Notes on the Osteology and Systematic Position of *Hypoptychus dybowskii* Steindachner and Other Elongate Perciform Fishes[1]

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Longer ago that can gracefully be admitted, Dr. Paul Kähsbauer of the Vienna Naturhis-historische Museum was kind enough to send me a specimen of *Hypoptychus dybowskii* from Steindachner's (1880) original series taken off "Northern Japan." Steindachner placed this fish alongside the Ammodytidae, and there has been a division of opinion ever since as to whether it should be included in or excluded from that family (cf, Regan, 1913; Jordan, 1923; Duncker and Mohr, 1939; Berg, 1940). In order to investigate its relationships, the Vienna specimen has been stained and dissected, and its osteology compared with that of the ammodytids *Bleekeria gilli* (Fig. 1*a*) and *Ammodytes tobianus*. The specimen of *Bleekeria* is Hawaiian and was retrieved from tuna spewings. *Ammodytes* is represented by two series, sent to me from the U. S. National Museum and the Museum of Comparative Zoology through the courtesy of Dr. L. P. Schultz and Dr. G. W. Mead, respectively.

That *Hypoptychus* belongs to the superfamily Ammodytoidae seems certain. The relationships of the superfamily Ammodytoidae are more obscure. A second objective of the present investigation has been to look into this matter, and a preliminary discussion of certain of the problems involved here will serve as an introduction to the paper.

In a typical percoid fish, e.g., *Epinephelus*, there are 24 vertebrae, and the dorsal fin is composed of an anterior spinous portion and a posterior soft portion. In such a fish the majority of the basal supporting elements, i.e., pterygiophores, of the spinous dorsal have a one-to-one relationship with the vertebrae below them; the soft dorsal rays and their pterygiophores, in contrast, are more closely spaced so that there is more than one ray and pterygiophore to each vertebra. Time and again, however, the percoids and their derivatives have become elongate. This change in shape is frequently accompanied by a whole series of other alterations. Thus, the cranial crests become low or disappear, the number of vertebrae increases, the distinction between dorsal spines and rays becomes reduced, both types of dorsal (and anal) rays develop an approximately one-to-one relationship with the vertebrae, and the caudal fin becomes rounded and its principal rays reduced in number. All of these changes are to be found among the percoids, e.g., the Cepolidae, trachinoids, ammodytoids, blennioids, schindlerioids, and most gobioids.

Indeed, it seems that all of these modifications occur together in the majority of elongate percoid derivatives and that those forms, such as the ophidioids, where there is more than one dorsal and anal ray per vertebra are the exception rather than the rule. On the other hand, the author is aware of no prepercoid teleost with a one-to-one relationship between soft dorsal and anal rays and the vertebrae. If what has just been said is correct, it follows that any fish with such a relationship is a percoid derivative, but that the unit correspondence between soft rays and vertebrae is of little use in distinguishing the various lineages of percoid derivation.

Here, the schindlerioids and gobioids will be dismissed from further consideration, as each of these groups has peculiarities by which it may easily be defined. However, Hawaiian specimens of the trachinoids *Parapercis schauinslandi* (Parapercidae, Fig. 1*c*) and *Crystallodytes cookei* (Trichonotidae, Fig. 1*b*), and of the blennioid *Tripterygion atriceps* (Tripterygiidae, Fig. 1*d*) have been stained and dissected. These specimens will be used both for purposes of com-

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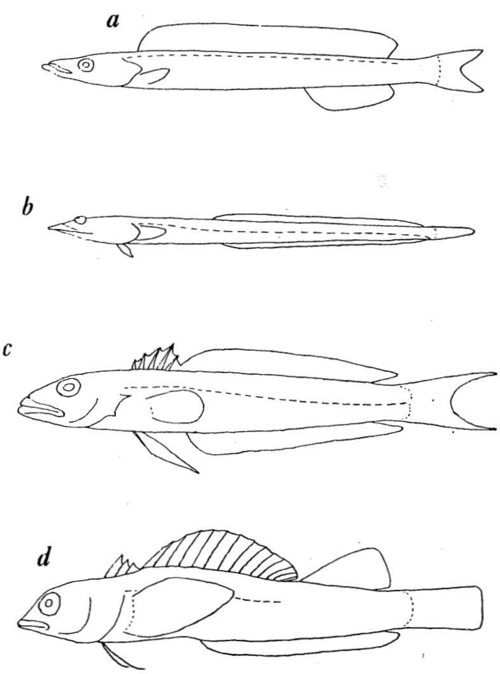

FIG. 1. Sketches of *a, Bleekeria gilli,* from Gosline and Brock, after Fowler, based on a specimen 3 inches in total length; *b, Crystallodytes cookei,* based on a specimen 2 inches long; *c, Parapercis schauinslandi,* from a 3-inch specimen; and *d, Tripterygion atriceps,* from a 1-inch fish.

parison with the three ammodytoids and in an attempt to obtain some understanding of the lineages to which each of them belongs.

With regard to these six fishes that have been investigated in some detail, it may be stated in advance that the author has not had any great success in discovering significant cranial differences between them. It is not so much that such differences do not exist, as that they appear to have rather slight systematic value. Though it may be that the author has simply overlooked significant differences, it would appear that the percoids and their immediate derivatives have a rather standardized skull pattern and that the major morphological differentiation of percoid groups has occurred in other features.

HEAD SKELETON

CIRCUMORBITAL BONES: In the typical percoid the circumorbital series is made up of the lacrimal (preorbital) followed by about five separately movable, canal-bearing ossicles (cf, Katayama, 1959: figs. 2–5). Above the fifth, the infraorbital lateral line canal joins the supraorbital canal. Of the five ossicles the uppermost is particularly variable and is sometimes fused to and sometimes free from the sphenotic.

