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Article IV.—THE WHALE SHARK, *RHINEODON TYPUS*. DESCRIPTION OF THE SKELETAL PARTS AND CLASSIFICATION BASED ON THE MARATHON SPECIMEN CAPTURED IN 1923

By E. Grace White[1]

Plates IV to XII; Figures 1 to 12

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INTRODUCTION

Rhineodon typus (*Rhincodon*, *Rhinodon typicus*), the only known species of whale shark, has had considerable attention as a rarity, but the scientific descriptions have been based on scanty material. With the exception of the original accounts by Dr. Andrew Smith (1829, 1849), no description has been made of the internal organs, and Smith made no mention of the skeleton, although he gave an excellent description of the digestive tract.

Rhineodon is a shark of the warm waters, and has been described from the more tropical waters of the Atlantic, the Pacific, and from the Indian Ocean, which is its main habitat. A complete survey of the literature will be found in Gudger's 'Natural History of the Whale Shark' (1915) and in his 'Further Notes' (1918).

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Because of its immense size, it has been handled with difficulty, and those who have had access to specimens have not always been able to land them, a fact which probably accounts for the lack of scientific data. It has been classified on the basis of the descriptions, and so has been assigned on external characters only, and to such different positions that it is the purpose of the present paper to determine the correct affiliations of the whale shark from the skeletal parts preserved from the specimen captured near Marathon, Florida, in 1923.

The capture and handling of this specimen has been described in a joint paper by Gudger and Mowbray (1930). Owing to the unfavorable weather conditions, the huge size of the fish, and other contributing circumstances, the specimen was too far gone from putrefaction, and too torn by tiger sharks for the skin to be preserved as had been hoped, and only as much of the skeleton could be preserved as the amount of formaldehyde immediately available in Key West would accommodate. The material at hand is, therefore, lacking in many important points, notably the forepart of the cranium and the pectoral fins. It is sufficient, however, to determine the relationships of the genus, since the jaws, the vertebræ, and the myxopterygia are in good condition.

This work has been undertaken at the suggestion of Dr. W. K. Gregory, Curator of Ichthyology at The American Museum of Natural History where the specimen has been preserved, and the Museum has placed the material at my disposal. Through the courtesy of Dr. E. W. Gudger, bibliographer and associate in Ichthyology, the description, measurements, and all necessary information concerning the capture of the specimen have been furnished, together with the photograph (Pl. V, fig. 2) showing the dental plates in position.

I wish to express my appreciation at this time to Dr. Gregory, Dr. Gudger, Dr. J. T. Nichols, to the photographic department of the Museum, and to other members of the museum staff for the many courtesies extended to me while engaged in this work. I wish also to thank Mr. B. A. Bean of the Smithsonian Institution in Washington for the loan of the dried dental plate of the Ormond specimen of whale shark which is shown photographed in plate X of this paper.

DESCRIPTION OF THE SKELETAL PARTS

The material includes the following parts:

1. A section of the occipital region of the cranium about nine inches thick. This was cut through the auditory capsules, and shows sections of the semicircular canals. On the right side the groove for the articulation of the hyomandibular is intact, and a series of anterior vertebræ are attached to the occiput.

2. In addition to the anterior series of vertebræ, there are vertebræ from various regions of the trunk. There are no caudal vertebræ.
3. The mandibular arch complete.
4. The hyoid arch with the exception of the basihyal.
5. The skeleton of the two claspers (myxopterygia), with all terminal appendages attached.
6. A piece of flesh twelve inches thick with the skin attached.
7. A small portion of the tooth-band with the teeth in position, and several loose teeth.

The external appearance of the whale shark is shown in plate IV which is Smith's original figure of the shark. In plate V, fig. 2, is a photograph of the mouth of the Marathon specimen taken at the dock before the tiger sharks had attacked it. The dental plates are in position.

TABLE 1.—Measurements of the Marathon Specimen of *Rhineodon* Taken at the Dock by L. L. Mowbray.[1]

	Ft.	In.
Length Over All	31	5
Girth of Body Over First Gill-slit	17	6
Girth of Body Immediately Behind Pectorals	23	..
Distance from Mouth to Base of First Dorsal	14	6
Distance from Mouth to Base of Second Dorsal	21	5
Distance from Mouth to Base of Caudal	25	9
Distance Along Upper Lobe of Caudal	7	..
Distance Along Lower Lobe of Caudal	5	7
Vertical Spread of Caudal	12	..
Length of Body Cavity	10	..
Width of Mouth-gape from Corner to Corner	3	8
Width of Head from Eye to Eye	5	3

These measurements give an idea of the immense proportions of the fish.

OCCIPITAL REGION OF CRANIUM

TABLE 2.—Measurements of Occipital Region of the Skull Cut Nine Inches Thick.

	Ft.	In.
Height, Posterior	..	5½
Height of Anterior Cut Surface	..	9¼
Width of Anterior Cut Surface, Dorsal	1	9
Width of Anterior Cut Surface, Ventral	1	7½
Width of Anterior Cut Surface Across Auditory Capsules	2	4
Height of Foramen Magnum	..	5½
Width of Foramen Magnum	..	3
Height of Medulla Cavity on Anterior Cut Surface	..	6¾
Width of Medulla Opening	..	8

[1]Courtesy, Dr. E. W. Gudger.

The nine-inch piece of the occipital region of the cranium shows this to be the usual undivided mass of cartilage which characterizes the elasmobranchs, but gives no idea of the length or height of the cranium.

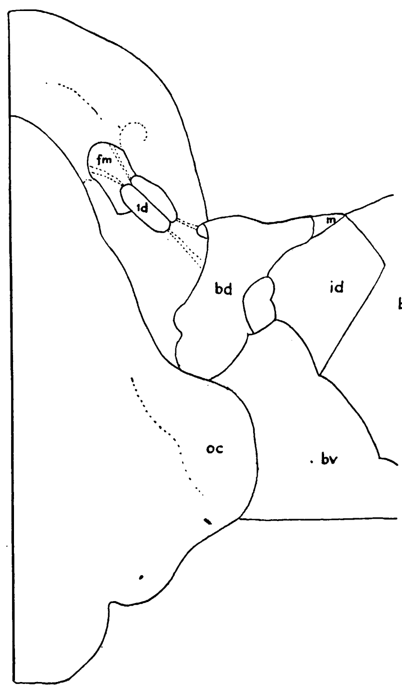

Fig. 1. First vertebra attached to cranium. ×¼.

fm, foramen magnum; *oc*, occipital condyle; *bd*, basidorsal cartilage; *id*, interdorsal cartilage; *bv*, basiventral cartilage; *m*, median cartilage.

In the midline of the posterior surface is the opening of the foramen magnum (5½×3 inches) which inclines slightly forward dorsally. Immediately below its ventral margin is a shallow excavation into which the apex of the first vertebra fits closely.

On either side of this excavation is a posteriorly projected occipital condyle (Fig. 1, oc) which articulates with one of the ventral lateral processes of the first vertebra.

Just above the condyles, in depressions lateral to the foramen magnum, are the openings for the branches of the vagus nerve. Lateral to these depressions the cranium widens to inclose the auditory capsules. Sections of the semicircular canals can be seen on the cut surface.

The articular surface for the hyomandibular includes an extension of the lateral boundary of the cranium to form an articular process beneath which are two grooves, the inner groove deeper and wider than

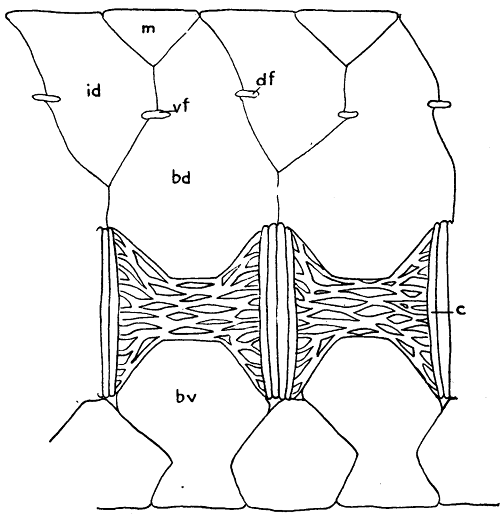

Fig. 2. Trunk vertebræ, side view. ×¼.

c, centrum; *df*, dorsal root nerve foramen; *vf*, ventral root nerve foramen; *iv*, interventral cartilage. Other labels as in Fig. 1.

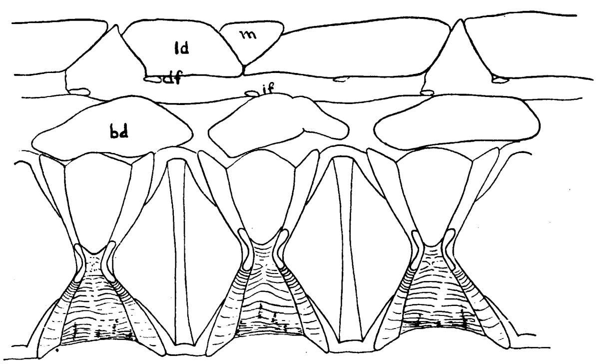

Fig. 3. Centra of anterior vertebræ, long. sec. ×¼.

the outer. Into these grooves fit the articular processes of the hyomandibular (Fig. 7).

The extreme forward and lateral positions of the eyes (Pls. IV–V) indicate that the postorbital region of the cranium is elongate and

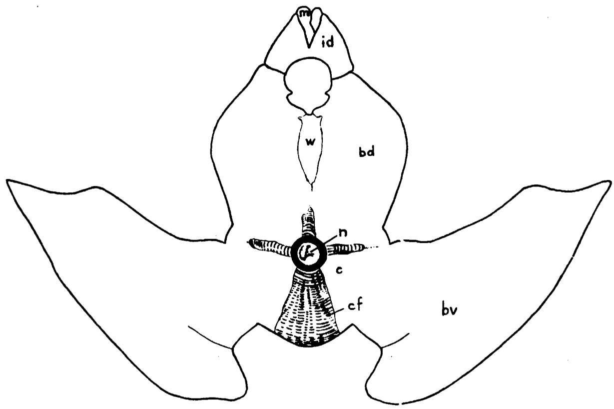

Fig. 4. Anterior vertebra cross-section through center of centrum. ×¼.

c, centrum; *n*, notochord; *w*, white fibrous tissue; *cf*, calcified area.

