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Niphon spinosus: A Primitive Epinepheline Serranid, with Comments on the Monophyly and Intrarelationships of the Serranidae

G. DAVID JOHNSON

Three reductive specializations (absence of the posterior uroneural, procurrent spur and third preural radial cartilages) define the percoid family Serranidae with respect to the ostensibly polyphyletic Percichthyidae (sensu Gosline, 1966). A single innovative specialization, the presence of three spines on the opercle, indicates that the Serranidae are monophyletic. All members of the serranid subfamily Epinephelinae, comprising five tribes, share a unique modification of the first dorsal pterygiophore, seemingly a specialization for support of the elongate dorsal spine of the larvae. The enigmatic *Niphon spinosus*, placed in the Percichthyidae by Gosline (1966), and in the Centropomidae by Rivas and Cook (1968), shares the epinepheline specialization, as well as the four specializations that characterize the Serranidae. It is hypothesized that the monotypic *Niphon* is the sister group of all other epinephelines. Identification of the larva of *Niphon* could provide corroborative evidence for this hypothesis.

NIPHON spinosus Cuvier is a percoid fish inhabiting shallow marine waters along the coasts of Japan, Korea, China and the Philippines. Its chief distinctive external features are a large spine at the angle of the preopercle and robust serrations along the ventral margin of the lacrimal (Figs. 1, 2). The evolutionary affinities of the monotypic *Niphon* within the Percoidae have been the subject of some debate. Although Jordan (1923) placed *Niphon* in a monotypic family, most authors prior to Gosline (1966), treated it as a serranid (Berg, 1940; Katayama, 1959; McCully, 1961; Norman, 1966; Greenwood et al., 1966). In 1966, Gosline removed a number of genera, including *Niphon*, from the Serranidae, and placed them in the Percichthyidae.

Rivas and Cook (1968) used a phenetic analysis of 22 characters to argue that *Niphon* is more similar to the Centropomidae than to the Percichthyidae or Serranidae and, therefore, placed *Niphon* in the Centropomidae. In their comparative analysis, Rivas and Cook considered only one species of centropomid, one percichthyid and no serranids. Greenwood (1977) pointed out that because *Niphon* shares 20 of these 22 characters with some serranids, percichthyids, or both, the similarity indices have little meaning. In addition, Rivas and Cook failed to consider that centropomids are variable in some of the characters that *Niphon* allegedly shares with them. Finally, Greenwood observed that *Niphon* does not exhibit either of the char-

acters that he regarded as diagnostic for the Centropomidae (expanded second neural spine and lateral line extending to the posterior margin of the caudal fin) and concluded that the closest relatives of *Niphon* would probably prove to be among the heterogeneous assemblage of genera placed by Gosline (1966) in the Percichthyidae. The purposes of this paper are to discuss the monophyletic integrity of the Serranidae, to consider certain aspects of serranid intrarelationships, and to present evidence that *Niphon spinosus* is a primitive member of the serranid subfamily Epinephelinae.

MATERIALS AND METHODS

Osteological features were studied primarily in specimens cleared and stained for bone and cartilage, but a few specimens were stained only for bone. Where specimens were not available for clearing and staining, certain osteological characters were determined from radiographs. Various aspects of soft anatomy were examined in whole specimens.

Cleared and stained specimens of representative genera from a wide variety of perciform families were examined for comparative purposes, including all nominal genera of the Percichthyidae and the serranid subfamilies Serraninae and Epinephelinae. Only the most pertinent material, that representing the Epinephelinae and the genera herein removed from the Serranidae, is listed.

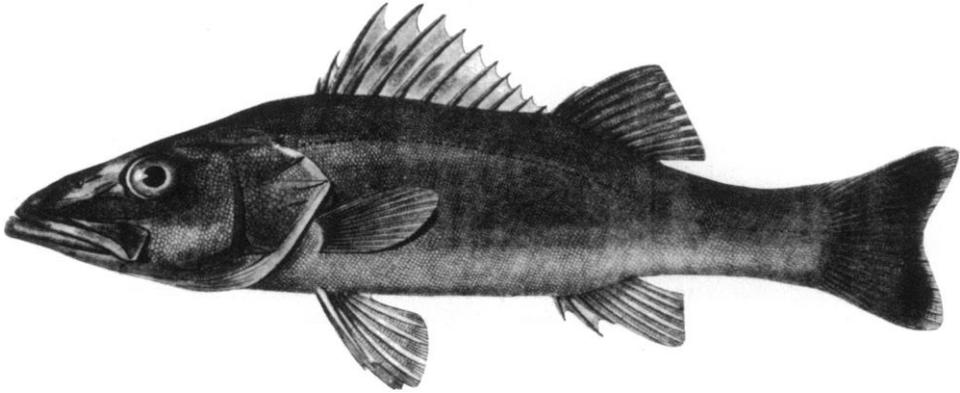


Fig. 1. *Niphon spinosus* Cuvier, 480 mm SL, Pusan, Korea (after Lindberg and Krasnyukova, 1971).

Abbreviations.—GMBL, Grice Marine Biological Laboratory, College of Charleston, Charleston, S.C.; ORI, Ocean Research Institute, University of Tokyo; RUSI, J. L. B. Smith Institute of Ichthyology, Rhodes University, South Africa; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZUMT, University Museum, University of Tokyo; C, cleared and stained; R, radiographed.

