

Niphon spinosus, a Primitive Epinepheline Serranid: Corroborative Evidence from the Larvae

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Abstract The larvae of *Niphon spinosus* are described based on seven specimens (4.2 mmNL–7.2 mmSL) collected in the East China Sea during October and November of 1980–1984. The morphology of these larvae, in particular the elongate third dorsal spine and the configuration of the developing anterior dorsal pterygiophore complex, corroborates the hypothesis that *Niphon* is a member of the serranid subfamily Epinephelinae. Within the Epinephelinae larval *Niphon* resemble most closely those of the tribe Epinephelini, but differ in several respects, such as the absence of serrations on the dorsal, pelvic and preopercular spines. Using outgroup comparison as a basis for character polarization, a character analysis demonstrates that it is most parsimonious to hypothesize that *Niphon* is the sister group of all other epinepheline tribes rather than the sister group of the tribe Epinephelini.

Niphon spinosus Cuvier is a bass-like percoid inhabiting shallow to relatively deep (>200 m) waters along the coasts of Japan, China, Korea and the Philippines. In Japan, where it is known as “ara”, *N. spinosus* is a highly prized food-fish and is seen frequently, though not abundantly, in the markets from Tokyo southward. There has been little research on the life history of this species and although there is some published information on spawning times, the larvae have remained unknown.

Johnson (1983) hypothesized that the monotypic *Niphon* is a primitive member of the serranid subfamily Epinephelinae and proposed that its larvae might resemble those of the tribe Epinephelini and should exhibit the elongate dorsal spine that characterizes all larvae of the subfamily. During a recent trip to Japan, I had the opportunity to examine unidentified serranid larvae in collections at the University of Kagoshima with the aim of identifying specimens of larval *Niphon*. Four preflexion, one flexion and two postflexion larvae were positively identified as *Niphon spinosus*. The purposes of this paper are to describe these specimens and to discuss their bearing on my earlier hypothesis of the phylogenetic relationships of this species.

Materials and methods

The seven larval *Niphon* were collected during four cruises of the T. S. Kagoshima-maru in the

East China Sea, south of Kyushu, Japan from 1980–1984. Collections were made using a 0.53 mm mesh, 1.6 m mouth diameter plankton net towed at a speed of about 2 kts. at the surface or subsurface with 100 m of wire out. All specimens came from samples collected in October or November, suggesting that peak spawning probably occurs in late summer and early fall; however a more exhaustive search of other collections is needed before any meaningful conclusions about spawning times can be made.

Specimens are deposited in the USNM collections of the National Museum of Natural History, Smithsonian Institution:

USNM 295390, 4.2 mm NL; 4 Oct., 1982, 20:06–20:26; 30°00'8"N, 127°23'3"E.

USNM 295391, 4.2 mm NL (cleared and stained), 5.2 mm NL; 3 Oct., 1982, 04:03–04:23; 31°00'0"N, 127°52'0"E.

USNM 295392, 4.5 mm NL; 11 Nov., 1984, 15:00–17:00; 31°09'42"N, 130°23'6"E.

USNM 295393, 4.9 mm NL (cleared and stained), 4 Oct., 1980, 20:09–20:29; 29°43'4"N, 127°14'2"E.

USNM 295394, 7.0 mm SL (cleared and stained); 5 Oct., 1982, 20:05–20:25; 30°29'2"N, 129°27'6"E.

USNM 295395, 7.2 mm SL; 9 Nov., 1983, 09:10–11:10; 31°14'0"N, 129°19'48"E.

Larvae were measured under a stereomicroscope using a calibrated ocular micrometer. Measurements are as defined by Leis and Rennis (1983). Unlabeled lengths are body lengths (noto-

