DEVELOPMENT OF THE VERTEBRAL COLUMN, FINS AND FIN SUPPORTS, BRANCHIOSTEGAL RAYS, AND SQUAMATION IN THE SWORDFISH, *XIPHIAS GLADIUS*[1]

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ABSTRACT

The development and structure of the fins and their supports, of the vertebral column, and the scales are described from 220 cleared and stained *Xiphias gladius*. Details on development and structure of the pectoral fin, the pectoral suspensorium, and the coraco-scapular cartilage are given. The pectoral suspensorium in *Xiphias* is slightly reduced; only one postcleithrum is present and intertemporals are absent. A cartilaginous distal radial was observed between the base of the dorsalmost pectoral ray during development. Dorsal and anal fin ray and pterygiophore development and structure are described. The anteriormost dorsal pterygiophore inserts in the second interneural space and originates from one and sometimes from two pieces of cartilage. The first anal pterygiophore inserts in the 16th interhaemal space and also originates from one but rarely from two pieces of cartilage. The posteriormost dorsal and anal pterygiophores insert in the 22d and 21st interneural-interhaemal spaces and have a stay and a serially associated double ray. Middle radials are absent in *Xiphias*. Details on hypural complex development and structure are given. *Xiphias* does not develop all basic perciform caudal complex parts. Missing are the centrum (PU_3) which has an autogenous haemal spine and a neural spine with articular cartilage, and the second (posterodorsal) uroneural pair. All other basic perciform caudal complex parts are present but some fuse during development; e.g., hypurals 1-4 fuse with each other and with the urostyle to form a plate. The three epurals, the first (anteroventral) uroneural pair, hypural 5, the parhypural, and one haemal spine remain autogenous in adults. The development of the vertebral column and the structure of the vertebrae are described in detail. The ribs in *Xiphias* are unusual because generally only one pair is present on centra 1-5, 15, and 16. Centra 6-14 usually have no ribs. Ribs in *Xiphias* develop from cartilage. Branchiostegal ray numbers are variable in *Xiphias*. There may be seven rays on both sides, or seven on one side and eight rays on the other, or there may be eight rays on both sides. The development of squamation is described. Two types of scales develop: large row scales in four parallel rows and smaller scatter scales between rows. All scales develop from one to seven posteriorly recurved spines. Our largest 668 mm ESL specimen was covered with scales, but the recurved spines had become blunt and scatter scales could not be distinguished from row scales anymore.

The development and structure of the fins and fin supports for the swordfish *Xiphias gladius* have not been described in the literature. The skull and vertebrae of adult *Xiphias* were studied by Gregory and Conrad (1937) and Nakamura et al. (1968) and brief description of vertebrae in adult *Xiphias* was given by Ovchinnikov (1970). Arata (1954) described the larvae and juveniles, and Yasuda et al. (1978) described embryonic and early larval stages. The purpose of this study is to document the development and anatomy of the fins and fin supports and vertebral column to afford comparisons of *Xiphias* with other fishes and to facilitate its phylogenetic placement. Although literature is abundant on larvae, juveniles, and adults of this monotypic species and genus (Palko et al. 1981), detailed osteological studies of *Xiphias* do not exist.

MATERIAL AND METHODS

The larvae and juveniles of *Xiphias gladius* were identified before clearing and staining according to the descriptions by Ehrenbaum (1905), Sanzo (1910, 1922), Regan (1924), Nakamura et al. (1951), Yabe (1951), Arata (1954), Tåning (1955), Jones (1958, 1962), Yabe et al. (1959), Markle (1974), and Yasuda et al. (1978). There were no identification problems (Richards 1974).

Cleared and stained larvae before and during notochord flexion were measured from the

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anterior orbit of the eye to the tip of the notochord (ENL) and those after notochord flexion were measured from the anterior orbit of the eye to the posteriormost edge of the hypural bones (ESL). The measurements were taken to the nearest 0.1 mm with a calibrated ocular micrometer for specimens <20 mm ESL, and for those >20 mm ESL, dial calipers were used. The reason for using ENL and ESL rather than standard length (SL) was that in most specimens the sword (bill) was damaged and standard length measurement would have been inaccurate.

A series of 220 *Xiphias gladius* from 3.7 mm ENL to 668 mm ESL captured with plankton nets, or by night light and dip netting, or taken from dolphin fish, *Coryphaena hippurus*, stomachs were cleared and stained for cartilage and bone by a combined method after Taylor (1967) and Dingerkus and Uhler (1977). Measurements of the specimens were taken after clearing and staining, because almost all *Xiphias* were twisted before clearing but were easily straightened after the clearing.

Although we had many smaller sized *Xiphias* larvae, we could have used more juveniles for our study (Fig. 1). Most of our specimens were collected in the Gulf of Mexico but a few were caught in the Caribbean Sea and Atlantic Ocean (Fig. 2).

All specimens were examined in 100% glycerin and under 100× to 150× magnification with a high-quality binocular dissecting microscope. Cartilage was viewed with the help of alcian blue stain, but cartilaginous structures that sometimes stained weakly or not at all were viewed by manipulating light intensity and the angle of the substage mirror. Onset of ossification was determined by light (pink) alizarin uptake, usually around the margin of a structure. Illustrations were drawn with the help of a camera lucida.

The osteological terms used in this study follow those used by Gosline (1961a, b), Nybelin (1963), Gibbs and Collette (1967), Monod (1968), and Potthoff (1975, 1980).

Counts of pterygiophores and fin rays include very small vestigial structures.

PECTORAL FIN

The pectoral fin rays in *Xiphias* were the first of all fin rays to begin development. The first rays were present at 4.8-5.6 mm ENL (Tables 1, 2). Development of the rays started on the dorsal border of the larval fin blade and proceeded in a

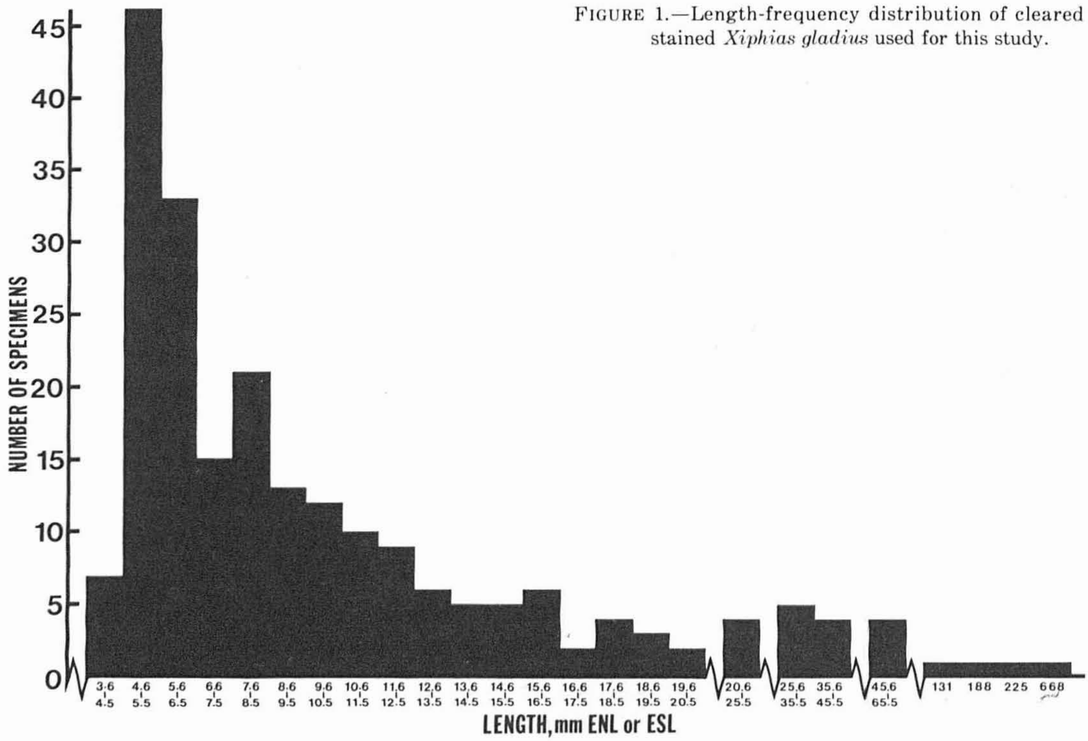


FIGURE 1.—Length-frequency distribution of cleared and stained *Xiphias gladius* used for this study.

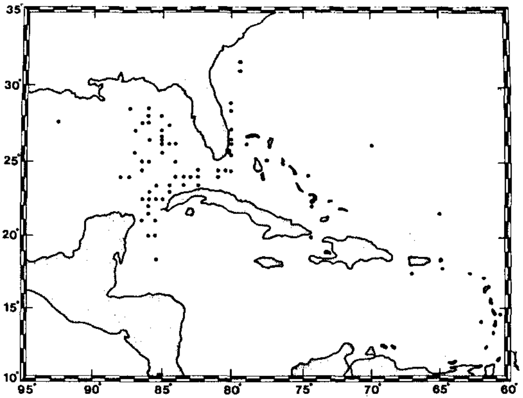


FIGURE 2.—Capture localities (black dots) of larval and juvenile *Xiphias gladius* used in this study. A locality may represent more than one capture.

TABLE 1.—Summary of fin development sequence in cleared and stained larvae of *Xiphias gladius*. PRC = principal caudal rays, SCR = secondary caudal rays.

Fin	Length ENL or ESL (mm)			Number of rays in fully developed fin
	First appearance of rays	All specimens have rays	Full complement of rays	
Caudal	5.4	6.1	26.7	34-38
PCR	5.4	6.1	8.8-11.0	17
SCR	7.8	11.6	26.7	8-10 dorsal 8-11 ventral
Dorsal fin	5.5	6.1	8.1-13.9	44-49
Anal fin	5.3	6.1	7.8-10.6	16-19
Pectoral fin	4.8	5.6	14.2-19.6	16-19

ventral direction. Adult counts of 16-19 rays were first obtained at 13.3 mm ESL and all specimens >19.5 mm ESL had the adult count (N = 20, $\overline{X}$ = 17.6, SD = 0.89) (Table 2).

Pectoral fin ray counts differed for individual specimens between sides. Of 154 specimens 4.6 mm ENL-19.5 mm ESL, in which the pectoral rays were still developing, 2 specimens differed by two rays (1.3%) between sides, 63 differed by one ray (40.9%), and 80 *Xiphias* (57.8%) had the same count on both pectoral fins. Of 20 specimens 19.6-668 mm ESL, which had adult counts, 10 differed by one ray between sides and 10 had the same count on both sides.

The position of the pectoral fin in *Xiphias* is on the side of larvae but changes during growth to ventrad in adults near the spot where the pelvic fin is located in most Perciformes. *Xiphias* lacks a pelvic fin and no vestiges of it were found during development (Gregory and Conrad 1937; Leim and Scott 1966; Ovchinnikov 1970; Yasuda et al. 1978).

PECTORAL FIN SUPPORTS

The pectoral rays were directly and indirectly supported by the bones of the pectoral girdle and its suspensorium. In fully developed juveniles the girdle consisted on each side of a scapula and a distal scapular radial (which supported the dorsalmost ray directly and which orginated from scapular cartilage), four large radials (which supported the remainder of the rays directly), a coracoid, and a cleithrum (Figs. 3-5). The scapula was connected to the coracoid by cartilage (Figs. 4, 5). The pectoral suspensorium consisted of a posttemporal, a supracleithrum, and a single postcleithrum. The posttemporal and supracleithrum were connected from the rear of the skull to the lateral side of the posterior process of the cleithrum. The single postcleithrum extended over the abdominal area and articulated on the medial side of the posterior process of the cleithrum (Figs. 3-5). The pectoral

TABLE 2.—Development of left pectoral fin rays for *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). $\overline{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number of rays																					
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	$\overline{X}$	SD
3.6-4.5	7																				—	—
4.6-5.5	20	5	6	8	3	2	1	1													1.6	2.03
5.6-6.5			1	3	2	5	2	6	5	5	1										6.4	2.19
6.6-7.5								1	5	3	4	1									8.9	1.12
7.6-8.5									1	2	6	6	5	1							10.7	1.37
8.6-9.5										1	2	3	5	2							11.3	1.08
9.6-10.5												1	6	1	2	1					12.6	1.33
10.6-11.5													3	3	2	1					13.1	1.20
11.6-12.5														1	6	2					14.1	0.60
12.6-13.5														1	2	—	—	1			14.5	1.80
13.6-14.5															2	2	1				14.8	0.89
14.6-15.5													1	—	—	2	2				14.8	1.57
15.6-16.5																	3	2			16.4	0.45
16.6-17.5																	1				—	—
17.6-18.5																1	1	1	1		16.5	1.20
18.6-19.5															1	—	—	1	1		16.3	2.08
19.6-668																	1	10	6	3	17.6	0.89

