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A REINTERPRETATION OF THE TELEOSTEAN FISH ORDER GOBIESOCIFORMES

By

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An intensive effort to interpret relationships among the old group "Jugulares" (Linnaeus, 1758, p. 249; Jordan, 1923, p. 228; etc.) led to a consideration of the Callionymidae and Draconettidae. For reasons dealt with below, the conclusion was reached that these two families (I do not agree with Davis, 1966, that they should be combined) are specialized derivatives of the notothenioid section of the perciform suborder Blennioidei (Gosline, 1968). Since, however, the Draconettidae and Callionymidae are morphologically well differentiated from the notothenioids, it appears best to remove them from the Perciformes entirely. Investigation also suggested that the Gobiesocidae has evolved from the notothenioid section of the perciform suborder Blennioidei and in small part at least over the same route as the draconettids and callionymids. The Callionymidae, Draconettidae, and Gobiesocidae are therefore combined here in the order Gobiesociformes.

The systematic position of the Callionymidae and Draconettidae has never been the subject of direct investigation. Various views concerning the relationships of these two families have, however, been suggested. Boulenger (1904, p. 708) included both the Callionymidae and Gobiesocidae in his Division Jugulares, and under his account of the Gobiesocidae stated: "The position of the ventral fins suggests, at first glance, affinity with the Callionymidae, and a comparison of the skeletons of these two types has convinced me that they are really related to each other, though highly modified in different directions." (My own conclusions are essentially those of Boulenger.) Starks (1905, p. 302) in connection with his account of the gobiescoid *Caularchus* [=*Gobiesox*] *maeandricus* wrote: "The Callionymidae, however, possess some important characters not possessed by the Gobiesocidae, and these probably more than counterbalance the characters held in common." Regan in 1913 (pp. 144, 145) placed the Callionymidae and Draconettidae in the "Division Callionymiformes" of the perciform suborder Percoidei. He stated that the Callionymidae "may be related to the Pinguipedidae, but is much more specialized [a suggestion with which I also agree]. The Gobiesocidae differ in many characters of importance." Referring again to the Callionymidae, Starks (1923, p. 267) said: "The osteology shows, however, that this family on account of several rather extraordinary and unique characters should be segregated in a suborder coördinate in value with the Batrachoid fishes." Regan in 1929 also recognized the Callionymoidei as a perciform suborder. The most recent comment on the systematic position of the Draconettidae and Callionymidae is that of Briggs and Berry (1959, p. 125). They summarized as follows: "Considering the paucity of our knowledge about these two families and their relationships with other percomorph groups, we see no present need for setting them aside in a separate suborder. Their morphology is no more peculiar than that of several other families that are traditionally retained without subordinal recognition within the vast assemblage of the Percomorphi."

The best and most complete account of the anatomy of the Gobiesocidae remains that of Guitel (1889). However, Guitel draws no conclusions regarding gobiesocid relationships within the Acanthopterygii. Since the days of Starks (1905)[1] and Regan (1909) the family has generally been allocated to an order of its own. In his monograph of the family, Briggs (1955, p. 7) wrote: "The Xenopterygii [=Gobiesociformes] seems to be most closely allied to the Haplodoci (batrachoids) but there is also some resemblance to the Callionymoidea. The order may be considered a highly specialized derivative of some still unknown primitive percomorph stock." McAllister (1968, p. 165) also suggests a gobiesocid-batrachoidid relationship. Apparently on the assumption that such exists Greenwood *et al.* (1966, pp. 389, 397) have assigned the Gobiesociformes to the superorder Paracanthopterygii, thus separating the group superordinally from the callionymoids.

Under the circumstances, it first seems advisable to discuss the possible relationship between the gobiesocoid and batrachoid fishes. Though both groups hold certain characteristics in common, *e.g.*, the usually scaleless body, the flattened head, anterior pelvics, incomplete circumorbital series, etc., it is my pro-

[1] Starks (1905, p. 292) attributed the creation of ordinal status for the gobiesocids to Gill, but neither Briggs (1955, p. 7) nor I have been able to find where Gill recognized more than subordinal rank for this family.

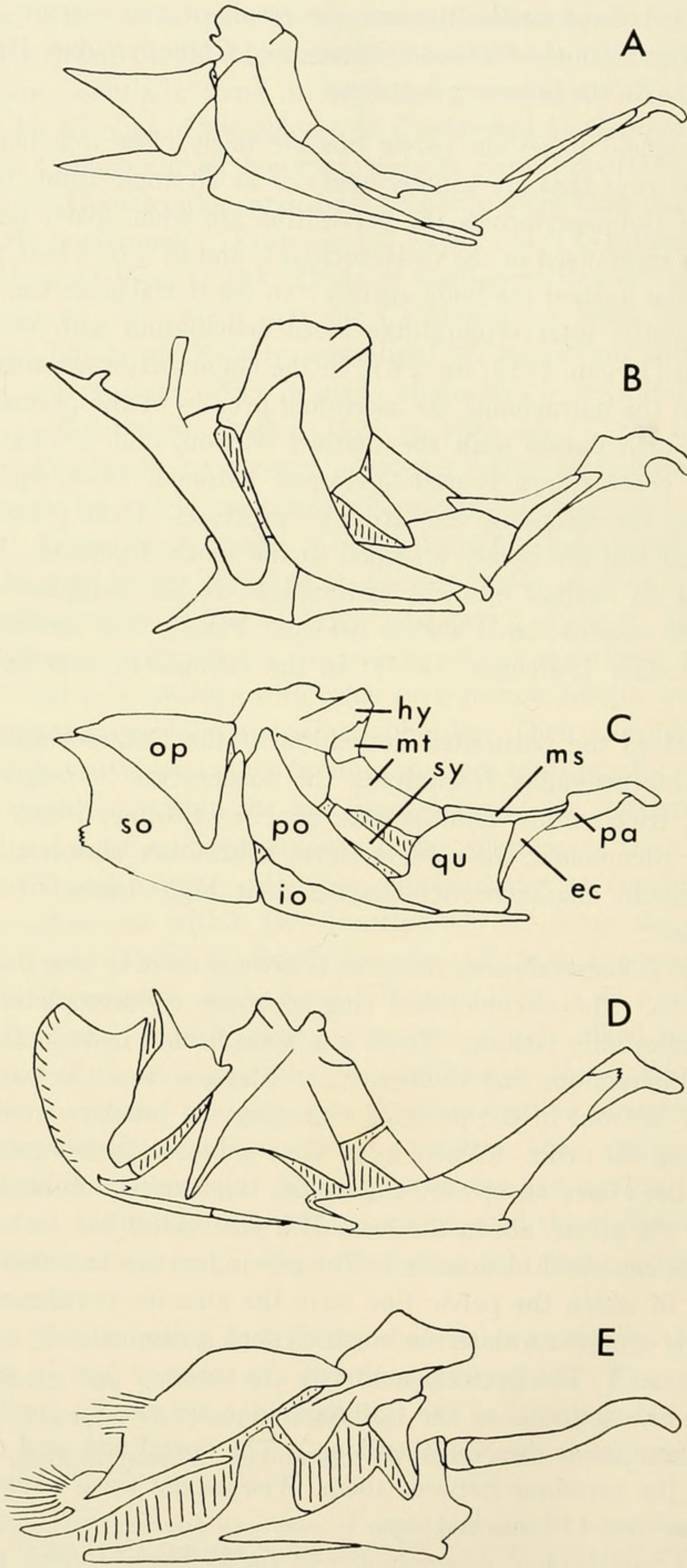
visional view that these similarities are the result of convergence. The batrachoid fishes differ from the Gobiesociformes, *i.e.*, Callionymidae, Draconettidae, and Gobiesocidae, in the following features:

In the batrachoid fishes the pelvic fins are fairly close together, small, and with 2 or 3 soft rays that are usually held out at an angle from the abdominal surface; in the Gobiesociformes the pelvic fins are wide apart, well developed (though highly specialized in the Gobiesocidae), and of 4 or 5 soft rays that are normally held flat against the body surface. In the batrachoids the upper hypurals have a peculiar intervertebral-like basal articulation with the rest of the caudal skeleton (Regan, 1912, fig. 2B); in the Gobiesociformes there is no such articulation. In the batrachoids the ascending process of the premaxillary has a movable basal articulation with the toothed portion, and a separate articular process of the premaxillary is well developed (Monod, 1960, fig. 49); in the Gobiesociformes the ascending and articular processes of the premaxillary have merged or fused and are firmly attached to the toothed portion. In the batrachoids there is no median ethmoid ossification; in the gobiesociform fishes a median ethmoid ossification is always present. Finally, the batrachoids have a peculiar gas bladder (Sørensen, 1884); in the Gobiesociformes there is no gas bladder.

With regard to the postulated derivation of the Gobiesociformes from the superfamily Notothenioidae (containing the parapercids [=mugiloidids], cheimarrichthyids, trichonotids, nototheniids, etc., see Gosline, 1968) of the perciform suborder Blennioidei, the gobiesociform fishes have almost all of the diagnostic notothenioid characteristics despite their high degree of specialization along other lines.

Thus in the Gobiesociformes the head is always more or less flattened, sometimes greatly so. The circumorbital ring of bones is incomplete. The medial tabulars are apparently lacking. There is a basisphenoid bone in *Draconetta* but not in the Callionymidae and Gobiesocidae. Flanges from the parasphenoid do not extend up in front of the prootics excluding the prootics from the internal cranial border of the orbit. (When, as in some gobiesocids and callionymids, the parasphenoid does have an upward expansion, this extends up between the middle portion of the orbits, not in the form of a postorbital bar such as occurs for example, in the zoarcioid blennioids.) The pelvic fins are as noted above. (The Gobiesocidae, in which the pelvic fins form the anterior portion of the sucking disc, is the only group known to me in which such a disc extends well forward of the pectoral bases.) The pectoral actinosts are three or four in number. (The 3 broad plate-like actinosts of the Callionymidae are closely duplicated in such notothenioid families as the Nototheniidae.) The dorsal and anal rays are equal in number to the vertebrae between them. The caudal fin is rounded or brush-like, with fewer than 15 branched rays.

Additional notothenioid resemblances of the Gobiesociformes are as follows.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The ventral sucking disc of the Gobiesocidae would seem to be to some extent foreshadowed in the ridges on the flat ventral surface of the notothenioid family Cheimarrichthyidae. The notothenioid genera *Prolatilus* and *Mugiloides* are the only members of the suborder Blennioidei known to me with the draconettid supraoccipital crest and with the body musculature extending well forward over the top of the cranium. Seven branchiostegal rays, said to be present in some members of the Gobiesocidae (Briggs, 1955) also occur in a number of notothenioids, but rarely elsewhere among the Blennioidei. Finally, the opercular peculiarities of *Draconetta* (fig. 1A) are largely duplicated in the notothenioid *Harpagifer* (fig. 1B) and would seem to be foreshadowed in the more generalized notothenioid *Parapercis* (fig. 1C).

The anatomical account of the draconettids, callionymids, and gobiesocids which follows is based primarily on alizarin-stained and dissected specimens from the following lots:

Callionymidae: *Callionymus flagris,* 125 mm. in standard length (U. S. National Museum no. 71082); *C. decoratus,* 50 mm. (University of Hawaii no. 2073); and *Pogonymus pogognathus,* 24 mm., paratype (UH 1626).

Draconettidae: *Draconetta acanthopoma,* 75 mm. (USNM 156956).

Gobiesocidae: *Gobiesox nigripinnis,* 70 mm. (USNM 131163), and *Trachelochismus pinnulatus,* 55 mm., an exchange specimen from New Zealand in the UH collections.

The external features of various other species of Callionymidae and Gobiesocidae in the U. S. National Museum were examined during tenure of a Smithsonian Research Associateship. I wish to express my deep obligation to the members of the Fish Division of that institution for help and facilities during that time and for sending me on loan the specimens of *Draconetta acanthopoma* listed above.

General features. The head and body of callionymids, draconettids, and gobiesocids are always scaleless, although Ochiai (1963, p. 66) finds "degenerate scales" partly surrounding the lateral line canal of the callionymid *Diplogrammus goramensis.* In callionymids the gill opening is a small hole; in *Draconetta* it is larger, but the gill membranes are broadly attached to the isthmus; and in the Gobiesocidae the gill membranes may be attached to or free from the isthmus (Briggs, 1955). The widely separate pelvic fin bases are entirely in front of the broad pectoral bases, which extend far down the sides; in some callionymids and

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Figure 1. Right suspensorium and opercular bones, external view, of A, *Draconetta acanthopoma*; B, *Harpagifer bispinis*; C, *Parapercis cephalopunctata*; D, *Callionymus flagris*; and E, *Gobiesox nigripinnis.* ec, Ectopterygoid; hy, hyomandibular; io, interopercle; ms, mesopterygoid; mt, metapterygoid; op, opercle; pa, palatine; po, preopercle; and sy, symplectic.

