Early development of the flathead, *Percophis brasiliensis* (Teleostei: Percophididae), from southeastern Brazil

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Abstract Morphological and osteological development of the flathead, *Percophis brasiliensis*, is described based on specimens collected from southeastern Brazilian waters. Identification of larvae was based on pigment pattern and meristic counts. Distinct melanophores were present on the bottom of the hindbrain, between the bases of the pelvic fins and on the bases of the pectoral fins. Within the family Percophididae only *Percophis brasiliensis* has 57 myomeres, which result in the larvae having an elongated body form. The larval pigment pattern and structure of the caudal complex suggest that the subfamilies Percophinae and Bembropinae are phylogenetically close, while the Hemerocoetinae belong to an advanced group within the family.

Key words. — Larval development; *Percophis brasiliensis*; southeastern Brazil.

The family Percophididae (suborder Trachinoidei) comprises three subfamilies: Percophinae, Bembropinae and Hemerocoetinae, with 13 genera and about 40 species (Nelson, 1994). The Percophinae includes a monotypic species, *Percophis brasiliensis* Quoy & Gaimard 1825, found in the western South Atlantic from Rio de Janeiro to Patagonia and is commonly caught by the bottom trawl fishery (Nakamura, 1986). Ribeiro (1915) provided a description of the species based on specimens collected from Rio de Janeiro. *Bembrops heterurus*, subfamily Bembropinae, has a similar distribution to *P. brasiliensis* (Menezes and Figueiredo, 1985; Das and Nelson, 1996).

Until recently, early life history data for the Percophididae has been scarce (Watson et al., 1984). A postflexion larva of *Hemerocoetes* sp. was first reported from New Zealand by Crossland (1982), Mori (1988) first described the early development of *Spinapsaron* sp. from Japanese waters and larvae of *B. anatirostris* were reported from the Gulf of Mexico by Richards (1990). Okiyama (1997) recently reviewed current knowledge of larval percophidid morphology and described the early development of *B. curvatura*, in addition to discussing the phylogenetic significance of the larval bubblemorph of *Bembrops* spp. and generic interrelationships of the family Percophididae.

In this paper we describe the morphological and osteological development of *P. brasiliensis* larvae, based on samples taken in southeastern Brazil.

Materials and Methods

Larvae used in this study were collected during the last 16 years in the southeast Brazil Bight between Cape Frio (23°00′S, 42°00′W) and Cape Santa Marta Grande (28°38′S, 48°50′W). Sampling was conducted using 60 cm Bongo nets, following the method described by Smith and Richardson (1977). Larvae were fixed in 10 % formalin solution. Stations sampled in the bight by the RV *Prof. W. Besnard*, were arranged in a systematic grid of about 20 n.m. intervals, from near the coast to the outer continental margin (Matsuura, 1998).

Larvae were examined under a dissecting microscope and measured using a micrometer attached to the objective lens. Body length (BL) was measured as notochord length for preflexion and flexion larvae and standard length for postflexion larva, taken from the tip of the upper jaw to the end of the notochord and to the posterior end of the hypural, respectively. Body depth (BD) was measured at the position of the shoulder girdle. Other measurements, including preanal length (PAL), prepelvic length (PPL), head length (HL), caudal peduncle depth (CPD) and snout length (SnL) were as defined by Moser (1996). Body

measurements were made on 78 larvae (2.6–22.5 mm BL: Table 1). Larvae were categorized as preflexion, flexion or postflexion stage, according to the state of notochord flexion (Ahlstrom et al., 1976). A series of 49 larvae (3.8–20.3 mm BL) was cleared with trypsin and stained with alizarin red and alcian blue for examination of skeletal development (Dingerkus and Uhler, 1977). All of the specimens used in this study are deposited at the Instituto Oceanográfico da Universidade de São Paulo (IOUSP).