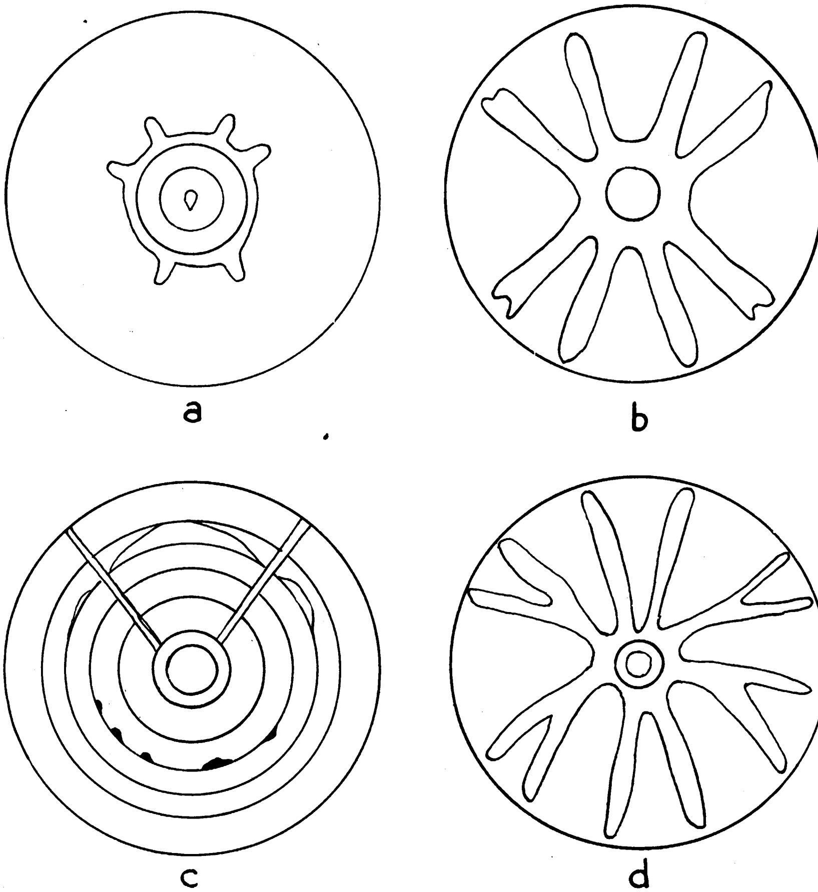

Fig. 5. Representative vertebræ from the suborders of the order Antacea. All after Hasse.

a, Hexanchea (*Heptanchus*); *b*, Heterodontea (*Cestracion*); *c*, Squalea (*Squatina*); *d*, Galea (*Ginglymostoma*).

the preorbital region greatly abbreviated. The absence of this portion of the cranium makes it impossible to determine the condition of the rostral cartilages, although it is probable that the region is greatly specialized, and that the cartilages are either atrophied or, at least, non-convergent.

VERTEBRÆ

The anterior vertebræ are distinctly marked off from the cranium (Fig. 1). The apex of the cone of the first vertebral centrum fits closely

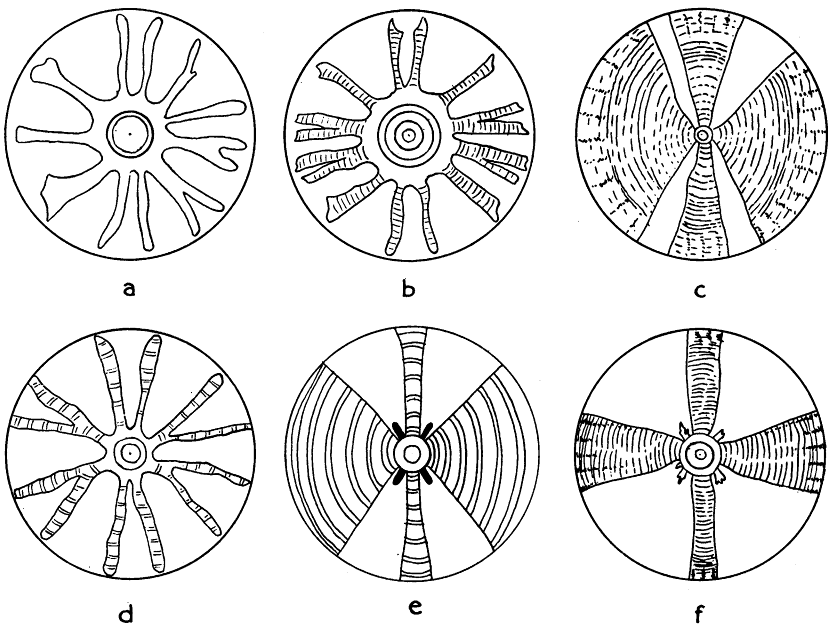

Fig. 6. Representative vertebræ from the superfamilies of the suborder Galea.

a, Carcharoidea (*Odontaspis*); *b*, Isuroidea (*Lamna*); *c*, Isuroidea (*Cetorhinus*); *d*, Catuloidea (*Ginglymostoma*); *e*, Carcharinoidea (*Galeocerdo*); *f*, *Rhineodon*.

a–e, after Hasse; *f*, original.

into an excavation in the basis cranii. Large lateral grooves in the basiventrals (bv) fit over the occipital condyles (oc), and two lateral processes extend forward to articulate with a horseshoe-shaped cartilage (bd) which is formed by the fusion of two basidorsals. From its apex, ligaments stretch forward and upward to the dorsal margin of the foramen magnum (fm). In these ligaments are suspended two small interdorsal cartilages (id).

The second vertebra is 7 inches high and 10 inches wide across the lateral wings of the ventral cartilages. There is an increase of one inch in height, and 2 inches in width in the first six vertebræ. The trunk vertebræ are 9¾ inches high and 8¼ wide across the ventrals.

At no place do the ventral cartilages meet in the midline, although they come very close together in the trunk series. Interventrals alternate with basiventrals, the latter being wider at the base and vertebral in position (Fig. 2).

The interdorsals are incompletely united above, and the intervening spaces are filled by a series of median cartilages (m) which complete the neural arch dorsally. The basidorsals are vertebral, and the interdorsals intervertebral in position (Fig. 2).

The centra are a series of double cones, their apices facing each other (Fig. 2). The inner layer of the centrum, immediately surrounding the notochord, is a white fibrous tissue laid down in concentric layers which grow narrower and narrower toward the apex of the cone, thus constricting the notochord in all regions (Pl. VI).

The centra are asterospondylous (Fig. 4 and Pl. VII). The outer cartilaginous layer is traversed by calcified areas which radiate outward to the edge of the cone (Fig. 4, cf). The lateral areas are slightly wider than the dorsal and ventral ones. Between the four main calcified areas are four very short irregular calcifications (Pl. VII, i) which extend only a few millimeters from the apex of the cone. These are undoubtedly a specialization since *Rhineodon* is a highly specialized type. They resemble somewhat the irregularity of the calcifications of many of the Isuroidea, but are entirely different from the rod-like calcifications intercalated between the calcified areas of the Carcharinoidea. Figures 5 and 6 will make this point clear.

The calcifications extend throughout the centrum, a point in which it agrees with all the Galea (Fig. 5). The variations within the group (Fig. 6) are so great that it is impossible to place the centrum of *Rhineodon* definitely in a superfamily from this characteristic. It might equally well agree with the Carcharinoidea (Fig. 6, e), and little importance can be attached to its resemblance to *Cetorhinus*, striking as that is (Fig. 6, c), since these two forms are both highly specialized and have several specializations in common.

Visceral Arches

Table 3.—Measurements of the Visceral Arches.

	Ft.	In.
Palatoquadrate Cartilage		
Length	2	9
Width at Proximal End	..	1¼
Width at Distal End	..	¾
Height at Proximal End	..	1¾
Height at Distal End	..	1
Width Over Palatobasal Process	..	3½
Height Over Palatobasal Process	..	5
Circumference, Proximal End	..	6½
Circumference, Distal End	..	3⅝
Circumference Over Palatobasal Process	..	11¾
Arch of the Upper Jaw When Mounted	5	6
Distance Between Proximal Articulations	5	7
Distance Between Palatobasal Processes	4	2
Distance Between Forward Curves	3	1½
Terminal Margin of Jaws	3	4
Meckelian Cartilage		
Length Along Margin	2	10
Width Upper and Lower Margins	..	¼
Width at Center	..	2½
Height at Proximal Curve	..	8¾
Height at Widest Portion	..	9¼
Height Distal End, Dorsal Surface	..	2¾
Height Distal End, Ventral Surface	..	1
Circumference at Widest Portion	1	6½
Arch of Lower Jaw When Mounted	5	8
Distance Between Jaws at Proximal Articulations	5	5
Distance Between Jaws at Widest Portion of Cartilage	3	3
Terminal Margin of Jaws	3	4
Hyomandibular		
Length, Anterior	1	1½
Length, Posterior	1	5
Circumference at Center	1	7½
Circumference at Distal End	1	11
Thickness of Anterior Face, Proximal	..	4
Thickness of Anterior Face, Distal	..	3
Thickness of Posterior Face, Proximal	..	3
Thickness of Posterior Face, Distal	..	5
Width, Proximal	..	7½
Width, Central	..	7
Width, Distal	..	5
Ceratohyal		
Length, Anterior	1	11½
Length, Posterior	1	10½
Circumference at Proximal End Over Articular Process	1	8

	Ft.	In.
Circumference at Center	1	4½
Circumference at Distal End	1	4¾
Thickness of Anterior Face, Proximal	..	1½
Thickness of Anterior Face, Center	..	½
Thickness of Anterior Face, Distal	..	3¼
Thickness of Posterior Face, Proximal	..	4
Thickness of Posterior Face, Central	..	2½
Thickness of Posterior Face, Distal	..	5
Width Over Proximal Articular Process	..	8½
Width Over Proximal Curve	..	5
Width Over Center	..	7
Width at Distal End, Outside	..	6
Width at Distal End, Inside	..	2½

The photographs (Pls. VIII–IX) show the mandibular arch reconstructed and mounted in position to show the arch of the jaws. Although the pterygoquadrates have been held together with splints, and the ends of the meckelian cartilages are missing on the left and spliced onto the right cartilage, the pictures give a good idea of the mouth of *Rhineodon*.

Table 3 shows the size of the arch and the distance between the cartilages when mounted. All descriptions, photographs and drawings of *Rhineodon* show a straight, almost terminal mouth (Plates IV–V) with the very small eyes close to its lateral margins. Mowbray found the mouth-gape of the Marathon specimen to be only 3 ft. 8 inches (Table 1) while the distance around the arches of the mounted specimens is 5 ft. 6–7 inches. The terminal line, however, formed by the centrally curved distal portions of the cartilages measures 3 ft. 4 inches. It is obvious, therefore, that the mouth-gape includes only this portion of the arches, the remaining portions being thickly covered with flesh. The flesh at the angles of the gape is loose since it must be greatly distended when the mouth is opened (Pl. V).

Pterygoquadrate Cartilages

The pterygoquadrates are slender and atrophied. Table 3 shows the small size compared to the size of the meckelian cartilages. The proximal portion anterior to the palatobasal process is thick and twisted. The articulation for the meckelian cartilage is double; a process extending forward which fits into a groove on the mandible, and a deep furrow which receives the meckelian process.