Epinephelinae.—Niphonini: *Niphon spinosus* Cuvier, ZUMT 49162, C; ORI uncat., C; USNM 57737, R. Epinephelini: *Anyperodon leucogrammicus* (Valenciennes), USNM 218817, C; USNM 22729, R; *Cromileptes altivelis* (Valenciennes), USNM 183245, R; *Epinephelus flavolimbatus* Poey, GMBL 78-132, C; *E. cruentatus* (Lacépède), USNM 218869, C; *E. inermis* (Valenciennes), USNM 8086, R; *E. itajara* (Lichtenstein), USNM 133692, R; *E. morio* (Valenciennes), GMBL 73-133, R; *E. multiguttatus* (Evermann and Radcliffe), USNM 128755, R; *E. niveatus* (Valenciennes), GMBL 76-254, C; *Gonioplectrus hispanus* (Cuvier), USNM 24952, R; *Gracila albomarginata* Randall, USNM 89985, R; *Mycteroperca phenax* Jordan and Swain, GMBL 78-132, C; *Paranthias furcifer* (Valenciennes), USNM 170020, C; *Plectropomus maculatus* (Bloch), USNM 218818, C; *Trisotropis dermatopus* (Temminck and Schlegel), USNM 177777, R; *Variola louti* (Forsk.) USNM 218820, C. Diploprionini: *Aulacocephalus temmincki* Bleeker, USNM 64640, R; USNM 22524, R; *Belonoperca chabanaudi* Fowler and Bean, USNM 217837, C; *Diploprion bifasciatum* Kuhl and van Hasselt, USNM 218889, C. Liopropomini: *Jeboehkia*

gladifer Robins, USNM 201422, R; *Liopropoma susumi* (Jordan and Seale), USNM 218726, C; *Pikea longilepis* (Garman), USNM 153602, R; *Rainfordia opercularis* McCulloch, USNM 203247, C. Grammistini: *Aporops bilinearis* Schultz, USNM 218920, C; *Grammistes sexlineatus* (Thunberg), USNM 218886, C; *Grammistops ocellatus* Schultz, USNM 218873, C; *Pogonoperca punctata* (Valenciennes), USNM 205491, R; *Pseudogramma polycantha* Bleeker, USNM 205491, C; *Suttonia lineata* Gosline, USNM 209705, C.

Incertae sedis.—*Dinoperca petersii* (Day), RUSI 76-4, C; *Hemilutjanus macrophthalmus* (Tschudi), USNM 77623, C; *Polyprion americanus* (Schneider), USNM 39897, R; *Stereolepis gigas* Ayres, SIO 68-382, C.

DISCUSSION

Monophyly of the Serranidae.—The Serranidae has historically served as a classificatory “wastebasket” within the percoids, providing a convenient pigeonhole for those generalized perch-like fishes whose relationships could not obviously be shown to lie with some other percoid family. Prior to 1966, the monophyly of the Serranidae was rarely questioned in the literature. Instead, efforts were directed toward subdividing the existing Serranidae into numerous subfamilies, usually with little suggestion as to how these might be interrelated (Jordan and Eigenmann, 1890; Jordan, 1923; Katayama, 1959; McCully, 1961).

A major advance in this regard resulted from

Gosline's (1966) attempt to redefine the limits of the Serranidae. On the basis of several shared morphological features (most of which are apparently primitive for the Perciformes) Gosline removed a number of genera and restricted the Serranidae to three subfamilies, the Serraninae, Anthiinae and Epinephelinae, and suggested that the Grammistidae forms a specialized serranid offshoot. Most of the newly excluded genera were placed in the Percichthyidae, originally erected by Jordan and Eigenmann (1890) for the South American genera *Percichthys* Girard and *Percilia* Girard. The value of Gosline's work lies not in his emendation of the Percichthyidae (which is almost certainly a polyphyletic assemblage defined solely on the basis of plesiomorphic characters) but in his restriction and redefinition of the Serranidae based on several character states that appear to be derived, at least in relation to those of the excluded genera. Although his survey of these character states was cursory and involved a relatively small portion of the total number of nominal serranid genera (for some characters he relied on Katayama, 1959, a considerably broader survey), Gosline nevertheless provided us with a testable hypothesis, i.e., that his Serranidae, "thus shorn of its accretions," represents a monophyletic family.

This hypothesis has not been seriously examined to date. Gosline's classification is in general use, but there seems to exist considerable doubt concerning the monophyly of the Serranidae. For example, Smith (1971), in his definition of the Serranidae, apparently chose not to use Gosline's work or his diagnostic characters, even though he cited Gosline's paper. More recently Greenwood (1977) referred to "the heterogeneous and aphyletic assemblage of serranid-percichthyid species." Because of this general state of doubt or confusion, I felt it would be useful to briefly review the available evidence for the definition of the Serranidae as a monophyletic family. In the following discussion, the terms Serranidae and Percichthyidae are *sensu* Gosline (1966).

An ongoing study of lower percoid phylogeny has led me to reconsider most of the characters used by Gosline and their bearing on the serranid-percichthyid problem. Essentially, this means that I have examined those characters in a broader range of genera than did Gosline, in the Serranidae, the Percichthyidae and several other percoid families. I conclude that all but a few of his characters are either too vari-

able (e.g., swimbladder projections), too subjective (e.g., relative length of postpelvic process; relative development of Baudelot's ligament), or both, to serve as valid phylogenetic indicators in these groups.

