

*Anatomy of the Head and Pelvic Fin of the  
Whale Shark, Rhineodon*

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# Article V.—ANATOMY OF THE HEAD AND PELVIC FIN OF THE WHALE SHARK, *RHINEODON*

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## INTRODUCTION

The specimen of *Rhineodon* described in this paper was caught near Islip, Long Island, in August, 1935. Its capture and subsequent history have been related by Gudger (1936), who has given also an account of its external features. It will suffice to state here that the total length of this shark was 31 feet 5 inches.

After removal of the skin, the following parts were collected for The American Museum of Natural History: the head and anterior branchial region; a small section of the esophagus; the heart; the claspers, pelvic fins and girdle. Due to the incompleteness of the material and decomposition of the soft parts, only the skeletal and mus-

cular anatomy could be determined satisfactorily. No attempt has been made to describe systematically the circulatory, nervous or other systems composed of soft tissues, but some notes on them are submitted.

The writer wishes to acknowledge the kind assistance of Dr. W. K. Gregory, Mr. H. C. Raven and Dr. E. W. Gudger throughout this work.

#### HEAD AND BRANCHIAL REGION

Although little is known of its habits, *Rhineodon* apparently feeds on small fish and minute forms of pelagic life (Gudger, 1931, p. 628). In correlation with this diet, unusual among sharks, there have been many modifications of the structure of the head. Most striking of these is the great enlargement of the mouth and its practically terminal position. There might be mentioned also the reduction of the teeth to fine denticles unfitted for seizing prey, the development of the gill rakers into a thick horny sieve for straining out fine organisms, and the reduction of the size of the eyes which are no longer of such primary importance in obtaining food. The size itself is correlated no doubt with the diet, as in the case of another group of vertebrates, the whalebone whales. These are but a few of the specialized or habitus characters of this strange shark which to a great extent tend to obscure its affinities. The scope of this paper, however, is largely descriptive, and no attempt is made to deduce relationships. The terminology used in the discussion of the head is that of Allis (1923).

#### NEUROCRANIUM

The cranium of *Rhineodon* is of a very peculiar shape. From the side (Fig. 1B) it is somewhat wedge-like, very flat ventrally, and dorsally sloping up gradually from the rostrum to its highest point in the posterior otic region from which there is a more abrupt descent into the occipital region. The maximum height is just one-third of the length. In the dorsal view (Fig. 2A) the great width of the cranium is striking. It is greatest across the flap-like postorbital processes where it much exceeds the length, but it equals the length across the nasal capsules and is only slightly less in the otic region. The dorsal surface is deeply incised by the V-shaped anterior cranial opening. The ventral surface of the cranium (Fig. 3A) is remarkable for its broad, flat expanse, only interrupted by a gentle upward slope in the occipital region. The rostrum is so reduced that it barely extends in front of the nasal capsules which are drawn out antero-laterally to overhang the palatoquadrate.



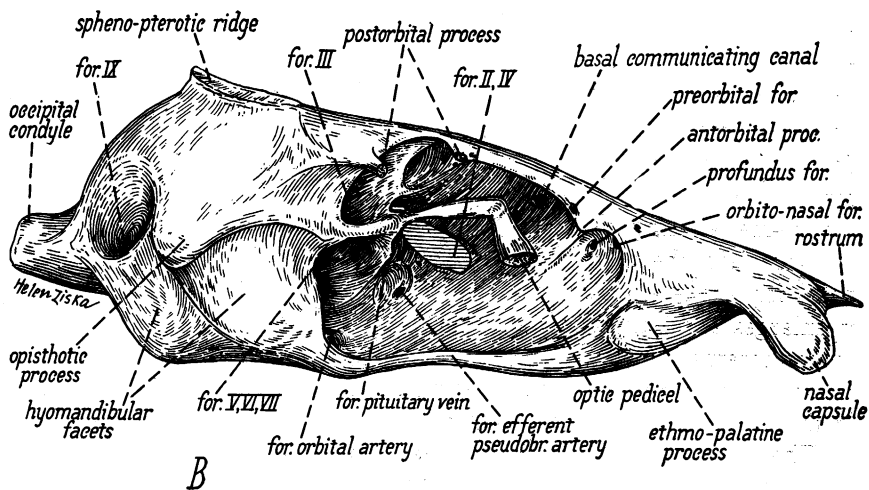
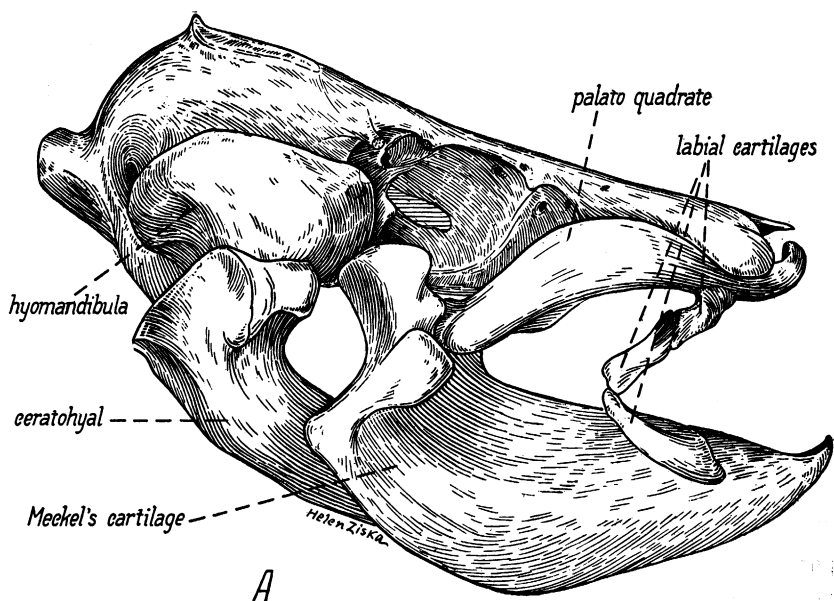


Fig. 1A. Skull. Lateral view.  $\times 1/8$ .

Fig. 1B. Neurocranium. Lateral view.  $\times 1/8$ .

## Ethmoidal Region

The rostrum of this specimen was not complete, but its general form could be determined with some certainty. It is so reduced that the mouth is practically terminal, the palato-quadrates extending to its front. Dorso-ventrally it is thin and flat; its anterior edge is nearly straight or perhaps slightly convex and has a pair of small notches laterally. On either side it is bounded by a shallow bay, the rostral-nasal notch, which separates it from the nasal capsule (Fig. 2A).

The nasal capsule is drawn out so far antero-laterally that it may be said to have a short stalk. The terminal part of the capsule was damaged in removing the skin, and the process of the ala nasalis which divides the fenestra nasalis was lost. However, the ala nasalis can be seen to form an oval-shaped ring surrounding the nostril except ventrally where the ring fails to close. The fenestra nasalis is of a twisted oval shape and is widely continuous ventrally with the nasal fontanelle. The latter, which according to Allis (1923, p. 132) is an unchondrified part of the subnasal plate and nasal capsule, is an oblong area on the ventro-mesial surface of the "stalk" of the nasal capsule. It is covered with a tough white membrane which forms the floor of the nasal chamber in this region.

From the lamina cribrosa of the nostril there extends postero-mesially the large, rounded olfactory canal through which passes the olfactory tract. This opens posteriorly into the anterior part of the precerebral chamber. Between the lining of the olfactory canal and the cartilaginous and membranous wall is the ectethmoidal chamber of Allis. In *Rhineodon*, however, it is not a broad chamber, but merely a canal for the orbito-nasal vein. Anteriorly it is small and located at the ventro-mesial angle of the olfactory canal. It receives a commissural vein through the postero-mesial corner of the membrane closing the nasal fontanelle as described by Allis in other selachians. Posteriorly it enlarges and curves laterally under the floor of the olfactory canal to the internal opening of the orbito-nasal canal of which it appears to be a continuation. This opening is on the ventro-lateral surface of the most posterior part of the olfactory canal.

The anterior cranial opening was shown by Allis (1923) to consist of two distinct parts, the fenestra praecerebralis and the cavum praecerebrale. The former is represented in *Rhineodon* by a narrow V-shaped notch, mutilated in this specimen, but apparently extending back nearly to the endolymphatic fossa, although its posterior limit is not certain (Fig. 2A). Its edges, formed by the thin cranial roof, sepa-



rate gradually as far anterior as the posterior opening of the olfactory canal. In front of this there is an abrupt change in the contour of the anterior cranial opening, the edges curving first laterally, then anteriorly and ventrally toward the rostrum. This part undoubtedly represents the *cavum praecerebrale*, and the point of change of contour is homo-

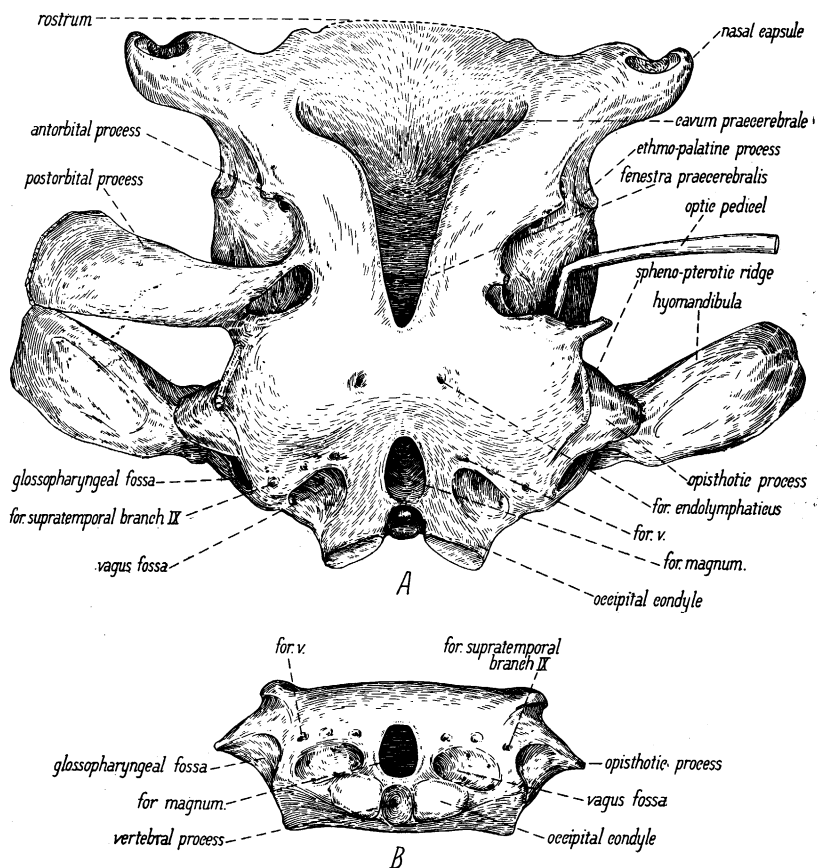


Fig. 2A. Neurocranium. Dorsal view.  $\times 3/40$ .