The palatobasal process is greatly reduced, and if any attachment to the cranium exists, it must be a very loose one. It appears to have

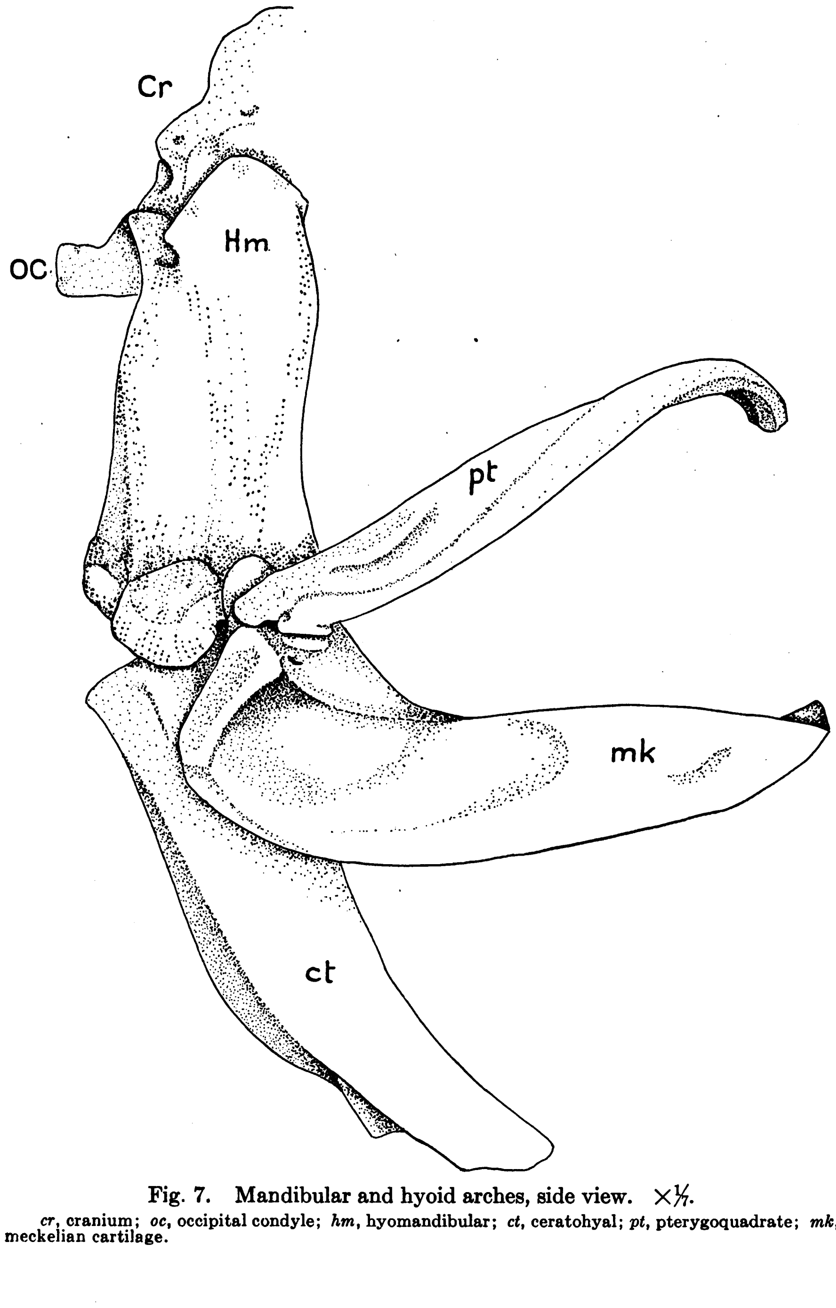

Fig. 7. Mandibular and hyoid arches, side view. ×1/7.

cr, cranium; *oc*, occipital condyle; *hm*, hyomandibular; *ct*, ceratohyal; *pt*, pterygoquadrate; *mk*, meckelian cartilage.

had a ligament attached, so that a loose articulation is probable. Just beyond the process, the cartilage narrows and turns abruptly in toward the midline, so that the two halves of the arch make a decidedly straight terminal line (Pls. VIII–IX).

Meckelian Cartilages

The meckelian cartilage is very wide but extremely thin, the edges being less than one inch thick. At the proximal end is a groove which receives the pterygoquadrate process, and a small knob-like process in a depression which fits into the groove on the pterygoquadrate, thus making a double articulation.

A large, rounded knob extends backward and inward to receive the articulation with the hyoid arch, and a flat, slightly depressed surface faces outward.

The cartilage dips in abruptly and curves forward, rising to form a slight elevation as it narrows and curves inward to meet the corresponding cartilage in a straight terminal line opposite the margins of the upper jaws (Pls. VIII–IX).

Hyomandibulars

The hyomandibular is a massive cartilage. Proximally it is deeply grooved and bears two large articular facets which fit into the grooves on the ventral surface of the cranium.

Distally a large knob with two glenoid surfaces indicates the articulation with the ceratohyal, and doubtless receives ligaments from the meckelian cartilage also. On its outer surface a long, thin process curves out toward the meckelian cartilage and articulates with the process extending in from that cartilage (Fig. 8, a–b).

At the proximal end a small cartilage embedded in a ligament is attached to the outer articular surface. This ligament is attached to the cranium.

Ceratohyals

The ceratohyal is also a massive cartilage but is longer and thinner than the hyomandibular. Proximally it is curved and bears an extensive articular surface with a long groove and a process which articulate with the hyomandibular. A projection on the outer surface just distal to the groove apparently receives the ligament which attaches it to the mandible.

The posterior surface is flat and narrows gradually toward the distal end. On it are the muscular attachments for the rays. Six of these

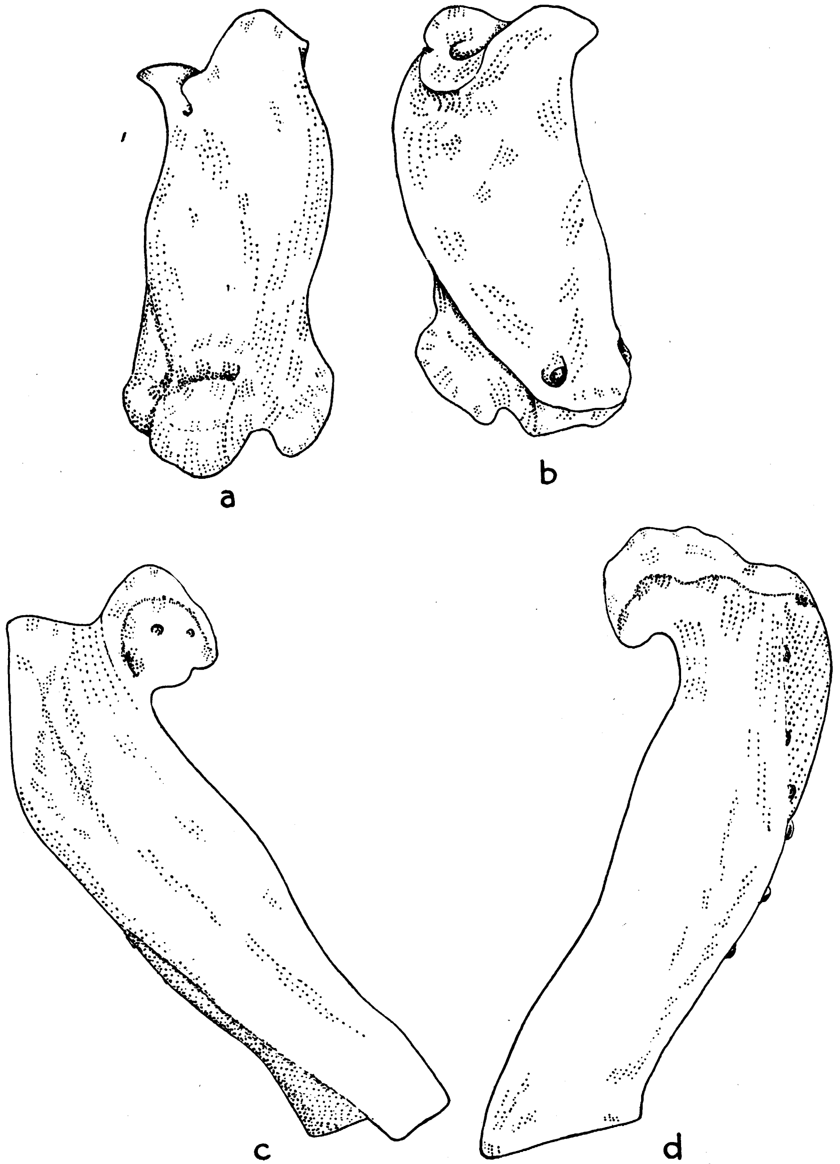

Fig. 8. Right hyomandibular and right ceratohyal. ×⅑.

a, hyomandibular, outside view; *b*, hyomandibular, inside view; *c*, ceratohyal, outside view; *d*, ceratohyal, inside view.

attachments remain. Two small cartilages embedded in cartilages are attached to the proximal end. Doubtless these ligaments are attached to the hyomandibular. (Fig. 8, c–d.)

Dental Bands

The dental bands of the Marathon specimen are seen in position on the jaws in plate V, figure 2 which is a photograph taken when the shark was first brought to Long Key. They are very narrow, less than two inches in width, and can be seen to curve to the arch of the jaws.

Since it was impossible to save the dental bands of the Marathon specimen, owing to the depredations of the tiger sharks while the specimen was being towed to the railroad dock, Mr. B. A. Bean of the Smithsonian Institution has very kindly loaned me the tooth-band of the Ormond specimen described by him in 1905. This band has been photographed at the museum and is reproduced in plate X. Figure 1 is the entire band and figure 2 a detail of the band reproduced natural size.

Comparison with plate XI, figure 1, which shows the teeth of the Marathon specimen natural size, will show the great difference in size between the two specimens. The Ormond specimen was an 18-foot shark and the cusps of its teeth are 1.5 mm. in length. The Marathon specimen was a 31-foot shark and the cusps of its teeth are 4.5 mm. long. While the shark was but twice the size of the Ormond specimen, its teeth are three times the size, doubtless due to the immature condition of the smaller shark.

The dental band consists of a thin layer of tissue 16 inches long and 1 inch wide. The teeth are arranged on this band in 292 vertical rows, in which the number of teeth vary from 10–13, except where the band narrows at either end when the number of teeth is reduced to 6–8 in a row. This makes approximately 3000 teeth on the band.

The teeth are embedded in the tissue so that only the cusp is free. This is sharply recurved backward so that all cusps point directly into the mouth of the shark. At the center of the band, which is at the junction of the two cartilages, the rows are fairly straight for about ¼ inch on each side, after which they begin to slant diagonally outward. Midway between the center and the two ends on each side the band widens slightly; the teeth increase in size and the rows in length. As they approach the ends, the angles of the rows grow sharper, curving in to the angle of the jaw; the teeth become smaller and the rows narrower and more crowded. The width of the rows at the center is ⅝ of an inch, at the widest portion ⅞, and at the ends only ⅜ of an inch.

In life the teeth are covered over by a very thin layer of tissue which has been removed from the dried band. The band is slightly shrunken from drying.

Comparison of the photograph in plate X with the photograph on plate XI, shows the bands of the two sharks to have been similar in form and arrangement of teeth.

TABLE 4.—Measurements of Teeth and Denticles in Millimeters.

DERMAL DENTICLES	
Height	0.75
Width	0.5
TEETH	
Height of Base	4.5
Width of Base	2.5
Length of Cusp	4.5

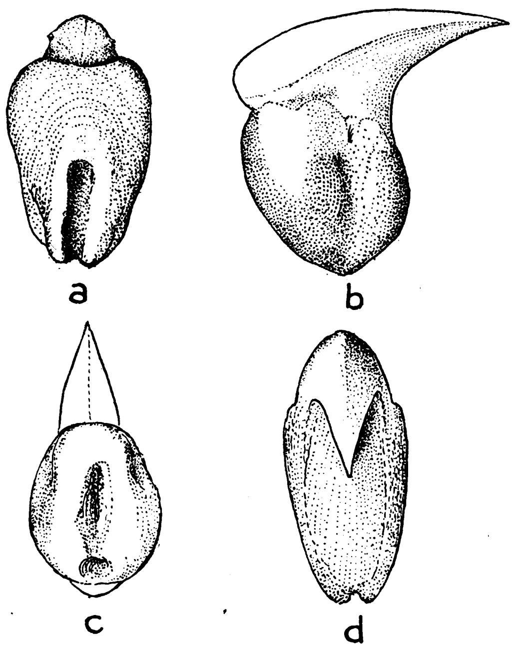

Fig. 9. Teeth. ×8.
a, view from rear; *b*, view from side; *c*, view from base; *d*, view from front.
Drawing by L. Nash.

Teeth

The loose teeth have been drawn in all positions in figure 9.[1] These are enlarged to show greater detail than the photographs. The teeth are

[1]Courtesy, Dr. E. W. Gudger.

seen to have a rounded base, deeply grooved in the center. From either side of the base rise two lateral prominences which lie at the base of the cusp, one on each side. They are very slight, but are doubtless the lateral denticles, or cusps, described for some species of *Isurus*,[1] and for *Odontaspis*. They indicate either a rudimentary or vestigial condition of a three-cusped tooth. The groove in the base is, also, probably an indication of a two-rooted base.

