

Some Thoughts about the Teleostean Fish Concept— the Paracanthopterygii

Thomas H. Fraser

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Abstract The brief history of the Paracanthopterygii is reviewed. Some relevant problems are discussed with the view that these aspects have not received sufficient attention or that their interpretations are equivocal with present data. No new information is presented. The group-concept is accepted as a reasonable hypothesis on which to base further testing. Nevertheless, the present constituents, in their sum, seem to be an unnatural group. The polymixioids and indostomoids are rejected as part of the overall group. The relationship of the gobiocoids, gobioids and ophidioids, as part of the Paracanthopterygii, are seen as tentative hypotheses either lacking strong evidence or with unexplained evidence against inclusion. The Ophidioidei are removed from the Gadiformes. Two other groups, the notothenioids and callionymoids, should also be studied.

Basic objections center on the acceptance of present myological and neurological evidence as being more than preliminary. Fundamental understanding of possible trends in these characters has not reached the level that is present in osteology. The effects of mode of life and plasticity of the myological and neurological systems are not yet known in detail.

Introduction

The term Paracanthopterygii, in the words of the authors, "represents a spiny-finned radiation more or less comparable morphologically with that of the Acanthopterygii". Greenwood et al. (1966 : 387) also propose that the group has a pre-acanthopterygian origin retaining some characters that preclude an acanthopterygian ancestor. Additions and refinements of this group appeared in Rosen and Patterson (1969), Banister (1970), and Freihofer (1970).

The Paracanthopterygii now contains two series and eight orders. Table 1 shows the major events in the brief history of the group with authors.

Proponents of the Paracanthopterygii have thus far suggested three possible ancestor groups: neoscopelid-like fish (Greenwood et al., 1966), polymixiids (Rosen and Patterson, 1969), and osmerids (Freihofer, 1970).

Discussion

Before reviewing evidence relating to the

two superorders in question, several criteria must be discussed. As Freihofer (1969 : 858–859) and Nelson (1970 : 378) correctly point out, morphological homology is supreme in these studies. This aspect will be construed rigidly—that is, phylogenetic homology in a narrow sense, not in the broad sense as used by some recent workers. It is the only criterion by which we can decipher the end results of characters with long evolutionary histories. Thus the function unit in question must be well understood anatomically with probable phylogeny of its own. Masking or confusing effects of mode of life and limits imposed by the environment must also be recognized. Without question, as many functional units as possible should be employed when trying to interpret relationships of the fishes in question. Here one tends to divide the characters into primitive and advanced (based on our interpretation of the unit's phylogeny). One argument suggests that we must completely abandon the primitive characters as being of no use in determining "sister" groups (see Rosen and Patterson, 1969 : 362; Nelson,

Table 1. Classification of the superorder Paracanthopterygii as of 1970 with authors responsible for placement given.

Superorder Paracanthopterygii	Greenwood et al., 1966.
Series Polymixiomorpha	Rosen & Patterson, 1969.
Order Polymixiiformes	Rosen & Patterson, 1969.
Series Salmopercomorpha	Rosen & Patterson, 1969.
Order Percopsiformes	Greenwood et al., 1966.
†Suborder Sphenocephaloidei	Rosen & Patterson, 1969.
Suborder Percopsoidei	Greenwood et al., 1966
Suborder Aphrederoidei (incl. Amblyopsoidei)	Rosen & Patterson, 1969.
Order Gobiiformes	Freihofer, 1970.
Order Gadiformes	Greenwood et al., 1966.
Suborder Muraenolepoidei	"
Suborder Gadoidei	"
Suborder Ophidioidei	"
Suborder Macrouroidei	"
Suborder Zoarcoidei	"
Order Batrachoidiformes	Greenwood et al., 1966.
Order Lophiiformes	Greenwood et al., 1966.
Suborder Lophioidei	"
Suborder Antennarioidei	"
Suborder Ceratioidei	"
Order Gobiesociformes	Greenwood et al., 1966.
Order Indostomiformes	Banister, 1970.

1969 : 21–22). This, in my opinion, is incorrect for several reasons:

1. These characters are part of the total gene pool and also have an evolutionary sequence of some value in determining relationships. To ignore, by fiat, these primitive characters after establishing a probable character phylogeny is not logical. Their analytical power is less, and this has been abused, but their power is not nil as some have suggested.
2. The question of a primitive versus advanced character is semantic and depends completely upon the narrow context of discussion. We must differentiate wherever possible the context in which the character is being discussed, for the same character, depending on minor changes, can be primitive or advanced at differing levels of classification.
3. Although many characters appear to be independent in their change (skull versus caudal skeleton), they may be only semi-independent (pleiotropic and/or polygenic effects).

