygiophore associated with a dorsal- or anal-fin segmented ray consists of fused proximal and middle radials and a bilateral pair of distal radials.

Bisegmental pterygiophores supporting spines and trisegmental pterygiophores supporting segmented rays are unspecialized perciform conditions.

8. There are no supraneurals, which primitively number three in perciforms;

however, spineless pterygiophores, which might be confused with supraneurals, are present, and may be numerous, at the anterior end of the dorsal fin in some dactyloscopids and clinids.

9. Branchiostegal rays 6; primitively number 7 in less specialized perciforms. One of the 15 species of the labrisomid genus, *Paraclinus* Mocquard, *P. walkeri* Hubbs, has 6 or 7 branchiostegals (usually 7, Hubbs, 1952: 70). I interpret the 7-rayed condition to be a new acquisition (autapomorphy) in this species. Nelson (1976: 270, 1984: 344) reported that the Tripterygiidae have 6 or 7 branchiostegals. I have not found 7 in any of the several genera and species of tripterygiids I have examined, nor do I know of any other published reports of 7 for this family.

10. Infraorbitals 2–5; in less specialized perciforms, there are 6 or 7.

Two unspecialized character states, whose importance will be discussed in the section on stichaeoids at the end of the paper: 11.—Basisphenoid present (except for the blennioid tribe Nemophini). 12.—Nostrils 2 on each side (except for a few species of the blennioid genus *Enchelyurus* Peters, tribe Omobranchini, in which there is only one on each side).

THE BLENNIOID FAMILIES

Tripterygiidae

Characterization (* denotes character is unspecialized, occurs in less specialized, nonblennioid perciforms; italics denote specialization unique to tripterygiids among blennioids; level at which other characters are specialized is undecided).—1: *no dorsal-fin spine articulating with pterygiophore serially associated with first segmented ray* (“*posteriormost*” dorsal-fin spine absent; as many as four of the posteriormost spines may be absent); 2: dorsal fin divided (membranes deeply or completely incised) into two spinous and one segmented-ray portions (membrane between spinous dorsal fins usually deeply or completely incised; wide space always present between last spine of 1st spinous dorsal fin and 1st spine of 2nd spinous dorsal fin); 3: dorsal-fin spines more numerous than segmented rays (nearly twice as many spines in all but the two species of *Notoclinus* Gill, in which the spines only slightly outnumber the segmented rays); 4: segmented dorsal-fin rays branched* or simple; 5: posteriormost dorsal-fin pterygiophore supporting 1 or 2* (“*last ray divided to base*”) fin-ray elements; 6: autogenous bony stay present* or absent following posteriormost dorsal-fin pterygiophore; 7: anal-fin spines 0, 1, or 2; 8*: anal-fin spines of mature males without fleshy bulbous distal swellings; 9: posteriormost anal-fin pterygiophore supporting 1 or 2* fin-ray elements (“*last ray divided to base*”); 10: autogenous bony stay present* or absent following posteriormost anal-fin pterygiophore; 11: branched pectoral-fin rays present* or absent; 12: dorsalmost pectoral-fin ray articulating entirely*, or in part, with scapula; 13*: coracoid autogenous; 14*: some caudal-fin rays branched; 15*: ventral hypural plate autogenous; 16: hypural 5 present* (most genera) or absent; 17: scales present*, some or most ctenoid*, bearing only one row of cteni (except scales all cycloid in the two species of *Notoclinus*), with radii only in anterior field*; 18*: lateral line contained on scales with free posterior margins (scales not embedded); 19*: lateral line extending half or more length of body (except restricted anteriorly in one undescribed Indo-Pacific genus); 20: rostral cartilage absent; 21: *septal bone present* or absent*; 22*: ecto- and mesopterygoids autogenous; 23*: posterior end of interopercle extending posteriorly past posterior end of epihyal; 24*: premaxillae protractile; 25*: no noticeably enlarged canine teeth posteriorly in jaws; 26*: free margins of lips entire (as opposed to fimbriate, crenulate, or with lappets); 27*: no cordlike ligament extending from dorsopos-

terior portion of each ceratohyal to anteromedial end of its respective dentary; 28*: urohyal lacking vertical pair of processes on each side (for specialized condition see section on Blenniidae); 29: gill membranes broadly attached across isthmus; 30*: free bony margins of opercular bones not fimbriate; 31: infraorbital bones 4 or 5; 32: palatine teeth present* or absent; 33*: nape cirri absent; 34: anterior ends of pelvises not extending anteriorly past their juncture with the cleithra (for contrasting condition see Fig. 4; for discussion see section on Dactyloscopidae).