The cusp is conical with a very sharp point. It is very similar to the cusp described for the teeth of *Cetorhinus*.[2]

We could have no more complete picture of the teeth of *Rhineodon*.

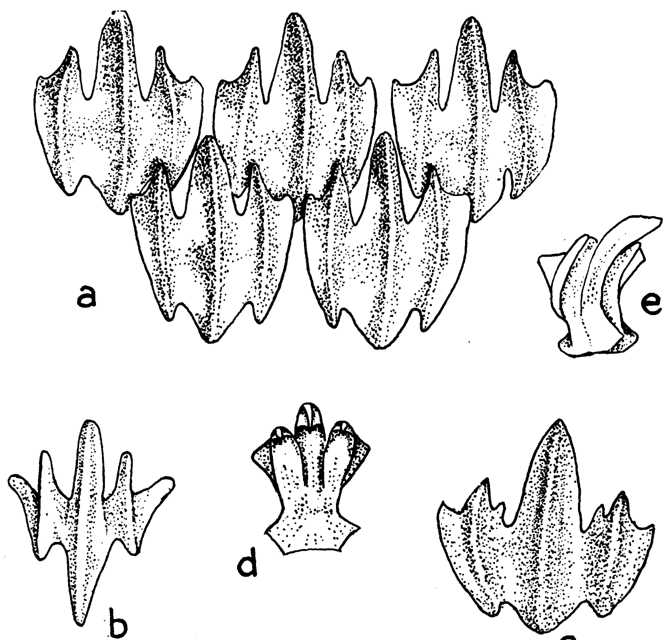

Fig. 10. Denticles. ×40.
a, group of denticles; *b–c*, types of denticles; *d*, face view; *e*, side view.

Dermal Denticles

The dermal denticles shown in figure 10 are from a piece of shagreen attached to a large muscular mass taken from the specimen. The denticles are minute, less than a millimeter in width (Table 4). The pedicel is relatively high, and the basal plate three-lobed.

[1]Jordan and Everman, 1896; Garman, 1913.
[2]Garman, 1913, p. 39.

The denticles vary slightly in shape and width (Fig. 10, a, b, c). They are arranged in diagonal rows and are slightly overlapping. In some parts the rows are closer together than in others.

The denticles are three-keeled but the apical margin is five-lobed. The median keel is thicker through so that the lateral keels appear to be

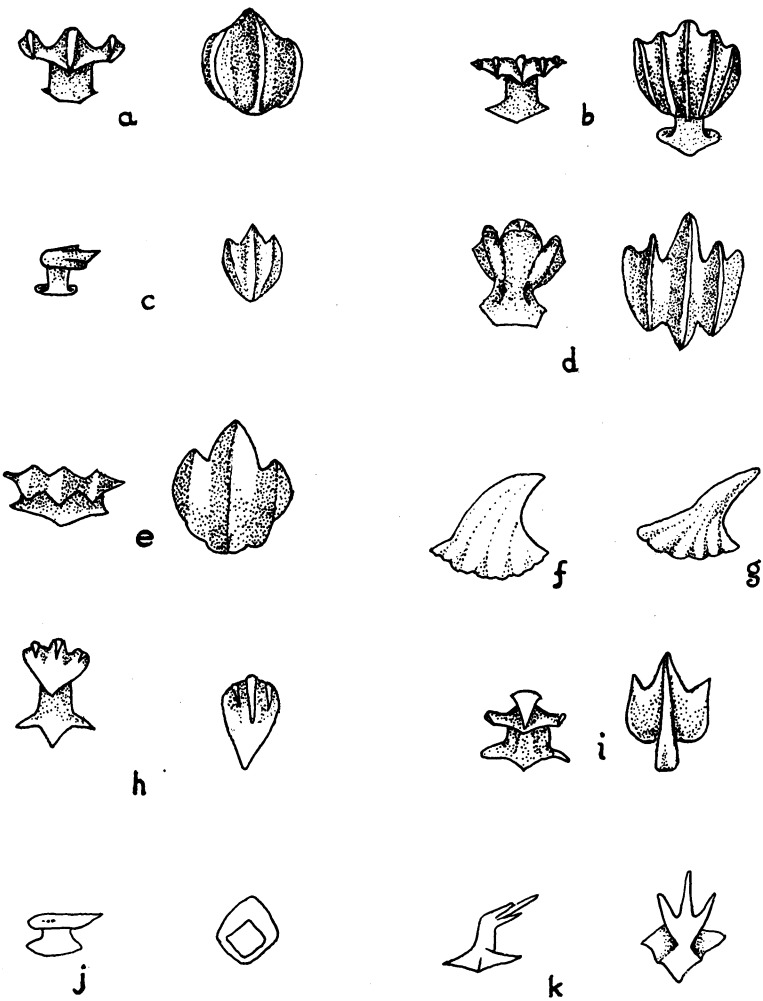

Fig. 11. Representative denticles of the Galea and Squalea.

a, Carcharoidea (*Carcharias taurus*)—*Odontaspis*: *b*, Isuroidea (*Vulpecula marina*); *c*, Isuroidea (*Carcharodon carcharias*); *d*. *Rhineodon*: *e*, Carcharinoidea (*Carcharinus limbatus*); *f*, Squalea (*Somniosus microcephalus*); *g*, Isuroidea (*Cetorhinus*); *h*, Catuloidea (*Ginglymostoma cirratum*); *i*, Squalea (*Squalus acanthias*); *j*, Squalea (*Centroscymnus owstonii*); *k*, Squalea (*Acanthidium aciculatum*).
a, *b*, *e*, *g*, *h*, and *i*, after Radcliffe; *c*, *f*, *j*, and *k* after Garman; *d*, original.

slightly forward in position (Fig. 10, d). The grooves are deep. The margins of the lateral keels curve forward, giving the five-lobed appearance to the margin.

The denticle does not make a sharp angle with its base, being only slightly tilted upward.

Comparison with figure 11 in which the denticles of various types are compared will show the great variation within the groups. Between the Galea and Squalea, however, is a radical difference in type, and there is no question of the resemblance of the *Rhineodon* denticles with the galeoid type.

An interesting instance is the resemblance between the denticles of *Cetorhinus* and *Somniosus* (Fig. 11, f, g). *Cetorhinus* resembles *Rhineodon* in so many of its physiological characters that this extreme modification is the more striking. Since *Cetorhinus* and *Somniosus* are both specialized forms living in arctic waters, it is probable that this is an adaptation to similar habitats. *Rhineodon* is always found nearer the tropical waters.

The denticles of the galeoid group most closely resembling those of *Rhineodon* are those of *Carcharodon, Carcharinus* and *Vulpecula.* No illustration could be found of the denticles of *Lamna* or *Isurus,* but both *Carcharodon* and *Vulpecula* are isuroid sharks. There is no sharp distinction between the superfamilies, however, as regards types of denticles, since they undergo variation in all groups.

Myxopterygia

Table 5.—Measurements of Myxopterygia.

	Ft.	In.
Axial Rod		
Length of Axial Rod	1	3½
Length of Dorsal Marginal at Surface	1	2½
Length of Ventral Marginal at Surface	..	11¾
Length of Chief Terminal Piece	..	7
Length of Dorsal Terminal Piece at Margin	..	5½
Length of Ventral Terminal Piece at Margin	..	3¾
Length of Spur	..	5½
Circumference of Basal Cartilage	..	9¾
Circumference of Axial Rod, Proximal	..	10¼
Circumference of Axial Rod, Central	..	9½
Circumference of Axial Rod, Distal	..	10

The myxopterygia are the skeletal parts of the claspers. In the description the terminology of Jungersen is used.

The myxopterygium is a continuation of the axial stem of the pelvic fin. The clasper of the specimen was cut through the distal portion of the basale metapterygii (B), the long cartilage by which the myxopterygium articulates with the pelvis (Pl. XII).

The stem of the myxopterygium consists of:

1.—The basale metapterygii which bears the rays. Four rays are attached to the basale in the specimen, two of which are broken off near the attachment. The two complete rays are long, tapering and unjointed. They curve in toward the cavity of the clasper. The last ray is partially attached to the next cartilage but appears to articulate on the basale.

2.—A thick, broad cartilage (b 1), widely triangular dorsally, and narrow and blunt ventrally. It touches both the basale and the axial rod on both sides.

3.—A small wedge-shaped cartilage (b 2) which fills in the space between b 1 and the axial rod on the ventral side.

4.—A long triangular cartilage on the dorsal side extending distally to fill in the gape formed by the dip in the dorsal marginal cartilage. (β) This is called the beta piece but does not extend forward to touch the basale as does the corresponding piece in the types described by Jungersen.

5.—The chief piece (b) of the myxopterygium, called the axial rod, or appendix stem. On the medial side it is rounded proximally and flattened distally. The sides are slightly dorsoventrally flattened. The entire skeleton is calcified on the surface, but the axial rod of the appendix stem carries on its dorsal and ventral edges two thin, completely calcified ridges: the dorsal and ventral terminal cartilages (Rd and Rv). These curve in to form the margins of the appendix slit, and are so close together in the anterior region as to approximate a tube. At no point is there any coalescence, however, since a very thin blade can be passed between them at any point.

The ventral marginal is but slightly shorter than the dorsal, but the dorsal extends a short distance beyond it at both ends. Both cartilages flare apart at the anterior and posterior ends to widen the appendix slit. At the anterior end the flare is foliaceous. Posteriorly, the cartilages separate gradually, beginning just anterior to the center, and the edges are thickened. Where the cartilages are closest together the ventral cartilage curves sharply outward so that its under surface is in contact with the dorsal, and not its margin. The margin is very thin and foliaceous, and flares outward.

The appendix stem curves forward on the medial side and is thickened on the edge, forming a collar. Ventrally the line of the collar is broken by a deep indentation. Posteriorly, the stem curves to a blunt margin, a half inch shorter on the ventral than on the dorsal side. The dorsal margin does not extend quite so far back as the dorsal marginal cartilage, and the ventral margin is shorter than the ventral marginal cartilage.

6.—The terminal pieces. To the appendix stem are attached four terminal pieces which are movable on the appendix stem and on each other.

a.—The axial piece (a). The main part of the terminal piece is formed of several distally pointed, irregularly conical pieces fused immovably together. En masse they form a thick, deeply furrowed axial piece, considerably thicker dorsally and concave on the inner surface. Distally the edges turn in and become thin and blade-like. A calcified ridge (l) extends like a lamella down the entire median length of the concave surface, joining the distal margins where they turn inward. Its edges are irregularly fluted proximally, and thicker distally. It divides the concave surface of the terminal piece into dorsal and ventral furrows which are covered over by two movable fan-like pieces: the dorsal and ventral terminal pieces (td, tv). These appear to correspond with the rhipidia of Leigh-Sharpe.

Since in all cases Leigh-Sharpe refers to the rhipidion on the dorsal side (Td) as the true rhipidion, it is presumable that the ventral flap (Tv) is a cover rhipidion. There seems to be no homology between the parts labelled rhipidion in Leigh-Sharpe's descriptions.

b.—The dorsal terminal piece (Td). The dorsal piece is elongate anteriorly and completely covers the dorsal furrow of the axial piece when closed. Posteriorly it fits into a groove on the surface of the lamella. The anterior elongation is narrow and roughened on the edge. It tapers into a finger-like projection which fits into a groove on the dorsal marginal cartilage.

c.—The ventral terminal piece (Tv). The ventral piece is shorter and thicker, and convex on the outward surface. It folds in over the ventral furrow and fits against the ventral surface of the lamella which curves slightly toward the dorsal side. Its edges are thin and irregular.

d.—A movable spur or thorn (T3). The spur is long, tapering, and conical in shape. It articulates on the distal margin of the ventral marginal cartilage, and lies in the ventral furrow of the axial terminal piece against the ventral surface of the lamella. Its tapering distal end lies over the ventral terminal piece so that the raising of the latter would undoubtedly aid in the erection of the spur. A thin calcified strip lies along its outer surface and runs forward to the inner surface of the ventral marginal cartilage.