Fig. 2B. Neurocranium. Occipital view.  $\times 3/40$ .

gous to the process separating the *cavum praecerebrale* and *fenestra praecerebralis* in *Chlamydoselachus*. The sides of the *cavum praecerebrale* are formed anteriorly by the mesial wall of the olfactory canal; its floor is nearly flat except for a slight upward curvature to the sides.

The membrane separating the cavum praecerebrale and the cavum cranii was not preserved, but its probable position is indicated by a very faint backwardly convex ridge extending from the inner wall of the olfactory canal on either side.

In *Rhineodon* there is no distinct wall or process limiting the ethmoidal region posteriorly. From the nasal capsule there is a smooth slope dorsally to the cranial roof, ventrally to the floor of the cranium, and laterally to the ethmo-palatine process and to the small crest of the antorbital process. There are no ethmoidal grooves as in other sharks.

#### Orbito-temporal Region

The orbito-temporal region (Figs. 1*B*, 2*A*) is large, occupying well over a third of the total length of the cranium. Its anterior wall is not prominent and slopes back gradually into the mesial wall. Dorsally there is a small antorbital process from which a crest slopes down anteriorly and laterally toward the ethmo-palatine process. Anterior to the antorbital process and beneath this crest is the large orbital opening of the orbito-nasal canal which extends through the ethmoidal region to the ectethmoidal chamber, entering it just anterior to the cranial opening of the olfactory canal. Behind the orbito-nasal foramen and below the antorbital process is the much smaller foramen for the profundus nerve. Its canal runs anteriorly and somewhat dorsally to open on the flat cranial roof in the posterior ethmoidal region. The preorbital canal for the ophthalmicus superficialis nerve is represented on the right side by a mere perforation of the overhanging posterior rim of the antorbital process; on the left side this nerve passes through the supraorbital membrane and does not perforate the cartilage.

Postero-mesial to the pre-orbital foramen and just below the overhanging edge of the base of the antorbital process is the moderately large orbital opening of a short canal which runs mesially, ventrally, then mesially again to the cranial cavity. Its cranial opening is five inches behind that of the orbito-nasal canal with which it has no communication. This canal is transversed by a vein, and seems to be homologous with the canal described by Allis in *Chlamydoselachus* (1923, p. 133), which transmits the anterior cerebral vein from the brain to the orbit. He considered it to be a remnant of the basal communicating canal of Gegenbaur.

Anteriorly, the roof of the orbit consists of a narrow, overhanging eave. Since the supraorbital branches of the ophthalmicus superficialis nerve pass up more laterally, it is unpierced by foramina with the



exception of the preorbital canal on the antorbital process. Posteriorly, there is a long, flat postorbital flap, arising from the cranial roof by two processes which are separated by a membranous fenestra (Fig. 2A). This peculiar cartilaginous extension passes laterally over the posterior orbital region toward the angle of the jaw, near which the eye is located. It serves as a roof for this part of the head and may also serve as a dorsal shield for the eye itself, but this could not be determined since its most distal part had been cut off.

The orbital region is limited ventrally by a subocular shelf (Fig. 1B) whose lower surface is flat and continuous with the base of the cranium. Its lateral edge, which forms a slight projection in the contour of the ventral view of the cranium, is moderately thin, and from it there is a concave slope up to the mesial wall and roof of the orbit. The lateral edge of the subocular shelf thickens anteriorly, and below the antorbital process passes into the relatively small orbital or ethmo-palatine process (= basal process? See Goodrich, 1930, p. 414). The latter is a flattened knob, elongated antero-posteriorly, and covered with a thick pad of connective tissue. Its articulation with the palato-quadrate is discussed below. In its posterior part, and under the trigemino-facialis foramen, the subocular shelf is pierced by the orbital artery. The short canal for this artery comes from a groove in the base of the cranium which is shallow as it starts near the edge of the cranium just anterior to the hyomandibula, but deepens as it runs mesially and somewhat anteriorly (Fig. 3A). In this groove runs the common carotid artery, off which the orbital artery branches three and a half inches from the edge, and passes up through the subocular shelf. The other branch, the internal carotid, follows the groove to its foramen six inches from the mid-line, then passes into the cranial cavity.

The mesial wall of the orbit (Fig. 1B) is pierced near the middle by a very large foramen communicating with the cranial cavity. Its shape is oval, much elongated in an antero-ventral direction. Through the most ventral part of this foramen passes the optic nerve, while another nerve, apparently the trochlear, makes its exit through the posterior and dorsal corner. Fusion of the optic and trochlear foramina in this manner is quite exceptional among selachians. On the left side the optic artery passes through this foramen also, but on the right side there is a small perforation of the postero-ventral edge of the foramen for this artery. Ventral to the posterior part of the large optic-trochlear foramen, and below the base of the eyestalk are two relatively small foramina within a single shallow depression. The more dorsal of these

is the orbital opening of the canalis transversus which transmits the pituitary vein. The more ventral and anterior is the foramen for the efferent pseudobranchial artery.

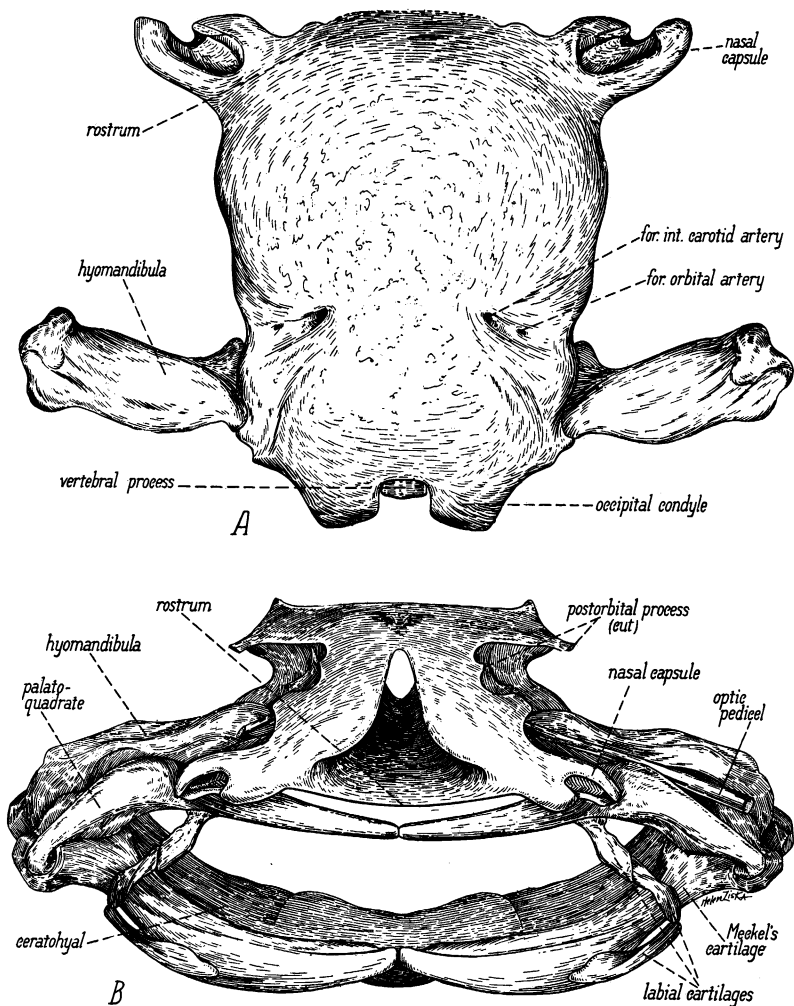


Fig. 3A. Neurocranium. Ventral view.  $\times 3/40$ .

Fig. 3B. Skull. Anterior view.  $\times 3/40$ .

In *Rhineodon* the otic region is widely expanded laterally, and its anterior wall limits the orbital region posteriorly and forms the



hind wall of the two large foramina for cranial nerves III, V, VI and VII. It is difficult to determine the homologue of the postorbital process described by Allis in *Chlamydoselachus* (1923) and by Gegenbaur (1872) in *Hexanchus*, *Heptanchus* and other sharks. The flap-like roof over the postorbital region, which was mentioned above, appears to be largely a secondary extension, but its basal processes by which it attaches to the cranium may well represent the postorbital process, *sensu stricto*. In any case, its ventral extension into the orbital region has been almost entirely lost.

Below and between the bases of each postorbital flap, in the most dorsal part of the orbit is a considerable fossa, completely filled with soft tissue. This fossa is deepened postero-mesially and is separated from the large oculomotor foramen posterior to it by a sharp, curving ridge. As far as could be determined, this fossa had no communication except externally, and its function and homology are unknown. On the ridge limiting this fossa anteriorly, that is, the ridge from the base of the anterior part of the postorbital process, there is a small foramen. This communicates by its canal with a correspondingly small opening in the cranial cavity over the optic-trochlear foramen. On the right side there is a second foramen just anterior to the postorbital process on the edge of the cranial roof. The cranial opening of its canal is close in front of the foramen just mentioned. On the left side only the posterior of these could be found, and appeared to carry a small blood vessel.

In the postero-dorsal corner of the orbital region is a large foramen opening into the cranial cavity in a postero-mesial direction. Its canal is separated laterally from the one below for the trigeminal, facial and abducens nerves by a shelf extending from the opisthotic process of the otic region anteriorly and mesially to the inner wall of the orbit. Dorsally it is continuous with a fossa directly posterior to the fossa beneath the anterior part of the postorbital process. Out through the ventral part of this foramen passes the oculomotor nerve, while the ophthalmicus superficialis branch of the fifth and seventh cranial nerves makes its exit dorsally.

In the postero-ventral corner of the orbit is a deep fossa into which open anteriorly the canals for the pituitary vein and efferent pseudo-branchial artery, laterally the canal for the orbital artery, and in whose posterior part is a large foramen for the trigeminal, facial and abducens nerves. The first of these nerves (V) makes its exit antero-ventrally, the second (VII) postero-ventrally, and the third (VI) dorsally. The

canal for these nerves unites with that for the oculomotor and superficial ophthalmic internally, and all of the nerves enter the acustico-trigemino-facialis recess of the cranial cavity together.