Results

Morphology. From the earliest stage, the larvae had large heads with long tapering tails (Fig. 1A). There were 56–57 myomeres, the last few being difficult to count in some specimens. The mouth was terminal (Fig. 1A, B), although the lower jaw protruded past the upper jaw in larger larvae (Fig. 1C–F). Tiny serial canine teeth were present on the premaxilla, palatine and dentary from the preflexion stage (Fig. 1B). A few of the anterior premaxillary teeth became fang-like in large specimens (Fig. 1D). No head spination was observed during the larval period. The head was laterally compressed in the preflexion stage (Fig. 1A), but became slightly depressed in the postflexion stage (Fig. 1E, F). The snout was short in the preflexion stage (27% HL; Fig. 1A), but became elongated in the postflexion stage (36% HL; Fig. 1E). The gut was tightly coiled in a single loop, being greatly expanded in some individuals due to the presence of several copepods or fish larvae. A partially digested 9 mm fish larva was found in the gut of a 13 mm BL cleared and stained specimen. The average PAL ranged from 38% BL in the preflexion stage to 42% BL in later stages (Table 1). The position of the pelvic fins was jugular, the average PPL remaining at 22–25% BL during the larval period. The CPD increased during formation of the caudal fin.

Pigmentation. Several characteristic pigment patterns were present in early stage larvae, external melanophores being present on the nape, between the pelvic fin bases and on the pectoral fin base (Fig. 1B). A series of melanophores was present in a single row along the ventral midline of the tail. Internal melanophores were present on the posterior dorso-lateral surface of the midbrain, anterior margin of the forebrain, ventral edge of the hindbrain and dorsal surface of the gut (Fig. 1A, B). Two to four small melanophores appeared on the jaw tips in the preflexion stage. One small melanophore, present laterally on the hypural lobe in the flexion stage (Fig. 1B), migrated to the posterior edge of the hypurals and increased in number thereafter (Fig. 1C). The number of melanophores on the dorsal surfaces of the gut and midbrain, and along the ventral margin of the tail increased as larvae grew (Fig. 1C, D). The pelvic fins were the first fins to become pigmented, some melanophores appearing on the membranous part by 4.5 mm BL and increasing in number with growth (Fig. 1B). All of these melanophores remained during the entire larval stage, whereas the melanophores on the bottom of the hindbrain became obscure in postflexion larvae (Fig. 1D). The hindbrain pigment is apparently unique to *P. brasiliensis* larvae.

Fin formation. The first fins to form in *P. brasiliensis* larva were the pectoral fins, membranous pectoral fins being present in the smallest larvae examined. Pectoral fin ray formation started during the flexion stage at 6.1 mm BL (Fig. 1C), the full complement of 17 or 18 rays being attained by 12.0 mm BL. Pelvic fin buds were observed in larvae as small as 3.7 mm BL. Membranous pelvic fins appeared at 4.2 mm BL and fin ray formation (I, 5) was completed at about 6.9 mm BL. A continuous median finfold extended posteriorly from the occipital region to the anus in the preflexion stage (Fig. 1A, B), fin-ray formation of the second dorsal and anal fins starting simultaneously at about 6.8 mm BL along the posterior part of the tail and proceeding anteriorly with growth (Fig. 1D). A full complement of soft rays of both fins

Table 1. Morphometric data of *Percophis brasiliensis* larvae from southeastern Brazil

Developmental stage	*n*	Head length	Prepelvic length	Body depth	Preanal length	Snout/head length
Preflexion (2.6–4.2 mm BL)	5	21.8–26.4	21.4–22.5*	18.9–21.4	35.9–40.5	21.4–31.8
Flexion (4.5–9.8 mm BL)	42	26.7–32.7	21.2–26.7	18.1–22.7	36.7–44.0	29.2–39.0
Postflexion (10.0–22.5 mm BL)	31	28.4–33.8	18.7–26.9	12.8–19.8	36.7–44.1	30.2–39.0

Proportion of body parts relative to body length as %. *Number of specimens for prepelvic length=2.