A few characters warrant discussion. Gosline pointed out that most serranids have 24 vertebrae, whereas percichthyids have 25 or more. However, anthiines have 26, the serranine *Acanthistius* Gill has 26 and occasional specimens of other serranids may have 25 or more. The phylogenetic significance of vertebral number within the percoids is difficult to evaluate. In some groups (e.g., lutjanids, sparids) it is remarkably constant, whereas in others, there is considerable intragroup variation, and there is no clear indication as to what might be the primitive percoid number. Cases of departure from the typical number by only one member of a family are also known.

Gosline noted that all his excluded genera have several trisegmental pterygiophores (those with separate medial radials) at the posterior portion of the median fins, whereas serranids have none, the medial radial apparently having fused to the proximal radial in all pterygiophores. His survey of this character in the serranids was inadequate, for a number of epinepheline genera have trisegmental pterygiophores, and grammistines (which he considered serranid offshoots) have more than most percichthyids. Nor does the configuration of the predorsal bones (one to three predorsals, the last interdigitating between the first and second neural spines) serve to define the family, because, as Gosline pointed out, the Serraninae is an exception, exhibiting the apparently primitive predorsal pattern (three predorsals, the last between the second and third neural spines) found in most percichthyids.

One of Gosline's reductive characters does seem to be consistent with his classification, although its significance is lessened by the fact that it has probably arisen independently a number of times in percoid evolution. This is the loss of the small posterior uroneural pair or its fusion to the larger anterior pair (Gosline, 1966: Fig. 10). All of Gosline's serranids have only one pair of uroneurals whereas most of the excluded genera have two.

Johnson (1975) supported Gosline's classification in reporting that the Serranidae lack a procurrent spur and that all but two genera (*Maccullochella* Whitley and *Niphon*) of the percichthyids examined have a well-developed pro-

current spur. This spur projects ventrally from the base of the posteriormost ventral procurrent caudal ray and is usually accompanied by a basal foreshortening of the preceding procurrent ray. Presence of this condition was interpreted as primitive for the Perciformes, suggesting that absence of the spur in the serranids represents a derived condition with respect to the percichthyids. The serranids are not unique, however, in lacking the procurrent spur. Its absence in a number of other percoid families may be the result of independent losses (Johnson, 1975).

Another apparently derived character state in serranids is absence of the third preural radial cartilages. In the Percichthyidae and many other lower percoid families (including the Centropomidae, Ambassidae, Apogonidae, Centrarchidae, Kyphosidae and Girellidae), a radial cartilage of variable size lies along the anterior margin of the distal ends of neural and haemal spines of the third preural centrum, just proximal to the bases of the procurrent caudal rays. This cartilage is also found in the Beryciformes, and its occurrence within the Perciformes seems to represent the primitive condition. Absence of this cartilage, here interpreted as the derived state, characterizes a number of percoid families, including the Serranidae. Again, it seems likely that loss of this cartilage has occurred independently several times.

Thus, there are at least three derived reductive character states that are consistent within the Serranidae (absence of a posterior uro-neural, absence of the procurrent spur and absence of a third preural radial cartilage). Because none of these apomorphous reductions is unique to serranids, even their co-occurrence here does not represent unequivocal evidence for serranid monophyly. There may well be non-serranid perciforms that also have these three structures absent. Nevertheless, their absence in serranids at least suggests the possibility of descent from an immediate common ancestor that had lost them and defines the family with respect to the Percichthyidae.

A single, apparently uniquely derived, innovative specialization has been identified for the Serranidae. As noted by Gosline (1966) all serranids share the presence of an opercular spine below the primary spine, making a total of three spines on the opercle (Fig. 2B). In almost all other percoids there are only two opercular spines, the primary one and a smaller one above this (excluding, as did Gosline, such genera as

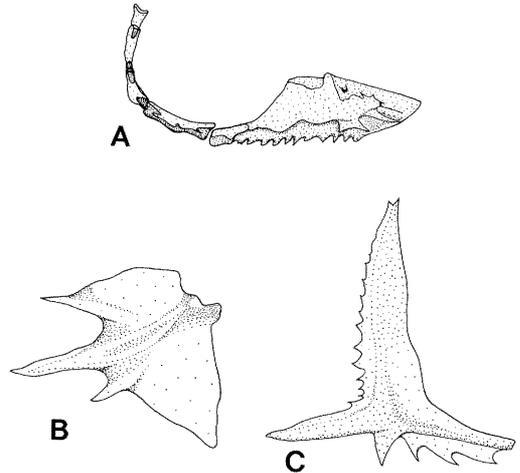


Fig. 2. *Nippon spinosus* (ZUMT 49162), right side. A) Infraorbital series. B) Opercle. C) Preopercle.

Archoplites Gill and *Howella* Ogilby where the primary spine has apparently splayed out to create many smaller spines, a condition in no way comparable to that of the serranids). The presence of three opercular spines is an uncommon perciform feature and I know of only one other percoid that exhibits it. The monotypic genus *Sphyraenops* Poey (= *Scombrosphyraena* Fraser and Fourmanoir) has an additional opercular spine below the main spine. This third spine is apparently independently derived, as *Sphyraenops* does not exhibit any of the other three serranid specializations mentioned above but instead shares at least one derived feature with the Epigonidae, rod-like elongation of the typically biconcave cartilaginous meniscus that lies between the vomer and the maxillary head. Other epigonids have only two opercular spines.

