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DEVELOPMENT OF *SCOMBROLABRAX HETEROLEPIS* (PISCES, SCOMBROLABRACIDAE) AND COMMENTS ON FAMILIAL RELATIONSHIPS

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ABSTRACT

Scombrolabrax heterolepis larvae were caught with plankton nets in the upper 200 m of the oceans from about 30°S to 30°N during all months with a peak catch in the seasonal winter months. Surface temperatures at capture stations ranged from 25.9° to 28.6°C. Development of 132 larvae (2.4 NL–14.7 mm SL) and three juveniles (22.5, 68.1, 69.5 mm SL) of *S. heterolepis* from the Pacific, Atlantic and Indian oceans is described. In small larvae, 2.6–5.0 mm SL, pigmentation resembled that of *Thunnus*. Larvae longer than 5.0 mm SL acquired distinct pigmentation on the jaws, brain, pectoral symphysis, gular membrane, dorsal body and lateral tail. Meristics are: 13 + 17 = 30 vertebrae; D XII, 15–16; A III, 16–17; P_1 18–19; P_2 I,5; C 8–9 + 9 + 8 + 9–10; 7 branchiostegal rays; first arch outer gill rakers 5–6 + 3; first closed haemal arch on 12th centrum; 9 pairs of dorsal, 11 pairs of pleural ribs. No predorsal bones were present. The proximal and distal radials of the median fin pterygiophores developed from one piece of cartilage. Middle radials and a stay were present in addition to the proximal and distal radials for five posteriormost dorsal and anal pterygiophores. The early pectoral fin supports were a bony cleithrum and a coraco-scapular cartilage. Later, four cartilaginous radials developed, and the scapula and coracoid ossified within the coraco-scapular cartilage. The basipterygium originated from rod-shaped cartilage that developed bony wings after ossification. Supporting elements of the caudal skeleton were those of a basal perciform: 3 centra (2 preural and 1 urostyle), 2 autogenous haemal spines, 1 parhypural, 5 hypurals, 3 epurals, 2 pairs of uroneurals, 1 specialized neural arch and 1 neural spine. No ontogenetic fusion of these elements occurred. Neural and haemal arches and spines were present first in cartilage. Their ossification occurred concurrently with segmentation and ossification of the notochord. Relationship of *S. heterolepis* to scombrids, gempylids and trichiurids is discussed, and it is suggested that *S. heterolepis* is a scombroid fish belonging to a separate family Scombrolabracidae.

In this paper we describe the larval development of the oceanic perciform fish *Scombrolabrax heterolepis* and discuss its relationships to other scombroid fishes. The familial relationship of *S. heterolepis* is unclear. In his original description, Roule (1922) placed it in a new family Scombrolabracidae, but since then it has been placed in the perciform families Apogonidae and Gempylidae (Grey, 1960). We have investigated its relation to the Scombridae, Gempylidae and Trichiuridae and make a provisional recommendation on its family status. Greenwood et al. (1966) considered the Scombroidei to consist of the families Scombridae, Gempylidae, Trichiuridae, Istiophoridae, Xiphiidae and Luvaridae. Gosline (1968) removed the Istiophoridae, Xiphiidae and Luvaridae from the Scombroidei to a separate suborder, the Xiphioidei. We agree with Gosline (1968) and tentatively recognize *S. heterolepis* in the family Scombrolabracidae, suborder Scombroidei. For this study, we consider the scombroids to consist of the families Scombridae, Gempylidae, Trichiuridae and Scombrolabracidae, although we did not study all species represented by these families (See Appendix).

Larvae of *S. heterolepis* are uncommon in fish collections. A few specimens are usually caught during offshore larval fish surveys in tropical waters and are often mistaken for tuna larvae.

Table 1. Comparison of characters among *Scombrolabrax*, *Morone* (a primitive percoid) and the species of Gempylidae, Trichiuridae and Scombridae examined by us (see Appendix)

	Scombrolabrax	Gempylidae	Trichiuridae	Scombridae	*Morone*
First dorsal fin develops before or after second dorsal	after	before*	before*	before*§	after
Predorsal bones	absent	absent†	absent	absent	present
Number of spines supported by first dorsal fin pterygiophore	2	2	2	2	3
First dorsal fin pterygiophore inserts in interneural space number	3	2‡	2	3	3
Number of stays for posteriormost dorsal and anal fin pterygiophore	1	2¶	1	1	1
Dorsal and anal finlets	absent	present or absent	absent	present	absent
Pelvic fin	I,5	I,5; I,4; I,2; I,1; I	I,3; I,2; I,1; I	I,5	I,5
Number of epurals	3	3	1 to 3**	2	3
Number of vertebrae supporting caudal fin rays (urostyle counted as one vertebra)	3	3	3**	4–5††	3
Procurrent spur (Johnson, 1975)	present	absent or present very reduced	absent**	absent	present
Number of vertebrae, precaudal and caudal	30 = 13 + 17	31 to 53, usually more precaudal, fewer caudal	58 to 192, usually fewer precaudal, more caudal	31 to 64, usually fewer precaudal, more caudal	25 = 11,12 + 13,14
Stay on pharyngobranchial of 4th arch	absent	absent	absent	present	absent

* In genera where larva are known.
† Except in *Ruvettus*, which has one predorsal bone.
‡ In *Epinnula*, *Neoepinnula* and *Rexea* we were unable to determine the exact insertion of the first two pterygiophores.
§ Except in *Scomber* and *Rastrelliger*.
¶ Except *Lepidocybium*, *Rexea* and *Gempylus* have one stay.
** For Trichiurids with tails.
†† 3 in *Scomber*, *Rastrelliger* and *Grammatorcynus*.

Figure 1. Capture localities of *Scombrolabrax heterolepis* larvae and juveniles used in this study. Some black dots may represent more than one geographic locality.

Materials and Methods

A total of 132 larvae (2.4 NL–14.7 mm SL) and 3 juveniles (22.5, 68.1, 69.5 mm SL) was used in this study. Larval specimens and the smallest juvenile (22.5 mm SL) were stored in 3% Formalin buffered with marble chips; the larger juveniles were stored in 40% isopropanol. All were measured with a calibrated ocular micrometer or with dial calipers. Notochord length (NL) was taken from the tip of the upper jaw to the tip of the notochord before and during notochord flexion. Standard length (SL) was taken from the tip of the upper jaw to the posterior border of the hypurals after complete notochord flexure. After pigment patterns were noted on all larvae and juveniles, 47 of them were cleared and stained for osteological study. Of these, 43 were cleared and stained after Taylor (1967) method and 4 were stained for cartilage and bone after Dingerkus and Uhler (1977). All specimens studied for fin ray and bone development were maintained in 100% glycerine and studied under 100× to 150× magnification. A structure was considered to be ossifying if it took up alizarin stain. The difficulty of viewing cartilage was overcome by changing light intensity and the angle of the substage mirror. Most drawings were executed with the aid of a camera lucida. For comparison with *S. heterolepis*, juvenile and adult specimens from the families Scombridae, Gempylidae, Trichiuridae and Percichthyidae were cleared and stained (Table 1 and Appendix).

We use a composite terminology for the caudal complex following Gosline (1961a,b), Nybelin (1963) and Monod (1968).

Distribution

One hundred and thirty-two larvae (2.4 NL–10.4 mm SL, 14.7 mm SL) and three juveniles (22.5, 68.1 and 69.5 mm SL) were collected in the tropical and subtropical waters of the Atlantic, Indian and Pacific oceans (Fig. 1). The specimens were collected in May, June, July, October and November in the Indian Ocean, in January through April, September, October and December in the Pacific, and in February, March, April and July through December in the Atlantic. This indicates that spawning probably occurs throughout the species range and throughout the year. A probable spawning peak during the seasonal winter months was indicated by greater numbers of larvae caught during those months. From localities where we have surface temperatures coupled with capture of *S. heterolepis* the range was 25.9° to 28.6°C. Sampling depths indicate that larvae

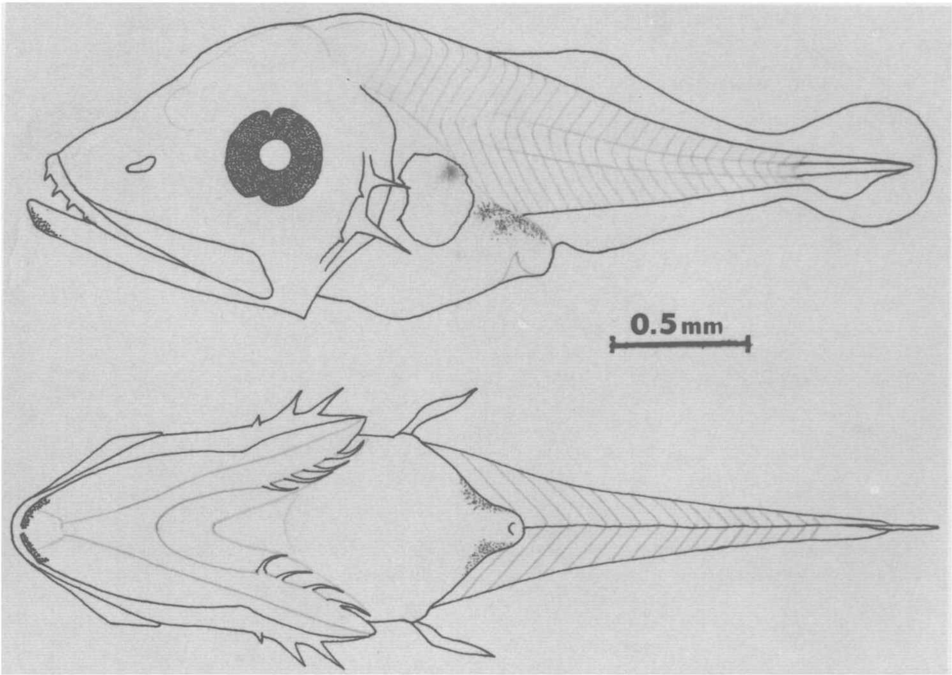

Figure 2. *Scombrolabrax heterolepis* larva, 3.1 mm NL, from the Indian Ocean. Top: left lateral view, bottom: ventral view.

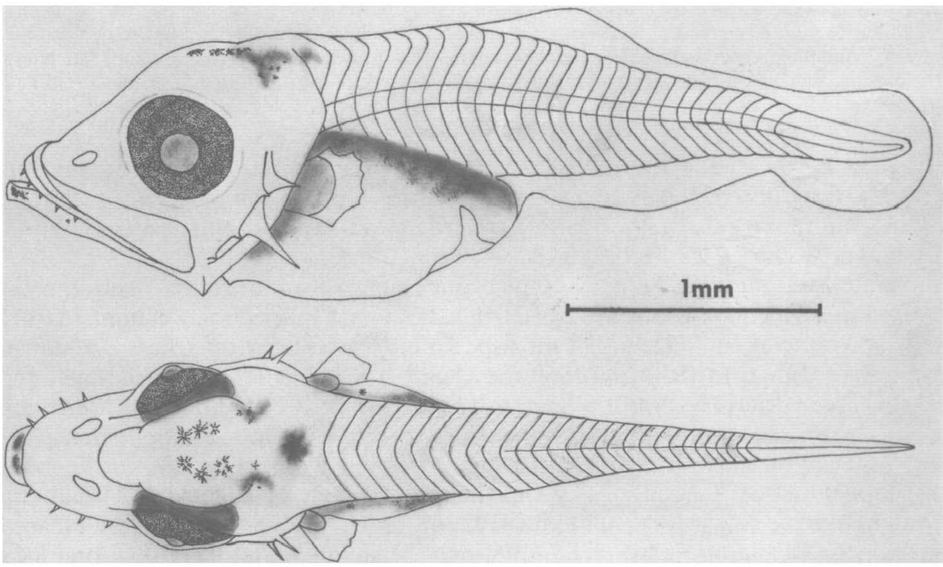

Figure 3. *Scombrolabrax heterolepis* larva, 3.7 mm NL, from the Atlantic Ocean. Top: left lateral view, bottom: dorsal view.