In *Parapercis* (Fig. 2*a*) the infraorbital canal is complete, passing through a lacrimal and six separate circumorbital bones. The uppermost of these is firmly attached to the cranium in *Parapercis.* Because six circumorbitals appeared to be a high number, the opposite side of the same specimen and of a larger specimen of *Parapercis schauinslandi* were checked; no variation was found. The circumorbital structures of *Tripterygion* differ from those of *Parapercis* in having three instead of six circumorbital bones and in the failure of the bone to close over the sensory canal externally. In *Crystallodytes* the circumorbital canal is still complete but there are only a lacrimal and two circumorbitals. The lacrimal and second circumorbital are large and laminar, but the anterior circumorbital is quite small.

In *Ammodytes* (Fig. 2*b*) there is a large lacrimal, followed immediately by a moderate-sized first infraorbital; then there is a broad gap followed by two small circumorbitals, the

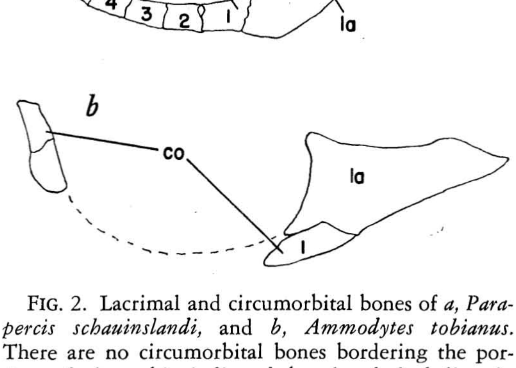

FIG. 2. Lacrimal and circumorbital bones of *a, Parapercis schauinslandi,* and *b, Ammodytes tobianus.* There are no circumorbital bones bordering the portion of the orbit indicated by the dashed line in *Ammodytes. co,* Circumorbital bones; and *la,* lacrimal.

upper of which articulates with the skull. In *Bleekeria* a similar break in the circumorbital ring occurs, but it is shorter than in *Ammodytes* and the posterior series seems to contain three or four small elements instead of two. *Hypoptychus* has the same two anterior elements followed by a broad gap; posteriorly, however, there is only a single ossicle, and it is fused to the sphenotic.

None of the six fishes have any subocular shelf from the circumorbitals.

JAWS: In sand-diving fishes like *Ammodytes* the mouth is usually not terminal; either it is withdrawn below an overhanging snout, as in *Crystallodytes,* or protected by a prognathous chin, as in *Ammodytes.* In *Ammodytes* the leading, lower jaw is firmly attached, but the upper has developed excessive powers of protrusion when the mouth is opened (van Dobben, 1935: 34–36). The great protrusibility of the upper jaw in *Ammodytes* is accompanied by a weakening of the bony elements, and it is probably in relation to this that *Ammodytes* and *Bleekeria* have edentulous premaxillaries. So far as jaw structure is concerned, *Hypoptychus* is intermediate between the normal percoid type and the specializations found in *Ammodytes* and *Bleekeria.*

The premaxillary of *Ammodytes* (Fig. 3*a*) consists of a long pedicel movably articulating at its base with the remaining portion of the premaxillary. The distal half of the maxillary tapers gradually to a point (Fig. 3*a*). The upper jaw of *Bleekeria* is essentially similar to that of *Ammodytes* except that a number of small ossicles are to be found in the ligamentous tissues connected with the jaw apparatus. Thus, there is an ossicle above the more lateral of the two pedicels of the premaxillary, another at the distal end of the premaxillary, and a whole series in the ligamentous tissue that runs between the upper and lower jaws.

The upper jaw of *Hypoptychus* (Fig. 3*b*) differs from those of *Bleekeria* and *Ammodytes* in the following features: the premaxillary bears a row of teeth (there are about 14 conical teeth in a single row on each side, not shown in Fig. 3*b*); the premaxillary is fused to its pedicel; and the tip of the maxillary is expanded distally.

A movable articulation between the premaxillary and its pedicel is also found in *Crystallodytes,* as well as in blennioids such as *Cirripectus* and *Istiblennius.* In *Parapercis* and *Tripterygion,* which have strong premaxillary teeth, the pedicel is stout and fused to the toothed portion.

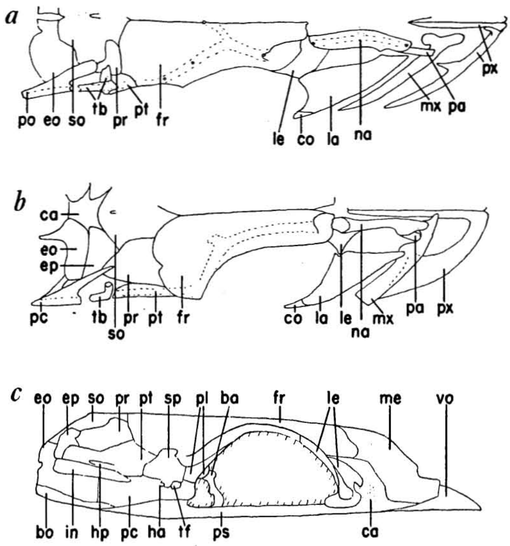

FIG. 3. Head skeletons of ammodytoids: superior views, with the premaxillary somewhat protruded, of *a, Ammodytes tobianus,* and *b, Hypoptychus dybowskii;* lateral view, *c,* of cranium of *Ammodytes tobianus. ba,* Basisphenoid; *bo,* basioccipital; *ca,* cartilage; *co,* circumorbital; *eo,* exoccipital; *ep,* epiotic; *fr,* frontal; *ha,* anterior hyomandibular socket; *hp,* posterior hyomandibular socket; *in,* intercalar; *la,* lacrimal; *le,* lateral ethmoid; *me,* mesethmoid; *mx,* maxillary; *na,* nasal; *pa,* palatine; *pc,* prootic; *pl,* pleurosphenoid; *po,* posttemporal; *pr,* parietal; *ps,* parasphenoid; *pt,* pterotic; *px,* premaxillary; *so,* supraoccipital; *sp,* sphenotic; *tb,* tabular; *tf,* trigemino-facial foramen; and *vo,* vomer. In the superior view of *Ammodytes, a,* the epiotic is covered by the posttemporal.