The myxopterygia are the most important of the skeletal pieces saved in the Marathon specimen, since they establish the affiliations of *Rhineodon* without question. The length of the ventral marginal cartilage precludes any relationship with the Squalea which have a short distal ventral cartilage (Fig. 12*c*); and approximation of the edges into a tube without coalescence at any point precludes relationship with the Catuloidea of the galeoid sharks (Fig. 12*a*).

SYSTEMATIC POSITION OF *RHINEODON*

The use of the name, *Rhineodon typus*, follows Gudger (1915) who claims priority for the name on the grounds that the printers mistook Smith's *e* for a *c* in the original paper (1829), so that the name appeared *Rhincodon*.

Rhinodon appeared in Smith's later paper (1849), but no reason for the change is apparent since the derivation of the name is from rhine (file) and odous (tooth).[1] *Rhinodon* is used in the classifications of Goodrich and Tate Regan, and is in more popular use today than the name *Rhincodon*.

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[1]Gudger, 1915.

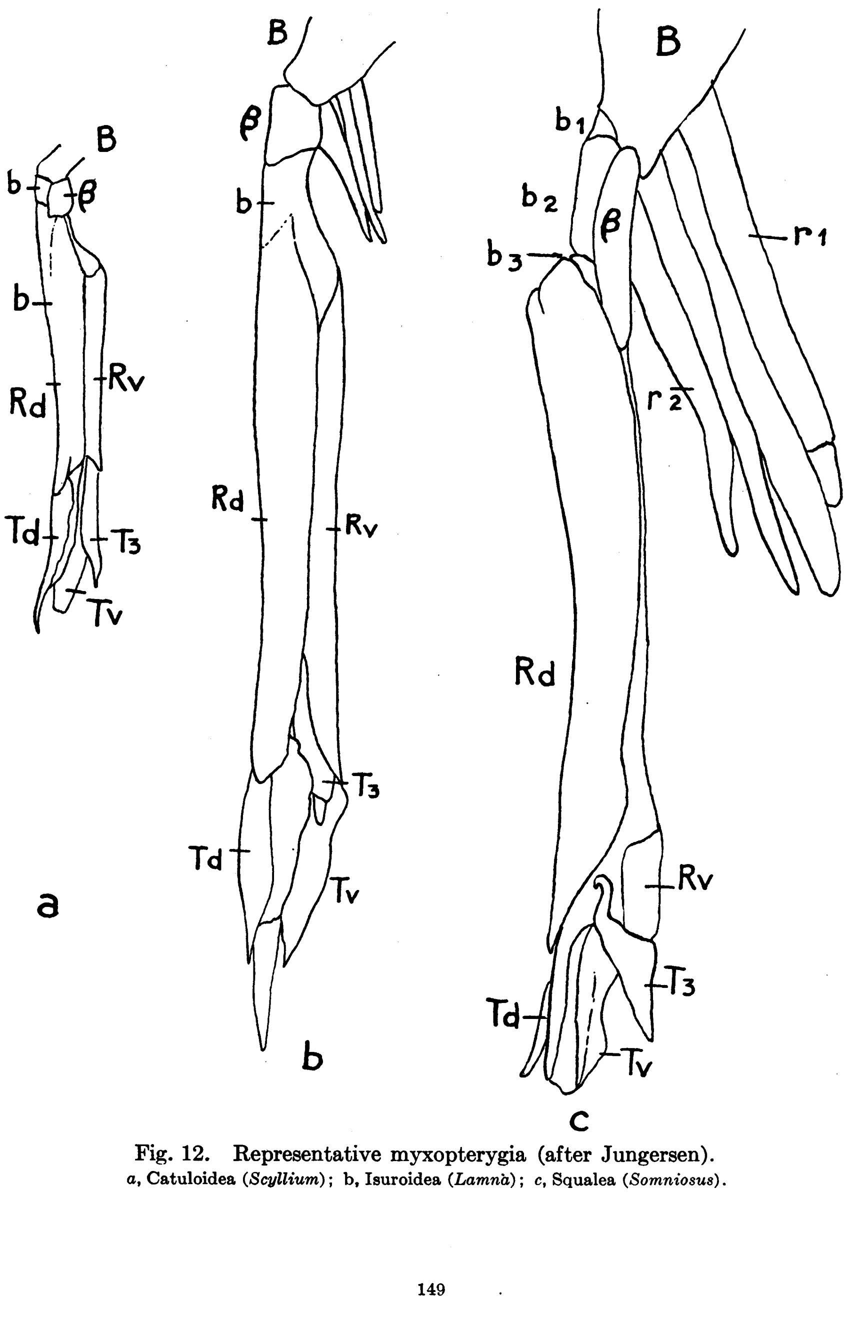

Fig. 12. Representative myxopterygia (after Jungersen).
a, Catuloidea (*Scyllium*); b, Isuroidea (*Lamnà*); *c*, Squalea (*Somniosus*).

The authors mentioned above have all given *Rhineodon* a place in their schemes of classification. Müller and Henle first recognized it as a type from Smith's description and placed it with the mackerel sharks on no more evidence than superficial resemblance. This position has been followed by all authors without question, except Tate Regan who, in 1906, placed the whale shark with the Orectolobidæ, or nurse sharks,—a very radical change. Goodrich, in 1909, followed Jordan and Everman without recognizing Tate Regan's position, but Garman, in 1913, returned *Rhineodon* to the mackerel sharks and substantiated his position as fully as the means at hand allowed.

It appears to the author that either position might be substantiated on the material available at the time, but both have been made on such scanty evidence that it seems wise to review the assignments in some detail.

TABLE 6.—Positions Assigned to *Rhineodon* and to Allied Forms by Various Authors.

MÜLLER AND HENLE (1841) AND JORDAN AND EVERMANN (1896)

Galei	Scylliorhinidæ	*Catulus* (*Scyllium*)
	Orectolobidæ	*Orectolobus*
	Ginglymostomidæ	*Ginglymostoma*
	Lamnidæ	*Lamna*
	Cetorhinidæ	*Cetorhinus*
	Rhincodontidæ	*Rhincodon*

TATE REGAN (1906)

Galeoidei	Lamnidæ	*Lamna*
		Cetorhinus
	Orectolobidæ	*Orectolobus*
		Ginglymostoma
		Rhinodon
	Scylliorhinidæ	*Scylliorhinus* (*Scyllium*)

GOODRICH (1909)

Scyllioidei	Scyliidæ	Scylliinæ	*Scyllium*
		Orectolobinæ	*Orectolobus*
			Ginglymostoma
	Lamnidæ	Lamninæ	*Lamna*
			Cetorhinus
		Rhinodontinæ	*Rhinodon*

Table 6—(*Continued*)

GARMAN (1913)

Isuroidei	Isuridæ	*Isurus* (*Lamna*) (*Cetorhinus*)
	Rhincodontidæ	*Rhincodon*
Catuloidei	Orectolobidæ	*Ginglymostoma* *Orectolobus*
	Catulidæ	*Catulus* (*Scyllium*)

WHITE (1930)

Galea	Isuroidea	Isuridæ	*Lamna* *Cetorhinus*
		Rhineodontidæ	*Rhineodon*
	Catuloidea	Orectolobidæ	*Orectolobus* *Ginglymostoma*
		Catulidæ	*Catulus* (*Scyllium*)

Table 6 shows diagrammatically the position assigned to the whale shark by Müller and Henle, Tate Regan, Goodrich, Garman, and the position proposed by the author. Since Jordan and Evermann follow Müller and Henle in all details, the one diagram illustrates the position of both equally well. In both cases a few external characters are noted as resembling the lamnoid sharks. Jordan states the feature of this group as being a lunate tail with a keel on either side as in the mackerels.[1]

To quote Tate Regan's position[1]: "Examination of a stuffed specimen of the large *Rhinodon typicus* leaves no doubt that it is closely related to *Ginglymostoma,* from which genus it differs only in those features in which it resembles the Basking Shark, *Cetorhinus maximus;* i.e., the small teeth, long gill rakers, wide gill clefts, etc., which are obviously of physiological rather than phylogenetic importance."

This point is well taken since both of these immense sharks are highly specialized and adapted to a sluggish mode of life which may well be responsible for parallel adaptations. This will be discussed at the end of this section.

In a later paper[3] Regan adds: "The curious dermal keels are like those met with in other sharks of the Orectolobidæ (*Stegostoma* and *Chiloscyllium*)." The keels of these sharks, like those of *Rhineodon,* run the length of the body and on into the tail. They differ from *Rhineodon,*

[1]Jordan, 1905.
[2]1906, p. 745.
[3]Idem, 1908, p. 353.

however, in that no single keel is strengthened at the side of the tail. Only one keel on either side of *Rhineodon* runs into the caudal fin, and this one is greatly strengthened to form the lateral keel which is so characteristic of the mackerel sharks. The shape of the caudal is also decidedly more lunate than in the orectolobid sharks mentioned. In *Chiloscyllium* the supracaudal hardly exists, whereas in *Rhineodon* it is sharply raised and very large. The keels on the body, therefore, may well belong to the physiological features, as do the gill rakers and small teeth. The spotted character of the skin is a feature found mainly in the small cat sharks which are related to the Orectolobidæ. The spottedness of *Rhineodon*, therefore, suggests this relationship but is of no phylogenetic importance.

The family characteristics of the Orectolobidæ, as Tate Regan outlines them, call for the presence of nasoral grooves, the position of the last two gill-slits over the base of the pectorals, and the rostral cartilages short and not convergent.

The position of the gill-slits is unquestioned (Pls. IV, V), but here again is a character which varies within the groups and has no systematic value by itself. The condition of the rostral cartilages may be of importance and, unfortunately, the material in the hands of the author does not settle this point. It seems very probable that the rostral cartilages fulfill this requirement, since the extreme forward position of the orbits precludes a long rostrum (see Pls. IV-V). Again, the question arises, however, whether the extreme specialization of the head of *Rhineodon* is not rather a symbol of its habits than of its relationships.

Of the nasoral grooves Tate Regan[1] says: "In most Selachians the nasal cavities are separate from the mouth. In three species of *Scyliorhinus* the nasal cavities are so near the mouth that the large anterior nasal valves overlie the edge of the upper lip but there are no oro-nasal grooves. In the Orectolobidæ the nasoral grooves divide the upper lip into a median and two lateral portions." Nasoral grooves have been claimed for *Rhineodon* by various authors but do not appear in any of the authentic descriptions. Examination of the photographs in plate V will show that the nostrils are terminal and that the flaps fold over the upper lip. In Pl. IV, fig. 1, which is a photo of the Miami specimen, the extent of the grooves cannot be seen, but in Pl. V, fig. 2, the photo of the Marathon specimen, the mouth is stretched in such a way that the ventral surface is visible. The nasal flap is just above the transverse rod which holds the fish to the dock. Although the jaw is damaged by the anchor

[1]1908, p. 347.

which has been placed in the mouth, the groove under the nasal flap can be seen to terminate just under the curve of the lip, and not to reach the margin of the jaw. While this is a terminal nostril, therefore, it cannot be said to be truly confluent with the mouth, and it does not appear to divide the jaw into three parts. It agrees with Tate Regan's description of *Scyliorhinus.* The presence of nasoral grooves, is, therefore, at least unverified and will bear further investigation.

This outlines Tate Regan's position and shows that, while the evidence from the external appearance of the whale shark is as good for the nurse sharks as for the mackerel sharks, if you discount the lunate tail, the evidence is largely unverified, and the majority of the external features of *Rhineodon* are to be looked upon as of "physiological rather than phylogenetic importance."