Discussion of Certain Tripterygiid Characters. — The single specialization that unites the members of the Tripterygiidae unequivocally (not present, even homoplastically in any other blennioid family) is the loss of at least the “last” dorsal-fin spine.

In many perciforms and in all nontripterygiid blennioids, each of the dorsal-fin spines, except the posteriormost, articulates with a single pterygiophore. The “last” dorsal-fin spine articulates with the pterygiophore that also supports the first segmented ray. (In fact, the dorsal-fin spines are displaced posteriorly, so that each spine rests on, or is most closely articulated with, the pterygiophore that is serially associated with the following spine, or in the case of the “last” spine, the pterygiophore of the first segmented ray.) In tripterygiids, no spine articulates with the pterygiophore of the first segmented ray, and in many tripterygiid taxa, several (up to 4) pterygiophores immediately anterior to that of the first segmented ray may also lack spines. A superficially similar condition exists only in the Blenniidae, in which the “last” dorsal-fin spine of many species is greatly reduced (and frequently overlooked in published descriptions), but some vestige of it is always present.

Hardy (1986: 166) reported that 5% of his specimens of the two species in the New Zealand tripterygiid genus *Ruanoho* Hardy had fully developed “last” dorsal-fin spines (I have seen radiographs of the specimens and confirm his observations). On this basis, he questioned the usefulness of the character as a specialization for defining the Tripterygiidae. None of the many specimens of many other genera and species of tripterygiids that Hardy, or I, or others have examined by radiograph or clearing and staining, have a “last” dorsal-fin spine.

I believe that the presence of the “last” spine in the exceptional specimens of *Ruanoho* is an uncommon reversal to a primitive state, hence, a specialization of *Ruanoho*. If by chance all specimens of *Ruanoho* had the last spine, close relationship with, and inclusion of *Ruanoho* among the Tripterygiidae would be unavoidable, with one exception: if *Ruanoho* is the sister group of the Tripterygiidae. The inclusion of *Ruanoho* in the Tripterygiidae is supported by certain of its other characters that are found otherwise only among tripterygiids within the Blennioidei, and it does not exhibit any specialization that characterizes unequivocally any other group of blennioids.

Three characters of tripterygiids that are specialized at some level in the family, and that *Ruanoho* also possesses, are the septal bone, a distinctly tripartite dorsal fin, and only unbranched rays in the segmented-ray dorsal-fin. Two of the unspecialized characters that *Ruanoho* has and that are otherwise unique to the tripterygiids among the blennioids are ctenoid scales and some branched pectoral-fin rays.

Among the blennioids, the septal bone occurs only in the Tripterygiidae, and it is present in many (most?), but not all the genera (see, however, character 21 in the Chaenopsidae). Among nonblennioid perciforms, the septal bone is found only in the enigmatic, monotypic Pholidichthyidae (Springer and Freihofner, 1976;

Holleman, 1982). Pending a cladistic analysis, it seems probable that the septal bone is a specialization defining a clade within the Tripterygiidae, and *Ruanoho* probably belongs in that clade.

The dorsal fin of most tripterygiids is divided into two spinous fins and a segmented-ray fin, with the notching between the fins complete or almost complete. Broad, membranous connections between the fins occur, however, in a few New Zealand species, and these species may have derived the connections secondarily. The anterior spinous dorsal fin comprises 3–9 spines (rarely more than 7 spines and only in *Obliquichthys* Hardy), and the last spine in the fin is well separated from the first spine of the second spinous fin.