One other perciform family, the Trachinidae, has three opercular spines arranged in a fashion similar to that of the Serranidae. This is probably an independently derived condition but could indicate a sister group relationship with the serranids. Future investigations of trachinoid fishes should address this question. Currently, the Trachinidae are placed in the suborder Trachinoidei, the other members of which do not possess three opercular spines. Gosline (1968) noted several features that trachinids share with other members of his superfamily Trachinoidea (Uranoscopidae, Leptoscopidae and Dactyloscopidae). These fea-

tures include a specialized ridge on the pelvic girdle, a hook-like process on the posterior rim of the hyomandibular, firmly connected and expanded circumorbital bones, and an enlarged scapular foramen. Trachinoids also have long soft dorsal and anal fins, pelvic fins placed well in advance of pectorals, reduced caudal fin ray counts and dorsally placed eyes. It thus seems likely that the three opercular spines of trachinids arose independently of those of serranids, perhaps in association with the opercular poison gland.

The Serranidae may currently be defined, then, on the basis of four shared specializations, 3 reductive and 1 innovative, the latter offering the strongest evidence in support of the hypothesized monophyly. Gosline noted that the family thus delimited "is restricted to the subfamilies Serraninae, Epinephelinae, and Anthiinae (except *Callanthias*), of Jordan and Eigenmann (1890)." This statement is somewhat misleading because Jordan and Eigenmann included in their Epinephelinae *Polyprion* Oken and *Stereolepis* Ayres, two genera which Gosline correctly excluded from the Serranidae. *Hemilutjanus* Bleeker, also considered an epinepheline by Jordan and Eigenmann, and *Dinoperca* Boulenger (= *Centrarchops* Fowler), treated as a serranid by most authors, should also be excluded. The affinities of these four genera are unclear, but none possess any of the four specializations diagnostic of the Serranidae.

The classification of Jordan and Eigenmann (1890) is clearly outdated and includes only European and American genera; a complete allocation of genera to the Serranidae and an understanding of their interrelationships can come only with a worldwide revision of the family, an undertaking not likely to be realized in the near future. Despite this, elaboration of certain aspects of serranid intrarelationships is warranted and will help to clarify my placement of *Nippon*.

Serranid intrarelationships.—The most recent analysis of serranid intrarelationships is that of Kendall (1976), based on a single character complex, the predorsals and associated bones (Fig. 3). Kendall agreed that Jordan and Eigenmann's three subfamilies are valid; he combined the liopropomines and the grammistids and pseudogrammids of Gosline (1960) as a fourth serranid subfamily, the Grammistinae.

Serranines have three predorsal bones and bear two supernumerary spines on the first dor-

sal pterygiophore (Fig. 4), both common percooid features. Supernumerary spines are those which have a secondary or non-serial association with the pterygiophore on which they are borne. Using the formula of Ahlstrom, Butler and Sumida (1976) the pattern is 0/0/0+2/1+1/. Within the Anthiinae, Kendall found two patterns—0/0+0/2/1+1/ and 0/0/2/1+1/, the third predorsal presumably having been lost in the latter configuration. Kendall considered the serranines and anthiines to form one lineage within the Serranidae and the epinephelines and grammistines to form another.

Although the epinepheline lineage can be clearly delineated, as discussed below, limits and relationships of the serranine-anthiine line await further clarification. The Serraninae cannot be defined on the basis of the predorsal pattern alone since this pattern is shared by many lower percoids. The two patterns seen within the Anthiinae are probably derived with respect to that of the serranines; however, McCully (1961) showed that although most genera now placed within the Anthiinae share a unique scale morphology, some have scales that are quite similar to those of the Serraninae. Additional morphological investigations will be required to resolve the limits of these two subfamilies.

More pertinent to the problem at hand (the placement of *Nippon*) is the other line of divergence, the epinepheline-grammistine lineage, which Kendall defined by loss of the posterior predorsal and of the first dorsal spine. All members of this group have no more than two predorsals and bear no more than one supernumerary spine on the first dorsal pterygiophore (Figs. 3, 5). Thus, the epinephelines (of Jordan and Eigenmann), the grammistids, the liopropomines (including *Rainfordia*) and the pseudogrammids were regarded as constituting a monophyletic group. Actually, neither loss of the third predorsal (also absent in anthiines) nor loss of the first dorsal spine is unique among percoids, and the shared absence of both structures does not categorically demonstrate monophyly. Although I concur with Kendall's treatment of this lineage as monophyletic, I base this conclusion on an additional synapomorphy, a unique modification of the first dorsal pterygiophore.