GILL COVERS: In *Ammodytes* (Fig. 4*b*) and *Crystallodytes* (Fig. 4*c*) the subopercles are expanded, presumably to protect the throat region. Indeed, the lower border of the articular in *Crystallodytes* is greatly expanded below as well (Fig. 4*c*).

SUSPENSORIUM: The suspensorium of *Ammodytes* is specialized in a number of regards (Fig. 4*b*). Most notable among these is the elongated palatine strut. The whole length of this strut from its forward tip to its articulation with the quadrate is made up of the palatine bone; the ectopterygoid is a minute triangular splint at the very base. In *Bleekeria* the structure of the suspensorium is essentially similar except that the ectopterygoid is somewhat larger so that the palatine does not meet the quadrate. The suspensorium of *Hypoptychus* (Fig. 4*a*) is a quite different structure. The palatine and ectopterygoid are about equal in size and are united to one another by a digitate suture. The metapterygoid is a small splint and the mesopterygoid appears to be absent.

Undoubtedly the greatest specialization in the suspensorium is that found in *Crystallodytes* (Fig. 4*c*). Here the suspensorium is divided into two well-developed and strong portions with the ectopterygoid forming a long, delicate strut between them. In the anterior portion a large, firm mesopterygoid forms a shelf under a large part of the eyeball; it is firmly attached to the strong palatine anteriorly, but only by membrane to the ectopterygoid.

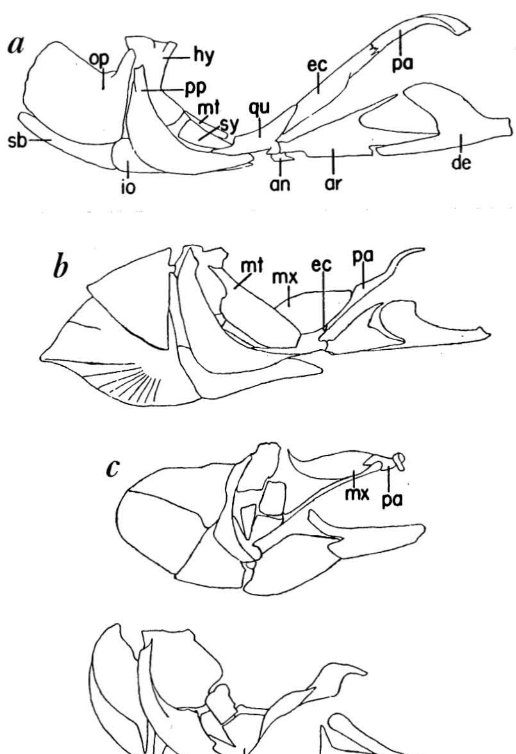

FIG. 4. Right gill covers, suspensoria, and lower jaws, external view, of *a, Hypoptychus dybowskii; b, Ammodytes tobianus; c, Crystallodytes cookei;* and *d, Tripterygion atriceps* (with the lower jaw dislocated). *an,* Angular; *ar,* articular; *de,* dentary; *ec,* ectopterygoid; *hy,* hyomandibular; *io,* interopercle; *mt,* metapterygoid; *mx,* mesopterygoid; *op,* opercle; *pa,* palatine; *pp,* preopercle; *qu,* quadrate; *sb,* subopercle; and *sy,* symplectic.

SKULL: In all of these fishes, there are no frontal-parietal crests, and the minute supraoccipital crest does not reach above the skull surface. *Tripterygion,* however, has a fringed, backwardly slanted crest running across the rear of the skull. This crest lies just behind the tabular ossicle on each side which bears the apparently incomplete supratemporal sensory canal commissure. (In the related *Entomacrodus* the supratemporal commissure is almost completely enclosed in the skull. Laterally, the commissure passes through a tabular ossicle that is fused to the cranium and thence medially through the rear of the parietals, leaving a large opening on the middorsal line.)

In *Parapercis* and *Tripterygion* the crania are somewhat more highly arched over the orbit than in the others. Probably in association with this, the wings of the parasphenoid extend farther up the sides of the postorbital bar than in the remaining four fishes. In all, however, the prootic extends over the top of the parasphenoid wings to the edge of the orbit. (In *Istiblennius,* related to *Tripterygion,* the parasphenoid wings meet the frontals in the usual blennioid fashion.)

In *Ammodytes* and *Bleekeria* the two exoccipital condyles lie adjacent to one another and form the upper portion of the facet for the articulation of the convex head of the first vertebra. In the other forms, including *Hypoptychus,* the exoccipital condyles lie at either side of the basioccipital articulation; the two exoccipital bones do not meet below the foramen magnum; and there is no rounded articular head on the first vertebra.

GILL ARCH SYSTEM: In *Ammodytes* the branchiostegal ray count is 8–7; in *Crystallodytes,* 7; in *Bleekeria,* 7; in *Parapercis* and *Tripterygion,* 6; and in *Hypoptychus,* 4–4.

In all the fishes under consideration the lower pharyngeals are separate. *Ammodytes* and

Bleekeria appear to be the only forms with 3 distinct upper pharnygeals on each side; *Hypoptychus* has separate upper pharyngeals on arches 2 and 3, but appears to have none on arch 4. *Parapercis and Crystallodytes* also have two pairs of upper pharyngeals, but the posterior pair seems to represent a combination of pharyngobranchials 3 and 4. *Tripterygion* appears to have only a single set of upper pharyngeals.

