

## Larval development of *Brotulotaenia nielseni* (Ophidiiformes, Ophidiidae, Brotulotaeniinae), with notes on relationships

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**Abstract** Ontogeny of the ophidiid fish, *Brotulotaenia nielseni*, is described based on seven specimens ranging from 10.0 mm NL to 69.5 mm SL, collected from tropical western Pacific. The so-called “rubaniform” is confirmed to represent larval stages of *Brotulotaenia*. Its selected features such as the slightly exterilium gut, enlarged first dorsal pterygiophore, unusually elongate ventral process of the coracoid, and peculiar structure of hypural plate are also observed and figured. Specialized larval morphs, i.e., rubaniform and exterilium (*sensu* Fraser and Smith, 1974; currently ascribed to larval *Lamprogrammus*) are compared in detail and their close relationship is suggested. It is likely that the Brotulotaeniinae is most close to some neobythitid genera including *Lamprogrammus*.

**Key words:** Rubaniform, exterilium, *Brotulotaenia nielseni*, *Lamprogrammus*.

### Introduction

*Brotulotaenia*, a genus of the ophidiid monotypic subfamily Brotulotaeniinae, comprises four species of meso- to bathy- and perhaps benthopelagic fishes in tropical and subtropical seas of the world (Cohen, 1974; Nielsen *et al.*, 1999), while *B. brevicauda* was recently reported from Flemish Cap bank (about 47°N, 45°W) in the northwest Atlantic (Bañón and Rodríguez-Marín, 1999). Although their taxonomy and morphology have been well studied (Cohen 1974; Kashkin, 1978; Shcherbachev, 1980; Machida *et al.*, 1997), available information on their ontogeny has been restricted to two large pelagic larvae called ‘rubaniform’ (Fourmanoir, 1976; Abousouan, 1980).

In the present paper, we describe the early ontogeny of *B. nielseni* based on a developmental series ranging from 10.0 mm NL to 69.5 mm SL (standard length) collected from the tropical and subtropical Pacific, and discuss the relationships of the ‘rubaniform’ with another remarkable larval morph, the ‘exterilium’ (*sensu* Fraser and

Smith, 1974), referable to *Lamprogrammus* (Fahay and Nielsen, 2001).

### Materials and Methods

Collection data of seven specimens (10.0 mm NL to 69.5 mm SL) of *B. nielseni* are summarized in Table 1.

NSMT-PL 108 was collected with horizontal tow of 2 m-conical larval net by R/V Shoyomaru, and NSMT-PL 109–144 with oblique tows of 15-foot IKPT-net by R/V Hakuho-maru, each from depths indicated in Table 1. Except for NSMT-PL 114 obtained during daytime (11:00–12:01), all specimens were collected during nighttime (20:10–03:00).

These larvae were preserved in 70% ethanol after initial fixation in 10% seawater formalin. Osteological observations were made after either double staining (10.0 mm NL, 69.5 mm SL) or alizarin red-S staining (14.5 mm, and 21.0, 22.5, 45 mm SL). Terminology follows Cohen (1974) and Markle and Olney (1990). Standard measurements are as defined by Okiyama (1988). Prenal

Table 1. Collection data of larval *Brotulotaenia nielseni*.

Cat. No.	SL, mm	Locality	Date	Depth, m
NSMT-PL108	31.5	13°10'S; 140°12'W	1964-2-17	ca. 30 m
NSMT-PL109	69.5	18°00'N; 131°00'E	1995-7-17	0-354
NSMT-PL110	14.5	12°00'N; 130°00'E	1995-7-26	0-307
NSMY-PL111	45.5	10°24'N; 143°12'E	1995-8-4	0-199
NSMT-PL112	21.0	7°58'S; 159°00'E	1995-9-6	0-158
NSMT-PL113	10.0	8°00'S; 160°25'E	1995-9-6	0-265
NSMT-PL114	22.5	3°53'S; 159°00'E	1995-9-7	0-202

length is the distance between tip of snout and the origin of anal fin, and head depth is measured as a vertical distance through dorsal fin origin.

#### Comparative materials:

*Brotulotenia nielseni*, SFC 1776, 312 mm SL (X ray photograph).

*Brotulotaenia nigra*, ASM I.22818-009, 260 mm SL.

*Brotulotaenia crassa*, ASM I.24347-002, 320 mm SL.

Exterilium larvae (*sensu* Fraser and Smith, 1974); uncatalogued, 15.1 mm NL (notochord length), KH95-2 st.021, 14°-01.2'N, 133°-57'E; uncatalogued, 70 mm SL (double stained and cleared for osteological study), KH95-2 st.045, 10°-24'N, 143°-27'E.

## Results

### Larval development (Figs. 1-2, Table 2).

*General morphology.*—Morphometric and meristic characters of all larvae are given in Table 2.

Larvae are laterally compressed throughout pelagic stages ranging from 10.0 mm NL to 69.5 mm SL in our collections. They are initially deep-bodied particularly at the level of the back of head. The body depth at the base of the pectoral fin gradually decreases from 31 per cent of the body length in the 10.0 mm late preflexion larva to 15-19 per cent in postflexion larvae larger than 45 mm long. The anus opens slightly anterior to the middle of the standard length in pre- and flexion larvae, shifting anteriorly thereafter until the snout to anus length reaches 38-39 per cent in postflexion larvae larger than 31.5 mm.