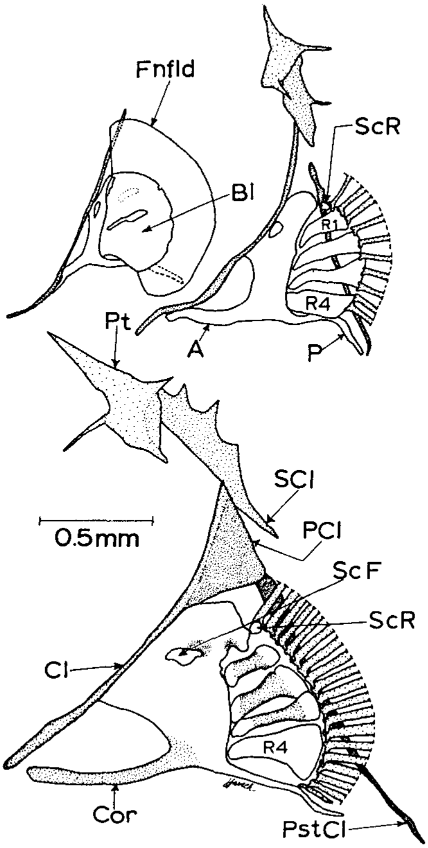
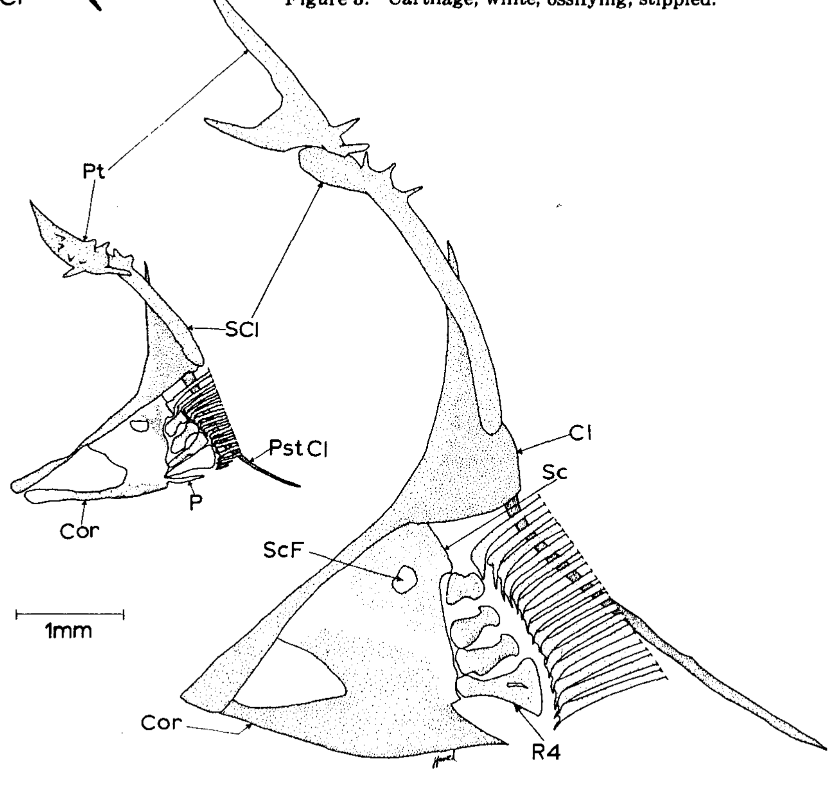


FIGURE 3.—Left lateral external view of the pectoral girdle and suspensorium from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.1 ENL; 7.6 ESL; bottom, 21.4 ESL. A, anterior process of the coraco-scapular cartilage; Bl, larval pectoral fin blade; Cl, cleithrum; Cor, coracoid; Fnfld, larval finfold; P, posterior process of the coraco-scapular cartilage; PCl, posterior process of cleithrum; PstCl, postcleithrum; Pt, posttemporal; R, radial orignating from larval fin blade; ScF, scapular foramen; SCl, supracleithrum; ScR, cartilaginous distal radial originating from scapular cartilage. Cartilage, white; ossifying, stippled.

FIGURE 4.—Left lateral external view of the pectoral girdle and suspensorium from *Xiphias gladius*, showing the ontogeny. The specimens' lengths in millimeters ESL are: left, 33.0; right, 64.6. Sc, scapula; for other abbreviations, see Figure 3. Cartilage, white; ossifying, stippled.



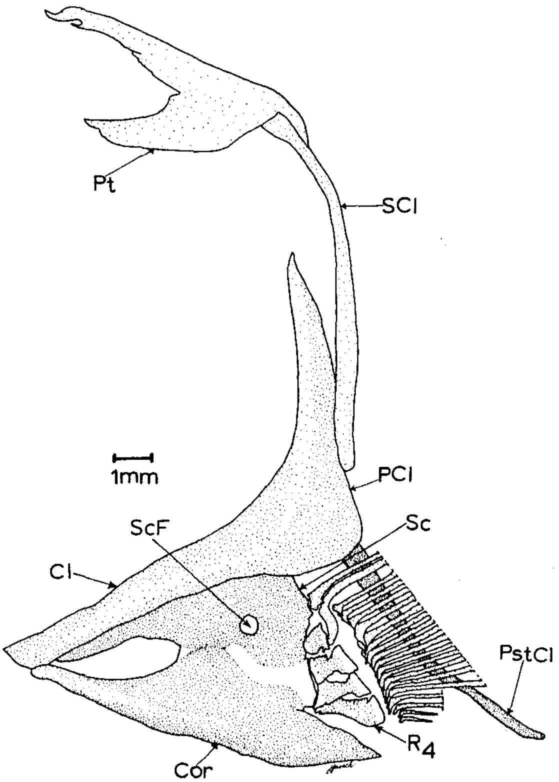


FIGURE 5.—Left lateral external view of the pectoral girdle and suspensorium from a 187 mm ESL *Xiphias gladius*. For abbreviations, see Figures 3 and 4. Cartilage, white; ossifying, stippled.

girdle is only briefly mentioned in Gregory and Conrad (1937) and no detailed description is given.

Our smallest 3.7 mm ENL specimen already had rudiments of a pectoral girdle, consisting of a rod-shaped bony cleithrum, an inverted Y-shaped coraco-scapular cartilage without scapular foramen, and a larval fin blade (similar to the 5.1 mm ENL specimen in Fig. 3) (Table 3). The cleithrum later developed a shelflike dorsal posterior process (Figs. 3-5). The coraco-scapular cartilage at first had long dorsal and long posterior processes and a short anterior process. It developed a foramen on the dorsal process, and the anterior process grew relatively larger and ossified into part of the coracoid, while the posterior process atrophied. Ossification of the scapula started around the scapular foramen and spread over the dorsal process forming the scapula (Figs. 3, 4; Table 3). The larval fin consisted of two parts: a flat cartilaginous semicircular blade surrounded on the circumference by a finfold containing larval actinopterygia (Fig. 3). The semicircular cartilaginous pectoral fin blade developed into the four large radials by first forming elongate holes in the blade. These holes then gradually enlarged to the border of the semicircular cartilage blade, forming separate cartilaginous radials, which later ossified (Figs. 3-5; Table 3).

TABLE 3.—Development of the pectoral girdle and suspensorium for 190 *Xiphias gladius* (3.7 mm ENL-64.6 mm ESL). Length ranges (mm, ENL, or ESL) are from "first observance" to "first observance in all specimens."

Part	Appearance in cartilage	Ossification
Posttemporal	—	5.3
Supracleithrum	—	5.3
Postcleithrum	—	5.3
Cleithrum	—	<3.7
Posterior process of cleithrum	—	6.2-6.9
Coraco-scapular cartilage	<3.7	—
Scapular foramen	4.6-5.1	—
Scapula	—	6.6-8.1
Coracoid	—	5.4-6.5
Scapular radial	5.5-9.3	10.6-15.0
Radial No. 1	5.2-5.6	8.8
Radial No. 2	5.2-5.9	9.0-10.0
Radial No. 3	5.4-9.1	9.1-12.0
Radial No. 4	6.8-9.1	13.3-14.7

The pectoral suspensorium, consisting of the posttemporal, supracleithrum, and postcleithrum, was of dermal origin (did not form from cartilage) and was first seen ossifying at 5.3 mm ENL (Table 3). The posttemporal was at first a flat rectangular bone with spines. The spines were lost and a dorsal and ventral process developed, giving the posttemporal the characteristic inverted C shape (Figs. 3-5; Table 3). The supracleithrum was short at first and had spines. It also lost its spines and developed a long posterior process which articulated laterally with the posterior process of the cleithrum (Figs. 3-5; Table 3). Lengthening of the supracleithrum accommodates the migration of the pectoral fin from a lateral position in the larvae to a more ventral position in the adults (Ovchinnikov 1970). The postcleithrum was an elongate rod-shaped bone without spines from the start and articulated medially with the posterior process of the cleithrum (Figs. 3-5; Table 3).

DORSAL FIN

Dorsal fin rays first appeared almost at the same sizes as the anal and caudal rays (Tables 1, 4). The dorsal fin rays developed in the dorsal finfold first at the middle of the body above the 10th-14th myomere in specimens 5.5-6.1 mm ENL. With growth, addition of dorsal fin rays

TABLE 4.—Summary of dorsal fin ray development for 208 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL).

Length, mm ENL or ESL	*N*	Range, number of dorsal fin rays	Mean, number dorsal fin rays	SD
3.6-4.5	7	0	0	—
4.6-5.5	47	0-32	1.3	6.17
5.6-6.5	31	0-38	23.0	13.92
6.6-7.5	14	27-42	35.7	4.49
7.6-8.5	21	36-45	41.0	2.75
8.6-9.5	13	40-44	42.2	1.44
9.6-10.5	11	40-45	42.2	1.66
10.6-11.5	8	42-47	43.8	1.70
11.6-12.5	9	40-48	44.9	2.40
12.6-13.5	4	42-46	43.8	1.80
13.6-14.5	5	43-48	44.8	2.01
14.6-668.0	38	44-49	46.4	1.23

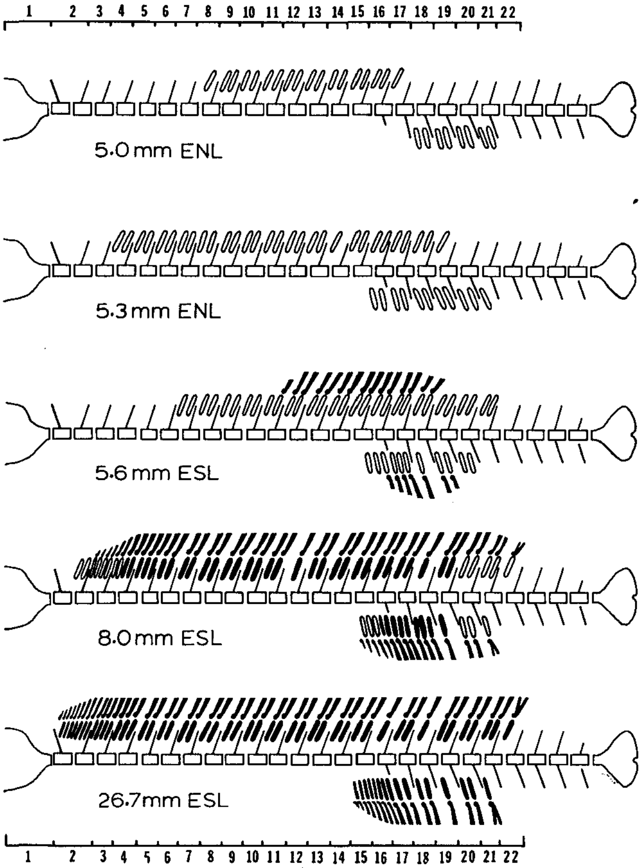


FIGURE 6.—Schematic representation of dorsal and anal fin and pterygiophore development in *Xiphias gladius* in relation to the vertebral column and head. Pterygiophores are represented white when cartilaginous and black when ossifying. Scales represent interneural and interhaemal space numbers and points on scales align with tips of neural and haemal spines.

was in an anterior and posterior direction. The posterior part of the dorsal fin was complete at a smaller size before the anterior part. Adult dorsal fin counts of 44-49 rays (14.6-668 mm ESL, $N = 38$, $\overline{X} = 46.4$, SD = 1.23) were first observed at 8.1 mm ESL, and all specimens longer than 13.8 mm ESL had the adult count (Fig. 6; Table 4). Our counts are in agreement with Arata (1954). Some of Arata's specimens, however, did not have adult counts. The sequence of dorsal fin ray development is similar in *Xiphias* to that of *Coryphaena* reported by Potthoff (1980).

DORSAL FIN PTERYGIOPHORES

In juvenile and adult specimens of *Xiphias* 14.1-668 mm ESL, the pterygiophores consisted of a jointed proximal and distal radial supporting a fin ray. The distal radial was located between the bifurcate base of the fin ray. Each proximal and distal radial and fin ray were forming a series, hence a serial association. Each fin ray also closely approximated the following posterior pterygiophore in a secondary association. Distal radials were present for all fin rays in 14 out of 37 juvenile specimens. Of the remaining 23 specimens 19 had one anteriormost ray and 4 had two anteriormost rays without distal radials (Table 5). Exceptions to the serial and secondary fin ray associations were found at the beginning and end of the fins. The anteriormost pterygiophore supported from one to three rays, most often two (Fig. 7). This pterygiophore consisted of one piece of cartilage, or of a Y-shaped piece, or of two fused pieces (Figs. 7, 8). In 1 of 38 speci-

TABLE 5.—Percent and number of anterior dorsal and anal fin rays without distal radials for 37 *Xiphias gladius* (14.7-668 mm ESL). Percent and number under 0 are specimens in which all fin rays had distal radials.

Item	Number of anterior dorsal and anal fin rays		
	0	1	2
Percent without dorsal distal radial(*N*)	37.8(14)	51.4(19)	10.8(4)
Percent without anal distal radial(*N*)	86.5(32)	13.5(5)	100.0(37)

Anteriormost dorsal pterygiophore shape	Number, dorsal fin rays associated with anteriormost pterygiophore		
	1	2	3
	4	23	2
			6
			2
Anteriormost anal pterygiophore shape	**Number, anal fin rays associated with anteriormost pterygiophore**		
	1	2	3
	1	21	
		10	4
	1		

FIGURE 7.—Threee possible shapes of anteriormost dorsal and anal pterygiophores for 37 *Xiphias gladius* 14.7-668 mm ESL and the number of fin rays associated with each pterygiophore shape.