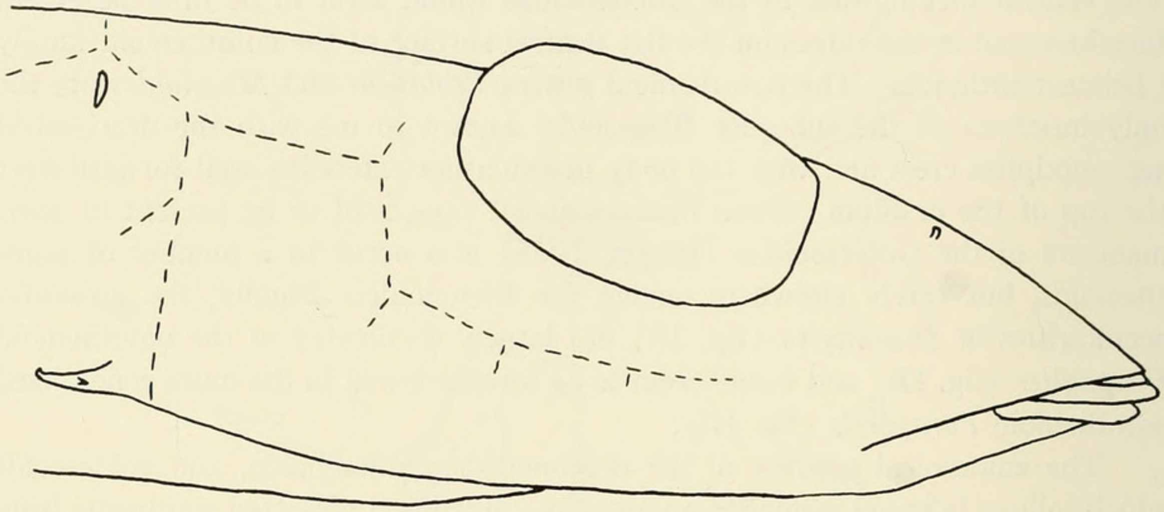

FIGURE 2. *Callionymus flagris*. Sketch of right side of head to show lateral line canals (dashed lines) that are not enclosed in head bones.

gobiesocids there is indeed a membrane extending from the innermost pelvic rays onto the outer surface of the pectoral fin. There is a short spinous dorsal in the Draconettidae and usually in the Callionymidae, but never in the Gobiesocidae.

FIN STRUCTURE. The Gobiesociformes show a transitional series from the usual percoid condition with spines and branched rays to that of the Gobiesocidae where the only spinous element is the flat outer pelvic plate and all the soft rays are simple. The loss of the spinous dorsal in this series has already been noted. As for soft rays, in the callionymid genera *Verutia* and *Synchiropus* all of the soft dorsal rays may be branched (Schultz, 1960, p. 399) and in large specimens of *Draconetta acanthopoma* all of the anal rays are branched, but elsewhere the dorsal and anal rays are mostly or all simple. In *Draconetta* and the callionymids examined, most of the pectoral and the 5 pelvic rays are branched. I count 8 branched caudal rays in *Draconetta acanthopoma*, 6 in *Callionymus flagris*.

THE LATERAL LINE SYSTEM. Those portions of the lateralis system enclosed in head bones will be dealt with below. Here, only the peculiar extension of the lateralis system in the Callionymidae will be mentioned. Such extensions occur on both the head (fig. 2) and body. In *Callionymus*, the system includes such peculiar features as a commissure across the top of the caudal peduncle. On the head of the same genus the canals behind the frontals all lie superficial to the skull bones, extending across the surface of the pterotic and forming a complete supratemporal commissure that is not contained in extrascapulars. Again the preopercular canal, instead of running up within that bone, exits from its lower limb, passes out superficially across the preopercular spine, and then up over the flesh behind the preopercle (fig. 2). None of the peculiarities mentioned are found in either the Draconettidae or the Gobiesocidae, although in the Draconettidae there are membranous extensions of the lateralis system.

Nasal apparatus. The nasal apparatus differs considerably among the gobiesociform fishes examined. It is most percoid-like in *Gobiesox nigripinnis* which has 2 nostrils, the anterior with a fringed flap and the posterior in a raised collar; these 2 nostrils lead into a nasal cavity, bordered mesially above by the nasal bone; the cavity contains a roundish nasal rosette. The nasal apparatus of *Callionymus flagris* is about the same except that there is only 1 nostril on each side. In *Draconetta acanthopoma* there are 2 tubular nostrils but no nasal bone; the nostrils lead into the two ends of a flattened, hollow, fleshy pad which seems to contain no specialized olfactory folds or lobes.

The circumorbital bones. The circumorbital series in the Gobiesociformes is always reduced to the lacrimal bone. Behind the eye in *Callionymus* and *Draconetta* a membrane-enclosed canal exits from the main lateralis canal and extends downward. In *Draconetta* this canal is short, ending behind the eye; in *Callionymus flagris* it extends forward below the eye towards the base of the lacrimal bone (fig. 2) but fails to connect with the lacrimal-enclosed canal.

Jaw structure. The peculiarity of the upper jaw protrusion of *Callionymus* has been described by van Dobben (1935, pp. 47, 48) and by Kayser (1962). In most percoids, the maxillary heads twist on their axes extruding the premaxillary articular processes before them like a squeezed cake of soap (van Dobben, 1935, pp. 10–13). In *Callionymus* the maxillary heads and associated cartilages and ligaments of the two sides form a ring around the long ascending processes of the premaxillaries. The ascending processes of the premaxillaries are free to move in and out within this ring. Upper jaw protrusion is entirely produced by the lowering of the mandible with the associated downward movement of the lateral end of the maxillary. Anatomically *Callionymus* is peculiar in having no articular processes on the premaxillaries lateral to their ascending processes.

The gobiesocids also have premaxillaries without articular processes (Guitel, 1889, pl. 25, fig. 16, and Briggs, 1955, figs. 74–81). In *Draconetta* there are long, narrow, articular processes that are all but fused to the ascending processes. So far as I determine from preserved specimens, *Draconetta* and most gobiesocids use the same peculiar method of upper jaw protrusion that *Callionymus* does. In at least the gobiesocid genus *Tomicodon,* however, the upper jaw does not appear to be protrusile.

Gill covers and suspensoria. With the extreme flattening of the head region that has taken place in the Callionymidae, Draconettidae, and Gobiesocidae, the operculum becomes squashed, so to speak, into a horizontally elongate structure. In at least some members of all three families, backwardly projecting spines are developed, but they are formed in different ways.