FINS, FIN SUPPORTS, AND AXIAL SKELETON

ANAL FIN: In the six fishes under consideration there is never more than a single unsegmented ray at the front of the anal fin, and even this is lacking in *Crystallodytes* and *Ammodytes.* All of the remaining anal rays are branched in *Parapercis,* some in *Hypoptychus,* only the last in *Tripterygion,* and none in *Crystallodytes, Bleekeria,* and *Ammodytes.*

Unlike the other three fishes, there is in the three ammodytoids a well-developed caudal peduncle behind the base of the last anal (and dorsal) ray; this is supported by about five vertebrae with bladelike neural and hemal arches.

DORSAL FIN: *Parapercis* and *Tripterygion* are the only fishes under consideration that have spinous dorsals. Furthermore, in these two the dorsal fins commence farther forward (over the 3rd vertebra in *Parapercis,* Fig. 5*a,* the rear of the skull in *Tripterygion,* Fig. 5*b*) than in the others (over the 5th vertebra in *Bleekeria,* and still farther back in the remaining forms). Structurally the spinous dorsal fin differs considerably in *Parapercis* and *Tripterygion.* In *Parapercis* it appears that the spinous dorsal has undergone some condensation, possibly as a result of forward movement of the soft dorsal, for the pterygiophores of the five spines interdigitate between neural arches 2 and 5 (Fig. 5*a*); one supraneural remains (rather than the three usually found in the lower percoids). In *Tripterygion* there are two spinous dorsals, the first of 3 spines and the second of 14; it appears very much as if the anterior 3 have appropriated the usual percoid supraneurals as their supporting bases. In the structure of the pterygiophores supporting the dorsal spines, *Parapercis* is considerably more generalized than *Tripterygion.*

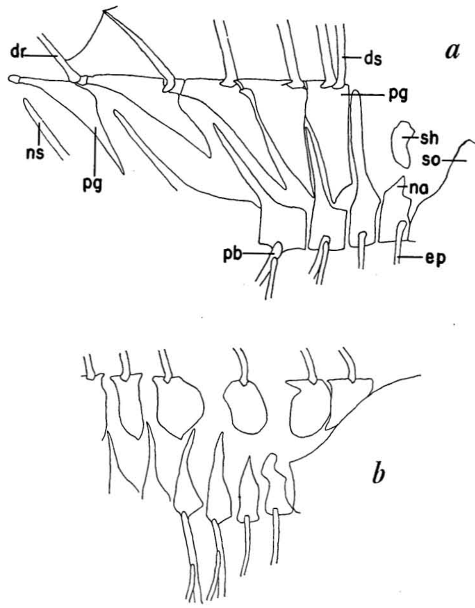

FIG. 5. Anterior vertebrae, ribs, dorsal rays and their supports in *a, Parapercis schauinslandi,* and *b, Tripterygion atriceps. dr,* Dorsal soft ray; *ds,* dorsal spine; *ep,* epipleural rib; *na,* neural arch; *ns,* neural spine; *pb,* pleural rib; *pg,* pterygiophore; *sh,* supraneural; *so,* supraoccipital.

In *Parapercis* the pterygiophores of the spines (except that of the first 2) retain their basic bisegmental structure (Fig. 5*a*); whereas in *Tripterygion* each pterygiophore is a fused monolithic unit (Fig. 5*b*).

In the soft dorsal, as in the anal, all the rays are branched in *Parapercis,* some in *Hypoptychus,* only the last in *Tripterygion,* and none in *Crystallodytes, Bleekeria,* and *Ammodytes.* In soft dorsal structure, there are again certain differences between *Parapercis* and *Tripterygion* on the one hand, and *Crystallodytes* and the ammodytoids on the other. In the first place, *Parapercis* and *Tripterygion* have the last dorsal (and anal) ray cleft to the base; *Crystallodytes* and the ammodytoids do not. Second, the pterygiophore of each soft dorsal ray in *Parapercis* and *Tripterygion* interdigitates deeply between a pair of neural spines (Fig. 5*a*), and there is an exact correspondence between vertebrae and soft dorsal rays. In *Crystallodytes* and the ammodytoids the pterygiophores of the soft dorsal (and anal) rays are short, weak structures