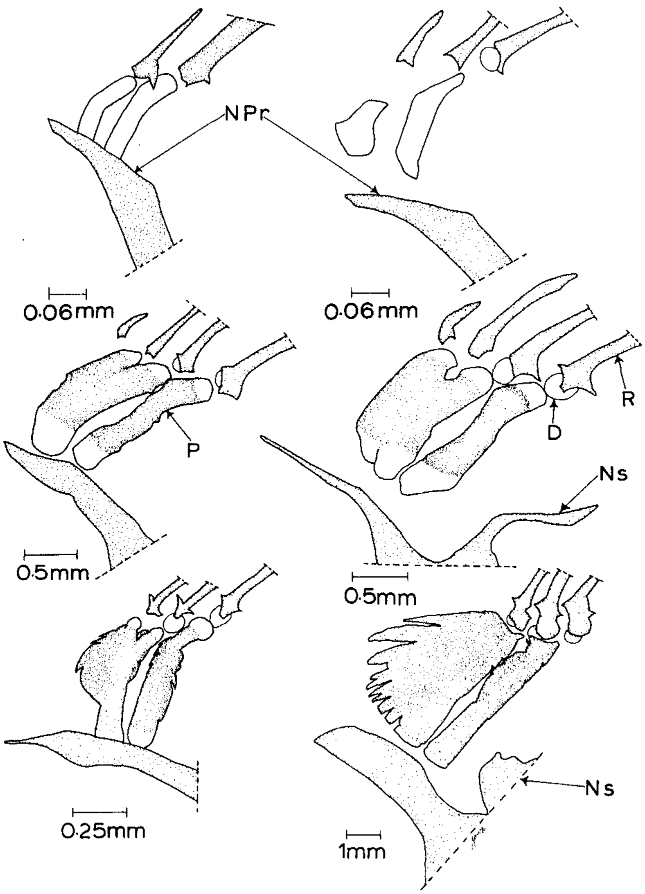


FIGURE 8.—Left lateral view of the two anteriormost dorsal fin pterygiophores with their associated rays in the second interneural space for various sizes of *Xiphias gladius*. Starting from left the specimens' lengths in millimeters ESL are: top row, 15.9, 20.4; middle row, 26.7, 33.6; bottom row, 52.4, 225. D, distal radial; NPr, neural prezygapophysis; Ns, neural spine; P, proximal radial; R, fin ray. Cartilage, white; ossifying, stippled.

mens, no rays were associated with the anteriormost pterygiophore. The posteriormost dorsal fin ray was double and was serially associated with the posteriormost pterygiophore (Figs. 9, 10). The double ray lacked a secondary association, but a stay was present under the double ray (Figs. 9, 10). Middle radials were absent in *Xiphias*. Total dorsal pterygiophore count was either equal to or one to two less than the dorsal fin ray count, depending on the number of rays associated with the anteriormost pterygiophore.

In larvae, juveniles, and small adults of *Xiphias* the dorsal proximal radials inserted in the interneural spaces. In 39 juveniles and small adults with fully formed fins, the first interneural space (bounded by head and first neural spine) lacked inserting pterygiophores or predorsal bones. The second interneural space (bounded by first and second neural spines) had four to seven ($\overline{X} = 5.2$), the third space had three to five ($\overline{X} = 4.2$), the fourth space had two to three ($\overline{X} = 2.9$), the fifth space had two to three ($\overline{X} = 2.4$), and the remainder of the interneural spaces had one to three pterygiophores, but usually two (Fig. 11). Usually the posteriormost dorsal pterygiophore inserted in the 22d interneural space and occasionally in the 21st (Fig. 11; Tables 6, 7).

In *Xiphias*, dorsal fin pterygiophores first appeared in cartilage before the fin rays at 4.8 mm ENL, but not until 6.0 mm ENL did all specimens have cartilaginous pterygiophores. Two *Xiphias*, 5.1 and 5.6 mm ENL, lacked dorsal pterygiophores but had some cartilaginous anal pterygiophores. Dorsal pterygiophores were first seen at the center of the body between the 11th and 18th interneural spaces (Fig. 6;

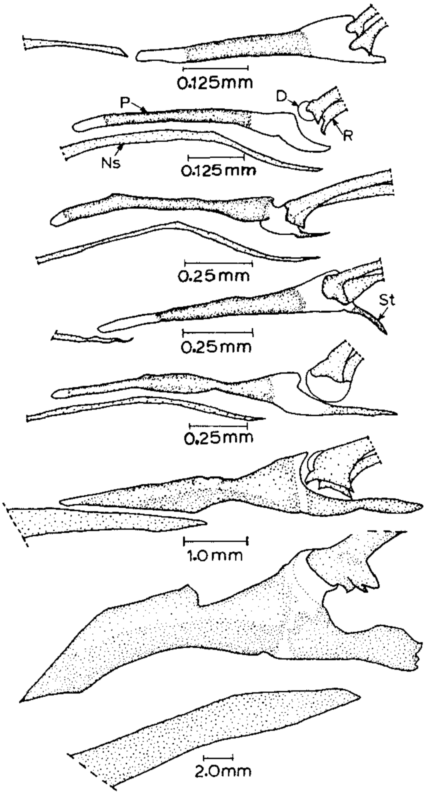


FIGURE 9.—Left lateral view of the posteriormost dorsal pterygiophore from *Xiphias gladius*, showing the ontogeny. Starting from the top and going to the bottom the specimens' lengths in millimeters ESL are: 15.9, 20.4, 26.7, 33.6, 52.4, 225, length unknown for last on bottom, weight 61 lb. St, stay; for other abbreviations, see Figure 8. Cartilage, white; ossifying, stippled.

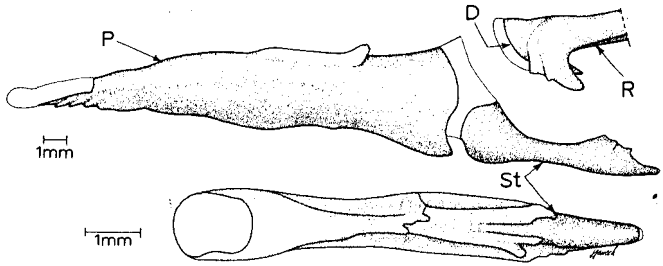


FIGURE 10.—Posteriormost dorsal pterygiophore and its stay from a 668 mm ESL *Xiphias gladius*. Top, left lateral view of proximal and distal radial, double ray and stay; bottom, dorsal view of stay, enlarged. For abbreviations, see Figures 8 and 9. Cartilage, white; bone, stippled.

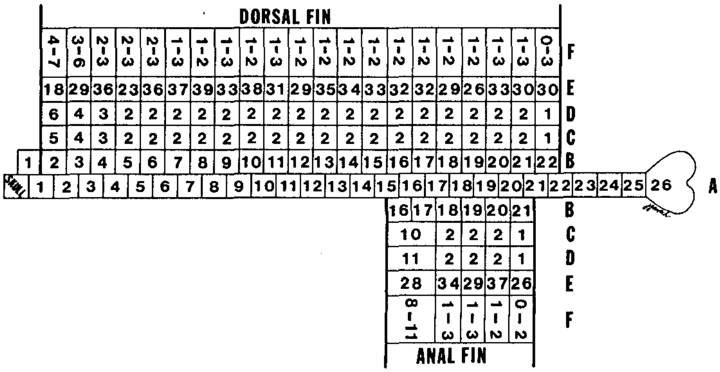


FIGURE 11.—Schematic presentation of common arrangement of pterygiophores and fin rays in relation to neural and haemal spines and vertebrae in 39 *Xiphias gladius* (14.7-668 mm ESL). Method of presentation modified after Matsui (1967). A, skull and vertebrae numbers; B, interneural and interhaemal space numbers; C, number of pterygiophores with highest frequency of occurrence found in the respective ("B") interneural or interhaemal space; D, number of fin rays associated with pterygiophores for indicated interneural or interhaemal space; E, highest frequency of occurrence in 39 *Xiphias* for the number of pterygiophores indicated in "C"; F, range of number of pterygiophores found in the respective ("B") interneural and interhaemal spaces.

TABLE 6.—Adult and juvenile position of posteriormost dorsal and anal fin pterygiophores in their interneural and interhaemal spaces for 116 *Xiphias gladius* (7.1-668 mm ESL).

	Interneural space numbers / Interhaemal space numbers			
Item	21/20	21/21	22/21	22/22
Number of specimens	29	7	79	1
Percent of specimens	25.0	6.0	68.1	0.9

Table 7). Addition of cartilaginous pterygiophores was in both anterior and posterior directions. The posteriormost interneural space number 21 or 22 was filled first (Fig. 6; Table 7). Addition of pterygiophores was then in an anterior direction until the anterior interneural space number 2 was occupied (Fig. 6; Table 7). Fin rays followed pterygiophore appearance at the center of the body. Addition of rays followed addition of pterygiophores, with some cartilaginous pterygiophores present anterior and posterior to the developing rays (Fig. 6).

Ossification of dorsal pterygiophores first started at 6.1 mm ENL in the same area and proceeded in the same direction as the cartilage development. Every specimen >8.0 mm ESL had some ossifying pterygiophores, and between 18.2 and 26.7 mm ESL all pterygiophores were ossifying. The last pterygiophore to ossify was the anteriormost in the second interneural space.

TABLE 7.—Development of dorsal and anal fin pterygiophores in the interneural and interhaemal spaces for 205 *Xiphias gladius*. $\bar{X}$ = mean.

Length, mm ENL or ESL	With pterygiophores				With ossifying pterygiophores			
	Anteriormost space no. ($\bar{X}$)		Posteriormost space no. ($\bar{X}$)		Anteriormost space no. ($\bar{X}$)		Posteriormost space no. ($\bar{X}$)	
	Interneural	Interhaemal	Interneural	Interhaemal	Interneural	Interhaemal	Interneural	Interhaemal
3.6-4.5	([1])	([1])	([1])	([1])	([2])	([2])	([2])	([2])
4.6-5.5	[1]3-11(5.0)	[1]16-18(17.1)	[1]17-22(20.0)	[1]19-21(20.1)	([2])	([2])	([2])	([2])
5.6-6.5	[1]2-6 (3.2)	16-18(16.5)	[1]20-22(21.4)	20-22(20.6)	[2]7-9 (8.0)	[2]16-17(16.8)	[2]16-18(17.0)	[2]17-19(18.0)
6.6-7.5	2-4 (2.8)	16-17(16.4)	21-22(21.6)	20-21(20.5)	[2]4-14(9.2)	[2]16-17(16.5)	[2]14-19(17.3)	[2]17-20(18.9)
7.6-8.5	2-3 (2.1)	16-17(16.5)	21-22(21.9)	20-21(20.9)	[2]3-11(5.4)	[2]16-18(16.4)	[2]13-22(19.1)	[2]17-21(19.0)
8.6-9.5	2-3 (2.1)	16-17(16.2)	21-22(21.8)	20-21(21.1)	3-12(4.7)	16-17(16.2)	14-22(19.4)	16-21(19.2)
9.6-10.5	2-3 (2.1)	16-17(16.3)	21-22(21.7)	20-21(20.6)	2-5 (3.5)	16-17(16.3)	19-22(20.5)	19-21(19.8)
10.6-11.5	2	16-17(16.4)	21-22(21.9)	20-21(20.9)	2-5 (3.8)	16-17(16.2)	18-22(20.7)	19-21(20.2)
11.6-12.5	2	16-17(16.4)	21-22(21.7)	20-21(20.6)	2-4 (2.8)	16-17(16.4)	18-22(20.8)	19-21(20.4)
12.6-13.5	2	16-17(16.8)	21-22(21.5)	20-21(20.8)	2-3 (2.5)	16-17(16.8)	21-22(21.3)	19-21(20.0)
13.6-14.5	2	16-17(16.4)	21-22(21.4)	20-21(20.6)	2-3 (2.2)	16-17(16.4)	20-22(21.0)	20-21(20.4)
14.6-15.5	2	16-17(16.6)	21-22(21.8)	20-21(20.8)	2	16-17(16.8)	21-22(21.8)	20-21(20.8)
15.6-16.5	2	16-17(16.2)	21-22(21.4)	20-21(20.4)	2-3 (2.4)	16	21-22(21.4)	20-21(20.4)
16.6-668	2	16-17(16.4)	21-22(21.5)	20-22(20.7)	2	16-17(16.4)	21-22(21.5)	19-21(20.6)

[1]No pterygiophores developed in all or some specimens; these were not used for calculation of means.
[2]No pterygiophores ossified in all or some specimens; these were not used for calculation of means.

Pterygiophores under the middle of the dorsal fin completed development first. Proximal and distal radials first appeared as one piece of cartilage. Then the distal radial cartilage separated from the proximal radial. Ossification of the proximal radial cartilage started at the middle and spread outwards proximally and distally toward the ends. The ends remained cartilaginous in adults, and small sagittal keels developed ventrad during ossification (Fig. 12). Extensive lateral keels were observed on the pterygiophores in the largest 668 mm ESL specimen.

The posteriormost pterygiophores ossified later, but in the same sequence as those in the middle area. The last pterygiophores supported a double ray in series and a stay was present (Figs. 9, 10). The posteriormost pterygiophore and the stay ossified from the same piece of cartilage (Figs. 9, 10).

The anteriormost pterygiophores were the last to ossify. The first anteriormost pterygiophore developed a large anterior sagittal keel (Fig. 8).

Distal radials developed from a piece of cartilage that separated during development from the distal portion of the cartilaginous pterygiophores and was situated between the bifurcate bases of the serial fin rays (Figs. 8, 12, 13). Ossification of all distal radials occurred after cartilage separation. At first the left and right sides of the distal radial cartilage ossified to form two pieces of bone. Ossification continued until the two bones were joined (Figs. 14, 15). All dorsal fin rays associated with the distal radials had bifurcated bases (Figs. 14, 15).

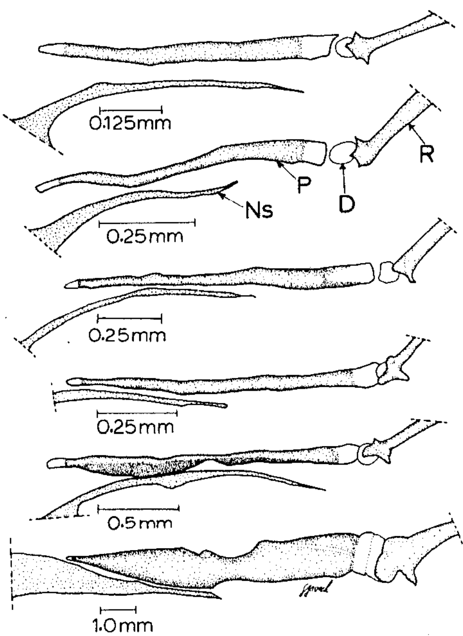


FIGURE 12.—Left lateral view of a dorsal pterygiophore from the 11th interneural space of *Xiphias gladius*, showing the ontogeny. Starting from the top and going to the bottom the specimens' lengths in millimeters ESL are: 15.9, 20.4, 26.7, 33.6, 52.4, 225. For abbreviations, see Figure 8. Cartilage, white; ossifying, stippled.