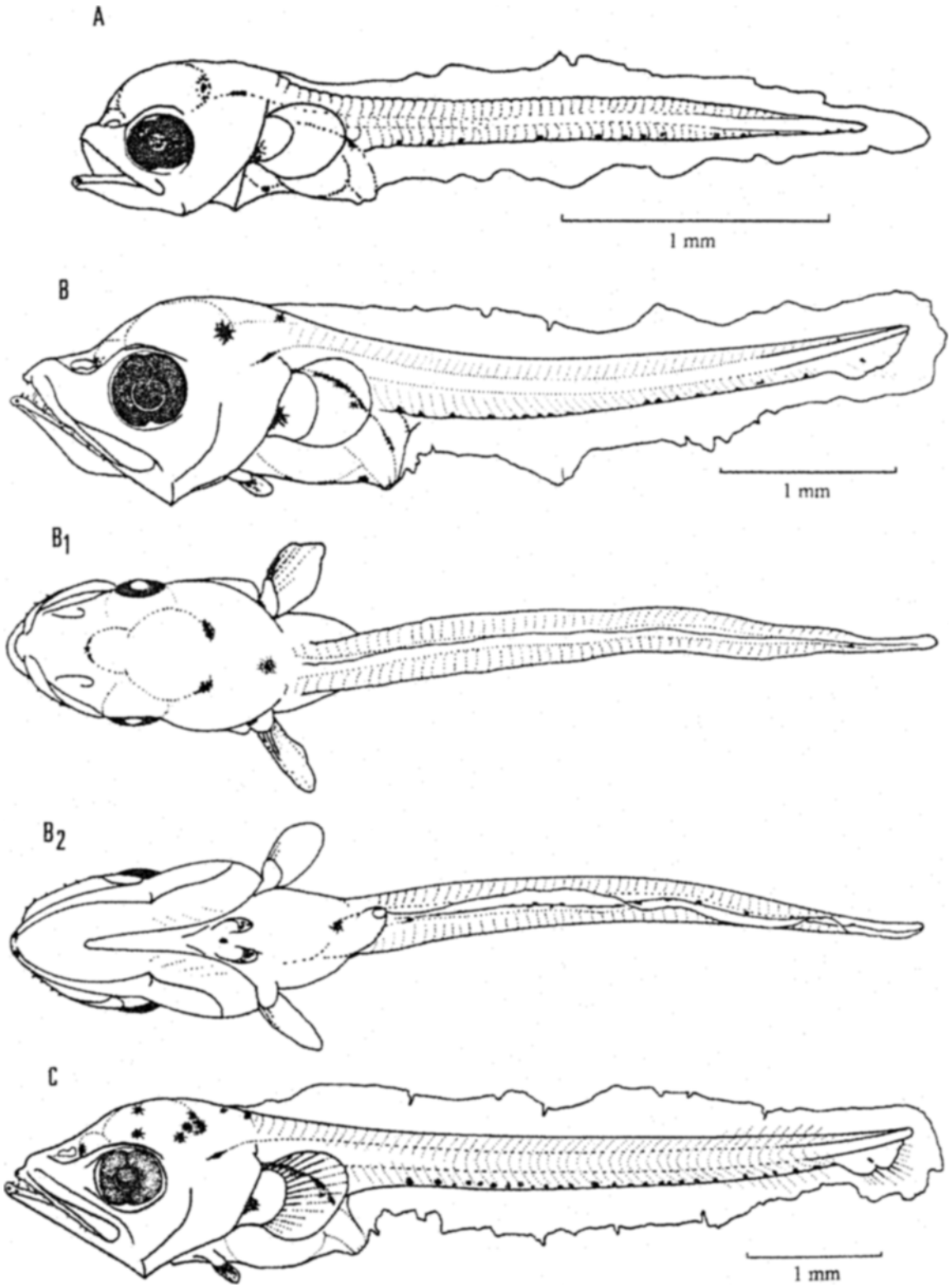

Fig. 1

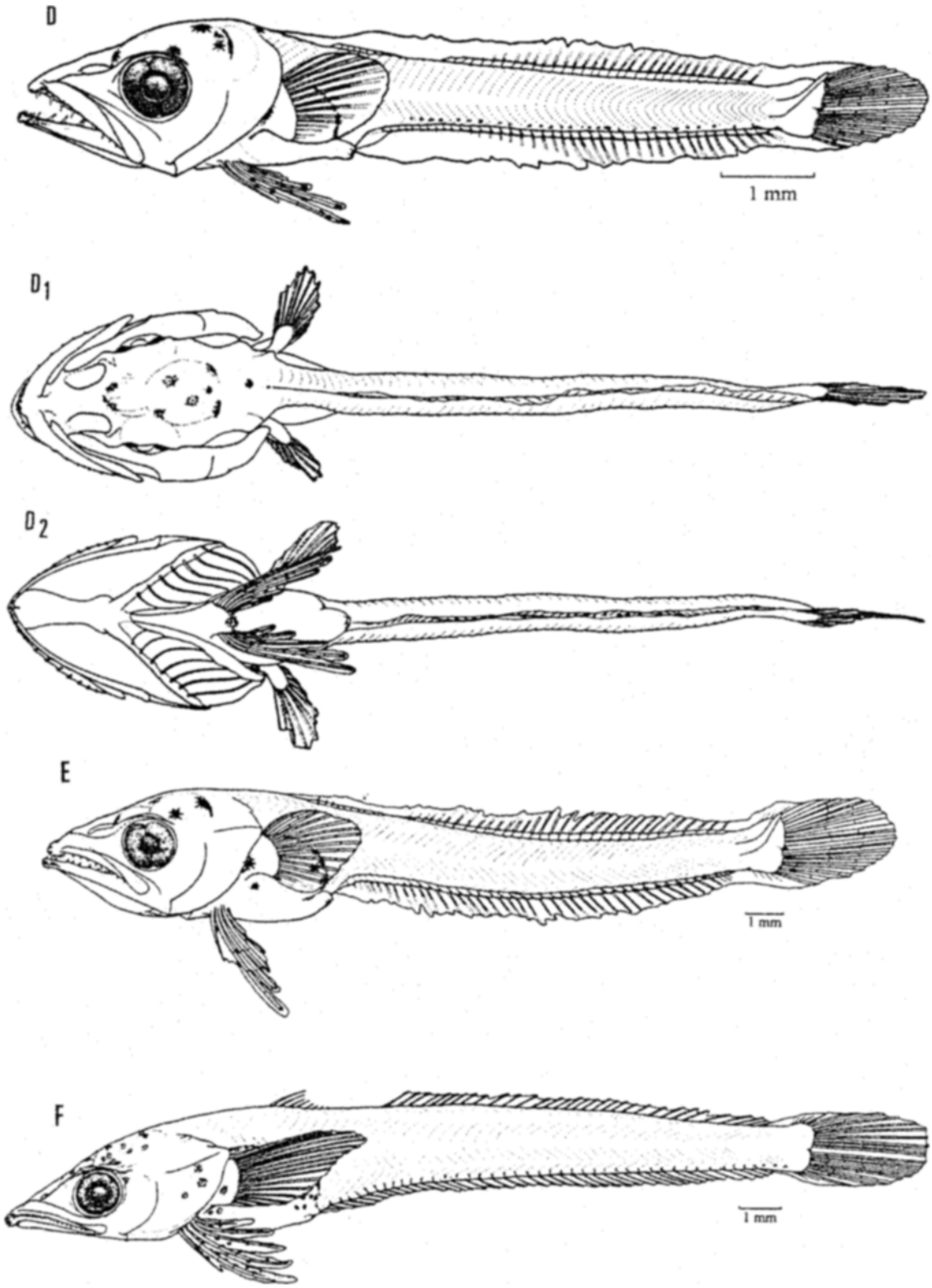

Fig. 1. Larval development of *Percophis brasiliensis* from southeastern Brazil. A) 2.6 mm BL (preflexion stage; IOUSP 3294); B) 5.0 mm BL (preflexion; IOUSP 1420-1); B_1) dorsal view; B_2) ventral view; C) 6.6 mm BL (flexion; IOUSP 3937); D) 9.0 mm BL (flexion; IOUSP 3536-1); D_1) dorsal view; D_2) ventral view; E) 11.3 mm BL (postflexion; IOUSP 1440); F) 22.5 mm BL (postflexion; IOUSP 2296).