The shelf which separates the oculomotor and trigeminal-facial-abducens canals expands lateral to the optic-trochlear foramen and forms a base for the optic pedicel (Figs. 1B, 2A). The latter starts

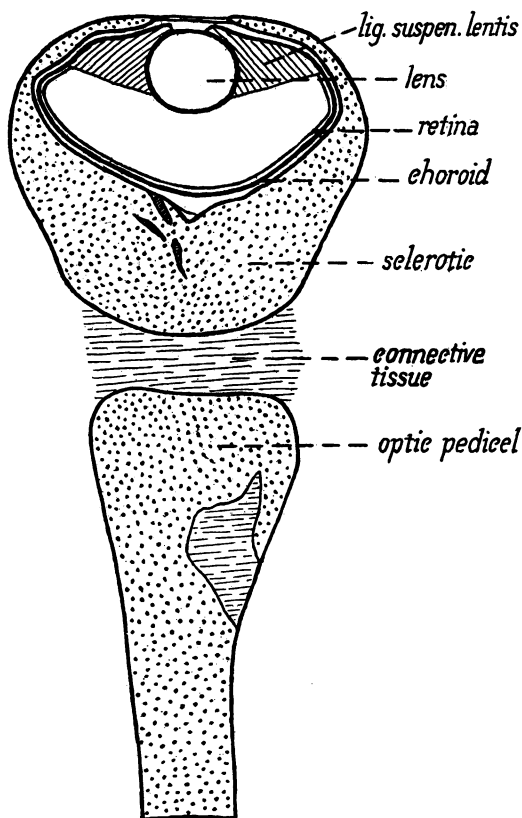


Fig. 4. Section through eyeball and optic pedicel.  $\times 3/4$ .

narrowly from this base and extends directly anteriorly for four and a half inches, expanding somewhat. At this point there is a right-angle bend and the eyestalk runs laterally and somewhat ventrally to the eyeball. Its section throughout this part is oval, flattened dorso-ventrally, with a maximum diameter of about one and a half inches. The length of this stalk from the bend could not be accurately determined



since the distal part had been cut off, but it must have been nearly fifteen inches.

The eye is located just dorsal to the articulation of the palatoquadrate and Meckel's cartilage, and is supported in this lateral position on the slightly swollen end of the elongate optic pedicel (Figs. 3B, 4). Relative to the size of the head it is very small, having a maximum diameter antero-posteriorly of two and a half inches. In lateral view the eyeball appears to be a sphere, but from the dorsal or anterior side it is seen to have its greatest diameter laterally and to taper rather rapidly toward the slightly convex mesial surface. In section (Fig. 4) the great thickness of the cartilaginous sclerotic layer is striking; on the proximal side it is as much as one inch of the total transverse diameter of two and a quarter inches. It is pierced postero-ventrally by the optic nerve, and is deeply pitted on its inner surface by canals for branches of this nerve and blood vessels. The sclerotic layer tapers rapidly toward the cornea near which its diameter is only one-eighth of an inch or less. The choroid and retina are very thin, and the former has only a slight protuberance representing the corpus ciliare. The lens is symmetrically placed dorso-ventrally and antero-posteriorly. It is nearly a perfect sphere and is only slightly flattened transversely; its maximum diameter is eleven-sixteenths of an inch. A ligamentum suspensorium holds the lens in place.

### Otic Region

The otic region is the most massively constructed part of the cranium. It is here that the depth is greatest, and the width across the laterally extended processes above the hyomandibula articulation is only slightly less than the width of the skull at the nasal capsules. In transverse section, the otic region is roughly rectangular, elongated transversely, but the ends of the rectangle are widely drawn out at the prominent lateral process just mentioned.

The dorsal surface of this region (Fig. 2A) is limited on either side by a ridge which corresponds to the spheeno-pterotic ridge of *Chlamydoselachus* as described by Allis (1923, p. 155). This ridge is highest posteriorly where it is cut off quite abruptly at the occipital region, but anteriorly it slopes down gradually to blend with the cranial roof just behind the posterior process of the postorbital flap. Between the two spheeno-pterotic ridges there is a slight bulge or convexity of the dorsal surface of the cranium, depressed medially by the two shallow endolymphatic fossae which are so close as to be nearly confluent. In the

postero-lateral and deeper corner of each fossa is a single opening, giving passage to the exterior to both the endolymphatic duct and the perilymphatic canal.

The lateral surface of the otic region (Fig. 1*B*) is dominated by a

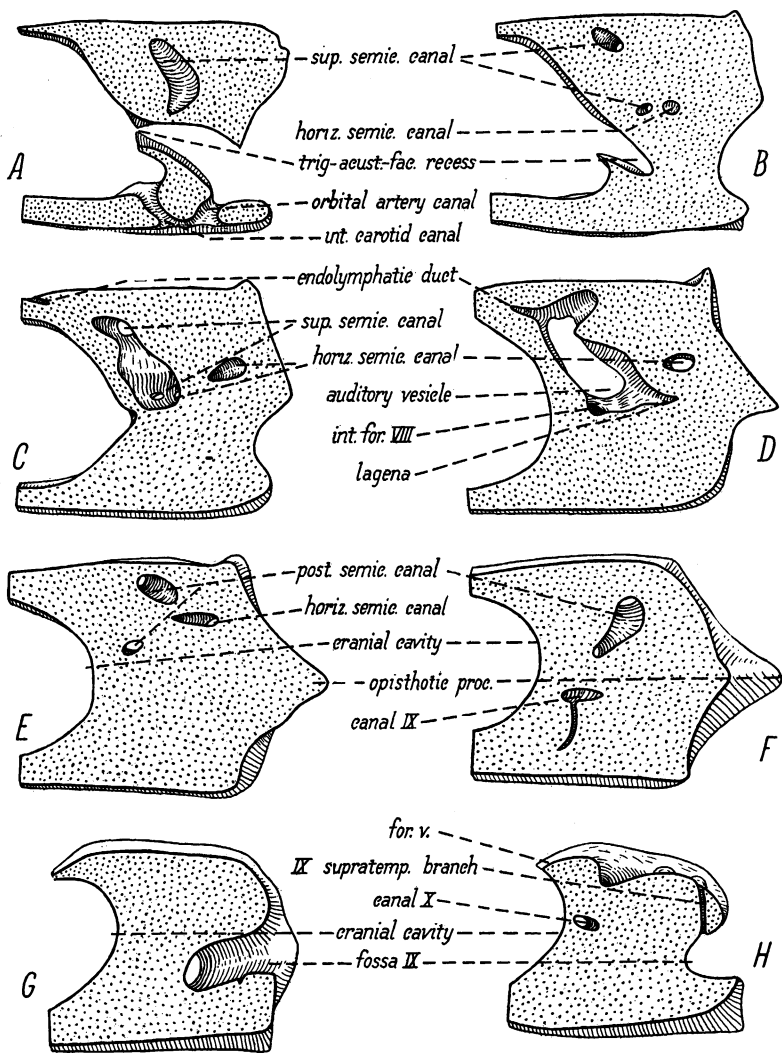


Fig. 5. Transverse sections through the otic region of the cranium. Right side. (A, anterior; H, posterior.)  $\times 1/8$ .

prominent process, broad and deep proximally, but tapering to a rounded point distally. It corresponds to the opisthotic ridge of Allis' description of *Chlamydoselachus* (1923, p. 157). Its dorsal surface slopes up mesially at an angle of about  $45^{\circ}$  to beneath the spheno-pterotic ridge, while its lower surface forms the upper part of the hyomandibular articulation and overlaps the hyomandibula considerably. The articulation for the latter consists of two grooves separated by a rounded ridge which extends from the posterior edge of the opisthotic process antero-ventrally to the ventral edge of the lateral surface of this region. The posterior groove, for the posterior articulatory process of the hyomandibula, extends antero-ventrally from below the glossopharyngeal foramen. The ridge, described above, which limits it anteriorly, fits into the deep proximal groove of the hyomandibula. From this ridge, the other groove extends anteriorly and slightly dorsally, and receives the anterior articulatory process of the hyomandibula. The latter groove is bounded above by the rather sharp antero-lateral edge of the opisthotic process, but is open in front toward the orbital region. The articulation of the hyomandibula will be discussed further below.

There is a slightly obtuse angle between the lower part of the lateral surface and the ventral surface of the otic region. From this angle arises the ridge separating the anterior and posterior hyomandibular facets. Mesially from this angle stretches the flat expanse of the ventral surface of the otic region.

The labyrinth region was studied by means of transverse serial sections at intervals of approximately one inch (Fig. 5). These showed little of the soft tissues, but the latter can be determined in part from the spaces in the cartilage which surrounds them. The auditory vesicle shows practically no constriction in the middle, but the dorsal utriculus enlarges gradually to pass into the ventral sacculus. From the latter there is a narrow, pointed, lateral extension representing the lagena. The auditory nerve passes from the cranial cavity through its short canal to the ventro-mesial corner of the vestibule. From the sacculus the endolymphatic canal leads upward through the vestibule, in the dorsal part of which it turns mesially toward its foramen in the endolymphatic fossa. The perilymphatic canal opens into the dorsal part of the perilymphatic space of the vestibule immediately below the turn in the endolymphatic duct, and follows close below the latter to its fenestra which is confluent with the foramen ductus endolymphatici. The semicircular canals appear to differ in no important respects from the typical shark type.

## Occipital Region

In *Rhineodon* the posterior occipital surface (Fig. 2B) is a rather steep, convex slope downward from the posterior roof of the otic region. Although this slope is interrupted by foramina and condyles, it may be thought of as extending to an edge, deepest medially, but higher laterally. This edge marks the beginning of the posterior part of the base of the cranium, which slopes down and anteriorly to its broad, flat expanse farther forward.

In the median and most ventral portion of the occipital surface is an oval-shaped, calcified, occipital process resembling half of an amphicoelous vertebra. Its posterior surface is a conical depression, perforated at the center for the passage of the notochord into the base of the cranium. Since the edges of this cone are raised above the surface of the occiput, it is a true process and not merely a depression as in *Chlamydoselachus*. It articulates through a notochordal intervertebral ring with the corresponding middle calcified ring of the first vertebral centrum.

Projecting from the occipital surface on either side of the vertebral process is a rounded, knob-like condyle. In section the condyles are oval, with a maximum diameter of three and a half inches transversely and a lesser diameter of two and a half inches dorso-ventrally. There are slightly convex articulatory surfaces on the posterior ends for corresponding depressions on the anterior surface of the first vertebral centrum. These surfaces are not parallel to the occipital surface, but are directed posteriorly as well as laterally from the median vertebral process.

The foramen magnum is situated directly above the median vertebral process in the sloping occipital surface. Its shape is oval, with a diameter of four and a half inches dorso-ventrally and three inches transversely.

On either side of the foramen magnum, and dorsal to each occipital condyle is a large, oval vagus fossa, deepest mesially where the vagus foramen is located. From the latter, the short vagus canal leads into the posterior cranial cavity. The cranium, as far as could be determined, includes only a single occipital nerve whose foramen is directly posterior to the vagus foramen on the rim of the vagus fossa. Its canal passes directly mesially to open just inside the foramen magnum. Within the vagus fossa there are three or four other foramina for small blood vessels which were not traced.

Above the mesial part of each vagus fossa is a relatively small

foramen, the external opening of a canal which passes anteriorly and inward to open in the cranial cavity above and in front of the inner vagus foramen. It transmits a vein and probably corresponds to foramen *v* of Gegenbaur (1872, p. 35) for the internal jugular vein. Lateral to foramen *v* there are two round depressions in the posterior occipital slope. The more lateral communicates by a small canal with the dorsal surface of the glossopharyngeal fossa and may be for the supratemporal branch of the ninth nerve. The more mesial of these shallow depressions, although resembling the other externally in every respect, appeared to have no internal communications.