One other criterion useful in assessing

relationships is the amount of parallel evolution of advanced characters. Fossils may also be helpful but these are no different from living fishes in having a mosaic of primitive and advanced characters (also see Nelson, 1969 : 22–23, 26).

Three major lines of evidence have been put forth in favour of recognizing the Paracanthopterygii—osteology, jaw musculature, and the ramus recurrens facialis (ramus lateralis accessorius), a specialized branch of the nervous system. Osteology has the strongest historical background of the three systems and is the most reliable. Jaw musculature and the nervous system have only begun to be applied seriously in systematics since about 1960 and are therefore less reliable, but have similar potentials (Nelson, 1969: 24, comments on the nervous system). In fact, interpretations of these systems are not yet based on comprehensive understanding either in terms of a probable phylogeny or from the standpoint of the effects from mode of life. Hence, an unknown but likely substantial

amount of uncertainty still exists in these two systems. Similar objections could be raised about osteological interpretations but in relative terms these would have less weight.

Characters and various trends for the Acanthopterygii have been compared in Greenwood et al., (1966). Two characters, a particular muscular arrangement of the upper jaw and type of caudal skeleton are the central criteria utilized (Rosen and Patterson, 1969 : 361)—though not initially indicated as such from the characters listed in Greenwood et al. (1966 : 387–388). As the former work is a refinement with regard to the characters analyzed, many of the following remarks deal with this work.

Rosen and Patterson (1969) review in great detail (1) a more or less specific type of caudal skeleton with the following characters: a complete neural spine on the second pre-ural centrum (PU-2), upper hypurals usually fused to the second ural centrum (U-2), never more than two epurals, and 9+9 principal caudal rays; and (2) the muscle organization of the mouth, particularly the levator maxillae superioris (LMS), an internal elaboration of the adductor mandibulae, versus other elaborations of the adductor mandibulae particularly the external portion. The other uniting features of the more primitive paracanthopterygian orders suggested by Greenwood et al. (1966 : 388), infraorbitals (when present) without a subocular shelf and Baudelot's ligament from the posteroventral edge of the supra-cleithrum to first vertebrae are not the subjects of much discussion.

Briefly, some of their conclusions are: (1) "We can conclude with some confidence that the second pre-ural neural spines of paracanthopterygians arose by elongation of a short neural spine, and that the two epurals are due to the loss of one epural, not to fusion of an epural with the neural arch of the second pre-ural centrum (p. 368). (2) The LMS is lacking in the Gobiesociformes and the lophiids but present in all other living paracanthops; the A division is "... absent from all ex-

amined members of the group save gadids, merluccids and percopsids." The LMS occurs in *Amia*, all members of the Myctophidae examined (5 genera, 13 species) and some Cyclopteridae; in some Carangidae, *Lampris*, *Polymixia*, *Gadopsis*, *Parapercis*, and a large number of blennies, a muscle like the LMS has developed (p. 371–2). (3) "There seems to be nothing else (subocular shelf, 3 predorsals, 3 epurals, loss of the pelvic splint, loss of the adipose fin, no true levator maxillae superioris) to distinguish the polymixioids from early percopsiforms" (p. 454). (4) "The conclusions to be drawn from these comparisons are that the gadiforms are very closely related to the percopsiforms, and originated from a Cretaceous fish resembling *Sphenocephalus* but with seven branchiostegals..." (p. 437). (5) "... we have found... evidence supporting the validity of the Paracanthopterygii, we have not found that any member of the group... is incorrectly placed, or any firm indications that other fishes should be included" (p. 361).

Let us consider their conclusions about the primitive paracanthopterygian caudal skeleton. The crux of their interpretation is "... did the ancestors of early percopsiforms such as *Amphiplaga* and *Sphenocephalus* have a low neural crest on the second pre-ural centrum, with which the first epural later fused, or did they have a short neural spine, one epural being lost?". The complete second pre-ural (PU-2) neural spine, occurring in some Zeiformes, Perciformes and more advanced acanthopterygians, is produced by a fusion of the first epural with the neural crest (Patterson, 1968; Monod, 1968). Patterson (1968) has shown that the primitive complement of epurals in teleosts is never more than three (but see Cavender, 1970) and that epurals appear to be detached neural spines which can lose their original metamery. The important facts here are: (1) polymixioids have a complete PU-2 neural spine and three epurals; (2) all known fossil and living percopsiforms have a complete PU-2 neural spine