All larvae have a slight exteriolum gut with a left-sided loop, which develops increasingly larger with growth. The gas bladder is moderately developed over the gut just posterior to the level of pelvic fin base. The head is large and deep, particularly in the early larvae. Head length decreases gradually relative to standard length from a maximum of 24 per cent in late preflexion larva to 13-16 per cent in postflexion larvae due to the progressive lengthening of the trunk and tail. The dorsal profile of the snout is nearly straight in late preflexion larva, becoming deeply concave in postflexion larvae. The eyes are small and rounded. Their diameter decreases from 15-18 per cent of the head length in the larvae less than 21 mm to 11-13 per cent in more advanced larvae. The nasal pores are completely separated in a 31.5 mm larva. The mouth is small, oblique, and extends below the level of the anterior rim of the eye. The upper jaw comprises a deep premaxillary and maxillary, and a small supramaxillary in the largest larva. Teeth observed in all larvae include a single or double rows of minute canines along most edges of the premaxillary and dentary. The scales and head pores are indistinct even in the largest larva.

*Fin Development.*—In the smallest larva at late preflexion, the dorsal and anal fin rays are developed except for those near the tail tip. The anteriormost three dorsal-fin rays, particularly the 2nd and 3rd, are elongate and nearly half as long as the body length; subsequent dorsal- and all anal-fin rays gradually decrease in sizes posteriorly. The second and third pelvic-fin rays are remarkably elongate, the longest being about 40 per cent of the body length. The pectoral and

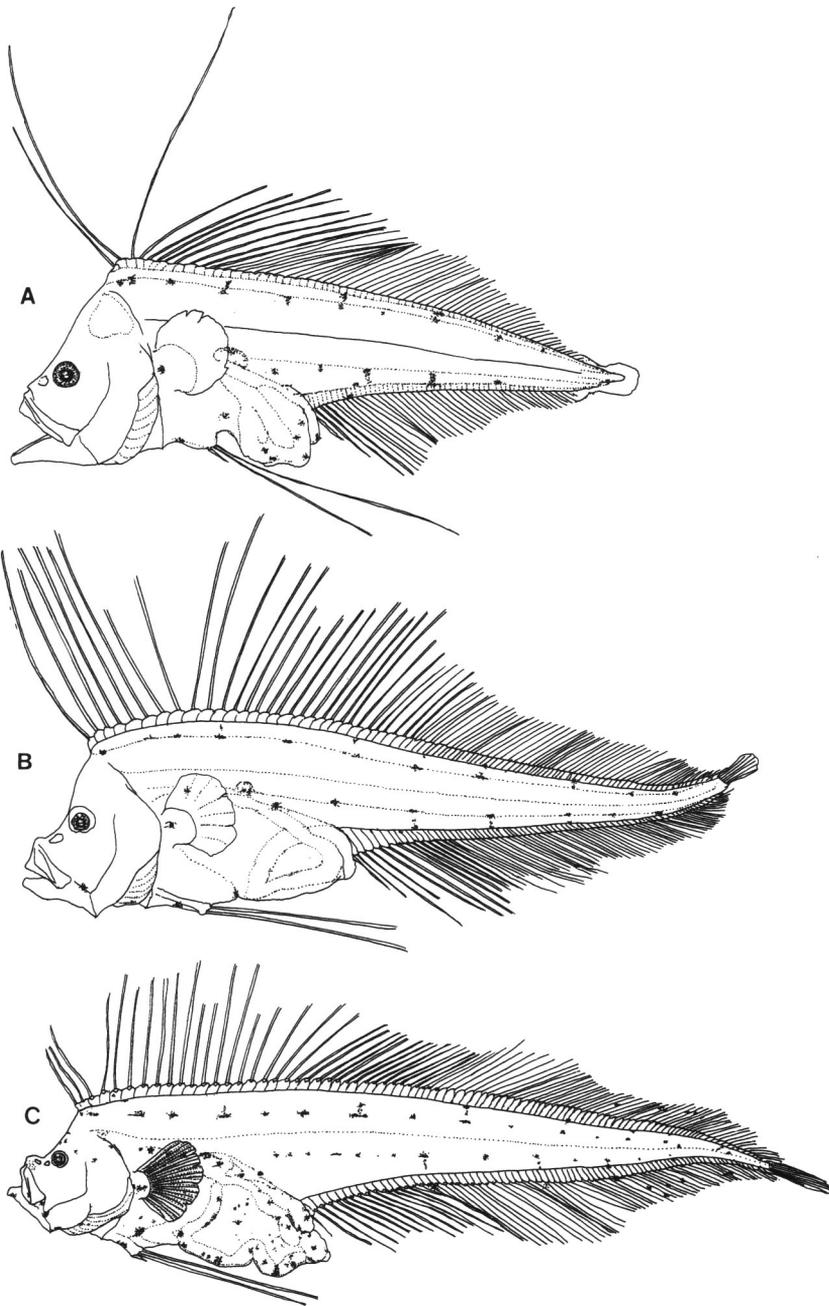


Fig. 1. Larvae of *Brotulotaenia nielseni*. A, 10.0 mm NL, NSM-TL113; B, 21.0 mm SL, NSM-TL112; C, 69.5 mm SL, NSM-TL109

caudal fins are membranous and include several incipient rays.