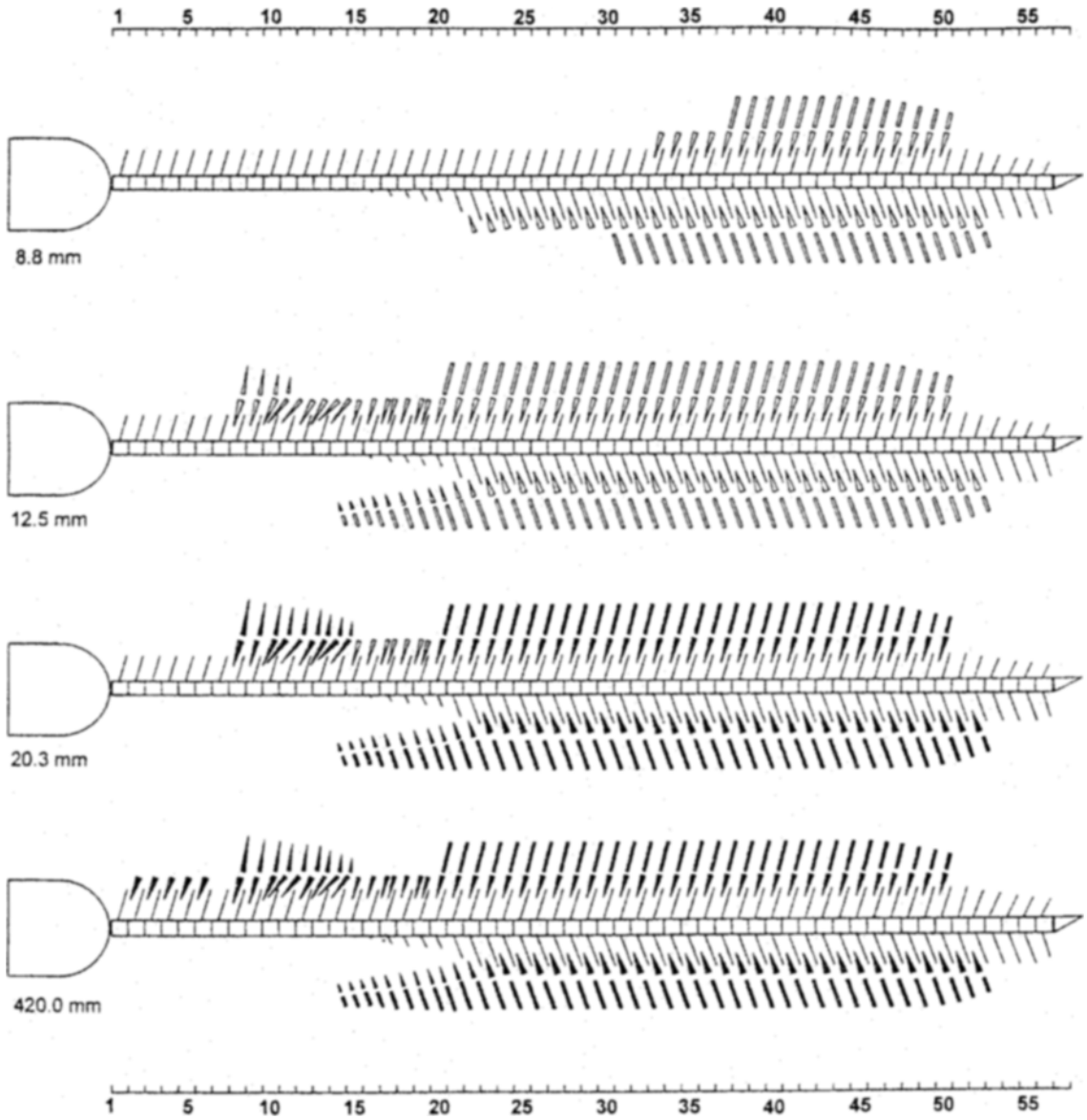

Fig. 2. Schematic representation of dorsal and anal fins and pterygiophore development in *Percophis brasiliensis* larvae relative to the vertebral column and head. Cartilaginous elements shown as white; ossified as black. Scale indicates vertebral number.

was attained at 14.2 mm BL, with 31 or 32 rays in the second dorsal fin and 40–42 rays in the anal fin. The spines of the first dorsal fin started to form at about 11.3 mm BL (Fig. 1E), being completed (8 or 9 spines) at 20.0 mm BL. Caudal fin ray formation started at 4.5 mm BL with the onset of notochord flexion (Fig. 1B). Hypurals and fin rays formed during the flexion stage, the adult complement of 9+8 principal rays being completed at about 9.0 mm BL. Procurrent caudal fin rays numbered 6 or 7+5. Thus, fin-ray development was completed in the sequence : pelvic,→caudal,→pectoral,→second dorsal and anal, and→first dorsal.