As already noted, the opercular apparatus of *Draconetta* (fig. 1A), with spinous opercles and subopercles, is essentially similar to that of the notothenioid *Harpagifer* (fig. 1B), although in *Harpagifer* an additional support for the opercle has been added by extending a vertical strut up to an abutment against the cranium. How the spinous arrangement in *Harpagifer* and *Draconetta* might have originated is suggested by the basal notothenioid *Parapercis* (fig. 1C). In *Parapercis* the opercle ends in the not unusual point; the subopercle has two structurally different sections, an upper, flap-like ossified membrane and a lower rigid plate ending posteriorly in a few serrations. Disappearance of the upper membranous portion of the subopercle and development of the lower would provide essentially the configuration of gill cover spines found in *Harpagifer* and *Draconetta*.

Now, if instead of developing the lower portion of the subopercle of *Parapercis,* the upper flap-like portion were enlarged, the lower eliminated, and the preopercle developed backward as a strong spine, the configuration found in *Callionymus* (fig. 1D) would result.

To arrive at the gobiesocid-type opercle (fig. 1E), one could hypothesize a form of *Callionymus* in which the subopercle loses its association with the interopercle and swings back onto the end of the opercle where it may form a spine in gobiesocids.

The changes in opercular structure just described are reflected in the interopercle. This bone, fairly long in *Parapercis* and longer in *Draconetta,* is pulled out into a long weakly ossified tendon in *Callionymus.* In *Gobiesox* the interopercle is wholly concealed by the preopercle and does not reach the subopercle at all but terminates in an abutment against the rear of the hyoid apparatus, as in the Blenniidae; the interopercle is, however, better developed in the more primitive *Trachelochismus,* where it nearly reaches the subopercle.

A last minor point about the gill cover structure of the Gobiesociformes should perhaps be made. In all three families those edges that are not rigid tend to have long, flexible bony fimbriae.

The "squashing" of the opercle would also seem to have had an effect on the suspensoria of callionymids, draconettids, and gobiesocids. The preopercles of the callionymids (fig. 1D) and gobiesocids (fig. 1E) have been extruded backward, so to speak, and the hyomandibular, preopercle, and quadrate have come to form the three points of a triangle. *Draconetta* (fig. 1A), however, has retained the usual configuration with the hyomandibular, preopercle, and quadrate all more or less in line. There is however no separate metapterygoid in the Draconettidae, Callionymidae, or Gobiesocidae.

The connection between the palatine and the posterior portion of the suspensorium has become rather tenuous. In *Draconetta* (fig. 1A) the palatine is attached to the quadrate by a long narrow strut composed of the ectopterygoid and mesopterygoid. In *Callionymus* (fig. 1D) these last two bones seem to have fused, but the strut is still present. In *Gobiesox* (fig. 1E) the palatine is only loosely connected with the rest of the suspensorium, the mesopterygoid is gone, and the minute ectopterygoid is only ligamentously attached to the palatine.

The hyoid apparatus and gill arches. The hyoid apparatus is close to,

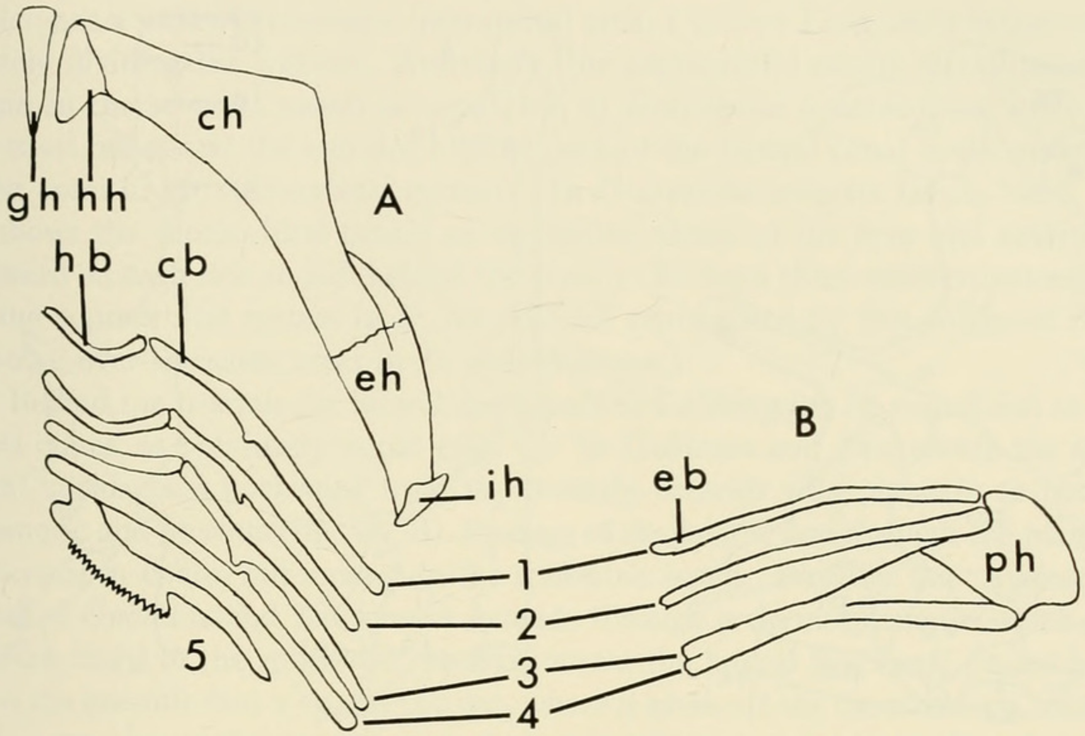

Figure 3. Hyoid and gill arches (1–5) in *Gobiesox nigripinnis*: A, hyoid arch and lower portions of the gill arches of the right side, from above; and B, the upper portions of the gill arches of the left side, from above. cb, Ceratobranchial; ch, ceratohyal; eb, epibranchial; eh, epihyal; gh, glossohyal; hb, hypobranchial; hh, hypohyal; ph, upper pharyngeal tooth plate.

and firmly connected by the anterior basibranchial with, the gill arches in *Callionymus*; in *Draconetta* and *Gobiesox* the hyoid arch is well separated from and unconnected with the other gill arches. In *Callionymus* and *Draconetta,* a well developed glossohyal extends forward from the hypohyals; in *Gobiesox* (fig. 3) the glossohyal is a small sliver of bone completely contained in the interspace between the hypohyals of the two sides. In *Draconetta* and *Callionymus* there are 6 branchiostegal rays on each side, in the gobiesocids 5–7 (Briggs, 1955, p. 9). In *Draconetta, Callionymus,* and *Gobiesox* there are 2 anterior branchiostegals attached to the inner surface of the hyoid arch; the other 4 close to its lower rim. In *Draconetta* and *Callionymus* the first 2 are short; in *Gobiesox* the first 3. In *Draconetta* 4 of the 6 branchiostegals are crowded back on the epihyal, in *Callionymus* 3, and in *Gobiesox* only 1 branchiostegal articulates with the epihyal.