Most of the fin rays are developed in the slightly larger 14.5 mm flexion larva. Several pre-

cociously elongated dorsal-fin rays become indistinct as growth proceeds, due to the increasing elongation of subsequent rays during the flexion stage. Lengths of dorsal-, anal- and pelvic-fin

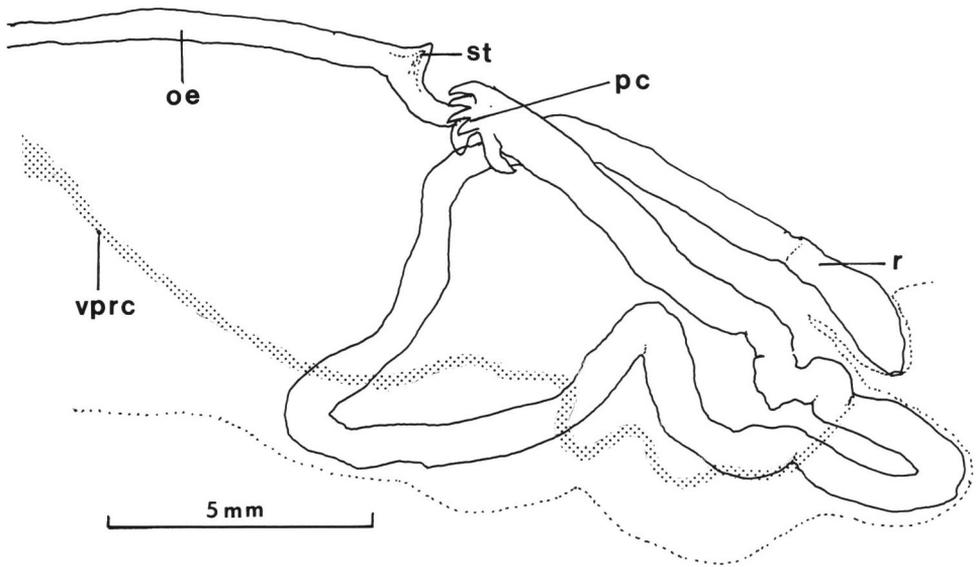


Fig. 2. Gut of larval *Brotulotaenia nielsenii*, 69.5 mm SL, NSM-TL109. oe — oesophagus; pc — pyloric caecum; r — rectum; st — stomach. Cartilaginous ventral process of the coracoid is also shown by a stipple.

Table 2. Morphometric and meristic characters of seven larvae of *Brotulotaenia nielsenii*.

	NSMT- PL113	NSMT- PL110	NSMT- PL112	NSMT- PL114	NSMT- PL108	NSMT- PL111	NSMT- PL109
Standard length (SL)	10.0	14.5	21.0	22.5	31.5	45.5	69.5
As % SL							
Body depth (max)	31.0	38.6	28.6	27.6	27.3	20.0	25.9
Head length (HL)	24.0	23.4	16.7	15.0	15.9	13.8	12.9
Distance from snout to anal	47.0	48.3	41.9	35.6	38.1	38.9	38.1
As % HL							
Eye diameter	16.7	14.7	15.7	18.2	16.0	12.9	11.1
Maxillary length	—	37.3	38.1	42.4	41.3	41.9	32.2
Snout length	—	—	31.4	33.3	34.0	—	27.8
Dorsal-fin rays	(88+)	(93)	96	90	93	97	95
Anal-fin rays	(56;)	(73)	75	70	69	73	72
Pectoral-fin rays	0	(23)-(23)	25-25	25-26	23-23	25-25	25-25
Pelvic-fin rays	3	3	3	3	3	3	3
Caudal-fin rays	(0)	(9)	5+4=9	5+4=9	5+4=9	5+4=9	5+4=9
Vertebrae			72		74		75

rays relative to body length are almost unchanged until early postflexion larvae around 20 mm SL. These features are retained in the largest postflexion larva although less conspicuous. On the other hand, anlagen of the pectoral and caudal fins change little during larval stages. Only pelvic and caudal fin rays are segmented.

*Pigmentation.* — The basic larval melanophore pattern is established in the smallest 10.4 mm

preflexion larva in the collection. The most characteristic feature is a longitudinal series of large or small melanophores evenly spaced on dorsal and ventral sides of body. The dorsal pattern comprises a total of nine dots ranging from nape to near the caudal tip below the 75<sup>th</sup> dorsal ray; these are in line along the dorsal corner of double chevrons of myotomes; several intermittent larger dots are paired with the more dorsally placed

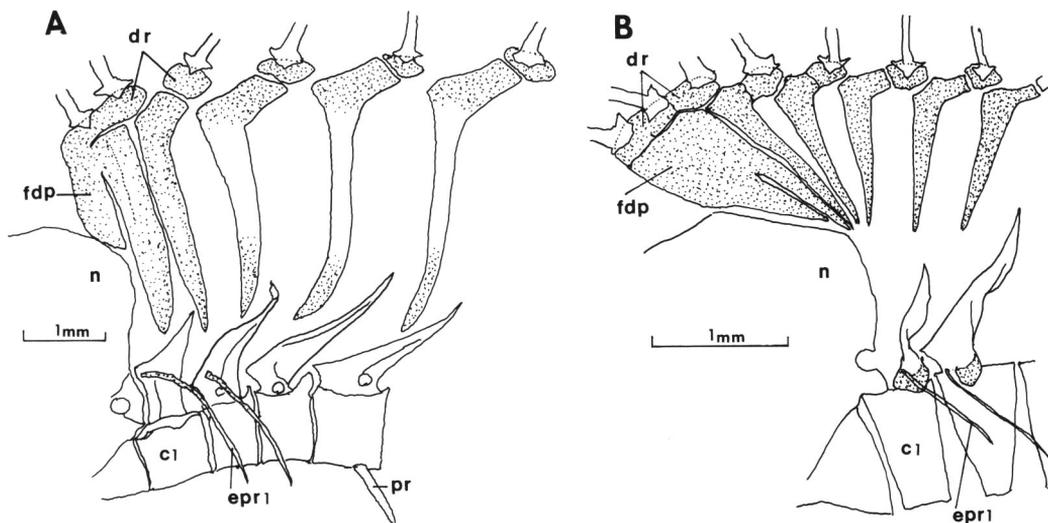


Fig. 3. Anterior axial skeleton of (A) larval *Brotulotaenia nielsenii*, 69.5 mm SL, NSM-TL109., and (B) larval *Lamprogrammus*, 70.0 mm SL, uncat. c1 — centrum 1; dr — distal radial; epr 1 — epural 1; fdp — first dorsal pterygiophore; n — neurocranium; pl — pleural rib. Cartilages are stippled.