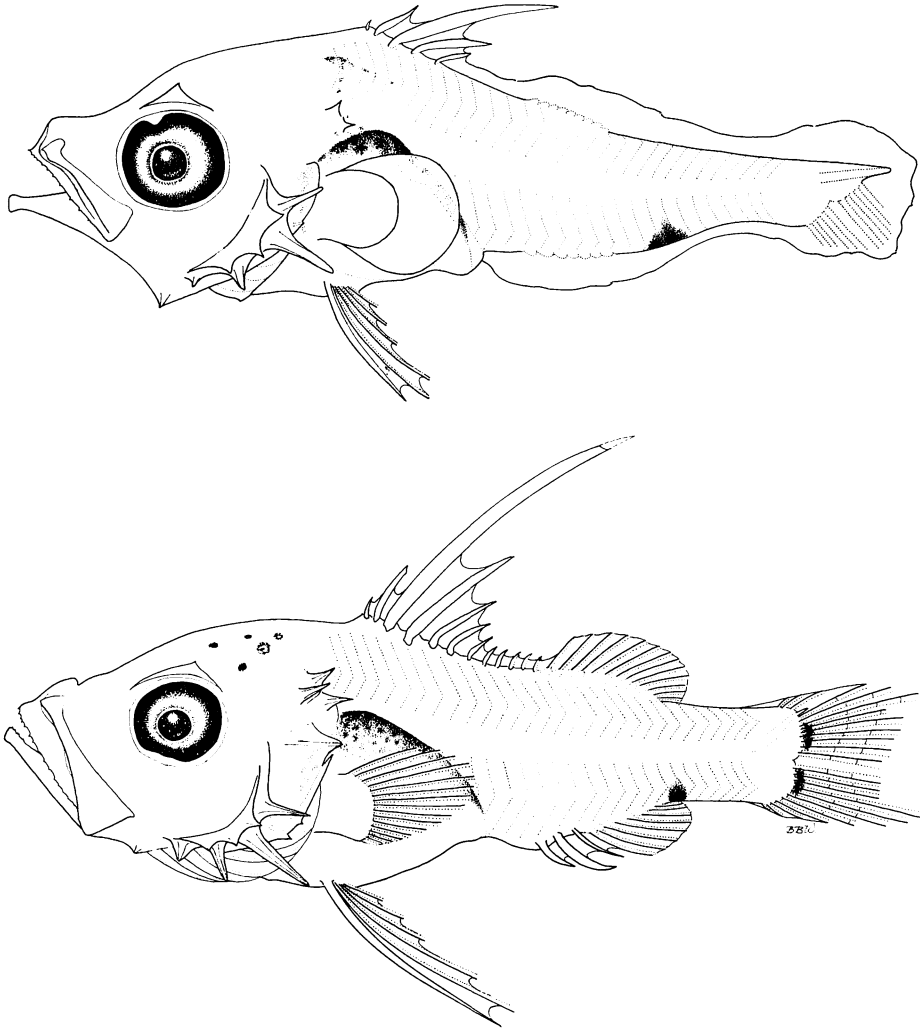


Fig. 1. Larvae of *Niphon spinosus*. Top, 4.9 mm NL; bottom, 7.0 mm SL. (Drawings by Betsy B. Washington.)

chord length in flexion and preflexion specimens, standard length in postflexion specimens). Drawings were prepared with the aid of a camera lucida. Two preflexion (4.2 mm, 4.9 mm) and one postflexion (7.0 mm) specimens were cleared and stained for bone and cartilage to allow more accurate observation of spination and internal pigment, and to allow observation of the dorsal pterygiophores and other aspects of the osteology.

Subfamilial and tribal categories for the Serranidae are sensu Johnson (1983). Two categories, subfamily Epinephelinae (epinephelins in the vernacular) and tribe Epinephelini (epinephelins in the vernacular), are referred to frequently and

the reader should take care not to confuse them.

Identification

The seven larvae were recognized as epinepheline serranids because of their resemblance to larvae of the epinepheline tribe Epinephelini, with which they share a somewhat kite-shaped body, a large midventral melanophore on the caudal peduncle, elongate dorsal and pelvic spines, and similarly configured spines on the preopercle, opercle, interopercle, supracleithrum, posttemporal and supraorbital ridge of the frontal. The two postflexion specimens were identified as *Niphon*

spinus by the myomere and dorsal fin-ray counts, 30 and XIII, 11, both of which are unique among serranids to this species. All other serranids have 24–26 vertebrae and fewer than XIII dorsal spines. Identification of the preflexion and flexion specimens, which lack a full complement of dorsal fin rays, was verified by their possession of 30 myomeres and other features shared with the postflexion specimens that are unique to *Niphon* among epinephelin serranids. The latter include absence of serrations on the elongate dorsal, pelvic and preopercular spines and the presence of two (versus one) short spines anterior to the elongate dorsal spine.

Description

(Fig. 1)

The most complete developmental description of larval Epinephelinae is that of Leis (1986) for *Plectropomus*, a member of the tribe Epinephelini. To facilitate comparison, a similar format is followed here for the description of larval *Niphon*. Morphometric and meristic data are given in Table 1.

The gut is tightly coiled in the smallest specimens (4.2 mm). The gas bladder, though obscured by

pigment, is well developed over the anterior portion of the gut. The laterally compressed body is "kite-shaped", being substantially deeper at the origin of the pelvic fins than it is just posterior to the anus. The head is relatively large (38–45% body length), as is the mouth, the maxilla reaching beyond the anterior margin of the orbit in all specimens. The snout is moderately long and slightly concave, and the rostral cartilage projects conspicuously at its tip. Minute, widely-spaced, conical teeth are present along the entire length of the premaxilla in preflexion specimens; the anterior two on each premaxilla are directed anteriorly, the remainder ventrally. In the postflexion specimens, only the anterior, exerted, premaxillary teeth are still well developed. A few small teeth are evident on the dentary only in the flexion and postflexion specimens. Scales are lacking in all specimens.

With the exception of the opercular spine and the more dorsal posttemporal spine, all head spines are present in the smallest specimens, and ontogenetic differences within this limited series involve only relative size, all spines being larger in the postflexion specimens. Sequence of initial development is probably similar to that described for *Plectropomus* by Leis (1986), but material is

Table 1. Morphometric and meristic data for larval *Niphon spinus*. Proportions are percentages of body length for each indicated measurement, as defined in Leis and Rennis (1983).

Stage	Preflexion	Preflexion	Preflexion	Preflexion	Flexion	Postflexion	Postflexion
Body length (mm)	4.2	4.5	4.9	5.2	4.2	7.0	7.2
Proportions (%)							
Head	42	38	38	40	45	42	39
Snout	14	12	12	14	17	14	14
Predorsal	38	39	35	38	43	42	39
Preanal	53	53	50	52	55	59	59
D spine, 3rd	25	22	24	30	39	37+	broken
P ₂ spine	26	22	20	28	31	31	30
Depth at:							
Pelvic fin	30	29	24	29	38	30	35
Anus	27	22	22	23	30	24	27
Caudal ped.					11	12	10
Counts							
Dorsal fin	IV	IV	V	VI	VII	Xiii, 11	Xiii, 11
Anal fin	0	0	0	1	1	III, 7	III, 7
Pectoral fin	0	0	0	4	8	15	17
Pelvic fin	I, 4	I, 5	I, 5	I, 5	I, 5	I, 5	I, 5
Caudal fin							
Principal	5+5	5+5	5+5	5+5	7+6	9+8	9+8
Procurent	0	0	0	0	0	3+3	3+3