ANAL FIN

Anal fin rays first appeared at about the same sizes as the dorsal and caudal rays (Tables 1, 8). The anal rays developed in the anal finfold first at the middle of the fin below myomeres 18-20 in specimens 5.3-6.1 mm ENL. Anal rays were

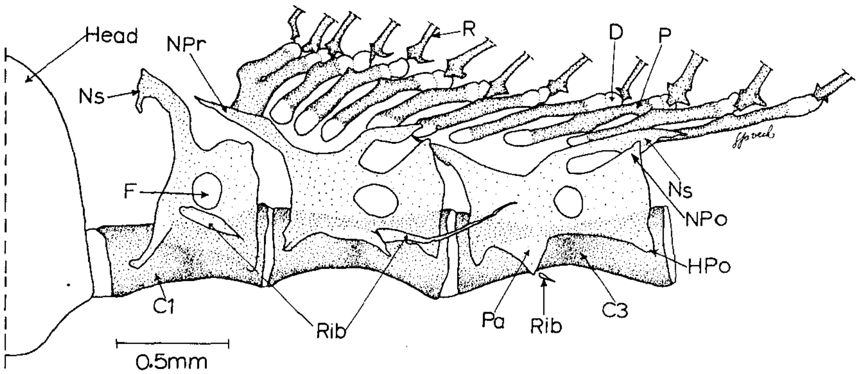


FIGURE 13.—Anteriormost three vertebrae and pterygiophores with fin rays from a 35.9 mm ESL *Xiphias gladius*. C, centrum; D, distal radial; F, neural foramen; HPo, haemal postzygapophysis; NPo, neural postzygapophysis; NPr, neural prezygapophysis; Ns, neural spine; P, proximal radial; Pa, parapophysis; R, ray.

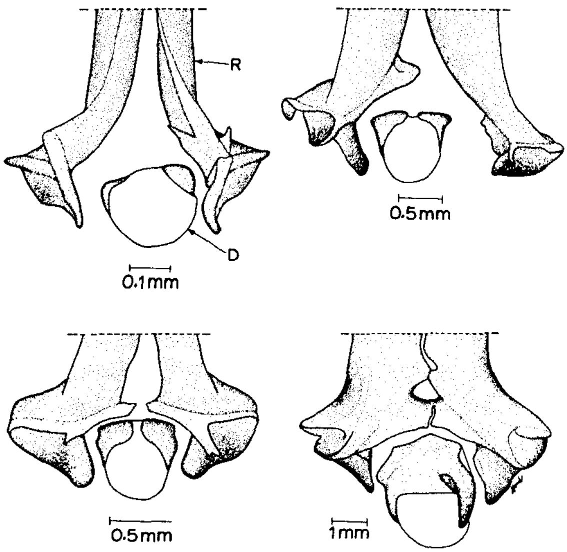


FIGURE 14.—Anterior view of the 12th dorsal ray and its distal radial from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters ESL are: top, 64.6, 187; bottom, 225, 668. D, distal radial; R, fin ray. Cartilage, white; ossifying, stippled.

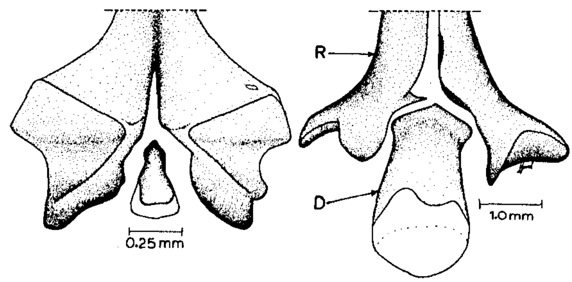


FIGURE 15.—Anterior view of two fin rays and their distal radials from juvenile *Xiphias gladius*. The specimens' lengths in millimeters ESL are: left, 225, first anteriormost dorsal ray; right, 668, next to last posteriormost dorsal ray. D, distal radial; R, fin ray. Cartilage, white; bone, stippled.

added in an anterior and posterior direction (Fig. 6). Adult anal counts of 16-19 rays (10.6-668 mm ESL, $N = 66$, $\overline{X} = 17.1$, SD = 0.81) were first observed at 7.8 mm ESL and all specimens longer than 10.6 mm ESL had the adult counts (Fig. 6; Table 8). Our counts generally agree with those of Arata (1954), except we had two specimens with 19 anal rays; Arata had none.

TABLE 8.—Development of anal fin rays for 213 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). $\overline{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number of anal fin rays																	
	0	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	$\overline{X}$	SD
3.6-4.5	7																	—	—
4.6-5.5	43	2	—	—	—	—	1	—	1									0.6	2.06
5.6-6.5	6	—	—	2	—	1	3	—	8	2	4	2	4	1				9.5	5.17
6.6-7.5									1	—	5	1	4	2	1			14.2	1.50
7.6-8.5												1	8	5	5	2		16.0	0.92
8.6-9.5													2	8	3			16.1	0.72
9.6-10.5													1	6	3	1	1	16.6	1.04
10.6-668														13	37	15	1	17.1	0.81

ANAL FIN PTERYGIOPHORES

The description of the dorsal fin pterygiophores in the previous section may be applied to anal fin pterygiophores because of the similarities between the two. Anal pterygiophores were inserted in the interhaemal spaces. These spaces were numbered the same as the opposing interneural spaces. Anteriormost (first) interhaemal space number 16 or 17 was bound anteriorly by the stomach, intestine, and anus and posteriorly by the first haemal spine. The first haemal spine was positioned on the 16th or 17th centrum. If it occurred on the 16th centrum, it was of variable length and often did not reach the pterygiophores. If the first haemal spine was on the 17th centrum, it always reached past the pterygiophores. The count for the 16th and 17th interhaemal space was summed because we were not always able to determine a division between the two spaces (Fig. 11).

Total number of anal pterygiophores in 31 of 37 specimens with full counts was one less than the anal fin ray count. In 2 of 37 specimens, it was the same and in 4 of 37 it was two less. The anteriormost anal pterygiophore supported from one to three rays, most often two (Fig. 7). This pterygiophore consisted of one piece of cartilage, normal in shape (Fig. 16), or of a vestige (Fig. 7). The vestigial piece may fuse to the next posterior pterygiophore to form an inverted Y shape (Fig. 16), or the inverted Y shape may originate from one piece of cartilage (Figs. 7, 16). An anterior sagittal keel developed on the anteriormost anal pterygiophore (Fig. 16), but this keel was not as large as on the first dorsal pterygiophore (Fig. 8).

The posteriormost anal pterygiophore had the same structure as its dorsal counterpart and inserted most often into the 20th or 21st interhaemal space, which was usually one space anterior to the posteriormost dorsal insertion (Fig. 11; Table 6).

In juveniles and small adults of *Xiphias* with fully formed fins the anteriormost interhaemal spaces 16 and 17 had 8-11 ($\bar{X}$ = 9.9, N = 40) pterygiophores. The remaining three or four interhaemal spaces had one to two or one to three pterygiophores each (Fig. 11). The posteriormost 21st interhaemal space had none or one to two pterygiophores. Only 1 specimen out of 116 had a pterygiophore in the 22d interhaemal space (Table 6).

Development and structure of the anal fin pterygiophores was the same as in the dorsal supports. Cartilaginous anal pterygiophores first appeared before anal fin rays and most of the time concurrently with dorsal pterygiophores below myomeres 18-20 (which approximately corresponds to interhaemal spaces 18-20) (Fig. 6; Table 7). Addition of cartilaginous pterygiophores was in an anterior and posterior direction. The posteriormost interhaemal spaces 20 or 21 were filled first. Last to develop was the anteriormost anal pterygiophore (Fig. 6). Fin rays followed pterygiophore appearance as in the dorsal fin (Fig. 6).

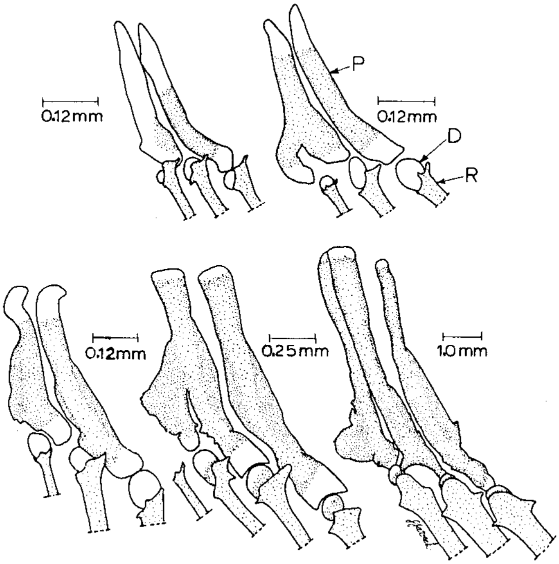


FIGURE 16.—Left lateral view of two or three anteriormost anal fin pterygiophores from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters ESL are: top row, 15.9, 20.4; bottom row, 33.0, 64.6, 225. D, distal radial; P, proximal radial; R, fin ray. Cartilage, white; ossifying, stippled.

Ossification of anal fin pterygiophores first started between 6.0 and 8.0 mm ENL or ESL in the same area of first appearance in cartilage and proceeded in the same directions as cartilage development (Fig. 6; Table 7). All anal pterygiophores were ossifying between 12.0 and 25.1 mm ESL.

Development and ossification of individual anal pterygiophores is similar to the dorsal pterygiophores (Fig. 16). The posteriormost anal pterygiophore develops a stay and supports a double ray serially as does its dorsal counterpart.

Distal radials developed in the anal fin as in the dorsal fin (Fig. 14). Almost all rays had a distal radial between their bifurcate base. Only 5 out of

37 specimens did not have a distal radial for the anteriormost ray (Table 5).

CAUDAL FIN

Caudal fin rays first appeared at about the same sizes as the dorsal and anal rays (Table 1). The caudal fin rays developed in the caudal finfold ventrad in preflexion larvae first on hypurals 2 and 3 and were added in an anterior and posterior direction. After complete notochord flexion between 6.3 and 8.0 mm ESL, the secondary caudal rays developed dorsad and ventrad in an anterior direction. Caudal rays were first seen in a 5.4 mm ENL specimen and all larvae longer than 6.1 mm ENL had some caudal rays developing (Table 9). The full complement of 9+8 principal rays developed between 8.8 and 11.0 mm ESL. All *Xiphias* longer than 26.6 mm ESL had the adult count of (8-10)+9+8+(9-11)=34-38 (N = 15, $\overline{X}$ = 35.9, SD = 1.55) rays (Tables 9, 10). The upper and lower caudal lobe had equal numbers of rays or they differed by one ray (Table 10). A procurrent spur (Johnson 1975) was not oberved in *Xiphias*.

TABLE 9.—Caudal fin ray development for 200 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). SCR, secondary caudal rays. PCR, principal caudal rays. $\overline{X}$ = mean, SE = standard error of the mean. Specimens are undergoing notochord flexion between dashed lines at 6.3-8.0 mm ENL.

Length, mm ENL or ESL	Upper		Lower		Total fin ray count			
	SCR	PCR	PCR	SCR	Range	$\overline{X}$	SE	N
3.6-4.5	0	0	0	0	0	—	—	7
4.6-5.5	0	0-3	0-3	0	0-6	0.2	1.36	46
5.6-6.5	0	0-6	0-8	0	0-14	4.9	3.83	30
6.6-7.5	0	2-7	2-8	0	4-15	9.9	2.99	14
7.6-8.5	0	4-8	4-8	0-1	8-17	13.7	2.62	19
8.6-9.5	0-1	5-9	6-8	0-2	11-19	15.5	2.77	12
9.6-10.5	0	7-9	8	0-2	16-20	17.6	1.33	11
10.6-11.5	0-1	7-9	8	0-2	16-20	18.1	1.50	9
11.6-12.5	0-2	9	8	2	19-21	19.6	0.85	8
12.6-13.5	0-3	9	8	1-3	18-23	21.3	2.20	4
13.6-15.5	0-3	9	8	2-3	19-23	21.5	1.41	8
15.6-17.5	3-5	9	8	3-5	23-27	24.3	1.71	6
17.6-26.5	4-7	9	8	4-8	25-32	26.0	1.99	11
26.6-668	8-10	9	8	9-11	34-38	35.9	1.55	15

TABLE 10.—Adult caudal fin ray counts for 15 *Xiphias gladius* (26.7-225, 668 mm ESL). USCR = upper secondary caudal rays, PCR = principal caudal rays, LSCR = lower secondary caudal rays.

Total fin ray count	USCR + PCR + LSCR	N
34	8 + 17 + 9	4
35	9 + 17 + 9	2
36	9 + 17 + 10	3
37	10 + 17 + 10	3
38	10 + 17 + 11	3

CAUDAL FIN SUPPORTS

The caudal fin rays were supported by some of the bones of the hypural complex and only two posteriormost centra (PU_2 and urostyle) were involved in the support (Fig. 17). The bones which supported the fin rays directly or indirectly in larvae and juveniles of *Xiphias* were two centra (PU_2 and urostyle), one specialized neural arch, three epurals, one paired uroneural, five autogenous hypural bones, one autogenous parhypural, and one autogenous haemal spine. One of 164 specimens examined had the unusual count of 16+11=27 vertebrae and had two autogenous haemal spines on preural centra 2 and 3. We were able to see all these supporting bones during development (Figs. 18-23; Table 11), but in the adults some parts were ontogenetically fused.