Among gobiesociform families the first spicular pharyngobranchial seems to have completely disappeared and there are never more than 2 sets of pharyngeal teeth on either side above. In *Draconetta* and *Callionymus* epihyal 2 extends up to the relatively small and narrow anterior tooth patch, while epihyals 3 and 4 articulate with the broader, posterior pharyngeal tooth patch[2]; in these two genera epihyals 3 and 4 are closely but movably attached to one another. In *Gobiesox*

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[2] Starks (1905, p. 302) stated that *Callionymus* had "three superior pharyngeals on each side" but in 1923 (p. 269) he describes 2 upper pharyngeals of the same shape as noted here.

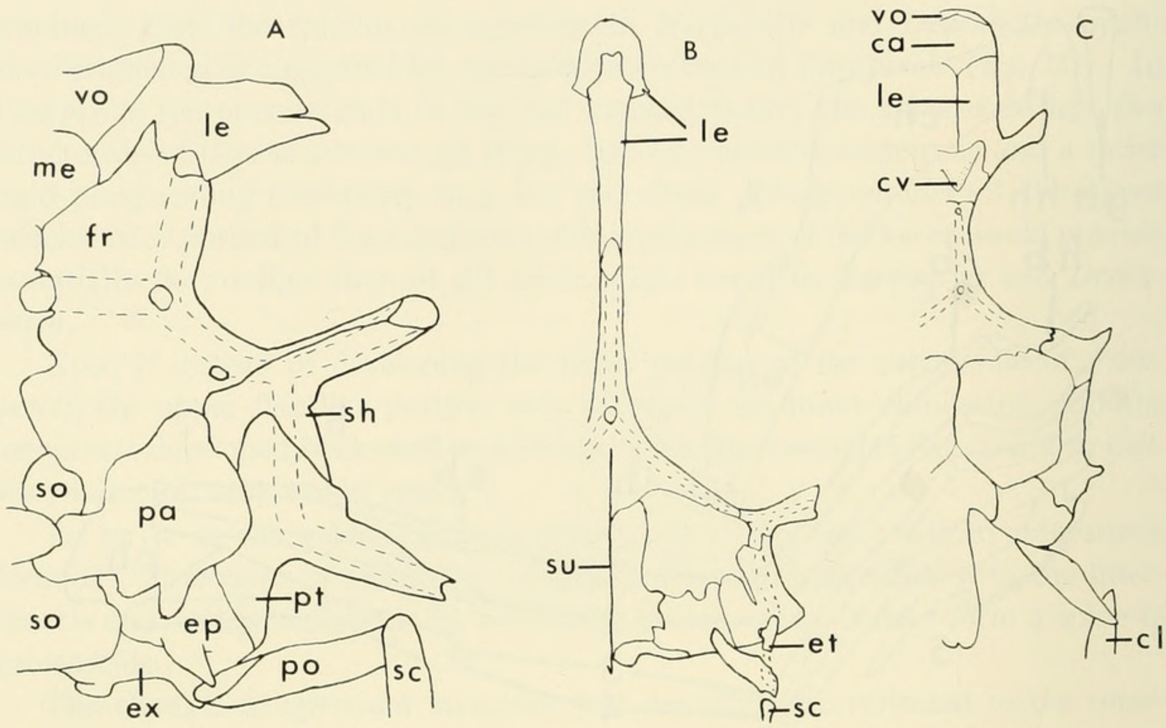

Figure 4. Cranium plus upper portion of pectoral girdle, right side, from above, of A, *Gobiesox nigripinnis;* B, *Draconetta acanthopoma* (only the upper surface of the rostral region is shown); and C, *Callionymus flagris.* Lateral line canals passing through cranial bones indicated by dashed lines. ca, Cartilage; cl, cleithrum; cv, cavity into which the ascending processes of the premaxillaries extend; et, lateral extrascapular; ex, exoccipital; fr, frontal; le, lateral ethmoid; me, mesethmoid; pa, parietal; po, posttemporal; pt, pterotic; su, supracleithrum; so, supraoccipital; st, sphenotic; su, supraoccipital crest; and vo, vomer.

(fig. 3) there are no chondrified or ossified basibranchials, and the gill arches are not interconnected below. Above, there is only 1 small pharyngeal tooth plate on each side; epihyals 2, 3 and 4 articulate with it, and epihyals 3 and 4 are rigidly united to one another.

Skull. In *Gobiesox* (which lives under rocks in the tidal zone) the head is broad with small eyes in strong laterally placed bony sockets. In *Callionymus* and *Draconetta* the eyes are close together on the top of the head. These differences are strongly reflected in the crania.

Lateral line and associated skull bones. In the Gobiesocidae the forward portion of the supraorbital canal on each side commences near the snout rim and passes back through the paired nasal and frontal bones. Between the wide-set eyes there is a complete, bone-enclosed frontal commissure (fig. 4A). In the Draconettidae and Callionymidae the narrow interorbital region has doubtless caused the fusion of the 2 supraorbital canals into a single median canal between the eyes (fig. 4B, C). Furthermore, in *Draconetta* the frontals themselves have fused into a single median bone. However, in the two species of *Callionymus* examined the frontals appear to be only partially fused, and in the callionymid *Pogonymus,* which has a somewhat broader interorbital area, I believe I can see a suture completely dividing the frontals. Anteriorly, the supraorbital canals of callionymids begin in the separate nasals as usual, but in *Draconetta acanthopoma* there are no nasal bones and the anterior median pore of the frontal canal is the anteriormost point in the supraorbital system. (In *Draconetta oregona* Davis, 1966, fig. 2, shows the supraorbital canals as separating ahead of the eyes and extending forward on each side to just behind the nostril. Perhaps these anterior extensions of the supraorbital system in *D. oregona* are represented by fine ridges of flesh running over the same areas in *D. acanthopoma.*)

Behind the frontals the lateral line canals of *Callionymus* lie superficial to the skull bones, as previously noted (fig. 1). In *Gobiesox* and *Draconetta* the temporal canals pass backward from the frontals through what appears to be the sphenotic and pterotic (fig. 4A, B). Passage of the lateral line through the pterotic is normal in fishes, but a canal in the sphenotic is not. Possibly the "sphenotic" canal of *Gobiesox* and *Draconetta* extends through a dermosphenotic which has become fused to the sphenotic. In *Draconetta* the lateral line canal passes back from the pterotic into a lateral tabular, where it gives off the membranous, incomplete supratemporal commissure, and then into the posttemporal, where it ends. In *Gobiesox* the lateral line canal ends in the pterotic; there is no tabular bone or posttemporal commissure.