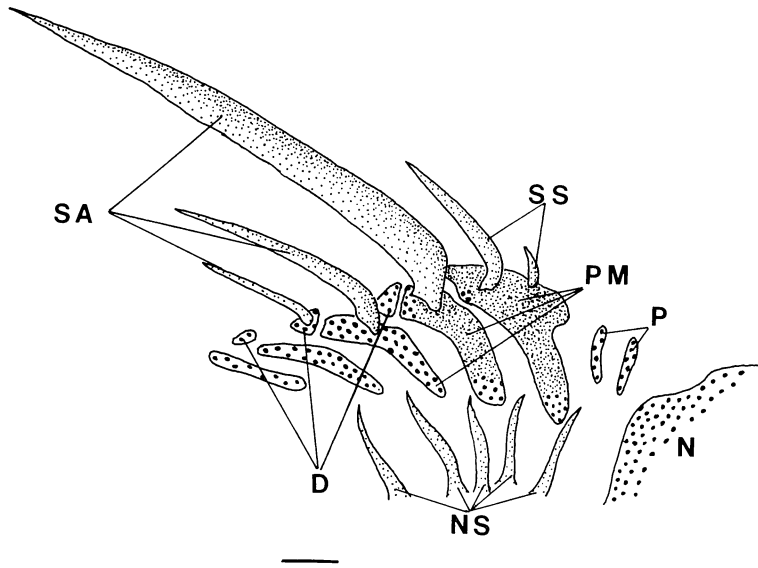


Fig. 2. Anterior dorsal pterygiophore complex of larval *Nippon spinosus* (4.9 mm SL), right lateral view; large stippling represents cartilage. D, distal radials; N, neurocranium; NS, neural spines; P, predorsals; PM, proximal-middle radials; SA, serially associated spines; SS, supernumerary spines. Scale bar represents 0.1 mm.

not available to confirm this. Unlike *Plectropomus* and other larval Epinephelini, all head spines have smooth margins.

There are three small spines of approximately equal size and spacing on the lateral margin of the preopercle. The posterior margin of the preopercle bears four spines, two on the lower limb, one at the angle, and one on the upper limb. In the smallest preflexion specimen the anteriormost of these is just visible and remains the smallest of the four spines throughout development. The longest of the four spines is the one at the angle (12–14% body length). A single small spine is present on the posterior margin of the interopercle near its junction with the subopercle. A very small spine is visible on the posterior margin of the opercle in all but the two smallest preflexion specimens.

The supraorbital ridge of the frontal extends dorsolaterally as a broad-based triangular spine. The posttemporal and supracleithrum each bear a single, posterolaterally directed spine; postflexion specimens have an additional posterolaterally directed spine on the posttemporal dorsal to the earlier developing spine.

In the two smallest preflexion specimens, dorsal spines two through five are present. Dorsal spine

one is the next to form and is present in the 4.9 mm specimen. The first two dorsal spines are borne in supernumerary association with the first dorsal pterygiophore (Fig. 2), thus dorsal spine two in *Nippon* corresponds to dorsal spine one in other epinephelins (wherein the first pterygiophore bears only a single supernumerary spine), three corresponds to two, and so forth. With completion of the first five spines, development of dorsal spines proceeds posteriorly. In the postflexion specimens, the full complement of spines (13) is present, but the last three remain bilaterally divided; they are identifiable as spine precursors (indicated by “i” in Table 1) by the nature of their serially associated distal radials and their articulation with them (Johnson and Keener, 1984; Johnson, 1984). The third dorsal spine is notably elongate, being about twice the length of the next longest (fourth) spine, and reaching 39% body length at flexion. The third spine is broken in both postflexion specimens, but it can be estimated to be about 40% body length in the 7.0 mm specimen. As in larvae of the tribe Epinephelini (Johnson and Keener, 1984), the elongate dorsal spine is chevron-shaped in cross section, but neither the apex ridge nor the lateral wing margins bear spinelets; the other dorsal spines are also smooth.

The distal tips of pterygiophores are evident near the mid-length of the soft dorsal fin in the smallest preflexion specimens, but incipient soft rays are not present at flexion. A full complement of dorsal soft rays (11) is present in the postflexion specimens.

Anal soft rays and pterygiophores form simultaneously with dorsal soft rays; incipient rays are lacking at flexion, and a full complement is present in the postflexion specimens. Unlike *Plectropomus* (Leis, 1986), anal spine two appears prior to the soft rays and is just visible in the largest postflexion (5.2 mm) and flexion specimens. A full complement of three anal spines is present in both postflexion specimens, but the tip of the third remains flexible, indicating that it is still in transition. Margins of all three anal spines are smooth.

Several incipient caudal-fin rays are present in the smallest preflexion specimens and a full complement of principal rays is present in both postflexion specimens (Table 1). Although the single flexion specimen measures 4.2 mm, three larger specimens (4.5–5.2 mm) show little evidence of onset of flexion. In addition to an expected variability in size at onset of flexion this apparent discrepancy is probably partially a result of the initial decrease in measured length at flexion due to the upturning of the notochord tip.

The moderately elongate (20–31% body length) pelvic spine is well developed in all specimens, and the full complement of five soft rays is present in all but the smallest preflexion specimen, in which the innermost ray is not yet formed. Like *Plectropomus* (Leis, 1986), there are only three (versus four in other epinephelin larvae) ridges along the length of the pelvic spine, and, as in *Plectropomus*, these appear to correspond to ridges 1, 2 and 3+4 as defined by Johnson and Keener (1984). All ridges are smooth.

A few incipient rays appear dorsally in the pectoral fin in the largest preflexion specimen; rays develop from dorsal to ventral and a full complement (17) is present in the largest postflexion specimen.

As in other larval epinephelins, the largest concentration of pigment is internally in the abdominal region, and there is little substantial ontogenetic difference in this pigment within the available series. The gas bladder and posterior portion of the gut are covered dorsally by an elongate cap of dense pigment that becomes more

sparse ventrally, extending to about the level of the ventral margin of the pectoral fin in preflexion specimens and only to about the middle of the pectoral fin in postflexion specimens. The anterior portion of the gut is covered by a similar, but less extensive, vertically oriented pigment sheet lying between the cleithra. A less dense sheet of pigment covers the notochord dorsolaterally, extending from the neurocranium to a point below the fourth or fifth dorsal spine.