and two epurals. The authors hypothesize that, because nearly all more primitive groups of fishes have a somewhat reduced neural spine on the PU-2 centrum, it must have elongated in polymixioids. Then they suggest "The similarity between percopsiforms and polymixioids suggests that their second pre-ural neural spine arose in the same way". This means that (1) the primitive percopsiform caudal skeleton originally had a short neural spine on the PU-2 centrum (not known) and (2) that this same caudal skeleton had three epurals and subsequently lost one (not known). Equally possible is the (1) shortening of the neural spine on the PU-2 centrum with (2) the subsequent fusion of the first epural to the low neural crest (neither process known in the Percopsiformes). In their Fig. 5 an arrow drawn between H to C would indicate another possible route similar to I-J. The data at hand do not favor either hypothesis contrary to their statement about "... *Sphenocephalus* appears both too primitive automatically and too ancient to have developed a second pre-ural neural spine secondarily by fusion of an epural with a neural crest, because this presupposes an ancestral series of forms in which the primitive short neural spine was reduced so that the first epural could come to lie above it". This statement cannot be accepted because, to quote them (p. 452): "What we find (in teleost phylogeny) is a mosaic of primitive and advanced features, the first lost and the second acquired...". Thus, I submit we cannot yet make any firm conclusion about the nature of the complete neural spine PU-2 in the percopsiforms or their relatives. The polymixioids have a long fossil record yet none shows the loss of an epural. (Note: Patterson (1964 : 374) is unsure of the placement of *Omosoma sinum* Arambourg, the oldest polymixioid known, of which Rosen and Patterson with some reservation state that there appear to be only two epurals).

With regard to the prototype of caudal skeleton, the characteristic paracanthoptery-

gian skeleton can be derived not only from polymixioids but also from ctenothrissoids, myctophoids, and berycoids. The prototype caudal skeleton cannot be derived from any known osmeroid (Table 2). Weitzman (1967 : 531) records substantial variation in the fusions of the ural centra in stomiatoids, even to the absence of the free second ural centrum in two species of *Borostomias* and its presence in a third species. The random nature of separate ural centra in stomiatoids indicates the danger of statements such as in Greenwood et al., (1966 : 387), where they state that no acanthopterygian is known to possess a caudal skeleton comparable to that of generalized paracanthopterygians. This, of course, is not true as both berycoids and polymixioids have the necessary structures (Regan, 1911 : Fig. 1; Gosline, 1961 : 14). As relatively few perciform fishes have been examined (none having a free second ural centrum) the possibility that some might have a free second ural centrum cannot be definitely excluded.

The second selected feature of the Paracanthopterygii is the levator maxilla superioris (LMS), an internal elaboration of the adductor mandibulae. The Acanthopterygii have tended to elaborate an external division of the adductor mandibulae known as A_1 . The occurrence of the LMS and a "pseudo" LMS in other groups indicates that selective pressures favoring this style of oral kinetics is not restricted to a single phyletic grouping. Material examined by these and other authors includes only a smattering of the acanthopterygian fauna; to accept that the major trends of the jaw muscle systems are well understood with respect to phylogeny and the masking effects of mode of life would be ill-advised.

The third conclusion relates to the distinction of polymixioids from early percopsiform fishes being analysed in conjunction with the fourth about *Sphenocephalus*. In their discussion summing up important differences and similarities relating to polymixioids and early percopsiforms, Rosen and Patterson (p. 454) state "There seems to be nothing else to distinguish