Between 3.7 and 6.2 mm ENL, *Xiphias* had a straight notochord in the caudal area. Notochord flexion was between 6.3 and 8.0 mm ENL. Before notochord flexion hypurals 1-4, the parhypural (Ph), and the haemal spine and arch (Hs) of the future preural centrum 2 were developing ventrad in cartilage (Fig. 18; Table 11). Dorsad the neural arch (Ns) of the future preural centrum 3, the specialized neural arch ("Na") of the future preural centrum 2, and the three epurals (Ep) were developing from cartilage (Fig. 19). Appearance of the cartilaginous parts was from anterior to posterior. After notochord flexion a cartilaginous hypural 5 (Hy) and a bony uroneural (Un) developed between 9.8 and 12.5 mm ESL (Figs. 20-21; Table 11).

The parhypural and hypurals 1-5 developed from separate pieces of cartilage. This is shown for the parhypural and hypurals 1-2 in Figure 18. Joining of the proximal portions of the parhypural and hypurals 1-2 by cartilage starts with the parhypural and hypural 1 between 5.4 and 5.6 mm ENL and extends to hypural 2 at 5.7 mm ENL. All specimens have the parhypural and hypurals 1-2 joined proximally with cartilage at 6.9 mm ENL or ESL as shown in Figures 19 and 20. Hypurals 3-5 are never joined by cartilage during development (Figs. 19-21). The cartilaginous proximal joint is lost during development when the hypurals are fully ossified between 27 and 34 mm ESL (Fig. 22).

Ossification of the cartilage bone in the caudal complex of *Xiphias* started with the preural

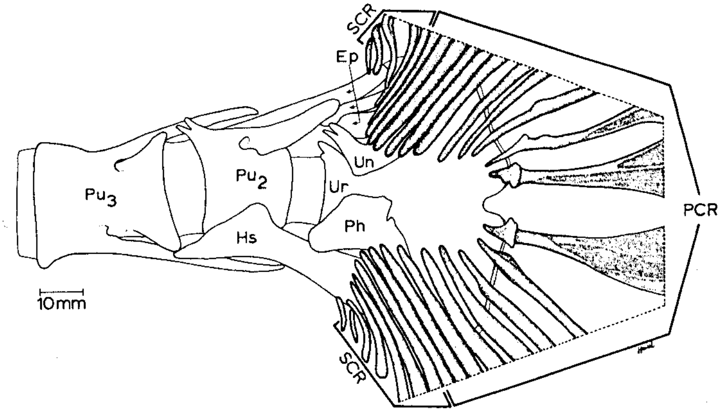


FIGURE 17.—Left lateral view of the adult caudal complex from *Xiphias gladius* of unknown length, 48 lb, showing fin ray articulation in relation to the caudal parts. Ep, epural; Hs, autogenous haemal spine; PCR, principal caudal rays; Ph, parhypural; Pu, preural centrum; SCR, secondary caudal rays; Un, uroneural; Ur, urostyle. Caudal complex bones, white; caudal rays, stippled.

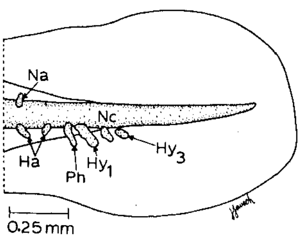


FIGURE 18.—Left lateral view of the caudal complex of a 5.1 mm ENL *Xiphias gladius*. Ha, haemal arch; Hy, hypural; Nc, notochord; Na, neural arch; Ph, parhypural. Cartilage, stippled.

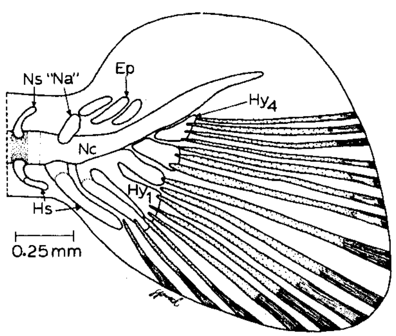


FIGURE 19.—Left lateral view of the caudal complex of a 8.8 mm ESL *Xiphias gladius*. Hs, haemal spine; "Na", specialized neural arch; Ns, neural spine; for other abbreviations, see Figures 17 and 18. Cartilage, white; bone, stippled.

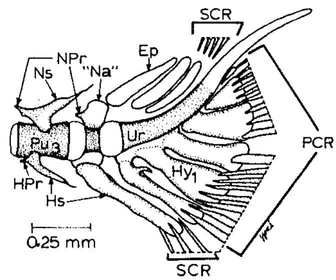


FIGURE 20.—Left lateral view of the caudal complex of a 12.6 mm ESL *Xiphias gladius*. HPr, haemal prezygapophysis; NPr, neural prezygapophysis; for other abbreviations, see Figures 17-19. Cartilage, white; ossifying, stippled.

TABLE 11.—Length ranges at which parts of the caudal complex appear in cartilage and ossify in 173 *Xiphias gladius* (5.4 mm ENL-225 mm ESL). Pu = preural centrum. Brackets denote fusion of separate structures during development.

	Length range (mm, ENL or ESL) of first appearance in cartilage	Length range (mm, ENL or ESL) of first evidence of ossification	First evidence of fusion (mm, ESL)
Pu_2 centrum	—	6.2- 9.0	
Specialized neural arch	5.4-6.5	7.1-12.3	
Epural			
anterior	5.7-6.8	10.3-13.7	
middle	5.4-6.8	10.3-13.7	
posterior	5.4-7.1	16.2-17.6	
Uroneural	—	9.8-12.3	
Hypural 5	9.8-12.5	16.0-17.7	
Hypural 4	5.7-7.9	9.4-13.7	17.2-26.7 (Hypurals 4 and 3)
Hypural 3	5.3-6.1	7.1-10.7	
Urostyle	—	6.2-9.1	131 -? (Hypural 4 to Hypural 1)
Hypural 2	5.1-5.6	7.1-9.7	17.2-22.6 (Hypurals 2 and 1)
Hypural 1	5.0-5.5	7.1-9.2	
Parhypural	5.0-5.5	7.1-9.2	
Pu_2 haemal spine	5.1-6.1	7.1-10.9	

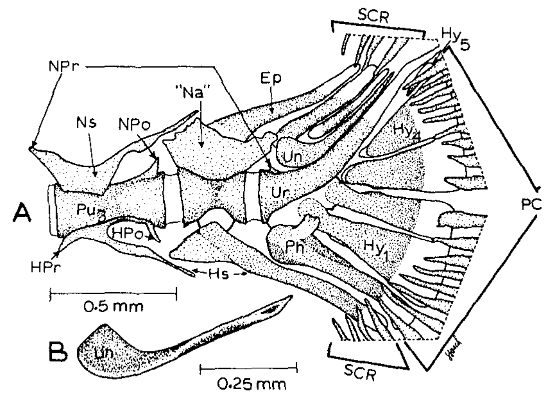


FIGURE 21.—The caudal complex of a 21.4 mm ESL *Xiphias gladius*. A, left lateral view of the complex; B, left lateral view of normal uroneural, enlarged. HPo, haemal postzygapophysis; NPo, neural postzygapophysis; for other abbreviations, see Figures 17-20. Cartilage, white; ossifying, stippled.

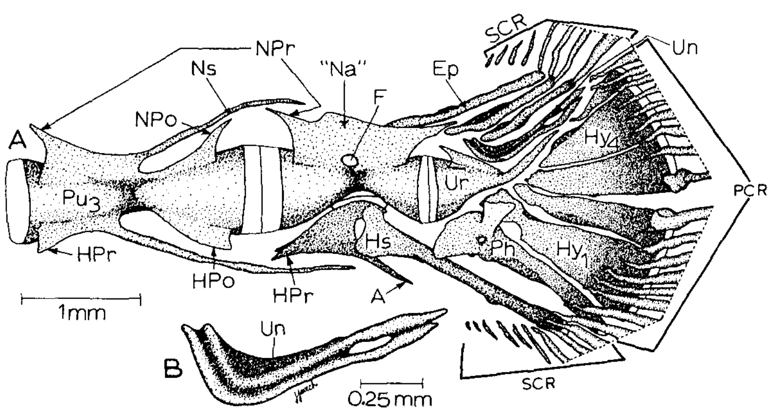


FIGURE 22.—The caudal complex of a 52.4 mm ESL *Xiphias gladius*. A, left lateral view of the complex; B, left lateral view of the anomalous uroneural, enlarged. A, anomalous secondary haemal spine; F, neural foramen; for other abbreviations, see Figures 19-21. Cartilage, white; ossifying, stippled.

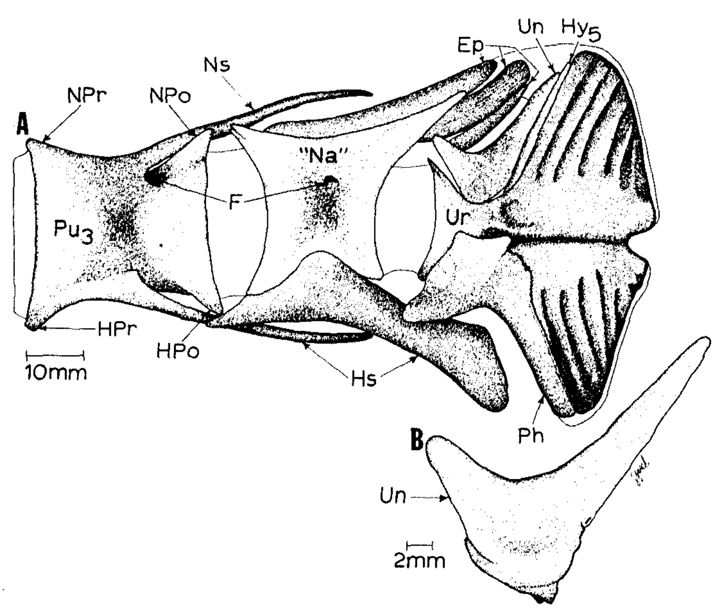


FIGURE 23.—The bones of the caudal complex from an adult *Xiphias gladius* length unknown, 61 lb. A, left lateral view of the caudal bones; B, left lateral view of the normal uroneural, enlarged. For abbreviations, see Figures 19-21. Cartilage, white; bone, stippled.

centrum 2 and the urostyle at 6.2 mm ENL-9.1 mm ESL. Ossification then proceeded from the haemal spine of the preural centrum 2 dorsad to the hypurals. Last to ossify between 16.0 and 17.7 mm ESL was hypural 5 (Table 11). The specialized neural arch of preural centrum 2 began ossification at 7.1-12.3 mm ESL followed by the three epurals. The posteriormost epural was last to ossify between 16.2 and 17.6 mm ESL (Table 11). The paired uroneural was not a cartilage bone and it was first present between 9.8 and 12.3 mm ESL before epural ossification (Table 11). In a few specimens the uroneural had an anomalous shape as if it had fused from two parts (Fig. 22).

During development of the hypural complex, a parhypurapophysis and a hypurapophysis (Lundberg and Baskin 1969; Nursall 1963) were observed on the parhypural and hypural 1. From a dorsal view the parhypural and hypural 1 are bifurcated as shown in Figure 24. This bifurcation can be observed in the adults on the autogenous parhypural but is absent on hypural 1, which then is fused to the hypural plate. A tunnellike foramen develops between the tips and rear of the parhypural prezygapophyses for the haemal canal on the proximal surface of the parhypural. This tunnel was not yet developed in a 44.1 mm ESL specimen (Fig. 24) but was fully formed in our 668 mm ESL specimen.

In adults of *Xiphias*, hypurals 1-4 fuse with each other and the urostyle, forming a single hypural plate with a notch posteriorly at the center. Grooves present on the plate formed because of articulating rays (Gregory and Conrad 1937) (Fig. 23). The epurals, the uroneural, hypural 5, the parhypural, and the haemal spine of preural centrum 2 remained autogenous in the adults. Fusion between hypurals 4 and 3 and 1 and 2 started distad from the articular cartilage in an anterior direction at 17.2-26.7 mm ESL (Figs. 21, 22; Table 11). Fusion of the two hypural plates, however, was in a posterior direction starting proximally. We could not determine the size at which the dorsal and ventral hypural plates fused with each other and with the urostyle because of insufficient samples (Fig. 1; Table 11).

The parhypural and hypurals 1-5 supported the principal caudal rays. Only on one occasion did the haemal spine of preural centrum 2 support a principal caudal ray, but this is not shown in Table 12. The distribution of principal rays on the hypural bones can only be seen in larvae and small juveniles (Figs. 19-22; Table 12).

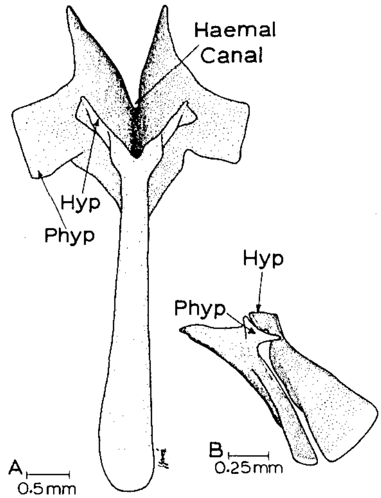


FIGURE 24.—The parhypural and hypural 1 from a 44.1 mm ESL *Xiphias gladius*. A, dorsal view, enlarged; B, left lateral view. Hyp, hypurapophysis; Phyp, parhypurapophysis. Cartilage, white; bone, stippled.

TABLE 12.—Distribution of principal caudal rays on the hypurals in 66 *Xiphias gladius* (8.8-64.6 mm ESL).

	Number of principal caudal rays					
Part	1	2	3	4	5	6
Parhypural	2	61	3			
Hypural 1			1	18	47	
Hypural 2	49	17				
Hypural 3		15	48	3		
Hypural 4			1	18	43	4
Hypural 5	38	28				

VERTEBRAL COLUMN

Of 164 *Xiphias* 5.3 mm ENL-668 mm ESL, 1 (0.6%) had 15+10=25 vertebrae, 95 (57.9%) had 15+11=26, 65 (39.7%) had 16+10=26, and 3 (1.8%) had 16+11=27 (Nakamura et al. 1968; Ovchinnikov 1970).