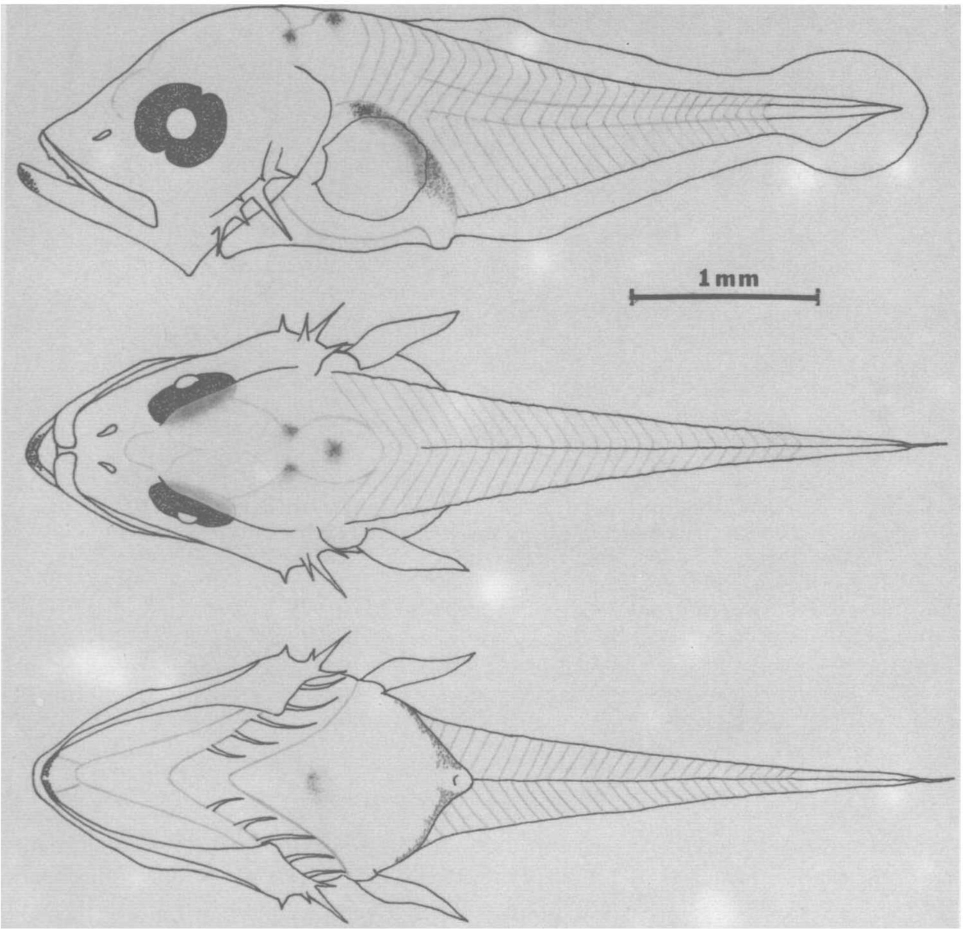

Figure 4. *Scombrolabrax heterolepis* larva, 4.4 mm NL, from the Pacific Ocean. Top: left lateral view, center: dorsal view, bottom: ventral view.

of *S. heterolepis* live in the mixed surface layer (upper 200 m). The most interesting distribution feature is their apparent absence from the eastern Pacific and eastern Atlantic oceans, although two records of adults from the eastern Atlantic are known (Roule, 1922; Arté, 1952).

Juvenile and adult *S. heterolepis* are uncommon in collections. The species was first described by Roule (1922) from a 259 mm TL specimen caught in 1915 south of Madeira. In 1952, a 278 mm specimen was caught off Cape Finisterre, Spain (Arté, 1952). In 1958 and 1960 the U.S. Fish and Wildlife Service research vessel OREGON caught several *S. heterolepis* in the Gulf of Mexico Sta. 2191 and 3102 with a 41-foot mid-water trawl. Of these, one 176 mm SL specimen was described by Grey (1960), another 140 mm specimen by Gosline (1968). We were loaned four of these specimens. Two of the four are deposited with the University of Miami Marine laboratory, UMML 7102, 68.1, 69.5 mm SL; both were cleared and stained. Of the other two (U.S. National Museum USNM 187651), one 83.9 mm SL specimen was cleared and stained and proved to be a stromateoid *Cubiceps pauciradiatus* (Family Nomeidae). The other is a *S. heterolepis* (98.3 mm

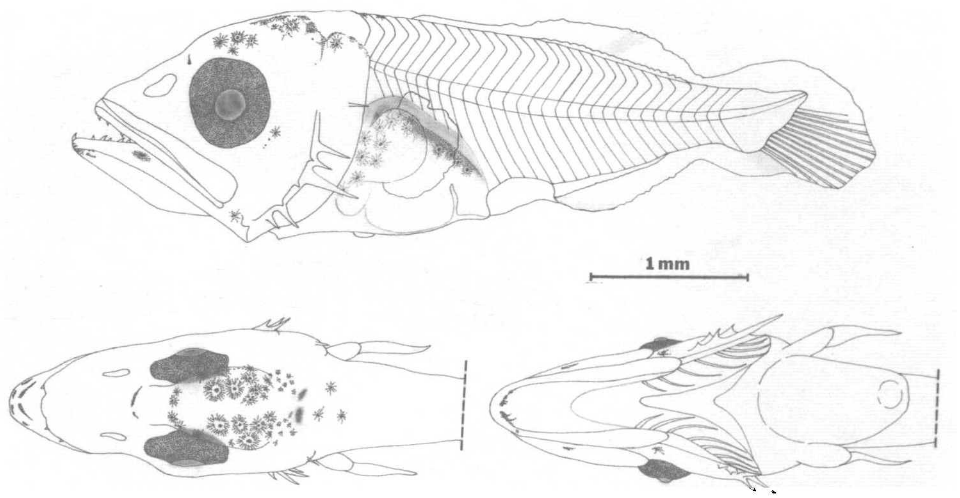

Figure 5. *Scombrolabrax heterolepis* larva, 4.4 mm NL, from the Atlantic Ocean. Top: left lateral view, bottom left: dorsal view, bottom right: ventral view.

SL) but was not cleared and stained. Higgins et al. (1970) reported that the U.S. National Museum has a total of about 25 *S. heterolepis* (USNM #187648–187652). They further reported on 37 *S. heterolepis* from the Indian and Pacific oceans, mostly taken from predator stomachs ranging 42–230 mm SL with a 108 mm SL mean. We did not examine those specimens.

PIGMENTATION

Pigmentation of *S. heterolepis* larvae is distinctive and the larvae superficially resemble scombrids, but the combination of characteristic melanophores and meristics exclude it from any known scombrid species (compare with Matsumoto et al., 1972; Richards, 1973; and Richards and Potthoff, 1974). Pigment characters of scombrids are compared with *S. heterolepis* in a later section.

Description.—Pigments acquired with length (Table 2, Figs. 2–11) increase and spread until body is covered with melanophores (Figs. 10, 11). Melanophores are acquired at shorter length in Atlantic Ocean than in Pacific and Indian oceans (Table 2, Figs. 4, 5). Smallest larvae (2.4–3.1 mm NL) only with melanophores at tip of lower jaw and over posterior portion of gut (Fig. 2). In larvae longer than 3.2 mm NL, melanophores form over anterior portion of gut and extend over into heart area in larvae longer then 4.0–4.3 mm NL (Table 2). Melanophores first observed over hindbrain at 3.2 mm NL in specimens with or without midbrain pigment, and forebrain melanophores acquired last at 4.3–5.4 mm NL or SL (Table 2). Melanophores form on head at tip and ramus of upper jaws and in angle of jaws and behind eye and these spread as larvae grow until whole head is covered in juveniles (Figs. 5–10). Characteristic lower jaw melanophores form at tip of jaw and at center of ramus at 3.5–5.7 mm NL or SL (Figs. 5, 6). After 6.0 mm SL melanophores added along entire ramus (Figs. 7, 8). Dorsal body melanophores first develop between 4.4 mm NL and 5.7 mm SL at nape, but spread posteriorly along left and right sides of first dorsal fin (Table 2, Figs. 5–9). Lateral body melanophores appear in larvae longer than 7 mm SL externally just above gut and spread dorsally, ventrally and posteriorly (Figs. 8, 9). Presence of

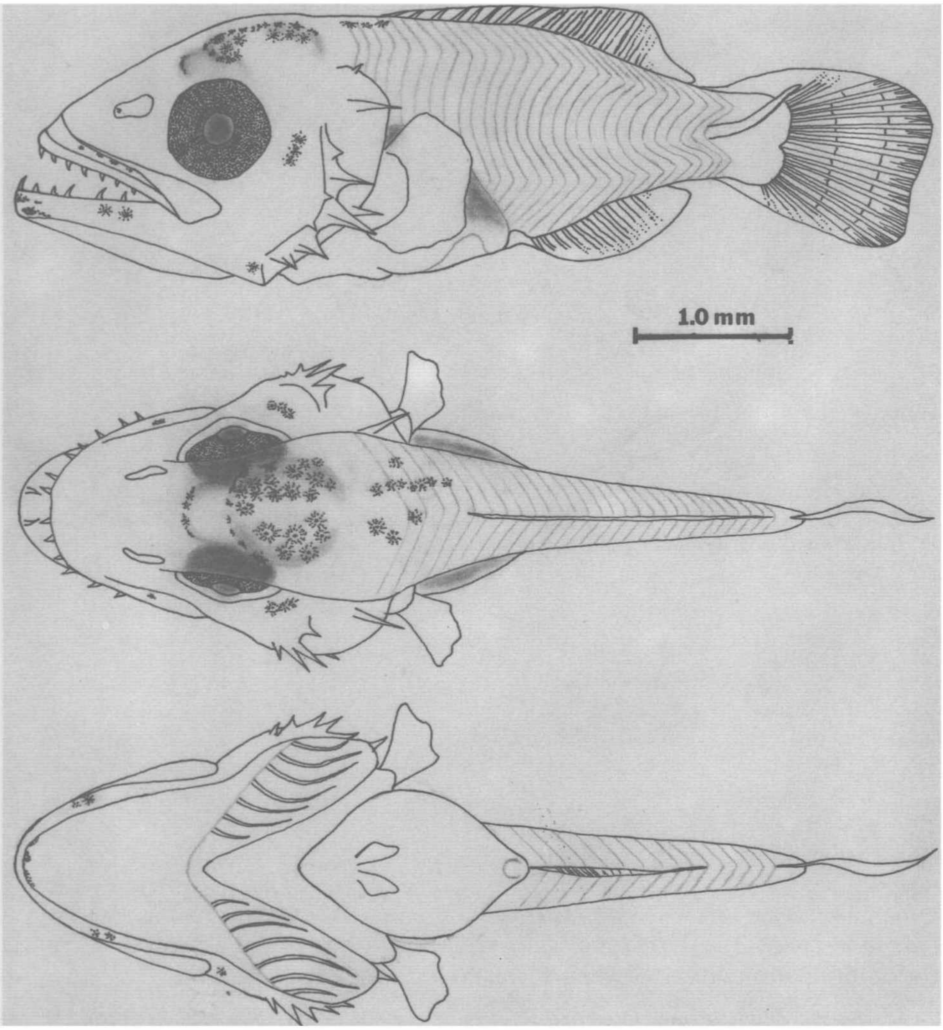

Figure 6. *Scombrolabrax heterolepis* larva, 5.0 mm SL, from the Atlantic Ocean. Top: left lateral view, center: dorsal view, bottom: ventral view.

lateral tail melanophores just anterior to caudal peduncle characteristic. Melanophores appear first as few internal cells at lateral midline (not figured) between 4.7 and 5.7 mm SL (Table 2); external melanophores then appear spreading dorsad and ventrad (Figs. 7–9). Body and tail melanophores eventually join covering all except hypural and ventral trunk area (Fig. 10); these areas become pigmented in larger juveniles (Fig. 11). Pigmentation observed in juvenile specimens on all fins except pectoral (observations on fin pigmentation limited because very few juveniles were available to us, and those were old and bleached).

Osteological Development

The development of the bones is described for each area of the skeleton with the exception of the jaws, suspensorium, opercular cover and neurocranium.

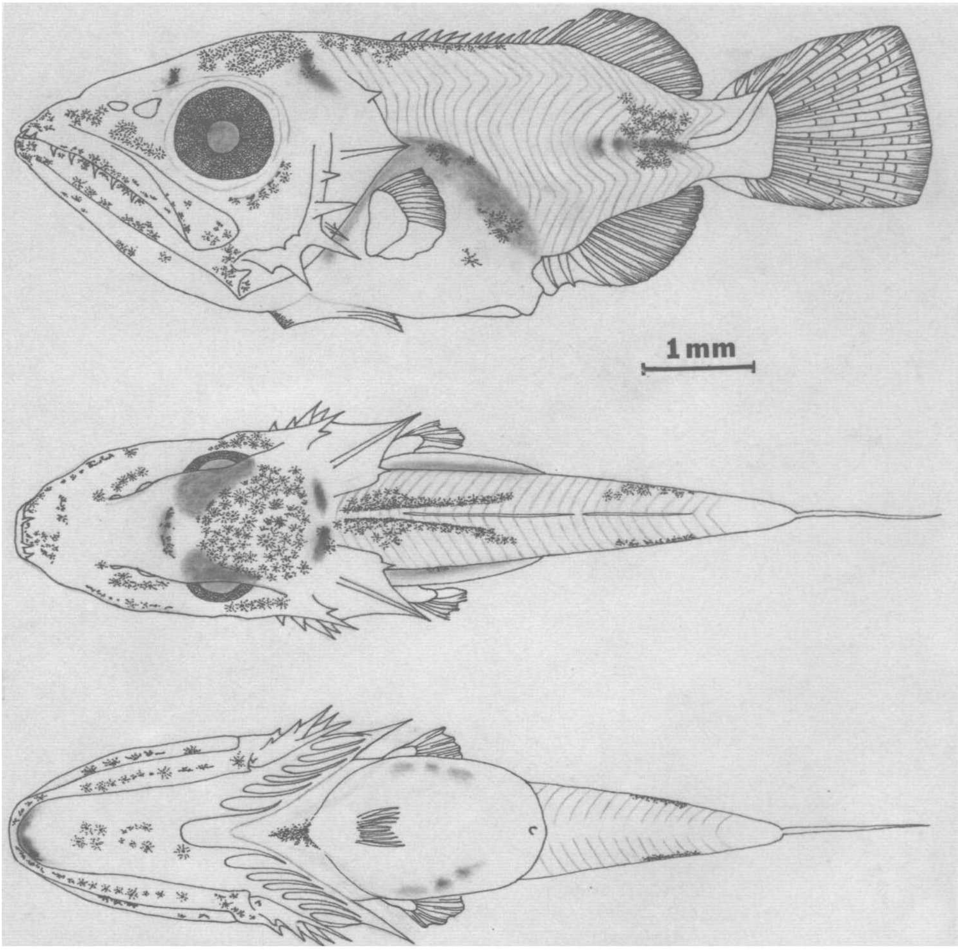

Figure 7. *Scombrolabrax heterolepis* larva, 6.1 mm SL, from the Atlantic Ocean. Top: left lateral view, center: dorsal view, bottom: ventral view.