In his characterization of the epinepheline-grammistine lineage, Kendall noted that the grammistines have the additional specialization of a uniquely shaped first dorsal pterygiophore (Fig. 3). He suggested that the thin, elongate

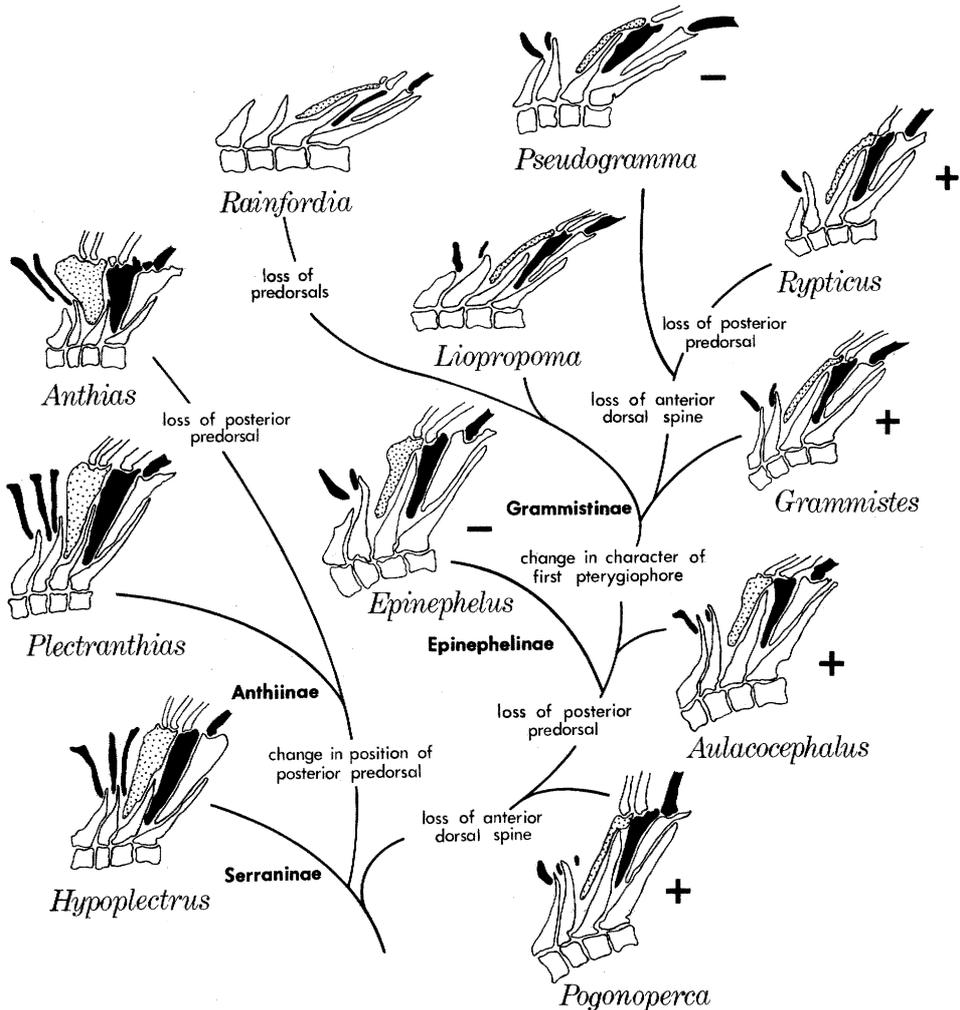


Fig. 3. Scheme of evolutionary relationships in some serranid fishes based on predorsal and associated bones (Kendall, 1976: Fig. 1). Predorsal bones solid; first pterygiophore stippled; second pterygiophore and its serially associated spine solid. Presence or absence of skin toxin grammistin indicated by + or - in those taxa examined for it.

grammistine pterygiophore was probably related to the support of the flexibly elongated second or second and third dorsal spines which are characteristic of the larvae. Larvae of the less specialized epinephelines, the groupers, also have a greatly elongated second dorsal spine (Fig. 6), although the general appearance of the first pterygiophore in these fishes is not particularly unusual.

On further examination, I have found that the first dorsal pterygiophore of all members of Kendall's epinepheline-grammistine line is uniquely modified in having no autogenous dis-

tal element (Fig. 7B, C). This element has either been lost or fused to the posterior portion of the proximal-medial element. The typical percoid condition is shown in Fig. 8A. The configuration of the posterior portion of this modified pterygiophore resembles that of a distal element in having a small hook-like process that projects through the foramen in the base of the serially corresponding spine, a condition that supports the hypothesis of fusion of the distal element rather than its loss. There is, however, no evidence of ontogenetic fusion (Fig. 6), and in Kendall's more primitive epinephelines, the

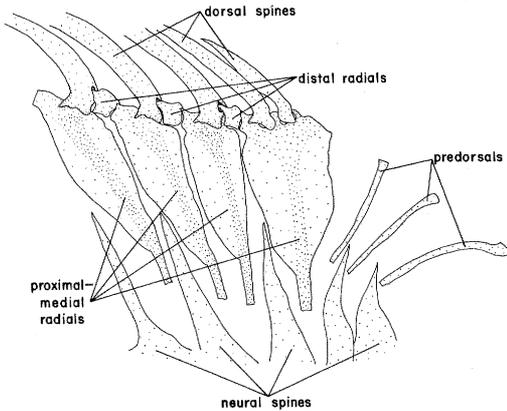


Fig. 4. *Centropristis striata* (GMBL 72-417), right side. Predorsal bones and anterior dorsal pterygiophores.