No further discussion of the matter is found in the literature until Garman's comprehensive memoir in 1913, all authors following Müller and Henle, except that Goodrich groups the families more logically by forming subfamilies. Garman justifies his position by a complete list of external characters, showing the resemblance of *Rhincodon* to *Cetorhinus,* and answers Tate Regan in the following statement[1]: "It has nasoral grooves, and has keels on the body as on some of the Orectolobidæ, but it differs from them in lacking nasal cirri, in size, in the disproportions of pectorals and caudals, in the erected supracaudal, the lobed subcaudal, and the lateral keels of the caudal pedicel." He places the shark once more with the mackerel sharks, using the preferred name isuroids for the mackerel group.

The author agrees with Garman that the position assigned by Müller and Henle is the correct one, but justifies the position on the correspondence of internal with external characters. The very argument outlined above shows how dangerous it is to base classification on external characters alone, since these are so frequently altered by the habitat, and since specializations appear within all groups. Many characters are duplicated in widely separated groups; such, for instance, as the position of the gill-slits over the base of the pectorals, which appears independently in several divisions under the Galea, but is specific for no one of them.

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[1]Garman, 1913, p. 41.

The known characters of *Rhineodon* have been listed in Table 7.

TABLE 7.—Characters of *Rhineodon*.

No.	Character	Authority[1]	Position
1.	Fish-like form	IV	Class Pisces
2.	Skeleton cartilaginous	VIII–IX	Subclass Chondropterygia
3.	Branchial arches 5	IV	"
4.	Teeth not implanted on jaws	V	"
5.	Spiral fold in intestine	Smith	"
6.	Paired claspers in male denoting internal fertilization	XII	"
7.	Absence of erectile dorsal spine	IV	Superorder Plagiostomia
8.	Vertebræ differentiated	2, 3, 4	"
9.	Teeth numerous	X–XI	"
10.	Gill-openings more than one	IV	"
11.	Body fusiform	IV	Order Antacea
12.	Gill-openings lateral	IV	"
13.	Pectorals not attached to the head	IV	"
14.	Pterygoquadrate has a palatobasal process	VIII	"
15.	The hyomandibular and ceratohyal bear rays	7	"
16.	The ceratohyal is a single cartilage attached to the lower end of the hyomandibular	7	"
17.	Vertebræ asterospondylous	VII	Suborder Galea
18.	Two dorsal fins without spines	IV	"
19.	Anal fin present	IV	"
20.	Jaws hyostylic	7	"
21.	Gill-slits 5	IV	"
22.	Spiracles small	V	"
23.	Myxopterygia: free ends of dorsal and ventral marginal cartilages approximate each other to form a tube	XII	"
24.	Myxopterygia: ventral cartilage elongate	XII (cf. 12)	"
25.	Dorsals unequal	IV	Superfamily Isuroidea
26.	Anterior dorsal large	IV	"
27.	Anterior dorsal just in advance of pelvics	IV	"
28.	Posterior dorsal small	IV	"
29.	Posterior dorsal just in advance of anal	IV	"

[1]Roman numerals refer to plates, arabic numerals to text figures illustrating this paper.

Table 7—(*Continued*)

No.	Character	Authority	Position
30.	Anal fin small	IV	Superfamily Isuroidea
31.	Caudal fin lunate	IV	"
32.	Caudal axis much raised	IV	"
33.	Lower lobe of caudal produced	IV	"
34.	Lateral keels on caudal	IV	"
35.	Gill-slits wide	IV–V	"
36.	Eyes very small, lateral	IV	"
37.	Nictitating membrane absent	Kishinouye	"
38.	Mouth large	IV	"
39.	Labial folds on both jaws, larger on upper jaw	V	"
40.	Nostrils terminal	V	"
41.	Nasal cirri absent	V	"
42.	Teeth have one root	9	"
43.	Several series of teeth in function	X	"
44.	Denticles three-keeled	10 (cf. 11)	"
45.	Vertebræ have four main calcified areas	VII (cf. 6)	"
46.	Myxopterygia: edges of marginals not coalesced	XII (cf. 12)	"
47.	Skin spotted	IV–V	Family Rhineodontidæ
48.	Vertical bands on sides	IV	"
49.	Longitudinal keels	IV	"
50.	Mouth terminal	IV–V	"
51.	Denticles minute	Table 4	"
52.	Teeth conical, recurved	XI	"
53.	Gill-rakers present	Smith	"
54.	Immense size	Table 1	"
55.	Skin mouse-color with yellow spots	Mowbray	*Rhineodon typus*

These characters are grouped under class, subclass, etc., following the classification of the elasmobranchs arranged by the author and now in use at the American Museum. This classification will be published at a later date.

An attempt has been made to verify all characters assigned to *Rhineodon* from the photographs and material at hand. Where this has been possible, the reference under authority is to photographs, figures, and tables in this paper. Where this could not be done, and the character has been described by an authentic observer, reference is made to the description. The descriptions used are those of Andrew Smith (1829, 1849), Kamakichi Kishinouye (1901), and L. L. Mowbray who was present at the capture of the Marathon specimen in 1923.

Table 8.—Characteristics of the Suborders of the Order Pleurotremata (Antacea) Compared with the Corresponding Characteristics of *Rhineodon*.

Character	Hexanchea	Galea	Heterodontea	Squalea	*Rhineodon*
Vertebræ	asterospondylous or undifferentiated	asterospondylous	asterospondylous	cyclo- to tecto-spondylous	asterospondylous
See Fig. 5	a	d	b	c	
Notochord	unconstricted anteriorly	constricted	constricted	constricted or unconstricted	constricted
Dorsal Fins	one	two	two	two	two
Dorsal Fin Spines	absent	absent	present	present or absent	absent
Anal Fin	present	present	present	absent	present
Gill-openings	6–7	5	5	5–6	5
Spiracle	small	small or closed	small	large	small
Jaw Suspension	amphystylic	hyostylic	amphi-hyostylic	hyostylic	hyostylic
Pteryogoquadrate Articulation	loose	loose or absent	extensive	absent	loose
Palatobasal Process	present	reduced	present	absent	reduced
Rostral Cartilages	single	three	single	single	unknown
Pectoral fin:					
Radials on Propterygium	none	one-several	one	one-several	unknown
Mesopterygium	on margin of fin	not on margin of fin	not on margin of fin	not on margin of fin	unknown
Myxopterygia:					
Axial Cartilage	cylindrical and pointed	dorso-ventrally flattened	cylindrical and pointed	cylindrical and pointed	dorsoventrally flattened
Ventral Marginal	short and distal	elongate	short and distal	short and distal	elongate

TABLE 9.—Characteristics of the Superfamilies of the Suborder Galea Compared with the Corresponding Characteristics of *Rhineodon*.

Character	Carcharoidea *Odontaspis Scapanorhyncus*	Isuroidea: *Isurus (Lamna), Cetorhinus, Carcharodon*	Catuloidea: *Ginglymostoma, Orectolobus, Scyllium*	Carcharinoidea *Carcharinus, Galeocerdo*	*Rhineodon*
Dorsals	almost equal	very unequal	almost equal	slightly unequal	very unequal
Posterior Dorsal	medium	very small	medium	medium	very small
Anterior Dorsal	medium, anterior to pelvics	large, anterior to pelvics	medium, posterior to pelvics	medium, far forward	large, anterior to pelvics
Caudal Axis	little raised	much raised	little raised	little raised	much raised
Lateral Keels	absent	present	absent	absent	present
Anal Fin	medium	very small	medium	medium	small
Gill-openings	wide	wide	medium	medium	wide
Last Two Over or Anterior to Base of Pectorals	anterior	over or anterior	over	over or anterior	over
Gill-rakers	absent	present or absent	absent	absent	present
Spiracles	small	minute or closed	large	small or closed	small
Nictitating Membrane	absent	absent	absent or rudimentary	present	absent
Nostrils	far from mouth	near mouth	far from mouth	far from mouth	terminal
Nasoral Grooves	absent or present	absent	present or absent	absent	unknown
Nasal Cirri	absent or present	absent	present	absent	absent
Mouth: Size	medium	large	small	medium	large
Mouth: Position	ventral	ventral	ventral	ventral	terminal
Mouth: Labial Folds	absent or on lower jaw only	on both jaws	on lower jaw only	absent, or, if present, on both jaws	on both jaws
Teeth: Size	large	large or small	large	large	very small
Teeth: Roots	two	one	two	two	one
Teeth: Cusps	more than one	one or more than one	more than one	more than one	one
Teeth: Series in Function	one	several	several	one	several
Teeth: Number	few	many	few	few	many
Myxopterygia: Edges of Marginals	not known	not united	united into a tube	not united	not united
Vertebræ: See text figure 6	a	b, c	d	e	f

Tables 8 and 9 are comparative lists of characteristics of the suborders and superfamilies within which question might arise. Reference to these tables will show the reason for assigning the position in the case of any characteristic of suborder or superfamily value.

DISCUSSION

Although several points remain to be verified; i.e., the presence of nasoral grooves, the condition of the rostrum, and of the pectoral fins; the material examined agrees very closely with the corresponding structures of the isuroid sharks. In the Carcharinoidea, while the tube of the myxopterygium is not fused, it is not described as having the edges as closely approximated as the isuroids. The vertebræ on first glance appear to be similar, but the four rod-like intercalations (Fig. 6, e) are so characteristic of the carcharinoids as to preclude any affiliation. Externally, the presence of nictitating membranes and the lack of differentiation in size and position of the fins is sufficient evidence of the separation between the groups.

The Catuloidea present more confusing external resemblances since both groups contain so many specialized forms. Spotting, for instance, is a feature of some of the smaller catuloids, and the longitudinal keels, the abbreviated head, and the position of the gill-slits over the base of the pectorals all suggest this group. These are largely physiological features, however, and marks of specialization rather than affiliation. The fusion of the tube in the myxopterygia is a characteristic so constant in the groups as to rule out this relationship and, when taken together with the differentiation of the fins, makes unquestionable the affiliation with the isuroid sharks.

It is the contention of the author that it is not in single characters, but in groups of characters, that relationships are shown, and that only where these groups appear consistently in conjunction with similar internal structure can the question of systematic position be safely determined.

The position of *Cetorhinus* has never been questioned, but the author suggests that a careful revision of the structure of this immense shark may throw interesting light on the subject. It is not usual for two such similar adaptations to appear in one group and yet have such striking differences.

Here are two immense sharks, both having wide gill-slits, gill-rakers, and very minute teeth, a group of modifications which denote the sluggish life and the habit of feeding on minute forms which both these sharks illustrate. In *Cetorhinus*, however, the gill-slits are so long that they almost meet ventrally and are all anterior to the base of the pectorals. The dermal denticles, also, show an extreme modification in *Cetorhinus*, which is paralleled in those of *Somniosus*, a squaleoid shark. The denticles of *Rhineodon* are so similar to those of the Carcharoidea that they are very little differentiated. This is probably a matter of climate, since *Rhineodon* inhabits warm waters, and both *Somniosus* and *Cetorhinus* are adapted to cold.

Since the differences between these two sharks are apparently of physiological rather than phylogenetic significance, it is possible that the likenesses are also, and that these are only cases of parallel adaptations. The structure of the internal organs of *Cetorhinus* may clear up tbis point, especially if the mature claspers could be obtained.

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PLATES IV TO XII

PLATE IV

Rhinodon typicus. Plate 26 of Smith's Illustrations of South African Zoölogy
(Bean, 1905).

Courtesy, N. Y. Zoological Society.