Branchiostegal Rays.—Full complement of 7 branchiostegal rays acquired during notochord flexion at 4.4–4.9 mm NL (Table 3). Four to five seen in smallest cleared and stained specimens from Atlantic Ocean at 3.6 and 3.7 mm NL (Table 3) and 3 seen in smallest specimen from Indian Ocean at 3.9 mm NL.

Gill Rakers and Pharyngeal Bones.—Five gill arches, first three support outer and inner row of gill rakers on ceratobranchials. Rakers on epi- and hypobranchials develop into toothpatches (Fig. 12); fourth arch has single row of rakers and toothpatches, and fifth arch consists of ceratobranchial with large toothplate (lower pharyngeal); epi- and hypobranchials absent from fifth arch.

Pharyngobranchial bones (upper pharyngeals) present on first four arches distad to epibranchials. First bone is suspensory pharyngeal and lacks teeth; remaining three pharyngobranchial bones have toothplates. Counts of outer row rakers of first arch ceratobranchial given in Table 3. Cartilaginous gill arches present in smallest 3.6 mm NL specimen. Single outer raker present in the dermis in two 4.1 mm NL specimens (Table 3) on first ceratobranchial slightly anterior to angle.

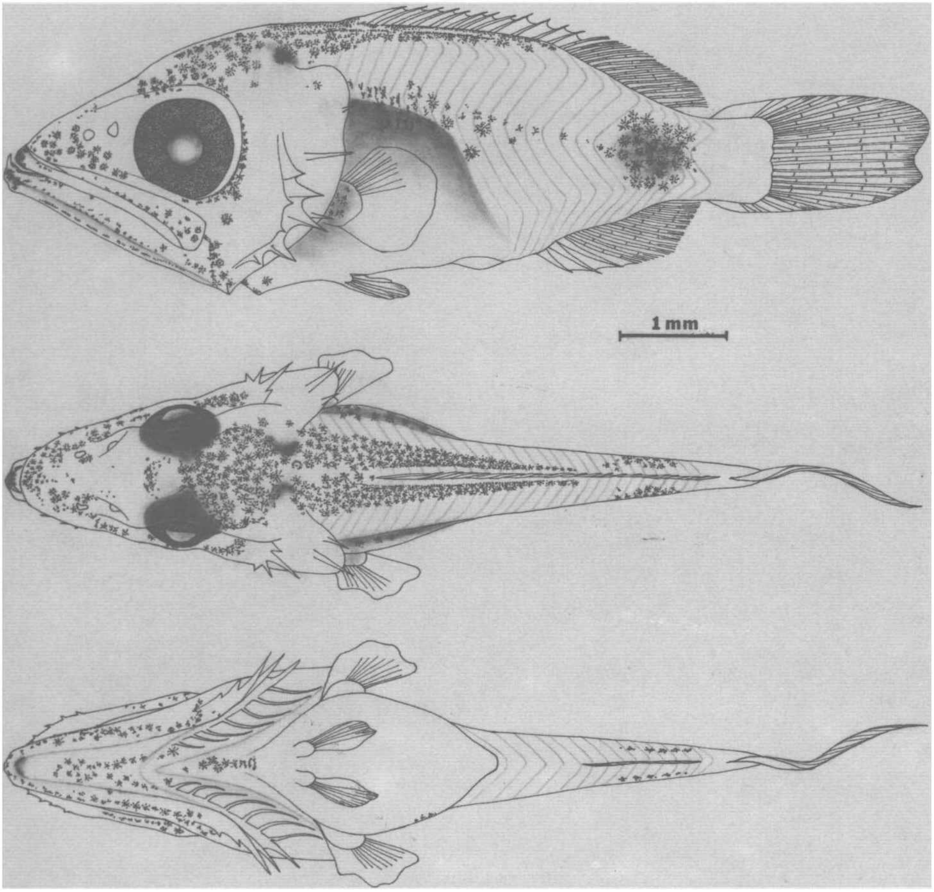

Figure 8. *Scombrolabrax heterolepis* larva, 7.2 mm SL, from the Atlantic Ocean. Top: left lateral view, center: dorsal view, bottom: ventral view.

During notochord flexion second raker appears in the dermis either anterior to first raker on ceratobranchial or posterior to first raker in angle (Table 3, Fig. 12A). More outer rakers appear after notochord flexion. Full complement for ceratobranchial eight or nine outer rakers, three anteriormost develop into toothpatches (Fig. 12D). (Gosline [1968] reported five rakers and additional toothpatches from a 140 mm specimen, whereas Grey [1960] found four well developed and one rudimentary raker and additional toothpatches in a 165 mm SL specimen).

First Dorsal Fin.—Development begins after some fin rays have appeared in second dorsal and anal fins (Table 4). Spines of first dorsal fin first appear at center of fin and then develop anteriorly and posteriorly. Anteriormost spine last to form. Full complement of 12 dorsal spines first observed at 4.7 mm SL in fully flexed specimen and all larvae longer than 6.1 mm SL have full counts (Table 4). (Gosline [1968] illustrated a *S. heterolepis* with 13 first dorsal fin spines, but Roule [1922], Arté [1952] and Grey [1960] counted 12 spines.)

First Dorsal Fin Supports.—Predorsal bones absent. Eleven pterygiophores support 12 spines (Table 3, Fig. 13). Each pterygiophore consists of a proximal and a distal radial, which are in series with spine (serial association) (Figs. 14A, 15A).

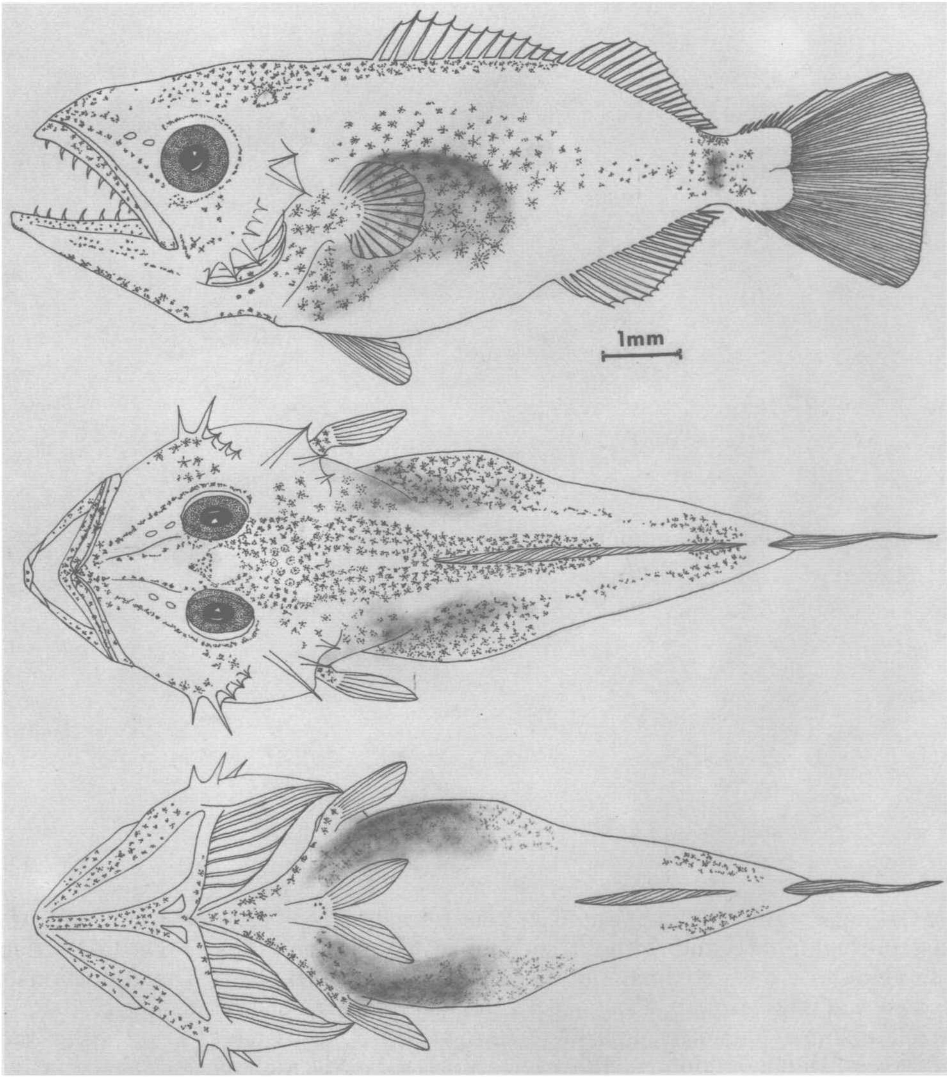

Figure 9. *Scombrolabrax heterolepis* larva, 9.7 mm SL, from the Atlantic Ocean. Top: left lateral view, center: dorsal view, bottom: ventral view.

Spine in series with next anterior pterygiophore articulates with distal portion of proximal radial in secondary association (Figs. 14A, 15A). Only anteriormost pterygiophore supports first spine without distal radial in secondary association and second spine in serial association, also without distal radial.

First dorsal fin pterygiophores similar to scombrids described by Kramer (1960) and Potthoff (1975). Pterygiophores have sagittal and lateral keels. Distal parts of proximal radials and distal radials themselves have characteristic palmate or alate shape only below first dorsal fin (compare A with B, C, D in Fig. 15).

First dorsal fin pterygiophores appear in cartilage during notochord flexion before fin spine development at future center of first dorsal fin (compare Tables 2, 3). Additional development in anterior and posterior direction. Ossification of first dorsal fin pterygiophores commences before second dorsal and anal fin pte-

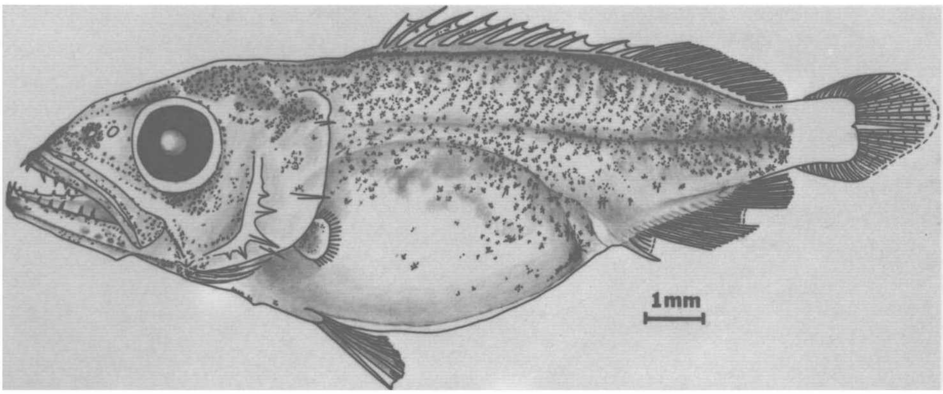

Figure 10. *Scombrolabrax heterolepis* larva, 14.7 mm SL, from the Atlantic Ocean. Left lateral view.

rygiophore ossification, starting with anteriormost pterygiophores at 6.1 mm SL. All first dorsal fin pterygiophores ossifying by 7.3 mm SL (Table 3).

Second Dorsal Fin.—Fin rays appear during notochord flexion at 5.0 mm NL simultaneously with anal fin rays before first dorsal fin spine development (Table 4). Rays first appear at center of second dorsal fin and more added anteriorly and posteriorly. Posteriormost double ray, counted as one ray, last to develop (Figs. 14D, 15D). Full counts of 15 second dorsal fin rays first observed at 5.7 mm SL and all specimens longer than 6.1 mm SL have full count of 15 (rarely 16) rays (Table 4). (Gosline [1968] illustrated *S. heterolepis* with 16 second dorsal fin rays, Grey [1960] counted 14–15 rays, and Roule [1922] and Arté [1952] found 15 rays.

Second Dorsal Fin Supports.—Juveniles have 15 (seldom 16) second dorsal fin pterygiophores (Table 3, Fig. 13); each ray serially associated with pterygiophore and secondarily with next posterior pterygiophore (Figs. 14B, C and 15B, C). Posteriormost two rays, counted as one branched ray, serially associated with last pterygiophore and without secondary association (Figs. 14D, 15D). Each pterygiophore has proximal and distal radial (Figs. 14B, 15B). Distal portions of second dorsal fin proximal radials and second dorsal fin distal radials lack palmate or alate shape. Posteriormost five or six pterygiophores have, besides proximal and distal radial, middle radial (Fig. 15C, D). Middle radials not shown in Fig. 14C, D because not yet ossified from cartilage. Posteriormost pterygiophore also

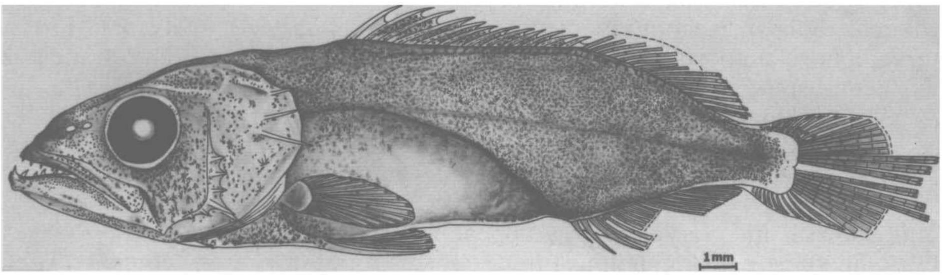

Figure 11. *Scombrolabrax heterolepis* juvenile, 22.5 mm SL, from the Pacific Ocean. Left lateral view.

