

# CARTILAGE AND BONE DEVELOPMENT IN SCOMBROID FISHES

THOMAS POTTHOFF, SHARON KELLEY, AND JOAQUIN C. JAVECH<sup>1</sup>

## ABSTRACT

Early development of cartilage and bone was examined in representative species of the scombroid fish families Scombridae, Gempylidae, Trichiuridae, Scombridae, Istiophoridae, and Xiphiidae from cleared and stained larval size series. Development of the dorsal and anal fins and their pterygiophore supports, development of the neural and haemal spines and hypural complex, and ossification of the vertebrae were studied. The first appearance and location of these skeletal elements in cartilage were noted, and then the direction of new additions was observed. Direction of ossification of these elements was also noted. There were three major kinds of vertebral column development: The first was shared by Scombridae, Scombridae in part - Scombrini, Scomberomorini, and Thunnini; the second was shared by Gempylidae, *Sarda* (Scombridae in part - Sardini), Istiophoridae, and Xiphiidae; the third kind was found in *Trichiurus* (Trichiuridae). Saddle-shaped ossifications of the vertebrae were found only in the Scombridae, and Gempylidae, and Scombridae. Four major kinds of fin and pterygiophore development were observed in the scombroid families: Scombridae and Scombridae in part - Scombrini shared one kind; Gempylidae, Trichiuridae, and Scombridae in part - Scomberomorini, Sardini, and Thunnini shared another kind, which had some variations for different taxa; Istiophoridae had the third kind; and Xiphiidae had the fourth kind. Initial ossification of the vertebral column started in one place in *Scombridae*, Gempylidae, *Trichiurus*, and *Xiphias*, in two places in *Scomberomorus*, *Sarda*, *Thunnus*, and *Istiophorus*, and in four places in *Scomber* and *Acanthocybium*. From our investigation, we are just beginning to learn about developmental characters and we cannot interpret their full meaning until more developmental work has been accomplished; we can only state that billfish (Istiophoridae, Xiphiidae) are very different from all other scombroids studied and that *Scombridae* shows affinity with the scombroids.

In this paper we describe development of selected osteological features of families in the suborder Scombroidei. We believe that this ontogenetic data will be useful in future taxonomic studies to aid in establishing familial relationships. Under current classification the scombroids comprise various numbers of families. Greenwood et al. (1966) recognized six families in the suborder Scombroidei: Scombridae, Gempylidae, Trichiuridae, Istiophoridae, Xiphiidae, and Luvaridae. Gosline (1968), Potthoff et al. (1980), and Collette et al. (1984) included the family Scombridae in the Scombroidei, but Johnson (in press) removed it recently. Collette et al. (1984), Leis and Richards (1984), and Tyler et al.<sup>2</sup> removed the Luvaridae from the Scombroidei. For this study we examined ontogenetic series of representative genera of the families Scombridae, Gempylidae, Trichiuridae, Scombridae (four tribes), Istiophoridae, and Xiphiidae.

Research on the larvae and young stages of scombroids, particularly tunas (Richards and Klawe 1972) has been extensive. In general, most papers deal with the external description of the larvae and juveniles (Okiyama and Ueyanagi 1978); few exist that address the internal morphology and development of scombroids and those are mostly on scombrids. Kramer (1960) described bone development in the mackerel (*Pneumatophorus diego* = *Scomber japonicus*). Potthoff and Richards (1970), Matsumoto et al. (1972), and Richards and Potthoff (1974) published osteological characters for juvenile scombrids. Cartilage and bone development were described in *Thunnus atlanticus* (Potthoff 1975), *Scombridae heterolepis* (Potthoff et al. 1980), and *Xiphias gladius* (Potthoff and Kelley 1982). Kohno et al. (1984) described fin and cartilaginous fin support development in *Scomber japonicus*. To our knowledge no developmental studies of cartilage and bone have been made for the scombroid families Istiophoridae and Gempylidae, although a part of the research presented here was published in Collette et al. (1984). Since Collette et al. (1984), we have conducted additional research and have discovered several errors in our published observations. We have added developmental series of *Scomber*

<sup>1</sup>Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

<sup>2</sup>Tyler, J. C., G. D. Johnson, I. Nakamura, and B. B. Collette. Osteology and relationships of the oceanic fish *Luvarus imperialis* (Luvaridae): an acanthuroid not a scombroid. Unpubl. manuscr. National Museum of Natural History, Wash., DC 20560.

spp., *Scomberomorus* spp., *Acanthocybium solanderi* and *Sarda sarda* (Scombridae), *Trichiurus lepturus* (Trichiuridae), and *Makaira nigricans* (Istiophoridae). We examined numerous juvenile and adult Trichiuridae; our findings are incorporated here. In

table 161 of Collette et al. (1984), observations from the gempylid *Diplospinus multistriatus* were erroneously listed under Trichiuridae. In this paper we have revised and corrected that table and incorporated all our new findings (Tables 1, 2).

TABLE 1.—Developmental and osteological features and counts

	Scombrobracidae ( <i>Scombrobrax</i> )	Gempylidae	Trichiuridae		Scombridae
			without tail and pelvic fin, <i>Trichiurus</i>	with tail and pelvic fin, <i>Benthodesmus</i> <i>Evoxymetapon</i> <i>Lepidopus</i>	Scombrini ( <i>Scomber</i> )
Predorsal bones: present or absent	absent	present or or absent <sup>2</sup>	absent	absent	absent
number	0	0 or 1	0	0	0
First anteriormost dorsal pterygiophore: supports number of fin spines	2	2	2	2	2
inserts in interneural space number	3	2	2	2	3
First anteriormost anal pterygiophore: supports number of spines or rays	3	<sup>3</sup> 2 or 3	2	<sup>4</sup> 3	2
Middle radials: present or absent	present	present <sup>5</sup>	present	present	present
Dorsal and anal stay: present or absent ossifies to one or two parts	present one part	present one or two parts <sup>6</sup>	not determined —	present one part	present one part
posteriorly bifurcated or nonbifurcated	nonbifurcated	bifurcated	—	nonbifurcated	bifurcated
Pelvic fin: spine, ray count	1,5	1,5;1,4;1,2; 1,1;	—	1,1;1,2	1,5
Preural centrum 3: neural spine with or without cartilage tip haemal spine autogenous or nonautogenous	with autogenous	with autogenous	— —	with ontogenetically fused	with autogenous
Vertebrae inclusive of urostyle supporting caudal rays: number	3	3	—	3	3
Number of vertebrae: precaudal + caudal = total	13 + 17 = 30	usually more precaudal, fewer caudal, total 31-67	40 + 126 = 166	fewer precaudal, more caudal, total 99-192	13,14 + 17,18 = 31
Epurals: number	3	<sup>7</sup> 3	—	1 (ontogenetic fusion from 2)	2
Anterior epural fused with neural arch of Pu <sub>2</sub>	No	No	—	No	No

<sup>1</sup>Data from Fritzsche and Johnson (1980) and G. D. Johnson (text footnote).

<sup>2</sup>*Ruvettus*, *Thyrsoptis* and *Tongaichthys* have one predorsal bone.

<sup>3</sup>*Rexea* and *Thyrsoptis* (*Leionura*) have two spines, *Nealotus* ontogenetically has three spines but second spine fuses to basipterygium during development.

<sup>4</sup>Two of these spines are extreme vestiges.

**METHODS**

Scombroid larvae were cleared and stained for cartilage and bone (Potthoff 1984) and subsequently measured in millimeters with a calibrated ocular

micrometer under a binocular microscope. Notochord length (NL) was measured on preflexion and flexion stage larvae from the anterior tip of the upper jaw to the posterior tip of the notochord. Standard length (SL) was measured from the anterior

for the scombroid families and *Morone*, a primitive perciform fish.

Scombridae—Continued						
Scomberomorini ( <i>Scomberomorus</i> )	Scomberomorini ( <i>Acanthocybium</i> )	Sardini ( <i>Sarda</i> )	Thunnini ( <i>Thunnus</i> )	Istiophoridae ( <i>Istiophorus</i> )	Xiphiidae ( <i>Xiphias</i> )	Percichthyidae ( <i>Morone</i> ) <sup>1</sup>
absent 0	absent 0	absent 0	absent 0	absent 0	absent 0	present 3
2	2	2	2	3	1 to 3, mostly 2	3
3	3	2	3	1	2	3
3	not known	3	3	2	1 to 3, mostly 2	3
present	present	present	present	present	absent	present
present one part	present one part	present one part	present one part	present one part	present one part	present one part
nonbifurcated	slightly bifurcated	bifurcated	bifurcated	bifurcated, sometimes non- bifurcated	non- bifurcated	nonbifurcated
1,5	1,5	1,5	1,5	1,2	0	1,5
with autogenous	with autogenous	with autogenous	with autogenous	with autogenous	without non- autogenous	with autogenous
4,5	5	5	4	3	2	3
(16-22) + (24-32) = (41-53)	(30-32) + (31-33) = (62-64)	26 + 25 = 51	fewer precaudal, more caudal, total 39-41	12 + 12 = 24 11 + 13 = 24	15 + 11 = 26 16 + 10 = 26	12 + 13 = 25 11 + 14 = 25
2	2	2	2	3	3	3
No	No	No	Yes	No	No	No

<sup>1</sup>*Neocybina* lacks middle radials.

<sup>2</sup>*Lepidocybium*, *Rexea*, *Diplospinus*, *Paradiplospinus*, *Tongaichthys*, and *Gempylus* have a one-part stay, all other gempylids have a two-part stay.

<sup>3</sup>*Diplospinus* ontogenetically usually has three epurals, posterior two epurals are fused to one in adults, but some *Diplospinus* develop only two epurals.

TABLE 1.—Continued.

	Scombrobracidae ( <i>Scombrobrax</i> )	Gempylidae	Trichiuridae		Scombridae
			without tail and pelvic fin, <i>Trichiurus</i>	with tail and pelvic fin, <i>Benthodesmus</i> <i>Evoxymetapon</i> <i>Lepidopus</i>	Scombrini ( <i>Scomber</i> )
Uroneural: number	2	2	—	1	1
Hypural 5: present or absent fused or separate	present separate	present separate	— —	absent not known	present fused to uroneural proximally
Ontogenetic hypural fusion: fusion of hypurals 1 & 2 to ventral plate is in cartilaginous or ossified state	no fusion	If present, ossified	—	not known	cartilaginous
fusion of hypurals 3 & 4 to dorsal plate is in cartilaginous or ossified state	no fusion	If present, ossified	—	not known	cartilaginous or ossified
Procurrent spur (Johnson 1975): present or absent	present	present, reduced or absent	—	absent	absent
Stay on 4th pharyngo- branchial (G. D. Johnson, text footnote): present or absent	absent	absent	absent	absent	present

TABLE 2.—Developmental features for the scombroid

	Neural and haemal arches and spines, parapophyses and hypural parts initially develop in the following places on the notochord by the following se- quence. Addition is in a given direction.	Developing pterygiophores and fin spines and rays are added in a direction.
Scombrobracidae ( <i>Scombrobrax</i> )	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteri- orly and anteriorly. 4. Dorsad at center, posteri- orly and anteriorly.	First dorsal: anteriorly and posteriorly. Second dorsal: an- teriorly and posteriorly. Anal: anteriorly and posteriorly.
Gempylidae ( <i>Gempylus</i> , <i>Nesiarchus</i> , <i>Diplospinus</i> )	1. Anterodorsad, posteriorly. 2. Posteroventrad, posteriorly and anteriorly. 3. Ventrad at center, posteri- orly and anteriorly.	First dorsal: posteriorly. Sec- ond dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Trichiuridae ( <i>Trichiurus</i> )	1. Anterodorsad, posteriorly. 2. Ventrad at center, posteri- orly and anteriorly.	Entire dorsal and anal: poste- riorly.

Scombridae—Continued

Scomberomorini ( <i>Scomberomorus</i> )	Scomberomorini ( <i>Acanthocybium</i> )	Sardini ( <i>Sarda</i> )	Thunnini ( <i>Thunnus</i> )	Istiophoridae ( <i>Istiophorus</i> )	Xiphiidae ( <i>Xiphias</i> )	Percichthyidae ( <i>Morone</i> ) <sup>1</sup>
1	1	1	1	1	1	2
present separate	present fused to uroneural proximally	present separate	present separate	absent —	present separate	present separate
cartilaginous	cartilaginous	cartilaginous	cartilaginous	cartilaginous or ossified	ossified	no fusion
cartilaginous	cartilaginous or ossified	cartilaginous or ossified	cartilaginous	cartilaginous or ossified	ossified	no fusion
absent	absent	absent	absent	absent	absent	present
present	present	present	present	present	present	absent

families and *Morone*, a primitive perciform fish.

Sequence of fin and associated pterygiophore development.	First anteriormost dorsal and anal pterygiophore develop from one or two pieces of cartilage.	Number of initial places of ossification along vertebral column; centra develop from saddle-shaped ossifications at bases of neural and haemal arches.
1. Second dorsal and anal concurrently. 2. First dorsal. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	1;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	1;Yes
1. All dorsal rays and pterygiophores dorsoanterior to anal fin. 2. All dorsal rays and pterygiophores opposite future anterior portion of anal fin. 3. All anal rays and pterygiophores.	Dorsal and anal from one piece.	1;No

TABLE 2.—Continued.

	Neural and haemal arches and spines, parapophyses and hypural parts initially develop in the following places on the notochord by the following sequence. Addition is in a given direction.	Developing pterygiophores and fin spines and rays are added in a direction.
Scombridae, Scombrini ( <i>Scomber</i> )	<ol style="list-style-type: none"> <li>1. Posteroventrad, posteriorly and anteriorly.</li> <li>2. Ventrad at center, posteriorly and anteriorly.</li> <li>3. Dorsad at center, posteriorly and anteriorly.</li> <li>4. Anterodorsad, posteriorly.</li> </ol>	First dorsal: pterygiophores anteriorly and posteriorly. Spines: one anteriorly, rest posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Scomberomorini ( <i>Scomberomorus</i> )	<ol style="list-style-type: none"> <li>1. Anterodorsad, posteriorly.</li> <li>2. Posteroventrad, posteriorly and anteriorly.</li> <li>3. Ventrad at center, posteriorly and anteriorly.</li> <li>4. Dorsad at center, posteriorly and anteriorly.</li> </ol>	First dorsal: posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Scomberomorini ( <i>Acanthocybium</i> )	Not entirely known. Smallest specimen available had already two centers of initial development: anterodorsad and posteroventrad.	First dorsal: probably posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Sardini ( <i>Sarda</i> )	<ol style="list-style-type: none"> <li>1. Anterodorsad, posteriorly.</li> <li>2. Posteroventrad, posteriorly and anteriorly.</li> <li>3. Ventrad at center, posteriorly and anteriorly.</li> </ol>	First dorsal: pterygiophores posteriorly. Spines: first one anteriorly, rest posteriorly. Second dorsal: probably anteriorly and posteriorly. Anal: anteriorly and posteriorly.
Scombridae, Thunnini ( <i>Thunnus</i> )	<ol style="list-style-type: none"> <li>1. Anterodorsad, posteriorly.</li> <li>2. Posteroventrad, posteriorly and anteriorly.</li> <li>3. Ventrad at center, posteriorly and anteriorly.</li> <li>4. Dorsad at center, posteriorly and anteriorly.</li> </ol>	First dorsal: pterygiophores posteriorly. Spines: first one anteriorly, rest posteriorly. Second dorsal: anteriorly and posteriorly. Anal: some anteriorly, most posteriorly.
Istiophoridae ( <i>Istiophorus</i> )	<ol style="list-style-type: none"> <li>1. Anterodorsad, posteriorly.</li> <li>2. Posteroventrad, posteriorly and anteriorly.</li> <li>3. Ventrad at center, haemal spines posteriorly, parapophyses anteriorly.</li> </ol>	Entire dorsal: very few anteriorly, most posteriorly. Anal: very few anteriorly, most posteriorly.
Xiphiidae ( <i>Xiphias</i> )	<ol style="list-style-type: none"> <li>1. Anterodorsad, posteriorly.</li> <li>2. Posteroventrad, posteriorly and anteriorly.</li> <li>3. Ventrad at center, posteriorly and anteriorly.</li> </ol>	Entire dorsal: anteriorly and posteriorly. Anal: very few anteriorly, most posteriorly.
Percichthyidae ( <i>Morone</i> ) <sup>1</sup>	Anterodorsad, posteriorly. Ventrad at center, posteriorly and anteriorly. Posteroventrad, posteriorly and anteriorly. Initial sequence not known, not known if neural arches and spines develop initially at center.	First dorsal: anteriorly and posteriorly. Second dorsal: anteriorly and posteriorly. Anal: anteriorly and posteriorly.