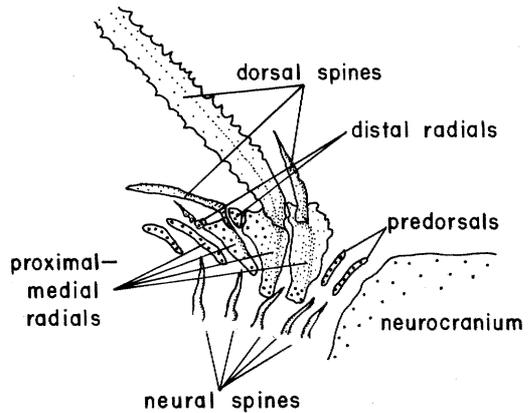


Fig. 6. Predorsal bones (cartilaginous) and anterior dorsal pterygiophores (first two ossified) of larval *Epinephelus* sp. (8 mm SL), right side. Second dorsal spine extends to three times length shown.

close approximation of the first and second pterygiophores relative to those remaining would seem to indicate loss of the distal element, or at least extreme reduction prior to fusion. In any case, whether lost or fused, the absence of an autogenous distal element and associated modification of the first dorsal pterygiophore is a specialization unique to the epinepheline-grammistine lineage, one undoubtedly related to support of the extremely elongate spine in the larvae. It probably serves no special function in the juvenile or adult.

Whereas Kendall's delineation of a monophyletic epinepheline-grammistine line appears

valid, his analysis of relationships within the lineage is less convincing, particularly his placement of the genus *Pogonoperca* (Fig. 3). This analysis involved only characters directly associated with the predorsal-dorsal pterygiophore complex. These characters are, in every case, reductive ones associated with a complex which had already undergone considerable reduction at the base of the lineage. Given the possible instability of such a complex it would seem that continued reductions and losses of component elements might be likely to occur independently within the group and thus should not necessarily be used as the sole transformation series on which to base a phylogeny. Consideration of additional morphological features indicates that the component genera of Kendall's epinepheline-grammistine lineage (hereafter treated as subfamily Epinephelinae) can be assigned to one of several ostensibly monophyletic tribes (Table

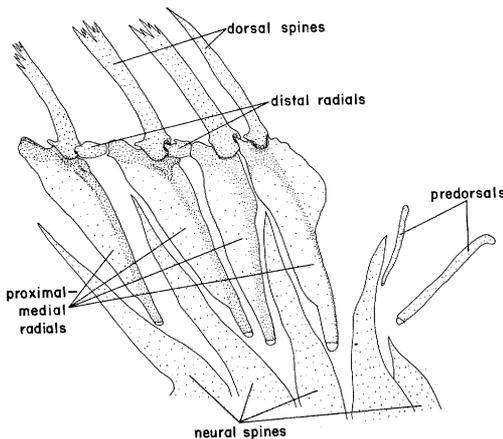


Fig. 5. *Mycteroperca phenax* (GMBL 78-132), right side. Predorsal bones and anterior dorsal pterygiophores.

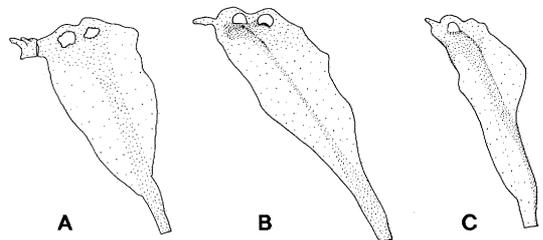


Fig. 7. First dorsal pterygiophore, spines removed. A) *Centropristis striata* (note free distal). B) *Niphon spinosus*. C) *Mycteroperca phenax*.

TABLE 1. ALLOCATION OF GENERA TO TRIBES OF SUBFAMILY EPINEPHELINAE.

| | |
|---------------|--|
| Niphonini | — <i>Niphon</i> Cuvier and Valenciennes |
| Epinephelini | — <i>Anyperodon</i> Gunther; <i>Cromileptes</i> Swainson; <i>Epinephelus</i> * Bloch; <i>Gonioplectrus</i> Gill; <i>Gracila</i> Randall; <i>Mycteroperca</i> Gill; <i>Paranthias</i> Guichenot; <i>Plectropomus</i> Oken; " <i>Trisotropis</i> " <i>dermopterus</i> ** (Temminck and Schlegel); <i>Variola</i> Swainson. |
| Diploprionini | — <i>Aulacocephalus</i> Temminck and Schlegel; <i>Diploprion</i> Kuhl and van Hasselt; <i>Belonoperca</i> Fowler and Bean. |
| Liopropomini | — <i>Jeboehlkia</i> Robins; <i>Liopropoma</i> Gill; <i>Pikea</i> Steindachner; <i>Rainfordia</i> McCulloch. |
| Grammistini | — <i>Aporops</i> Schultz; <i>Grammistes</i> Bloch and Schneider; <i>Grammistops</i> Schultz; <i>Pogonoperca</i> Gunther; <i>Pseudogramma</i> Bleeker; <i>Rypticus</i> Cuvier; <i>Suttonia</i> Smith. |

* Including subgenera *Epinephelus*, *Promicrops*, *Cephalopholis*, *Dermatolepis* and *Alphistes* after Smith (1971).

** This Japanese species is currently the only one referred to *Trisotropis* Gill, which is a junior synonym of *Mycteroperca* (type species *guttatus* Schneider = *venenosa* Linnaeus). Examination of specimens of this species indicates that it is a distinct genus, and should therefore be renamed.

1) and suggests an alternate hypothesis regarding the placement of *Pogonoperca*.