The large glossopharyngeal fossa (Fig. 1*B*) is located in the posterolateral corner of the cranium between the posterior occipital slope and the opisthotic process. Inwardly the deep pit or fossa grades into a true canal which passes antero-mesially to the cranial cavity. It is posterior and ventral to the labyrinth region from which it is widely separated by cartilage (Fig. 5). Into the lateral portion of the canal, or more properly the fossa, opens dorsally the canal for the supratemporal branch of the glossopharyngeal nerve, as mentioned above.

### Cranial Cavity

The cranial cavity (Fig. 6) is very large relative to the size of the brain, which occupies only a small area on the floor of the posterior third of the cavity. The remainder of the space is loosely filled with a tangled network of fibrous connective tissue. In the anterior and shallowest part of the cranial cavity, the fenestra praecerebralis, described above, forms a long, V-shaped gap in its cartilaginous covering, and is closed dorsally and anteriorly by a membrane, not preserved in this specimen. Just behind the anterior part of the membrane in the antero-lateral corner of the cavity is the inner opening of the olfactory canal. Postero-dorsal to the latter on the side wall is the inner opening of the so-called basal communicating canal. The floor in this anterior region is smooth, flat and relatively thin, and there is no indication of an angulation called by Gegenbaur the "Basalecke" (1872, p. 59).

The large foramen for the optic and trochlear nerves is just anterior to the middle of the cranial cavity. Above it are the two small foramina of uncertain homology and function, which communicate with the postero-dorsal part of the orbital region. As mentioned above, only the posterior of these foramina was found on the left side and appeared to transmit a small blood vessel.



On the floor of the cranial cavity is a swelling or ridge extending from beneath the optic-trochlear foramen on either side postero-mesially to the mid-line. Directly behind this ridge is a groove into which opens the canal for the internal carotid artery four and a half inches from the mid-line, and that for the efferent pseudobranchial artery farther laterad under the optic-trochlear foramen. The efferent pseudobranchial artery passes down the groove mesially from its foramen, joins the internal carotid artery, and the common artery thus formed extends as a commissural vessel to join that of the opposite side. The ridge bounds the pituitary fossa anteriorly, but is evidently homologous with the ridge which forms the anterior boundary of the posterior and

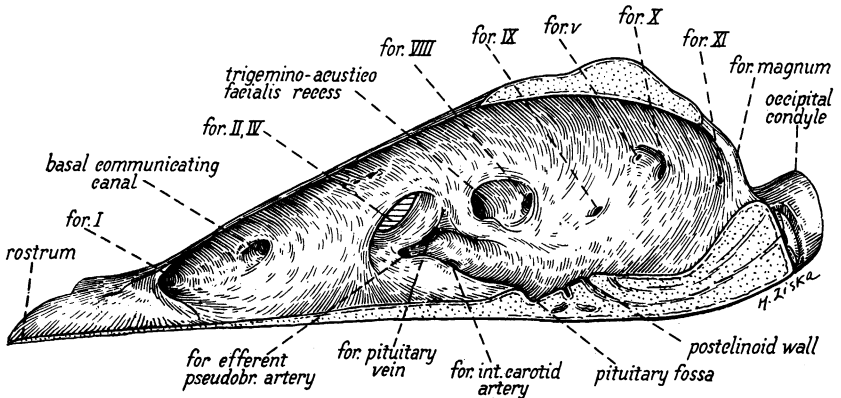


Fig. 6. Median view of right half of sectioned cranium.  $\times 1/8$ .

deeper portion of the pituitary fossa of *Chlamydoselachus* (Allis, 1914, p. 228). In the latter shark, the pituitary fossa extends anteriorly to the presphenoid process which is not found in *Rhineodon*.

The pituitary fossa is bounded posteriorly by the postclinoid wall, a rounded swelling whose apex is indicated by an intermittent streak of notochordal tissue which extends into it. This wall extends laterally to the side wall of the cranium below and anterior to the trigemino-acustico-facialis recess. In the latter region it is hollowed out to form a fossa and is pierced by the canalis transversus for the pituitary vein. The opening of the latter is only a short distance posterior to the foramen for the efferent pseudobranchial artery. The pituitary vein passes mesially in the posterior part of the pituitary fossa, and in the mid-line appears to receive a branch coming from the cartilage of the floor of the cranium below the notochordal tip.

In the wall of the cranial cavity above and behind the inner opening of the canalis transversus is a deep pit known as the trigemino-acustico-facialis recess. The abducens nerve issues through the dorsal part of this recess, the trigeminus and facialis nerves through the ventral part, while the auditory nerve enters its foramen in the postero-mesial portion. In contrast to the typical selachian condition, the oculomotor nerve likewise leaves the cranial cavity through the trigemino-acustico-facialis recess. Half way to the exterior of the cranium it separates from the other nerves, except the ophthalmicus superficialis with which it issues by a separate dorsal foramen. The trigemino-acustico-facialis recess is separated from the pituitary fossa and the anterior foramina by a thin wall, directed obliquely postero-ventrally. This wall is not homologous to the "alisphenoid" cartilage of Sewertzoff (1899) or the prootic ridge of Allis (1914) since it is anterior to the oculomotor nerve.

In the otic region the cranial cavity is deep, but it is narrowed by the inward swelling of the walls of the labyrinth. The roof is thicker here than elsewhere in the cranium and is hollowed out on either side of the mid-line by the endolymphatic fossae. The floor is likewise thick and shows in section an interrupted streak of notochordal tissue extending from the vertebral process to the postelinoid wall. Dorsal to the notochordal streak in the basis cranii is a broken band of soft connective tissue leading to a pit behind the postelinoid wall. A similar inclusion of soft tissue in the basis cranii of *Chlamydoselachus* was considered by Allis (1914, p. 231) to be a possible remnant of an extension of the ligamentum longitudinale dorsale inferius of the vertebral column. The floor of the cranial cavity shows a strong upward flexure posteriorly toward the foramen magnum. The relatively small brain is correspondingly flexed as it extends from the foramen magnum to the postelinoid wall. As far as could be determined under the poor conditions of preservation, the brain does not extend in front of the postelinoid wall.

The foramen for the auditory nerve is in the posterior part of the trigemino-acustico-facialis recess, as mentioned above. Directly posterior to it is the foramen for the glossopharyngeal nerve, while the vagus foramen and foramen *v* for the internal jugular vein are dorsal and posterior to the glossopharyngeal foramen. The roof of the cranial cavity slopes down and the floor slopes up to the foramen magnum in the middle of the occipital surface. Just inside the foramen magnum is the inner foramen for the only occipital nerve.

## VISCERAL SKELETON

The mandibular and hyoid arches of *Rhineodon* have been illustrated and briefly described by E. Grace White (1930), but with this more complete material it is possible to make certain additions to her description. Figures 1A and 3B show the mandibular and hyoid arches mounted on the neurocranium. Unfortunately the position of the elements in these reconstructions cannot be considered as typical in every respect, but illustrates the peculiar adaptation of this strange shark which consists primarily in great enlargement of the mouth, especially transversely, brought about by a laterally directed suspensorium.

## Labial Cartilages

Three labial cartilages (Figs. 1A, 3B) were found, arranged in a single series which is attached loosely by connective tissue dorsally to the palato-quadrate and ventrally to Meckel's cartilage. From these points of attachment, the labial cartilages form an acute angle with the apex directed postero-laterally, and limit the mouth on either side. The dorsal element is short, widened where it is attached to the lower and outer surface of the palato-quadrate in front of the ethmo-palatine process, constricted in the middle, and widened again distally where there is an oblique surface on its end for the second cartilage. The second element is also short and is directed ventro-postero-laterally as is the dorsal piece. It has an oblique surface on its upper end by which it articulates with the upper cartilage and a rounded knob-like end for the lower labial. The ventral element, which forms the lower side of the angle of the mouth is more than twice as long as either upper piece. Laterally it is slender and rod-like, but anteriorly and mesially it expands into a thick, wide blade, an extension of which fits into a depression on the dorsal part of the outer surface of Meckel's cartilage anterior to the middle.

The homologies of these elements with those of other selachians are not certain. The two ventral pieces, however, appear to correspond to the two labials of the posterior series of *Chlamydoselachus*, *Scymnus*, *Mustelus* and other sharks, while the dorsal piece is probably the homologue of the anterior labial of those sharks, which has moved into line with and become attached to the dorsal one of the posterior labials. This is borne out by the fact that the levator labii superioris muscle passes dorsally posterior to it.

### Mandibular Arch

The palato-quadrate cartilage (Figs. 1A, 3B) is extremely reduced, and consists merely of a twisted rod, stoutest proximally, but very slender distally. It articulates with Meckel's cartilage at two points, first at the knob which forms its proximal end, and second at a concave facet on the ventral surface four inches antero-mesial. From this point, the palato-quadrate rod curves dorsally, anteriorly and somewhat mesially, and rapidly separates from Meckel's cartilage. This type of double articulation seems to indicate that the mouth is kept open habitually and only closed spasmodically to gulp in water or food. Near the middle of the palato-quadrate, the ethmo-palatine process is represented by a slight knob-like swelling on the mesial surface opposite the corresponding process in the anterior orbital or posterior ethmoidal region of the cranium. Both processes are thickly covered with a pad of capsular connective tissue and have no ligamentous connection. This articulation of the palato-quadrate with the cranium is obviously very loose; in fact it was not possible to bring the two processes into contact in setting up the specimen, although no doubt this is accomplished in life in certain positions of the jaws. In front of the ethmo-palatine process the palato-quadrate diminishes rapidly in diameter as it curves mesially under the nasal capsule and then passes straight to the mid-line to meet the opposite half below the end of the flat rostrum (Fig. 3B). The straight anterior part is flattened dorso-ventrally and bears a band of minute teeth on its ventral surface (White, 1930, pp. 142-144, text-fig. 9, Pls. x, xi).

Compared to the palato-quadrate, Meckel's cartilage (Fig. 1A, 3B) is tremendously developed, and is very deep, especially posteriorly, although it is rather thin. From the posterior part of the main ramus, a large knob-like process extends postero-mesio-dorsally to articulate with the hyomandibula. Projecting laterad from the main ramus at its posterior end is a large process, swelling dorsally where it receives the proximal articulation of the palato-quadrate in a concave facet; this is the sustentaculum of Gegenbaur. The second palato-quadrate articulation is a small knob, antero-mesial to the first and on the dorsal edge of the main ramus of the palato-quadrate.

Posteriorly Meckel's cartilage is deep and thin with a sharp dorsal edge, but as it curves antero-mesially toward the opposite half it becomes shallower and thicker. Toward the front the dorsal surface is wide, with a groove in the middle for the tooth band. The groove is bounded in front and laterally by a sharp edge, and postero-mesially by

a ridge which approaches the lateral edge and disappears posteriorly. The two opposite Meckel's cartilages meet in the mid-line only dorsally, where they are attached loosely by a ligamentous band, but ventrally and posteriorly they are separated by a small, oval, median basimandibular cartilage (Fig. 10*B*). The latter underlies the coraco-mandibularis muscle.