<sup>1</sup>Data from Fritzsche and Johnson (1980) and G. D. Johnson (text footnote 3).

Sequence of fin and associated pterygiophore development.	First anteriormost dorsal and anal pterygiophore develop from one or two pieces of cartilage.	Number of initial places of ossification along vertebral column; centra develop from saddle-shaped ossifications at bases of neural and haemal arches.
1. Second dorsal and anal concurrently. 2. First dorsal.	Dorsal and anal from one piece.	4;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	2;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal separated from second dorsal during part of development.	Dorsal probably from one piece, anal not known.	4;Not known
1. First dorsal. 2. Second dorsal and anal concurrently. Not known if first dorsal is separated from second dorsal during part of development.	Dorsal from one piece, anal probably from two pieces.	2?;Yes
1. First dorsal. 2. Second dorsal and anal almost concurrently. First dorsal separated from second dorsal during part of development.	Dorsal from one piece, anal from two pieces.	2;Yes
1. First dorsal. 2. Second dorsal and anal concurrently. First dorsal <i>not</i> separated from second dorsal during development.	Dorsal from one piece, anal from two pieces.	2;No
1. Second dorsal and anal concurrently. 2. First dorsal. First dorsal and first anal <i>not</i> separated from second dorsal and second anal during development.	Variable, dorsal and anal may develop from one or two pieces.	1;No
1. Second dorsal and anal concurrently. 2. First dorsal. Separation or continuity of first and second dorsals not known.	Dorsal and anal from two pieces.	?;No

tip of the upper jaw to the posterior margin of the hypural bones. *Xiphias* larvae were measured from the anterior margin of the eye to the posterior tip of the notochord for eye notochord length (ENL) or from the anterior margin of the eye to the posterior margin of the hypural bones for eye standard length (ESL).

## FAMILY SCOMBROLABRACIDAE

Figure 1

Thirty *Scombrolabrax heterolepis* larvae (2.9-10.4 mm NL or SL) were available.

Development of the vertebral column initially started in four places on the notochord: 1) antero-dorsad (neural arches and spines of future centra 1-3), 2) posteroventrad (parhypural, hypurals), 3) ventrad at the center (haemal arches and spines on future centra 16-21), and 4) dorsad at the center (neural arches and spines on future centra 12-28). The anterior neural spines were added in a posterior direction whereas the neural and haemal spines at the center of the body were added anteriorly and posteriorly. The two areas of neural spine development coalesced around the eighth neural spine anteriorly and just anterior to the hypural complex posteriorly. The hypurals were added in a posterior direction, but the parhypural and the two autogenous haemal spines were added anteriorly (Table 2). Ossification of the vertebral column in *Scombrolabrax* initially started in one place with the anteriormost neural arches and spines and proceeded in a posterior direction. The hypural complex was the last along the vertebral column to start ossifying. Vertebrae first ossified by forming saddles of bone dorsad and ventrad around the notochord. As ossification proceeded the saddles merged laterally forming an hourglass-shaped vertebra in the lateral view.

Cartilaginous second dorsal and anal fin pterygiophores developed first simultaneously above interneural spaces 15-17 and below interhaemal spaces 16-19 before the anterior neural arches and spines had coalesced. The addition of cartilaginous second dorsal and anal fin pterygiophores was in an anterior and posterior direction. First dorsal fin pterygiophores appeared second above interneural spaces 4-7, to which pterygiophores were added anteriorly and posteriorly, terminating anteriorly in the third interneural space and joining with the second dorsal fin pterygiophores posteriorly. Dorsal and anal fin rays and spines developed in the same sequence as their corresponding pterygiophores, but a little later (Table 2).

*Scombrolabrax heterolepis* does not develop pre-dorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three spines (two supernumerary spines). The posteriormost five or six dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double ray and had a nonbifurcated stay (Table 1).

In *S. heterolepis*, first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the anterior development of the neural spines and the central appearance of haemal spines. The hypural complex development was described by Potthoff et al. (1980). *Scombrolabrax heterolepis* had the basic perciform caudal skeleton (Gosline 1968), with no hypural fusion observed in adults. The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. A procurrent spur was present on the posteriormost ventral secondary caudal ray with a basally foreshortened ray anterior to it (Johnson 1975) (Table 1).

## FAMILY GEMPYLIDAE

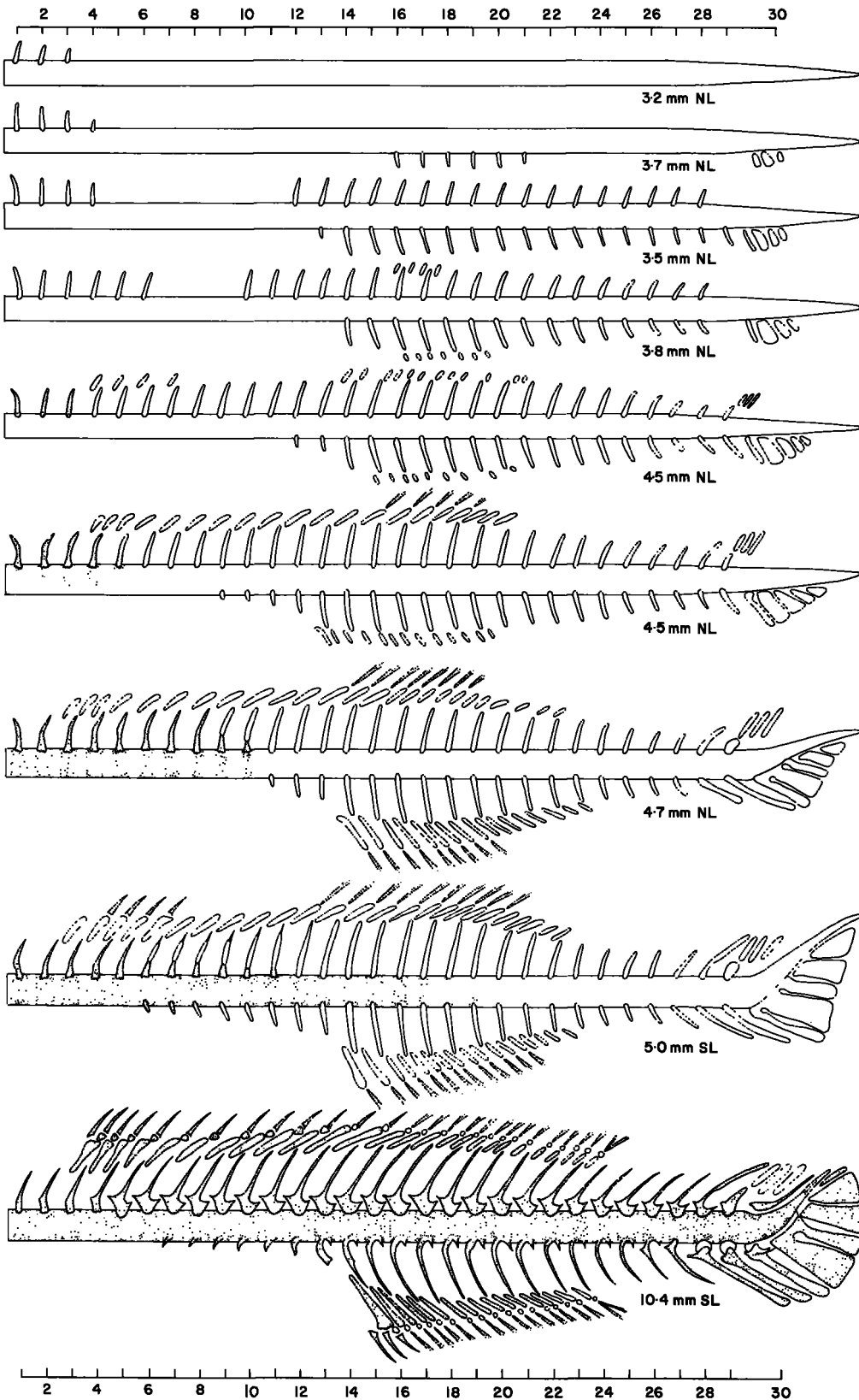
Figures 2-4

One hundred and ten gempylids in 11 genera were available: 33 *Gempylus serpens* (3.7-9.9, 160 mm NL or SL), 23 *Nesiarchus nasutus*, (2.6-10.2, 55, 242 mm NL or SL), 7 *Neoepinnula orientalis* (3.3-7.1, 112 mm NL or SL), 11 *Nealotus tripes* (3.4-11.9, 24-140 mm NL or SL), 5 *Lepidocybium flavobrunneum* (5.5-35.3 mm NL or SL), 5 *Promethichthys prometheus* (26.4-161 mm SL), 2 *Rexea* sp. (132, 155 mm SL), 2 *Ruwettus pretiosus* (209, 212 mm SL), 1 *Thyrsitops lepidopoides* (160 mm SL), 16 *Diplospinus multistriatus* (3.4-13.5 mm NL or SL), 5 *Thyrsites atun* (= *Leionura*, 83-254 mm SL). Of these, *G. serpens*, *D. multistriatus*, and *N. nasutus* yielded complete developmental series.

Development of the vertebral column initially started in three places on the notochord: 1) antero-dorsad (neural arches and spines on future centra 1-6); 2) posteroventrad (hypurals); and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were

FIGURE 1.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scombrolabrax heterolepis*, Scombrolabracidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.





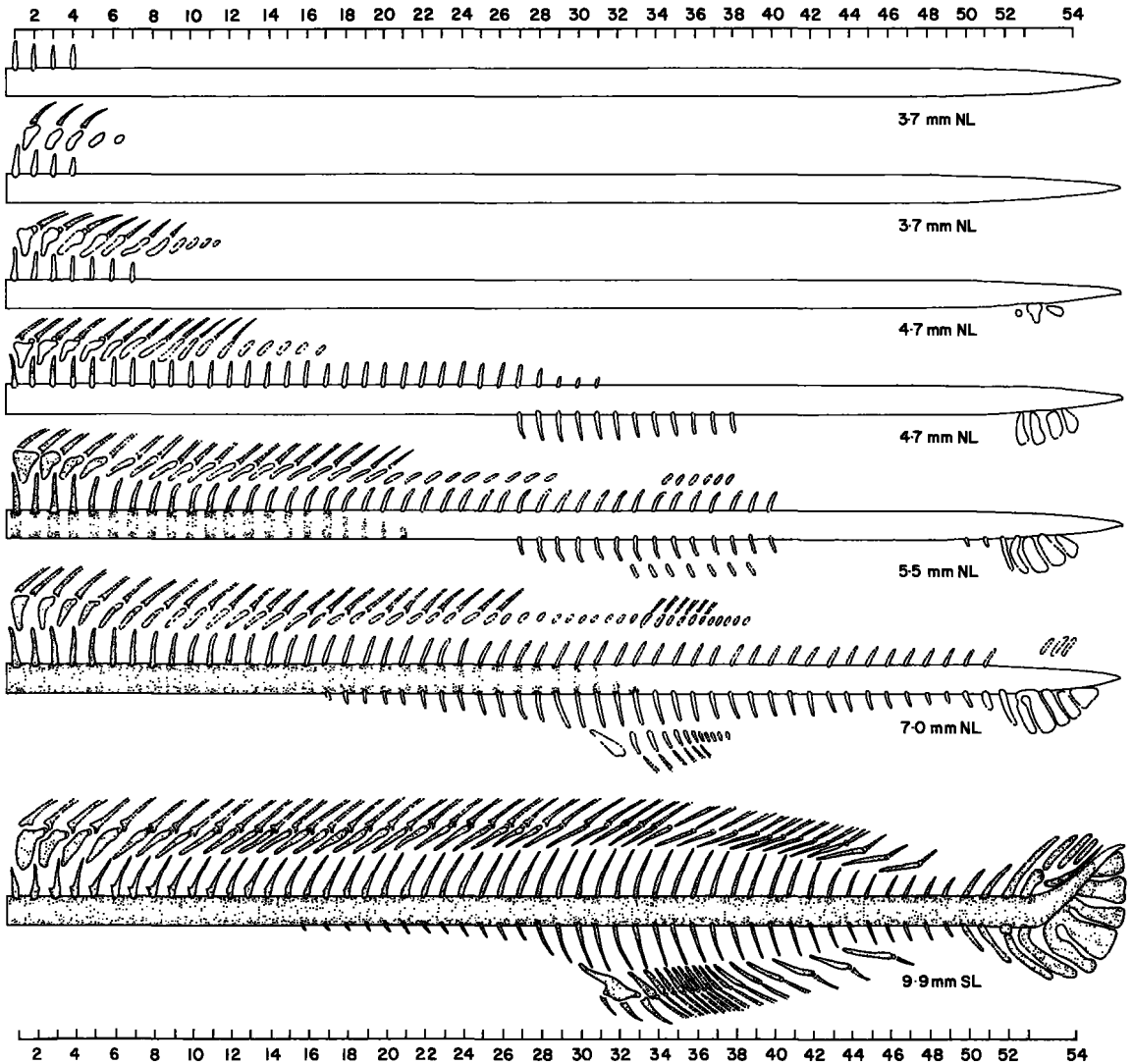


FIGURE 2.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Gempylus serpens*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

added in a posterior direction. Haemal arches and spines developed only when the neural spines reached the caudal area, and they were added in a posterior direction. Parapophyses were added anteriorly. The hypurals were added posteriorly, the parhypural and the autogenous haemal spines were added anteriorly (Table 2). Ossification of the vertebral column in the gempylid genera examined by us initially started in one place and was similar to the ossification in *Scombrolabrax*, except in *Diplospinus* the vertebral column was ossified to preural centrum 6 when the urostyle and the hypurals initially started to ossify. Saddle-shaped vertebral ossifications were

observed in all gempylids examined, similar to those described for *Scombrolabrax*.