Table 2. Lengths at which pigment develops for Atlantic, Pacific and Indian ocean *Scombrolabrax heterolepis*. Notochord and standard lengths are in mm for the first appearance of pigments in some specimens and for the presence of these pigments in all specimens

	Atlantic		Pacific, Indian	
	First	All	First	All
Hindbrain	3.2	3.3	3.2	4.7
Midbrain	3.2	3.3	3.2	4.7
Forebrain	4.3	4.6	4.5	5.4
Tip upper jaw	3.7	5.8	4.3	5.9
Ramus upper jaw	4.2	5.2	4.3	5.7
Tip lower jaw	—	<2.4	—	<2.9
Ramus lower jaw	3.5	4.5	4.5	5.7
Angle of jaws	4.2	5.1	5.7	5.7
Gular membrane	5.6	6.8	8.6	8.6
Behind eye	4.4	5.1	5.0	5.4
Nape (dorsal body)	4.4	4.6	5.7	5.7
Above gut	—	<2.4	—	<2.9
Above heart	4.0	5.0	4.3	5.4
Pectoral symphysis and isthmus	4.7	5.6	5.7	5.9
Lateral tail	4.7	5.2	5.7	7.4

has stay (Figs. 14D, 15D) similar to stay observed by Weitzman (1962) in *Brycon meeki*, Potthoff (1974, 1975) in *Thunnus*, Gomez Gaspar (1976) in *Lile piquitinga* and Houde and Potthoff (1976) in *Archosargus rhomboidalis*. All proximal radials of second dorsal fin pterygiophores have sagittal and lateral keels. First rod-shaped cartilaginous pterygiophores of second dorsal fin appear before and during notochord flexion (before any rays develop) at center of future second dorsal fin in myomeres 15 to 19 (compare Tables 3, 4). More cartilaginous pterygiophores added anteriorly and posteriorly as development proceeds. Ossification of second dorsal fin pterygiophore starts at anterior portion of second dorsal fin at 7.3 mm SL as continuation of first dorsal fin pterygiophore ossification and continues in

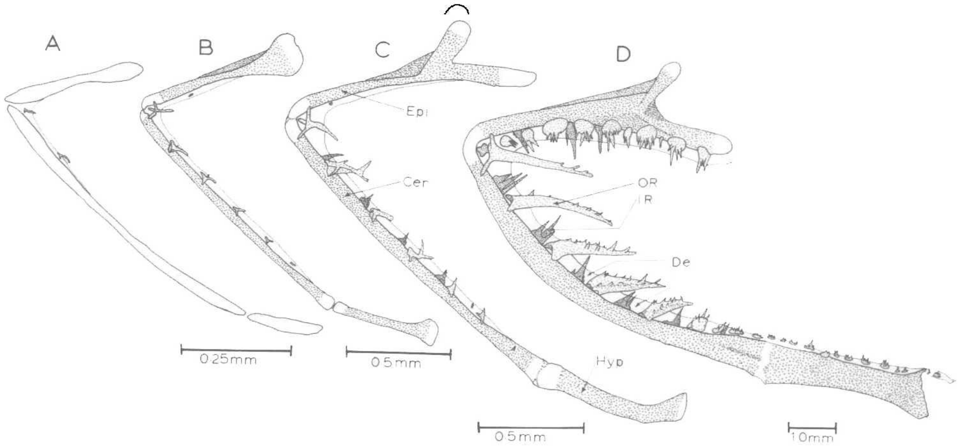

Figure 12. Lateral external view of the first (external) right gill arch from *Scombrolabrax heterolepis* showing the ontogeny. A, 4.9 mm NL, Atlantic Ocean; B, 9.7 mm SL, Atlantic Ocean; C, 14.7 mm SL, Pacific Ocean; D, 68.1 mm SL, Atlantic Ocean. Cer, ceratobranchial; De, dermis; Epi, epibranchial; Hyp, hypobranchial; IR, inside raker; OR, outside raker.

Table 3. Some meristic and osteological characters of 47 cleared and stained *Scombrolabrax heterolepis* larvae and juveniles. Vertebral counts for specimens from 4.0 NL to 8.1 mm SL were derived from neural and haemal spine counts. Specimens between dashed lines are undergoing notochord flexion. A, Atlantic Ocean; I, Indian Ocean; P, Pacific Ocean. C, cartilaginous. O, ossifying

Notochord or Standard Length, mm	Number, branchiostegals (one side)	Number, first ceratobranchial outer rakers	Number, pterygiophores: First dorsal fin C	First dorsal fin O	Second dorsal fin C	Second dorsal fin O	Anal fin C	Anal fin O	Number vertebrae, precaudal and caudal	Number, ossifying neural spines	Number, ossifying haemal spines + parhypural	Found on vertebra number: First closed haemal arch	First haemal zygapophyses Pre	First haemal zygapophyses Post	First ventral parapophysis	Number Rib Pairs Dorsal	Number Rib Pairs Pleural	Area
3.6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	A
3.7	4	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	A
3.9	3	0	0	0	0	0	0	0	?	0	0	0	-	-	12	0	0	I
4.0	4	0	0	0	0	0	0	0	? + 17	0	0	?	-	-	13	0	0	A
4.0	5	0	0	0	0	0	0	0	?	0	0	-	-	-	-	-	-	A
4.1	6	1	0	0	0	0	6	0	13 + 17	0	0	?	-	-	12	0	0	A
4.1	6	1	0	0	9	0	8	0	13 + 17	0	0	?	-	-	11	0	0	A
4.1	5	0	0	0	0	0	0	0	- -	0	0	-	-	-	12	0	0	I
4.2	-	-	11	0	14	0	14	0	13 + 17	4	0	?	-	-	10	0	0	A
4.3	6	1	7	0	8	0	10	0	13 + 17	0	0	-	-	-	9	0	0	A
4.3	-	1	10	0	13	0	14	0	13 + 17	4	0	?	-	-	7	0	0	I
4.4	7	1	10	0	9	0	16	0	13 + 17	3	0	-	-	-	8	0	0	A
4.5	7	2	4	0	12	0	9	0	13 + 17	3	0	-	-	-	12	0	0	P
4.5	6	2	0	0	0	0	0	0	13 + 17	0	0	?	-	-	-	0	0	P
4.9	7	2	11	0	15	0	16	0	13 + 17	6	0	12	-	-	7	0	0	A
4.9	-	-	11	0	15	0	16	0	13 + 17	9	0	-	-	-	11	0	0	P
4.9	-	-	11	0	15	0	-	-	13 + 17	-	-	-	-	-	7	0	0	A
5.0	7	2	11	0	?	0	16	0	13 + 17	5	0	?	-	-	8	0	0	A
5.0	7	1	10	0	14	0	16	0	13 + 17	7	0	?	-	-	9	0	0	A
5.3	7	2	11	0	15	0	16	0	13 + 17	5	0	-	-	-	7	0	0	P
4.7	7	3	11	0	14	0	16	0	13 + 17	20	6	12	-	-	7	0	0	A
4.9	7	-	11	0	?	0	?	0	13 + 17	19	4	12	-	-	8	0	0	P
5.0	7	3	11	0	15	0	15	0	13 + 17	11	0	-	-	-	7	0	0	I
5.0	7	2	?	0	?	0	?	0	13 + 17	10	3	-	-	-	8	0	0	A
5.2	-	3	11	0	15	0	16	0	13 + 17	15	4	12	-	-	7	0	0	A
5.4	7	3	11	0	14	0	16	0	13 + 17	18	6	12	0	0	7	0	0	P
5.6	7	4	?	0	?	0	?	0	13 + 17	25	7	12	0	0	7	0	0	A
5.7	7	4	11	0	15	0	17	0	13 + 17	20	8	12	0	0	8	0	0	I
5.7	7	4	11	0	15	0	17	0	13 + 17	23	7	12	0	0	7	0	0	?
5.8	-	4	11	0	15	0	16	0	13 + 17	22	12	-	0	0	7	0	0	A
5.9	7	5	11	0	15	0	17	0	13 + 17	24	10	-	0	0	7	0	0	A
6.0	7	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
6.0	7	4	11	0	16	0	16	0	13 + 17	25	12	12	0	0	7	0	0	A
6.1	7	4	6	5	15	0	?	0	13 + 17	25	11	12	0	0	8	0	0	A
6.6	7	4	-	-	-	-	-	-	13 + 17	25	12	13	-	-	7	0	0	A
7.3	7	5	0	11	11	4	14	3	13 + 17	27	13	12	0	15	8	1	3	A
7.4	7	5	0	11	13	2	16	1	13 + 17	27	14	12	0	13	8	1	3	P
7.5	7	5	0	11	15	0	16	1	13 + 17	23	12	12	0	13	8	0	2	A
8.1	7	6	0	11	10	5	11	6	13 + 17	29	17	12	20	13	8	0	3	A
8.6	7	5	0	11	8	7	11	6	13 + 17	28	17	12	21	13	8	1	4	I
9.5	7	6	0	11	5	10	7	10	13 + 17	29	17	12	21	13	9	2	5	P
9.7	7	6	0	11	6	10	10	8	13 + 17	29	17	12	20	13	7	2	5	A
10.4	7	6	0	11	7	8	6	10	13 + 17	29	17	12	20	13	8	3	5	P
14.7	7	6	0	11	0	15	3	14	13 + 17	29	17	12	21	13	7	4	11	P
22.5	7	7	0	11	0	15	0	17	13 + 17	29	17	12	19	13	8	4	11	P
68.1	7	6 + 3	0	11	0	15	0	17	13 + 17	29	17	12	14	13	6	9	11	A
69.5	-	5 + 3	0	11	0	15	0	17	13 + 17	29	17	13	16	12	6	9	11	A

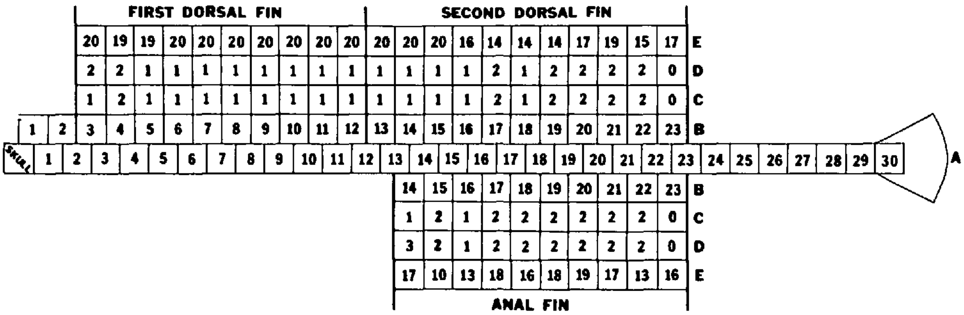

Figure 13. Common arrangement of pterygiophores, fin spines and fin rays in relation to the vertebral column and skull for 20 *Scombrolabrax heterolepis* from all world oceans. Modified after Matsui (1967). A, skull and vertebrae numbers; B, interneural and interhaemal space numbers; C, number of pterygiophores in the respective interneural or interhaemal space; D, number of fin spines or fin rays associated with the pterygiophores; E, frequency of occurrence in 20 specimens for the pterygiophore number in the respective interneural or interhaemal spaces.

posterior direction (Table 3). Posteriormost pterygiophores from interneural space number 22 start to ossify at 14.7 mm SL. Segregation of distal and proximal radials from rod-shaped pterygiophore cartilage occurs before ossification (Fig. 14B, C, D), but middle radials segregate from proximal radial by ossification (Fig.

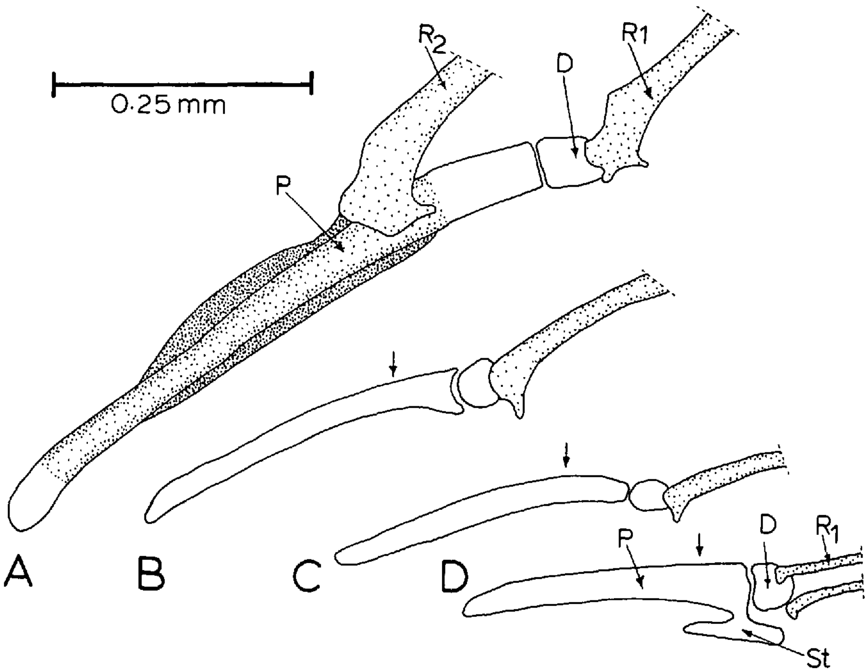

Figure 14. Left lateral view of selected pterygiophores from a 9.7 mm SL *Scombrolabrax heterolepis* from the Atlantic Ocean, showing the various stages of development of pterygiophores from one specimen. Counting from anterior in a posterior direction: A, 5th pterygiophore from the first dorsal fin; B, 19th pterygiophore from the second dorsal fin; C, 22nd pterygiophore from the second dorsal fin; D, 26th or posteriormost pterygiophore from the second dorsal fin. Arrows indicate place of secondary association with fin ray. D, distal radial; P, proximal radial; R_1, serially associated ray; R_2, secondarily associated ray; St, stay. Cartilage, white; ossifying, stippled.