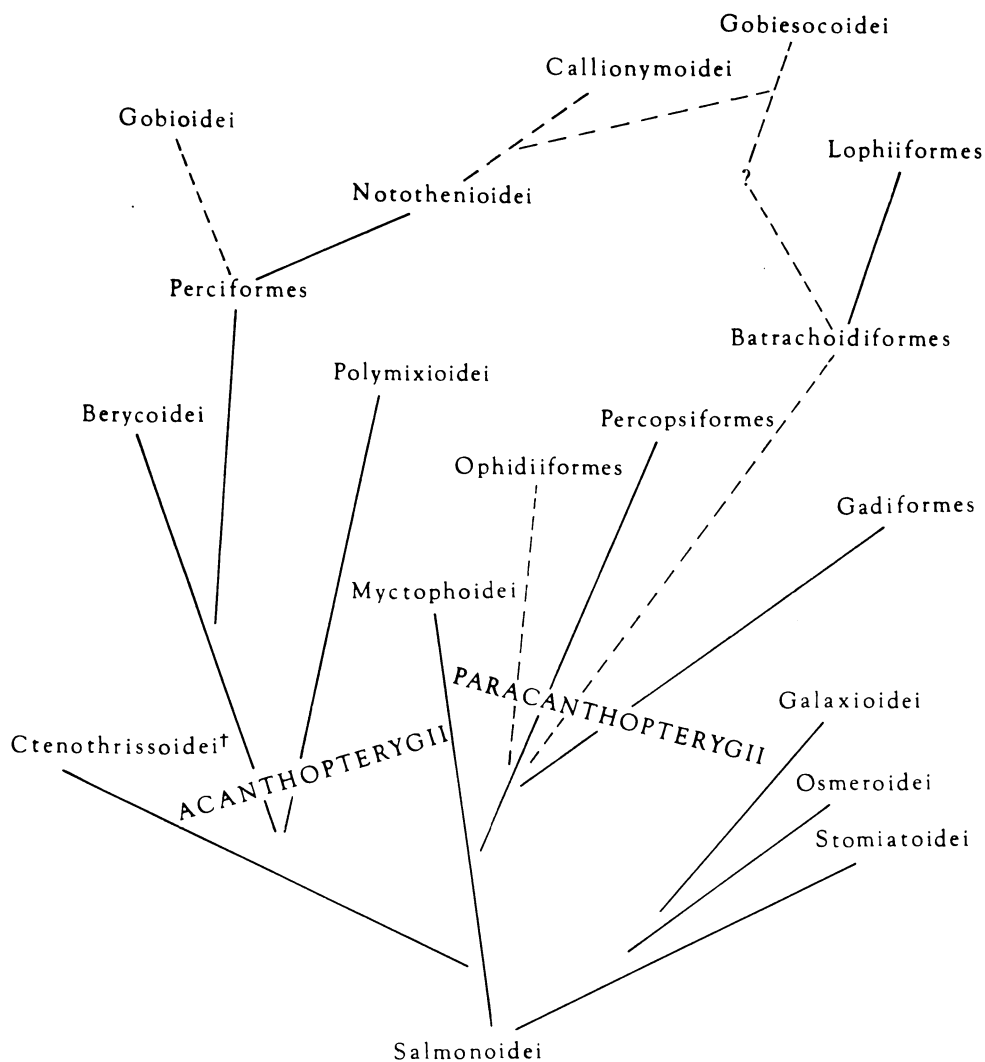


Fig. 1. One interpretation of relationships in the radiation of some spiny-rayed teleosts and their possible ancestors. Dashed lines indicate the existence of a greater degree of uncertainty than solid lines.

the polymixioids from early percopsiforms.” The characters referred to are: a subocular shelf, three predorsals, loss of the pelvic splint, loss of the adipose fin and no true levator maxillae superioris. Had they tabulated the data in their last section (starts p. 445) such a statement would not have been made for two other differences (exoccipital condyles and supramaxillae) are mentioned (p. 446-447). Moreover, seven other characters (identified in Table 2) which can be found in Patterson

(1964) and Rosen and Patterson (1969) will further define polymixioids and early percopsiforms. These character states would probably be classed as “advanced” ancestral Paracanthopterygian characters.

Rosen and Patterson (1969 : 454) admit that no Cretaceous or recent polymixioid was the common ancestor of the paracanthopterygians because “... all known polymixioids have elongated median fins and can have no adipose fins The fact that we have had to make

Table 2. A comparison of selected characters of the early Paracanthopterygii and other important groups. Most information is compiled from literature cited in this paper.