melanophores. Ventrally, five dots occur opposite the 4<sup>th</sup> to 8<sup>th</sup> of the dorsal pattern, while larger melanophores are not always arranged in parallel, due to irregular addition of two dots over the anal pterygiophores between 3<sup>rd</sup> and the 4<sup>th</sup> ventral pattern. Melanophores are scattered over abdomen chiefly along the ventral border including the pelvic fin basis, and on the roof of the gas bladder. There is a single spot at the base of the pectoral fin. No head melanophores are observed externally, but several dots occur inside the bottom of otic capsule and in the nape. Pigmentation slightly changes thereafter chiefly due to the addition of melanophores to the previously formed patterns. In the early postflexion larva of 21 mm SL, two dots are added to both the dorsal and ventral series, besides new occurrences of melanophores at the posterior corner of the upper jaw and on the head. In the largest postflexion larva of 69.5 mm SL, melanophores further increase in several body parts such as on the head, around the upper and lower jaws, and over the abdomen, along with intermittent additions of small dots particularly in the ventral series, and new occurrences of several dots over the distal halves of the posterior one third of the dorsal and

anal fins.

*Gut.* — In the largest postflexion larva, the gut is a simple narrow tube, with moderate zigzags around the first turn of the intestine. The stomach is a small cone-like projection associated with six minute pyloric caeca (Fig. 2).

### Osteology

The following descriptions are made chiefly on the basis of the largest specimen, with supplementary notes from smaller larvae.

*Ossification* — The 10.0 mm preflexion larva shows the beginning of membranous bone formation in many elements such as the jaws, frontal, parasphenoid, palatine, preopercle, branchiostegal rays, and cleithrum, besides anterior dorsal- and anal-fin rays and pelvic-fin rays including precociously elongate rays. The axial skeleton and most of the opercular apparatus do not start to ossify until 14.5 mm flexion, but even in the largest 69.5 mm larva, the hyoid arch, brachial arches, pectoral and pelvic girdles, and caudal skeleton are largely unossified,

*Anterior axial skeleton* (Fig. 3A) — In the largest larva (69.5 mm), the anterior vertebral column is differentiated with slightly reduced

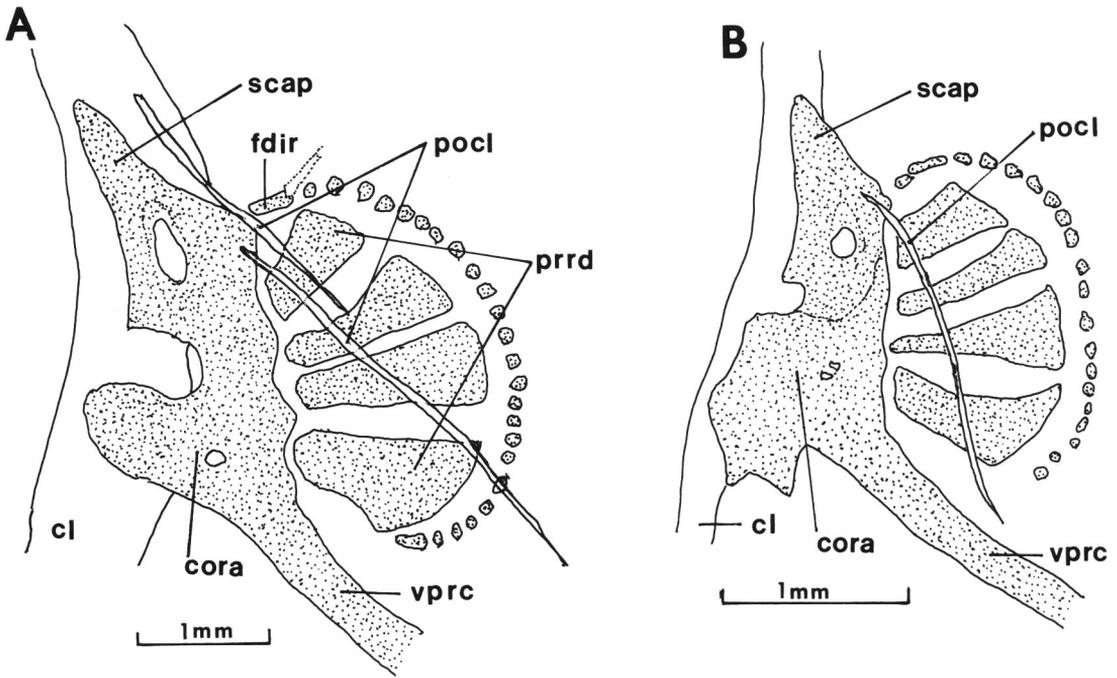


Fig. 4. Pectoral-fin girdle of (A) larval *Brotulotaenia nielsenii*, 69.5 mm SL, NSM-TL109., and (B) larval *Lamprogrammus*, 70.0 mm SL, uncat., right side, medial view. clei—cleithrum; cora—coracoid; fdir—first distal radial; pocl—postcleithra; prrd—proximal pectoral-fin radials; scap—scapula; vprc—ventral process of coracoid. Cartilage are stippled.

first neural spine relative to the second. Filamentous epipleurals occur on the first two centra with articulation to the anterodorsal corner of the pedestal of the neural spine. Pleurals occur ventrally on the fourth and succeeding centra. The first dorsal pterygiophore is poorly ossified and peculiarly modified (Fig. 3). It is deeply two-forked proximally with the anterior arm overlying the neurocranium and the elongate posterior one interdigitating with the first neural spine. Dorsally, it is also fused anteriorly with the large distal radial and supports two dorsal-fin rays. The second dorsal pterygiophore is an intact element with slight modification to fit closely along the posterior corner of the preceding one. Remaining dorsal and anal pterygiophores are similarly elongate and widely spaced, and become progressively shorter posteriorly. All pterygiophores interdigitate more or less with neural or haemal spines by the ratios of 1.33 or 1.36, respectively.