All centra except the first anteriormost, the urostyle, and preural centrum 2 had neural pre- and postzygapophyses, and neural arches and spines (Figs. 25-27). The first anteriormost centrum lacked a neural prezygapophysis (Figs. 13, 27), preural centrum 2 had a neural prezygapophysis, a specialized (open) neural arch, and a neural postzygapophysis (Figs. 22, 23). The urostyle had only a neural prezygapophysis (Figs. 21-23). All precaudal vertebrae except the anteriormost had parapophyses (Figs. 13, 25,

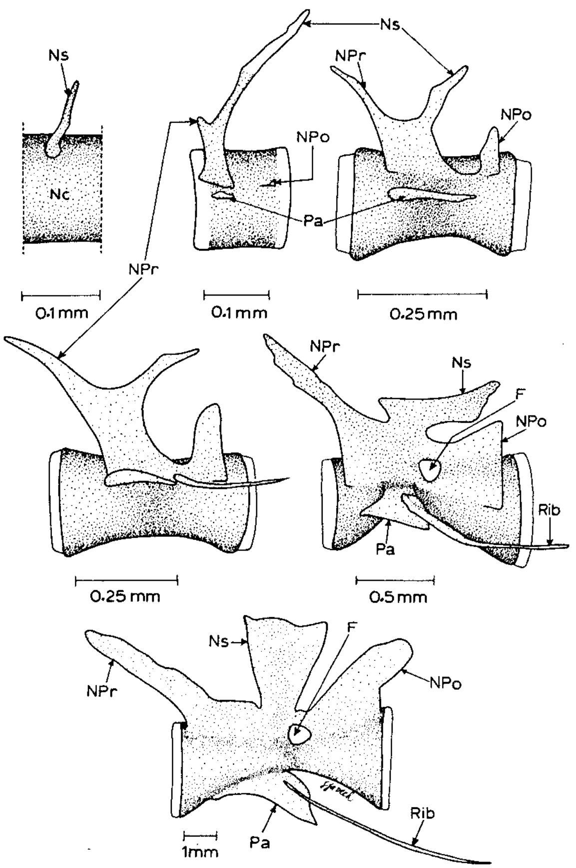


FIGURE 25.—Left lateral view of the second anteriormost vertebra from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.1 ENL, 7.8 ESL,12.6 ESL; center, 21.4 ESL, 52.4 ESL; bottom, 225 ESL. F, neural foramen; Nc, notochord; NPo, neural postzygapophysis; NPr, neural prezygapophysis; Ns, neural spine; Pa, parapophysis. Cartilage, white (except in 5.1 mm ENL specimen in top row left where entire stippling signifies cartilage); ossifying, stippled.

26). Haemal postzygapophyses were present on precaudal vertebrae numbers 3 to 15, sometimes on 2 to 15 (Figs. 13, 26).

All caudal vertebrae had nonautogenous haemal spines, except preural centrum 2 and the urostyle. Preural centrum 2 had an autogenous haemal spine. The urostyle had an autogenous parhypural with a tunnellike foramen for the haemal canal. The parhypural is homologous to the autogenous haemal spine of preural centrum 2 (Figs. 20-24). The 16th centrum sometimes lacked a haemal spine, sometimes had a vestigial haemal spine, or it had a normal haemal spine. Haemal pre- and postzygapophyses were present on all caudal centra except on preural centrum 2 and the urostyle. Neural foramina were present on most precaudal and caudal centra on larger specimens (Figs. 13, 22, 23, 25-28).

Five out of eight *Xiphias* with all ribs developed had six paired ventral ribs, which loosely articulated with the parapophyses on centra 1-4, 14, and 15 (Figs. 25-27). Two specimens had seven pairs of ribs on centra 1-5, 14, and 15 and on centra 1-4 and 13-15. One *Xiphias* had nine pairs on centra 1-6 and 14-16.

The neural arches fuse distally during ossification to form neural spines. The fusion and spine formation is over a size range and proceeds from posterior in an anterior direction (Fig. 27; Table 13). Our largest four specimens of *Xiphias*, 131-668 mm ESL, had three to six anterior neural arches and spines split. These arches and spines remain split in adults (Bruce B. Collette[3]).

Development of the centra starts with the appearance of distally opened cartilaginous neural arches. One arch was seen behind the head on top of the notochord in our smallest 3.7 mm ENL specimen (Fig. 29). As length in *Xiphias* increased, more arches were added in a posterior direction (Fig. 29; Table 14). All specimens >6.5 mm ENL had the complete count of 25 neural arches.

Two cartilaginous split haemal arches were first observed at 5.0 mm ENL when 16 neural arches were present. The two haemal arches were opposite the 16th and future 17th neural arch. Additional haemal arches and spines were added in a posterior direction (Fig. 29; Table 15).

[3]Bruce B. Collette, Systematic Zoologist, National Marine Fisheries Service, NOAA, Systematics Laboratory, Washington, DC 20560, pers. commun. July 1981.

TABLE 13.—Number of split neural arches and spines counted from anterior to posterior for various size ranges in 159 *Xiphias gladius* 5.5 mm ENL-668 mm ESL. N=number of specimens, $\overline{X}$=mean.

Length, mm	Centrum number with split neural arches and spines																							
ENL or ESL	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\overline{X}$
5.5-6.9									1	5	2	5	3	3	5	1	1	3	1	1	2	5	38	17.1
7.0-13.3					5	5	12	18	18	10	3	2	1	—	2	—	—	—	—	—	—	1	77	10.7
13.6-64.6				2	6	8	17	6	—	1													40	8.6
131-668	1	—	2	1																			4	4.8

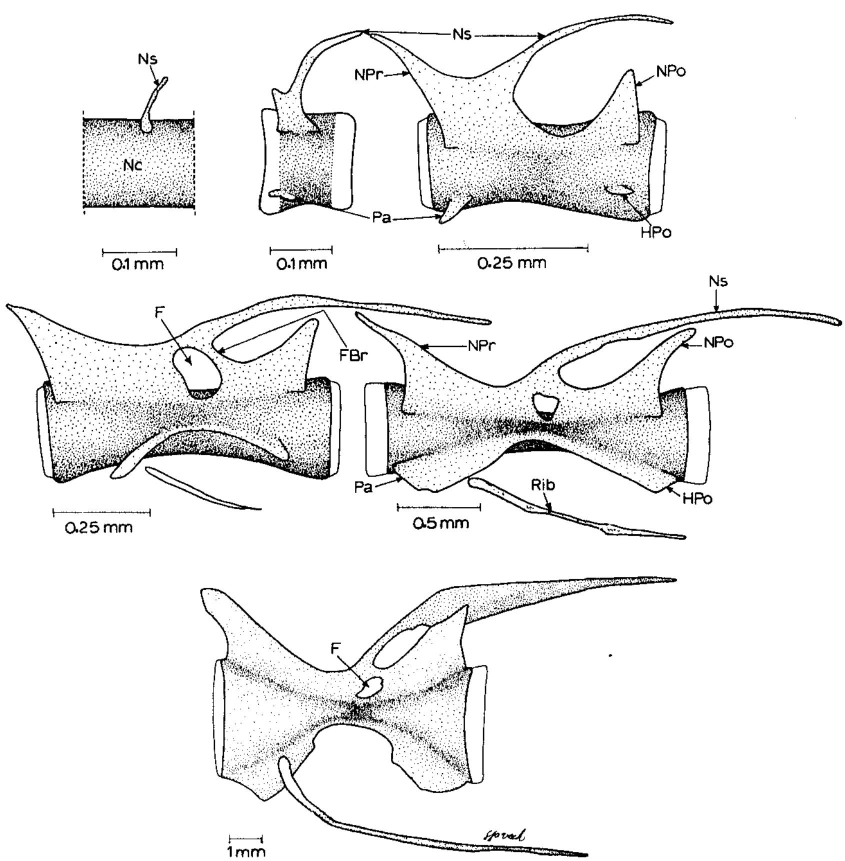


FIGURE 26.—Left lateral view of the 15th vertebra from *Xiphias gladius*, showing the ontogeny. Starting from top left the specimens in millimeters ENL or ESL are as in Figure 25. FBr, foraminal bridge; HPo, haemal postzygapophysis; for other abbreviations, see Figure 25. Cartilage, white (except in 5.1 mm ENL specimen in top row left, where entire stippling signifies cartilage); ossifying, stippled.

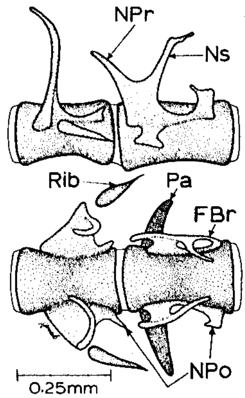


FIGURE 27.—First and second anteriormost vertebrae from a 12.8 mm ESL *Xiphias gladius*. Top, left lateral view; bottom, dorsal view. For abbreviations, see Figgures 25 and 26.

All specimens >6.0 mm ENL had the complete count of eight or nine haemal arches and spines.

Ossification of the vertebral column started at 4.4 mm ENL anteriorly at the bases of the neural arches. All specimens longer than 5.0 mm ENL had some anterior vertebral column ossification. The ossification was in a posterior direction as length increased until all centra including the urostyle were ossifying in some specimens between 6.1 mm ENL and 8.1 mm ESL (Fig. 29). In specimens >8.1 mm ESL all entra had some ossification.

The development of the neural and haemal pre- and postzygapophyses is shown in Figures 20-23 and 25-28. Neural prezygapophyses developed on all centra except the anteriormost centrum (Figs. 13, 27) and neural postzygapophyses developed on all centra except the urostyle (Figs. 21-23, 25-28). Haemal prezygapophyses developed on all haemal spines and shifted dorsad and anteriorly onto the centrum during ontogeny (Figs. 20-23, 28); the haemal prezygapophyses on preural centrum 2 and on the parhypural remained on the autogenous haemal spine and the autogenous parhypural (Figs. 21-23).

A neural foramen developed on each centrum except on the urostyle by first developing a neural postzygapophysis (Figs. 25-28). Then an anteriorly directed process developed on the anterodorsal side of the postzygapophysis, which joined the neural spine forming a neural foraminal bridge (Figs. 27, 28).

The neural prezygapophysis of the second anterior centrum developed an entirely different shape than all other prezygapophyses and could be taken for a neural spine on small juvenile or

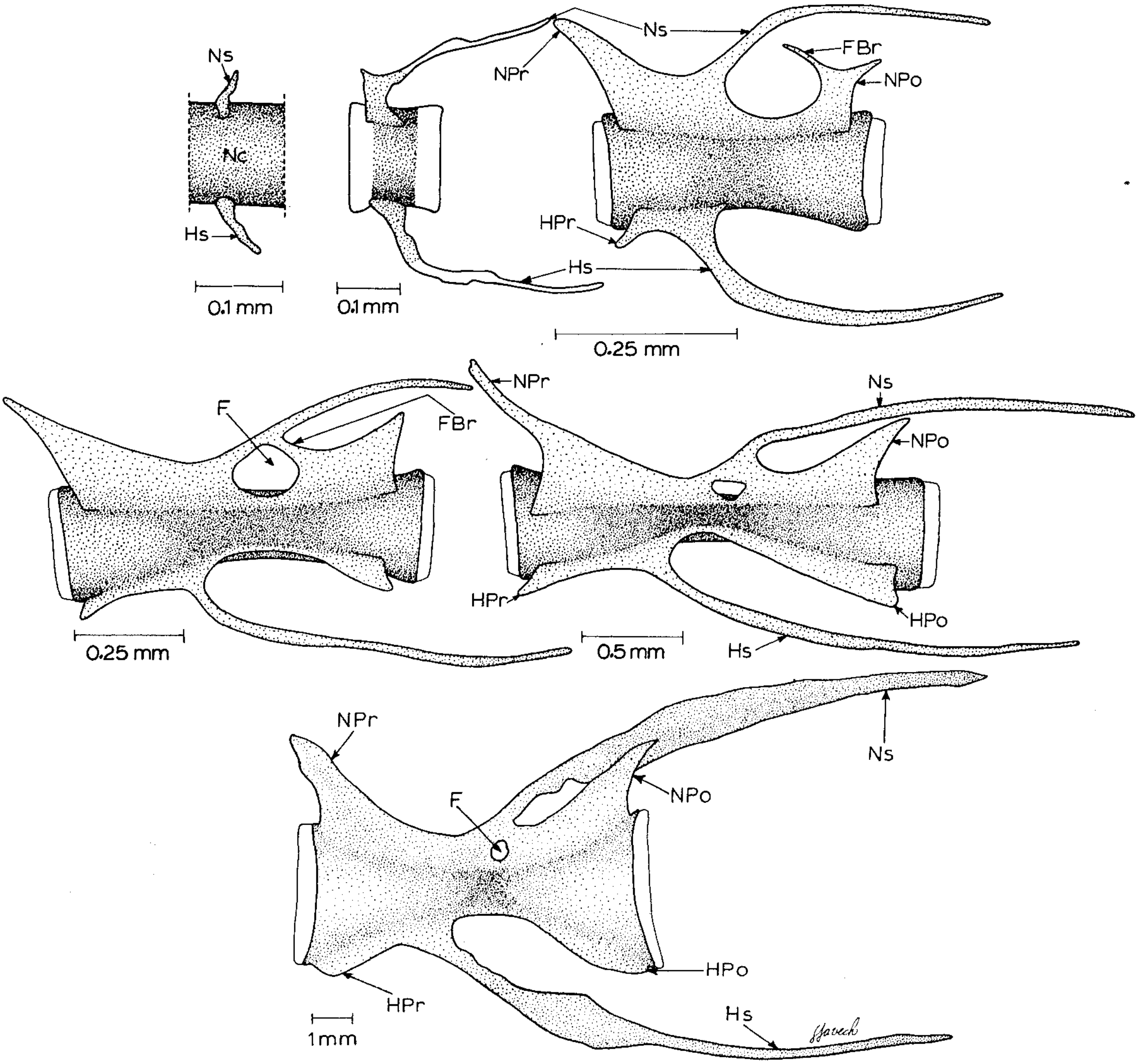


FIGURE 28.—Left lateral view of the 17th vertebra from *Xiphias gladius*, showing the ontogeny. Starting from top left the specimens in millimeters ENL or ESL are as in Figure 25. Hs, haemal spine; HPr, haemal prezygapophysis; for other abbreviations, see Figures 25 and 26. Cartilage, white (except in 5.1 mm ENL specimen in top row left, where entire stippling signifies cartilage); ossifying, stippled.