Between the palato-quadrate and hyomandibula are two small cartilages related to the spiracle. The more anterior and ventral has the form of a short rod, while the other is a mere nodule at its postero-dorsal end. They lie morphologically anterior to the pseudobranchial artery and ventral to the musculus levator maxillae; they also appear to be in the anterior wall of the spiracular canal, and thus are probably true spiracular cartilages.

#### Hyoid Arch

The hyomandibula (Figs. 2*A*, 3*A*) is a tremendously massive cartilage, projecting normally almost directly laterad from the cranium. Its articulation with the cranium consists of a rounded groove cutting across its proximal end from the postero-dorsal to the antero-ventral corner. Above the anterior part, and below the posterior part of this groove are two flange-like processes which fit into the anterior and posterior grooves of the otic region as described above. These two flanges restrict antero-posterior movement of the hyomandibula to some extent, but dorso-ventral movement is quite free except as it may be limited dorsally by the opisthotic process of the cranium.

The massive ramus of the hyomandibula has a greater diameter antero-posteriorly than dorso-ventrally. Its ventral surface is convexly rounded while the dorsal surface is somewhat hollowed out and is bounded posteriorly by a ridge which curves anteriorly around the distal end above the articulatory surface for the ceratohyal. This articulatory surface is irregularly rounded and bears no very distinct facets, grooves or processes. An ill-defined ridge or swelling in the middle of the ventral part of the surface fits into the groove on the corresponding surface of the ceratohyal. But the movement of the latter cartilage on the hyomandibula is very free, and is limited dorsally only by a small cartilage nodule. The articulation of Meckel's cartilage is even less restricted. The knob-like extension of Meckel's cartilage has no corresponding facet on the hyomandibula, but moves freely against the rounded antero-ventral part of the distal end of the latter. There was found no long, thin process for the articulation with Meckel's

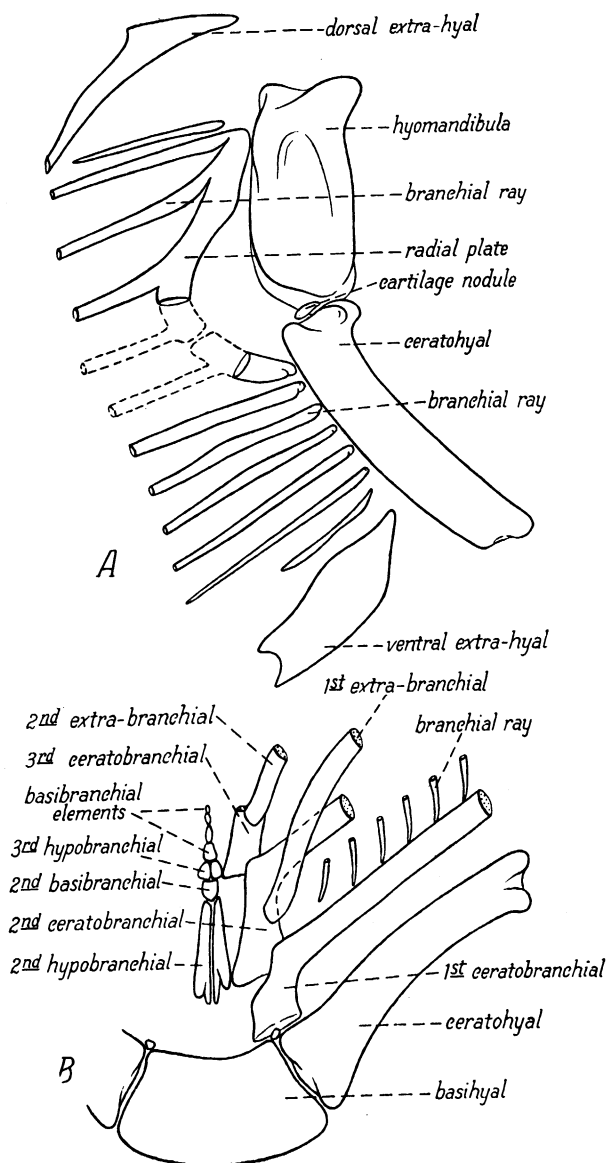


Fig. 7A. Diagrammatic representation of the hyoid arch and its branchial rays.  $\times 1/16$ .

Fig. 7B. Ventral view of the hyoid arch and parts of the first to third branchial arches.  $\times 1/16$ .



cartilage as described by White (1930, p. 140). A complex arrangement of ligaments binds together the various cartilages of the mandibular and hyoid arches in this region.

The ceratohyal (Figs. 1A, 7) is a strongly developed cartilage, thicker than Meckel's cartilage, but not as long or as deep. Its proximal end rises above the main shaft, and has a rounded and shallowly grooved surface for the hyomandibula and the small cartilage nodule which bounds it dorsally. Ventrally, its proximal end is extended posteriorly to form a right angle which serves as an attachment for a ligament. The main shaft is of rather uniform shape, and is flattened-oval in section. It curves mesially then anteriorly, and broadens and flattens distally toward the basihyal. The articulation with the latter is thin and wide, directed antero-laterally, and is brought into a nearly horizontal plane by a slight twisting of the shaft of the ceratohyal.

The median basihyal (Fig. 7B) joining the two ceratohyals, has a broad, flat form. The flat upper surface has a transverse width of eighteen inches at its widest part near the front, but tapers posteriorly; its greatest antero-posterior measurement is eight inches. The lower surface is deepest half-way between the anterior and posterior edges. From here it slopes up to meet the dorsal surface in the sharp, anteriorly convex front edge, and it also slopes up to the posterior edge which is not as thin and is concave anteriorly. The basihyal fits inside the inner surface of Meckel's cartilage and continues the contour of the floor of the mouth which is marked anteriorly by Meckel's cartilage.

The branchial rays of the hyoid arch of this specimen had been partly cut away, but enough remained to show the general arrangement (Fig. 7A). In the upper or hyomandibular segment only four rays were preserved. Of these the proximal ray, which is the shortest and most slender, is free from the hyomandibula and the other rays. The other three rays arise from the posterior edge of a flat rod to which they are fused. This rod articulates proximally with the posterior surface of the hyomandibula, then curves backward so that the branchial rays become quite widely separated from the hyomandibula. The distal part of the rod and any rays which were attached to it had been cut off, but it extended undoubtedly as far as the hyomandibula-ceratohyal joint and may have carried one or two additional branchial rays.

The arrangement is more simple in the lower or ceratohyal segment. There are seven rays of which the most distal or ventral is small and free as is the dorsal ray in the upper segment. The next five rays are long, slender, simple rods which articulate with the ceratohyal on its

postero-ventral surface. The most dorsal or proximal ray of this segment also articulates with the ceratohyal, but is a larger and flatter cartilage and curves dorso-laterally. Its distal part had been cut off, but it seems likely from its position and shape that it extended upward to meet the ray-bearing rod of the dorsal segment, and may itself have carried one or two branchial rays.

The arrangement of the hyoid branchial rays in *Rhineodon* is not unlike that described by Fürbringer in some other selachians. *Cestracion*, for example (Fürbringer, 1903, p. 445, Pl. XVIII, fig. 34), has several of the rays of both the dorsal and ventral segments carried on dorsal and ventral plates distinct from the hyomandibula and ceratohyal. He considers these "Radienplatte" (radial plates) to be formed by the concrescence of the bases of several radials; together with attached rays they form a "Radienkamm" or radial comb.

There is an extra-hyal cartilage in both the dorsal and ventral segments. The dorsal extra-hyal is long and rod-like with an antero-posteriorly expanded dorsal end. The ventral extra-hyal is long, thin and flat; it has a narrow, pointed anterior or ventral end, and a posterior or dorsal end with two processes separated by a bay.

### Branchial Arches

Only fragments of the branchial arches were preserved, but in view of the rarity of *Rhineodon* it is considered worth while to describe them briefly. The first pharyngobranchial consists of a deep vertical plate passing forward into a short rod-like extension which terminates in a convex articulatory surface for the epibranchial. The plate-like portions is located beneath the lateral part of the first vertebrae. Only the proximal part of the first epibranchial was preserved. The dorsal part of this cartilage is somewhat flattened transversely and extended antero-posteriorly, and bears a rounded concave facet for the pharyngobranchial at its postero-dorsal corner. Anteriorly, at the base of this expanded portion is a small process bearing a minute, pointed cartilage nodule terminally. The proximal or dorsal part of the epibranchial passes rapidly into a cylindrical rod which bears the branchial rays.

In the ventral segments of the branchial arches (Fig. 7B), parts of the first three ceratobranchials were preserved. Each of these consists of a long, somewhat curved, cylindrical rod extending dorsally toward the corresponding epibranchial and bearing the branchial rays on its posterior border, and a flattened, antero-mesially directed ventral portion. The latter part of the first ceratobranchial articulates

anteriorly with the posterior border of the hyoid arch at the joint between the ceratohyal and basihyal; there is a small cartilage nodule at this joint. Posteriorly it overlaps ventrally the flat extension of the second ceratobranchial with which it articulates. The second ceratobranchial has a similar articulation with the third; it also meets ventrally its related hypobranchial.

Arranged along the median line is a series of small median and paired cartilages representing all that remains of the hypo- and basibranchial elements. Anteriorly is a pair of long, flat cartilages, meeting in the mid-line and expanding slightly in front to meet the most anterior part of the second ceratobranchial. These are evidently the second hypobranchials, and thus there are no hypo- or basibranchials related to the first arch. A median element posterior to these hypobranchials is the second basibranchial, which is succeeded by two small paired cartilages, the hypobranchials of the third arch, which articulate with the anterior part of the third ceratobranchial. Behind these are four or more small median cartilage nodules of irregular shape and position. They represent the posterior basibranchials in a degenerate condition.

The ventral extra-branchials (Fig. 7*B*) are long, curved, cylindrical rods. That of the first branchial arch arises from the ventral flattened surface of the lower part of the second ceratobranchial, then curves postero-dorso-laterally behind the branchial rays of the first arch. The second extra-branchial arises similarly from the third ceratobranchial.