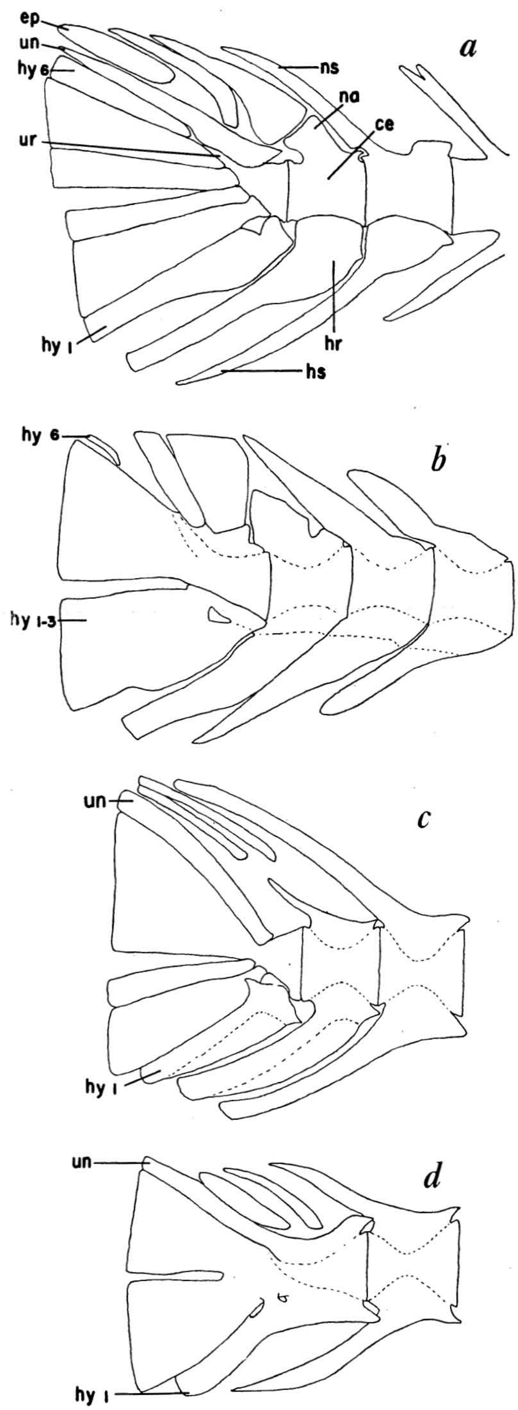

FIG. 6. Caudal skeletons of *a, Parapercis schauinslandi; b, Tripterygion atriceps; c, Bleekeria gilli;* and *d, Hypoptychus dybowskii. ce,* Centrum; *ep,* epural; *hr,* hemal arch; *hs,* hemal spine; *hy,* hypural; *na,* neural arch; *ns,* neural spine; *un,* uroneural; and *ur,* urostyle.

that interdigitate little if at all between the tips of the neural spines, and there is a rough but inexact correspondence between soft dorsal (and anal) rays and vertebrae.

CAUDAL FIN: The tails of the ammodytoids are somewhat forked, those of the other fishes under investigation more or less rounded. In all, there is a reduction in the caudal ray number from the typical percoid count of 17 principal rays, 15 branched. In *Parapercis* there are 15 branched rays, but no outer principal unbranched rays. In *Ammodytes* and *Bleekeria,* there are 15 principal rays, 13 branched. In *Hypoptychus,* there are 13 principal rays; apparently 11 of these were branched, but since the fin rays of the available specimen are broken the branched ray count cannot be definitely established (the same is true of the dorsal, anal, and pectoral fins). *Tripterygion* and *Crystallodytes* have 10 principal rays, 8 branched.

With regard to the caudal skeleton, *Parapercis* (Fig. 6*a*) is quite typically percoid (Gosline, 1961). There are six separate hypurals, one uroneural, and three epurals; none of these elements are fused to the urostyle. In the caudal skeleton of the other five fishes, considerably more fusion and/or reduction has occurred. Hypurals 4 and 5 are always fused with the urostyle, and, in *Crystallodytes* (Gosline, 1955: fig. 7d) and *Hypoptychus* (Fig. 6*d*), two or three of the lower hypurals as well. (Fig. 6*d* must be viewed with some reservation, as the specimen from which it was drawn may have been aberrant in having the last two vertebrae fused.) There are two epurals in *Tripterygion* (Fig. 6*b*) and the three ammodytoids, and only one in *Crystallodytes.*

PECTORAL FIN: The total number of pectoral rays in the fishes investigated is 15 in *Tripterygion* and *Parapercis,* 13 in *Ammodytes* and *Bleekeria,* 12 in *Crystallodytes,* and 9 in *Hypoptychus.* Of these, all are segmented in *Tripterygion* and the ammodytoids; however, there is a small, unsegmented, splintlike uppermost ray in *Parapercis* and *Crystallodytes*. Judging from the material available, it appears that the uppermost pectoral ray is homologous whether splintlike or segmented, for it has the same very peculiar basal structure. Like other soft rays it consists of two halves. However, in the uppermost pectoral ray the two halves are usually not mirror images of one another. Rather, the scapula articulates with a facet that lies entirely on the inner "half" of the ray (except, among the fishes investigated, in *Hypoptychus* and *Tripterygion*). An inquiry into this peculiarity has shown that the scopeliform genus *Synodus* has a small bony nodule that lies between two equal halves, but is attached to the inner. As Starks (1930: 238) noted,

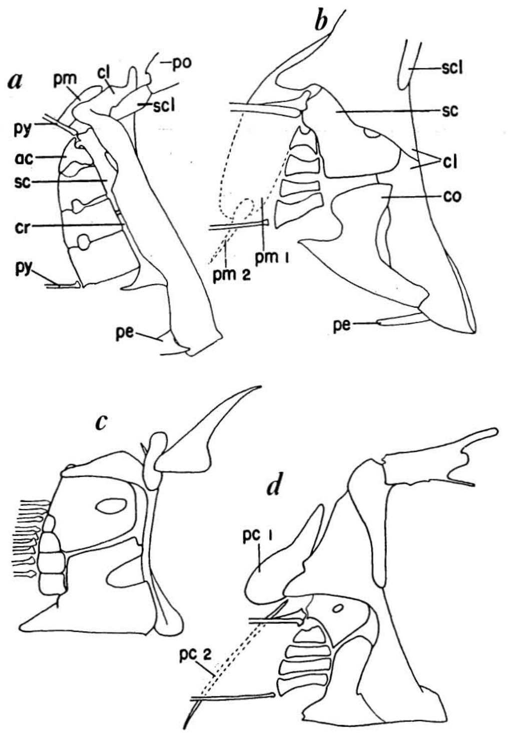

FIG. 7. Right pectoral girdles, external view, of *a*, *Tripterygion atriceps; b, Bleekeria gilli; c, Hypoptychus dybowskii;* and *d, Ammodytes tobianus.* Only the uppermost and lowermost pectoral rays are shown in *a, b* and *d;* the top of the pectoral girdle is not drawn in *b;* and the lower postcleithrum is not indicated in *a. ac,* Actinost; *cl,* cleithrum; *co,* coracoid; *pc,* postcleithrum; *pe,* pelvic girdle; *pm,* postcleithrum; *py,* pectoral ray; *sc,* scapula; and *scl,* supracleithrum.

this nodule probably represents a modified actinost, which in many higher teleosts became incorporated into the inner, articular "half" of the uppermost pectoral ray (Fig. 7*b*, *d*).

The pectoral girdles of *Tripterygion* and of the ammodytoids are shown in Fig. 7. Those of the ammodytoids are peculiar in having the supracleithra and cleithra more or less vertically aligned.