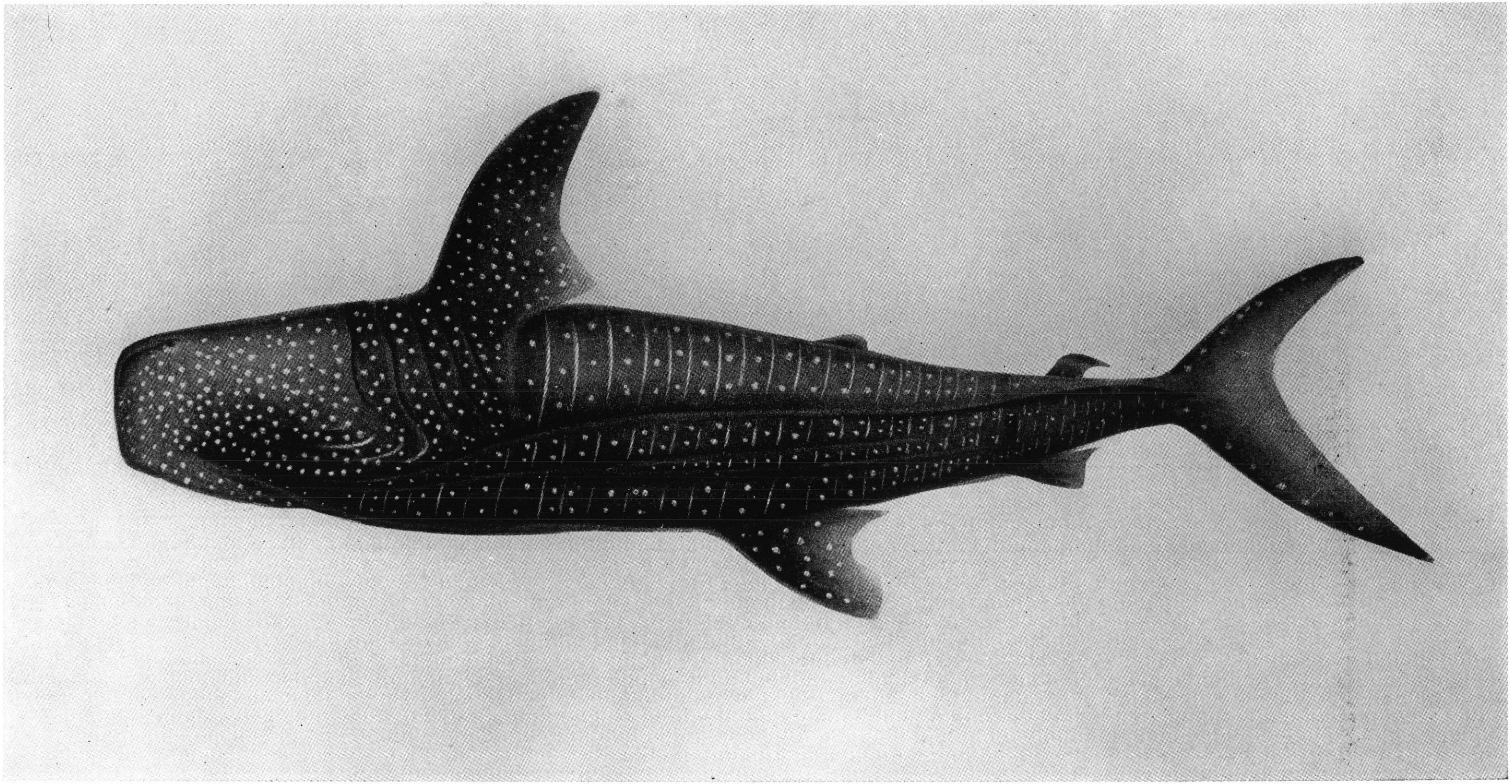


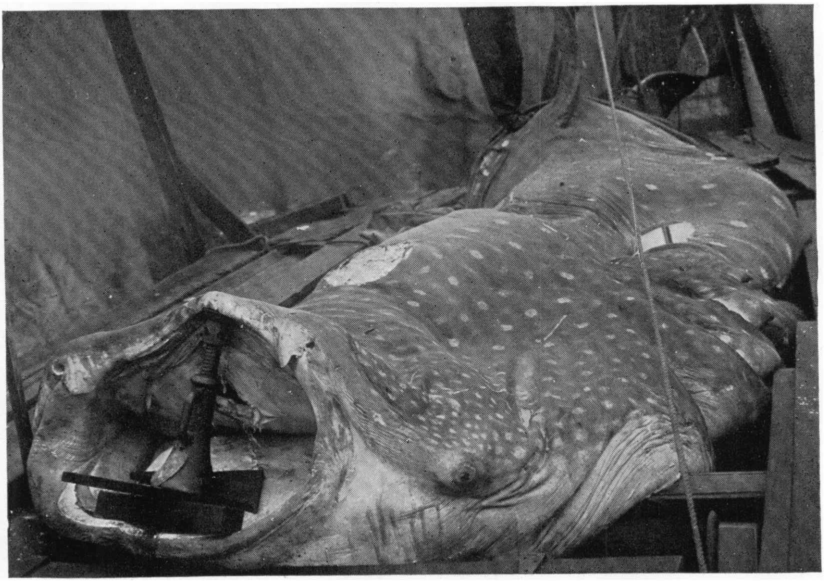
PLATE V

Fig. 1. A whale shark on the marine railway at Miami, showing mouth, teeth, nasal flaps, spiracle and gill-slits.

Courtesy, N. Y. Zoölogical Society.

Fig. 2. Marathon specimen at the dock at Long Key, Florida, showing dental plates in position.

Courtesy, Dr. E. W. Gudger.



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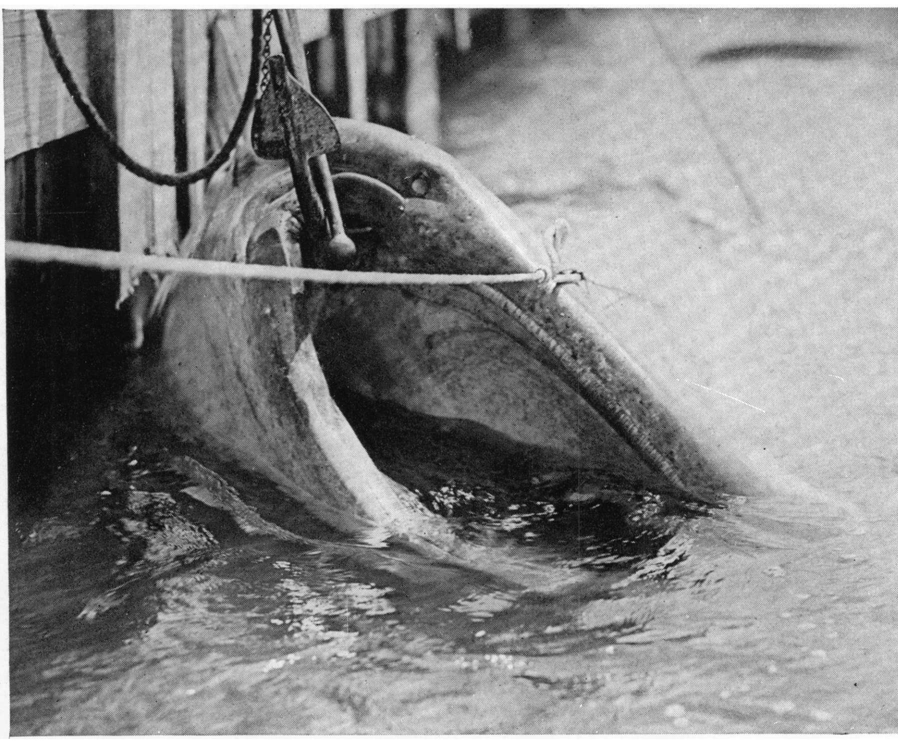

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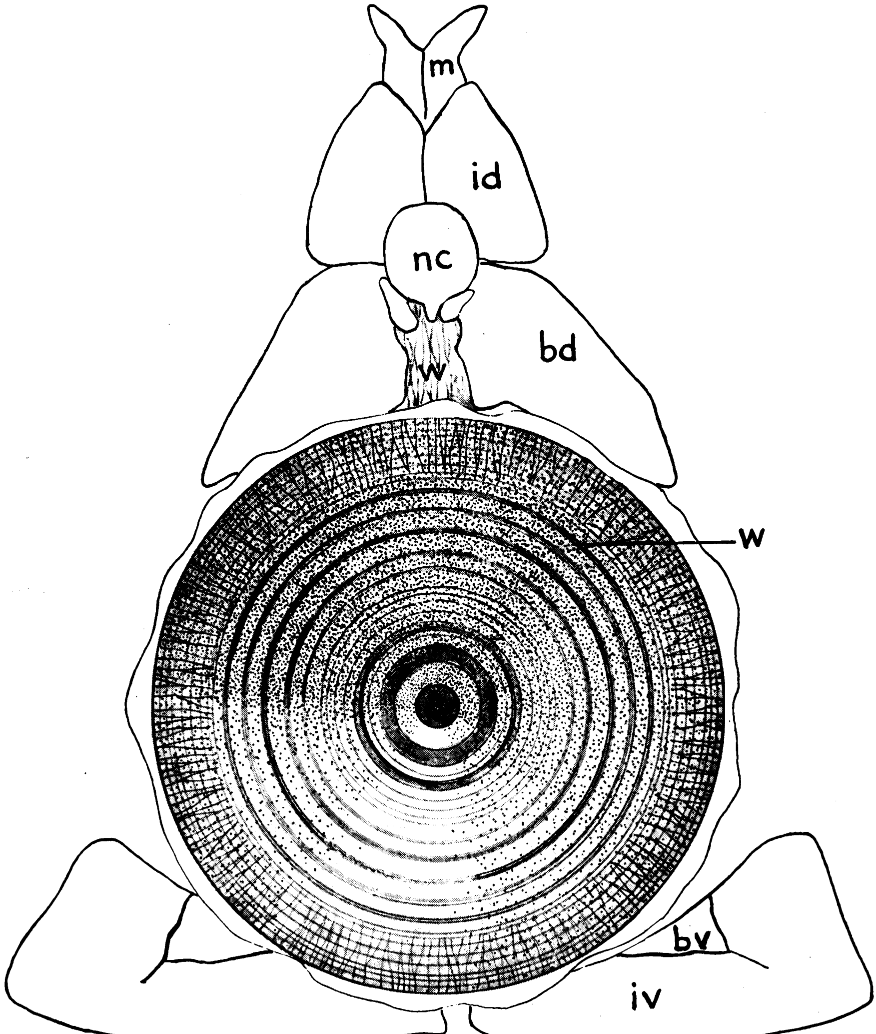


Plate VI

Trunk vertebra, end view.

bd, basidorsal cartilage; *id*, interdorsal cartilage; *bv*, basiventral cartilage; *iv*, interventral cartilage; *m*, median cartilage; *nc*, neural canal; *w*, white fibrous tissue.