TABLE 14.—Development of the neural spines on the anterior to posterior numbered centra for 97 *Xiphias gladius* 3.7-7.0 mm ENL or ESL. N = number of specimens, $\overline{X}$ = mean.

Length, mm	Centra with neural spines																										
ENL or ESL	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	N	$\overline{X}$
3.6-4.0	1																									1	—
4.1-4.5	3	1	—	1	—	—	—	1																		6	2.8
4.6-5.0		1	2	8	5	2	—	1	—	—	1	—	—	—	—	1										21	5.3
5.1-5.5				1	1	1	1	1	—	—	2	—	—	1	1	—	—	—	—	—	1	—	6	5	5	26	18.7
5.6-6.0																				1	2	—	3	6	5	17	23.5
6.1-6.5																							3	3	11	17	24.5
6.6-7.0																									9	9	25.0

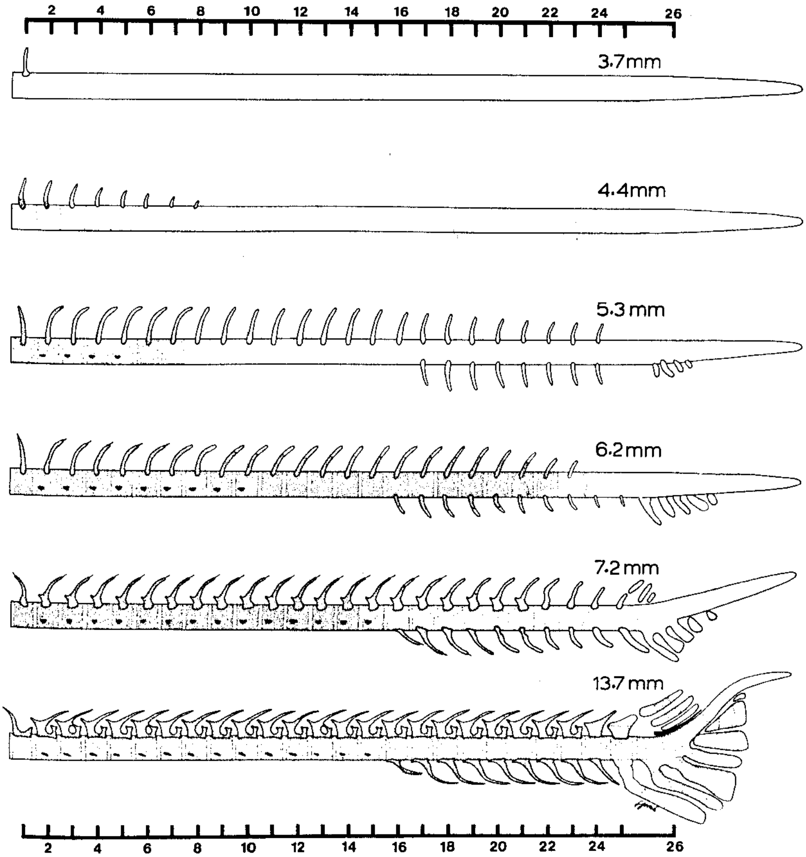


FIGURE 29.—Schematic presentation of the vertebral column development in *Xiphias gladius.* Ticks on scale denote centra number and are aligned with the middle of the centrum. Indicated millimeter measurements are ENL or ESL. Cartilage, white; ossifying, stippled.

TABLE 15.—Development of the haemal spines on the anterior to posterior numbered centra for 53 *Xiphias gladius* 5.0-6.5 mm ENL. N = number of specimens, $\overline{X}$ = mean.

Length, mm ENL or ESL	Centra with haemal spines 17	18	19	20	21	22	23	24	25	N	$\overline{X}$
5.0	1									1	17.0
5.1-5.5		1	1	—	1	1	4	3	8	19	23.4
5.6-6.0			1	—	2	1	2	1	9	16	23.6
6.1-6.5									17	17	25.0

larger specimens (Figs. 8, 13, 25, 27). This prezygapophysis is considerably longer than the neural spine except in large juveniles and adults (Fig. 25).

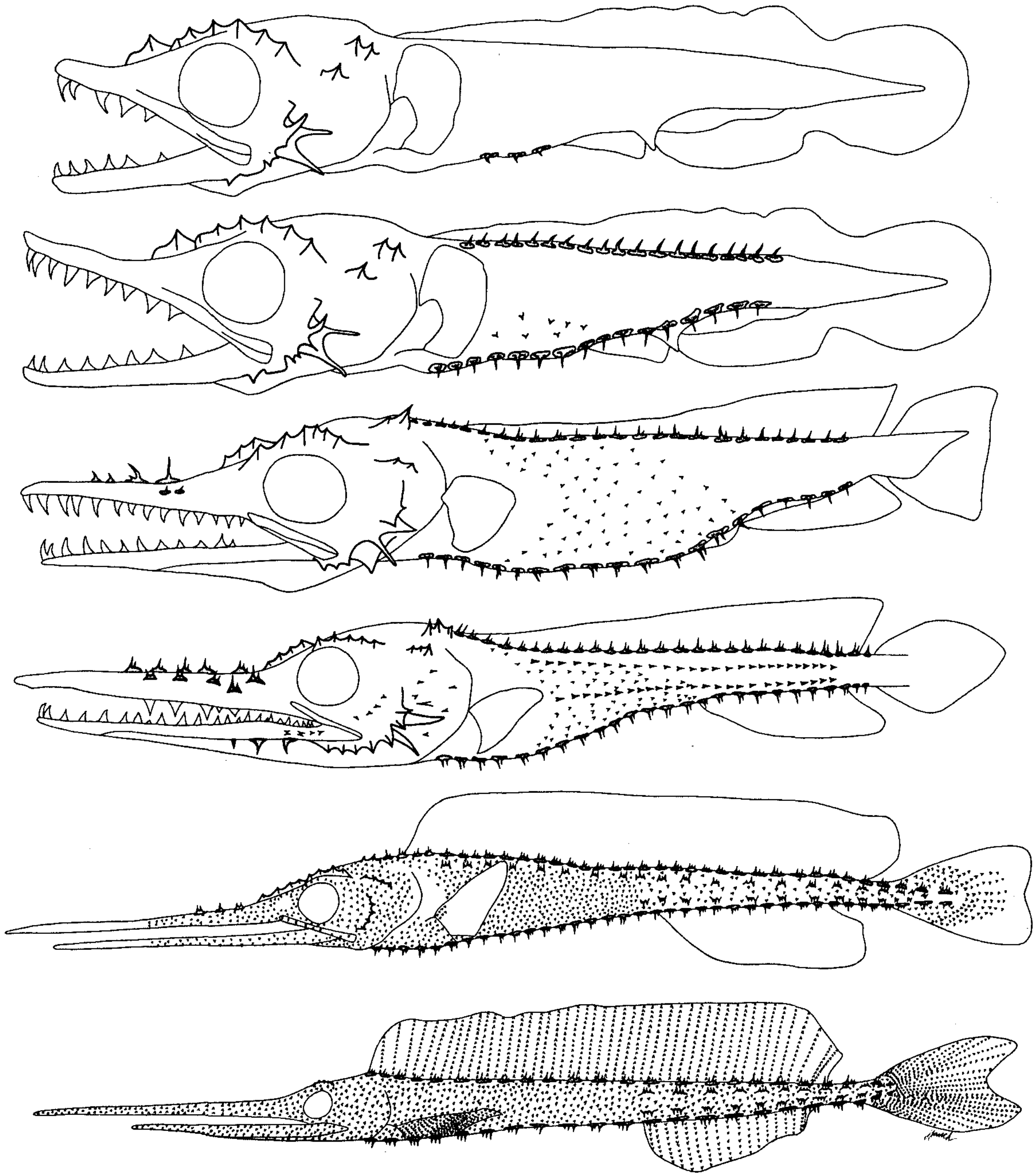
Ribs developed from a short piece of proximal cartilage. The cartilage later ossified and bone cells were added distally directly in the lengthening process of the rib during development. One pair of ribs was first seen on the anteriormost centrum at 8.0 mm ESL in some specimens. All *Xiphias* >12.2 mm ESL had at least one pair of ribs developing. Development was in a posterior direction on the first four centra and in an anterior direction on centra 15 and 14. When centra 1-3 had developing ribs, usually a pair also was present on centrum 15. Ribs developed over a wide size range. The smallest specimen with a full set of ribs on centra 1-4, 14, and 15 measured 25.1 mm ESL and all specimens larger than 55.1 mm ESL had the full rib complement. *Xiphias* usually developed ribs on centra 1-4, 14, and 15, but a few specimens also had ribs on centra 5, 6, 13, and 16.

BRANCHIOSTEGAL RAYS

Branchiostegal rays were first seen in a 4.2 mm ENL specimen and all *Xiphias* >4.2 mm ENL had some rays. The 4.2 mm ENL *Xiphias* had four rays on each side but a 4.5 mm ENL specimen had only two (Table 16). Branchiostegals were added from posterior to anterior direction. specimens with developing branchiostegals had either the same count on both sides or differed by one ray between sides. Adult counts of seven or eight rays were first observed at 5.0 mm ENL and all *Xiphias* >6.6 mm ENL had

TABLE 16.—Development of the branchiostegal rays on the left and right sides for 211 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). N = number of specimens, $\bar{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number branchiostegal rays, left												Number branchiostegal rays, right										
	0	1	2	3	4	5	6	7	8	$\bar{X}$	SD	N	0	1	2	3	4	5	6	7	8	$\bar{X}$	SD
3.6-4.5	1	—	1	—	3	1	1			3.6	2.12	7	1	—	1	1	2	1	1			3.4	2.12
4.6-5.5					7	8	11	19		5.9	1.34	45					8	6	13	16	2	6.0	1.34
5.6-6.5							2	24	6	7.1	0.57	32							3	21	8	7.1	0.57
6.6-668								71	56	7.4	0.45	127								78	49	7.4	0.45



adult counts (Table 16). Of 127 *Xiphias* (6.6 mm ENL-668 mm ESL), 59 (46.4%) had seven branchiostegals on both sides, 37 (29.2%) had eight on both sides, and 31 (24.4%) had seven rays on one side and eight on the other.

SQUAMATION

Larvae of *Xiphias* developed four rows of scales on each side with smaller "scatter" scales between the rows (Fig. 30). First to appear between 5.3 and 6.1 mm ENL were some ventral "row" scales on the stomach. These scales were added during growth anterior to the pectoral symphysis and posteriorly to the ventral hypurals. Dorsal row scales were first seen between 5.7 and 6.9 mm ENL, approximately between the 3d and 15th centrum. The addition of dorsal row scales during growth was in an anterior direction to the top of the head and in a posterior direction to the dorsal hypurals. The two lateral scale rows were first seen in some specimens between 6.5 mm ENL and 8.6 mm ESL, extending from the posterior border of the pectoral fin to about the 16th centrum. Scales were added anteriorly only to the dorsal lateral row to about the operculum and posteriorly to the urostyle. Scatter scales, between the dorsal, ventral, and lateral scale rows first developed between 6.2 and 7.1 mm ENL on the stomach just posterior to the pectoral fin and dorsad to the ventral scale row (Fig. 30). Scatter scales, which were smaller than row scales, spread from the stomach dorsad during growth until the left and right sides in an area from the 4th centrum to the 18th centrum were covered (Fig. 30). Further addition of scatter scales was then in an anterior and posterior direction covering the whole body, the sword, and the caudal fin rays at 61.5 mm ESL, but not the pectoral, dorsal, and anal fins. In our 187 mm ESL specimen the dorsal, anal, and pectoral fin rays were covered with scatter scales. In the literature, Arata (1954); Leim and Scott (1966); Nakamura et al. (1968), and Palko et al. (1981) stated that adult *Xiphias* lack scales.

FIGURE 30.—Larval and juvenile *Xiphias gladius*, depicting the ontogeny of squamation. The size of scales was exaggerated in proportion to the body. Starting from the top and going to the bottom the specimens' lengths in millimeters are: 5.3 ENL, 6.2 ENL, 7.6 ESL, 11.5 ESL, 35.4 ESL, 188 ESL.

Our largest 668 mm ESL specimen had scales (Fig. 31), seen through the dissecting microscope on a cleared and stained piece of skin. In this specimen the row scales could no longer be distinguished from the scatter scales.

Development of individual scales is similar for the row and scatter scales, except scatter scales start out smaller than row scales but increase in size to equal the row scales during development. Each scale starts as an oval-shaped structure with one posteriorly recurved spine. During development more posteriorly recurved spines are acquired in a row at the center of the scales and the scale margins become progressively crenated (Fig. 32). Finally, in specimens >200 mm ESL the marginal scale crenations become fewer and the recurved spines develop into blunt stubs (Fig. 32).

Individual row scales have approximately the same number of spines in a developing specimen, but this does not apply for the scatter scales. Our largest 668 mm ESL *Xiphias* had developed variable scales which had from one to seven blunt stubby spines; row scales were not distinguishable from scatter scales in this specimen (Figs. 31, 32). Arata's (1954) work on scale development agrees with our findings.