Formation of pterygiophores. The formation of cartilaginous pterygiophores of the dorsal and anal fin ray started posteriorly at about 6.8 mm BL and proceeded anteriorly (Fig. 2). Ossification of the pterygiophores started at about 20 mm BL. The first and second pterygiophores of the first dorsal fin were inserted into the seventh and eighth interneural spaces, respectively, and the third and fourth ptery-

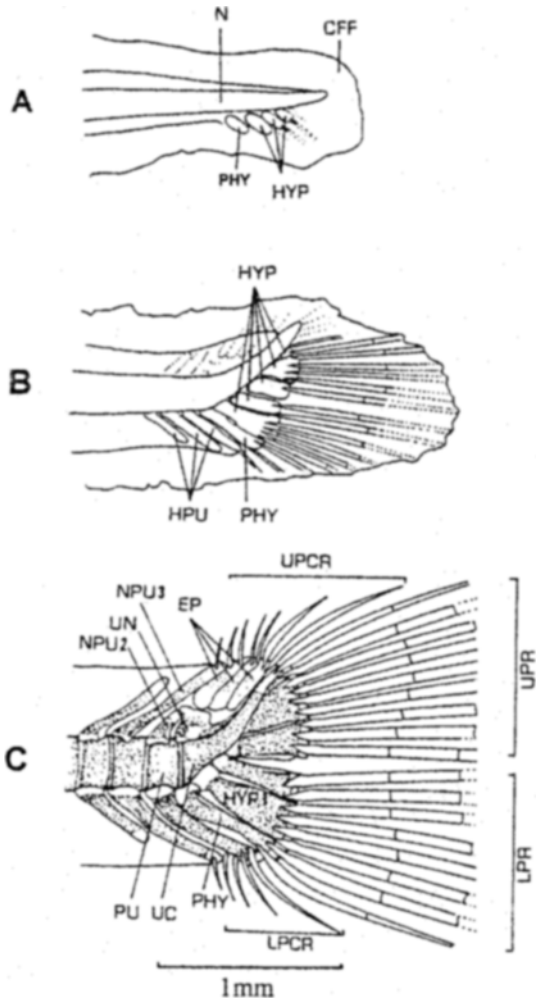

Fig. 3. Caudal complex of *Percophis brasiliensis* larvae. A) 5.5 mm BL (preflexion stage; IOUSP 3536-2); B) 8.0 mm BL (flexion; IOUSP 1420-2); C) 20.3 mm BL (postflexion; IOUSP 1437). Ossified region stippled; cartilaginous region blank; dotted line indicates initial formation of cartilaginous structures. CFF-caudal finfold; EP-epural; HYP-hypural; LPR-lower principal caudal rays; LPCR-lower procurrent rays; N-notochord; NPU-neural spine of preural centra; PHY-parhypural; PU-preural centrum; UC-ural centrum (=urostyle); UN-uroneural; UPCR-upper procurrent rays; UPR-upper principal caudal rays.