Characters	†Sphenocephaloidei	Per-copsoidei	Poly-mixioidei	Berycoidei	Mycto-phoidei ¹	Osmeroidei	†Ctenoth-rissoidei ²
Ural centrum two	Present	Present	Present	Present	Present	Absent or fused	Present
Autogenous hypurals	6	6	6	6	6	6	6
Pairs of uroneurals	2	2	2	2	2	2	2
Neural spine on second pre-ural centrum	Long	Long	Long	Short	Short	Short	Short or long
Epurals	2	2	3	3	3	2	3
Principal caudal rays	9+9	9+9	9+9	9+9	10+9	10+9	10+9
Endopterygoid teeth	Present	Absent	Present	Present	Present	Present	Present
Ectopterygoid teeth	Present	Present	Present	Present	Present	Absent	Present
Perforate ceratohyal	Present	Absent	Present	Present	Absent	Absent	Present
Ceratohyal-epihyal suture	Absent	Present and Absent	Absent	Absent	Absent	Absent	Present
Branchiostegal rays*	6(2+4)	6(2+4)	8(4+4)	8(4+4)	up to 16	8-10	9(5+4)
Pelvic splint	Present	Present	Absent	Absent	Present	Present	Present
Pelvic girdle articulating with post cleithrum	Yes	Yes	Yes	Yes	No	No	Yes
Pelvic spine	Absent	Absent	Present	Present	Present	Absent	Present
Pelvic position	Subthoracic	Subthoracic	Subthoracic	Subthoracic	Subthoracic (Abdominal)	Abdominal	Subthoracic
Adipose fin	Present	Present	Absent	Absent	Present	Present	Absent
Dorsal spines	5	3	5	2-12	1	Absent	Absent
Anal spines	5	3	5	1-4	1	Absent	Absent
Supramaxillae	1	Absent	2	2	2	1	2
Antorbital	Present	Present	Present	Present	Present	Present	Present
Mesocoracoid arch	Absent	Absent	Absent	Absent	Absent	Present	Absent
Supraoccipital	Large	Medium	Large	Large	Small	Small	Small
Parietals meet at midline	No?	No	No	No	Yes	Yes	Yes
Supratemporal fossa*	Rudimentary?	Absent	Present	Present	Absent	Absent	Absent
Posttemporal fossa roofed	No	No	No	No (partially)	Yes	No	No (partially)
Maxilla in gape	Excluded	Excluded	Partially included	Partially included	Excluded	Included	Included
Maxilla toothed	No	No	No	Posteriorly in some	No (except some larvae)	Yes	Yes
Premaxilla alveolar process	Long	Long	Long	Long	Long	Short	Short
Ascending premaxillary process	Developed	Developed	Developed	Developed	Developed	Rudimentary	Rudimentary
Sensory canals on head*	Little enclosed by bone	Partially enclosed by bone	Enclosed by bone	Enclosed by bone	Enclosed by bone	Open canals	Enclosed by bone
Orbitosphenoid*	Absent	Absent	Present	Present	Present	Absent	Present
Basisphenoid*	Absent	Absent	Present	Present	Present	Absent	Present
Separate opening for hyomandibular and facialis nerve branches in pars jugularis	Not given	Yes	Yes	Yes	Yes	Not given	Yes
Epineural ribs*	Absent	Absent	Present	Absent	Present	Present	Present
Epipleural ribs*	Absent	Reduced	Present	Present	Present	Present	Present
Exoccipital condyles	Separate	Separate	Simple (joined)	Simple (joined)	Simple (joined)	Not given	Simple (joined)
Predorsals (supraneurals)	1	1	3	3	3	17	Not known
Infraorbital shelf	Absent	Absent	Present	Present	Present or Absent	Absent	Present or Absent

Table 2. (Cont.).

Characters	†Sphenocephaloidei	Per-copsoidi	Poly-mixioidei	Berycoidei	Mycto-phoidei ¹	Osmeroidei	†Ctenoth-rissoidei ²
Tooth plates on basibranchials	—	Present	Present	Absent	Present	Present	Present
Baudelot's ligament	—	to 1st vertebra	to 1st vertebra	to basi-cranium	to 1st vertebra	Not given	—
Levator superioris maxillae (LSM)	—	Present	Absent	Absent	Present	Not given	—
A ₁ bundle of adductor mandibulae	—	Present (reduced)	Present	Present	Present	Not given	—
"Pseudo" levator superioris maxillae	—	Absent	Present	Absent	Absent	Not given	—
Ramus lateralis accessorius	—	Present	Absent	Absent	Absent	Absent	—
External fin-ray innervation	—	Absent	Not given	Not given	Not given	Not given	—
Ramus canalis lateralis	—	Present	Not given	Present	Present	Present	—

* Character not used by Rosen and Patterson (1969) in discussions of polymixioid and percopsiform relationships.

¹ There is some question about whether †*Nematonotus* is classified as a myctophoid (Rosen and Patterson, 1969), or as a nematonotoid (Goody, 1969).

² Excluding the Macristiidae.

the necessary search to confirm this statement is sufficient indication of the existence of a close relationship between the percopsiforms and polymixioids". The attitude expressed in this last sentence is unrealistic and not suitable for determining relationships. A suggestion is made (p. 406–407) that *Sphenocephalus* as a percopsiform might have shared a common ancestor with *Berycopsis*, a polymixioid. Then on p. 437 another suggestion is made that a Cretaceous fish resembling *Sphenocephalus* is the ancestor of the Gadiformes. For both cases a number of primitive characters must be assumed to be present which are not known in any fossil or living percopsiforms.

Another study on nerve patterns is also a further attempt to define the Paracanthopterygii (Freihofer, 1970). I have commented on this study from a limited point of view (Fraser, 1972). As with musculature, specific nerves and their branches have only recently come to be investigated with the view of gaining systematic information. Nevertheless, basing his conclusions on limited material (three gobiids, *Acanthogobius*, *Bathygobius*, and *Eleotris*) and some listed evidence from McAllister (1968 : 116–117), Freihofer raises the Gobioidi to ordinal level and places it next

to the Percopsiformes in the Paracanthopterygii. The new nerve evidence involves the ramus canalis lateralis system and an accessory pectoral ventral lateralis branch of the lateral line nerve which occur together in the gobiids and percopsiform fishes examined, but not in the other spiny-rayed fishes which were studied. Conservative action perhaps would not do more than raise possible relationships at this time. Wholesale transfer of a large, diverse group into another conceptual framework based on admittedly preliminary information (Freihofer, 1970 : 216) is a weak practice. Surely, a detailed study should precede such an action. Rosen and Patterson (1969) overlooked or dismissed McAllister's suggestion (also on p. 123) of a possible relationship with the Percopsiformes for they did not examine a single gobioid.