## MUSCLES

### Muscles of the Eyeball

The muscles of the eyeball are of exceptional length, of course. The four rectus muscles are peculiar in arising from a single tendon (Fig. 9), which has its origin just behind that of the optic pedicel on the shelf separating the oculomotor from the trigemino-facialis foramen. This tendon passes laterally, and at a distance of six inches from its origin gives rise to the four slender rectus muscles which extend on the four sides of the eyestalk the rest of the distance to the eyeball. The rectus externus (posterior), the smallest of the rectus muscles, passes along the posterior edge of the optic pedicel to be inserted on the posterior rim of the eyeball (Fig. 8*A, B*). As is the case with the other rectus muscles, it divides near its insertion into two parts, a deeper slip being inserted directly on the eyeball, and a more super-

ficial slip inserted on connective tissue covering the eyeball. The rectus externus is innervated by the abducens except in its most proximal part where it appears to receive a small branch of the oculomotor. The rectus inferior (Fig. 8B) extends down the anterior half of the ventral surface of the eyestalk, then curves posteriorly to be inserted on the most ventral part of the rim of the eyeball. The rectus internus (anterior) and rectus superior muscles are united for part of their extent into a single, large flat muscle. Three inches from the eyeball

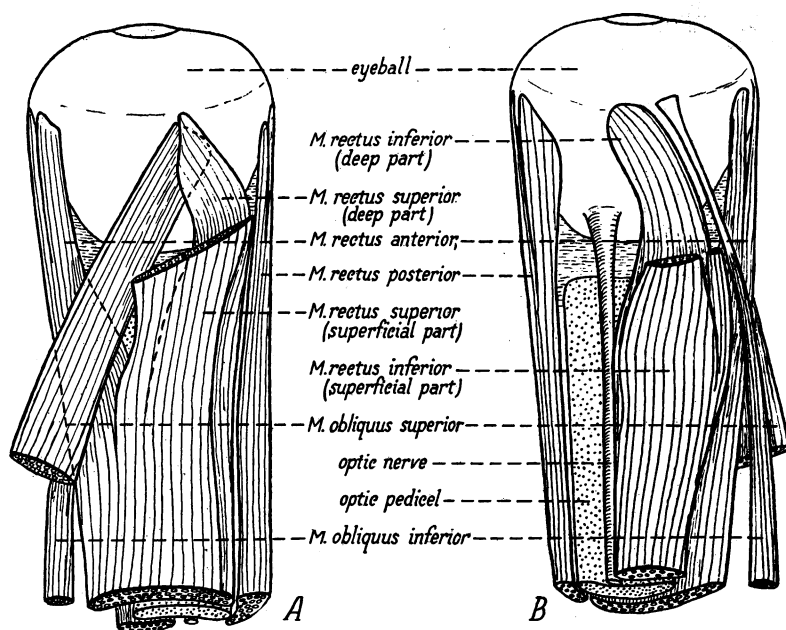


Fig. 8. Distal portion of eyeball muscles. A. Dorsal view. B. Ventral view.  $\times 1/2$ .

this divides into its two components, of which the smaller rectus internus passes below the obliquus superior, and is inserted on the anterior part of the rim of the eyeball. From the point of separation, the rectus superior has a narrow but thick deep portion, and a wide but thin superficial portion. Its insertion on the dorsal rim of the eyeball covers that of the obliquus superior (Fig. 8A).

The tendon of the rectus muscles forms the hypotenuse of a triangle of which the two limbs of the optic pedicel form the other sides.

This triangular space is filled proximally by a muscle mass of peculiar appearance, whose bundles curve between their origin on the eyestalk and their insertion on the rectus tendon (Fig. 9). It is likely that this muscle is derived from one or more of the rectus muscles, but this is uncertain since its innervation was not determined. It serves as a retractor of the eyeball.

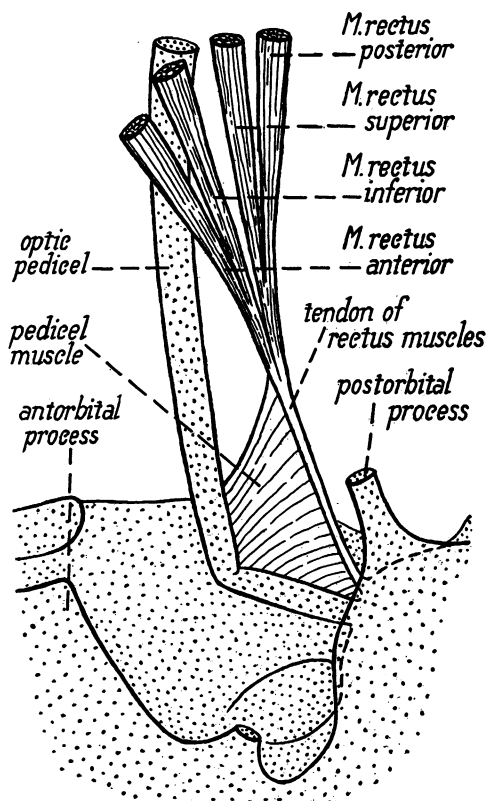


Fig. 9. Proximal portion of rectus muscles of eyeball and of optic pedicel. Dorsal view.  $\times 3/16$ .

The origin of the oblique muscles was not found, but is probably tendinous. Distally these muscles approach the eyeball from the front at a low angle (Fig. 8). Of the two oblique muscles, the obliquus superior is much the larger. It crosses the rectus internus dorsally, passes below the superficial portion of the rectus superior, and is inserted directly beneath the insertion of the deeper portion of the

latter on the dorsal rim of the eyeball. The obliquus inferior, the smallest of the eye muscles, is extremely slender and is tendinous in its most distal one and a half inches. It crosses the rectus internus ventrally, follows the anterior edge of the rectus inferior, and is inserted just anterior to the latter on the ventral surface of the eyeball.

#### Muscles of the Mandibular Arch

The levator labii superioris muscle (Fig. 10A) is inserted by means of two rather short tendons among the fibers of the adductor mandibulae lateralis muscle opposite the dorsal edge of Meckel's cartilage. It enlarges rapidly as it curves dorsally, mesial to the labial cartilages and lateral to the palato-quadrato. At the latter, the muscle had been cut and could not be traced directly to its origin. However, its origin is indicated almost certainly by a group of muscle fibers attached to the dorsal surface of the cranium and spread from in front of the antorbital process to the anterior part of the postorbital process. The usual ventral origin of the levator labii superioris is made impossible by the terminal position of the palato-quadrato.

The adductor muscle of the mandibular arch (Fig. 10A) may be divided into three parts comparable to those in some rays (see Tiesing, 1896, p. 87-90), although not approaching the complexity of the latter. *Musculus adductor mandibulae lateralis* is inserted near the middle of the outer surface of Meckel's cartilage on which it reaches nearly to the ventral border and to the insertion of the ventral constrictor. It extends dorsally on the anterior border of the main adductor mass, receives the tendons of the levator labii superioris, and apparently passes outside the latter to its origin on the middle part of the outer surface of the palato-quadrato. The adductor mandibulae medialis forms the main part of the adductor mass, and may be divided into two portions itself. The deeper part (*M. adductor mandibulae medialis I*) arises from the outer surface of the palato-quadrato, from the proximal end of the latter to the origin of the lateralis portion of the muscle. Its fibers pass ventrally, arching out and back around the angle of the mouth, and are inserted near the lower border of Meckel's cartilage from the proximo-ventral angle to the insertion of the lateralis portion. The smaller, more superficial part (*M. adductor mandibulae medialis II*) arises from the adductor mandibulae medialis I muscle immediately underlying it and from the proximo-lateral corner of the palato-quadrato. It passes postero-ventrally as an ellipse-shaped muscle, widest at the middle, and narrowest at the ends, and is inserted on the



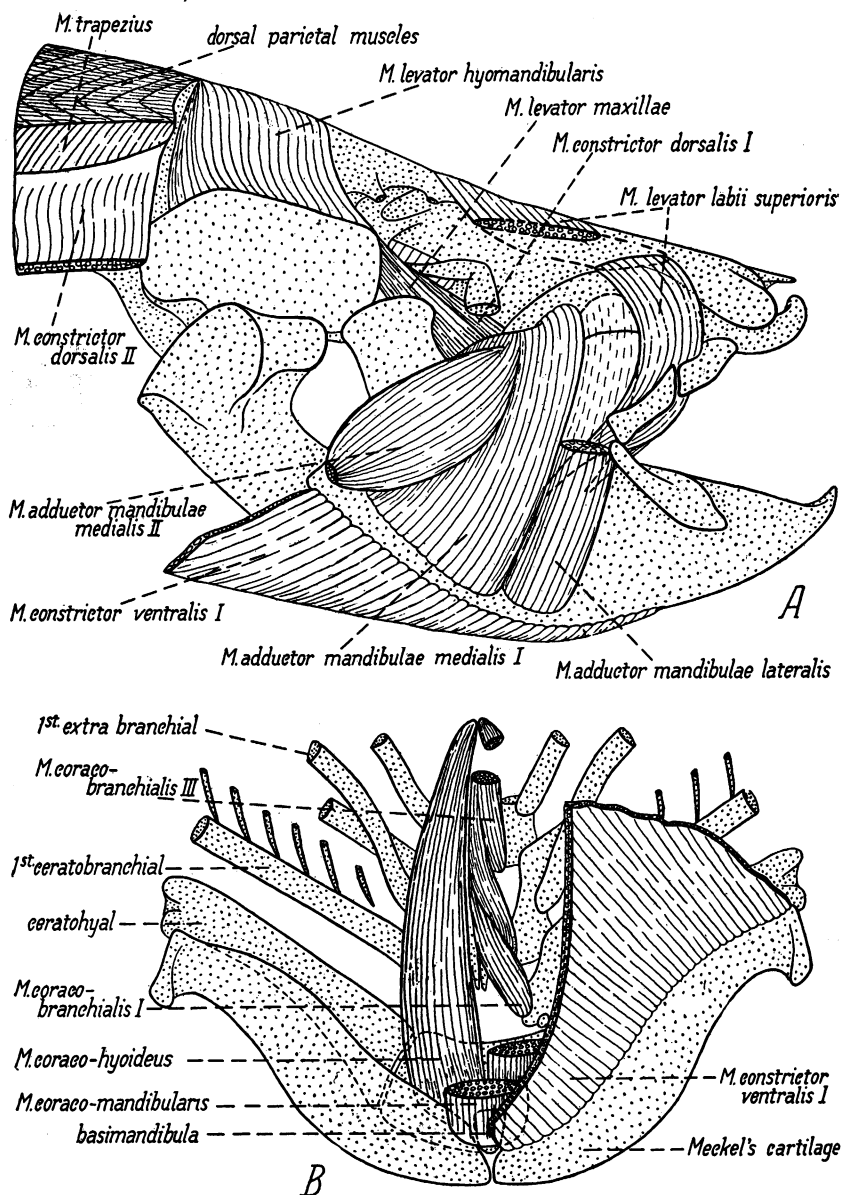


Fig. 10A. Muscles of skull. Right side.  $\times 1/8$ .

Fig. 10B. Hypobranchial muscles. Ventral view.  $\times 1/16$ .

postero-ventral angle of Meckel's cartilage, and also apparently in the second ventral constrictor muscle.