In Kendall's scheme (Fig. 3), the epinepheline lineage is composed of two subfamilial groupings, Epinephelinae* [Hereafter all subfamilial categories followed by an asterisk are sensu Kendall. Subfamilial and tribal categories not so marked refer to the proposed classification (Table 1).] and Grammistinae* (the latter including liopropomines and pseudogrammids). Three of the genera he examined, *Pogonoperca*, *Diploprion* and *Aulacocephalus* (representative of itself and *Diploprion* in Kendall's diagram) were not included in either subfamily, but were placed as early offshoots on the line leading to these two groups. Kendall cited as a hallmark of the grammistine* line the thin and elongate character of the first dorsal pterygiophore (in other serranids it is relatively stout). The absence of this uniquely modified pterygiophore, the absence of a highly modified nasal rosette, and the higher dorsal spine number led Kendall to exclude *Aulacocephalus* and *Diploprion* from the Grammistinae* despite their possession of the skin toxin grammistin. These two genera, together with *Belonoperca* (not considered by Kendall) are here considered to comprise the monophyletic Diploprionini, based on their common possession of rugose areas on the neurocranium and infraorbitals and a unique scale type (described by McCully, 1961, for *Aulacocephalus* and *Diploprion*).

A major discrepancy in Kendall's scheme is his placement of *Pogonoperca*. As noted earlier, the epinepheline-grammistine* lineage is characterized by the absence of the third predorsal. The exception is the genus *Pogonoperca*, in which there is a small nubbin of bone in the usual

position of the third predorsal. The presence of this "third predorsal" led Kendall to treat *Pogonoperca* as the most primitive member of this lineage (and thus well separated from his Grammistinae*). Because *Pogonoperca* possesses grammistin, this scheme would require that the toxin was present primitively, and was secondarily lost in the Epinephelinae* while being retained in *Aulacocephalus*, *Diploprion* and the Grammistinae*. This conclusion is untenable when additional characters are considered, for it is clear that *Pogonoperca* is a member of the more specialized Grammistini. It shares with all other members of that tribe a nasal rosette with a single row of longitudinally oriented lamellae, specialized preopercular spine configuration, loss of articulation between the third and fourth dorsal pterygiophores, reduced number of procurrent rays and increased number of trisegmental pterygiophores in the median fins. In addition, it shares with the grammistine genera *Rypticus*, *Grammistes* and *Grammistops*, modified cycloid scales (McCully, 1961) and the presence of the toxin grammistin not only in the epidermis (as in the Diploprionini) but also in flask-shaped dermal glands (Randall et al., 1971). Biochemically, the grammistin of *Pogonoperca* is more like that of *Grammistes* than that of *Aulacocephalus* or *Diploprion* (Oshima et al., 1974). Finally, *Pogonoperca* exhibits the grammistine hallmark, a thin elongate first dorsal pterygiophore. The evidence clearly indicates that *Pogonoperca* cannot be placed at the base of Kendall's epinepheline-grammistine* line, but belongs in the well-defined tribe Grammistini. The third predorsal is most parsimoniously interpreted as secondarily acquired.

Kendall considered *Liopropoma* (including *Je-*

boehlkia and *Flagelloserranus*), *Pikea* (not shown in his diagram) and *Rainfordia* to be closely related and placed them as what might be considered the sister group of his remaining grammistines*. This seems reasonable because these genera (tribe Liopropomini) share a distinctive scale type (McCully, 1961), a hook-like extension of the posteroventral corner of the maxillary and a subocular shelf extending from more than one infraorbital. The Liopropomini share with the Grammistini an elongate nasal rosette, thin curved first dorsal pterygiophore and reduced number (1–3) of pyloric caeca.

Although synapomorphies of adult Epinephelini have not been identified, monophyly of this tribe is evidenced in the unique larval type shared by the component genera. All larval Epinephelini are characterized by robust serrations on the elongate second dorsal, pelvic and preopercular spines and a distinctive pigment spot on the caudal peduncle (Kendall, 1979; Johnson and Keener, in press).

A complete phylogenetic analysis of the subfamily Epinephelinae is beyond the scope of this study. For reasons discussed above, I believe the classification proposed here represents an improvement over the existing scheme based on available evidence. In addition, it provides a clear and readily testable hypothesis. Justification for the single remaining tribe, Niphonini, is discussed below.

The relationships of Niphon.—It is apparently a misunderstanding of the limits of the Serranidae and its monophyly that has resulted in the confusion associated with the relationships of *N. spinosus*.

The phenetic approaches of both Gosline (1966) and Rivas and Cook (1968) led them to dismiss the significance of the unique specialization shared by *Niphon* and the serranids (three opercular spines). Gosline argued that *Niphon* could not be a serranid because, unlike all other serranids, it has a serrated lacrimal. This autapomorphic feature, however, does not preclude serranid affinities. Rivas and Cook, on the other hand, were more concerned with the overall similarity of *Niphon* to centropomids based on a subjectively chosen suite of characters, most of which are primitive ones and none of which is unique to the centropomids.