Preflexion specimens lack pigment on the neurocranium. In the flexion specimen there is a single melanophore over the right frontal just above the posterior margin of the midbrain. In the postflexion specimens, three to five melanophores are scattered over the posterior surface of each frontal above the midbrain. A small but distinct melanophore is present at the junction between the articular and ascending processes of each premaxilla in the flexion specimen. This melanophore is detectable on one side in two of the preflexion specimens, and apparent remnants of the pigment are visible in the postflexion specimens.

No pigment is apparent on the dorsal or anal fins. A very small dusky area appears on the pelvic fin membrane near the distal tip of the outermost soft ray in all specimens. Preflexion specimens have a single melanophore near the base of one of the two uppermost ventral principal caudal rays, just distal to the tips of the hypurals. Three additional melanophores are present in the flexion specimen near the bases of the lowermost three dorsal principal rays. In the postflexion specimens this pigment has developed into two dusky bars along the bases of several of the uppermost ventral and lowermost dorsal principal rays.

A single, large midventral melanophore is present just posterior to the termination of the anal fin. Its ventral portion lies near the surface at the midventral body margin; its dorsal extension is internal, reaching nearly to the vertebral column in preflexion specimens and about half that distance in postflexion specimens. Longitudinally, it extends across myomeres 22–24 in the former and 23–24 in the latter.

Relationships

Johnson (1983) reviewed the classificatory history of *Niphon*. Briefly, most authors prior to

Gosline (1966) placed *Niphon* in a broadly defined Serranidae; Gosline (1966) restricted the Serranidae and placed *Niphon* in his newly delineated Percichthyidae; Rivas and Cook (1968), based on a phenetic analysis, placed *Niphon* in the Centropomidae; Greenwood (1977) convincingly refuted the hypothesis of Rivas and Cook and agreed with Gosline (1966) that *Niphon* was probably closely related to at least some genera of Gosline's "heterogeneous" Percichthyidae. Johnson (1983) argued that *Niphon* is a serranid (*sensu* Gosline) because it exhibits the innovative specialization (three opercular spines) that is unique among percoids to the Serranidae, and the three reductive specializations (a single uroneural and absence of the procurrent spur and third preural radial cartilages) that diagnose the Serranidae with respect to Gosline's percichthyids.

Johnson (1983) agreed with Gosline's division of the Serranidae into three subfamilies, Serraninae, Anthiinae and Epinephelinae, and recognized five tribes within the latter, Niphonini, Epinephelini, Diploprionini, Grammistini and Liopropomini. He argued that *Niphon* is a member of the Epinephelinae because it shares with all members of that subfamily a unique specialization: absence of an autogenous distal radial on the first dorsal pterygiophore. He noted that this modified pterygiophore probably serves no particular function in adult epinephelines, but that it almost certainly evolved as a larval specialization to provide special support for the serially associated spine, which in the larvae, unlike the adults, is always elongate and variously modified. In the tribe Epinephelini, this elongate spine is pungent and bears variously configured spinelets along its apex ridge and lateral wing margins (see Johnson and Keener, 1984). Larval *Niphon* were unknown at the time. In larvae of the other epinepheline tribes, Diploprionini, Liopropomini and Grammistini, the elongate spine is flexible and encased in a fleshy, variously pigmented sheath that may extend distally well beyond the tip of the spine and, in the Liopropomini, bears a series of rather fanciful, bulbous swellings (see Kendall, 1984: fig. 268B). In larval Liopropomini the next posterior spine is also elongate and in the Diploprionini the next one (*Diploprion*, Hubbs and Chu, 1934) to several (*Belonoperca*, pers. obs.) spines are elongate, but the pterygiophores associated with these additional elongate

spines are unmodified.

All members of the Epinephelinae, with the exception of *Niphon*, share an additional specialization. Whereas other serranids, including *Niphon*, and most percoids have two supernumerary (non-serially associated) spines on the first dorsal pterygiophore (Johnson, 1983: figs. 3, 9), the anteriormost of these has been lost in the remaining epinepheline tribes (Johnson, 1983: fig. 5). Thus, the serially associated spine of the first pterygiophore (the one that is elongate in the larvae) is the second rather than the third. In some liopropomini and grammistini, both supernumerary spines are lacking, so that the elongate spine is the first.

Johnson (1983) suggested that, in light of the above, the larvae of *Niphon* could provide corroborative evidence for his hypothesized phylogenetic placement of the genus. If *Niphon* is an epinepheline serranid and if the function of the modified first dorsal pterygiophore is as postulated (i.e., to support an elongate spine in the larvae), then larval *Niphon* should have an elongate dorsal spine. Moreover, because *Niphon* retains two supernumerary spines on the first dorsal pterygiophore, this elongate spine should be the third, rather than the second or first as it is in other epinephelines.

As noted in the preceding description, the larvae of *Niphon* do have an elongate third dorsal spine and the hypothesis that *Niphon* is an epinepheline serranid is thereby corroborated.