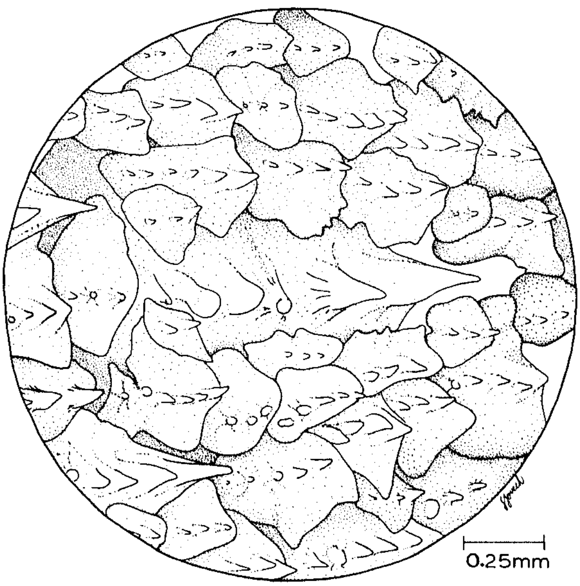


FIGURE 31.—Enlarged view of the skin from a 668 mm ESL *Xiphias gladius*, showing scales with two to six posteriorly recurved spines. White spaces between scales are skin. Anterior is to the left.

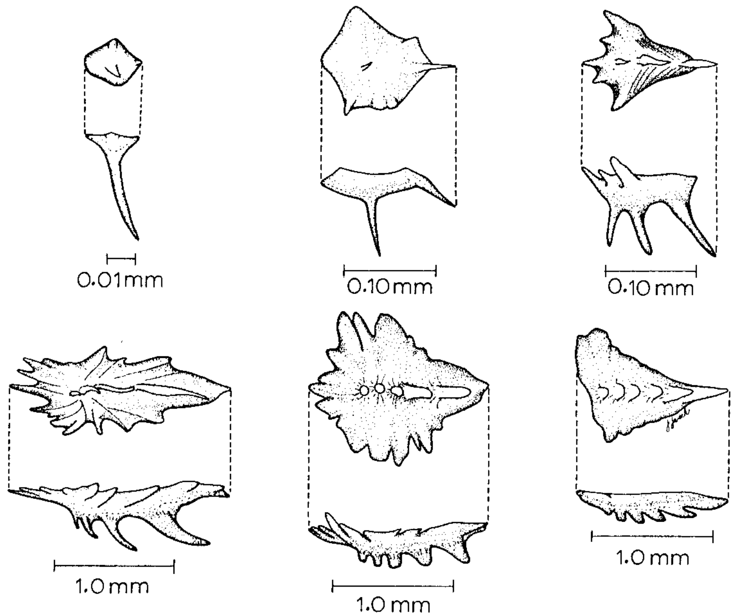


FIGURE 32.—Scales from *Xiphias gladius*, showing ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.4 ENL, 6.2 ENL, 25.1 ESL; bottom, 61.5 ESL, 225 ESL, 668 ESL. Each size in top and bottom rows has an external view (top) and a lateral view (bottom).

DISCUSSION

Xiphias gladius is a highly modified perciform fish which, in our opinion, should not be placed as the monotypic family Xiphiidae in the suborder Scrombroidei, as was done by Greenwood et al. (1966). We agree with Gosline (1968) and Fierstine (1974), who placed the monotypic family Xiphiidae under the separate suborder Xiphiioidei. However, Gregory and Conrad (1937) compared *Xiphias* bones with those of *Istiophorus* and concluded that xiphiids and istiophorids are separate but parallel families of common scombroid stock. G. David Johnson, who examined the branchial arches of *Xiphias*, istiophorids, and scombrids (unpubl. data), has evidence that *Xiphias* belongs with the scombroids. We will discuss the modifications and variations that we noted in *Xiphias* and compare these with other fish families.

The pectoral fin position in *Xiphias* larvae is lateral, but during growth to adults the fin moves ventrad to an almost pelvic position. *Xiphias* probably lost its pelvic fin during phylogeny. Remnants of a basipterygium were not found by us or other workers during development of the larvae (Yasuda et al. 1978).

Pectoral fin ray counts of the left and right sides were equal or differed by one ray in juvenile *Xiphias*. Similar results were obtained for *Archosargus* (Houde and Potthoff 1976), *Coryphaena* (Potthoff 1980), and *Scombrolabrax* (Potthoff et al. 1980). In tunas, larger differences in pectoral fin ray counts between sides were found (Potthoff 1974).

With the publication of Dingerkus and Uhler's (1977) cartilage staining technique, Fritzsche and Johnson (1980) reported the development of pectoral radials from a sheet of cartilage in *Morone*. Swinnerton (1905) reported the same for *Salmo salar* by using the "reconstruction in wax from serial sections" technique; he called the cartilaginous blade "fin-plate." We saw the same happening in *Xiphias* and labeled the sheet of cartilage "blade" (Bl) in Figure 3. It is likely that pectoral radials develop from a cartilaginous blade in all Perciformes, and perhaps all lower fishes. Starks (1930) reported a cartilaginous blade (radial plate) in adult *Dallia pectoralis* and Roberts (1981) in the salmoniform Sundasalangidae; we believe this to be an example of a neotenic structure.

The pectoral girdle in *Xiphias* is reduced as compared with a basic perciform pectoral girdle such as that found in *Coryphaena* (Potthoff 1980) and in at least some scombrids, e.g., *Sardini* (Collette and Chao 1975), *Acanthocybium* (Conrad 1938), and *Thunnus* (de Sylva 1955). In *Xiphias*, the supratemporal and intertemporal bones are absent and there is only one postcleithrum.

Adult *Xiphias* have two dorsal and two anal fins (Leim and Scott 1966; Ovchinnikov 1970), but larvae and juveniles have one continuous dorsal and anal fin (Nakamura et al. 1951; Yabe et al. 1959). During development the fin rays in the center of the fins stop growing and the rays become subcutaneous. The subcutaneous rays and their pterygiophores are present in the adults and were dissected in our largest 668 mm SL specimen. In three scombrid genera, *Scomber*, *Rastrelliger*, and *Auxis*, we find a first dorsal and second dorsal fin separation similar to that in adult *Xiphias*, except that in these scombrids the two fins are separate initially even though the first and second dorsal fin pterygiophores are continuous (Kramer 1960; Potthoff pers. obs. on *Auxis*). There is only one anal fin in these three scombrid genera, whereas adult *Xiphias* have two anal fins.

All dorsal rays in *Xiphias* are bifurcated at their bases (Figs. 14, 15) as in *Coryphaena* (Potthoff 1980). This probably is not the case in most perciforms where the spinous rays of the first dorsal fin have a closed base with a foramen and the distal radials are situated outside the bases of the first dorsal fin spinous rays (Kramer 1960; Potthoff 1974, 1975; Potthoff et al. 1980).

The anteriormost dorsal pterygiophores in *Xiphias* insert in the second interneural space (Figs. 11, 13), as in the gempylids and trichiurids (Potthoff et al. 1980), but not as in the serranids, sparids, apogonids, scombrolabracids, and scrombrids where the anteriormost pterygiophores insert in the third interneural space (Matsui 1967; Fraser 1972; Potthoff 1974, 1975; Houde and Potthoff 1976; Fritzsche and Johnson 1980; Potthoff et al. 1980), and not as in the coryphaenids in which they insert in the first space (Potthoff 1980). No predorsal bones were present in *Xiphias*. All scombrids and most scombroids also lack predorsal bones, however some gempylids, e.g., *Ruvettus* (Potthoff et al. 1980), have one predorsal. Most other perciformes have predorsals in the first and second interneural spaces.

The first dorsal pterygiophore in *Xiphias* is variable in development (Figs. 7, 8) and originates either from one or two pieces of cartilage. In scombrids (Potthoff 1974, 1975), a two-part development of the first dorsal pterygiophore was not evidenced, but in *Morone* it was (Fritzsche and Johnson 1980).

The last (posteriormost) pterygiophore of *Xiphias* has a serially associated double ray and a stay (Figs. 9, 10). In *Xiphias*, as probably in all Perciformes, the stay develops from the proximal radial cartilage. The stay is not posteriorly bifurcated as in most scombrids (Potthoff pers. obs.), nor does it ossify into two parts as in most gempylids and some trichiurids (Potthoff et al. 1980).

Xiphias lacks middle radials as does *Coryphaena* (Potthoff 1980), whereas many Perciformes probably have middle radials at least for some of the posteriormost dorsal and anal pterygiophores (Kramer 1960; Berry 1969; Potthoff 1974, 1975; Houde and Potthoff 1976; Potthoff et al. 1980; Fritzsche and Johnson 1980).

In *Xiphias* the caudal rays are supported by only two centra (urostyle and preural centrum 2) (Figs. 17, 21, 22). This is unusual, because in most perciforms three centra support the caudal rays (Berry 1969; Houde and Potthoff 1976; Potthoff 1980; Potthoff et al. 1980; Fritzsche and Johnson 1980), and in most scombrids four or five centra support the caudal rays (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978), except in *Scomber* and *Rastrelliger* where three centra support caudal rays (Potthoff pers. obs.).

Xiphias lacks a second uroneural in the caudal complex which is present in the basic perciform caudal such as in *Archosargus* (Houde and Potthoff 1976), *Elagatis* (Berry 1969), *Scombrolabrax* (Potthoff et al. 1980), *Morone* (Fritzsche and Johnson 1980), and *Coryphaena* (Potthoff 1980), but is absent in the scombrids (Potthoff 1975). The single uroneural of *Xiphias* does not fuse to the urostyle in adults as in Thunnini and Sardini (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978), but in several specimens anomalous shapes of the uroneural were observed (Fig. 22).

We believe that *Xiphias* has lost preural centrum 3, because a centrum having an autogenous haemal spine and a neural spine with articular cartilage is lacking (Figs. 20-23). However, 1 specimen out of 164 examined with the unusual vertebral count of 16+11=27 (typical counts 15+11 or 16+10=26) had two autogenous haemal spines on preural centra 2 and 3. To our knowledge, a perciform caudal with only one autogenous haemal spine as in *Xiphias* has not been reported previously. We cannot totally rely on Monod (1968) or any other osteological descriptive work dealing only with adult fish because Potthoff (1975) showed that some autogenous hypural parts fuse during development and cannot be recognized in adults.

There is considerable fusion of caudal complex bones in *Xiphias*. Hypurals 1-4 and the urostyle fuse to one posteriorly notched hypural plate during development (Fig. 23); the three epurals, the uroneural pair, hypural 5, and the parhypural remain autogenous, whereas in Thunnini and Sardini only one epural remains autogenous and the paired uroneural fuses to the urostyle (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978). In *Xiphias*, hypurals 1-4 develop initially from distinctly separate pieces of cartilage and fusion of the hypurals into the notched hypural plate occurs. In Scombridae a similar yet different development takes place, because in Thunnini hypurals 1 and 2 originate from one distinctly larger piece of cartilage, whereas in *Scomber* (*Pneumatophorus*), hypurals 1 and 2 originate from separate pieces of cartilage as in *Xiphias* (Kramer 1960).

The caudal rays in adult scombrids, except Scombrini, cover the whole hypural plate (Collette and Chao 1975; Collette and Russo 1978), whereas in *Xiphias* a smaller area is covered by the rays (Figs. 17, 22, 23). When the rays are disarticulated from the hypural plate in adult *Xiphias*, long vertical depressions caused by the rays can be observed on the hypural plate (Fig. 23).

Xiphias has a greater number of precaudal than caudal vertebrae (Fig. 6) (Leim and Scott 1966; Ovchinnikov 1970). The same tencency was observed in the gempylids (Matsubara and Iwai 1958; Potthoff et al. 1980) and the opposite tendency in the scombrids (Conrad 1938; de Sylva 1955; Mago Leccia 1958; Kramer 1960; Gibbs and Collette 1967; Matsui 1967; Potthoff and Richards 1970; Collette and Chao 1975). Generally, the tendency in the perciform fishes is to have a higher caudal vertebral count; the most typical count being 10+14=24 vertebrae (Johnson 1981).

The neural and haemal arches in *Xiphias* first develop distally opened (split) (Fig. 27). During development the neural and haemal arches fuse forming spines. Fusion of the neural and haemal spines proceeds from posterior in an anterior direction (Table 13). In other perciforms studied by Potthoff, split arches were sometimes observed on small larvae on the anteriormost first and second centra only, but these two arches fused to spines during development. Adult *Xiphias* retain three to six anteriormost split neural arches (Bruce B. Collette footnote 3).

Rib development and position is unique in *Xiphias*. Commonly, perciforms have pairs of dorsal (epipleural) ribs on the precaudal vertebrae starting on the first centrum and pleural ribs starting on the third centrum (Houde and Potthoff 1976; Potthoff et al. 1980). These ribs develop from anterior in a posterior direction. *Xiphias*, however, has lost many of its ribs. Generally, there are only one pair of ribs on each of the first four centra, which develop from anterior in a posterior direction and one pair on the last two precaudal vertebrae which develop from posterior in an anterior direction. We do not know if the ribs in *Xiphias* were originally epipleural, pleural, or a combination of epipleural and pleural. We were able to determine, however, the cartilage origin of ribs in *Xiphias*. Tibbo et al. (1961) stated that ribs in adult *Xiphias* are short and poorly developed, but no details on rib position were given.

An account of rib development in lower and higher fishes is given by Emelianov (1935). He found that some bony fish develop ribs from cartilage, in others rib development from cartilage is bypassed and ribs develop directly from bone cells, and still in others, parts of the ribs develop from cartilage and other parts of the same rib develop directly from bone. In *Xiphias* the proximal portions of each rib originate from cartilage, the distal portions develop directly as bone.

The branchiostegal ray count in *Xiphias* may vary by one ray from specimen to specimen or it may vary between left and right sides in a specimen. Usually, branchiostegal ray counts are conservative and characterize fish families and sometimes genera (Kishinouye 1923; McAllister 1968; Fraser 1972; Ahlstrom et al. 1976; Kendall 1979; Matsuura 1979), however variability has been reported in some groups such as Carangidae (McAllister 1968).

We cannot make firm conclusions about the phylogenetic status of *Xiphias*. From our study we conclude that *Xiphias* is a perciform fish that differs from other perciforms to warrant the separate suborder Xiphiioidei. We were unable to determine relationship with the scombroids (gempylids, scombrids). A comparison with istiophorids remains to be done, and we believe we furnished sufficient material to facilitate such a comparison.

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