There are two postcleithra in *Parapercis, Tripterygion, Ammodytes,* and *Bleekeria,* and apparently not any in *Crystallodytes* and *Hypoptychus.*

PELVIC FIN: Pelvic fins are lacking in the three ammodytoids studied here. However, two splintlike pelvic girdle elements are to be found in *Bleekeria* (Fig. 7*b*), and a small pelvic fin of a spine and three rays, located somewhat ahead of the pelvic bases, occurs in the related ammodytid genus *Embolichthys* (Jordan, 1902). The three other fishes studied here also have the pelvics originating ahead of the pectoral bases. *Parapercis* has a pelvic spine and five branched rays, the fourth considerably the longest. *Crystallodytes* has a short pelvic consisting of a spine and five unbranched but segmented rays. In *Tripterygion* there are two well-developed unbranched, but segmented, rays; there is no spine. In all three fishes the pelvic girdle articulates anteriorly with the cleithra. In *Crystallodytes* (Fig. 8*d*), the two halves of the pelvic girdle are rather widely separated anteriorly; in *Parapercis* (Fig. 8*b*) they are united for nearly their entire length; in *Tripterygion* (Fig. 8*c*) the two halves are not only united, but anteriorly they seem to have completely fused. Futhermore, *Tripterygion* has the pelvic girdle firmly wedged between the cleithra.

VETEBRAL COLUMN AND RIBS: *Parapercis* has 30 (10 + 20) vertebrae (including the urostyle); *Tripterygion,* 34 (10 + 24); *Crystallodytes,* 55 (29 + 26); *Ammodytes lanceolatus,* according to Regan (1913: 137), 69 (40 + 29); *Bleekeria gilli,* according to Duncker and Mohr (1939: 13), 57 (32 + 25); and *Hypoptychus,* 55 (31 + 24).

In *Parapercis, Tripterygion, Ammodytes,* and *Bleekeria* there are two sets of ribs. The lower, or pleural, ribs start from the 3rd vertebra; the upper, or epipleural, ribs start from the 1st,

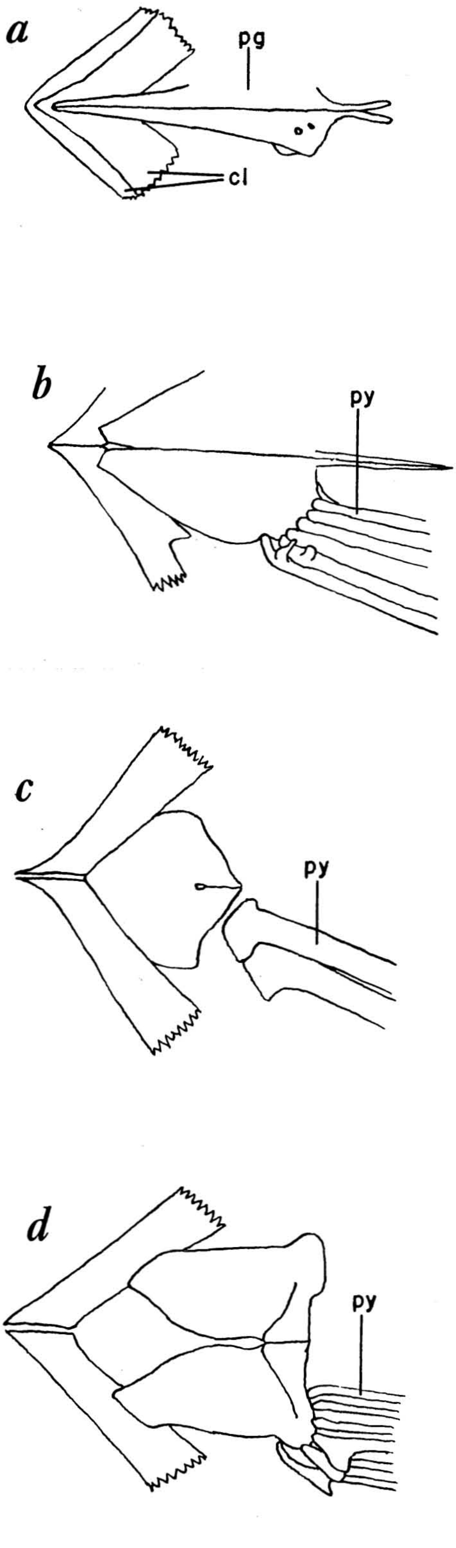

FIG. 8. Pelvic girdles, from above, of *a, Caranx ignobilis; b, Parapercis schauinslandi; c, Tripterygion atriceps;* and *d, Crystallodytes cookei.* The pelvic rays are not indicated in *a. cl,* Cleithrum; *pg,* pelvic girdle; and *py,* pelvic ray.

articulating with the upper surface of the pleural ribs from the 3rd vertebra on (Fig. 4*a, b*). In *Crystallodytes* there is only one set of ribs which starts with the 1st vertebra; this set would appear to represent the epipleurals. In *Hypoptychus,* there is also only one series of ribs, but it starts from the 3rd vertebra and would appear to represent the pleural series.

DISCUSSION

On the basis of osteological characters, *Parapercis, Crystallodytes, Tripterygion,* and the three ammodytoids could be grouped in a number of ways. One such system would separate the more elongate forms, i.e., *Crystallodytes* and the ammodytoids, from the shorter, stockier *Parapercis* and *Tripterygion.* Such a division could be expressed osteologically as follows.

Parapercis and *Tripterygion.* Premaxillary pedicels stout, firmly fused to the toothed portions. Wings of the parasphenoid expanded, forming the lower portion of the postorbital bar. The abdominal portion of the vertebral column shorter than the caudal portion, consisting of 10 vertebrae. Dorsal with an anterior spinous portion which commences over or ahead of the 3rd vertebra. Last dorsal and anal rays cleft to their bases. Pterygiophores of the dorsal and anal rays deeply interdigitating between successive neural and hemal spines, respectively.