Further corroboration is found in the precocious development of the anterior spinous dorsal pterygiophore complex of these larvae (Fig. 2), details of which confirm the homology of this complex with that of other epinephelines. The first two dorsal pterygiophores are the first to form. They are present as robust cartilaginous rods in the 4.2 mm preflexion specimen, only the second having an autogenous distal radial at its tip. They have begun to ossify in the 4.9 mm specimen, in which there are only five dorsal spines, no soft rays and some of the posterior soft dorsal pterygiophores have not yet formed. The configuration of the first two pterygiophores at this stage is essentially identical to that seen in larvae of the tribe Epinephelini (see Johnson, 1983: fig. 6). The slightly larger first pterygiophore projects posterodorsally over the anterodorsal corner of the second; the tip of the former, still lacking a distal radial, inserts

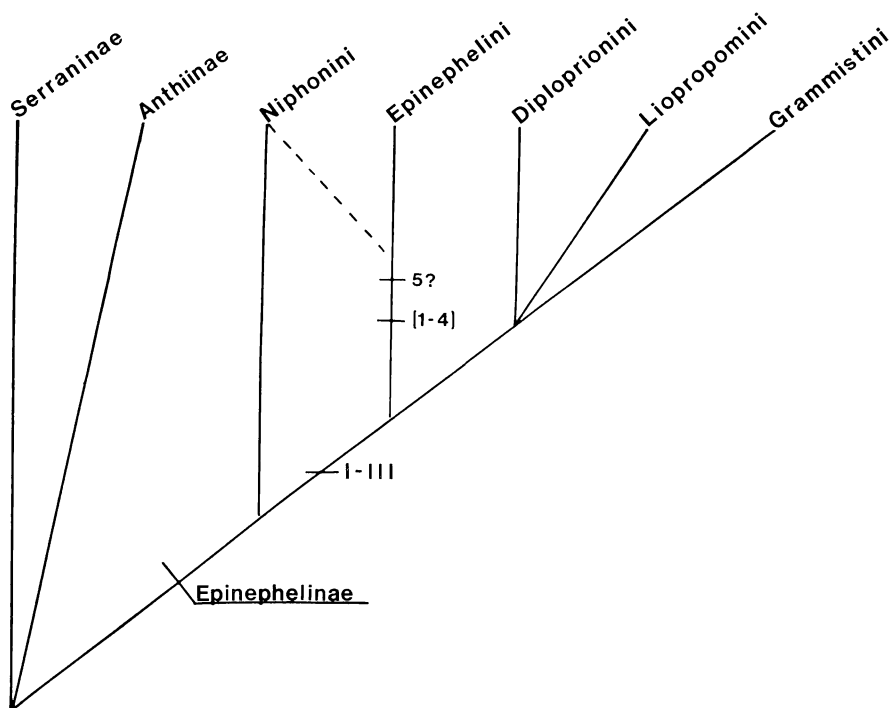


Fig. 3. Cladogram of hypothesized relationships of serranid subgroups. Dotted line represents refuted hypothesis. Numbers refer to characters in text: I-III, valid synapomorphies; 1-4, characters shown to be plesiomorphies or for which polarity is equivocal; 5, possible synapomorphy.

into the foramen in the base of its moderately elongate, serially associated spine. Development of this anterior pterygiophore complex is similar in all epinepheline tribes, although the first pterygiophore is reduced to a thin, elongate rod in adult liopropomins and grammistins.

Within the Epinephelinae, Johnson (1983) placed *Niphon* in a separate tribe, Niphonini, which he diagnosed by several specializations that are unique to adult *Niphon* among serranids—predorsal pattern 0+0/2/1/1/, dorsal fin rays XIII, 11, vertebrae 30, serrate lacrimal, elongate preopercular spine. *Niphon* also has uniquely configured ctenoid scales (see McCully, 1961). These autapomorphies provide no information about the relationships of *Niphon* to other epinepheline tribes. However, two primitive features, two supernumerary spines on the first dorsal pterygiophore and robust predorsal bones, led Johnson (1983) to hypothesize that *Niphon* is the sister group of all other epinephelines, which exhibit the derived states of one or no supernumerary spines and reduced predorsals.

Although the morphology of the larvae of

Niphon confirms its relationship to the subfamily Epinephelinae, these larvae resemble larvae of the tribe Epinephelini more closely than those of any other serranids, raising the possibility that *Niphon* is the sister group of the Epinephelini rather than the sister group of all other epinepheline tribes; to date, only larval characters support the monophyly of the Epinephelini (Johnson, 1983). The two conflicting hypotheses (see Fig. 3) can be tested by a parsimony comparison; placement of *Niphon* with the Epinephelini is refuted if *Niphon* shares fewer apomorphies with the Epinephelini than the Epinephelini share with the other three epinepheline tribes.

In the character analysis that follows, character polarities for the subfamily Epinephelinae are hypothesized based on outgroup comparison following the methodology of Maddison et al. (1984). Because relationships among the three subfamilies of the Serranidae are unresolved (Fig. 3), I treat Serraninae plus Anthiinae as a single outgroup for the Epinephelinae. In the absence of a hypothesized sister group for the Serranidae (which would serve as the second outgroup for the

Epinephelinae if serranines plus anthiines are the first), hypotheses of character polarity are unaffected if either serranines or anthiines, rather than the two together, are shown to be the sister group of the Epinephelinae. Regardless of the relationships among the three subfamilies, a character state exhibited by both serranines and anthiines is hypothesized as the ancestral state for the Epinephelinae, and for characters in which serranines and anthiines exhibit different states, polarity for the Epinephelinae is equivocal.

There has been considerable debate concerning the validity of the ontogenetic criterion ("direct" method of Nelson, 1978) for determining character polarity as opposed to the criterion of outgroup comparison (e.g., Nelson, 1973; Lundberg, 1973; Brooks and Wiley, 1985; Kluge, 1985; Nelson, 1985; De Queiroz, 1985) and, I believe, some confusion about the strict application of the former. Further discussion is warranted here, because larval characters are important in this analysis, and because in another recent study (Leis, 1986) some of these characters were polarized based on ontogenetic information.

In an analysis of the relationships among selected genera of the tribe Epinephelini Leis (1986) polarized several larval characters based on knowledge of their development within the tribe, without specific reference to comparable ontogenetic transformations in closely related outgroups. With this method, which essentially ignores the possibility of heterochrony, a feature that develops (e.g., B in the transformation A→B) during the known ontogeny of a species or group of species within the ingroup is considered derived, even though the same transformation (A→B) may exist in immediate outgroups. The more parsimonious interpretation of such a character transformation distribution is that the transformation A→B is a synapomorphy at a more inclusive level than the ingroup (and thus primitive at the ingroup level) and that the absence of B in one or more ingroup taxa is derived, presumably through pedomorphosis.