giophores into the ninth interneural space (Fig. 2). The first pterygiophore of the second dorsal fin was inserted into the 19th interneural space and each following pterygiophore into the adjacent interneural space in a 1 : 1 ratio. Although supraneural bones had not formed in the largest cleared and stained specimen (20.3 mm BL), adult specimens had five enlarged supraneurals inserted into the anterior five interneural spaces (Fig. 2).

Formation of vertebrae. The formation of cartilaginous vertebral centra started anteriorly at about 11.3 mm BL, thereafter proceeding posteriorly. The posteriormost cartilaginous preural centra started to form at about 12.2 mm BL, development proceeding anteriorly. Ossification of the vertebral centra started at about 17.0 mm BL in the anteriormost vertebral centra and proceeded posteriorly. The largest cleared and stained specimen (20.3 mm BL) had 22 precaudal and 35 caudal vertebrae.

Formation of caudal complex. Several fin rays were present in the caudal finfold at 5.0 mm BL. The cartilaginous hypurals and parhypural started to form at about 5.5 mm BL, during the flexion stage (Fig. 3A). At 11.5 mm BL the urostyle and principal caudal rays were partially ossified, although the epurals had not formed. The complete caudal complex was attained at about 20.3 mm BL (Fig. 3 C). The five hypurals were not fused each other, being loosely attached to the urostyle.

Identification

The high count of 56–57 myomeres separates the larvae of *Percophis brasiliensis* from those of all other percophidids, the long second dorsal and anal fin bases also being a characteristic of the former species. *Percophis brasiliensis* larvae are usually separated from the larvae of other families characterized by jugular pelvic fins and long second dorsal and anal fin bases by their large head, elongated body and distinctive pigment pattern. Flexion larvae of Chiasmodontidae are similar to *P. brasiliensis*, but have more posterior pelvic fins and fewer vertebrae (33–46) (Watson and Sandknop, 1996).

The Blenniidae, Clinidae and Labrisomidae also have jugular pelvic fins and a long dorsal fin base, but their dorsal fins are not separated and they have fewer than five pelvic fin rays.

Okiyama (1997) described the characteristic larval bubblemorph of some *Bembrops* species and discussed their ecological and phylogenetic significance. Because the expansion of the dermal sac in the head region was observed only in *Bembrops* larvae from the Pacific (not in those from the Atlantic), this character can be considered as a morphological adaptation of the Pacific larval form rather than a specialization of the genus *Bembrops*. The formation of pelvic and pectoral fin rays of *Bembrops* larvae seems to occur simultaneously (Richards, 1990; Okiyama, 1997), the pelvic fins having a surface pigment simi-

lar to those of *P. brasiliensis*.

A large patch of melanophores on the ventral surface of the caudal peduncle is common to larvae of three *Bembrops* species (Okiyama, 1997), but was not found in *P. brasiliensis*. Pigments in common observed in *Percophis* and *Bembrops* included: melanophores on the posterior dorso-lateral surface of the midbrain, anterior margin of the forebrain, base of the pectoral fins and between the pelvic fin bases. Postflexion larvae or planktonic prejuveniles of other percophidids (*Chrionema*, *Matsubaraea*, *Hemerocoetes* and *Spinapsaron*) do not share these pigment patterns (Okiyama, 1997). Another similarity between *Percophis* and *Bembrops* was found in the caudal complex. Within the family Percophididae, only the latter two genera have five hypurals unfused in the adults. The hypurals of *Matsubaraea* (subfamily Hemerocoetinae) are fused to form upper and lower plates (hypurals 1+2 and 3+4+5), a character common to many trachinoid taxa (Fujita, 1990).