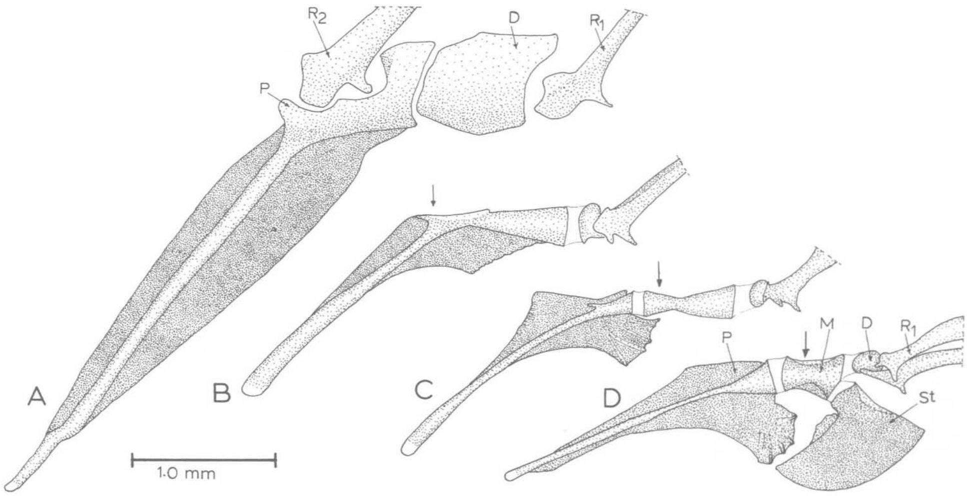

Figure 15. Left lateral view of selected pterygiophores from a 69.5 mm SL *Scombrolabrax heterolepis* from the Atlantic Ocean, showing fully developed pterygiophores. Counting from anterior in a posterior direction, pterygiophores A, B, C and D are the same numbers as in Figure 14. Arrows indicate place of secondary association with fin ray. M, middle radial; for other abbreviations, see Figure 14. Cartilage, white; ossifying, stippled.

15C,D). (Potthoff [1975] described same for *Thunnus atlanticus*.) Stay of posteriormost pterygiophore originates from proximal radial cartilage (Fig. 14D).

Anal Fin.—Fin rays appear during notochord flexion at same time as second dorsal fin rays and before first dorsal fin spines (Table 4). Development sequence same as second dorsal fin, posteriormost anal ray consists of 2 rays counted as one; full counts, III, 16, first seen at 5.7 mm SL and all specimens longer than 6.1 mm SL have full count III, 16 (rarely III, 15 or III, 17) (Table 4). (Gosline [1968] illustrated a *S. heterolepis* without anal spines and with only 15 anal rays, but stated in text that 3 anal spines are present in species; Roule [1922] reported I, 15, Arté [1952] II, 16 and Grey [1960] II, 18 anal rays.)

Anal Fin Supports.—Juveniles have 17 (seldom 16 or 18) anal fin pterygiophores (Table 3, Fig. 13). Structure and development same as second dorsal fin, except for first anteriormost anal pterygiophore. This pterygiophore probably represents fusion of two pterygiophores as in *Thunnus atlanticus* (Potthoff, 1975) and supports 3 spines.

Pterygiophore Relationship to the Interneural and Interhaemal Spaces.—Pterygiophores insert in interneural and interhaemal spaces. These spaces defined by neural and haemal spines. Only first interneural space delineated by skull and first anteriormost neural spine. First anteriormost interhaemal space designated number 14 because of opposite interneural space 14 and delineated by parapophysis of 13th precaudal centrum and first haemal spine of first caudal centrum (centrum number 14). Common pattern and number of pterygiophores for each interneural and interhaemal space given in Figure 13. Pattern almost constant for first dorsal fin pterygiophores and for first anteriormost three pterygiophores of second dorsal fin. Variability occurs under posterior two thirds of second dorsal fin and above entire anal fin. Pterygiophores of first and second dorsal fins insert into interneural spaces 3 to 22, rarely into interneural space 23 (Fig. 13). Anal fin

Table 4. Fin spine and ray counts of 47 cleared and stained *Scombrolabrax heterolepis* larvae and juveniles. Specimens between dashed lines are undergoing notochord flexion. A, Atlantic Ocean; I, Indian Ocean; P, Pacific Ocean

Notochord or Standard Length, mm	Dorsal Fin, Spines and Rays	Anal Fin, Spines and Rays	Pectoral Fin Rays (right)	Pectoral Fin Rays (left)	Pelvic Fin, Spine and Rays (one side)	Caudal Fin Rays Upper Secondary	Caudal Fin Rays Upper Principal	Caudal Fin Rays Lower Principal	Caudal Fin Rays Lower Secondary	Area
3.6	0	0	0	0	0	0	0	0	0	A
3.7	0	0	0	0	0	0	0	0	0	A
3.9	0	0	0	0	0	0	0	0	0	I
4.0	0	0	0	0	0	0	1	1	0	A
4.0	0	0	0	0	0	0	2	2	0	A
4.1	0	0	0	0	0	0	4	3	0	A
4.1	0	0	0	0	0	0	2	2	0	A
4.1	0	0	0	0	0	0	2	2	0	I
4.2	0	0	0	0	0	0	7	8	0	A
4.3	0	0	0	0	0	0	5	5	0	A
4.3	0	0	0	0	0	0	7	7	0	I
4.4	0	0	0	0	0	0	5	7	0	A
4.5	0	0	0	0	0	0	5	6	0	P
4.5	0	0	0	0	0	0	0	0	0	P
4.9	0	0	0	0	0	0	7	8	0	A
4.9	0	0	0	0	0	0	7	8	0	P
4.9	0	0	0	0	0	0	9	8	0	A
5.0	0,?	0,9	0	0	0	0	7	7	0	A
5.0	0	0	0	0	0	-	-	-	-	A
5.3	0,8	0,9	0	0	0	0	7	8	0	P
4.7	XII,12	III,14	4	4	0	0	9	8	1	A
4.9	VI,8	II,8	4	4	0	0	8	7	0	P
5.0	XI,10	II,13	0	0	0	-	-	-	-	I
5.0	VIII,10	II,8	0	0	0	0	9	8	1	A
5.2	X,10	II,9	0	0	I,2	0	9	8	1	A
5.4	XI,13	II,12	3	3	I,1	-	-	-	-	P
5.6	XII,13	III,15	-	5	I,0	1	9	8	2	A
5.7	XII,15	III,16	-	7	I,3	3	9	8	3	I
5.7	XII,12	III,13	3	2	I,0	2	9	8	2	?
5.8	XII,15	III,15	-	-	I,3	3	9	8	4	A
5.9	XII,15	III,15	0	0	I,2	3	9	8	2	A
6.0	XII,14	III,15	7	8	I,4	-	-	-	-	P
6.0	XII,16	III,15	-	5	I,4	2	9	8	2	A
6.1	XI,14	III,13	-	-	I,3	0	9	8	2	A
6.6	XII,16	III,16	6	6	I,4	4	9	8	4	A
7.3	XII,15	III,16	11	11	I,4	4	9	8	5	A
7.4	XII,15	-	10	13	I,5	-	-	-	-	P
7.5	XII,15	III,16	9	-	-	3	9	8	4	A
8.1	XII,15	III,16	12	12	I,5	6	9	8	6	A
8.6	XII,15	III,16	13	13	I,5	6	9	8	6	I
9.5	XII,15	III,16	15	15	I,5	8	9	8	9	P
9.7	XII,16	III,17	14	15	I,5	7	9	8	8	A
10.4	XII,15	III,15	15	-	I,5	8	9	8	8	P
14.7	XII,15	III,16	18	-	I,5	9	9	8	10	P
22.5	XII,15	III,16	19	19	I,5	9	9	8	10	P
68.1	XII,15	III,16	19	19	I,5	8	9	8	9	A
69.5	XII,15	III,16	18	18	I,5	9	9	8	10	A

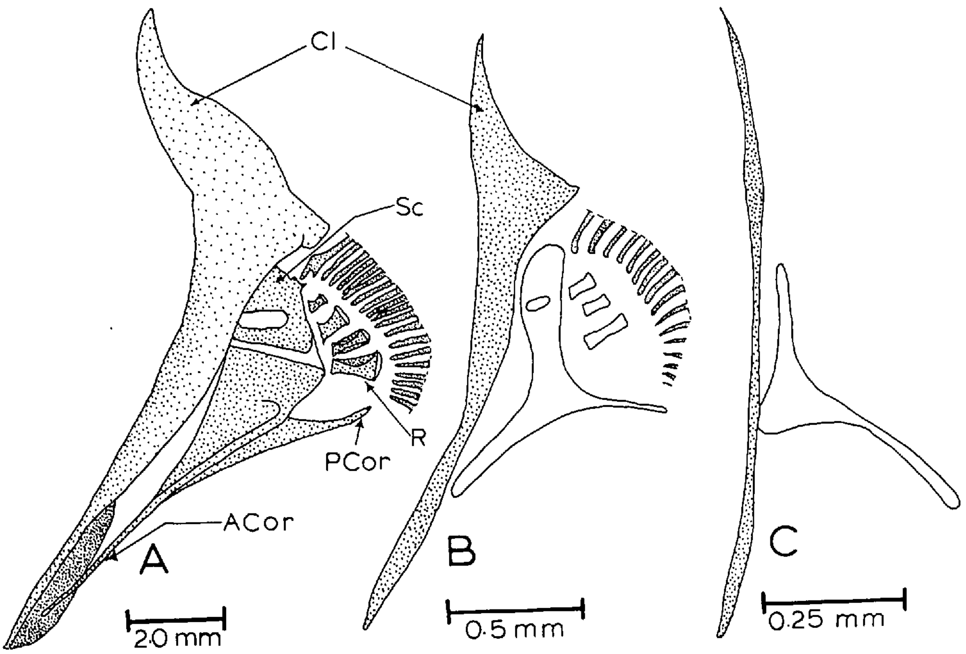

Figure 16. Left lateral external view of the pectoral girdle from *Scombrolabrax heterolepis*, showing the ontogeny. A, 68.1 mm SL, Atlantic Ocean; B, 10.4 mm SL, Pacific Ocean; C, 4.2 mm SL, Atlantic Ocean. ACor, anterior process of coracoid; Cl, cleithrum; PCor, posterior process of coracoid; R, radial; Sc, scapula. Cartilage, white; ossifying, stippled.

pterygiophores insert into interhaemal spaces 14 to 22, seldom into interhaemal space 23. First anal pterygiophore always anterior to first haemal spine.

Pectoral Fin.—Smallest larvae (3.1–5.3 mm NL) have larval pectoral fins consisting of base and rayless blade (Fig. 2, Table 4). Fin rays develop in dorsal portion of blade in some larvae after notochord flexion at 4.7 mm SL and all larvae longer than 5.9 mm SL have pectoral fin rays developing. Development of rays from dorsal edge of blade ventrad. Full pectoral fin ray count of 18 or 19 rays observed in 14.7 mm SL specimens and larger (Table 4). Left and right pectoral fins have the same count or differ by one to two rays during development and no differences between left and right sides observed in three specimens with full counts. (Roule [1922] counted 17, Arté [1952] counted 19 and Grey [1960] counted 18 pectoral rays.)