A completely, or almost completely, separate anterior spinous dorsal fin (comprising three spines) occurs commonly in the Dactyloscopidae and Clinidae, and uncommonly in the Labrisomidae and Chaenopsidae. A deep separation between the spinous and segmented-ray dorsal fins also occurs in the Dactyloscopidae and Blenniidae, but a tripartite dorsal fin occurs only in a few dactyloscopids and in the highly specialized, monotypic labrisomid genus *Haptoclinus* Böhlke and Robins (1974).

Haptoclinus has what might be interpreted to be four dorsal fins: a completely separate 1st fin comprising three spines, a completely separate 2nd fin comprising a single spine, a 3rd fin comprising 13–14 spines that is deeply incised at its connection to a 4th fin comprising simple segmented rays.

The tripterygiids share no specialization with any other blennioid family to the exclusion of all the other families. If the presence of branched rays in the dorsal and pectoral fins of tripterygiids is plesiomorphic for the tripterygiids, then the presence of only simple rays in the dorsal and pectoral fins is a synapomorphy for the other blennioid families.

After this paper had gone to press, Michael Brogan called to my attention that I had overlooked a character that essentially defines the Tripterygiidae. Hubbs (1952: 50) first differentiated the Tripterygiidae from the other blennioids in noting that the sensory canals of the infraorbital bones and preopercle are unroofed by bone. I confirm his findings for the osteology of all the tripterygiids I have examined except the highly specialized New Zealand genus *Notoclinus* Gill, in which these canals are roofed with bone. The canals are roofed with bone in all the other blennioids, including the Dactyloscopidae, which Hubbs did not recognize as blennioids. It is undecided whether unroofed canal bones is a synapomorphy of the tripterygiids. Unroofed sensory canal bones appear in various preperciforms (e.g., beryciforms) and the condition is generally considered to be unspecialized in perciforms. If this assumption is true, the condition might be a plesiomorphy retained by the Tripterygiidae (hence, roofed bones would be a synapomorphy of the other blennioid families and probably an autapomorphy for *Notoclinus*).

Dactyloscopidae

Characterization (* denotes character is unspecialized, occurs in less specialized, nonblennioid perciforms; italics denote specialization that occurs only in dactyloscopids among blennioids; level at which other characters are specialized is undecided).—1*: dorsal-fin spine articulates with pterygiophore serially associated with first segmented ray (“posteriormost” dorsal-fin spine present); 2: dorsal fin various, divided (membranes deeply or completely incised) into two spinous and one segmented-ray portions, or divided into anterior 2-, 3-, or 4-spined fins (with spines variably completely separate) and continuous posterior spinous and segmented-ray fin, or fin undivided* (continuous); 3: dorsal-fin elements variable,

ranging from many more spines than segmented rays to many more segmented rays than spines; 4: segmented dorsal-fin rays simple; 5: posteriormost dorsal-fin pterygiophore supporting only 1 fin-ray element ("last ray not divided to base"); 6: no autogenous bony stay following posteriormost dorsal-fin pterygiophore; 7: anal-fin spines 2; 8*: anal-fin spines of mature males without fleshy bulbous distal swellings (however, *bone of anterior rays thickened in males*); 9: posteriormost anal-fin pterygiophore supporting only 1 fin-ray element ("last ray not divided to base"); 10: no autogenous bony stay following posteriormost anal-fin pterygiophore; 11: all pectoral-fin rays unbranched; 12: dorsalmost pectoral-fin ray articulating entirely,* or in part, with scapula; 13*: coracoid autogenous; 14: some caudal-fin rays branched* or all unbranched; 15: ventral hypural plate fused to urostylar complex; 16: hypural 5 absent; 17: scales, cycloid, not embedded,* with radii only in anterior field*; 18*: lateral line contained on scales with free posterior margins (scales not embedded); 19*: lateral line extending entire length of body; 20: rostral cartilage absent; 21*: septal bone absent; 22: *ecto- and mesopterygoids presumably fused* (represented by a single bone occupying the position one would expect the two bones to occupy; probably a synapomorphy of the Dactyloscopidae, but character state is also present in some Chaenopsidae); 23*: posterior end of interopercle extending posteriorly past posterior end of epihyal; 24*: premaxillae protractile; 25*: no noticeably enlarged canine teeth posteriorly in jaws; 26: free margins of one or both lips with fimbriae or lappets (entire* in the monotypic *Leurochilus* Böhlke); 27*: no cordlike ligament extending from dorsoposterior portion of each ceratohyal to anteromedial end of its respective dentary; 28*: urohyal lacking vertical pair of processes on each side (for specialized condition see section on Blenniidae); 29: gill membranes free*, *broadly overlapping ventrally*; 30: *free bony margins of all three opercular bones fimbriate, those of opercle produced externally*; 31: infraorbital bones 5; 32: palatines edentate; 33* nape cirri absent; 34: *anterior ends of the pelvises extending anteriorly (or dorsoanteriorly) past their juncture with the cleithra* (Fig. 4).