Gempylids developed first dorsal fin pterygiophores and fin spines first, after only a few cartilaginous neural spines had developed. Development of first dorsal fin pterygiophores and spines was in a posterior direction. During early development the neural spines were anterior to the first dorsal fin pterygiophores and fin spines, but later they developed faster and were posterior to the pterygiophores. Pterygiophores of the second dorsal and anal fins developed before the developing first dorsal fin pterygiophores and had joined with the second dor-

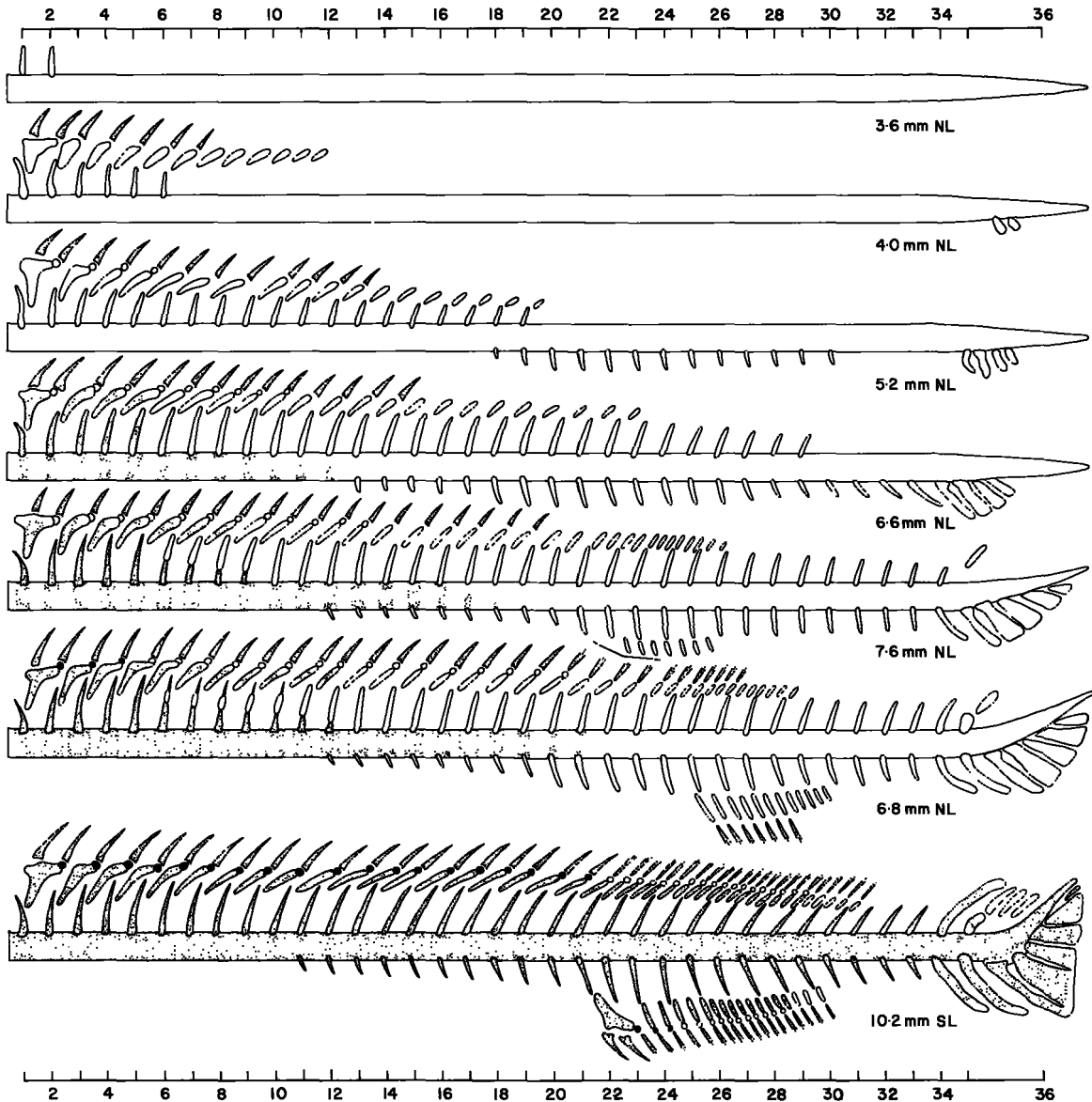
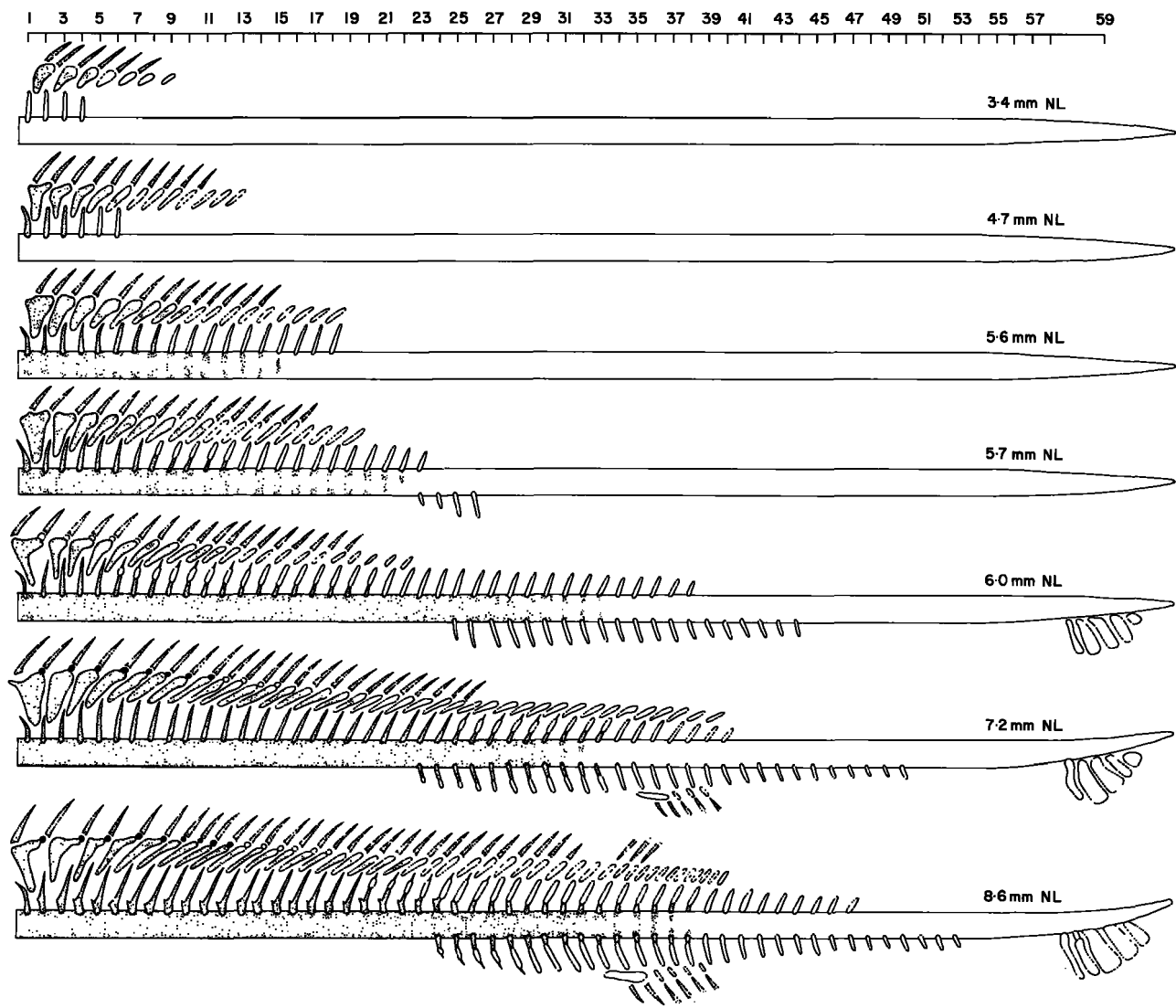


FIGURE 3.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Nesiarichthys nasutus*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

sal fin pterygiophores. Addition of second dorsal and anal pterygiophores was then in an anterior and posterior direction. The same development was observed for the second dorsal and anal fin rays and anal spines at slightly greater size (Table 2).

Most gempylid genera lack predorsal bones, except *Tongaichthys* (Nakamura and Fujii 1983), *Ruvettus* (Potthoff's pers. obs.), and *Thyrsitops* (Sato 1983) which have one predorsal bone. The first dorsal pterygiophore originated from one piece of

cartilage and inserted in the second interneural space supporting two fin spines (one supernumerary spine). In three Atlantic *Lepidocybium*, the first dorsal pterygiophore inserted in the second interneural space, but in two Pacific specimens it was found in the third space. The first anal pterygiophore was considerably larger than the following pterygiophores and presumably developed from two pieces of cartilage. It supported three anal spines (two supernumerary spines) except in adults of *Rexea*,



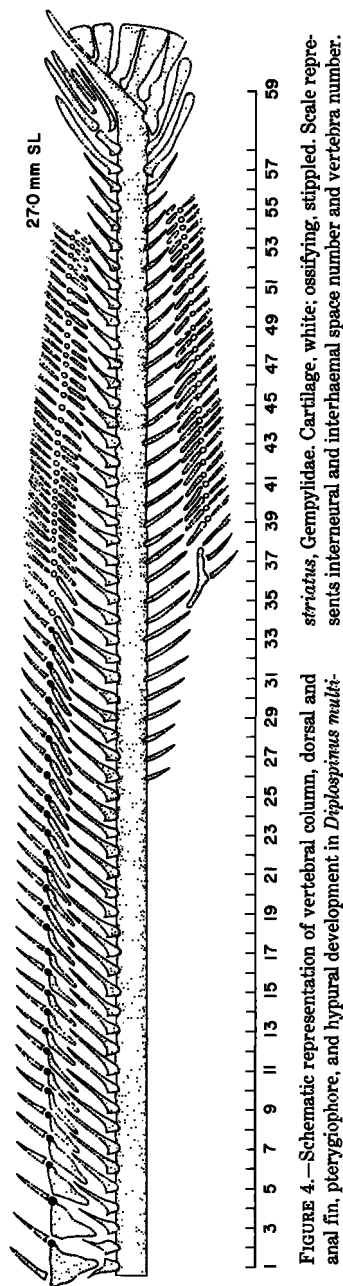


FIGURE 4.—Schematic representation of vertebral column, dorsal and anal fin pterygiophore, and hypural development in *Diplospinus multistriatus*, Gempylidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

*Thyrssites* (*Leionura*), and *Nealotus* where only two spines were supported (one supernumerary). Larvae of *Nealotus* have three spines associated with the first anal pterygiophore, but in juveniles the second anal spine was fusing to the posterior process of the pterygiophore. No evidence of a similar fusion was observed in *Rexea* or *Thyrssites* (*Leionura*). Gempylids had middle radials in one to six posterior-most dorsal and anal pterygiophores (except *Neopinnula* lacked middle radials). A double ray, and a two-part posteriorly bifurcated stay was associated with the last dorsal and anal pterygiophore in approximately one half of the genera. *Lepidocybium*, *Gempylus*, *Diplospinus*, *Paradiplospinus*, *Tongaichthys*, and *Rexea* had a one-part posteriorly bifurcated stay (Table 1).

First caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with anterior development of a few neural spines and some first dorsal fin pterygiophores and fin spines. The gempylid genera studied by us developed all parts found in basic perciform caudal skeletons (Gosline 1968), even the smaller second uroneural. Caudal parts then fuse differently in the various genera of adults (Matsubara and Iwai 1958). The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. In the gempylids the procurrent spur on the posteriormost ventral secondary caudal ray may be present, reduced, or absent. Johnson (1975) examined two species in which it was absent (Table 1).

## FAMILY TRICHIURIDAE

### Figures 5-8

Seventy-three trichiurids in four genera were available: 61 *Trichiurus* (4.5-26, 300, 303, 510 mm TL), 8 *Benthodesmus* (4.5, 12 mm NL, 65-120, 541, 545 mm SL), 3 *Evoxymetapon* (210-550 mm SL), 1 *Lepidopus* (280 mm SL). Only *Trichiurus* yielded a complete developmental series.

Development of the vertebral column in *Trichiurus* initially started in two places on the notochord: 1) anterodorsad (neural arch and spine on future centrum 1), and 2) ventrad at the center (anterior haemal arches and posterior parapophyses). Cartilaginous neural arches and spines were added in a posterior direction. Haemal arches and spines developed when the neural spines reached the anterior future caudal vertebrae. Addition of haemal arches and spines was also in a posterior direction (Table 2). *Trichiurus* lacked a caudal complex. Ossification of the vertebral column started initially in one place, with the anteriormost neural spines and

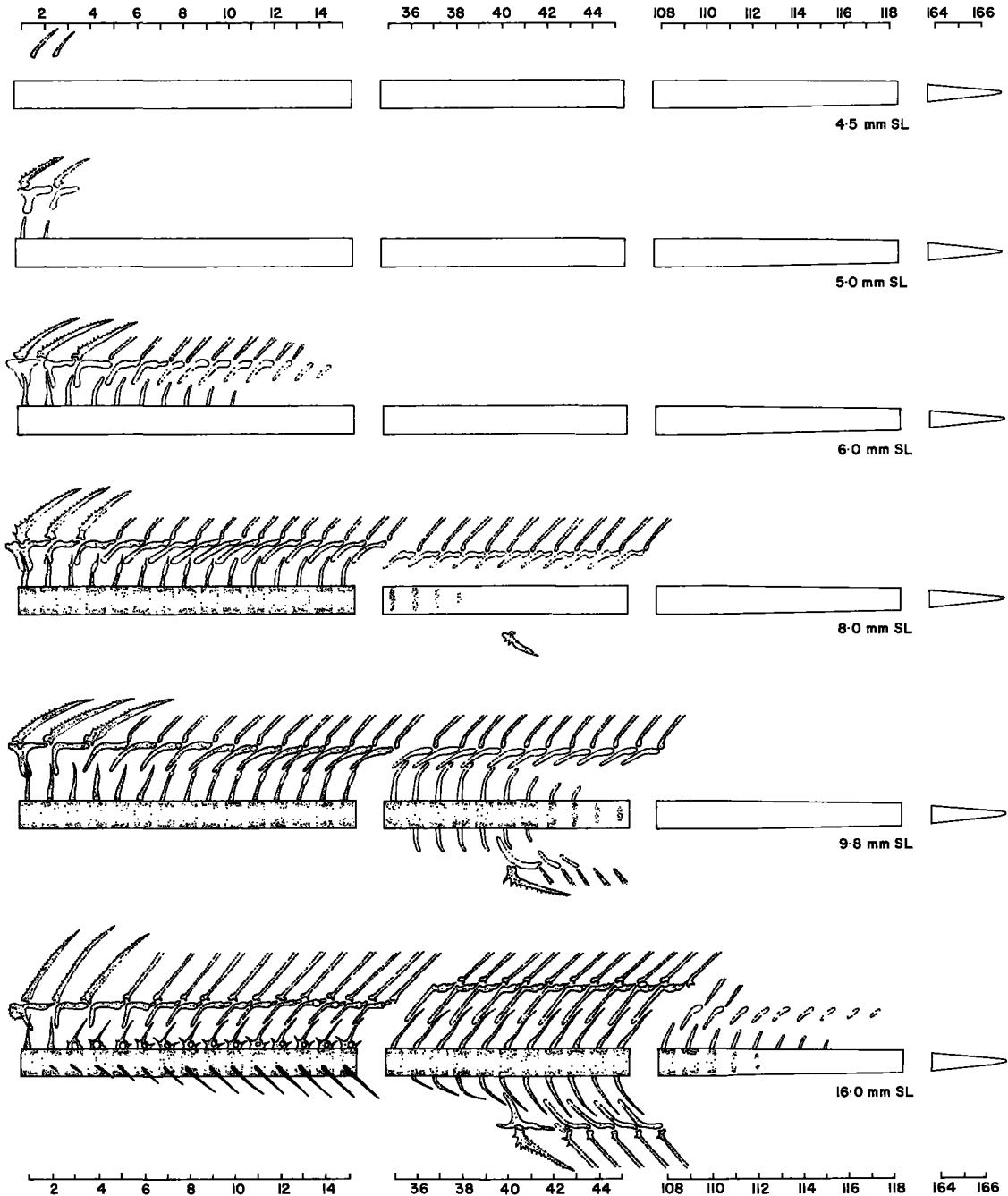


FIGURE 5.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Trichiurus lepturus*, Trichiuridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

