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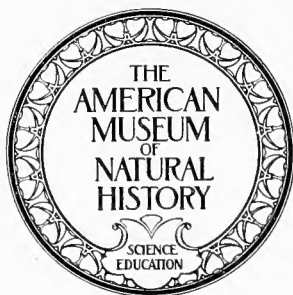
THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

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AND
ANALYTICAL SUBJECT INDEX



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OBITUARY

BERTRAM GARNER SMITH, 1876-1945

DR. E. W. GUDGER

AMERICAN MUSEUM OF NATURAL HISTORY

DR. SMITH was born October 7, 1876, at Painesville, Ohio, the son of Albert W. and Ella Garner Smith. He died of a heart attack at his home in Albuquerque, N. M., July 30, 1945. He is survived by his wife and a daughter. He was of New England ancestry, through his grandmother Smith, from the Mortons who settled New Salem, Mass., about 1660.

When Smith was about two years old, his parents moved to Youngsville, Warren Co., northwestern Pennsylvania. There he received his early education, graduating from high school in 1893. In 1894, he entered the Pennsylvania State Normal School at Edinboro and graduated in 1896. For the next two years he taught in the public grade schools of his section of Pennsylvania. From 1899 to 1902, during the winters, he taught the sciences in the High Schools of Warren, Dubois, and Corry, Pa., and between times attended the summer sessions of Cornell University. In 1903, he matriculated at the University of Michigan, where he was assistant in zoology to Professor J. E. Reighard 1904-07, and from which he graduated A.B. in 1907.

He was instructor in biology at Lake Forest College in the spring of 1907, in zoology at Syracuse University 1907-09, and at Wisconsin in 1909-11. In 1911, he entered Columbia University as a graduate student in zoology under Dr. Bashford Dean, and because of much published research, he was able to take his Ph.D. in 1912. From this year's work stemmed a lifelong friendship with Dr. Dean. From 1912-16, he was assistant professor of zoology at Michigan State Normal College and associate professor 1916-21. From 1921 to 1930 he was associate professor of anatomy in New York University



BERTRAM GARNER SMITH

Medical College and professor of anatomy from 1930 until his retirement in September 1942.

Over the years 1906–1929, Smith's scientific work was chiefly done on amphibians. Of his 49 published papers, 22 were on members of this group, and 13 of these dealt with the giant salamander, *Cryptobranchus allegheensis*. His interest in this dates from boyhood, when, fishing in the stream near his home, he would frequently catch a *Cryptobranchus* instead of a fish. Thus, when he learned of the importance of this animal from a zoological point of view, he knew where to find it. The breeding season and habits of this amphibian, sought for almost a generation, were a mystery until it was discovered that, unlike other amphibians, it breeds not in the spring but in the fall. Smith studied its habits and found how oviposition and fertilization are effected. His field observations ranged from 1905–1911, and his laboratory work from 1906–1929.

The difficulties of the field work of collecting and "fixing" the egg and life history stages were great. But quite as great were those of the laboratory work of embedding and sectioning these yolk-laden amphibian eggs averaging 6.2 mm. in diameter and exceeded in size only by those of *C. japonicus* (c. 7 mm. in diameter). Smith was a good artist and his papers are illustrated by his own drawings and photographs. The work on his articles, from start to finish, was done with his own hands. Unlike many researchers, he never had the help of assistants.

Smith's thirteen papers on the natural history and embryology of *Cryptobranchus* (published mainly in the *Biological Bulletin* and *Journal of Morphology*), range in date from 1906–1929. They comprise 484 pages and 590 drawings and photographs. Even a general examination of his papers on *Cryptobranchus* reveals what a prodigious amount of meticulous histological work he did on the development stages of these huge eggs and early embryos. I do not recall any vertebrate whose natural

history and embryology have been more thoroughly and successfully studied. These studies, together with those on *Amblystoma* and *Necturus*, comprise the major interest of the first period of his scientific activities.