Discussion of Certain Dactyloscopid Characters.—Dawson (1982: 17) stated erroneously that dactyloscopids lack a parasphenoid. I believe that he meant they lacked pterosphenoids, as was first reported by Starks (1923). The absence of pterosphenoids is probably a dactyloscopid synapomorphy. Some omobranchin blenniids appear to have lost the pterosphenoids independently. The dactyloscopid basisphenoid appears to consist only of the meningost portion (a specialization), whereas, at least some taxa in all the other blennioid families have a basisphenoid consisting of both meningost and belophram portions (Springer, 1968: 43–44).

The dactyloscopids and clinids share in always having the ventral hypural plate fused with the complex urostylar centrum (also true of all chaenopsids) and, with the exception of the clinid *Springeratus* Shen, in lacking palatine teeth (also true of all Blenniidae, and several Labrisomidae).

The presence of vomerine teeth is a common condition among basal perciforms. Among the blenniids, all tripterygiids and chaenopsids have vomerine teeth, and the teeth may be present or absent in the blenniids, clinids, and chaenopsids. All dactyloscopids, however, lack vomerine teeth, and this character is possibly a synapomorphy of the family.

Among the blennioids, only the dactyloscopids have the anterior ends of the pelvises extending anteriorly (or dorsoanteriorly) past their juncture with the cleithra (Fig. 4). A similar relationship between the ends of the pelvises and the cleithra occurs in a wide array of relatively unspecialized perciforms (including

uranoscopids and trachinids, which have been considered to be close relatives of the dactyloscopids; Starks, 1923). In keeping with my flagging of other, apparently plesiomorphic characters with an asterisk, this character should also be flagged. In this case, however, I have arbitrarily assumed that the character state in the dactyloscopids evolved independently. If my assumption is correct, the other state for the character (pelvises not extending past their junction with the cleithra) is plesiomorphic for the Blennioidei.

The dactyloscopids are also unique among the blennioids in having the gill membranes separate and free from the isthmus, a condition that is typical of less specialized perciforms. The condition either represents a synapomorphy of the dactyloscopids or retention of a primitive character.