Pectoral Fin Supports.—Fin rays supported on each side directly and indirectly by bones of pectoral girdle and suspensorium. Pectoral girdle consists of four radials, scapula, coracoid and cleithrum (Fig. 16A). Dorsalmost ray supported by scapula and remaining rays supported by four radials. Scapula and coracoid connected by cartilage. Suspensorium (not illustrated) consisted of supratemporal, posttemporal, supracleithrum and two postcleithra. (Intertemporal bones found in *Notropis* [Harrington, 1955] and *Coryphaena* [Potthoff, 1980] were not present in *S. heterolepis*.) Specimens at onset of notochord flexion have rod-shaped, bony cleithrum and coraco-scapular cartilage with long dorsal and long posterior processes and short but expanded anterior process (Fig. 16C). After notochord flexion, scapular foramen develops in dorsal process of the coraco-scapular car-

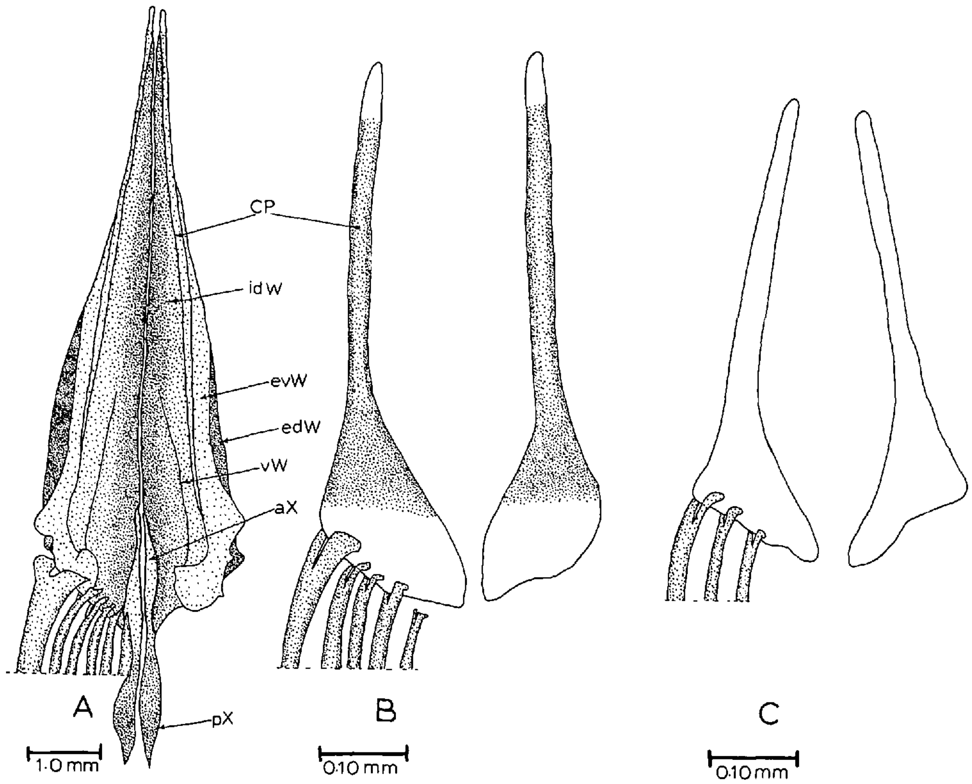

Figure 17. Ventral view of left and right basipterygia from *Scombrolabrax heterolepis*, showing their ontogeny. A, 68.1 mm SL, Atlantic Ocean; B, 7.3 mm SL, Atlantic Ocean; C, 5.2 mm SL, Atlantic Ocean. The fin rays from the left basipterygium have been removed. aX, anterior xiphoid process; CP, central part; edW, external dorsolateral wing; evW, external ventral wing; idW, internal dorsolateral wing; vW, ventral wing; pX, posterior xiphoid process. Cartilage, white; ossifying, stippled.

tilage, cartilaginous radials appear posterior to dorsal process and anterior process of coraco-scapular cartilage grows larger. Cleithrum develops posterior shelf dorsally (Fig. 16B). Further development consists of ossification of coraco-scapular cartilage to two bones (coracoid and scapula), ossification of radials and further expansion of cleithrum (Fig. 16A). Anterior process of coracoid lengthens, almost reaching ventral tip of cleithrum; posterior process shortens in relation to all other structures of pectoral girdle. (Origin of coracoid and scapula from one piece of cartilage has been observed in fishes [Swinnerton, 1905; Starks, 1930; Houde and Potthoff, 1976; Potthoff, 1980]). Suspensorium development not studied. (Pectoral bones of some gempylid fishes studied by Matsubara and Iwai [1958], but they did not mention supratemporals.)

Pelvic Fin.—Fin buds first seen after notochord flexion at 4.7 mm SL. First three fin elements, spine and two rays appear on outside edge of pelvic blade at 5.2 mm SL. Additional rays added inward until full complement of I, 5 rays reached at 7.4 mm SL (Table 4, Fig. 17).

Pelvic Fin Supports.—Two basipterygia support pelvic fin spine and rays. Basipterygium divided into three parts corresponding to ontogeny of bone (Figs. 17,

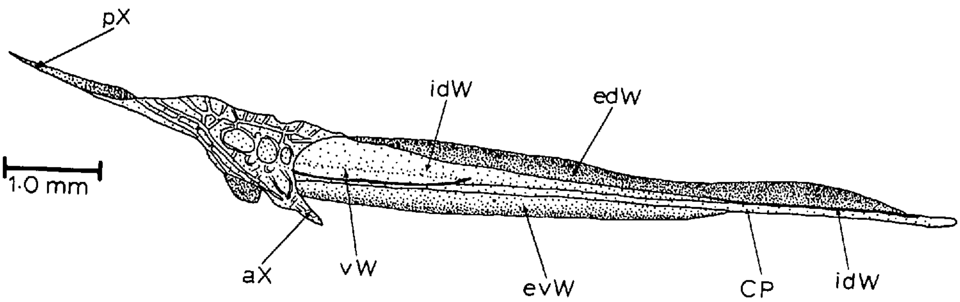

Figure 18. Internal lateral view of left basipterygium from a 68.1 mm SL *Scombrolabrax heterolepis* from the Atlantic Ocean. The fin rays have been removed. For abbreviations, see Figure 17. Cartilage, white; ossifying, stippled.

18): central part (original cartilage), wings (membranous bone origin) and anterior xiphoid process (membranous bone origin), and posterior xiphoid process (cartilage origin). Central part carries four wings, similar to two sagittal and two lateral keels of pterygiophores. Wings termed internal dorsolateral, external dorsolateral, external ventral and ventral (Figs. 17, 18). Grooves formed at juncture of wings with central part. Xiphoid processes located internally at midline. Anterior xiphoid process is anteroventral extension of dorsal process. Basipterygia are closely approximated at internal surfaces of four xiphoid processes and at edges of two internal dorsolateral wings (Fig. 17A). Development of two basipterygia shown in Figure 17. Rod-shaped pieces of cartilage with expanded bases appear first (Fig. 17C), then cartilage ossifies (Fig. 17B). After ossification of central part, wings and anterior processes develop as membranous bone (Figs. 17A, 18). (Pelvic bones of some gempylid fishes briefly described by Matsubara and Iwai [1958].)

Caudal Fin.—First fin to develop rays (Table 4, Figs. 19–21) with principal caudal rays first appearing in ventral lobe of caudal finfold before notochord flexure at

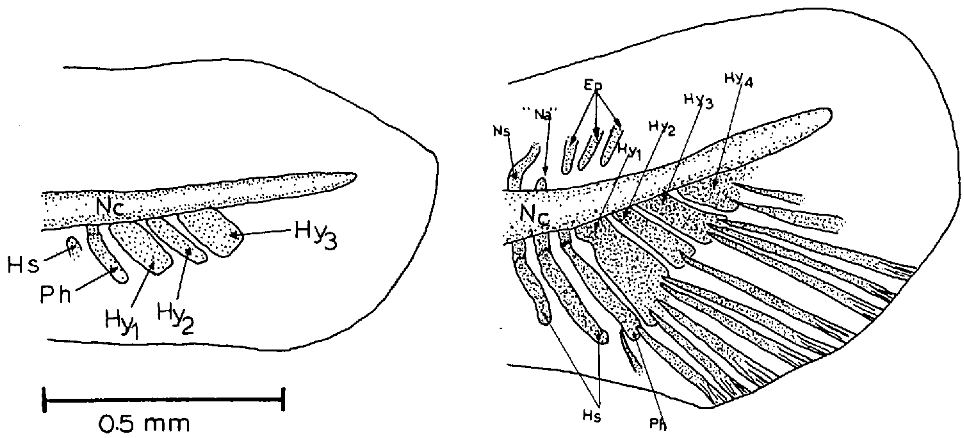

Figure 19. Left lateral view of two caudal complexes of *Scombrolabrax heterolepis*. Left: 3.9 mm NL, Indian Ocean. Right: 4.4 mm NL, Atlantic Ocean. Ep, epural; Hs, haemal spine; Hy, hypural bone; "Na," specialized neural arch; Nc, notochord; Ns, neural spine; Ph, parhypural. Cartilage, stippled.

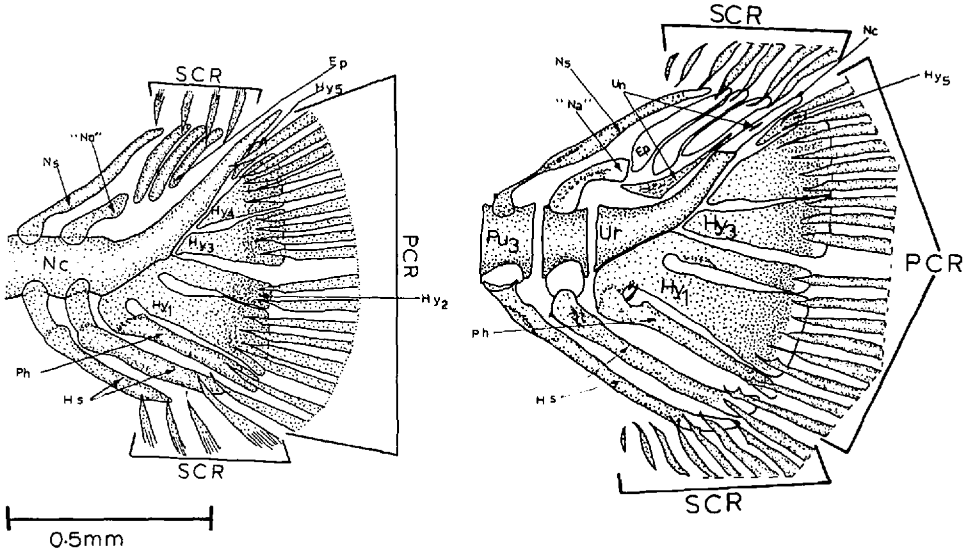

Figure 20. Left lateral view of two caudal complexes of *Scombrolabrax heterolepis*. Left: 6.6 mm SL, Atlantic Ocean, both cartilage and ossifying cartilage, stippled. Right: 9.7 mm SL, Atlantic Ocean, cartilage, white; ossifying, stippled. PCR, principal caudal rays; Pu, preural centrum; SCR, secondary caudal rays; Un, uroneural; Ur, urostyle. For other abbreviations, see Figure 19.

4.0 mm NL. Rays develop from point, between hypurals 2 and 3, outward. Notochord begins flexion at 4.2 mm NL after more than half of principal rays present. Smallest specimen 4.7 mm SL with full complement of 17 principal rays (9 dorsal, 8 ventral) and fully flexed notochord. All specimens 5.0 mm SL and longer have full principal ray complement. Secondary caudal rays start developing first in lower ventral lobe at 4.7 mm SL. Full complements of 8 or 9 upper and 9 or 10 lower secondary rays acquired between 9.5–14.7 mm SL. Ventral posteriormost secondary caudal ray in two larger juveniles has reduced procurrent spur (Johnson, 1975) and base of preceding secondary ray shortened (Fig. 21).

Caudal Fin Supports.—Caudal bones support caudal fin rays and have following parts: 3 centra (2 preural and the urostyle); 1 neural spine; 2 autogenous haemal spines; 1 autogenous parhypural; 5 autogenous hypurals; and 2 paired uroneurals; 3 epurals; 1 specialized neural arch (Figs. 19–21). (Gosline [1968] described and figured caudal skeleton of 140 mm *S. heterolepis* with same number of parts as described by us.)

Caudal fin supports develop at 3.9 mm NL (Fig. 19), with only haemal spine of preural centrum 2, parhypural and hypurals 1, 2 and 3 developing as small cartilaginous buds ventral to unflexed notochord. Notochord flexion starts at 4.2 mm NL. Ventrad, two autogenous haemal spines, the parhypural and hypurals 1 to 4 develop in cartilage. Dorsad, neural spine, specialized neural arch and 3 epurals present in cartilage (compare to Figure 19 right of slightly larger 4.4 mm NL specimen). Fifteen principal caudal rays (7 + 8) ossifying in caudal finfold. Notochord flexion complete at 4.7–5.4 mm SL. During flexion, hypural 5 and more caudal fin rays added to caudal complex. (Figure 20 left shows flexed specimen representative of immediate post flexion stage.) Urostyle first bone to start ossification at 5.6 mm SL, larger anterior uroneural pair appears in bone at 5.7 mm SL but not present in all specimens until 7.3 mm SL; smallest posterior