The subfamilies Percophinae and Bembropinae have common characters in both pigment pattern and structure of the caudal complex, suggesting a phylogenetically close relationship, whereas the Hemerocoetinae may belong to a more advanced group within the family due to the presence of fused hypurals (Dunn, 1983). In order to verify the phylogenetic relationship within the family Percophididae, information on the early development of the subfamily Hemerocoetinae is necessary, especially that of the preflexion and flexion stages.

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Literature Cited

Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci., 26: 285–402.

Crossland, J. 1982. Distribution and abundance of fish eggs and larvae from the spring and summer plankton of north-east New Zealand, 1976–78. Fish. Res. Bull., New Zealand, 24: 11–57.

Das, M. K. and J. S. Nelson. 1996. Revision of the percophid genus *Bembrops* (Actinopterygii: Perciformes). Bull. Mar. Sci., 59: 9–44.

Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technol., 52: 229–232.

Dunn, J. R. 1983. The utility of developmental osteology in taxonomic and systematic studies of teleost larvae : A review. NOAA Tech. Rep., NMFS Circ., 450: 1–19.

Fujita, K. 1990. The caudal skeleton of Teleostean fishes. Tokai Univ. Press, Tokyo. 897 pp.

Matsuura, Y. 1998. Brazilian sardine (*Sardinella brasiliensis*) spawning in the southeast Brazilian Bight over the period 1976-1993. Rev. bras. oceanogr. 46: 33–43.

Menezes, N. A. and J. L. Figueiredo. 1985. Manual de peixes marinhos do sudeste do Brasil. V. Teleostei (4). Museu de Zoologia, Universidade de São Paulo, São Paulo. 105 pp.

Moser, H. G. 1996. Introduction. Pages 1–72 *in* H. G. Moser, ed. The early stages of fishes in the California Current region. CalCOFI Atlas, No. 33. Allen Press, Lawrence.

Mori, K. 1988. Trichonotidae, Creediidae and Percophidae. Pages 724–725 *in* M. Okiyama, ed. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo.

Nakamura, I. 1986. Important fishes trawled off Patagonia. Japan Marine Fisheries Resource Research Center, Tokyo. 369 pp.

Nelson, J. S. 1994. Fishes of the world, third edition. John Wiley & Sons, New York. 600 pp.

Okiyama, M. 1997. Two types of pelagic larvae of *Bembrops* (Trachinoidea: Percophidae), with notes on their phylogenetic implication. Bull. Mar. Sci., 60: 152–160.

Ribeiro, A. de M. 1915. Fauna Brasiliense. Peixes. V. (Eleutherobranchios Aspirophoros). Physoclisti. Arch. Mus. Nac., Rio de Janeiro. 17: 1–679.

Richards, W. J. 1990. List of the fishes of the western central Atlantic and the status of early life stage information. NOAA Tech. Mem., NMFS-SEFC-267: 1–88.

Smith, P. E. and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap., 175:1–100.

Watson, W. 1996. Blenniidae: combtooth blennies. Pages1182–1199 *in* H.G. Moser, ed. The early stages of fishes in the California Current region. CalCOFI Atlas, No. 33. Allen Press, Lawrence.

Watson, W., A. C. Matarese and E. G. Stevens. 1984. Trachinoidea: development and relationships. Pages 554–561 *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. Am. Soc. Ichthyol. Herpetol., Spec. Publ. 1. 760 pp.

Watson, W. and E. M. Sandknop. 1996. Chiasmodontidae: swallowers. Pages 1131–1137 *in* H.G. Moser, ed. The early stages of fishes in the California Current region. CalCOFI Atlas, No. 33. Allen Press, Lawrence.