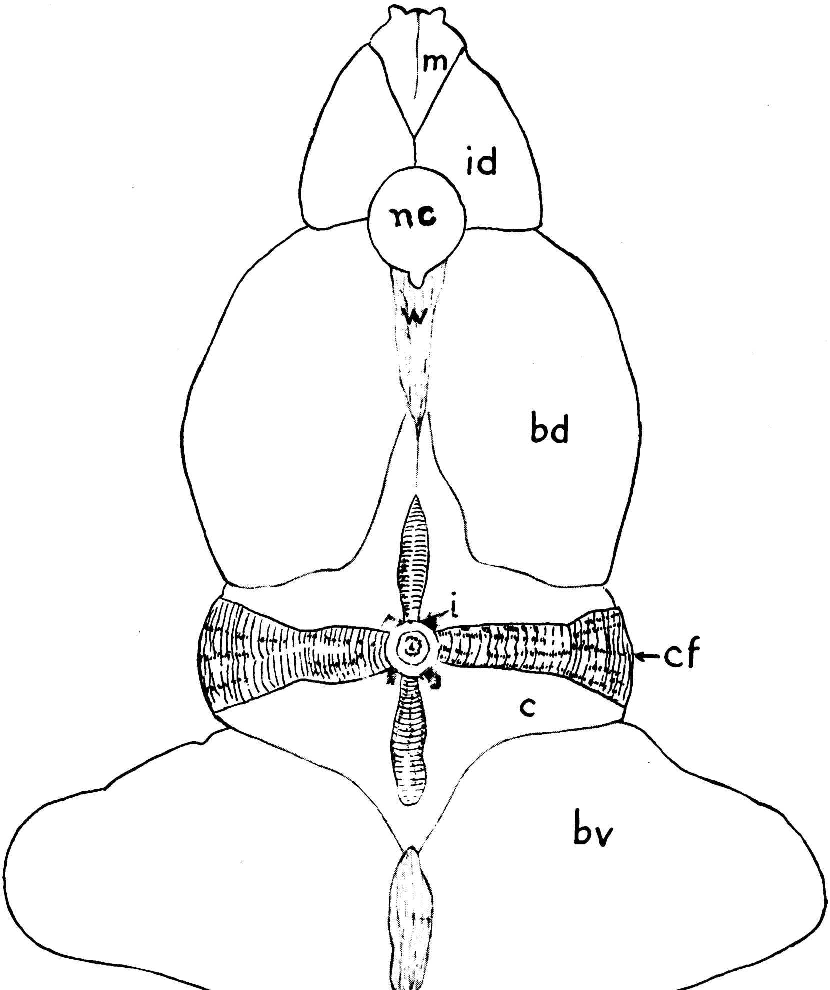


PLATE VII

Trunk vertebra, cross-section through center.

cf, calcified area; *i*, intercalated calcifications; *w*, white fibrous tissue.

PLATE VIII

Mandibular arch, dorsal view. A. M. N. H. photograph.

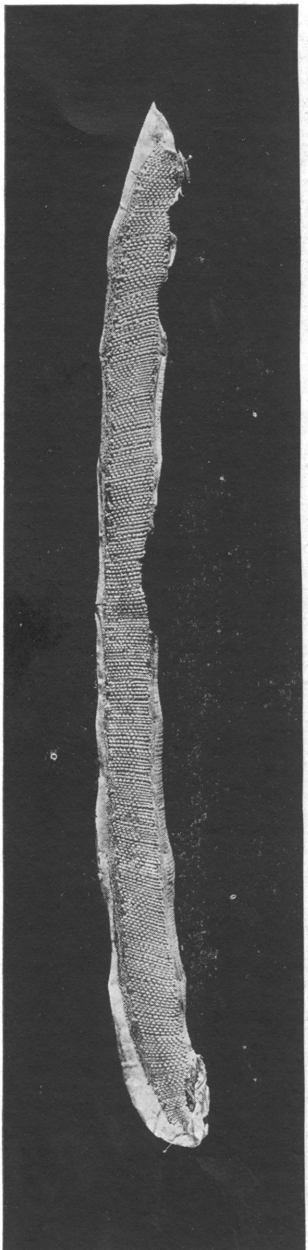
Plate IX

Mandibular arch, ventral view. A. M. N. H. photograph.

Plate X

Dental band from Ormond specimen of whale shark. A. M. N. H. photograph.

Fig. 1. Entire band, ×⅓. Fig. 2. Detail of band, natural size.
Dental band loaned by B. A. Bean, U. S. National Museum.



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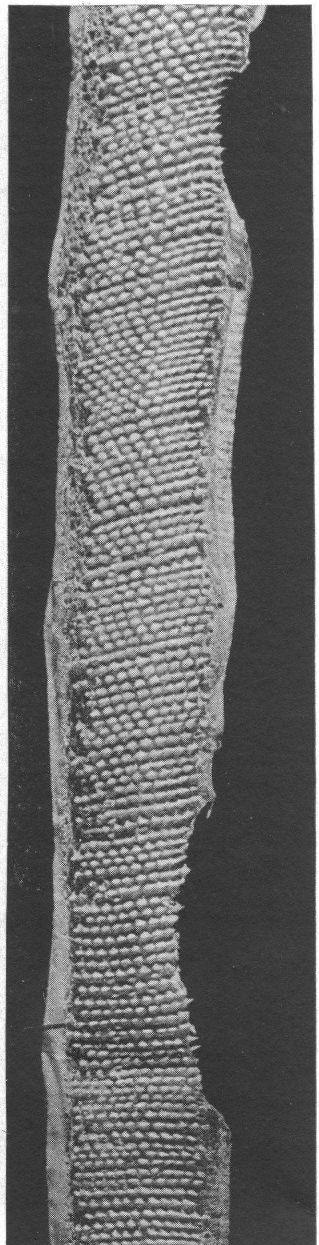

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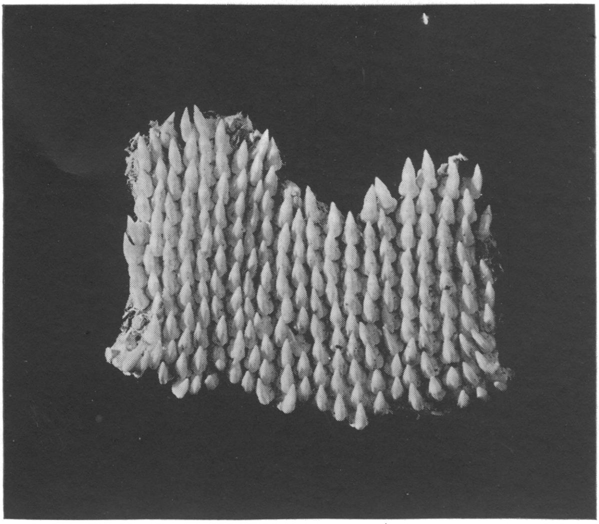
PLATE XI

Teeth of the Marathon specimen. A. M. N. H. photograph.

Fig. 1. Natural size. Fig. 2. ×2.



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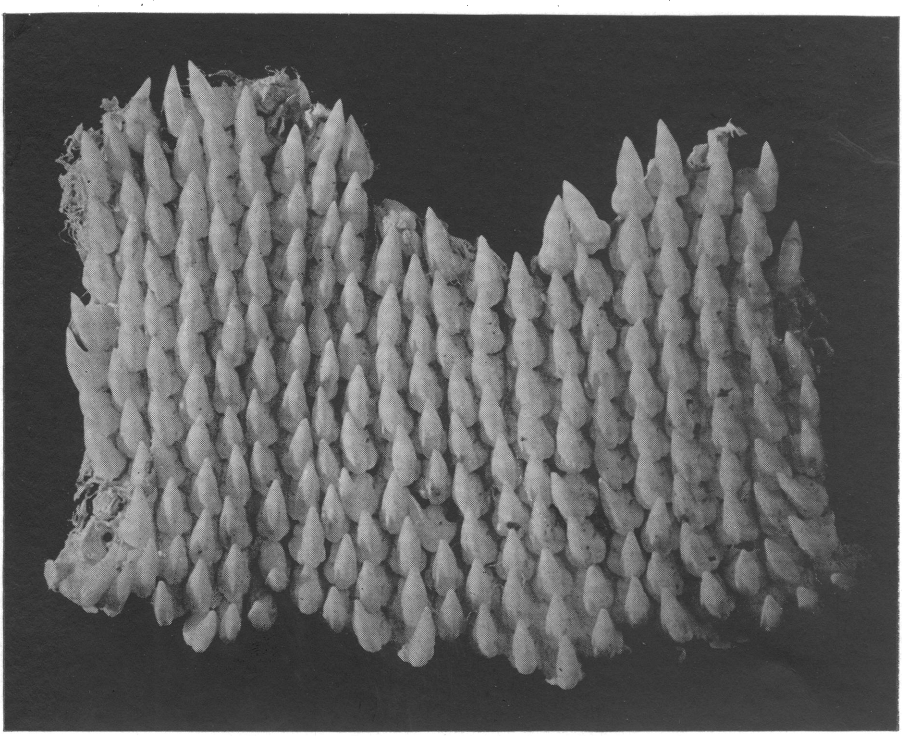

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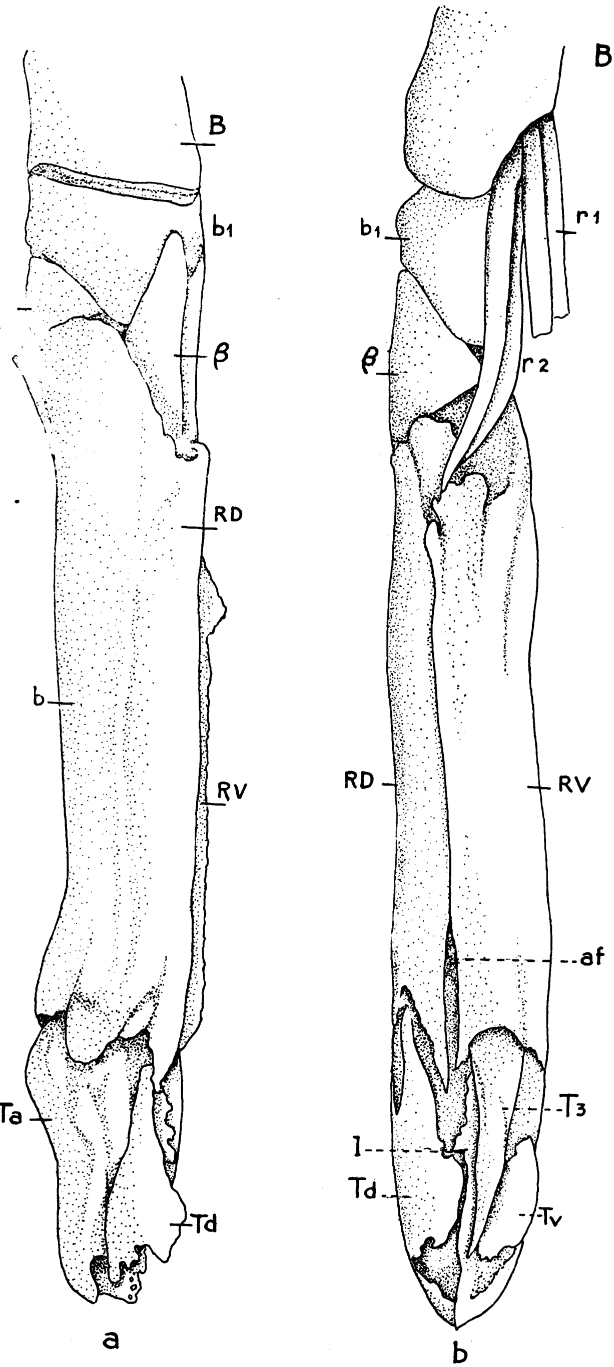
PLATE XII

Right myxopterygium. ×1/2. *a*, dorsal view; *b*, ventral view.

B—Basale metapterygii
r^1 —jointed ray
r^2 —unjointed ray
b —appendix stem
af —appendix slit
b_1, b_2—stem joints
β —Beta piece

Rd—dorsal marginal cartilage
Rv—ventral marginal cartilage
Ta—axial terminal piece
Td—dorsal terminal piece
Tv—ventral terminal piece
T_3—spur
L —lamella


B
b1
b2
β
RD
b
RV
Ta
Td
a
B
r1
b1
β
r2
RD
RV
af
T3
l
Td
Tv
b