In the smallest larva (10 mm), the anterior dor-

sal fin pterygiophores are more closely arranged, the anteriormost being more deeply two-forked distally with the slightly shorter anterior arm.

*Pectoral- and pelvic-fin girdles* (Fig. 4A)—Except for the ossified cleithrum and two postcleithra, pectoral and pelvic girdles are mostly composed of cartilaginous elements even in the largest larva. The scapula and coracoid are fully fused, lying deep inside the cleithrum. There are large and small foramina besides a deep anterior incision in the basal part of this complex. The coracoid is peculiar in having an extremely elongated ventral process extending from its posteroventral corner to near the anus. There are four proximal pectoral radials of slightly different sizes and slightly constricted shapes, the ventral-most one being the largest. A total of 25 distal radials are closely spaced along the posterior border of the proximal radials with the first and last elements slightly enlarged. The two postcleithra are thin and elongate bones lying in parallel; the

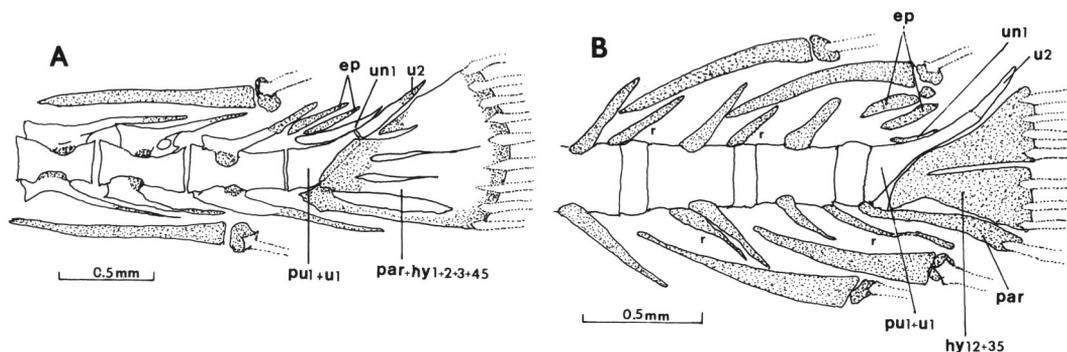


Fig. 5. Caudal skeleton of (A) larval *Brotulotaenia nielsenii*, 69.5 mm SL, NSM-TL109., and (B) larval *Lamprogrammus*, 70.0 mm SL, uncat. For dislocated pairs of laterally divided neural and haemal spines in (B), right side components are indicated by “r”. ep — epural; hy15 — hypural 1–5; par — parhypural; pu 1 — preural 1; un — uroneural; u1, 2 — ural 1, 2. Cartilages are stippled.

ventral element is longer.

The pelvic girdle of the largest larva comprises a pair of distally expanded cartilaginous rods, articulating to the cleithrum at the proximal tip.

The pectoral girdle of the smallest larva (10 mm) comprises the ossified cleithrum and the cartilaginous scapula-coracoid complex already bearing an unusually elongate cartilaginous ventral process and a large anterior incision.

**Caudal skeleton** (Fig. 5A)—The caudal skeleton is weakly ossified even in the largest larva (69.5 mm), forming a large single hypural fan formed by the distal fusions of associated bones. The unossified parhypural and the ossifying hypural 4+5 fuse only distally, whereas the hypurals 1–3 have a further connection along their cartilaginous proximal bases articulating with the preural 1 and ural 1; the hypural 4+5 is supported by the ural 2 without articulation. Open or closed splits among them are variously developed with the largest one present between the parhypural and the hypural 1. The preural 1 and ural 1 bear dorsally an uroneural 1 and overlying two cartilaginous epurals. Nine principal caudal fin rays are evenly spaced along the cartilaginous semi-circular frame of the hypural fan. Cartilages are also observed at the distal and proximal portions of neural and haemal spines.

According to the definitions of Fujita (1990), number of the hypurals in this largest larva

should be counted as one, although the 21.0 mm larva at early postflexion stage has the fully separated hypurals and parhypural including the independent hypural 5.

### Ecology

**Distribution** (Fig. 6)—All larvae but a single specimen collected by R/V Shoyo-maru, were collected during cruise KH95-2 of R/V Hakuohomaru, July 17 to September 9, 1995. These larvae were found in plankton collections taken with 15 f-IKPT net or 2 m-conical larval net in the surface waters down to 350 m. Except for a single larva (22.5 mm), all positive collections were made during night time. Their localities were broadly distributed in the tropical and subtropical Pacific west of 140°W between about 18°N and 13°S.

**Feeding**—Guts of three larval specimens ranging from 10.0 to 69.5 mm SL were observed; no items were identified in 10.0 mm larva, but a 21.0 mm larva fed a total of 13 copepods and a single amphipod, and a 69.5 mm larva contained a single copepod and amphipod. The presence of food materials throughout the long gut in the 21.0 mm larva indicates active feeding in the night time in these larvae.