Clinidae

Characterization (* denotes character is unspecialized, occurs in less specialized, nonblennioid perciforms; italics denote specialization that occurs only in clinids among blennioids; level at which other characters are specialized is undecided).— 1*: dorsal-fin spine articulates with pterygiophore serially associated with first segmented ray (“posteriormost” dorsal-fin spine present); 2: dorsal fin either continuous* or divided (membranes deeply or completely incised) into anterior 3-spined fin and continuous posterior spinous and segmented-ray fin; 3: dorsal fin with many more spines than segmented rays; 4: segmented dorsal-fin rays simple; 5: posteriormost dorsal-fin pterygiophore supporting only 1 fin-ray element (“last ray not divided to base”); 6: autogenous bony stay following posteriormost dorsal-fin pterygiophore absent; 7*: anal-fin spines 2; 8: anal-fin spines of mature males without fleshy bulbous distal swellings; 9: posteriormost anal-fin pterygiophore supporting only 1 fin-ray element (“last ray not divided to base”); 10: autogenous bony stay absent following posteriormost anal-fin pterygiophore; 11: all pectoral-fin rays unbranched; 12: dorsalmost pectoral-fin ray articulating only with dorsalmost proximal radial; 13*: coracoid autogenous; 14: all caudal-fin rays unbranched; 15: ventral hypural plate fused to urostylar complex (see also discussion of fossil described by Bannikov, 1989, in Blennioid Specializations section, character 2); 16: hypural 5 present* or absent; 17: scales present* (except scales absent in monotypic *Clinoporus* Barnard), cycloid, *with radii in all fields*; 18: *lateral line contained on embedded scales*; 19: lateral line extending entire length of body* or restricted to anterior half with pits continuing to end of body; 20: rostral cartilage absent; 21*: septal bone absent; 22*: ecto- and mesopterygoids autogenous; 23*: posterior end of interopercle extending posteriorly past posterior end of epihyal; 24*: premaxillae protractile; 25*: no noticeably enlarged canine teeth posteriorly in jaws; 26*: free margins of both lips entire (as opposed to fimbriate, crenulate, or with lappets); 27: *cordlike ligament extending from dorso-posterior portion of each ceratohyal to anteromedial end of its respective dentary* (except absent in monotypic, highly specialized *Cancelloxus* Smith); 28*: urohyal lacking vertical pair of processes on each side (for specialized condition see section on Blenniidae); 29: gill membranes broadly attached across isthmus; 30*: free bony margins of opercular bones not fimbriate; 31: infraorbital bones 5; 32: palatines toothed* (perhaps only in *Springeratus* Shen) or edentate; 33*: nape cirri absent; 34: anterior ends of pelvises not extending anteriorly past their juncture with the cleithra (for contrasting condition see Fig. 4; for discussion see section on Dactyloscopidae).

Discussion of Certain Diagnostic Characters.—The presence of scales with radii in all fields and a cordlike ligament extending from the ceratohyal to the dentary

are unique specializations for the clinids among the blennioids. These two characters also occur in nonblennioids, but with the exception of some pseudochromids and stichaeoids (A. C. Gill, pers. comm.) do not occur together. Scales with radii in all fields are also present, at least, in *Plesiops* Oken (Plesiopidae), some labrids (A. C. Gill, pers. comm.), and *Rypticus* Cuvier (Serranidae).

The clinids, and a few species of *Malaccoctenus* Gill (Labrisomidae), are distinguished by the presence of a specialized modification of the dorsolateral, external, margin of the cleithrum. Usually this modification takes the form of a deep notch, and is referred to as a "hook" (Fig. 5) in the literature. The modification may also take the form of a jutting ridge or knob (see Penrith, 1969: fig. 41 for illustrations of various forms of this modification).

Blenniidae

Characterization (* denotes character is unspecialized, occurs in less specialized, nonblennioid perciforms; italics denote specialization that occurs only in blenniids among blennioids; level at which other characters are specialized is undecided. — 1*: dorsal-fin spine articulates with pterygiophore serially associated with first segmented ray ("posteriormost" dorsal-fin spine present); 2: dorsal fin either continuous* or divided (membranes deeply or completely incised) into anterior spinous fin and continuous posterior segmented-ray fin; 3: dorsal fin with more segmented rays than spines (some specimens of a few species of *Ecsenius* McCulloch and *Pereulixia* Smith may have the numbers of spines and segmented rays equal, and some specimens of one species of *Stanulus* Smith may have as many as two more spines than segmented rays); 4: segmented dorsal-fin rays simple; 5: posteriormost dorsal-fin pterygiophore supporting only 1 fin-ray element ("last ray not divided to base"); 6: autogenous bony stay following posteriormost dorsal-fin pterygiophore absent; 7: anal-fin spines 2; 8: anal-fin spines of mature males of many species *with* or without* fleshy bulbous, often rugose, distal swellings; 9: posteriormost anal-fin pterygiophore supporting 1 or 2* fin-ray elements (variable within those species that exhibit "last ray divided to base"); 10: autogenous bony stay absent following posteriormost anal-fin pterygiophore; 11: all pectoral-fin rays unbranched; 12: dorsalmost pectoral-fin ray articulating only with dorsalmost proximal radial; 13: *coracoid ankylosed to cleithrum*; 14: caudal fin with some branched rays* or all rays unbranched; 15: ventral hypural plate autogenous* or fused to urostyle complex; 16: hypural 5 present* or absent; 17: scales absent (except scale-like flaps present in lateral line anteriorly in a few species); 18: lateral line present* (in skin, may contain tiny ossified tubes anteriorly) or absent (only in some highly specialized taxa, e.g., *Plagiotremus*, some species of *Alticus* Valenciennes); 19: lateral line highly variable; ranging from extending entire length of body* to absent; 20: rostral cartilage present* or absent; 21*: septal bone absent; 22*: ecto- and mesopterygoids autogenous; 23: posterior end of interopercle not extending posteriorly past posterior end of epihyal (extending past end of epihyal in tribe Omobranchini, in which a posteriorly projecting spur at posterior end of interopercle appears to have developed secondarily); 24: *premaxillae not protractile*; 25: *most species with noticeably enlarged canine teeth posteriorly in one or both jaws*; 26: free margins of one or both lips entire* or fimbriate (crenulate, scalloped or lappeted); 27*: no cordlike ligament extending from dorsoposterior portion of each ceratohyal to anteromedial end of its respective dentary; 28: *urohyal has vertical pair of processes on each side, with strong ligamentous attachments to hypohyals* (see Springer, 1968, fig. 8; or Williams, 1990, fig. 3); 29: *gill membranes confluent with sides of head restricting gill*