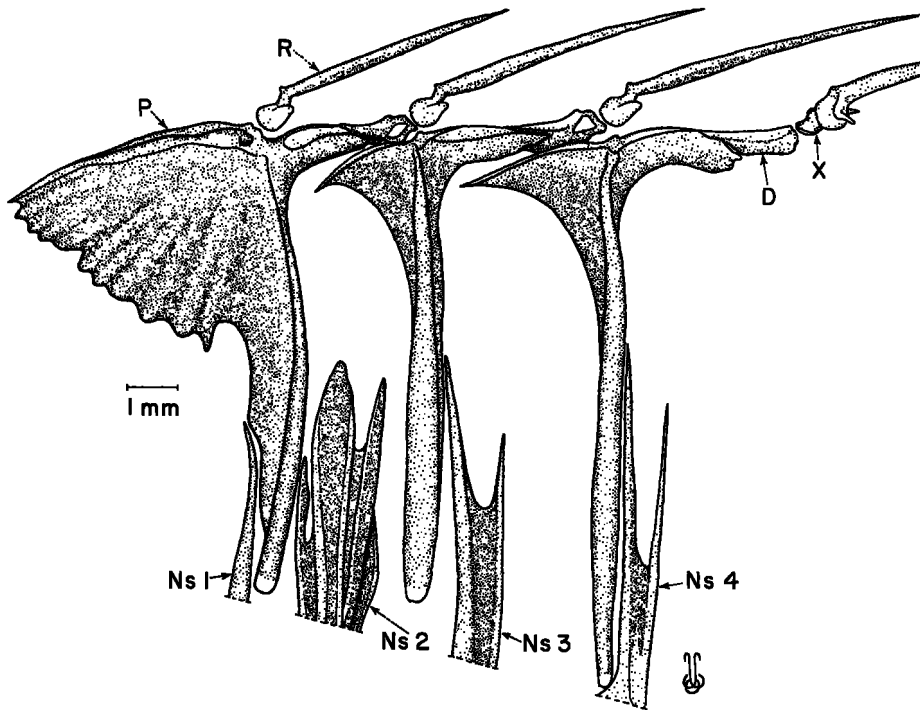


FIGURE 6.—Left lateral view of the anteriormost three dorsal pterygiophores inserting in the interneural spaces 2-4 from a juvenile *Trichiurus lepturus* 510 mm TL. D, distal radial; Ns, neural spine; P, proximal radial; R, ray or spine; X, a new pterygiophore element of unknown homology. Cartilage, white; bone, stippled.

arches and proceeded in a posterior direction. Saddle-shaped ossifications of the vertebrae as seen in Scombrolabrociidae, Gempylidae, and Scombridae were not observed in *Trichiurus*, instead vertebral ossification started laterally on both sides of the notochord as a thin strip of bone. During further development the lateral strip elongated dorsad and ventrad joining the strip from the opposite side and forming a ring of bone around the notochord.

*Trichiurus* first developed two of the three anterior dorsal fin spines. Next the first dorsal pterygiophore developed. Then dorsal pterygiophores, the third dorsal fin spine, and the dorsal fin rays were added in a posterior direction, with the pterygiophore development being slightly posterior to the ray development and considerably posterior to the neural arch and spine development. The single large anal spine developed first after dorsal fin ray and pterygiophore development had dorsally passed the anterior portion of the anal fin fold. Next, the large first anal fin pterygiophore and some haemal arches and spines developed. Further development consisted of the addition of anal fin rays, pterygiophores,

and haemal arches and spines in a posterior direction. The haemal arches and spines and the anal fin rays developed slightly anterior to the anal pterygiophores. The anal pterygiophores were slightly anterior to the dorsal fin ray and pterygiophore development (Table 2).

*Trichiurus* lacked predorsal bones. The first dorsal pterygiophore supported two fin spines (one supernumerary) and originated from one piece of cartilage. In larvae the first dorsal pterygiophore inserted between the split neural arch and spine of the first centrum, thus inserting into the first and second interneural spaces. However, in adults the first dorsal pterygiophore inserted into the second interneural space. All following interneural and interhaemal spaces accommodated one pterygiophore per space. The first anal pterygiophore was larger than the following pterygiophores, but it developed from one piece of cartilage and supported one supernumerary spine and one ray (Table 1).

The pterygiophores in *Trichiurus* and probably in most if not all species of the Trichiuridae are anatomically different from those of other scom-

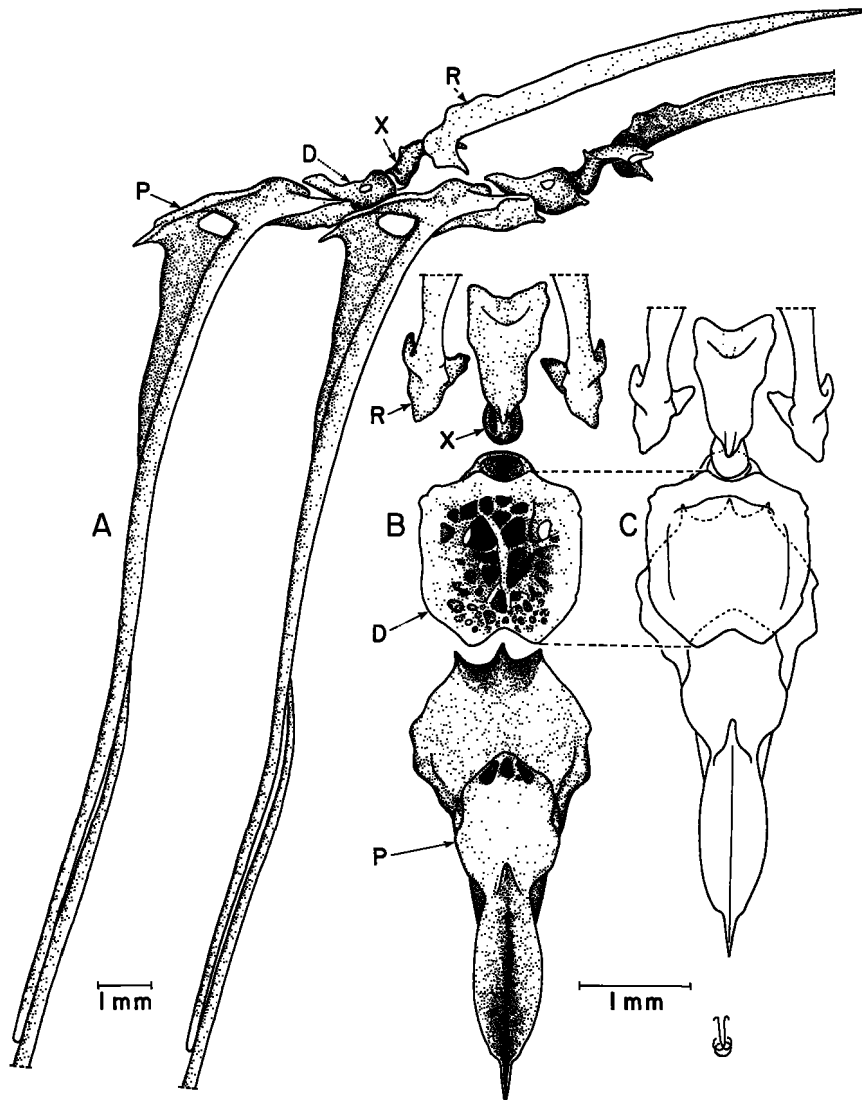


FIGURE 7.—Two dorsal fin pterygiophores from *Trichiurus lepturus* 510 mm TL, taken directly from opposite the anterior portion of the anal fin. A, left lateral view of the pterygiophores and rays; the left side of the posterior ray has been removed. Cartilage, white; ossifying, stippled. B, dorsal view of one of the two pterygiophores; unfused parts have been disarticulated. C, dorsal view of pterygiophore in B, unfused parts have been left articulated. For abbreviations see Figure 6.

broids (G. D. Johnson<sup>3</sup>). The anteriormost two dorsal pterygiophores supported three spines, which were the only dorsal fin spines and which had serrations in larvae and juveniles, but were smooth in adults. The anterior two pterygiophores had two parts each and supported fin spines. The 3d-127th pterygiophores had three parts and supported fin

rays, the distal parts being located between the bifurcate bases of the rays. These distal parts were not homologous with distal radials and are labeled "X" in Figures 6-8. The 128th-130th pterygiophores had four parts, and the last three pterygiophores (131st-133d) had become vestigial having a variable number of parts, usually from two to four. Anal fin pterygiophores were anatomically similar to the dorsal fin pterygiophores. The first anal fin spine was large and serrated in larvae and juveniles but became small and smooth in adults. *Trichiurus* lar-

<sup>3</sup>G. David Johnson, Curator (Fishes), Smithsonian Institution, National Museum of Natural History, Wash., DC 20560, pers. commun. 1985.



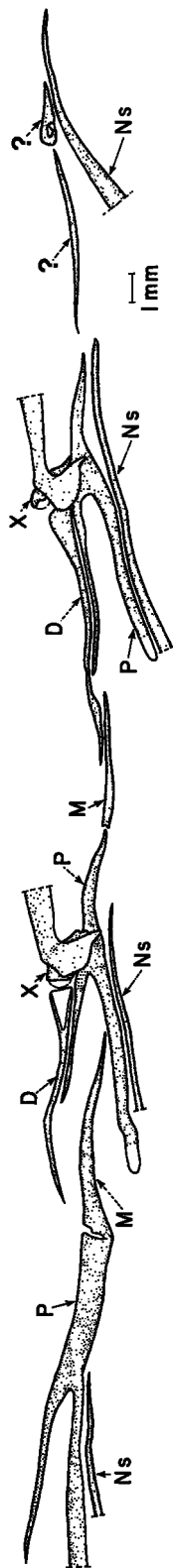


FIGURE 8.—Left: lateral view of the three posteriormost dorsal fin pterygiophores from *Trichiurus lepturus* 303 mm TL. M, middle radial; P, pterygiophore parts where

homology cannot be determined; for other abbreviations see Figure 6. Cartilage, white; bone, stippled.

vae and juveniles developed an anal fin in which the rays were of the same length as those in the dorsal fin, but the anal rays became very short and vestigial in adults. In adult *Trichiurus* the posterior end of the dorsal fin was anterior to the posterior end of the anal fin. Other trichiurids (*Benthodesmus*, *Evoxymetapon*, *Lepidopus*) examined by us had pterygiophore arrangements similar to *Trichiurus*.

## FAMILY SCOMBRIDAE

The family is a very speciose group which is divided into two subfamilies (Collette et al. 1984). For the monotypic Gasterochismatinae, larvae were not obtainable, but one or more species for each of the four tribes of the Scombrinae was studied.

### Tribe Scombrini

#### Figure 9

Twenty-two *Scomber japonicus* (4.4 mm NL - 9.6 mm SL, 100, 103 mm SL) and 12 *S. scombrus* (5.7 mm NL - 8.2 mm SL) were used in this study. Many more *Scomber* smaller than 5.5 mm NL were available but showed no cartilage development along the notochord. In addition, developmental studies on *Scomber* by Kramer (1960) and Kohno et al. (1984) were consulted.

Development of the vertebral column in *Scomber* initially started in four places on the notochord: 1) posteroventrad (parhypural, hypurals 1 and 2), 2) ventrad at the center (anterior haemal arches and spines), 3) dorsad at the center (neural arches and spines above developing haemal arches and spines), and 4) anterodorsad (neural arches and spines of future centra 1-3). The anterior neural spines were added posteriorly, the neural spines at the center of the notochord were added anteriorly and posteriorly, the haemal spines were added posteriorly, but the parapophyses were added anteriorly. The hypurals were added in a posterior direction, but the two autogenous haemal spines were added anteriorly. The dorsal and ventral areas of development coalesced completing the cartilaginous ontogeny of the vertebral column. Ossification of the vertebral column (neural and haemal spines, vertebrae, and hypural complex) initially started in four places: 1) dorsoanteriorly (anteriormost neural arches and spines), 2) ventrad at the center (anterior haemal arches and spines and posterior parapophyses), 3) posteriorly (hypural complex), and 4) dorsad at the center (neural arches and spines). The four initial areas of ossification coalesced as ossification progressed. Vertebrae in *Scomber* initially had saddle-