For most characters polarized for the Epinephelini by Leis (1986), outgroup comparison supports the ontogenetically hypothesized polarities; where conflicts exist, they are discussed under each character following discussion of the polarity hypothesis for the Epinephelinae. The reader is cautioned once again not to confuse subfamily

Epinephelinae (epinephelines) and tribe Epinephelini (epinephelins); character polarity for the two groups may be different. Polarization for the subfamily Epinephelinae is based on the outgroup statement given above. Polarization of characters for the tribe Epinephelini is based on the relationships among the tribes of the Epinephelinae proposed by Johnson (1983) and supported by the present analysis. Although not clearly indicated, Table 1 of that paper listed tribes in hypothesized phyletic sequence: Nipponini, Epinephelini, Diploprionini, Liopropomini, Grammistini. Relationships among the latter three tribes are not well resolved, and they are treated here as an unresolved trichotomy (Fig. 3). Those three tribes together constitute the sister group and first outgroup for the Epinephelini, and Nipponini (*Nippon*) is the second outgroup. The majority of characters treated by Leis (1986) pertain only to relationships within the Epinephelini and are not considered here.

Evidence putatively supporting the first hypothesis (represented by dotted line in Fig. 3), that the relationships of *Nippon* lie with the tribe Epinephelini, is examined first. *Nippon* larvae share with larvae of all or most members of the Epinephelini the following features not present in larvae of other epinepheline tribes:

- 1) The supraorbital ridge develops dorsolaterally as a large, broad-based, triangular spine. Development of a similar spine is the primitive condition for anthiines (i.e., it is present in the cladistically primitive members such as *Plectranthias*, based on the partial phylogeny proposed by Olmi, 1986), but serranines lack it as do other epinephelines. Polarity for the Epinephelinae is thus equivocal, and the supraorbital spine cannot be considered a synapomorphy of *Nippon* and epinephelines. An alternative interpretation, equally parsimonious, is that development of a large supraorbital spine is a synapomorphy uniting anthiines and epinephelines, with a reversal within epinephelines at the Diploprionini-Liopropomini-Grammistini node. The latter interpretation would offer an even stronger refutation of the spine as a synapomorphy of *Nippon* and epinephelins.

As regards polarity for the Epinephelini, Leis (1986) concluded, based on ontogeny, that a large supraorbital spine (lacking in *Plectropomus*) is derived within the tribe. Outgroup comparison

indicates that polarity for this character within the Epinephelini is also equivocal: the spine is lacking in the first outgroup (the three other epinepheline tribes), and present in the second outgroup (*Niphon*).

2) An elongate spine develops at the angle of the preopercle. Anthiine larvae develop a similar spine, but serranines lack it as do other epinephelins. Polarity for epinephelins is thus equivocal, and an elongate preopercular spine cannot be considered a synapomorphy of *Niphon* and epinephelins. As with the supraorbital spine, the preopercular spine could also be interpreted as a synapomorphy uniting anthiines and epinephelins, with a reversal within the latter.

3) The posterior one to three dorsal spines develop initially as soft rays. Leis (1986) considered this condition derived within the Epinephelini, because "indirect formation of spines is a specialized case of soft ray formation." In a phylogenetic context, "specialized" is a relative term, and the latter surmise cannot be established for a given taxon without outgroup comparison. Moreover serial homology of the spines involved is fundamental to the hypothesis of synapomorphy. The polarity argument is complicated by the problem of serial homology, because serranines (total spines 9–11), anthiines (9–11) and *Niphon* (13) have an additional supernumerary spine on the first pterygiophore. In order to compare serial elements posteriorly among all serranids it is necessary to subtract one spine from the total number present in serranines, anthiines and *Niphon*. For comparative purposes, then, the range of dorsal spine counts for each serranid subgroup are as follows: Serraninae, 8–10. Anthiinae, 8–10. Epinephelinae, 5–12, by tribe—Niphonini, 12; Epinephelini, 8–11; Diploprionini, 8–9; Liopropomini, 8; Grammistini, 5–8. In the latter three epinepheline tribes, all spines form directly (no transformation from soft rays). Information is limited, but it appears that all spines also form directly in serranines and anthiines.

Based on the above, indirect formation of some posterior spines occurs only in *Niphon*, where spines 10–12 form indirectly, and some epinephelins, where, according to Leis (1986), all spines form directly in those with eight spines (*Plectropomus*), the ninth spine forms indirectly in those with nine spines, and spines 10–11 form indirectly in those with 11 spines (it is probably safe to as-

sume that the ninth or ninth and tenth form indirectly in those epinephelins with ten spines). Thus indirect formation of the serially homologous tenth and eleventh spines might be interpreted as a synapomorphy of *Niphon* and the Epinephelini, but only if that condition is primitive for the Epinephelini. If the primitive state for the Epinephelini is eight or nine spines (i.e., failure of succeeding soft rays to transform into spines) then it is more parsimonious to conclude that the additional spines (i.e., transformation of elements 10–11 into spines) in *Niphon* and in most epinephelins have developed independently. Leis (1986) postulated, based on ontogeny, that eight spines in *Plectropomus* is primitive for epinephelins. However, the distribution of dorsal spine number among serranid subgroups (see above) is such that it is equally parsimonious to hypothesize that the primitive state for the Epinephelini is either eight or nine spines; it is not possible to unequivocally select one or the other as the primitive state. Whether eight or nine spines is primitive, ten or more and the associated indirect formation of the additional spines is clearly derived within the Epinephelini and is thus refuted as a synapomorphy of *Niphon* and that tribe. (Placement of *Niphon* as the sister group of only the Epinephelini, with the primitive spine number for the latter hypothesized as 10–11, offers an equally parsimonious hypothesis, if only dorsal spine number is considered, however that hypothesis is incongruent with the distribution of other characters).