Freihofer (1970) noted that the fin-ray nerves are internal in living percopsiforms but external on all other paracanthopterygians: that *Merluccius* has no ramus lateralis accessorius (RLA) but all other gadiform fishes examined have a well-developed system; that the RLA of *Percopsis* and *Chologaster* differs strongly from that of *Aphredoderus*, and that no group other than percopsiform fishes yet examined

has the 4b branch of the ramus canalis lateralis system; that "*Porichthys* does not have independent branches of the ramus canalis lateralis system" (p. 252) although, in the summary (p. 258, j), a well-developed RCL system is claimed for batrachoidids. Most of these differences are given without comment or interpretations of these facts.

Other conclusions by Freihofner are at odds with those of Rosen and Patterson. He believes that the batrachoidiform fishes are related to percopsiforms but says nothing about gadiform fishes, whereas Rosen and Patterson discuss a batrachoidiform-gadiform relationship with little mention of the percopsiforms. Freihofner suggests an osmeroid ancestor for the Percopsiforms instead of a ploymixioid ancestor. In other respects Freihofner's evidence supports the general concept of the Paracanthopterygii.

There are a number of crucial problems that need to be resolved before the Paracanthopterygii in its present form can be readily accepted. Some have been mentioned above. Other problems are related to the expanding of the paracanthopterygian boundaries and altering concepts.

The Percopsiformes and Gadiformes are said to be related, yet some similarities given by Rosen and Patterson (1969 : 435) such as (3) similarity of skull roofs (their text figs. 28 and 50) between fossil forms and (8) pterospheonoid-paraspheonoid contact which is also common in other groups lacking the basisphenoid, i.e., blennies and some percoids, are questionable. Further, none of the percopsiforms has been found with more than six branchiostegals while all gadiform fishes have at least seven branchiostegals.

The concept of the Gadiformes is strained by the addition of the ophidioid fishes. The ophidioid differ from other gadiform fishes in having a separate opening in the pars jugularis for the hyomandibular branch of the facial nerve. They are the only group (apart from *Sphenocephalus*) to possess a supramaxilla, the only gadiform to possess a pelvic spine,

and the only gadiform (except for some macrouroids) to have a foramen completely within the scapula. Rosen and Patterson (1969) have argued that these differences are not enough to preclude inclusion in the Gadiformes. They further suggest that the Ophidioidei are as ancient as the Gadoidei and definitely a separate lineage of long standing. Nonetheless, in view of these and other questions raised herein, the ophidioid-gadoid relationship should be accepted only as a tentative hypothesis. Gosline (1968 : 28) widely separates the two groups and McAllister (1968 : 115) states that the gadiform fishes could not have given rise to ophidioid fishes, listing reasons, but relates the groups.

Some discussion, at this point, about the pars jugularis is desirable. Patterson (1964 : 434–438, fig. 96) outlined the trend of simplification of the trigeminal chamber in elopoids, ctenothrissoids, berycoids, and percoids. Gosline (1968 : 23–24) pointed out that a more simplified system occurs in the Gadiformes (also see Rosen and Patterson, 1969 : 430–431). Rosen and Patterson (1969 : 422) note that certain cottoid fishes also possess this typically gadoid feature but that it is obviously an independent development. The main point here is that the more complex system present in the ophidioid fishes cannot be derived from the gadiform condition. Derivation of the batrachoidiform-lophiiform lineage suffers from this same weakness. The Gadiformes are seen here as a more or less deadend group. One has either to postulate characters not known to occur in the Gadiformes or fall back on a percopsiform fish in order to derive groups with the more complicated system in the pars jugularis. Outside a perciform context the ophidioid fishes are best treated as an order (see McAllister, 1968 : 114–116).

With regard to the more specialized orders Batrachoidiformes, Lophiiformes, and Gobiociformes, some evidence is still equivocal for relating these three groups, especially the Gobiociformes (no LMS, fused ural centra).