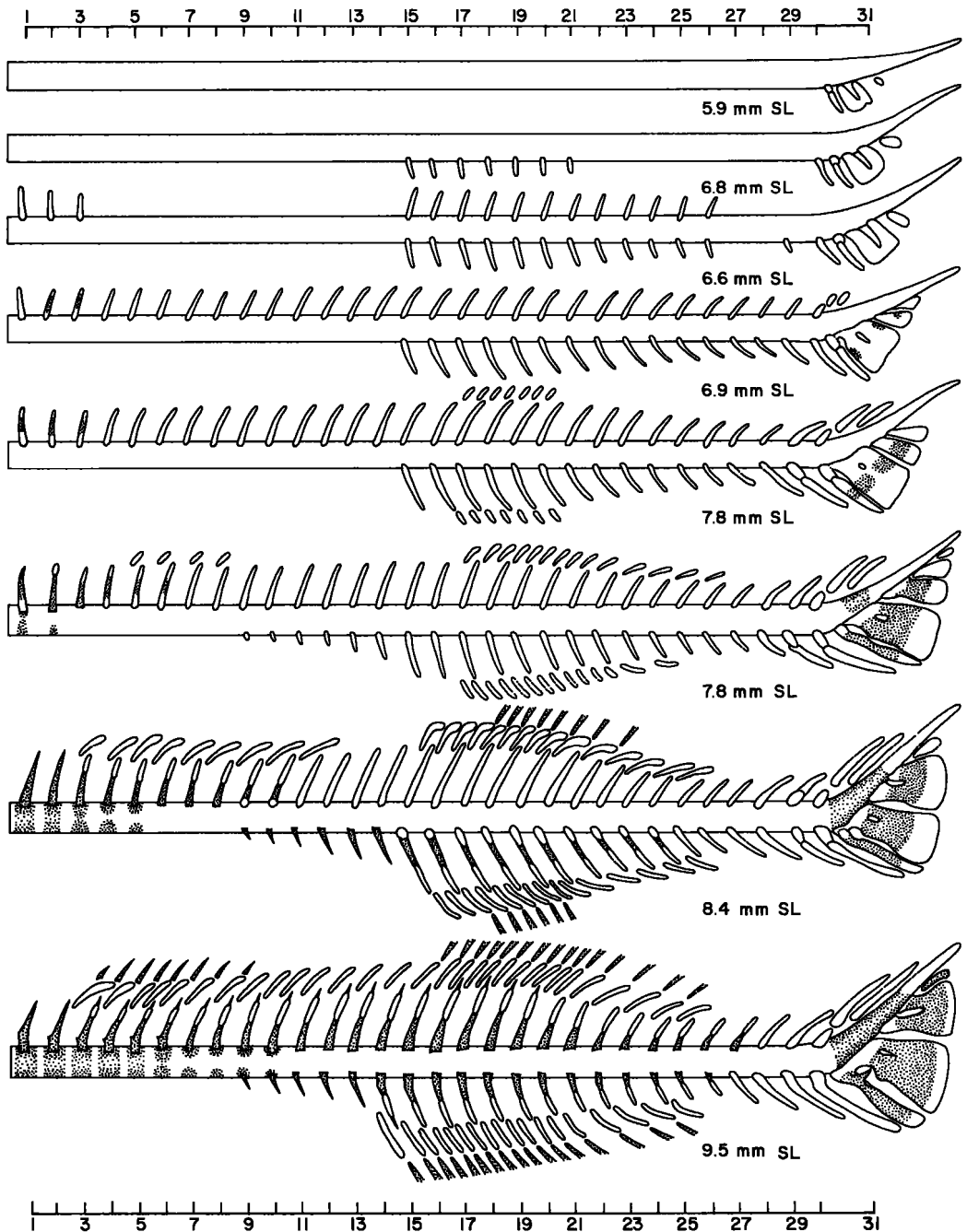


FIGURE 9.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scomber japonicus*, Scombrini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneutral and interhaemal space number and vertebra number.

shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

Cartilaginous second dorsal and anal fin pterygiophores developed first simultaneously above interneural spaces and below interhaemal spaces 17-19. The addition of cartilaginous second dorsal and anal fin pterygiophores was in an anterior and posterior direction. Cartilaginous first dorsal fin pterygiophores appeared second above interneural spaces 5-8 and were added anteriorly and posteriorly, terminating anteriorly in the third interneural space and joining with the second dorsal fin pterygiophores posteriorly. Second dorsal and anal fin rays developed in the same sequence as their corresponding pterygiophore, but a little later. The first dorsal fin spines developed from anterior in a posterior direction, but the anteriormost (supernumerary) spine first developed when seven first dorsal fin spines were already present (Table 2).

*Scomber* lacked predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore was considerably larger than all other pterygiophores, but it originated from only one piece of cartilage supporting two anal spines (one supernumerary spine). The posterior-most six dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a posteriorly bifurcated stay (Table 1).

In *Scomber*, caudal development of the cartilaginous parhypural and hypurals 1 and 2 was first before any other development of cartilaginous haemal or neural arches and spines along the notochord. The development of the hypural complex from the first appearance of cartilaginous hypurals to ossification onset was described by Kohno et al. (1984) and our findings are in agreement with theirs. Kramer (1960) described the ossification sequence in the hypural complex of *Scomber*. In our specimens, hypurals 1 and 2 were fusing to a ventral hypural plate before ossification onset. Hypurals 3 and 4 were fusing in some larvae before and in others after ossification onset. The neural and haemal elements of preural centra 2 and 3 supported the procurrent caudal rays. A procurrent spur and a basally foreshortened ray were absent in *Scomber* (Johnson 1975) (Table 1).

### Tribe Scomberomorini

Figures 10, 11

Thirty-nine specimens were available: 9 *Scomber-*

*omorus cavalla* (4.1-6.2 mm NL), 17 *S. maculatus* (6.1 mm NL - 10.2 mm SL, 40.5-67.5 mm SL), 3 *S. regalis* (5.3, 6.5 mm NL, 85.0 mm SL), 4 *S. tritor* (6.0 mm NL - 8.0 mm SL), 6 *Acanthocybium solanderi* (6.2 mm NL - 10.8 mm SL). None of the above five species yielded complete developmental series. However, *S. cavalla* specimens showed the cartilaginous ontogeny of the vertebral column, of the dorsal and anal fin pterygiophores and of the hypural complex. The *S. maculatus* specimens showed the latter phases of pterygiophore and hypural complex development, dorsal and anal fin development, and the ossification of the vertebral column and the hypural complex. Specimens of *S. regalis* and *S. tritor* provided evidence that development for the Atlantic species of *Scomberomorus* is very similar. Specimens of *A. solanderi* gave incomplete information on cartilaginous vertebral column development, but adequate information on dorsal and anal pterygiophore, on dorsal and anal fin, on hypural complex development, and on the ossification sequence of the vertebral column.

Development of the vertebral column in *Scomberomorus* initially started in four places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1-3), 2) posteroventrad (parhypural, hypurals 1 and 2), 3) ventrad at the center (four haemal arches and spines), and 4) dorsad at the center (six neural arches and spines above initial haemal spine development). The anterior neural spines were added posteriorly, the neural spines at the center of the notochord were added anteriorly and posteriorly, the haemal spines were added mostly posteriorly but a few were added in an anterior direction. All parapophyses were added in an anterior direction. The hypurals were added in a posterior direction, but the two autogenous haemal spines were added in an anterior direction. The dorsal and ventral areas of development coalesced and thus cartilaginous ontogeny of the vertebral column was complete. Ossification of the vertebral column initially started in two places: 1) anteriorly (neural arches and spines, and centra) and 2) posteriorly (hypural complex). Ossification of the neural arches and spines and centra was in a posterior direction. In the hypural complex ossification started with the urostyle and proceeded anteriorly to preural centrum 3. Then the ventral hypural plate started to ossify followed by the dorsal plate, the parhypural, and the two autogenous haemal spines. Last to start ossification were the epurals, the uroneural, and the neural spines. Vertebrae in *Scomberomorus* had saddle-shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

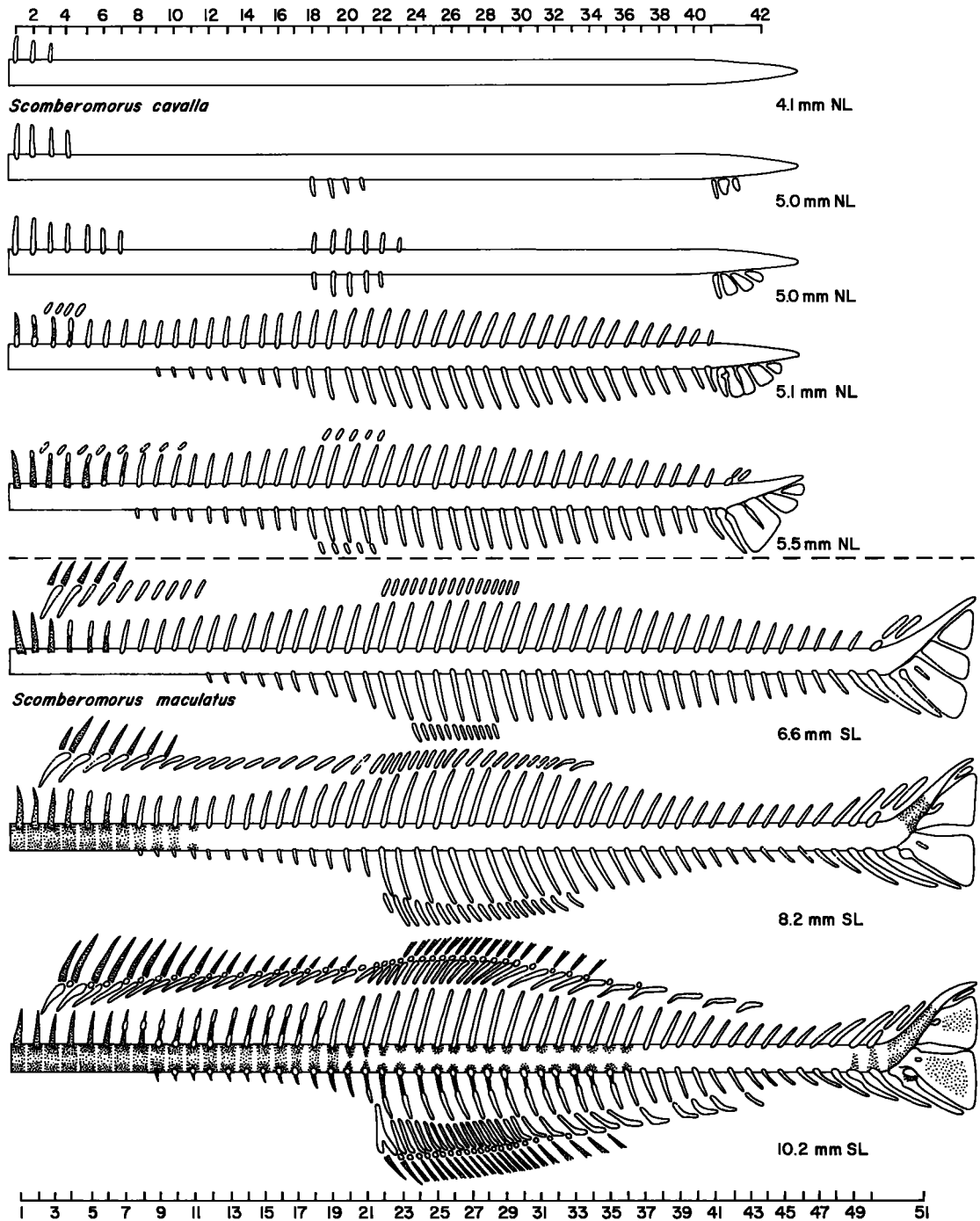


FIGURE 10.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Scomberomorus cavalla* and *S. maculatus*, Scomberomorini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents inter-neural and interhaemal space number and vertebra number.

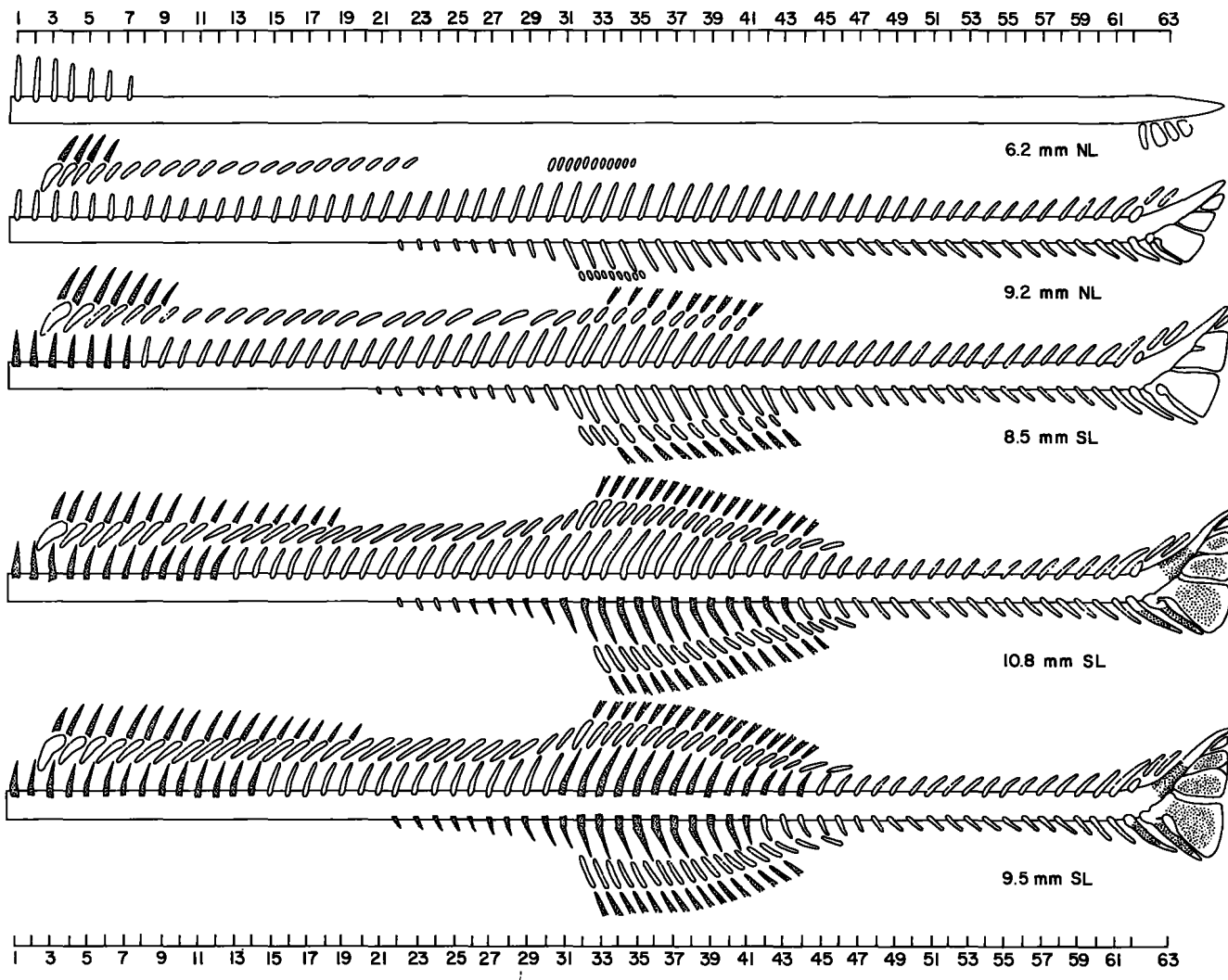


FIGURE 11.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Acanthocybium solanderi*, Scomberomorini, Scombridae. Cartilage, white; ossifying, stippled.

Scale represents interneural and interhaemal space number and vertebra number.

Two to five cartilaginous first dorsal fin pterygiophores developed first above interneural spaces 3-5 at the time of ossification onset of the anterior-most neural arches and spines. The addition of cartilaginous first dorsal fin pterygiophores was in a posterior direction. Five cartilaginous second dorsal and anal fin pterygiophores developed second simultaneously in the anterior portions of the future second dorsal and anal fins. Some addition of cartilaginous second dorsal and anal fin pterygiophores occurred in an anterior direction, but most of the addition was posteriorly. Dorsal and anal fin rays and spines developed in the same sequence as their corresponding pterygiophores, but a little later (Table 2).

*Scomberomorus* does not develop predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three spines (two supernumerary spines). The posteriormost nine dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a non-bifurcated stay (Table 1).

In *Scomberomorus*, first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the anterior development of the neural spines and the central appearance of haemal spines. Hypurals 3-5 were added posteriorly, the two autogenous haemal spines anteriorly. Hypurals 1 and 2 and hypurals 3 and 4 fused before ossification onset to a cartilaginous ventral and dorsal hypural plate. The dorsal and ventral plates fused after ossification to a single hypural plate with a central notch (Collette and Russo 1984). Hypural 5 gradually fused with the paired uroneural forming an autogenous bone resembling a third epural and mistaken as such by Leccia (1958). Two epurals developed anterior to the uroneural-hypural 5. These epurals remained autogenous. The neural and haemal elements of preural centra 2, 3, 4, and 5 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in *Scomberomorus* (Johnson 1975) (Table 1).