Crystallodytes and the ammodytoids. Premaxillary pedicels long and/or movably articulated with their lateral portions. Wings of the parasphenoid little developed, not extending up as a portion of the postorbital bar (Fig. 3*c*). The abdominal portion of the vertebral column longer than the caudal portion, of more than 10 vertebrae. No spinous dorsal, the soft dorsal commencing over or behind the 5th vertebra. Last dorsal and anal rays undivided. Pterygiophores of the dorsal and anal rays interdigitating little or not at all between the neural and hemal spines, respectively.

To group the fishes under consideration in the above fashion is to separate those nearer the generalized percoid type from those that are more specialized. Such a division may merely represent levels of structural organization rather than relationships.

Parapercis is much the least differentiated from the typical percoids of any of the six fishes dealt with in this paper. All of the remaining five fishes (*Tripterygion, Crystallodytes, Ammodytes, Bleekeria,* and *Hypoptychus*) have in common the following specializations over and beyond those found in *Parapercis*: circumorbital series of bones incomplete or complete and consisting of a lacrimal and only 2 or 3 circumorbitals; no pungent dorsal spines; caudal with 13 or fewer principal rays; urostyle fused to the upper hypurals; pelvics reduced (i.e., without branched rays) or absent.

Most of the minor specializations that *Parapercis* does exhibit seem to be associated with fin structure. Thus the pelvics are advanced in position and have the inner (actually the 4th) soft rays the longest, but there appears to be no great specialization of the pelvic girdle (Fig. 8*b*). The caudal fin lacks the usual principal unbranched rays, though the caudal skeleton is typically percoid (Fig. 6*a*). The spinous portions of the dorsal and anal have been reduced. In the anal there is a single small unsegmented splint at the front of the fin. The spinous dorsal seems to have been pushed forward and concentrated as well as reduced in size, for there is only one supraneural and the pterygiophores for all five spines extend between neural arches 2 and 5. The soft dorsal and anal retain a typical percoid condition. However, their pterygiophores interdigitate deeply between successive neural and hemal spines and bear a one-to-one relationship with the vertebrae. Now in typical percoid families, though not apparently in the Cepolidae, the soft dorsal and anal rays usually do not interdigitate deeply between the neural and hemal spines, and there are usually about two pterygiophores per vertebra. This is true of even fairly elongate forms like the goatfish, *Mulloidichthys samoensis.* To change this arrangement to a one-to-one relationship between pterygiophores and vertebrae requires either an increase in the spacing between soft dorsal and anal rays, or an increase in the number of vertebrae, or both. The cigar-shaped labrid *Cheilio inermis* seems to be an instance where a one-to-one ratio has been brought about by increased spacing between rays, for this fish retains 24 vertebrae. In most elongate fishes, however, an increase in vertebrae has also taken place.

On the basis of *Parapercis* alone it is impossible to evaluate Regan's (1913) percoid "Division Trachiniformes" (equals superfamily Trachinoidae). Suffice it here to remark that there does appear to be a somewhat extensive group of usually rather deep-water bottom fishes having essentially the fin characters described above for *Parapercis.* Whether these fishes are really related is impossible to say at this point. The relationship of *Crystallodytes* to this group is also doubtful. Certainly *Crystallodytes* represents a much higher degree of differentiation from the typical percoids than *Parapercis.* (For certain characteristics of *Crytallodytes,* see below.) Some knowledge of less specialized (or at least of other) forms of the *Crystallodytes* lineage should provide far better indications of its relationships than are available from a study of this form alone. (Throughout this paper, *Crystallodytes* has been considered a trichonotid, but that this is a correct family allocation is dubious, cf, Schultz, 1960: 273.)

Tripterygion is generally agreed to be a member of the perciform suborder Blennioidei. However, this suborder, since it was defined and later restricted by Regan (1912, 1929), has undergone considerable disintegration and rearrangement (Starks, 1923; Smith, 1952; Hubbs, 1952; Gosline, 1955; and Makushok, 1958). Even after certain nonblennioid groups have been removed, Hubbs and Makushok feel that most or all of the remaining families may be divided into a northern (cold water) group and a southern (warm water) group which may have had independent origins among the percoid families.

Tripterygion is, in many respects, one of the more generalized, i.e., percoid, members of the whole warmwater group. This group differs radically from the remaining fishes under consideration here in its mode of life. The southern blennies characteristically use their thickened pelvic rays to prop the anterior end of the body away from the hard substratum on which they feed. The more elongate forms at least characteristically rest with the tail bent, and, when disturbed, retreat into holes in the rock and coral by means of sinuous movements of the body. A number of the characteristic external features of the southern blennies are probably associated with this mode of life. For example, the pelvic rays though reduced in number are stout, and are attached to a short pelvic girdle that is firmly wedged between the wings of the cleithra. The dorsal fin extends far forward, in the extreme case of *Xiphasia* to above the eye. There is often a pair of tentacles or a transverse fringe of them, e.g., *Cirripectes,* on the nape; in *Tripterygion* there is a low transverse fringe across the nape in exactly the same position as in *Cirripectes,* but it is made up of bony flaps extending upward from the skull.