### Discussion

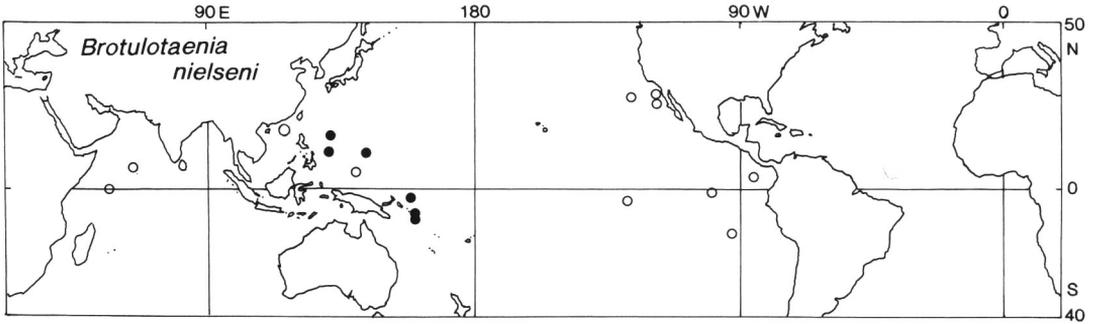


Fig. 6. Distributions of larvae (closed circle) and adults (open circle) of *Brotulotaenia nielsenii*.

### Identification

Apart from larval Carapidae diagnosed by the presence of vexilifer stage, no other larvae of Ophidiiformes have diagnostic characters peculiar to the order. "Larve rubaniforme" was first reported on the basis of a 59 mm specimen as "incertae sedis" in the Pleuronectiformes (Fourmanoir, 1976). Subsequently, Aboussouan (1980) described a similar type of larva (62.7 mm SL) in full details, suggesting its possible affinity with *Brotulotaenia* of Ophidiidae, although several internal features were misinterpreted there probably due to inadequate staining technique as follows: Baguette copulatoire mâle (bcop) may be excretory organ, anteriormost two dorsal pterygophores are not separated but partly fused, angular (an) is not discriminated from the articular, and metapterygoid (mtp) and postcleithrum (pc) should read "symplectic" and "ventral process of coracoid", respectively.

Markle and Olney (1990) suspected his identification, because there are morphological differences between his larva and adults (Cohen, 1974), particularly in arrangement and position of anterior dorsal pterygiophores. As stated above, however, our studies reveal that improper staining of cartilaginous elements might be responsible for this confusion. Although our specimens fit closely with the *Brotulotaenia* larva of Aboussouan (1980) in overall appearance, their meristic characters, particularly those of dorsal fin rays counts (Cohen, 1974; Nielsen *et al.*, 1999), readily referred them to *Brotulotaenia nielsenii*. Geographic distribution of this species

(Fig. 6) also substantiate our conclusion. On the other hand, two previously known rubaniform larvae (Fourmanoir, 1976; Aboussouan, 1980) are safely identified with *B. crassa*.

Since these larvae represent both of two species groups in the *Brotulotaenia*, i.e., long- and short- bodied forms (Cohen, 1974), the so-called "rubaniform" may be commonly shared by all congeners.

### Metamorphosis

The smallest juveniles recorded were 78.8 mm SL in *Brotulotaenia brevicauda* (Cohen, 1974), and 82 mm SL in *B. nielsenii* (Parin *et al.*, 1977), respectively. If their body sizes do not decrease at metamorphosis, "rubaniform" larvae are expected to be transformed into juveniles between about 70 and 80 mm SL. Due to the poor morphological information on these juveniles, adult features (Cohen, 1974) were compared with those of the largest larvae regardless of species. Major metamorphosis events follow:

The head shape transforms from concave to a straight dorsal profile, with slight to little ventrad flexion at nape, and the mouth changes from oblique to horizontal, with associated increases in relative sizes of the head, eyes and mouth. The gut transforms from a slightly extirium shape to a compact feature comprising a prominent thick-walled stomach. The relative lengths of the dorsal and anal fin rays are reduced. The pelvic fins and the dorsal postcleithrum are lost. The scapula and coracoid ossify and separate, associated with resorption of the elongate posteroventral

coracoid cartilage. The anteriormost dorsal fin pterygiophore shifts from the levels over the first to the second vertebra associated with its change of inclination from forward to posteriad.

Of these less drastic events, the abdominal transformation is of particular interest, because opportunistic feeding habit inferred from the long gut peculiar to rubaniform appears to be retained even in the adults, which also develop some integumental features such as the seemingly distensible belly skin and scales in the form of small, nonimbricate prickles (Cohen, 1974).

Contrary to Cohen (1974), X-ray photographs of our comparative materials comprising adult *Brotulotaenia crassa* and *B. nigra* revealed clear distal overlapping of the dorsal- and anal-fin pterygiophores with associated neural and haemal spines. The same photographs, however, did not provide clear enough images to locate the anterior dorsal pterygiophores, suggesting their poor ossification even in the adult.

### Relationships

Cohen and Nielsen (1978) placed the *Brotulotaenia* in a separate new subfamily Brotulotaeniinae within the Ophidiidae. Although its probable relationship with some neobythitine genera was suggested by Cohen (1974), the current state of ophidiid classification (Nielsen *et al.*, 1999) is still in chaos. This seems particularly true in the Neobythitiinae, because Howes (1992) suggested that it may be a paraphyletic assemblage related to various arrays of ophidiiformes. *Brotulotaenia* was not included in Howes' (1992) materials.