Only six *Acanthocybium solanderi* were available. We were therefore unable to ascertain a complete developmental sequence. Our smallest 6.2 mm NL specimen had two cartilaginous development centers along the notochord: some neural spines and arches anteriorly and the parhypural, hypural 1-3 posteriorly. The next larger specimen 9.2 mm SL had all neural and haemal arches and spines developed, thus

we were unable to tell if in *Acanthocybium* four initial centers (as in *Scomberomorus*) or only three centers (as in *Xiphias* and *Sarda*) of cartilaginous development along the notochord were present. In all our *Acanthocybium* specimens, hypurals 1 and 2 gradually fused before ossification onset to a ventral cartilaginous hypural plate. In the 8.5 mm SL *Acanthocybium*, hypurals 3 and 4 were fusing before ossification onset; in the larger 9.5 and 10.4 mm SL specimens hypurals 3 and 4 were ossifying while still separate. The dorsal and ventral hypural plates were fused in adults to one plate with a notch (Conrad 1938; Collette and Russo 1984) (Table 1). Ossification of the vertebral column initially started in four places and was similar to the ossification in *Scomber*.

The development of the dorsal and anal fins and their supporting pterygiophores in *Acanthocybium* was similar to that described in *Scomberomorus*.

### Tribe Sardini

#### Figure 12

Ninety-nine *Sarda sarda* (2.4-9.0 mm NL or SL, 59-102 mm SL) were available. Of the larval specimens (2.4-9.0 mm NL or SL) only 32 were larger than 5 mm NL, and of these 10 were between 6.0 and 6.9 mm NL or SL, 6 were between 7.0 and 7.9 mm NL or SL, and 3 were larger than 8 mm SL. Thus, since development of the vertebral column in *Sarda* begins around 5 mm NL, only 32 specimens were useful to our study and they were too few to yield a complete developmental series. Our conclusions on Sardini development are not as well supported as for most other scombroids.

Development of the vertebral column in *Sarda* initially started in three places on the notochord: 1) anterodorsad (neural arch and spine of future centrum 1), 2) posteroventrad (parhypural, hypurals 1 and 2), and 3) ventrad at center (haemal arches and spines, parapophyses). The anterior neural spines were added in a posterior direction and the haemal spines probably first appeared when the corresponding neural spines developed above them at the center of the notochord. Our evidence, however, is only indirect, because one 7.5 mm NL specimen had 21 neural spines and no haemal spines, but our 8.1 mm SL specimen had all neural and haemal spines developed. The cartilaginous hypurals were added posteriorly, but we could not observe the anterior addition of the autogenous haemal spines, although we assume that it happens in *Sarda* as in other scombroids with tails. Ossification of the vertebral column in *Sarda* initially started in two places: anteriorly (neural arches and spines) and posteriorly

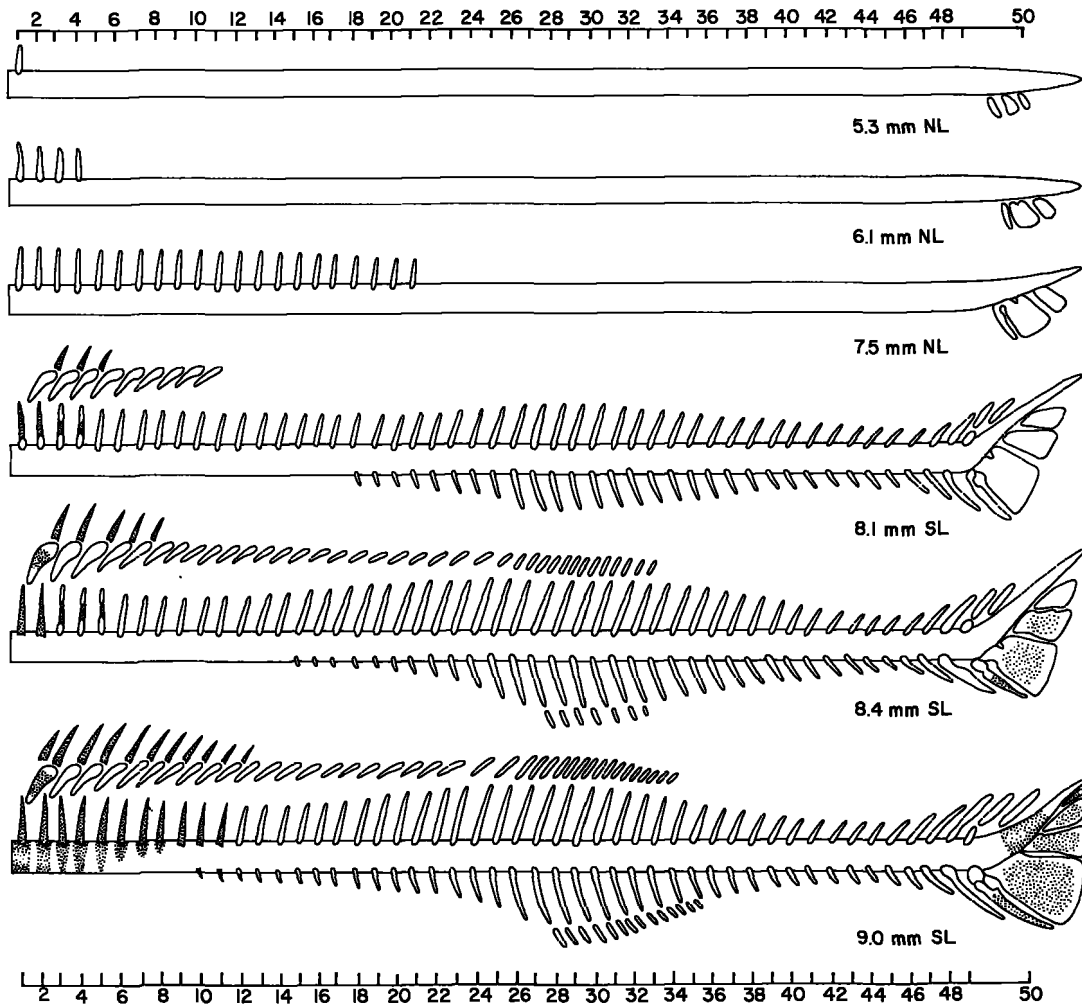


FIGURE 12.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Sarda sarda*, Sardini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

(hypural complex). Our largest 9.0 mm SL specimen showed ossification to the 11th neural spine. We do not know if ossification in *Sarda* proceeds entirely posteriad or if in *Sarda*, as in *Scomber* and *Acanthocybium*, there is some central ossification of neural and haemal spines before the anterior ossification has reached the center of the column. The hypural complex started to ossify early at the time ossification on the neural spines began anteriorly. Vertebrae in *Sarda* had saddle-shaped ossifications similar to those described for *Scombrolabrax* (Table 2).

Cartilaginous first dorsal fin pterygiophores developed first anteriorly above interneural spaces 2-10 in the 8.1 mm SL specimen. Addition of cartilaginous first dorsal fin pterygiophores was in a posterior direction. The 8.4 mm specimen had all first dor-

sal fin pterygiophores and some second dorsal and anal fin pterygiophores and they were continuous with each other. Therefore, we are unable to determine if second dorsal and anal fin pterygiophores in *Sarda* developed before first dorsal fin pterygiophores were joined with the second dorsal fin pterygiophores. Three first dorsal fin spines were present in the 8.1 mm SL specimen, serially associated with the first three pterygiophores. Addition of first dorsal fin spines was in a posterior direction, except for the anteriormost first spine (supernumerary), which developed later in the 9.0 mm SL *Sarda*. Second dorsal and anal fin rays were not developed in our 9.0 mm SL specimen. Our 59 mm SL specimen had the full adult compliment of fin rays (Table 2).

*Sarda* did not develop predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the second interneural space supporting two spines (one supernumerary spine). We do not know if the first anal pterygiophore originated from one or two pieces of cartilage, but it is most likely that it originated from two pieces because it supported three fin elements (two supernumerary spines). The posteriormost seven to nine dorsal and anal pterygiophores had middle radials. The last dorsal and anal pterygiophore supported a double finlet and had a posteriorly bifurcated stay (Table 1).

In *Sarda* first caudal development of the cartilaginous parhypural and hypurals 1 and 2 was concurrent with the beginning development of the anteriormost neural arches and spines. Hypurals 1 and 2 fused in the cartilaginous state to form the ventral hypural plate. In three specimens, hypurals 3 and 4 were separate after ossification onset. These hypurals were fused to the dorsal hypural plate in juveniles. Hypural 5, the uroneural and two epurals were separate in our juveniles. Collette and Chao (1975) found that in adults the dorsal and ventral plates fused to one hypural plate without a notch and that the uroneural fused with hypural 5, but the two epurals remained autogenous. The neural and haemal elements of preural centra 2, 3, 4, and 5 supported the procurrent caudal rays. A procurrent spur and a basally foreshortened ray were absent in *Sarda* (Johnson 1975) (Table 1).

### Tribe Thunnini

#### Figure 13

More than 86 specimens were available: 86 *Thunnus* (mostly *T. atlanticus* and a few *Thunnus* spp., 3.7-9.7 mm NL or SL), and a small number of *Auris*, *Euthynnus*, and *Katsuwonus*. We were unable to observe early cartilaginous development in all genera except *Thunnus*.

Development of the vertebral column in *Thunnus* initially started in four places on the notochord: 1) anterodorsad (neural arches and spines of future vertebrae 1-3), 2) posteroventrad (hypurals 1 and 2), 3) ventrad at the center (anteriormost five haemal arches and spines and posteriormost two parapophyses), and 4) dorsad at the center (five neural arches and spines above initial haemal arch and spine development). The anterior neural arches and spines were added in a posterior direction, the central neural arches and spines were added anteriorly (coalescing around the future 14th centrum) and posteriorly toward the epurals. The parapophy-

ses were added in an anterior direction, whereas the haemal arches and spines were developing in a posterior direction. In the hypural complex hypurals were added posteriorly, but the parhypural and the two autogenous haemal spines were added in an anterior direction, coalescing with the central haemal arches and spines. Ossification of the vertebral column in Thunnini initially started in two places similar to the ossification described for *Scomberomorus*. Saddle-shaped vertebral ossification development was observed in all Thunnini examined, similar to the development described for *Scombrolabrax* (Table 2).

In Thunnini, cartilaginous first dorsal fin pterygiophores developed anteriorly in interneural spaces 3-6 when only few cartilaginous neural spines were present. Additional pterygiophores were added in a posterior direction. Later, small cartilaginous second dorsal fin pterygiophores appeared in the middle of the vertebral column above interneural spaces 15-22. As the first dorsal fin pterygiophores developed in a posterior direction, the second dorsal fin pterygiophores developed in an anterior and posterior direction until all the dorsal pterygiophores were continuous. Anal pterygiophores appeared below interhaemal spaces 20-25 and developed in an anterior and posterior direction. Addition of the first dorsal fin spines was in a posterior direction, except for the anteriormost spine (supernumerary), which developed when the second and third spine were already present. The second dorsal and anal fin rays developed in the same sequence as their corresponding pterygiophores but a little later (Table 2).

All Thunnini species examined lacked predorsal bones. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the third interneural space supporting two fin spines (one supernumerary spine). The first anal pterygiophore developed from two pieces of cartilage and supported three fin spines (two supernumerary spines) (Potthoff 1975). Middle radials were present on the posterior eight or nine finlet supporting dorsal and anal pterygiophores. A one-part posteriorly bifurcated stay developed with the posteriormost dorsal and anal fin pterygiophores (Table 1).

In *Thunnus*, the caudal complex began to develop very early concurrently with the first anteriormost neural spines. Hypurals 1 and 2 and hypurals 3 and 4 developed separate cartilages and fused to a cartilaginous dorsal and ventral hypural plate. Potthoff (1975) stated that hypurals 1 and 2 developed as one piece of cartilage from the start, but he examined only specimens larger than 5.0 mm NL not stained for cartilage. The dorsal and ventral hypural plates



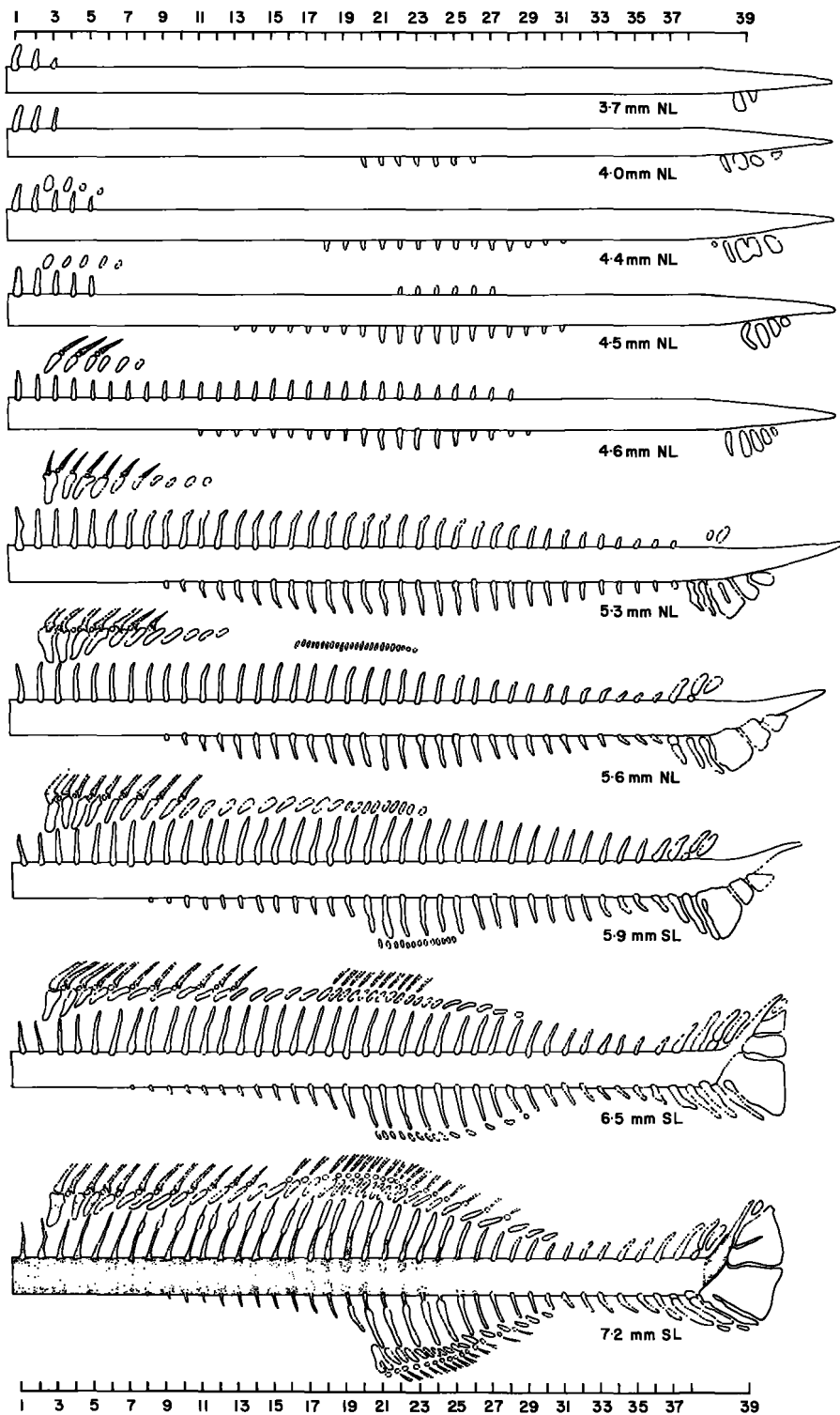


FIGURE 13.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Thunnus atlanticus*, Thunnini, Scombridae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

fused after ossification, but the small hypural 5 remained separate. Preural centra 2 and 3 each had an autogenous haemal spine. Two epurals and one uroneural developed dorsad. The anterior epural fused with the neural arch of  $Pu_2$  and the uroneural fused to the urostyle (Potthoff 1975). The neural and haemal elements of preural centra 2, 3, and 4 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in the Thunnini (Johnson 1975) (Table 1).