A few other characters of *Tripterygion atriceps* may be mentioned because of their bearing on blennioid classification. The lateral line canal of the lacrimal and three circumorbitals is not covered by bone externally (Hubbs, 1952: 48, 50). A basisphenoid is present (Makushok, 1958: 58). The lowermost actinost in the pectoral girdle is not greatly longer than deep (Makushok, 1958: 58; compare Fig. 7*a* of the present paper with Makushok's fig. 25). Finally, in the caudal skeleton of *Tripterygion* (Fig. 6*b*) the three lower hypurals have fused to one another. Hypurals 4 and 5 (above the axis) have also fused to one another and to the urostyle and uroneurals. Hypural 6 is a small separate ossicle (the "minimum hypural" of Makushok, 1958), and there are two broad epurals. In the northern blennies, by contrast, the upper or epaxial hypurals are usually, though not always, separate from the urostyle (Makushok, 1958: 38, and fig. 22). Also, the northern blennioids usually have three epurals, rather than the two of *Tripterygion.* (In 1955: fig. 7f, I provided a sketch of the caudal skeleton of *Istiblennius gibbifrons.* I have not been able to relocate the specimen from which the drawing was made, but judging from specimens of *Entomacrodus marmoratus* and *Istiblennius zebra,* which have caudal skeletons very like that of *Tripterygion,* the figure is incorrect in showing a fusion of the lower hypurals and the epurals with the rest of the urostylar vertebra.)

The investigation of *Tripterygion* reported on here would support, in its small way, Hubbs' (1952) and Makushok's (1958) thesis that the "northern" and the "southern" blennies are diphyletic. But whether they are diphyletic in the sense that the two groups have wholly different origins or in the sense that they have diverged in two different directions from the same or from two closely related stocks would seem to remain an open question. That *Tripterygion* has little relationship to the congrogadids (cf, Smith, 1952) also seems clear.

Among the more elongate fishes investigated, i.e., *Crystallodytes* and the ammodytoids, *Crystallodytes* and *Ammodytes* at least are sand divers. The pointed heads, long bodies, low vertical fins, small or absent pelvics, modified scales, and peculiarities of the lateral line of the body are probably associated with this mode of life. The habits of the other two ammodytoids, *Bleekeria* and *Hypoptychus,* are unknown.

That there is any phylogenetic relationship between *Crystallodytes* and the ammodytoids seems extremely doubtful. *Crystallodytes* differs immediately from the ammodytoids in the following characters. The lower jaw is included and the upper appears to be nonprotrusile. The circumorbital series of bones is complete. The cleithra are very oblique with the lower ends far forward of the upper. The dorsal and anal extend far back, and there is no well-demarcated caudal peduncle. Both the principal and procurrent fin rays are reduced in number. The lateral line runs low on the body posteriorly, just above the anal base. Finally there is a series of specializations related to the eye and suspensorium of *Crystallodytes.* In the first place, the eye itself is very characteristic, for *Crystallodytes* is a pop-eyed fish (Fig. 1*b*) with the small pupil protruding notably beyond the rest of the eyeball. This eyeball is supported below by a large and firm subocular shelf composed of the greatly expanded mesopterygoid. This bone, together with the palatine, forms a nearly separate portion of the suspensorium only weakly attached to the rest of this structure by the long, weak ectopterygoid (Fig. 4*c*). Neither the suspensorium nor the peculiar eyeball shows any relationship whatever to those structures in

Parapercis, which is typically percoid in these respects. Nor does *Crystallodytes* show any relationship to any of the other fishes investigated in these structures. Indeed, the only fishes that would seem to have a suspensorium anything like that of *Crystallodytes* are the congrogadids (cf, Regan, 1912: fig. 2b, and Smith, 1952: pl. 6B).

The three ammodytoid fishes may be defined as follows: elongate fishes with premaxillaries highly protrusile. Circumorbital bones incomplete, the lacrimal and first circumorbital separated from the rest of the series. Fins without spines or unsegmented rays except for the procurrent rays of the caudal (pelvic rays of *Embolichthys?*). Caudal forked or emarginate, preceded by a well-marked caudal peduncle which is supported by five or more vertebrae with bladelike neural and hemal spines. Pelvics absent (of a spine and three rays in *Embolichthys,* Jordan, 1902). Vertebrae 55 to 69, the abdominal vertebrae more numerous than the caudal, in approximately a one-to-one relationship with the dorsal and anal rays above and below them. Cleithra and supracleithra almost vertically aligned.

The analysis of *Hypoptychus* indicates that it is widely separated from *Ammodytes* and *Bleekeria.* Though the three genera hold a number of features in common it would seem that *Hypoptychus* has evolved in quite a different direction from the other two. Thus, while *Hypoptychus* remains more percoid in jaw structure and skull–vertebral column articulation, it has become more specialized (degenerate?) in almost every other feature: the bones are thin; the branchiostegal rays and fin rays are reduced in number; the scales have been completely lost; etc. *Hypoptychus* well warrants the separate family Hypoptychidae apparently first assigned to it by Jordan (1923: 230).

The families Hypoptychidae and Ammodytidae may be contrasted as follows.

Hypoptychidae. Scales entirely lacking. Jaws subequal, the premaxillary with teeth and with its long pedicel firmly attached. Branchiostegal rays 4. Articular facets of the exoccipitals widely separate. Dorsal and anal fins equal in length, of about 20 rays. Caudal with 13 principal rays; pectorals with 9.

Ammodytidae. At least some scales present. Lower jaw protruding, sharptipped. Premaxillary without teeth and with its pedicel movably attached to its lateral portion. Branchiostegal rays 7 or 8. Articular facets of exoccipitals contiguous. Dorsal extending far forward of the anal. Caudal with 15 principal rays; pectorals with 13.

The problem of ammodytoid origin remains obscure. The majority of features point to a percoid origin of some sort, but none of the percoid families known to the author would seem to provide a suitable ancestor.

The ammodytoids in turn would appear to have led to nothing with the exception of one highly speculative possibility. If the terminal vertebra of *Hypoptychus* is not merely the result of fusion in an aberrant specimen, then a progressive evolution along many of the lines already apparent in that fish might end in a neotenic form very like *Schindleria* (cf, Gosline, 1959).

Whatever the ancestors and derivatives of the ammodytoids may be, they remain, so far as known, sufficiently isolated and characterized to warrant fully the superfamily status among the Percoidei that has generally (cf, Regan, 1913) been assigned to them.

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