Nor is the evidence strong for suggesting that the Batrachoidiformes are related to the Gadiformes. All of these groups are not yet well known anatomically and character trends are only preliminary. Other authors, Gosline (1968 : 7) and Böhlke and Robins (1970), believe that the Callionymoidei must go with the gobiesocoids. I believe that the Notothenioidei should be examined with regard to these two groups (See Gosline, 1968). No real effort has been made to test the hypothesis suggested by Gosline.*

Little can be said about whether *Indostomus* is incorrectly placed in the Paracanthopterygii, as Banister (1970 : 204) admits a great deal of speculation. The presence of dermal armor raises much doubt concerning any relationship with the Gobiesociformes or Batrachoidiformes. If any groups outside the Gasterosteiformes are remotely related to the Indostomidae it may be the Agonidae or Pegasidae, neither of which is well known anatomically (see Banister, 1970; McAllister, 1968 : 167). The Indostomidae appear to be *incertae sedis* for the moment if they are not considered to belong in the Gasterosteiformes. Banister's arguments (p. 197-198) for withdrawal to another order are not compelling but indicate that *Indostomus* has few of the primitive characters of gasterosteoids and few of the syngnathoid characters. He only mentions dermal armor, snout shape, and an elongated mandible as similarities. Nearly all the reasons for removal are negative (loss) characters and thus not very satisfying.

Although I agree with Freihofner (1969 : 858-859) that function or ecology is not needed for determination of morphological homologies, these unneeded factors are important when one begins to compare and interpret various points of evolution. What are the

effects that differing environmental demands (pelagic, burrowing) may impress on these systems. Within the paracanthopterygian concept of general unifying characters, I have noted, with increasing uneasiness, that obvious exceptional convergent patterns are tending to be described most frequently in other benthonically oriented fishes. (1) Examples for the LMS can be found in the Cyclopteridae (Rosen and Patterson, 1969), Sciaenidae, Gobiidae, Microdesmidae (Freihofner, 1970), and the Amiidae (Rosen and Patterson, 1969). (2) In the "pseudo" LMS group are the Gadopsidae, Mugiloididae, Polymixiidae, and members of the Blennioidei (Rosen and Patterson, 1969). (3) External fin-ray nerves are present in the Liparidae, Cottidae, and Stichaeidae (Freihofner, 1970). (4) The strong resemblance of the RLA patterns present in the Gobiesocidae, Cottidae, and Liparidae (Freihofner 1963). (5) The specific similarity of *Anguilla*, *Nemacheilus*, *Parupeneus*, *Brotula*, and *Percopsis* in having the cranial exit of the RLA through the facial foramen beside the hyomandibular trunk (Freihofner 1970). (6) The strong tendency for these fish (mostly benthic) with depressed or slightly depressed neurocrania to lack the basisphenoid and have contact between the parasphenoid and pterosphenoid or frontal bones. (7) Simplification of the foramina of the trigeminal chamber occurs in the Cottidae and in the Gadiformes. Whether all of these apparent similarities are interrelated to similar environmental demands remains in doubt. If some of these characters are fundamental environmental requirements for biological success then their importance for determining phyletic relationships is greatly diminished. Present studies do not permit an unequivocal decision. Several long term studies by a number of workers will be necessary before some of these complex problems will be resolved.

One remaining problem, that of a possible ancestor, may be partially answered here. Three different groups have been proposed: osmeroids, polymixioids, and myctophoids. Based on information in Table 2, some com-

* A paper dealing with the possible notothenioid derivation of gobiesocoid (including callionymoids) fishes by William A. Gosline (1970) is relevant to the last few sentences. I was unaware of this paper until after this manuscript was submitted in March 1972.

ments are in order. Freihofer (1970) proposed that some osmeroids gave rise to the percopsiform fishes. There are several difficulties in accepting this proposition. The Osmeroidei, as conceived by Weitzman (1967), do not have a free second ural centrum, they lack ectopterygoid teeth, have only one supramaxilla and a large number of predorsals (supraneurals). They show no tendencies toward the development of the modern trends present in the spiny-rayed groups. The last objection is probably more important than the former ones. To carry this problem further, the Percopsiformes as conceived by Rosen and Patterson (1969) cannot possibly give rise to the Beryciformes as Freihofer suggests (also see McAllister, 1968 : 123) for the Percopsiformes lack two supremaxillae, the orbitosphenoid, basisphenoid, epineural ribs, an infraorbital shelf, and have fewer branchiostegals, separate exoccipital condyles, two epurals, only two openings in the pars jugularis, and reduced number of epipleural ribs. The alternative possibility of the Percopsiformes being a direct ancestor of the Perciformes is not as easily refuted, but seems unlikely, for the Percopsiformes lack the basisphenoid and an infraorbital shelf and have one less epural and branchiostegal ray. Tendencies within the group also indicate, as Rosen and Patterson (1969) state, changes away from perciform characters.