opening to relatively small opening on each side of head or broadly attached across isthmus; 30*: free bony margins of opercular bones not fimbriate; 31: infraorbital bones 2–5; 32: palatines edentate; 33: nape cirri present or absent*; 34: anterior ends of pelvises not extending anteriorly past their juncture with the cleithra (for contrasting condition see Fig. 4; for discussion see section on Dactyloscopidae).

Discussion of Certain Blennioid Characters. — Although there are several blennioid synapomorphies, either the fusion (ankylosis) of the coracoid with the cleithrum or the structure of the urohyal appears to be adequate for defining the Blenniidae to the exclusion of all other perciforms. The jaw teeth of blennioids are also distinctive and specialized among the blennioids. The teeth are essentially uniserial, and, except for the emphasized posterior canines, are incisoriform and close-set (often referred to as “comb-like” in the literature). The jaw teeth of almost all other blennioid species are pointed and, in all but a relatively few species, in more than one row in some portion of the jaws.

Chaenopsidae

Characterization (* denotes character is unspecialized, occurs in less specialized, blennioid perciforms; italics denote specialization that occurs only in chaenopsids among blennioids; level at which other characters are specialized is undecided). — 1*: dorsal-fin spine articulates with pterygiophore serially associated with first segmented ray (“posteriormost” dorsal-fin spine present); 2: dorsal fin either continuous* or divided (membranes deeply or completely incised, characterizes *Emblemaria hyltoni* Johnson and Greenfield) into anterior spinous fin and continuous posterior spinous and segmented-ray fin; 3: dorsal fin varying from having about equal numbers of spines and segmented rays to spines considerably more numerous than segmented rays (most species with more spines than rays; however, one undescribed species of *Ekemblemaria* Stephens, with XVI–XVII,27, P. A. Hastings, in litt., 1991); 4: all segmented dorsal-fin rays simple; 5: posteriormost dorsal-fin pterygiophore supporting only 1 fin-ray element (“last ray not divided to base”); 6: autogenous bony stay absent following posteriormost dorsal-fin pterygiophore (in some *Acanthemblemaria* species, at least, a small, cartilaginous stay is present); 7: anal-fin spines 2; 8*: anal-fin spines of mature males without fleshy bulbous swellings; 9: posteriormost anal-fin pterygiophore supporting 1 fin-ray element (“last ray not divided to base”); 10: autogenous bony stay following posteriormost anal-fin pterygiophore absent (but a cartilaginous stay present in at least some species of *Acanthemblemaria*); 11: all pectoral-fin rays unbranched; 12: dorsalmost pectoral-fin ray articulating only with dorsalmost proximal radial; 13*: coracoid autogenous; 14: caudal fin with all rays unbranched; 15: ventral hypural plate fused to urostylar complex; 16: hypural 5 present* or absent; 17: scales absent; 18: *lateral line absent on body* (however, the lateral line is also lacking in some highly specialized blennioids); 19: not applicable; 20: rostral cartilage absent; 21*: septal bone absent (but see discussion following this listing of characters); 22: ecto- and mesopterygoids autogenous* or fused; 23: posterior end of interopercle ranging from not extending to extending* posteriorly past posterior end of epihyal; 24*: premaxillae protractile (not or scarcely protractile in *Mccoskerichthys sandae*, which is sometimes included in the Chaenopsidae, but which may be the sister group of the Chaenopsidae; Hastings and Springer, 1990); 25*: no noticeably enlarged canine teeth posteriorly in jaws; 26*: free margins of both lips entire (as opposed to fimbriate, crenulate, or lappeted); 27*: no cordlike ligament extending from dorsoposterior portion of each ceratohyal to antero-medial end of its respective dentary; 28*: urohyal without vertical pair of processes