Ethmoid region of the skull. The peculiarities of the ethmoid region of the cranium of *Callionymus* (Starks, 1923, pp. 267–268) and of *Draconetta* can, I think, have developed through a pinching together of the broader, more normal ethmoid area of the Gobiesocidae. In the Gobiesocidae the ethmoid overlaps the vomer in the usual percoid fashion but lies behind the level of the lateral ethmoids (Guitel, 1889, pl. 25, fig. 1). In the narrower-snouted draconettids and callionymids the mesethmoid is completely separated from the vomer by cartilage and by the medial bases of the two lateral ethmoids which meet (fig. 4C) or nearly meet on the midline. In *Draconetta* (fig. 5) the mesethmoid is above and behind the lateral ethmoid bases, but in the callionymids it is entirely behind them. In both families the mesethmoid forms part of the orbital border. In the callionymid *Pogonymus* the ascending processes of the premaxillaries extend up and back over the rostral surface as usual; here the mesethmoid does not extend down into the interorbital space. But in *Callionymus* the ascending processes are more horizontal and their tips extend back into a medial rostral cavity; here the mesethmoid has been pushed down and back, as it were, into the infraorbital space (Starks, 1923, pl. 4, fig. 5). The same sort of thing seems to have happened in the chaetodontid percoids, as Starks (1926, p. 301, footnote 35) has noted.

Upper surface of rear of skull. Major differences on the upper surface of the skull posteriorly have to do with the extent to which it is covered by the body musculature. In *Callionymus* the rear face of the skull drops away abruptly, and no musculature at all extends forward over its upper surface. The supraoccipital

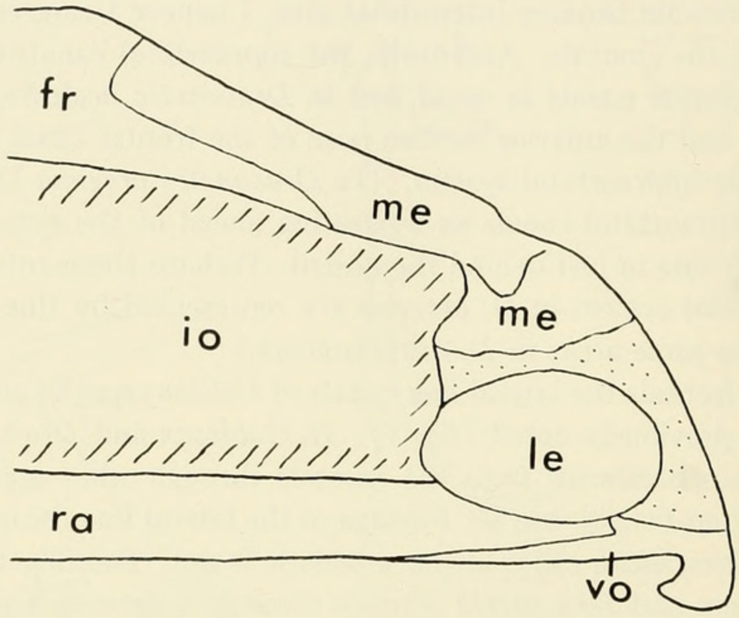

Figure 5. *Draconetta acanthopoma.* Lateral view of forward end of cranium with only the base of the lateral ethmoid indicated. Cartilage stippled. fr, Frontal; io, infraorbital fenestra; le, lateral ethmoid; me, mesethmoid; ra, parasphenoid; and vo, vomer.

extends back from the skull as a flat superficial cap (fig. 4C) the bottom of which forms a surface for muscular attachment. In *Gobiesox* the rear face of the skull slopes more obliquely and two large lateral lobes of musculature extend forward nearly to the rear borders of the eyes. The musculature does not extend forward over the central portion of the skull and there is no median crest. The flat supraoccipital bone (fig. 4A) in *Gobiesox* is pinched off into two parts by the overlapping parietals, but this is not true of at least certain other gobiesocid genera (see Guitel, 1889, pl. 25, fig. 1, and Starks, 1905, p. 283—Starks's *Caularchus* equals *Gobiesox* and his *Gobiesox* equals *Sicyases* according to Briggs, 1955). In *Draconetta* (fig. 4B) the musculature extends forward along either side of the midline to just behind the eye, and a median crest extends forward on the supraoccipital and even a short way on the fused frontals.

Sphenoid region of the skull. In *Draconetta* a pleurosphenoid and small basisphenoid bone are present; the two bones are, however, widely separated, the basisphenoid ending posteriorly in the membrane lining the orbits posteriorly. In neither *Callionymus* nor *Gobiesox* are pleurosphenoids or basisphenoids present.

As is true of all notothenioids, there is little upward extension of the parasphenoid into a postorbital bar, and the prootic borders the orbit in all the Gobiesociformes. In *Gobiesox,* however, the parasphenoid is considerably expanded anteriorly, forming a broad shelf below and between the orbits; this expansion is greater than that of the parasphenoid just behind the orbits.

Otic and occipital regions of the skull. In none of the Gobiesociformes examined is there an expanded auditory bulla. In *Draconetta* there is a triangular