The levator maxillae and first dorsal constrictor muscles (Fig. 10A) are indistinctly separated, and arise together from below the posterior part of the postorbital process. The levator maxillae arises from the outer posterior border of the oculomotor-ophthalmicus superficialis foramen and from the overlying first dorsal constrictor. The first dorsal constrictor arises largely from the ventral surface of the postorbital flap and also from the lateral surface of the cranium below the postorbital flap. Together the two muscles pass antero-laterally and slightly ventrally in front of the spiracle to the inner surface of the palato-quadrate, on which they insert in front of the anterior articulatory facet for Meckel's cartilage.

Of the ventral superficial constrictor muscles, only the first and part of the second were preserved. They form a thin sheet of muscle extending between the ventral elements of the mandibular and hyoid arches and covering the hypobranchial muscles (Fig. 10B). The more superficial layer of this sheet is the first ventral constrictor. It arises from a median aponeurosis and the fibers pass diagonally antero-laterally to be inserted on the ventro-lateral edge of Meckel's cartilage along its whole length. The insertion is entirely distinct from the adductor mandibulae muscle except posteriorly where a few fibers of *M. adductor mandibulae medialis* II apparently pass into the first ventral constrictor. The deeper layer of this muscular sheet, which is the anterior part of the second ventral constrictor, also arises from a median aponeurosis. The fibers run antero-laterally, parallel to those of the first ventral constrictor, and are inserted on the postero-ventral surface of the ceratohyal and on the ventral surface of the basihyal up to the mid-line.

### Muscles of the Hyoid Arch

The levator hyomandibularis (Fig. 10A) is a large, powerful muscle, entirely distinct from the rest of the second dorsal constrictor from which it is derived. It arises from the speno-pterotic ridge on the dorso-lateral angle of the otic region, and its fibers pass laterally then curve anteriorly to be inserted on the distal end of the dorsal surface of the hyomandibula.

The rest of the second dorsal constrictor arises from fascia surrounding the dorsal parietal muscles and curves laterally, then ventrally as a thin sheet. Its most lateral part had been cut away.

The second ventral constrictor, a muscle related to the hyoid arch, was described above in connection with the first ventral constrictor.

### Hypobranchial Muscles

Only the insertion of the median coraco-mandibularis muscle was preserved, but this shows it to be a very powerful muscle with an oval transverse section and a maximum diameter of approximately seven inches. It is inserted by means of a short tendon on the postero-medial corners of the ventral surfaces of Meckel's cartilages and on the basi-mandibular cartilage (Fig. 10*B*).

The paired coraco-hyoideus muscles are extremely powerful, and lie on either side of the mid-line dorsal to the coraco-mandibularis. Posteriorly near their origin from an aponeurotic septum (of the coraco-arcuales communis) they are rather slender, but they enlarge gradually anteriorly until they nearly equal the coraco-mandibularis in size. Their fibers are inserted directly, without any tendinous bridge, on the ventral surface of the basihyal.

The coraco-branchialis muscles (Fig. 10*B*), the deepest of the hypobranchial system, were preserved only anteriorly. The first and most anterior coraco-branchialis muscle arises from the second and from an aponeurosis surrounding the coraco-hyoideus muscle dorsally. Its fibers run antero-laterally to be inserted on the ventral surface of the antero-mesial flange of the first ceratobranchial; there is no connection with the hyoid arch. The second coraco-branchialis muscle arises in part in common with the first from the aponeurosis on the dorsal surface of the coraco-hyoideus muscle, and in part from the third. It is inserted on the ventral surface of the antero-mesial flange of the second ceratobranchial. The third coraco-branchialis muscle has a similar insertion on the third ceratobranchial.

The coraco-arcuales communis muscles were not preserved in this specimen.

### Other Muscles

The dorsal parietal muscles (Fig. 10*A*) are inserted on the posterior occipital slope of the cranium, and extend onto the roof of the otic region as far anteriorly as the endolymphatic fossa in the middle and as far as the speno-pterotic crest at the side; laterally they are inserted over the glossopharyngeal foramen. They extend posteriorly on either side of the mid-line as a thick mass of muscle on the concave

dorso-lateral surface of the vertebrae. The myocommata are directed first postero-ventrally then antero-ventrally.

The anterior part of the trapezius is represented evidently by a tongue of muscle between the dorsal parietal muscles and the dorsal constrictor muscle sheet. The fibers, which run obliquely postero-ventrally, arise from fascia of the dorsal parietal muscles, and also from the cranium above and behind the glossopharyngeal foramen.

The various muscles of the branchial arches, the adductors, interarcuales and interbranchiales, were not well enough preserved to merit description.

#### PELVIC FIN AND CLASPERS

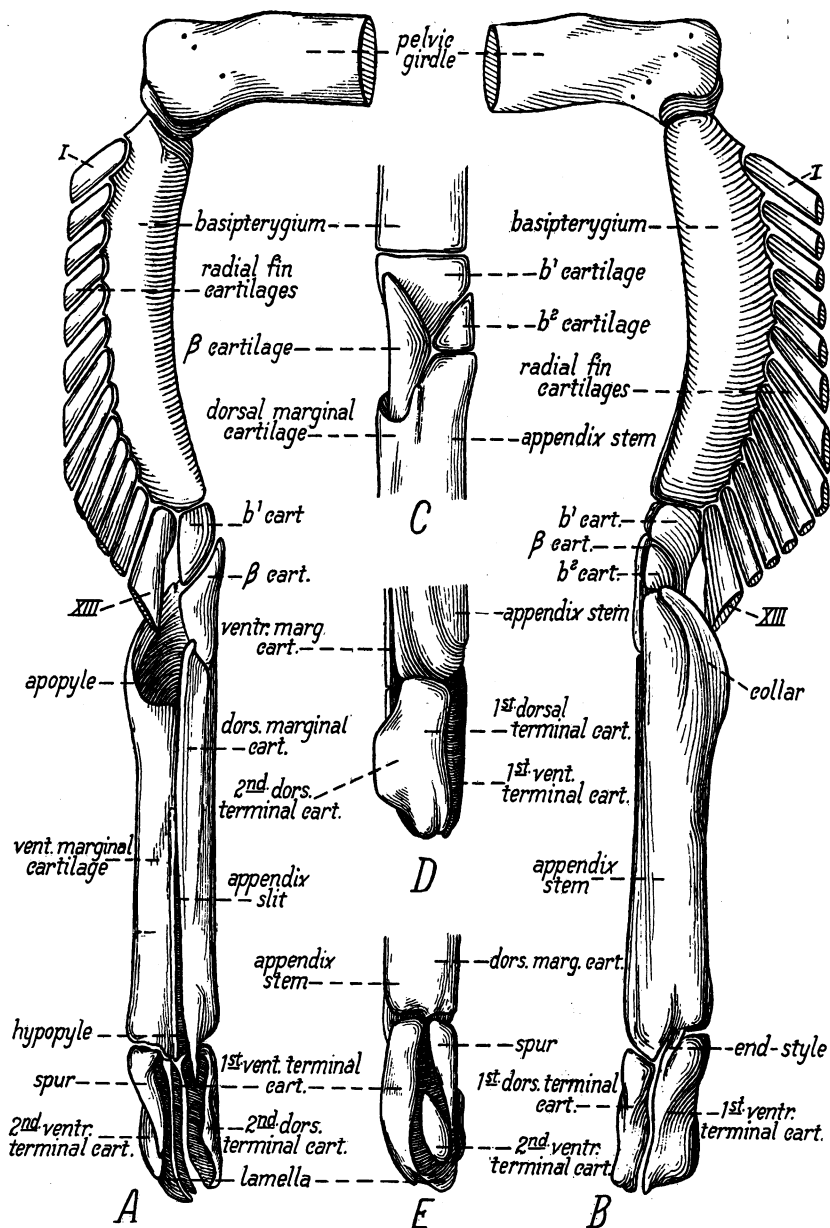
The myxopterygia or skeletal parts of the claspers have been described by E. Grace White (1930), but in view of the greater completeness and better preservation of this material it is considered worth while to make certain additions to her description. The muscles of the fin and claspers have also been determined.

#### SKELETON

The pelvic girdle (Fig. 11A, B) is a rather wide, flat cartilage having slightly concave articulatory surfaces at its postero-lateral corners for the basipterygia. Ventrally there are four foramina for diazonal nerves, but due to union of the two posterior canals, there are only three foramina on the dorsal surface. The greatest transverse measurement of the pelvis is sixteen inches, while its antero-posterior dimension at the middle is three and a half inches.

The basipterygium (Fig. 11A, B) is a massive cartilage articulating with the pelvis proximally by a flattened concave surface. Its greatest length, not following the outward curvature at the middle, is thirteen and three-quarters inches. Laterally there are concave facets for the radial fin cartilages of which there are thirteen on the left and fourteen on the right side. The posterior radial on both sides is considerably larger than the others, and articulates with cartilage  $b^1$  as well as with the basipterygium. That it may be of double origin is suggested by a division of its dorsal radial muscle.

The main joint in the myxopterygium (Fig. 11C) consists of three relatively small cartilages ( $b^1$ ,  $b^2$  and  $\beta$ ) between the basipterygium and the appendix stem. The position of these small elements when the pelvis is directed in its normal ventro-lateral direction is such that the joint is nearly twice as thick dorso-ventrally as it is transversely.



Figs. 11A and B. Skeleton of left pelvic fin and clasper. A. Dorsal view. B. Ventral view.  $\times 1/7$ .

Fig. 11C. Joint between basipterygium and appendix stem. Mesial view.  $\times 1/7$ .

Figs. 11D and E. Terminal cartilages of left clasper. D. Mesial view. E. Lateral view.  $\times 1/7$ .

This hinge-like arrangement means that the appendix stem may be moved with very little difficulty in a transverse direction, but that dorso-ventral movement is strictly limited. It has been stated that the claspers of some sharks are bent forward nearly  $180^\circ$  during copulation, but it is difficult to see how this could occur in *Rhineodon* with this type of joint, even if the basipterygium were so twisted on the pelvis that the hinge were horizontal. During dissection it was impossible to bend the appendix stem more than  $45^\circ$  from the relaxed or horizontal position, but movement may have been restricted to some extent by drying of ligaments.

The myxopterygia figured and described by Dr. White (1930) are peculiar in the pitted surface of the cartilage and in the rough, irregular edges of the various pieces. This condition does not occur in the present specimen, and is thought to be due to preservation in formalin and eating away of the limy portions of the skeleton.

The chief elements of the myxopterygium, the appendix stem and its marginal cartilages, have been described quite completely by Dr. White and little need be added. There is some confusion, however, in the determination of the position of the myxopterygium in her plate (1930, Pl. XII). Morphologically (that is, according to the terms used in morphological descriptions) the appendix slit is lateral and the appendix stem mesial. But actually, in *Rhineodon*, the appendix slit is dorsal and the appendix stem ventral in the relaxed position. Thus in the plate mentioned, Figure *a* is correctly labeled "dorsal" from a morphological point of view, though it is really mesial. Figure *b*, labeled "medial," is morphologically lateral, actually dorsal. In this paper, all references are to the actual position while the clasper is relaxed and directed posteriorly.