on each side* (for specialized condition see section on Blenniidae); 29: gill membranes broadly attached across isthmus; 30*: free bony margins of opercular bones not fimbriate; 31: *infraorbital bones* 2–3 (normally 2 in all but females of *Coralliozetus* Evermann and Marsh (P. Hastings, in litt., 14 Jan 1991); 4 in the monotypic *Mccoskerichthys*); 32*: palatines toothed; 33*: nape cirri absent; 34: anterior ends of pelvises not extending anteriorly past their juncture with the cleithra (for contrasting condition see Fig. 4; for discussion see section on Dactyloscopidae).

Discussion of Certain Chaenopsid Characters.—The presence of two epurals is probably plesiomorphic for the Blennioidei. One or two epurals are present in various taxa within each of the blennioid families, except the chaenopsids, all of which have only one epural. The presence of only one epural is probably a synapomorphy of the Chaenopsidae.

Of a considerable number of specimens and taxa of chaenopsids that P. A. Hastings has examined, he informs me (pers. comm.) that only his two cleared and stained specimens of *Ekemblemaria nigra* (Meek and Hildebrand) and one of several of his cleared and stained specimens of *Coralliozetus angelicus* (Böhlke and Mead) have a small isolated ossification in the interorbital septum. This ossification is probably a specialization within the Chaenopsidae.

Labrisomidae

Diagnosis (* denotes character is unspecialized, occurs in less specialized, non-blennioid perciforms; level at which other characters are specialized is undecided).—1*: dorsal-fin spine articulates with pterygiophore serially associated with first segmented ray (“posteriormost” dorsal-fin spine present; a few species are specialized in having only spines in the dorsal fin); 2: dorsal fin either continuous* or divided (membranes deeply or completely incised) into anterior spinous fin and continuous posterior spinous and segmented-ray fin (for a specialized exception see discussion of the labrisomid *Haptoclinus* in the section on the Tripterygiidae); 3: dorsal fin with more spines than segmented rays (only spines in *Stathmonotus* and some *Paraclinus* species); 4: all segmented dorsal-fin rays simple; 5: posteriormost dorsal-fin pterygiophore supporting 1 or 2* (“last ray divided to base”) fin-ray elements; 6: autogenous bony stay present* or absent following posteriormost dorsal-fin pterygiophore; 7: anal-fin spines 2; 8*: anal-fin spines of mature males without fleshy bulbous swellings; 9: posteriormost anal-fin pterygiophore supporting 1 or 2* (“last ray divided to base”) fin-ray elements; 10: autogenous bony stay present* or absent following posteriormost anal-fin pterygiophore; 11: all pectoral-fin rays unbranched; 12: dorsalmost pectoral-fin ray articulating only with dorsalmost proximal radial; 13: coracoid autogenous*; 14: caudal fin with some rays branched* or all rays unbranched; 15: ventral hypural plate autogenous* or fused to urostylar complex; 16: hypural 5 present* or absent; 17: scales present* or absent (absent only in *Stathmonotus* and *Neoclinus nudus* Stephens and Springer); scales, when present, cycloid, with radii only in anterior field*; 18: lateral line present* or absent (absent only in *Stathmonotus* and monotypic *Haptoclinus* Böhlke and Robins, in both of which it is represented by pits); 19: lateral line, when present, usually extending entire length of body* on nonembedded scales* (restricted anteriorly in *Neoclinus* and monotypic *Nemaclinus* Böhlke and Springer); 20: rostral cartilage absent; 21*: septal bone absent; 22*: ecto- and mesopterygoids autogenous; 23*: posterior end of interopercle extending posteriorly past posterior end of epiphyal; 24*: premaxillae protractile; 25*: no