The polymixioids and myctophoids have many fewer objections as possible ancestor groups to the Percopsiformes. The basic problems with the polymixioids are that none is known to have an adipose fin or a pelvic splint and all have an infraorbital shelf, orbitosphenoid, and basisphenoid (showing no tendency to lose the last three characters). Whereas, the myctophoids do possess an adipose fin and a pelvic splint, lack the infraorbital shelf (except the Myctophidae) and do show the tendency to lose the orbitosphenoid and basisphenoid. Further, the myctophoids, in addition to other parallelisms, show the tendency to develop a true levator superioris

maxillae which is not present in polymixioids (Rosen and Patterson, 1969 : 450–451). For these reasons I favor a myctophoid ancestry for the percopsiform fishes (Fig. 1) (also see Goody, 1969 : 228–229). The polymixioids are viewed as part of the berycoid radiation without a close relationship to percopsiform fishes.

Much remains to be clarified and supported with additional evidence concerning the integrity of the various acanthopterygian groups and their origins. Two relatively recent systems, myology and nerve patterns, bring unused characters to bear on this problem. These systems may provide compelling information but present data are small and the interpretations are subject not only to this error but also to nature's own tricks of convergences not yet discerned. Equal weight cannot yet be accorded present myological and nervous evidence with that of osteology. Fortunately, controversy does tend to stimulate work in the field. In my opinion, much data must be added and analyzed and existing data re-analyzed—hence the critical nature of this review. A return to Regan's system is not advocated, but this portion of the newer system has not yet withstood repeated examinations that time will bring.

Acknowledgments

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(The J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, South Africa)

真骨魚類の Paracanthopterygii 上目に関する考察

T. H. Fraser

硬骨魚類真骨魚類の分類において近年問題になっている Paracanthopterygii 上目について、最近の研究を比較検討しながら考察を行った。その結果、一応この上目を分類学上の一つのたき台とすることの意義を認めるが、単系的自然群とは認め難い。なおギンメダイ類と *Indostomus* 類は Paracanthopterygii 上目からとり除かれるべきである。ウバウオ類・ハゼ類・アシロ類を一応仮にこの上目に含めるとしても、これ等の魚と他のメンバーとの近縁関係を立証する強力な事実は現在のところ発見されていない。アシロ類はタラ目から除かれるべきである。*Notothenia* 類とネズボ類の2グループも更に研究する必要がある。筋肉や神経系の解剖結果を、類縁関係推察の資料として、深く検討することなしに用いるのには反対である。これ等のデータの系統学的意味はよく判っておらず、適応に伴って起る変化やその可塑性はまだ詳細には理解されていないのが現状である。

(The J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, South Africa)

投稿者へのお願い

編集の実務にたずさわって気がついたことを書いてみます。なおこの欄は 20 巻 1 号にもあります。

文章一般について。長い文章は主語と述語や修飾語と被修飾語の関係等があいまいになるので、可能な限り避けて下さい。文章毎に主語と述語を確認するのは良い習慣だと思います。

日本語について。but の意味で使われる場合を除き、接続詞「が」の使用を避けて下さい。これは長い文章を避けることにも関連があります。

英文について。the former, the latter, that, this, it などを用いる時は、ごく慎重に願います。先行詞の候補が 2 つも 3 つもあって、意味がとりにくいばかりか、誤解を招きかねない例が多々見受けられます。重複や稚拙さをおそれるよりも「何をいいたいのか」が不明なるのをおそれて下さい。respectively を最後にくっつけて、幾つかのことがらを併列する表現も慎重に願います。

日本の地名について。英文部分（和文論文の場合は abstract または図や表の説明）に緯度、経度を入れることを勧めます。

なみがたの使用について。A から B までという場合は、ハイフンやダッシュでなく A~B を使うことにしました。~は数学記号マイナスとも紛れることが

なく良い記号だと思っています。引用文献のページや図等に用いるのも~です。

謝辞について。相手の所属と姓名の名の方も略さずはっきり書いて下さい。

引用文献欄について。雑誌名を日本語で表示する場合略さないで下さい。魚雑ではなく、魚類学雑誌です。論文のページの他に figs. や pls. を忘れず表示して下さい。著者が三人以上の場合、文中では A ら（和文論文の場合）A et al.（英文の場合）と引用しますが、引用文献欄には A・B・C・D.（和文の場合）A, B, C, and D.（英文の場合）というように全ての著者を略さずに表示して下さい。（Y. T.）

訂正・Errata

魚類学雑誌 19 巻 4 号。233 頁の Table 1. Ceratioidei ← Ceratioidei. 237 頁の Table 2. Berycoidei の行の principal caudal rays は 10+9 ← 9+9. 239 頁の左列。17 行。polymixioid ← ploymixioid.

Japanese Journal of Ichthyology 19(4) p. 233. Table 1. Ceratioidei, not Ceraioidei. p. 237. Table 2. Principal caudal rays of Berycoidei are 10+9, not 9+9. p. 239. Left column. Line 17. polymixioid, not ploymixioid.

(We regret that a mix-up in communication prevented us from adequately processing the galley proof for Dr. Fraser's paper).