Greenwood's (1977) failure to recognize the serranid affinities of *Niphon* clearly resulted not from his methodology, but from his reluctance to accept the monophyly of the Serranidae. He

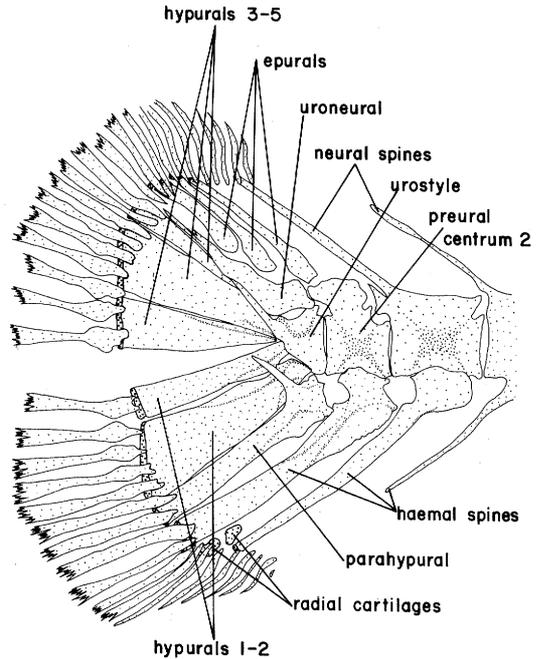


Fig. 8. Caudal skeleton of *Niphon spinosus* (ZUMT 49162), right side.

believed that *Niphon* would probably eventually be shown to be closely related to some, if not all, of Gosline's percichthyids. Greenwood was apparently also misled by his interpretation of the caudal skeleton. He reported that *Niphon* has two uroneurals and thus concluded that its "caudal skeleton is virtually identical with that in the percichthyids" he had examined (all serranids have only one uroneural). However, as Greenwood himself noted, these "two uroneurals" are fused basally, and thus, I believe, should be interpreted as one. There is no reason to believe that the distal processes on the uroneural actually represent remnants of two uroneurals. One specimen I examined (Fig. 8) showed two of these processes on one side and three on the other. They are most likely secondary in origin.

Niphon possesses all four derived characters that are diagnostic of the Serranidae. Besides the three opercular spines (Fig. 2) and single uroneural, the procurrent spur is absent, and there are no radial cartilages anterior to the third preural neural and haemal spines (Fig. 8). On this basis alone, there is good reason for the placement of *Niphon* within the Serranidae. In

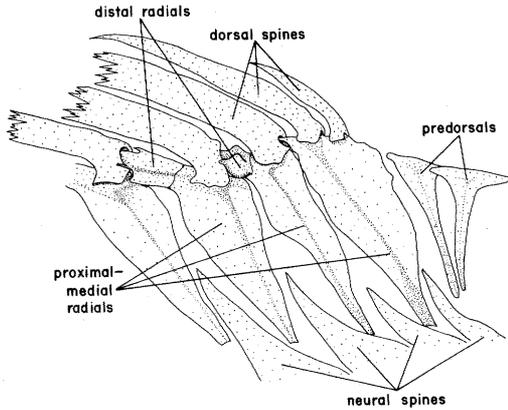


Fig. 9. *Niphon spinosus* (ZUMT 4916), right side. Predorsal bones and anterior dorsal pterygiophores.

addition, *Niphon* shares the uniquely modified first dorsal pterygiophore of the serranid subfamily Epinephelinae. As illustrated in Fig. 7B, this pterygiophore has no autogenous distal element and its posterior portion bears a small process that projects through the foramen in the base of the serially corresponding spine. It will be noted that in *Niphon* (Fig. 9), the spine that has serial correspondence with the first dorsal pterygiophore is the third rather than the second. This is because the first pterygiophore bears two (rather than one) supernumerary spines. In the Epinephelini there is only one supernumerary spine and in some genera of the more specialized epinepheline tribes (e.g., the Grammistini) there are none. In these cases the serially corresponding spine of the first dorsal pterygiophore (the one which is strongly produced in the larvae) is the second or first respectively. Because two supernumerary spines is the most common percoid condition, and is found in other serranid subfamilies, *Niphon* appears to be primitive in this feature with respect to the other epinephelines. An additional (although not unique) specialization that *Niphon* shares with the epinephelines is the presence of only two predorsal bones. Here again, the robust nature of these two bones is a primitive condition. The other epinephelines have considerably reduced predorsals (Figs. 3, 5).

Niphon differs from other serranids in several respects (presumably autapomorphies of the genus). The predorsal pattern (0+0/2/1/1/) is unusual for percoids and is unlike that of any

other serranid. *Niphon* also differs from other serranids in having an unusual dorsal fin count (XIII, 11), a higher vertebral number (30 vs 24–26), a serrated lacrimal and an enlarged preopercular spine (characteristic of many percoid larvae, including those of the Epinephelini, but uncommon in adults). These character states could be primitive ones, but this does not seem likely because the affinities of *Niphon* lie with the specialized Epinephelinae, and the more primitive Serraninae do not possess them. As autapomorphies, these characters support the monophyly of the monotypic tribe Niphonini. Absences of the third supernumerary spine and the third predorsal bone in the remaining epinepheline tribes unites them as a monophyletic group. *Niphon*, being primitive in these two features, is hypothesized to be the sister group of all other epinephelines. Corroborative evidence for this hypothesis could be provided through identification of the larva of *N. spinosus*, to date unknown. This evidence relates to the presence, in *Niphon*, of two supernumerary spines on the first dorsal pterygiophore. If the relationships of *Niphon* (and the function of the modified first dorsal pterygiophore) are as postulated, its larva should have an elongate dorsal spine as do other epinepheline larvae. However, other epinephelines always have the first or second spine elongate, whereas in *Niphon* these first two spines are supernumerary and should not be produced. The larva of *N. spinosus*, then, should have an elongate third dorsal spine.

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