noticeably enlarged canine teeth posteriorly in jaws; 26*: free margins of both lips entire (as opposed to fimbriate, crenulate, or with lappets); 27*: no cordlike ligament extending from dorsoposterior portion of each ceratohyal to anteromedial end of its respective dentary; 28*: urohyal without vertical pair of processes on each side (for specialized condition see section on Blenniidae); 29: gill membranes broadly attached across isthmus; 30*: free bony margins of opercular bones not fimbriate; 31: infraorbital bones 4–5 (except for the monotypic *Exerpes* Jordan and Evermann, which has only the lachrymal and dorsoposteriormost two infraorbitals); 32: palatines toothed* or edentate; 33: nape cirri present or absent*; 34: anterior ends of pelvises not extending anteriorly past their juncture with the cleithra (for contrasting condition see Fig. 4; for discussion see section on Dactyloscopidae).

Hastings and Springer (1990) hypothesized *Stathmonotus* (arbitrarily, and provisionally, allocated herein to the Labrisomidae) to be the sister group of the Chaenopsidae + *Mccoskerichthys* (arbitrarily, and provisionally, allocated herein to the Chaenopsidae). They hypothesized *Neoclinus* (arbitrarily and provisionally allocated herein to the Labrisomidae) to be the sister group of *Stathmonotus* + *Mccoskerichthys* + Chaenopsidae. I have no evidence favoring the monophyly of the Labrisomidae, even if I exclude *Neoclinus* and/or *Stathmonotus* from that family.

General Biogeography of the Blennioidei

The Blenniidae and Tripterygiidae are circumglobally distributed in tropical and warm temperate marine waters (a few blenniids enter freshwater and a few occur in cool-temperate marine waters). The Clinidae are restricted to the major continental lithospheric plates (Springer, 1982: fig. 15), where they occur almost exclusively, antitropically, in warm temperate waters (perhaps 5 of the approximately 75 species occur in the tropics of the Indo-west Pacific). The Chaenopsidae and Dactyloscopidae are restricted to the tropical marine waters of the eastern Pacific and western Atlantic. With the exception of *Neoclinus*, which ranges from the Pacific coast of northern Baja California northward to about midway along the California coast, and from southern Japan to Taiwan, the Labrisomidae are restricted to the tropical and warm temperate marine coasts of the Western Hemisphere and eastern Africa. A Miocene fossil, *Labrisomus pronuchipinnis* Arambourg, is well documented for Oran, in the southwestern Mediterranean area).

Suborder Stichaeoidei

These so-called “northern blennioids” exhibit no specializations that might indicate a close relationship with the Blennioidei, often called the “tropical-blennioids.” Stichaeoids primitively have infrapharyngobranchials 2–4, 3 epurals, an autogenous hemal spine on preural centrum 2, autogenous hypurals 3 and 4, a hypurapophysis, 6 infraorbitals, rod-like pelvises with branched pelvic-fin rays, etc., all relatively plesiomorphic states not found among the Blennioidei. The stichaeoids do have a specialized triangular coracoid process like that of the blennioids, but the stichaeoid coracoid and scapula are much longer than the radials. Among the specializations that the stichaeoids share to the exclusion of the blennioids, except in some secondarily specialized blenniids, are the absence of the basisphenoid and the presence of a single nostril on each side of the head. They share these two characters with the zoarcoids, which are, perhaps, their sister group.

Terming the stichaeoids "northern blennioids" causes confusion, and this common name should be avoided. I suggest that they be called "stichaeoids" or "spiny wormfishes."

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