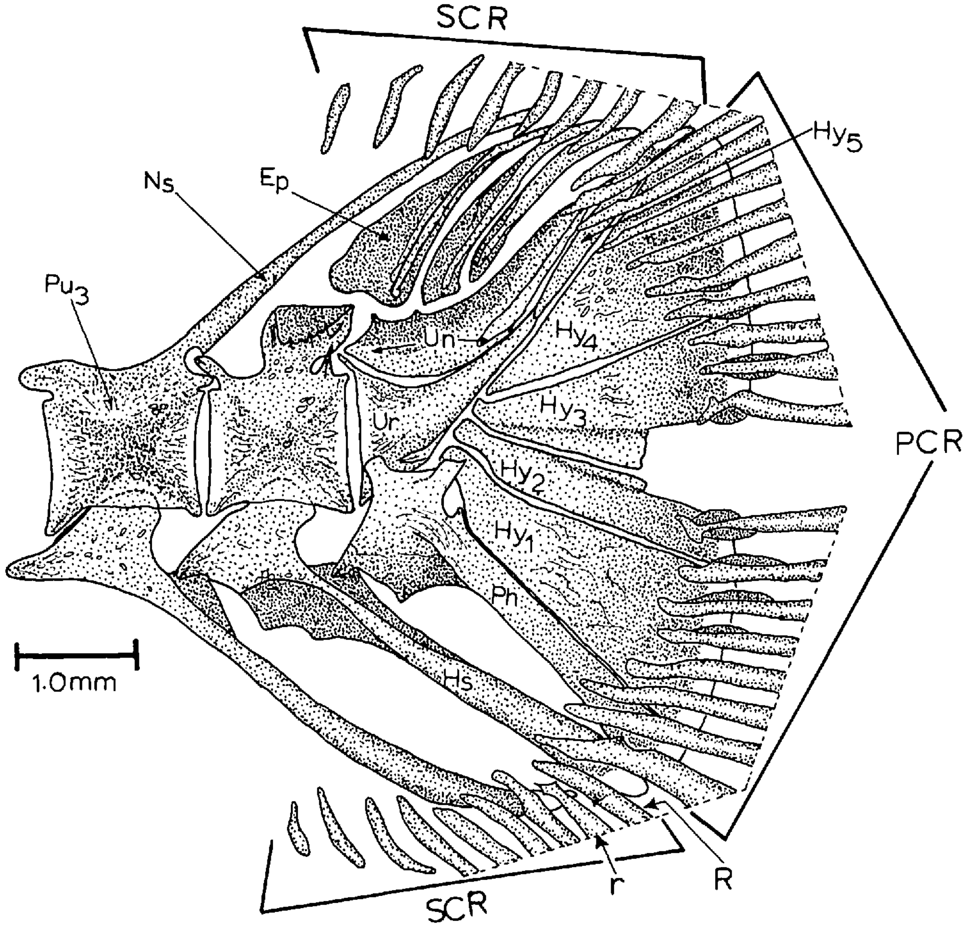

Figure 21. Left lateral view of the caudal complex of a 68.1 mm SL *Scombrolabrax heterolepis* from the Atlantic Ocean. R, secondary ray with procurrent spur; r, secondary foreshortened ray. For other abbreviations, see Figs. 19, 20. Cartilage, white; ossifying, stippled.

uroneural pair first seen in a 9.5 mm SL specimen (Fig. 20 right); hypural ossification starts at 7.3 mm SL; three epurals last to ossify at 14.7 mm SL. Completion of development of caudal complex consists of further ossification and closer articulation of various parts (Fig. 21). No fusion of caudal bones observed.

Caudal fin rays indirectly associated with urostyle and preural centra 2 and 3 (Figs. 20, 21). Rays supported by distal margins of neural spine of preural centrum 3, 3 epurals, 5 hypurals, parhypural and haemal spines of preural centra 2 and 3 (Figs. 20, 21). Nine upper principal caudal rays supported by hypurals 5, 4 and 3; and 8 lower principal rays supported by hypurals 2 and 1, parhypural and often by haemal spine of preural centrum 2. Hypural 5 supports one or two principal rays, usually one; hypural 4 supports four or five principal rays; hypural 3 supports two, three or four principal rays, usually three; hypural 2 supports one or two principal rays; hypural 1 supports three to six principal rays, usually four or five; parhypural supports one or two principal rays, usually one; haemal spine of preural centrum 2 supports none or one principal caudal ray, usually one. Principal caudal ray absent on haemal spine of preural centrum 2 in 3 of 21 specimens.

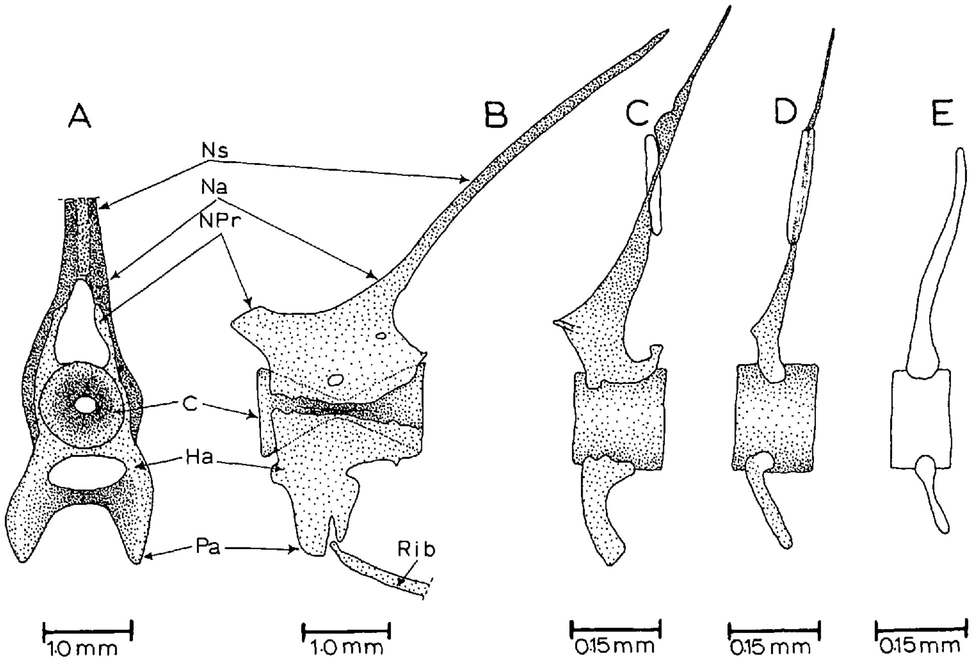

Figure 22. Left lateral view of the 12th centrum from *Scombrolabrax heterolepis*, showing the ontogeny, except A which is an anterior view. A, B, 69.5 mm SL, Atlantic Ocean; C, 8.1 mm SL, Atlantic Ocean; D, 6.6 mm SL, Atlantic Ocean; E, 4.9 mm NL, Atlantic Ocean. C, centrum; Ha, haemal arch; Na, neural arch; NPr, neural prezygapophysis; Ns, neural spine; Pa, parapophysis. Cartilage, white; ossifying, stippled.

Vertebral Column.—Thirty vertebrae, 13 precaudal and 17 caudal vertebrae (Table 3). (Roule [1922] in his original description reported 14 + 16 vertebrae, but Gosline [1968] gave 13 + 17.) Smallest cleared and stained specimen (3.6 mm NL) had straight unsegmented notochord with no neural or haemal cartilaginous arches. Cartilaginous neural and haemal arches first observed at 3.7 mm NL, first complete count obtained at 4.1 mm NL. Neural arches develop at two centers: one at anteriormost portion of notochord, other posterior to center of notochord approximately under future center of second dorsal fin. Cartilaginous neural arches develop from these centers anteriorly and posteriorly. Cartilaginous haemal arches develop from center at middle of future anal fin. Ossification of vertebral column and neural and haemal arches and spines from anterior in posterior direction. Notochord segmentation followed by ossification, similar to vertebral development observed in *Archosargus rhomboidalis* (Houde and Potthoff, 1976), but not as in *Thunnus atlanticus* (Potthoff, 1975) where no segmentation observed and ossification spreads from bases of neural and haemal arches towards center of notochord. Neural and haemal arches and spines ossify in same mode as *Thunnus atlanticus* (Potthoff, 1975) (Figs. 22, 23). Evidence of vertebral column ossification first seen in 4.2 mm NL flexion stage specimen, in which first four anteriormost neural arches stained red at bases (Table 3), and six anteriormost centra were segmented in the notochord. All centra, neural and haemal arches and spines ossifying in specimens 8.1–9.5 mm SL and longer. First closed haemal arch usually on 12th centrum (Table 3, Fig. 22). First haemal postzygapophysis usually on the 13th centrum (Table 3, Fig. 23A). First haemal prezygapophysis

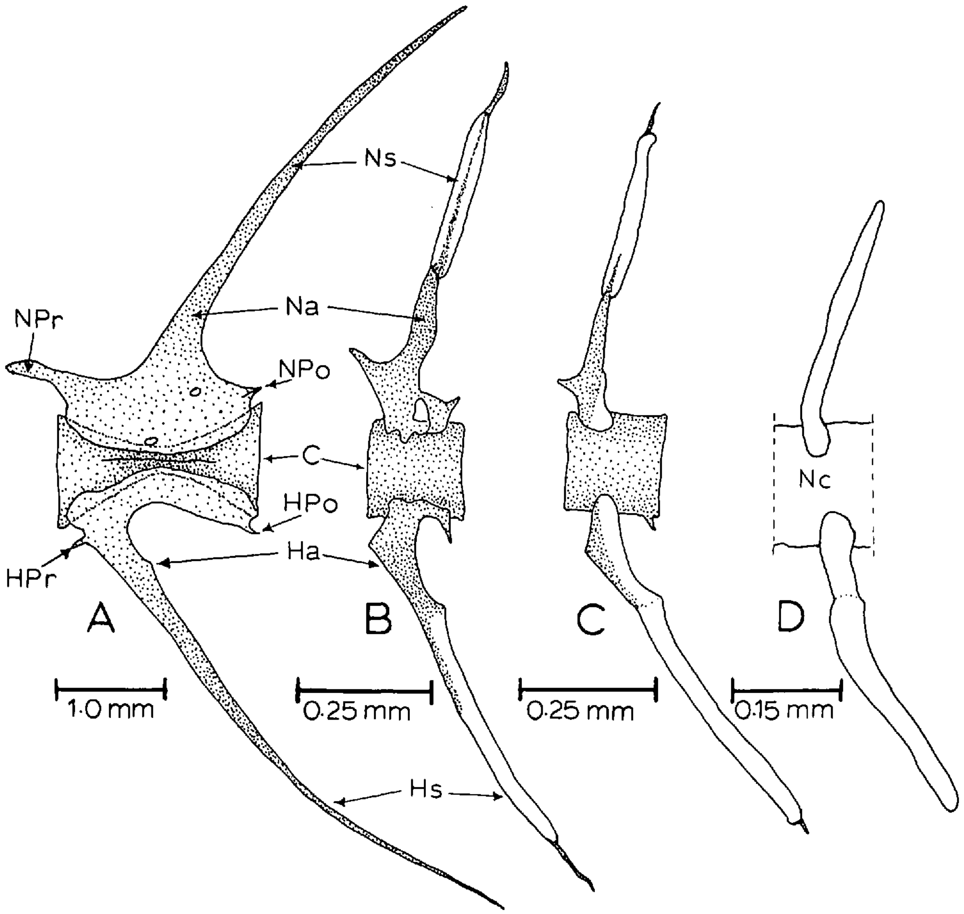

Figure 23. Left lateral view of the 15th centrum from *Scombrolabrax heterolepis*, showing the ontogeny. A, 69.5 mm SL, Atlantic Ocean; B, 8.1 mm SL, Atlantic Ocean; C, 6.6 mm SL, Atlantic Ocean; D, 4.9 mm NL, Atlantic Ocean. Hs, haemal spine; HPo, haemal postzygapophysis; HPr, haemal prezygapophysis; NPo, neural postzygapophysis. For other abbreviations, see Figure 22. Cartilage, white; ossifying, stippled.

seems to develop anteriorly during growth because it is found on 19th to 21st centrum in 8.1–22.5 mm SL specimens and on 14th and 16th centrum in two juveniles 68.1 and 69.5 mm SL (Fig. 23A). The first ventrally directed parapophysis is on 6th to 9th centrum (Table 3, Fig. 22).

Dorsal and Pleural Ribs.—Nine pairs of dorsal ribs on centra 1–9 and 11 pairs of pleural ribs on centra 3–13 (Table 3). First two dorsal rib pairs articulate near right and left bases of two anteriormost neural arches, other seven dorsal rib pairs loosely articulate with pleural ribs ventrad to haemal parapophyses. Anteriormost pleural rib pair articulates with left and right base of third neural arch. Remaining ten pairs articulate with haemal parapophyses (Fig. 22B). Parapophyses found lateral to centra 4, 5 and sometimes 6, 7 and ventral to centra 7–13 (Table 3). Dorsal and pleural ribs develop from anterior in posteriad direction, starting at 7.3 mm SL (Table 3). Full complement of 11 pairs of pleural ribs first attained at 14.7 mm SL when only four pairs of dorsal ribs present. Length at which full complement of dorsal ribs first develop unknown due to lack of specimens in size range 22.5–68.1 mm SL (Table 3). Uncertain if ribs develop first from cartilage and then ossify or if develop directly as bone.

Identification of Larvae and Juveniles

A count of 30 myomeres separates the larvae of *S. heterolepis* from all scombrids. *Scomber* and *Rastrelliger* have 31 myomeres but are also separable from *S. heterolepis* larvae based on body shape and presence of ventral tail pigment for all larval sizes (Kramer, 1960; Matsui, 1963). In larvae larger than 5.0 mm NL, which have cartilaginous neural and haemal spines, vertebral counts may be obtained for separation of the genera after clearing and staining. *Rastrelliger* has 13 + 18 (Matsui, 1963), *Scomber* has 14 + 17 (Kramer, 1960) and *S. heterolepis* has 13 + 17 vertebrae.