## FAMILY ISTIOPHORIDAE

### Figure 14

One hundred and sixteen istiophorids (3.0-227 mm NL or SL) were available. Most specimens were caught in the Gulf Stream off Miami, FL. In 67 of the specimens we were able to count vertebrae; all had a count of 12+12. This identified them as *Istiophorus platypterus* or *Tetrapturus* spp. (Merrett 1971; Richards 1974). The 67 specimens with the 12+12 vertebral count, and the remainder, which were too small for vertebral counts, probably were *I. platypterus* because most adult istiophorids captured in the Gulf Stream off Miami are that species. In addition, 12 *Makaira nigricans* (3.3-5.9 mm NL, 13.3 and 220 mm SL) identified by W. J. Richards<sup>4</sup> were examined. The 13.3 and 220 mm SL specimens had a count of 11+13 vertebrae.

Development of the vertebral column initially started in three places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1 and 2), 2) posteroventrad (hypurals), and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were added in a posterior direction. The haemal arches and spines also were added in a posterior direction at the time when neural arches and spines appeared above on the notochord. Parapophyses were added anteriorly. Hypural bones were added in a posterior direction, but the parhypural and the two autogenous haemal spines were added anteriorly. Ossification of the vertebral column in istiophorids initially started in two places: ossification of the anteriormost neural spines and arches proceeded in a posterior direction. The hypural complex started ossification before all neural and haemal spines were ossifying. Saddle-shaped ossifications of the vertebrae as observed in the Scombrabrachidae, Gempylidae, and Scombridae were not observed in the

Istiophoridae during ontogeny. First ossification of vertebrae in Istiophoridae was evidenced by the formation of rings of bone around the notochord (Table 2).

Cartilaginous dorsal pterygiophores appeared first above interneural spaces 3-5. Dorsal pterygiophore addition was mostly in a posterior direction, except that those pterygiophores over interneural spaces 2 and 1 were added in an anterior direction. When dorsal pterygiophore development extended to above the anterior portion of the anal fin fold, cartilaginous anterior anal pterygiophores were seen below interhaemal spaces 13 and 14, and their addition was posteriorly abreast of the dorsal pterygiophores. At larger sizes dorsal and anal finrays developed in the same sequence as their supporting pterygiophores (Table 2).

Istiophorids did not have predorsal bones, instead the first three interneural spaces were filled with fin spine supporting pterygiophores. The first dorsal pterygiophore originated from one piece of cartilage and inserted in the first interneural space supporting three spines (two supernumerary spines). The anteriormost spine was either small, reduced, or vestigial. The first anal pterygiophore developed from two pieces of cartilage supporting two fin spines (one supernumerary spine). Istiophorids had one middle radial and one posteriorly bifurcated (sometimes nonbifurcated) stay with the posteriormost dorsal and anal pterygiophore. The posteriormost dorsal and anal ray were double (Table 1).

In istiophorids, the caudal complex started to develop after the precaudal neural spines had developed. The parhypural and hypurals 1-4 developed as separate cartilages. In most istiophorid specimens the cartilages of hypurals 1 and 2 and hypurals 3 and 4 fused to a lower and upper hypural plate before ossification; in some specimens fusion did not take place until after ossification onset for the upper and lower hypurals. Also, there were specimens in which none of the cartilaginous hypurals fused. The 5th hypural did not develop in istiophorids. Dorsad 3 epurals and 1 uroneural developed. Preural centra 2 and 3 each had one autogenous haemal spine. In adult istiophorids, the fusion of the bones in the caudal complex was extensive (Gregory and Conrad 1937); we examined adult specimens of *Istiophorus*, *Tetrapturus*, and *Makaira* and found identical hypural fusions in the three genera. The three epurals remained autogenous, but the uroneural, hypurals 1-4, and the parhypural were fused with each other and with the urostyle to form a notched hypural plate. The neural and haemal

<sup>4</sup>W. J. Richards, Senior Scientist, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. 1983.

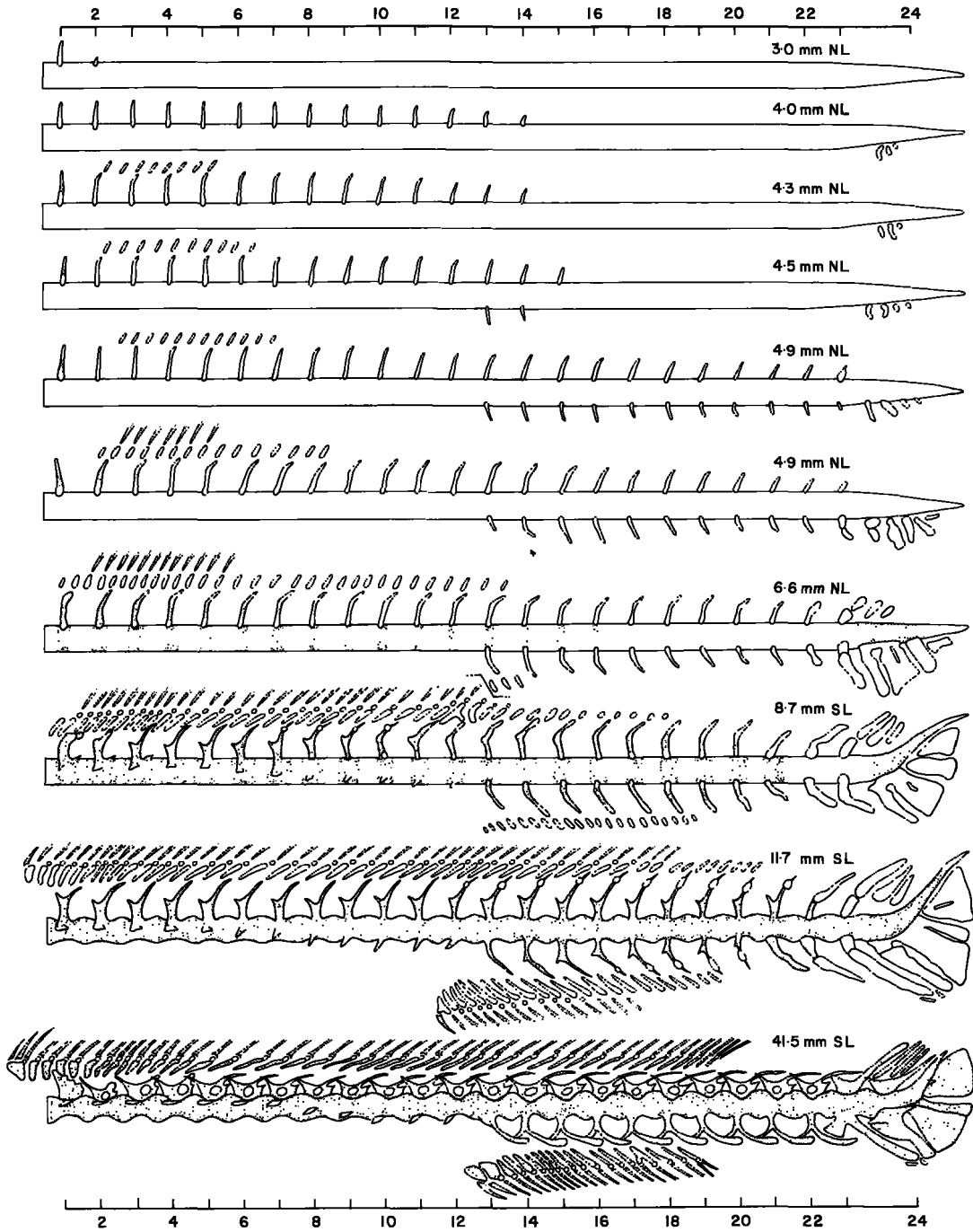


FIGURE 14.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Istiophorus platypterus*, Istiophoridae. Cartilage, white; ossifying, stippled. Scale represents interneuronal and interhaemal space number and vertebra number.

elements of preural centra 2 and 3 supported procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in the Istiophoridae (Johnson 1975) (Table 1).

## FAMILY XIPHIIDAE

Figure 15

Ninety-five *Xiphias gladius* specimens (3.7-19.5 ENL or ESL) of this monotypic genus and species studied by Potthoff and Kelley (1982) were reexamined by us.

Development of the vertebral column initially started in three places on the notochord: 1) anterodorsad (neural arches and spines on future centra 1-3), 2) posteroventrad on the notochord (hypurals), and 3) ventrad at the center (anterior haemal arches and posterior parapophyses). The neural arches and spines were added in a posterior direction. When the developing neural spines had passed the pre-caudal area, some of the anterior haemal spines started to develop (except the anteriormost two of

the future caudal vertebrae). Addition of cartilaginous neural and haemal spines was in a posterior direction, except the first two haemal spines which developed anteriorly. Hypural complex bones were added in an anterior and posterior direction. Ossification of the vertebral column in *Xiphias* initially started in one place with the anteriormost neural arches and spines. Ossification then proceeded in a posterior direction with the hypural complex ossifying last. Saddle-shaped ossifications of the vertebrae as observed in the Scombrobracidae, Gempylidae, and Scombridae was not observed in *Xiphias* during ontogeny. Instead, vertebral ossification was first noted in *Xiphias* by the appearance of dorsoventral fractures on the notochord followed by the appearance of ossified vertebrae between the fractures (Table 2).

Cartilaginous dorsal and anal pterygiophores developed simultaneously before the neural and haemal spines had reached the area. The dorsal pterygiophores first developed in a group below the future middle of the dorsal fin above the future inter-

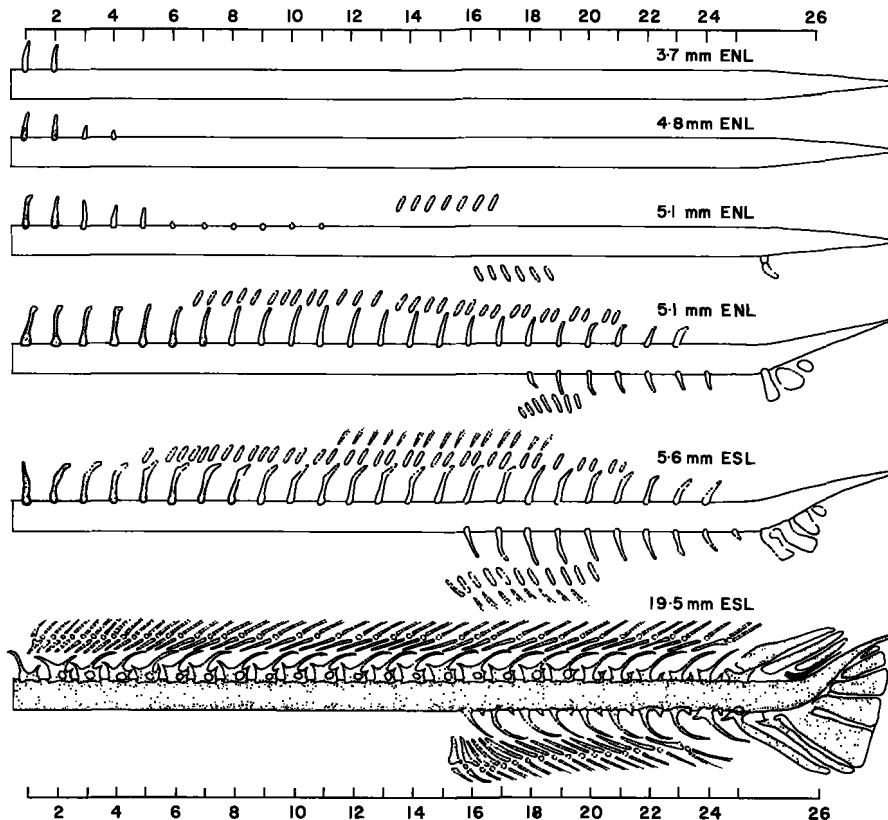


FIGURE 15.—Schematic representation of vertebral column, dorsal and anal fin, pterygiophore, and hypural development in *Xiphias gladius*, Xiphiidae. Cartilage, white; ossifying, stippled. Scale represents interneural and interhaemal space number and vertebra number.

neural spaces 13-16. The anal pterygiophores first developed in a group above the future anterior part of the anal fin below interhaemal spaces 16-18. Further addition of cartilaginous dorsal and anal pterygiophores was in an anterior and posterior direction. The posterior pterygiophore additions dorsad and ventrad were completed before the anterior additions ceased. The full complement of anal pterygiophores was reached before the full dorsal complement. Dorsal and anal fin rays first originated in the same areas as the pterygiophores, but at larger sizes with addition of rays in the same directions (Table 2).

*Xiphias* did not have predorsal bones. The first dorsal pterygiophore originated from one or two pieces of cartilage and inserted in the second interneural space, supporting from one to three fin spines. The first anal pterygiophore developed from one or two pieces of cartilage, supporting from one to three fin spines. *Xiphias* had no middle radials in the dorsal or anal pterygiophores, but a double ray and a nonbifurcated stay were associated with the posteriormost dorsal and anal pterygiophores (Potthoff and Kelley 1982) (Table 1).

In *Xiphias*, cartilaginous hypurals were first seen before precaudal neural spine development was complete, but after dorsal and anal pterygiophore development had started. The hypural complex development was described by Potthoff and Kelley (1982). Hypurals 1-5 and the parhypural developed from separate cartilages, and there was no cartilage fusion. There were three epurals and one uroneural. Only one autogenous haemal spine was present on preural centrum 2. In adults the three epurals, the uroneural, hypural 5, and the parhypural remained autogenous, but hypurals 1-4 fused with each other and the urostyle forming a notched hypural plate (Gregory and Conrad 1937). The neural and haemal elements of only preural centrum 2 supported the procurrent caudal rays. A procurrent spur and basally foreshortened ray were absent in *Xiphias* (Johnson 1975) (Table 1).

## DISCUSSION AND CONCLUSION

Developmental features observed in our study are illustrated in Figures 4-5 and 9-15. These features along with meristic and osteological characters are compared among the six scombroid families and the primitive percoid *Morone* in Tables 1 and 2. Although our conclusions are still preliminary because of lack of adequate developmental series for many genera, some comparisons, based largely on development, are worth noticing.