4) A single, large, partially internal melanophore develops on the midventral margin of the caudal peduncle, just posterior to the termination of the anal fin; in most epinephelins, but not in *Niphon*, this melanophore migrates dorsally to a midlateral position. An enlarged, partially internal, midventral melanophore posterior to the anal fin is also a common feature of larval serranines and anthiines (see Kendall, 1979), and, although the latter groups usually have additional, smaller midventral melanophores, I see no convincing evidence to unequivocally reject the homology of the enlarged melanophore with that of *Niphon* and the Epinephelini. If my surmise is correct, an enlarged midventral melanophore is primitive for the Epinephelinae and cannot be considered a synapomorphy of *Niphon* and epinephelins.

Leis (1986) interpreted the presence of an en-

larged midventral melanophore as derived within the Epinephelini, the presence of several small ventral melanophores on the tail in *Plectropomus* and *Cephalopholis* being primitive. I disagree with Leis' polarity assessment, in support of which he presented both ontogenetic and outgroup evidence. The ontogenetic evidence was based on the observations of Mito et al. (1967) who reported that in reared specimens of *Epinephelus akaara* the large midventral spot is preceded by, and apparently derived from coalescence of, a series of midventral melanophores during the late yolk-sac stage. Although this developmental pattern may characterize *E. akaara*, it does not appear to be the general pattern of development for epinephelins. Based on examination of large numbers of yolk-sac stage epinephelin larvae representing several species and at least three genera from the Atlantic, I have not seen specimens with a series of small spots initially that eventually coalesce to form the single large spot, nor does Leis (1986) report having seen this pattern in other epinephelin species, nor is it reported in other descriptions of the early development of reared epinephelin larvae (e.g., Guitart Manday and Juarez Fernandez, 1966; Chen et al., 1977; Hussain and Higuchi, 1980). The available evidence, then, suggests that an initial series of midventral melanophores is less general among epinephelins (as well as in the immediate outgroups, see below) than a large single spot. Interpretation of a series of spots as primitive for epinephelins, based on a developmental sequence that is known to occur in only one of many species, is not consistent with strict application of the ontogenetic criterion; in Nelson's (1978) terms, the biogenetic law is falsified, and heterochrony should be invoked.

As for outgroup evidence, Leis (1986) noted that a ventral series of melanophores is common among preflexion percoid larvae, including the other two serranid subfamilies (serranines and anthiines), which he believed supported his interpretation of that pattern as primitive for epinephelins. However, serranines and anthiines and other percoids are not the appropriate immediate outgroups for the Epinephelini, which are instead, as noted above, the Diploprionini-Grammistini-Liopropomini lineage (first) and *Niphon* (second). I have observed a single midventral melanophore posteriorly in some *Liopropoma*, and

others have no midventral pigment. In *Diploprion* a broad band of pigment encircles the tail in the area where the midventral spot occurs in epinephelins; this band does not form through coalescence of a ventral series of melanophores, nor is there any other midventral pigment present. Other members of the three tribes that form the first outgroup for the Epinephelini lack midventral pigment altogether. The second outgroup, *Niphon*, has an enlarged midventral melanophore, but also lacks all other midventral pigment. It is therefore most parsimonious to hypothesize that the absence of a series of small midventral melanophores is the primitive state for the Epinephelini. Consequently, contrary to Leis (1986), the presence of this series should be interpreted as derived in *Plectropomus* and *Cephalopholis*.

5) The pelvic spines develop early in conjunction with the anterior dorsal spine-pterygiophore complex and become moderately (*Niphon*) to extremely (Epinephelini) elongate. In some anthiines and some serranines pelvic spines may develop precociously, but this condition does not appear as extreme as in *Niphon* and the epinephelins. The three other epinepheline tribes lack precocious, elongate pelvic spines. Extremely precocious, elongate pelvic spines might be interpreted as a synapomorphy of *Niphon* and the Epinephelini, although a more detailed comparison of the development of these spines in serranines, anthiines, *Niphon* and epinephelins would be desirable to resolve questions of homology that could affect polarity assessment.

Of the five characters discussed above, only the last, precocious elongate pelvic spines, can be interpreted as a synapomorphy of *Niphon* and the Epinephelini and some questions of homology for that character remain. Other features shared by larvae of *Niphon* and the Epinephelini, such as small spines on the interopercle, subopercle, posttemporal and supracleithrum are common features of larvae of most other serranids and thus also fail as synapomorphies for the two taxa.

In contrast, at least three valid synapomorphies, lacking in *Niphon*, unite the Epinephelini with the three other epinepheline tribes, Diploprionini, Liopropomini and Grammistini:

1. *The two predorsal bones are substantially reduced; they are relatively short and unequal in size, the first being larger than the second, neither being expanded at the distal end* (see Kendall,

1976, Fig. 1). (In some, the second is lacking, and the first may be lost as well.) In serranines and anthiines, both of which have three predorsals primitively, the predorsals are notably longer, subequal in length, and the anteriormost is usually expanded distally. The two predorsals of *Niphon* are long and subequal like those of serranines and anthiines, being even more robust and expanded distally.

II. *The first supernumerary spine on the first dorsal pterygiophore is lacking.* In all serranines, anthiines and *Niphon* there are two supernumerary spines on the first dorsal pterygiophore.

III. *The serially-associated (second) spine of the first dorsal pterygiophore is extremely elongate in the larvae, reaching well over one-half SL in all known larvae and one to several times the body length in most.* In larvae of most other serranids, the serial homologue of this dorsal spine (the third), though produced relative to the other spines in some species (e.g., *Niphon*) does not attain one-half the body length (longer in some species of *Anthias*). Although the spine differs considerably in configuration among these epinepheline tribes, in all of them it develops initially with a distinctive fleshy sheath, a condition not observed in larvae of serranines and anthiines. The fleshy sheath may be an additional synapomorphy for epinepheline tribes, exclusive of *Niphon*; however the earliest development of this spine is unknown for *Niphon*.