S. heterolepis most closely resembles *Thunnus* in pigmentation at sizes less than 4.3 mm SL when forebrain and pectoral symphysis pigments are not developed. The presence of the latter pigments would separate *S. heterolepis* from *Thunnus*. *Thunnus* has 39 myomeres, but if myomeres cannot be counted, the following are useful diagnostic features for *S. heterolepis*: the pigment on the tip of the lower jaw is similar to that in *Thunnus* but larger and always occurs on both sides of the lower jaw. *S. heterolepis* cannot be confused with *Auxis* or *Euthynnus* because these two genera, besides having 37 to 39 myomeres, have a row of melanophores on the ventral tail margin. *Katsuwonus pelamis* has 41 myomeres and has forebrain pigment at small sizes (3.2 mm NL) and at least one large melanophore on the ventral tail margin. Both *Scomberomorus* and *Sarda* have more than 41 myomeres and also have a row of melanophores on the ventral tail margin. As pigmentation increases with growth in *S. heterolepis*, the presence of pigment on the lateral rami of the jaws, on the gular membrane and near the caudal peduncle and the absence of pigment on the first dorsal fin and along the ventral tail margin distinguish it from any scombrid larva. For juveniles the combination of meristics distinguishes *S. heterolepis* from scombrids: 12 first dorsal fin spines, 3 anal fin spines and no dorsal and anal finlets.

Relationships

Scombrolabrax heterolepis shares morphological features with the scombroids, which we consider to be the scombrids, gempylids and trichiurids. We were unable to examine all species of the scombroids, and our placement of *S. heterolepis* in the Scombroidei, Family Scombrolabracidae, is tentative and based on the scombroid species examined by us (See Appendix).

The pterygiophores of *S. heterolepis* are similar in most aspects to those of scombrids: predorsal bones are absent, the anteriormost dorsal pterygiophore supports only two spines and it inserts in the third interneural space (Table 1; compare Fig. 13 with Potthoff, 1974, Fig. 10), the alate structure of first dorsal fin distal and proximal radials is similar (Fig. 15A) (Kramer, 1960; Potthoff, 1975), middle radials are present in the posteriormost dorsal and anal fin pterygiophores (scombrids have more middle radials than *S. heterolepis*), the posteriormost dorsal and anal fin pterygiophores have one stay (Kramer, 1960) (compare Fig. 15D with Potthoff, 1975, Fig. 18). In scombrids the first anal pterygiophore supports two indistinct spines and a soft ray whereas in *S. heterolepis* three spines are supported. Finlets present posterior to the dorsal and anal fins in scombrids are lacking in *S. heterolepis*. Predorsal bones are also absent in the gempylids and trichiurids (except in *Ruvettus*, which has a small predorsal bone in the first interneural space) (Table 1). Smith and Bailey (1961) considered this absence advanced and showed that in 47 percoid families only five lacked predorsal bones; however, they did not examine scombroids. In gempylids and trichiurids examined by us the first dorsal pterygiophore supports two spines and inserts in the second interneural space (Table 1). In *Epinnula, Neoepinnula* and *Rexea* we were unable to determine the interneural space for the first dorsal pterygiophores. The first dorsal fin pterygiophores are specialized in gempylids and trichiurids, because the distal radials articulate closely with the proximal radials. The second dorsal fin pterygiophores have separate distal radials between the fin ray base. Middle radials are present posteriorly in the gempylids and trichiurids examined. Gempylids examined by us had two stays posterior to the last dorsal and anal pterygiophores (except in *Lepidocybium, Rexea* and *Gempylus* where we found only one stay), whereas trichiurids and *Scombrolabrax* have only one stay, which is typical of most perciforms. The posteriormost double ray of gempylids is in series anterior to the two stays with the distal and proximal radial, indicating that the two stays are truly stays and not vestiges of radials. Three spines are supported by the first anal pterygiophore of *Scombrolabrax* and of gempylids and trichiurids examined (except *Rexea,* where only two spines are supported). Finlets are present posterior to the dorsal and anal fins in some gempylids examined but are lacking in trichiurids and *Scombrolabrax* (Table 1).

The pelvic fin, with a count of I, 5, and the basipterygium are similar in *S. heterolepis* and in all scombrids (Table 1; compare Figs. 17, 18 with Collette and Chao, 1975, Figs. 66, 67; Kishinouye, 1923; de Sylva, 1955). In gempylids the pelvic fin ray count may be I,5; I,4; I,2; I,1 or I and the basipterygium may be developed, slightly reduced or reduced (Matsubara and Iwai, 1952, 1958). In trichiurids, the pelvic fin may be reduced or absent (Tucker, 1956).

The gill rakers of the first arch of *S. heterolepis* are typically gempylid (compare Fig. 12D with Matsubara and Iwai, 1952, Figs. 2, 4, 9, 12). In a recent investigation of the pharyngobranchial complex of scombroids, G. David Johnson has observed a bony stay on the fourth infrapharyngobranchial in the Scombridae, Istiophoridae and Xiphiidae. This stay was not present in the Gempylidae, Trichiuridae or *Scombrolabrax,* and thus far has not been observed in any other perciform family (G. David Johnson, personal comm.[1]).

The caudal complex of *S. heterolepis* shows none of the fusion of elements seen in the Gempylidae (Matsubara and Iwai, 1958), Scombridae (Monod, 1968 and Potthoff, 1975), Istiophoridae (Monod, 1968), Carangidae (Berry, 1969), and Coryphaenidae (Potthoff, 1980). It is the most basic primitive perciform caudal structure (Gosline, 1961a; E. H. Ahlstrom, personal comm.[2]) and is similar to that of *Archosargus rhomboidalis* described by Houde and Potthoff (1976), except *A. rhomboidalis* lacks the procurrent spur (Johnson, 1975). *Scombrolabrax,* the gempylids (Matsubara and Iwai [1958] reported 2 epurals for *Lepidocybium,* but our specimens had 3 epurals) and some trichiurids have 3 epurals, although some trichiurids have only 1 epural (Table 1). All scombrids have 2 epurals (Kramer, 1960; Fierstine and Walters, 1968; Collette and Chao, 1975; Potthoff, 1975). The processes of the posteriormost two centra and the urostyle support the caudal fin rays in *S. heterolepis* and in the Gempylidae and Trichiuridae (Table 1). Scombrids have narrow caudal peduncles, and thus the processes of the posteriormost

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[2] National Marine Fisheries Service, NOAA, Southwest Fisheries Center, La Jolla, CA. Deceased.

three or four centra and the urostyle support the caudal fin rays (Collette and Chao, 1975; Potthoff, 1975), except in *Grammatorcynus* (B. B. Collette and J. L. Russo, personal comm.[3]), *Scomber* and *Rastrelliger* where only 2 centra and the urostyle support the caudal fin rays. Gempylids may have some fusion and loss of elements in the caudal complex (Matsubara and Iwai, 1958), but this is not as extensive as in the scombrids and some trichiurids. The bases of the principal caudal rays are forked in juvenile *S. heterolepis* and cover about one third of the hypural bones distad (Fig. 21). The same is true for all other adult gempylids (Matsubara and Iwai, 1958; Collette and Russo, 1978, Fig. 2B) and trichiurids with tails. Adult and juvenile scombrids also have forked caudal rays, but in contrast, these rays cover most of the hypural bones in adults (Munro, 1943; Collette and Chao, 1975, Fig. 57; Collette and Russo, 1978, Fig. 2A). In *Scomber* and *Rastrelliger,* only part of the hypural bones are covered. The procurrent spur on the posteriormost ventral secondary caudal ray and a foreshortened adjacent secondary ray described on many percoids by Johnson (1975) are lacking in all scombrids and trichiurids examined, but the spur is present in an extremely reduced state in some gempylids without the foreshortening of the adjacent secondary caudal ray. In *S. heterolepis,* both the spur and the foreshortened ray are present (Fig. 21, Table 1).

S. heterolepis has a lower total count of vertebrae (30) than any gempylid, trichiurid or scombrid and a greater number of caudal (17) than precaudal (13) vertebrae. Total vertebral counts for gempylids range from 31 to 53 (Munro, 1943; Matsubara and Iwai, 1958); for trichiurids 58 to 192 (Tucker, 1956); and for scombrids 31 to 64 (Munro, 1943; Mago Leccia, 1958; Kramer, 1960; Matsui, 1963 and 1967; Gibbs and Collette, 1967; Potthoff and Richards, 1970; Collette and Chao, 1975; Collette and Russo, 1978; Collette et al., 1978) (Table 1). Most gempylids have more precaudal than caudal vertebrae (Matsubara and Iwai, 1958) whereas scombrids and trichiurids have fewer precaudal than caudal vertebrae (exceptions are some Sardini, *Auxis* and *Euthynnus* in the Scombridae). *Diplospinus* (Trichiuridae) has, according to our observations, fewer precaudal than caudal vertebrae, although Tucker (1956) reported the opposite. *Benthodesmus* (Trichiuridae) has fewer precaudal than caudal vertebrae if the first anal pterygiophore is used to delineate precaudal from caudal centra. If the first haemal spine is used to delineate the vertebrae then *Benthodesmus* has more precaudal than caudal vertebrae.

Grey (1960) indicated that *S. heterolepis* is related closest to *Neoepinnula orientalis.* We compared *S. heterolepis* with *N. orientalis* from the Caribbean and found little internal resemblance between the two genera. *Neoepinnula* has 16 + 16 = 32 vertebrae; D XVI, 19; A III, 18; caudal rays 10 + 9 + 8 + 10 rays supported by 2 centra and the urostyle, 3 epurals, 1 pair uroneurals (2 fused?), a dorsal and ventral hypural plate and a parhypural. There are no predorsal bones anterior to the dorsal fin pterygiophore. Insertion of the first pterygiophore could not be determined because the first two neural spines were too short.

The larvae of *S. heterolepis* superficially resemble scombrid larvae more than they do gempylid or trichiurid larvae. The sequence of fin development (second dorsal fin develops before first) in *S. heterolepis* resembles that of *Scomber* and *Rastrelliger,* but in all other known scombroid larvae the first dorsal fin develops first (Table 1). Okiyama and Ueyanagi (1978) discussed the interrelationships of larvae in the Scombridae. They pointed out the usefulness of the sequence in fin

[3] National Marine Fisheries Service, NOAA, Systematics Laboratory, Washington, DC 20235.

development, but unfortunately repeated a typographical error made in transposition by Richards (1973). Richards intended to state for *Scomber*: second dorsal fin develops before the first dorsal fin. The development of gempylid and trichiurid larvae is not well studied. In *Gempylus serpens* (*Gempylus* B in Voss, 1954), *Nesiarchus nasutus* and *Diplospinus multistriatus (Gempylus* A in Voss, 1954), the first dorsal fin develops first.

We conclude that *S. heterolepis* is a scombroid fish because the larvae superficially resemble tuna larvae and because predorsal bones are absent in *S. heterolepis* and all other scombroids except *Ruvettus*. The insertion of the first dorsal fin pterygiophore in the third interneural space and the following two pterygiophores in the fourth interneural space are found in *S. heterolepis* and in the Scombridae (compare Fig. 13 with Potthoff's [1974] Fig. 10; our observations for other scombrid genera). In the Gempylidae and Trichiuridae examined by us, the first dorsal pterygiophore inserts in the second interneural space. In *Epinnula, Neoepinnula* and *Rexea* we could not determine the exact insertion. We know of no other fish families that have retained a similar scombrid pterygiophore insertion sequence with the loss of the predorsal bones (Smith and Bailey [1961]; G. D. Johnson, personal comm.[1]) except *Astrapogon, Pseudamiops* and *Gymnapogon,* in the family *Apogonidae* (Fraser, 1972). The vertebral number of 30 vertebrae also favors scombroid relationship since many percoids have 24 or 25. We propose that *S. heterolepis* should be placed, for the time being, in the separate family Scombrolabracidae, because *S. heterolepis* has a reduced procurrent spur followed by an adjacent reduced secondary ray (Fig. 20; Johnson, 1975) (not shared with any members of other scombroid families), a basic caudal complex (not shared with all members of other scombroid families) and lacks a stay on the pharyngobranchial of the fourth arch (present in Scombridae and in the non scombroid istiophorids and xiphiids, absent in Gempylidae and Trichiuridae) (Table 1).

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APPENDIX

The following species were examined by us for characters listed in Table 1 and discussed in the "Relationships" section.

Family Scombridae. *Thunnus atlanticus* (4, 64–85, 504 mm SL), *T. thynnus* (3, 105–120 mm SL), *Katsuwonus pelamis* (4, 100–140 mm SL), *Euthynnus alletteratus* (4, 80–120 mm SL), *Auxis* spp. (5, 105–125 mm SL), *Sarda sarda* (2, 68, 104 mm SL), *Scomberomorus regalis* (2, 161, 181 mm SL), *Rastrelliger* spp. (2, 112, 127 mm SL), *Scomber japonicus* (3, 103–113 mm SL), *Grammatorcynus bilineatus* (examined only stay, 2, 382, 424 mm SL), *Gasterochisma melampus* (examined only caudal fin and stay, 3, 1,050–1,280 mm SL).

Family Gempylidae. *Lepidocybium flavo-brunneum* (2, 830, 1,020 mm SL), *Ruvettus pretiosus* (3, 210–220 mm SL), *Neoepinnula orientalis* (5, 170–200 mm SL), *Epinnula magistralis* (x-ray, 1, 437 mm SL), *Thyrsites atun* (2, 170, 180 mm SL), *Rexea* spp. (2, 132, 155 mm SL), *Promethichthys prometheus* (3, 100–236 mm SL), *Nealotus tripes* (4, 83–159 mm SL), *Nesiarchus nasutus* (2, 241, 275 mm SL), *Gempylus serpens* (5, 105–271 mm SL).

Family Trichiuridae. *Diplosinus multistriatus* (3, 64–217 mm SL), *Paradiplospinus gracilis* (1, 324 mm SL), *Benthodesmus simonyi* (1, 528 mm SL), *Evoxymetapon taeniatus* (3, 368–750 mm SL), *Trichiurus lepturus* (3, 420–600 mm TL).