There are three major kinds of early development and addition of the cartilaginous neural and haemal arches and spines along the notochord. Each kind may differ slightly between taxa. *Scombrobrax*, *Scomber* (Scombrini), *Scomberomorus* (Scomberomorini), and Thunnini have one kind in which there are four initial developments on the notochord, but not necessarily in the given order, e.g., anteriorly dorsad, centrally dorsad, centrally ventrad, and posteriorly ventrad with a subsequent merger of the initial areas. Gempylidae, *Sarda* (Sardini), Istiophoridae, and Xiphiidae have a second kind in which there are three initial developments, e.g., anteriorly dorsad, centrally ventrad, and posteriorly ventrad; then the addition is from anterior in a posterior direction with a merger in the posterior, near the hypural complex. *Trichiurus*, which lacks hypurals, has the third kind in which there are two initial developments, e.g., anteriorly dorsad and centrally ventrad with addition in a posterior direction. We could not fully determine the cartilaginous development for *Acanthocybium*, because of an incomplete series, and for trichiurids with tails, because a series was lacking.

In the Scombrobracidae, Gempylidae, and Scombridae, the vertebrae first develop by coalescence of saddle-shaped ossifications positioned dorsad and ventrad. We were not able to observe saddle-shaped ossification in *Acanthocybium* because we lacked specimens. The other scombroid families, Trichiuridae (*Trichiurus*), Istiophoridae, and Xiphiidae, and the primitive percoid *Morone* did not have these saddle-shaped ossifications. Saddle-shaped ossifications have been observed during ontogeny in other perciform fish such as *Enchelyurus brunneolus* (Blenniidae) by Watson<sup>6</sup> and *Lutjanus campechanus* (Lutjanidae) by Potthoff and Kelley<sup>6</sup>. We are unable to comment at this time on the significance of these saddle-shaped ossifications until the ontogeny of many more taxa is studied.

In the Scombrinae two species belonging to two different tribes share a peculiar ossification sequence not observed by us in any other scombroids. Both in *Scomber* (Scombrini) and *Acanthocybium* (Sardini), initial ossification of the neural and haemal arches and spines and the hypural complex started at four locations on the vertebral column (Kramer

<sup>6</sup>Watson, W. Larval development of *Enchelyurus brunneolus* from Hawaiian waters (Pisces: Blenniidae: Omobranchini). Unpubl. manuscript. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Soloma Beach, CA 92075.

<sup>6</sup>Research on the development of *Lutjanus campechanus* is in progress at the Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

1960). In other scombroids initial ossification was only anterior and posterior (*Scomberomorus*, *Sarda*?, *Thunnus*, Istiophoridae) or only anterior (*Scombrolabrax*, Gempylidae, *Trichiurus*, *Xiphias*). We believe that the relationship of *Acanthocybium* to the Sardini should be re-examined in the future.

The Scombrini and *Scombrolabrax* (Figs. 1, 9) share a primitive development in which the second dorsal fin, anal fin, and pterygiophores develop first from a center anteriorly and posteriorly, and the first dorsal fin and pterygiophores develop second, from a center anteriorly and posteriorly in *Scombrolabrax*, but posteriorly only in *Scomber* except for the first dorsal fin spine, which was added later. The Gempylidae, Thunnini, and *Scomberomorus* (Figs. 2, 3, 4, 10, 13) share an advanced development in which the first dorsal fin and pterygiophores develop first from the anteriormost element in a posterior direction, and the second dorsal fin, anal fin, and pterygiophores develop second from a center anteriorly and posteriorly, the first dorsal fin being separate from the second dorsal fin during part of the ontogeny. In *Acanthocybium*, *Sarda*, and Thunnini, the development is similar to the advanced development of the Gempylidae and *Scomberomorus* except in *Acanthocybium*, *Sarda*, and Thunnini, the second dorsal fin spine developed first, the first dorsal fin spine was added later. The first dorsal fin was separate for part of the ontogeny from the second dorsal in *Acanthocybium*, but we were unable to observe this in *Sarda* because of the lack of an adequate size series. In *Trichiurus* (Fig. 5), the dorsal fin and pterygiophores develop from the anteriormost element posteriorly. When dorsal fin development reaches above the anal fin, the anal fin develops from its anteriormost element in a posterior direction. Dorsal and anal fin development then proceed posteriorly at about the same pace. *Trichiurus* has a peculiar developmental feature, which was not observed in any other scombroid. It was that the anteriormost dorsal fin spines and anal spine and rays develop before their corresponding pterygiophores. Pterygiophore development soon overtook fin ray development and during further development more pterygiophores are present than fin rays. In the Istiophoridae and Xiphiidae, dorsal and anal fin development differ from the previously described groups. In the Istiophoridae (Fig. 14) the first dorsal fin and pterygiophores develop first from a center anteriorly and posteriorly. When the posterior portion of the first dorsal fin development reaches above the anterior portion of the anal fin, anal rays and pterygiophores are added mostly pos-

teriorly, although a few elements develop in an anterior direction. The second dorsal fin develops only in a posterior direction consecutive to the first dorsal fin. In *Xiphias* (Fig. 15), the second dorsal and anal fins and pterygiophores develop first from a center anteriorly and posteriorly. Development of the first dorsal fin and pterygiophores then is continuous with the second dorsal fin in an anterior direction only.

The hypurals in all scombroids develop as separate cartilages. Only in *Scombrolabrax* is there no fusion of the hypurals in the adults. In the Gempylidae the extent of the hypural fusion varies for different genera and we did not observe fusion in the cartilaginous state. For the trichiurids with tails, not enough specimens were available to make observations on hypural fusion. In the remaining scombroids (Scombridae, Istiophoridae, Xiphiidae) hypurals 1-4 are fused to one hypural plate in adults. Fusion to one hypural plate came about during ontogeny by fusion of hypurals 1 and 2 to a ventral and hypurals 3 and 4 to a dorsal hypural plate, with subsequent fusion of these into one plate. For the ventral plate, cartilaginous fusion occurs in all tribes of the Scombridae, but in the Istiophoridae fusion is either from cartilaginous or ossifying hypurals 1 and 2 and in *Xiphias* it is always from ossifying hypurals (Table 1). In *Scomber*, *Acanthocybium*, and Istiophoridae, the fusion of hypurals 3 and 4 to the dorsal hypural plate is variable and occurs either during the cartilaginous or ossifying state. In *Sarda* three specimens have fusion of hypurals 3 and 4 in the ossifying state. In *Scomberomorus* and *Thunnus* the fusion to the dorsal hypural plate occurs always in the cartilaginous state, whereas in *Xiphias* it is always in the ossifying state (Table 1).

The number of centra supporting the caudal rays varies in the scombroids. In *Scombrolabrax*, Gempylidae, Trichiuridae with tails, *Scomber*, and Istiophoridae, three vertebrae (including the urostyle) support the caudal rays. In *Xiphias* only two vertebrae support the rays. In the Scombridae more vertebrae are involved with the support of the caudal rays, except in *Scomber*. In the *Scomberomorus* species examined by us, five centra support the rays, but in some species of *Scomberomorus* only four centra are involved (Collette and Russo 1984). In *Acanthocybium* (Collette and Russo 1984) and *Sarda*, five centra are involved with the support of the rays, whereas in *Thunnus* only four centra support the caudal rays (Table 1).

Johnson (fn. 3; in press) is of the opinion that *Scombrolabrax* does not belong in the Scombroidei because it lacks most defining specializations of this

group. Bond and Uyeno (1981) removed *Scombrolabrax* from the Scombroidei on the basis of one specialized character. We are of the opinion that *Scombrolabrax* should be retained in the Scombroidei until we fully understand the significance of developmental characters. *Scombrolabrax* shares many characters with other scombroids, in particular the absence of predorsal bones coupled with the anterior pterygiophore interneural insertion sequence, the saddle-shaped ossifications of the vertebrae, the sequence of neural and haemal arch and spine development and the striking resemblance of *Scombrolabrax* to Thunnini larvae.

Gempylid and trichiurid relationships await further study when complete series of larvae of more species become available. We believe that *Gempylus* and *Diplospinus* are similar and very closely related. We also believe that the gempylids and trichiurids are very closely related, the trichiurids representing an advanced gempylid group.

Johnson (in press) has discovered a specialization (a stay on the 4th pharyngobranchial) unique to the Scombridae, Istiophoridae, and Xiphiidae but absent in other Perciformes. From our study we believe that the billfish (*Xiphias* and Istiophoridae) do not belong in the Scombroidei because they differ in many developmental and meristic characters from other scombroid members (Tables 1, 2). However, until more developmental studies are done to determine the meaning and significance of developmental characters, it would be premature to suggest rearranging the Scombroidei.

The full value of early developmental studies for systematic purposes will be realized when similar studies have been completed on a greater variety of fishes. Only then will we be able to interpret the meaning and significance of some developmental characters presented here.

## ACKNOWLEDGMENTS

We thank G. L. Beardsley, B. B. Collette, A. C. Jones, G. D. Johnson, and W. J. Richards for critically reading the manuscript and P. Fisher for typing many drafts of the manuscript. We thank B. B. Collette, R. H. Gibbs, M. F. Gomon, G. D. Johnson, W. J. Richards, and J. L. Russo for providing gempylid and trichiurid fishes for clearing and staining. The *Scomberomorus* and *Acanthocybium* material was loaned to us by M. Leiby and J. Gartner from the SEAMAP collections. M. P. Fahay, G. H. Moser, and B. Sumida MacCall generously provided *Scomber* and *Sarda* specimens.

## LITERATURE CITED

- BOND, C. E., AND T. UYENO.  
1981. Remarkable changes in the vertebrae of perciform fish *Scombrolabrax* with notes on its anatomy and systematics. *Jpn. J. Ichthyol.* 28:259-269.
- COLLETTE, B. B., AND L. N. CHAO.  
1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). *Fish. Bull., U.S.* 73: 516-625.
- COLLETTE, B. B., AND J. L. RUSSO.  
1984. Morphology, systematics and biology of the spanish mackerels (*Scomberomorus*, Scombridae). *Fish. Bull., U.S.* 82:545-692.
- COLLETTE, B. B., T. POTTHOFF, W. J. RICHARDS, S. UEYANAGI, J. L. RUSSO, AND Y. NISHIKAWA.  
1984. Scombroidei: development and relationships. In H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (editors), *Ontogeny and systematics of fishes*, p. 591-620. *Am. Soc. Ichthyol. Herpetol., Spec. Publ.* 1.
- CONRAD, G. M.  
1938. The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombroid fish. *Am. Mus. Nov.* 1000, p. 1-32.
- FRITZSCHE, R. A., AND G. D. JOHNSON.  
1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. *Trans. Am. Fish. Soc.* 109:387-406.
- GOSLINE, W. A.  
1968. The suborders of perciform fishes. *Proc. U.S. Natl. Mus.* 124(3647):1-78.
- GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS.  
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.* 131:341-355.
- GREGORY, W. K., AND G. M. CONRAD.  
1937. The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). *Am. Mus. Novit.* 952, p. 1-25.
- JOHNSON, G. D.  
1975. The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications. *Occas. Pap. Calif. Acad. Sci.* 121, p. 1-23.  
In press. Scombroid phylogeny: an alternative hypothesis. *Bull. Mar. Sci.* 39.
- KOHNO, H., M. SHIMIZU, AND Y. NOSE.  
1984. Morphological aspects of the development of swimming and feeding functions in larval *Scomber japonicus*. *Bull. Jpn. Soc. Sci. Fish.* 50:1125-1137.
- KRAMER, D.  
1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-56. *U.S. Fish Wildl. Serv., Fish. Bull.* 60:393-438.
- LECCIA, F. M.  
1958. The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. *Bull. Mar. Sci. Gulf. Caribb.* 8:299-341.
- LEIS, J. M., AND W. J. RICHARDS.  
1984. Acanthuroidei: development and relationships. In H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (editors), *Ontogeny and systematics of fishes*, p. 547-551. *Am. Soc. Ichthyol. Herpetol. Spec. Publ.* 1.

- MATSUBARA, K., AND T. IWAI.  
1958. Anatomy and relationships of the Japanese fishes of the family Gempylidae. Mem. Coll. Agric. Kyoto Univ., Fish. Ser. Spec. No., p. 23-54.
- MATSUMOTO, W. M., E. H. AHLSTROM, S. JONES, W. L. KLAWE, W. J. RICHARDS, AND S. UHEYANAGI.  
1972. On the clarification of larval tuna identification, particularly in the genus *Thunnus*. Fish. Bull., U.S. 70:1-12.
- MERRETT, N. R.  
1971. Aspects of the biology of billfish (Istiophoridae) from the equatorial western Indian Ocean. J. Zool. 163:351-395.
- NAKAMURA, I., AND E. FUJII.  
1983. A new genus and species of Gempylidae (Pisces: Perciformes) from the Tonga Ridge. Publ. Seto Mar. Biol. Lab. 27(4/6, Art. 10):173-191.
- OKIYAMA, M., AND S. UHEYANAGI.  
1978. Interrelationships of scombroid fishes: an aspect from larval morphology. Bull. Far Seas Res. Lab. 16, p. 103-113.
- POTTHOFF, T.  
1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the blackfin tuna (*Thunnus atlanticus*, Pisces Scombridae). Bull. Mar. Sci. 25:205-231.  
1984. Clearing and staining techniques. In H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson (editors), Ontogeny and systematics of fishes, p. 35-37. Am. Soc. Ichthyol. Herpetol., Spec. Publ. 1.
- POTTHOFF, T., AND S. KELLEY.  
1982. Development of the vertebral column, fins and fin supports, branchiostegal rays, and squamation in the swordfish, *Xiphias gladius*. Fish. Bull., U.S. 80:161-186.
- POTTHOFF, T., AND W. J. RICHARDS.  
1970. Juvenile bluefin tuna, *Thunnus thynnus* (Linnaeus), and other scombrids taken by terns in the Dry Tortugas, Florida. Bull. Mar. Sci. 20:389-413.
- POTTHOFF, T., W. J. RICHARDS, AND S. UHEYANAGI.  
1980. Development of *Scombrobrax heterolepis* (Pisces, Scombrobracidae) and comments on familial relationships. Bull. Mar. Sci. 30:329-357.
- RICHARDS, W. J.  
1974. Evaluation of identification methods for young billfishes. In R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 62-72. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- RICHARDS, W. J., AND W. L. KLAWE.  
1972. Indexed bibliography of the eggs and young of tunas and other scombrids (Pisces, Scombridae), 1880-1970. NOAA Tech. Rep. NMFS SSRF-652, 107 p.
- RICHARDS, W. J., AND T. POTTHOFF.  
1974. Analysis of the taxonomic characters of young scombrid fishes, genus *Thunnus*. In J. H. S. Blaxter (editor), The early life history of fish, p. 623-648. Springer-Verlag, Berlin, Heidelberg, New York.
- SATO, S.  
1983. Identificação, Distribuição e desenvolvimento larval de "Lanceta" *Thyrstitops lepidoides* (Cuvier, 1931) (Pisces: Gempylidae) da região compreendida entre cabo frio (23°S) e cabo de sta. Marta Grande (29°S). M.S. Thesis, Univ. São Paulo, Brasil, 64 p.