With regard to the terminal pieces (Fig. 11 *A, B, D, E*) there is great confusion, and it is difficult to make homologies of the various elements with those of other sharks. This is due in part to the use of different names in the literature, and in part to the great variability of these terminal elements even in closely related forms. It is possible, however, to make general homologies with some certainty.

The cartilage continuous with the axial rod or appendix stem in the terminal region was named the end-style by Jungersen (1899, p. 18). This is represented evidently in *Rhineodon* by a slender, conical rod of soft cartilage which forms part of the "axial terminal" of Dr. White. This does not show clearly as a separate element in the present specimen, but is distinct at least proximally in the specimen described by Dr.



White. There it appears as a ventral process of the distal end of the appendix stem which is fused with the lateral elements forming the "axial terminal" more distally.

On either side of the end-style of sharks is a variable number of elements which are movable continuations of the dorsal and ventral marginals. These are the dorsal and ventral terminals of Jungersen (1899, p. 19). The dorsal terminal of *Rhineodon* is made up of two parts firmly attached to each other, though not fused. That next to the end-style (first dorsal terminal) is the most medial element of the "axial terminal" of Dr. White; it is not fused, however, to the end-style or other parts of her "axial terminal," but is entirely distinct from them. The other element (second dorsal terminal) is the dorsal terminal of Dr. White.

If the homology of the end-style in *Rhineodon* is correct, most of the "axial terminal" of Dr. White, that is, all lateral to the end-style, is really a ventral terminal (first ventral terminal); this would include the prominent lamella. Her ventral terminal would then be correctly identified, but it would be the second one.

The spur is evidently "T<sup>3</sup>" of Jungersen, which he considers a third ventral terminal. The thin calcified strip described by Dr. White on its outer surface is without doubt calcified connective tissue.

#### MUSCLES

The adductor (Fig. 12A, B) is a large, flat muscle which has its origin on the ventral and posterior surfaces of the pelvic girdle nearly to the mid-line. Ventrally it is divided into bundles which correspond to the ventral radial muscles of the fin, but this division does not appear on the dorsal surface. The fibers run posteriorly and laterally to be inserted on the mesio-ventral surface of the basipterygium. The last bundle is more distinct distally than the others and is inserted on the mesio-ventral surface of b<sup>1</sup> and b<sup>2</sup>; some of its fibers pass into the dilatator muscle. The proximal part of the large first radial muscle is continued onto the pelvis and is in series with the adductor bundles.

The internal flexor (Fig. 12A) arises broadly from the mesial edge of the distal half of the basipterygium. As the fibers curve mesially then back, the size of the muscle diminishes, and it passes into a short tendon before being inserted on the mesial edge of the  $\beta$  cartilage.

The external flexor (Figs. 12A, B) arises by a broad, flat tendon from the posterior edge of the pelvis near the mid-line, and its fibers run nearly directly posteriorly just dorsal to the adductor. Distally it

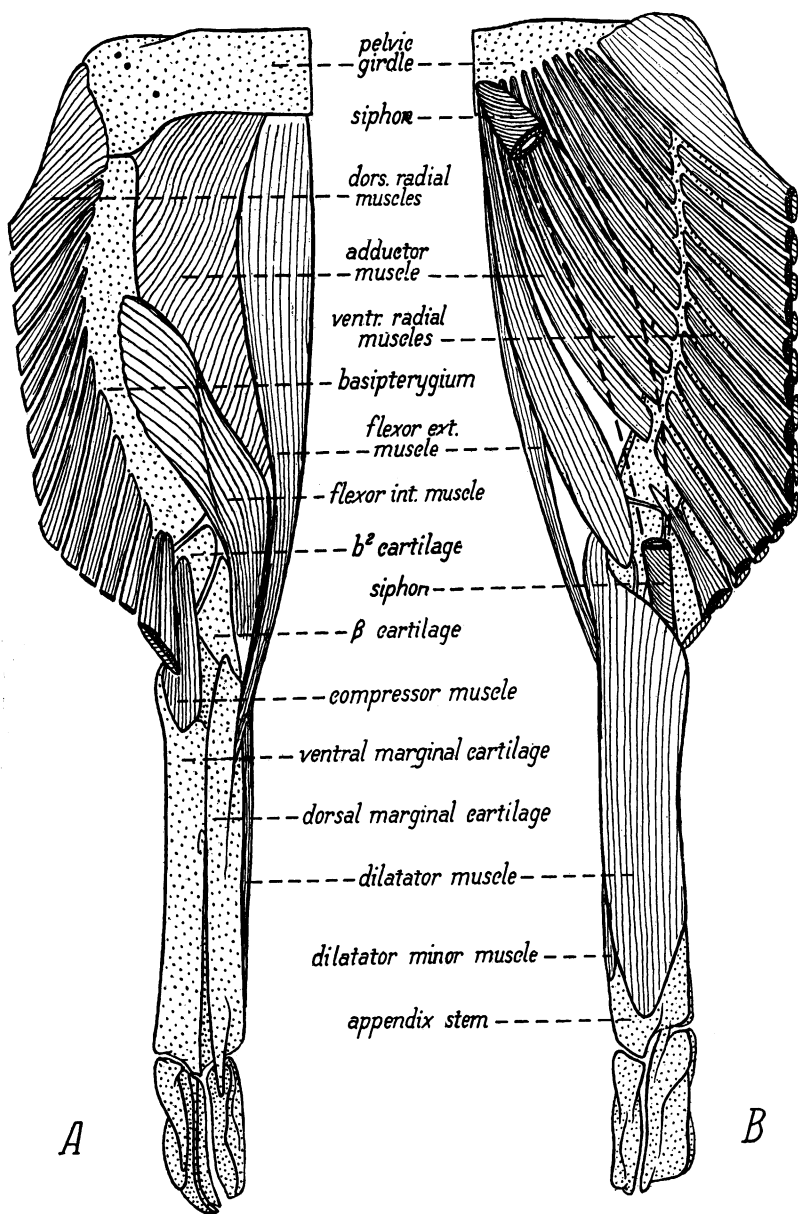


Fig. 12. Muscles of left pelvic fin and clasper. A. Dorsal view. B. Ventral view.  $\times 1/7$ .

diminishes in size, unites with the internal flexor and is inserted just posterior to the latter on the  $\beta$  cartilage and appendix stem; some fibers pass into the dilatator muscle.

The dilatator muscle (dilator of Daniel, 1934, p. 95) arises largely from the prominent collar of the ventral marginal cartilage which extends over the proximo-ventral edge of the appendix stem; but an anterior extension has its origin on the mesial surface of  $b^1$ ,  $b^2$  and  $\beta$ , to reach which it passes between the adductor and external flexor. The muscle fibers run posteriorly, wrapping the appendix stem, and are inserted in aponeurotic connective tissue near the distal part of that cartilage. Mesially and distally there is a slip which has been distinguished as *M. dilatator minor* by Huber (1901).

The compressor (Fig. 12A) is a small muscle arising from the distal and lateral edge of  $b^1$  just posterior to the origin of the last radial muscle. The fibers run posteriorly and are inserted on the edge of the ventral marginal cartilage just over the apophyle. Laterally and distally it is connected with the constrictor muscle of the siphon.

The siphon (Fig. 12B) is a tube or sac arising blindly near the midline just ventral to the pelvis, and running posteriorly and laterally to the apophyle where it is connected with the compressor muscle. It lies between the adductor muscle and the skin. Its walls are thick and muscular, and are composed of strongly striated fibers running in an obliquely circular direction. There is no sharp distinction, as in some sharks, between a siphon sac and a siphon tube (see Leigh-Sharpe, 1920-1926).

The dorsal radial muscles (Fig. 12A) arise from the dorsal surface of the basipterygium and more superficially from the body muscles dorsal to the basipterygium. The first is large and arises from the lateral margin and dorsal surface of the pelvis. The last is large also and shows some indication of a division into two parts. The bundles extend posteriorly and laterally and are inserted on the radial cartilages. There are thirteen radial muscles on the left side to correspond to the thirteen cartilages.

The ventral radial muscles (Fig. 12B) have a similar double origin. The deeper fibers arise from the basipterygium, while the more superficial arise from the belly muscles. They pass postero-laterally to their corresponding radials, but their insertion overlaps slightly onto the radial in front, a condition not found in the dorsal radial muscles. The first ventral radial is large and has a broad origin from the ventral surface of the pelvis in series with the adductor bundles. The last or

twelfth radial muscle is small, arising by a narrow tendon from the distal end of the basipterygium, and is inserted on both the twelfth and thirteenth radial cartilages. Thus there is one less ventral radial muscle than cartilage.

### MEASUREMENTS

Length of cranium from vertebral process to rostrum.....	31.0 in.
Width of cranium at nasal capsules.....	33.0
Width of cranium across ethmo-palatine processes.....	27.5
Width of cranium across opisthotic processes.....	28.5
Greatest depth of cranium (in otic region).....	11.0
Length of upper labial cartilage.....	4.7
Length of middle labial cartilage.....	5.5
Length of lower labial cartilage.....	13.0
Length of palato-quadrate following outside curve.....	34.5
Antero-posterior diameter of palato-quadrate in front.....	1.5
Dorso-ventral diameter of palato-quadrate in front of articulation for Meckel's cartilage.....	3.5
Length of Meckel's cartilage following curve of dorsal edge.....	34.0
Depth of Meckel's cartilage at posterior end.....	8.0
Greatest length of hyomandibula.....	18.0
Antero-posterior diameter of hyomandibula at middle.....	7.5
Dorso-ventral diameter of hyomandibula at middle.....	5.0
Greatest length of ceratohyal following curve.....	24.5
Depth of ceratohyal at middle.....	6.5
Greatest transverse diameter of basihyal.....	18.0
Antero-posterior diameter of basihyal along mid-line.....	8.7
Total length of pelvic fin and clasper extended.....	39.0
Length of basipterygium (not following curve).....	13.7
Transverse diameter of basipterygium at middle.....	3.3
Length of appendix stem.....	16.5
Transverse diameter of appendix stem at middle.....	2.8

### SUMMARY

A recent dissection of the head of the whale shark, *Rhineodon typus*, showed the skull to be a highly specialized derivative of the more normal shark type. The more striking modifications are the great increase in size, the enlargement of the mouth and its terminal position, the widening of the neurocranium, the reduction of the teeth to minute denticles, and the development of the gill rakers into complex horny sieves. These are all habitus characters, correlated more or less directly with its diet of minute forms of pelagic life. In the fundamental or heritage characters, however, *Rhineodon* corresponds closely with *Chlamydoselachus* and other sharks.

While the muscles of the neurocranium and visceral skeleton are typically selachian in their basic relationships and arrangement, they differ considerably in details of their form and attachments, as would be expected in such a highly specialized type.

The pelvic fin and clasper are not unlike those of other sharks, the greatest differences being in the always variable terminal cartilages of the claspers.

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