The phylogenetic implications of ontogeny have also been poorly founded in Ophidiiformes except for Carapidae (Gordon *et al.*, 1984; Markle and Olney, 1990), due to the paucity of larval information. Markle and Olney (1990) frequently referred to larval *Brotulotaenia* (Abousouan, 1980), as outgroups to the Carapidae, in their systematics of pearlfishes.

The so-called "extrilium" larvae (*sensu* Fraser and Smith, 1974), have been studied by Nielsen (1963), Fraser and Smith (1974), Moser (1981),

Gordon *et al.* (1984) and Okiyama (1988) chiefly based on large specimens (29.5 to 74 mm SL) comprising several forms. Their association with the neobythitine genus *Lamprogrammus* is suggested (Fahay and Nielsen, 2001).

In view of striking resemblances between the rubaniform and exterilium larvae, special attention was paid to their relationships in the following discussion, where Brotulinae and Ophidiinae were used as subfamily outgroups to *Brotulotaenia* (Brotulotaeniinae) and *Lamprogrammus* (Neobythitiinae). The Carapidae was also used as a family outgroup, when necessary.

*Body form and development pattern*—The 15.1 mm exterilium larva at preflexion stage (Fig. 7A) is remarkable in having several precociously elongated anterior dorsal-fin rays as in the rubaniform. Otherwise, it has essentially the same morphology as larger specimens (e.g., Okiyama, 1988; Fig. 7B). Despite marked differences in gut morphology and pelvic-fin development, these two larval morphs also share many distinct features such as a deep, laterally compressed body attaining about 70 mm SL and a characteristic melanophore pattern.

Although the so-called eterillium-like larvae have been described in some neobythitine ophidiids (Okiyama, p338, 1988; Nielsen and Evseenko, 1989), besides *Brotulotaenia*, these shared characters are peculiar to the rubaniform and exterilium, probably representing the highly specialized character state for the family.

*Gut configuration*—At a glance, one may consider that there are remarkable contrasts in the gut configuration between these two larval morphs. It is of interest, however, that the preflexion rubaniform (Fig. 2) has a peculiar gut with the anus separate from the ventral body profile, which is similar to the condition observed in the exterilium and the carapid genus *Eurypleuron* (Markle and Olney, 1990). Furthermore, they share the same coiling pattern of a remarkably long gut, supported by an exceptionally elongate cartilaginous ventral process of the coracoid, suggesting their homologous gut configuration. As in the typical exterilium gut independently

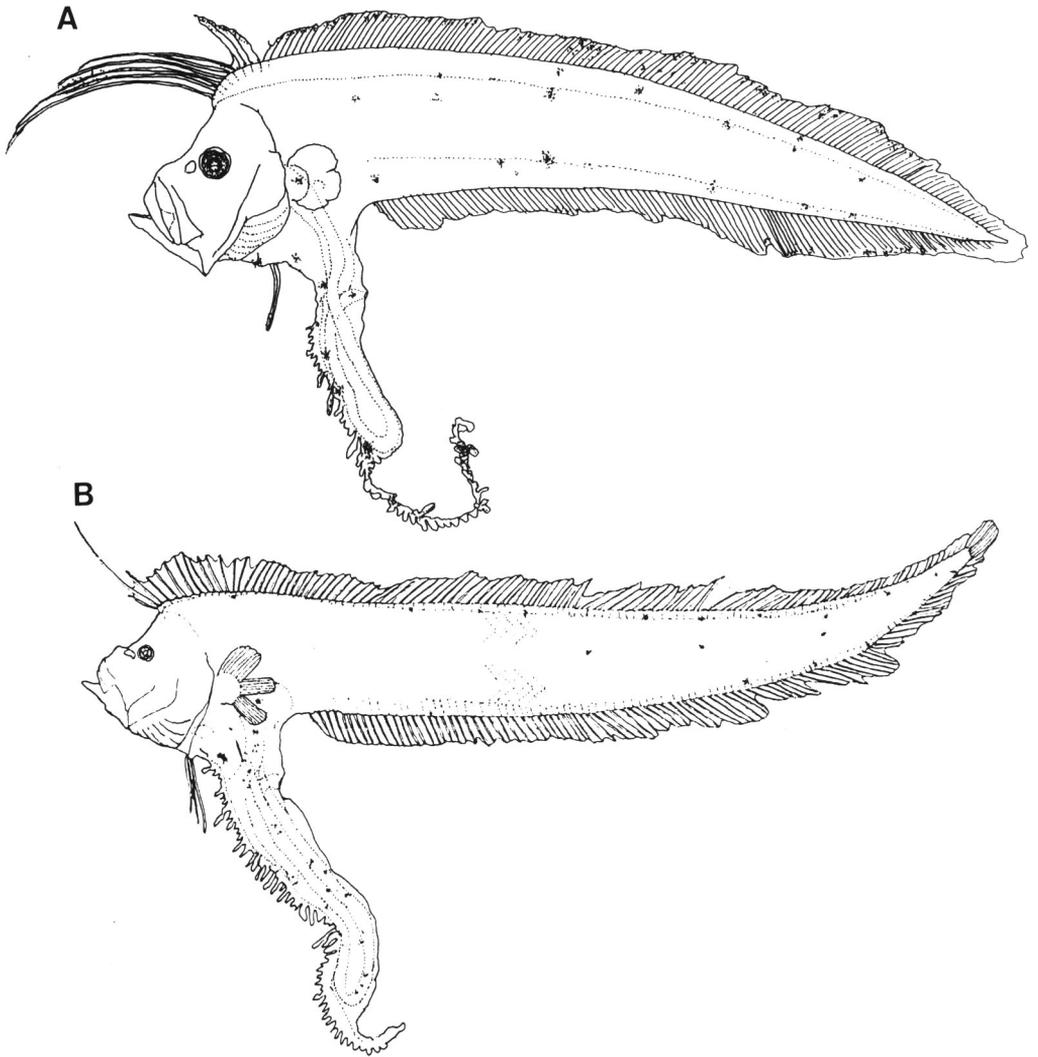


Fig. 7. Larvae of *Lamprogrammus* sp. (A) 10.0 mm NL, unctalogued, and (B) 38.0 mm SL (after Okiyama, 1988).

occurring in *Eurypleuron* (Markle and Olney, 1990), the shared gut configuration in these larval morphs may also represent the derived state in the Ophidiidae.