In conclusion, the available evidence supports the hypothesis that *Niphon* is the sister group of all other epinephelines (Fig. 3). The alternative hypothesis, that *Niphon* is the sister group of only the tribe Epinephelini, would require that an extremely elongate dorsal spine, similarly reduced predorsal bones and loss of the anterior supernumerary spine on the first dorsal pterygiophore have arisen independently within the Epinephelini and in the three other epinepheline tribes.

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Literature cited

- Brooks, D. R. and E. O. Wiley. 1985. Theories and methods in different approaches to phylogenetic systematics. *Cladistics*, 1: 1-11.
- Chen, F. Y., M. Chow, T. M. Chao and R. Lim. 1977. Artificial spawning and larval rearing of the grouper, *Epinephelus tauvina* (Forsk.) in Singapore. *Singapore J. Prim. Ind.*, 5(1): 1-21.
- De Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Syst. Zool.*, 34: 280-299.
- Gosline, W. A. 1966. The limits of the fish family Serranidae, with notes on other lower percoids. *Proc. Calif. Acad. Sci.*, 33: 91-111.
- Greenwood, P. H. 1977. A review of the family Centropomidae (Pisces, Perciformes); an appendix. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, 31: 297-301.
- Guitart Manday, D. and D. Juarez Fernandez. 1966. Desarrollo embrionario primeros estadios larvales de cherna criolla, *Epinephelus striatus* (Bloch) (Perciformes: Serranidae). *Acad. Ci. Cuba Estud.-Inst. Oceanol.*, 1: 35-45.
- Hubbs, C. L. and Y. T. Chu. 1934. Asiatic fishes (*Diploprion* and *Laeops*) having a greatly elongated dorsal ray in very large post-larvae. *Occ. Pap. Mus. Zool. Univ. Mich.*, 229:1-7.
- Hussain, N. A. and M. Higuchi. 1980. Larval rearing and development of the brown spotted grouper, *Epinephelus tauvina* (Forsk.). *Aquaculture*, 19: 339-350.
- Johnson, G. D. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae. *Copeia*, 1983: 777-787.
- Johnson, G. D. 1984. Percoidei: development and relationships. Pages 464-498 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. *Ontogeny and systematics of fishes*. Amer. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- Johnson, G. D. and P. Keener. 1984. Aid to identification of American grouper larvae. *Bull. Mar. Sci.*, 34: 106-134.
- Kendall, A. W., Jr. 1976. Predorsal and associated bones in serranid and grammistid fishes. *Bull. Mar. Sci.*, 26: 585-592.
- Kendall, A. W., Jr. 1979. Morphological comparisons of North American sea bass larvae (Pisces:

- Serranidae). NOAA Tech. Rep., NMFS Cir. No. 428., 50 pp.
- Kendall, A. W., Jr. 1984. Serranidae: development and relationships. Pages 499–510 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Amer. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- Kluge, A. G. 1985. Ontogeny and phylogenetic systematics. Cladistics, 1: 13–27.
- Leis, J. M. 1986. Larval development in four species of Indo-Pacific coral trout *Plectropomus* (Pisces: Serranidae: Epinephelinae) with an analysis of the relationships of the genus. Bull. Mar. Sci., 38: 525–552.
- Leis, J. M. and D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales Univ. Press, Sydney and Univ. of Hawaii Press, Honolulu., 269 pp.
- Lundberg, J. G. 1973. More on primitiveness, higher level phylogenies and ontogenetic transformations. Syst. Zool., 22: 327–329.
- Maddison, W. P., M. J. Donoghue and D. R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33: 83–103.
- McCully, H. H. 1961. The comparative anatomy of the scales of serranid fishes. Unpubl. Ph. D. Diss., Stanford Univ., 248 pp.
- Mito, S., M. Ukawa and M. Higuchi. 1967. On the larval and young stages of a serranid fish, *Epinephelus akaara* (Temminck et Schlegel). Bull. Naikai Reg. Fish. Res. Lab., 25: 337–347.
- Nelson, G. 1973. The higher-level phylogeny of vertebrates. Syst. Zool., 30: 197.
- Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Syst. Zool., 27: 324–345.
- Nelson, G. 1985. Outgroups and ontogeny. Cladistics, 1: 29–45.
- Olmi, C. B. 1986. Morphology of the larvae of American Anthiinae (Pisces: Serranidae) with comments on relationships within the subfamily. Unpubl. Masters Thesis, College of Charleston.
- Rivas, L. R. and B. A. Cook. 1968. Relationships of the western Pacific “percichthyid” fish *Niphon spinosus*, with the family Centropomidae. Wassman J. Biol., 26: 201–208.

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原始的ハタ亜科魚類アラの分類学的位置に関する仔魚形態からの考察

G. David Johnson

東シナ海産の 7 個体 (脊索長 4.2 mm–標準体長 7.2 mm) にもとづき、アラ仔魚の形態を記載した。これらの個体は 1980–1984 年の 10–11 月に採集された。仔魚の形態的諸特徴の中でも、伸長した第 3 背鰭棘と発達中の前部背鰭担鰭骨要素の配置はアラ属がハタ亜科に所属することを確証するものである。ハタ亜科内ではアラ仔魚はマハタ族仔魚と最も類似するが、背・腹鰭棘および前鰓蓋棘上に鋸歯が発達しないなどの点で異なっている。外接群比較によって形質の極性を決めて、形質分析をおこなったところ、アラ属はマハタ族の姉妹群とするよりも、むしろハタ亜科の他の全族の姉妹群と仮定するのが、最も節減の原則にかなうことが示唆された。