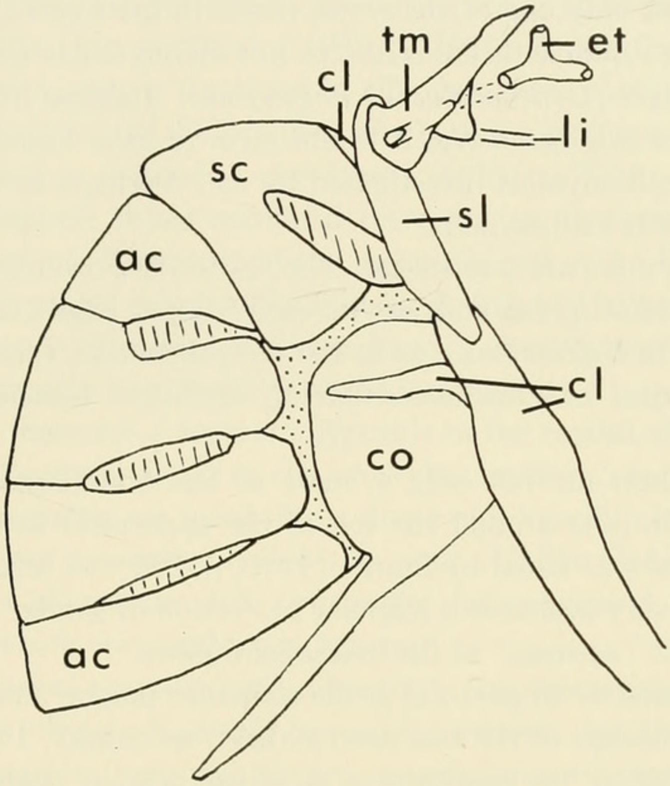

FIGURE 6. *Draconetta acanthopoma.* Pectoral girdle of right side, except postcleithra. Lateral line canal indicated by dashed lines. ac, Actinost; cl, cleithrum; co, coracoid; et, lateral extrascapular; li, ligament to intercalar; sc, scapula; sl, supracleithrum; and tm, posttemporal.

intercalar on the lower surface of the cranium which serves for the attachment of the ligament from the short lower wing of the posttemporal. In *Gobiesox* and *Callionymus* there is neither an intercalar nor a lower wing to the posttemporal.

The exoccipital condyles in *Draconetta, Callionymus,* and *Gobiesox* are widely separated from one another and indeed are practically or quite lateral to the basioccipital condyle. As Starks (1905, p. 293, footnote 1) has noted, this configuration of the occipital condyles is one frequently associated with a depressed body form.

PECTORAL GIRDLE. In gobiesocids the supracleithrum and posttemporal bones are both present. The cleithrum and primary pectoral girdle extend up the sides of the body. From an articulation on the top of the cleithrum, the supracleithrum extends horizontally forward, and from the front of the supracleithrum the posttemporal extends horizontally inward to an articulation with the skull. The axes of the cleithrum, supracleithrum, and posttemporal thus lie primarily in three different planes (Guitel, 1889, pl. 24, fig. 3). In *Draconetta* the supracleithrum and posttemporal are present (fig. 6) but the supracleithrum and cleithrum have the same axes. Among callionymids Briggs and Berry (1959) and Ochiai (1963) state that a supracleithrum and supratemporal are both present, though the latter author shows only one of these two bones in his figures. Starks (1923, p. 268) says that the supracleithrum is absent in Callionymidae and I can find none in *Callionymus flagris, C. decoratus,* or *Pogonymus.* Judging from the position of the supracleithrum in *Draconetta,* it would seem to have become fused with the cleithrum in the callionymids investigated by me. Perhaps its loss as a separate element is variable in callionymids.

In *Draconetta* there are 4 actinosts. The lower 3 are columnar, but the uppermost tapers to a basal point and has its entire upper edge contiguous with the scapula (fig. 6). In *Callionymus,* as in the Nototheniidae, there are only 3 actinosts, the uppermost of *Draconetta* having doubtless become fused with the scapula.

In *Gobiesox* there are not only 4, more or less hourglass shaped, actinosts, but the scapula projects around the top of the uppermost in such a way as to resemble a fifth, as was noted by Starks (1930, p. 220; see also Guitel, 1889, pl. 24, fig. 10). It is very probably a scapular projection of similar sort that provides the uppermost fifth "actinost" of the batrachoid fishes.

A further peculiarity of pectoral girdle structure unique among the Gobiesocidae is the specialization of the two postcleithra (see Starks, 1905; Guitel, 1889, pl. 24, fig. 3). Both of the postcleithra on either side are plate-like. The upper is vertically alined and has numerous fimbriae extending from its posterior surface; it appears to be only ligamentously attached to the main pectoral girdle. The lower extends inward from the side of the abdomen and, with its counterpart from the opposite side, supports the rear rim of the adhesive disc. I do not know of a similar specialization elsewhere in fishes, the postcleithra of *Cheimarrichthys,* for example, being quite normal. In *Draconetta* there is only a single, long, scimitar-like postcleithrum with the usual ligamentous attachment to the top of the cleithrum. *Callionymus* has an even longer, thinner postcleithral strut, but it is made up of 2 pieces closely bound together where they overlap.

PELVIC GIRDLE. The pelvic girdle of the Gobiesociformes is short and broad, as in many notothenioids. The only peculiarity that I can find is in the flat, spatulate pelvic spine of *Gobiesox,* already mentioned.

AXIAL AND CAUDAL SKELETONS. In *Draconetta* there are 7 abdominal and 16 caudal vertebrae, including the urostylar centrum. In the Callionymidae, so far as is known, there are 7 + 14 vertebrae. Briggs (1955, p. 9) gives the vertebral counts of Gobiesocidae as ranging from 25–54; in *Gobiesox* the count given by Starks (1905, p. 300) is 13 + 19.

In all the Gobiesociformes the ribs start on the second vertebra. In *Draconetta* and *Callionymus* there is only 1 pair of ribs per vertebra. These, in *Draconetta,* extend out and up away from the abdominal cavity, which suggests that they are epipleurals. In *Gobiesox* the same set of ribs occurs, but from the third vertebra on there is another set of ribs extending lateroventrally from the lower surface of the main ribs about half way out along their length (Runyon, 1961, p.

136 and fig. 27). These supplementary lower ribs are, despite their configuration, probably pleural ribs (but see Starks, 1905, p. 301). In the flattened nototheni-oid *Bembrops* there is only a single set of ribs, but these commence on the first, not the second vertebra (for the problem of whether a single set of ribs in acanthopterans is pleural or epipleural, see Starks, 1923, p. 290).

In the gobiesociform fishes examined there are no predorsal bones, and the first interneural extends down behind the second neural arch. In *Draconetta* the neural arch to interneural relationship is normal, but in *Callionymus* and *Pogonymus* the third and following vertebrae have V-shaped neural processes that extend out laterodorsally on either side of the interneurals.

In *Draconetta* there are 2 separate hypurals in the caudal skeleton, the lower autogenous, and the upper fused to the urostylar centrum. In *Callionymus* and *Gobiesox* these 2 hypurals are fused into a single unit basally. In *Draconetta* and *Callionymus* there are 2 epurals, in *Gobiesox* none. Unlike *Gobiesox,* the penultimate vertebra of *Callionymus* and *Draconetta* has expanded, plate-like neural and hemal arches which are fused to the centrum.

So far as the fishes examined are concerned, the characters described above may be grouped as follows. It should be noted, however, that the wider the spectrum of variation within the group the less any definition based on one or a few species, such as those given below, can be expected to hold.