*Anterior axial skeleton:* The first dorsal pterygiophore is similarly modified into a compound structure in both larval morphs (Figs. 3A, B), although the first distal radial bearing the anterior-most two fin rays is free from the pterygiophore in the exterillum, and an additional free bone supporting the third dorsal fin ray occurs immediately posterior to it in the rubaniform. The ex-

terillum is also peculiar in the anterior shift and inclination of the first three dorsal pterygiophores over the neurocranium. These differences seem to imply a progressive specialization of the relevant features, with the condition in the exterillum being more advanced than in the rubaniform.

As in the vexillum of carapids, there are various conditions in ontogenetic modification of the anterior dorsal pterygiophores in the ophidiids, including a contrasting pattern between the rubaniform, exterillum, and *Benthocometes ro-*

*bustus*. The first dorsal pterygiophores are shifted slightly posteriad and modified as “an interesting flattened structure that resembles the predorsal bone of *Snyderidia* and *Pyramodon*” (Markle and Olney, 1990) in the former two, whereas 8-10 “predorsal” pterygiophores are retained after losing associated fin rays in *Benthocometes robustus* (Nielsen and Evseenko, 1989). Surely, these represent different states of derived features associated with precocious development of elongate dorsal-fin rays, because several larval ophidiids including *Brotula* (without such elongate dorsal fin rays) have 2–5 simple supraneural cartilages (Markle and Olney, 1990; Okiyama, unpublished). In this regard, it is of interest that the carapid genus *Encheliophis* has a uniquely derived feature, the presence of some anterior dorsal pterygiophores that do not support fin rays (Markle and Olney, 1990).

On the other hand, *Brotula* and the larval morphs under discussion here shares the presumed primitive state such as the reduced first neural spine relative to the second that is inclined posteriad (Markle and Olney, 1990), and epipleurals on at least the first two centra (Markle, 1989). Comparative information is unavailable concerning the peculiar pattern of pleural ribs being absent on the 3<sup>rd</sup> centrum in the rubaniform larvae and the 3<sup>rd</sup>–4<sup>th</sup> centra in the exterilium.

It is probable that the anterior dorsal pterygiophores and the anterior centra have independent developmental histories, the former being highly specialized in these two larval morphs.

*Pectoral- and pelvic-fin girdles*—The pectoral-fin girdle of the exterilium is almost identical with that of the rubaniform (Figs. 4A, B), except that the former has one postclethrum and the latter has two. This condition in the rubaniform (*Brotulotaenia*), also differs from the single postclethrum in adults described by Cohen (1974), suggesting the ontogenetic loss of the dorsal element. Since *Brotula* and the neobythitine *Dicrolene* have two postcleithra whereas other ophidiids lack them (Markle and Olney, 1990), the above features appear to represent the primitive

state.

Among the variously developed cartilaginous ventral processes of the coracoid in larval Ophidiiformes (Gordon *et al.*, 1984; Markle and Olney, 1990; Okiyama and Kato, 1997), those in the rubaniform and exterilium are unusually elongate as they are in the carapid *Eurypleuron*. Therefore, the suggestion that the relevant process appears to be a functional analogue of the postcleithra in carapids (Markle and Olney, 1990) does not hold true in these larval morphs.

The pelvic fins are precociously formed in both larval morphs, but their fin rays are greatly elongate in the rubaniform whereas short or fairly elongate (Fahay, pers. comm.) in the exterilium. Since the exterilium larva is referable to *Lamprogrammus* (Fahay and Nielsen, 2001), the elongate or short pelvic fins of these larval morphs are considered to be commonly lost after metamorphosis. This ontogenetic loss can be identified as the derived state from the character distribution throughout the Ophidiidae.

*Caudal skeleton*—The caudal skeleton of the rubaniform (*B. crassa*, 62.7 mm SL) originally described by Aboussouan (1980) was revised after reference to other specimens (*B. nielseni*, 69.5 mm SL) (Fig. 5A), which seem to share similar structure with that of the adults studied through X-ray photograph (Cohen, 1974). We also examined the caudal fin of a large exterilium (70 mm SL) (Fig. 5B). Despite several teratological features in the latter, they share a common pattern of caudal skeleton including two epurals, a uroneural and a ural 2, whereas there are several minor differences between them as follows: ossification is more advanced in the rubaniform than in the exterilium; the posterior edge of the hypural plate is rounded vs vertical; caudal-fin rays are 9 vs 8; pattern of the hypural fusion is irregular vs regular; and the parhypural is fused vs distinct.

A paucity of relevant information precludes further discussion on this character. It can be said, however, that there are significant differences in the ontogeny of hypural fusions between these larval morphs and *Brotula* (Markle and

Olney, 1990; Fujita, 1990).

In summary, the above descriptions reveal that the rubaniform and exterilium larvae commonly share many putative synapomorphies. From the ontogenetical point of view, therefore, it is likely that *Brotulotaenia* is more closely related to the neobythitine genus *Lamprogrammus* than current systematics of the Ophidiiformes suggest (Nielsen *et al.*, 2000), and the former is less derived than the latter.

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