Gobiesociformes.—Head and body scaleless. Circumorbital bones represented only by the lacrimal. Premaxillary with its articular process absent or merged with the ascending process (in *Draconetta*). Opercular apparatus with 1 or 2 backwardly projecting spines (except some Gobiesocidae). Metapterygoid absent. Ribs commencing on second vertebra.

Gobiesocoidei.—An abdominal adhesive disc. No spinous dorsal fin. None of the fin rays branched. Outer pelvic ray flattened and spatulate, followed by 4 segmented rays. Palatine separated by membrane from the ectopterygoid. No basibranchials. A single upper pharyngeal tooth plate on each side. Frontals separate. Mesethmoid not forming part of the orbital boundaries. Parasphenoid expanded below and between the orbits. Postcleithra expanded, platelike, the lower supporting the rear border of the adhesive disc. More than 10 abdominal vertebrae, more than 24 in all. Two sets of ribs from the third vertebra. Penultimate vertebra with its neural and hemal arches not expanded. No epurals.

Gobiesocidae.—Lateral line system limited to the head. A nasal bone on each side of head. Two nostrils on either side, which lead into a nasal sac containing a well-developed olfactory rosette. A single spine, if any, on the opercular apparatus, formed by the subopercle. Gill openings not restricted to a small hole above or behind the opercle. Mesopterygoid absent. Supratemporal commissure lacking. No median supraoccipital or frontal crest. Pleurosphenoid, basisphenoid, and intercalar absent. Posttemporal present. Four actinosts. Two postcleithra. Neural arches normal. Hypurals fused into a single plate.

Callionymoidei.—No abdominal adhesive disc. A spinous dorsal fin present, except *Draculo.* At least 1 soft ray in each fin branched or divided to the base. Outer pelvic ray spinous, followed by 5 soft rays. Palatine firmly attached to the ectopterygoid. Basibranchials present. Two upper pharyngeal tooth plates on each side. Frontals fused or mostly so. Mesethmoid forming part of the orbital boundaries. Parasphenoid forming a narrow strut below and between the orbits. Postcleithral strut narrow. Seven abdominal vertebrae, fewer than 24 in all. A single set of ribs. Penultimate vertebra with its neural and hemal arches expanded and plate-like. Two epurals.

Draconettidae.—Lateral line system limited to head. No nasal bone. Two nostrils on each side of head; no nasal rosette. Two spines on the opercular apparatus, one on the opercle and one on the subopercle. Gill openings not restricted to a small hole above or behind the opercle. Mesopterygoid present. Supratemporal commissure incomplete. A low supraoccipital crest extending forward onto the rear of the frontals. Pleurosphenoid, basisphenoid, and intercalar present. Posttemporal present. Four actinosts. One postcleithrum. Neural arches normal. Two separate hypurals.

Callionymidae.—Lateral line continued on body. A nasal bone on each side. One nostril leading into a nasal sac with a well developed olfactory rosette. Spine on the opercular apparatus single, formed by the preopercle. Gill openings restricted to a small hole above or behind the opercle. Mesopterygoid absent. Supratemporal commissure complete. No median crest on supraoccipital or frontals. Pleurosphenoid, basisphenoid, and intercalar absent. Posttemporal absent. Three actinosts. Two postcleithra. Neural arches of third and succeeding vertebrae with V-shaped flanges. Hypurals fused into a single plate.

Of the developments which characterize the Gobiesociformes as a whole, some are of a type that have repeatedly occurred in higher acanthopterans, *e.g.*, the "simplification" of skull and fin ray structure. Perhaps the absence of scales and the loss of the circumorbital bones behind the lacrimal should be placed in the same category. In my opinion the definitive peculiarities held in common by the various members of the Gobiesociformes are those of the upper jaw, gill cover, and rib configuration.

That the various members of the Gobiesociformes have diverged widely is obvious. In the first place, there is a most remarkable difference in habitat between the callionymoids, which are mostly quiet water bottom fishes, and many gobiesocids. At least some of the latter, including the close relatives of one dissected here, live among the boulders of wave-washed rocky beaches.

The way in which the gobiesocids have evolved from a proto-gobiesociform ancestor is suggested by the notothenioid *Cheimarrichthys,* which has the same

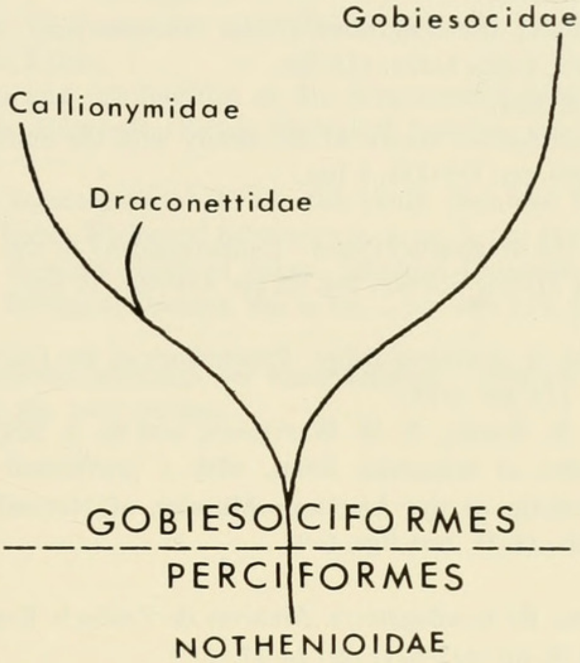

Figure 7. Suggested gobiesociform relationships.

sort of broad, flat head, small, wide-set eyes, and incipient adhesive organ on the abdomen as *Gobiesox*. However, the gobiesocids, in addition to having the premaxillary, opercular, and rib structure, etc., of all the gobiesociformes, which *Cheimarrichthys* does not have, have incorporated the postcleithra into the adhesive disc in a unique way. In short, the gobiesocids are much more highly specialized fishes than *Cheimarrichthys*.

The callionymoids would seem to have diverged from their proto-gobiesociform ancestors in two principal respects. One is that the high-set eyes have left little room for the interorbital portion of the cranium. The frontals have not only fused, but their anterior portion appears to have been pinched off and replaced in part by the mesethmoid from the preorbital region. Second, there has been a reduction in the number of vertebrae.

Between the draconettids and callionymids, the quite different opercular specializations of the two groups preclude the possibility of the one group having evolved directly from the other. In general, however, the draconettids have remained at a lower stage of specialization than the callionymids as indicated by the much lower degree of fusion in the draconettid skeleton.

In my opinion then, the relationships between the three gobiesociform groups may be diagrammed as in fig. 7.

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