The second period of Smith's productive scientific work began shortly after the death (December 6, 1928) of his teacher at Columbia, Dr. Bashford Dean. An organization of Dr. Dean's associates, students, friends and family was set up to establish memorials to him. Bronze plaques were cast and mounted in the American and Metropolitan Museums. Then came the question of what to do with four sets of splendid drawings (some in color) of certain archaic fishes—myxinoids and sharks—made for reproduction by lithography, and it was decided that these should be published as a Memorial Atlas under the direction of Dr. Smith and the writer (as editor).

After much thought, I determined that, instead of a Memorial Atlas, we would publish a Memorial Volume if I could have Smith's help, since his training in embryology and anatomy would be invaluable. And when next he came to my office, I announced my proposed plan and without a moment's hesitation he held out his hand and said—"I came to tell you just that thing. I, too, owe it to Dr. Dean." Nothing more clearly illustrates the spirit of the man. Then began work that covered 13 years and in which we did five of the eight articles in the volume. This was especially hard for Smith, who was carrying a full teaching load in the department of anatomy of New York University Medical College. Furthermore, it was time-consuming for him to come to and return from the American Museum. But for all that—he came.

In 1931 and 1933, we published two joint papers—one on the natural history of the frilled shark. Then came the long hard pull for more than three years in which Smith prepared his great "Anatomy of the Frilled Shark, *Chlamydoselachus anguineus*," (published 1937) of 190 quarto pages, 7 half-tone plates and 128 text-figures. In shark anatomy this book, on one shark only, measures up

to J. F. Daniel's "Elasmobranch Fishes" (3rd. ed., 1934, octavo, 322 pp., 270 figs.).

But even this was equalled by the final article in the Memorial Volume, "The Heterodontid Sharks: Their Natural History and the Development of *Heterodontus japonicus*, Based on Notes and Drawings by Bashford Dean."—138 quarto pp., 7 lithographed plates (5 in natural color) and 69 text-figs. This I (as editor) had held for Smith and for the final article in the Memorial Volume, and when (October 1, 1942) I handed him the first copy from the binder, I said, "This is the high note of the Volume, and also of your scientific writings." But little did I apprehend how true the latter statement was to be.

Dr. Smith retired from his work in N. Y. University, September 1, 1942, settled up his affairs in the East and presently went to Albuquerque, N. M., where he bought a house and settled down to adapt it and the grounds (with his own hands) to make it a home. Things went well until in the Spring of 1945 he began to have heart attacks, to one of which he succumbed on July 30. Thus passed a fine man, who made elaborate studies of the natural history and embryology of one of the least known American amphibians. Later he made similar additions to our knowledge of the natural history, anatomy and embryology of two archaic sharks. These notable monographs, the outcome of ability and persistent hard work, are the monuments in American Zoology to Dr. Bertram Garner Smith.

THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE VI

THE ANATOMY OF THE FRILLED SHARK
CHLAMYDOSELACHUS ANGUINEUS Garman

By BERTRAM G. SMITH
Professor of Anatomy
New York University College of Medicine
New York City



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ARTICLE VI

THE ANATOMY OF THE FRILLED SHARK
CHLAMYDOSELACHUS ANGUINEUS Garman

By BERTRAM G. SMITH

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THE ANATOMY OF THE FRILLED SHARK *CHLAMYDOSELACHUS ANGUINEUS* Garman

BY BERTRAM G. SMITH
Professor of Anatomy
New York University College of Medicine

INTRODUCTION

Interest in *Chlamydoselachus* centers around the problem of its affinities. It has been said (Garman, 1884.1, .2) to have "a certain embryonic look." It has been called a living fossil. It has been designated (Garman, 1884.3, .4; Gill, 1884.1, .2) the oldest living type of vertebrate. More conservatively, Woodward (1921, p. 37) regards *Chlamydoselachus* as one of the most primitive of the true Selachii. On the other hand, a study of the external characters alone (Gudger and Smith, 1933) is sufficient to indicate that *Chlamydoselachus* possesses many structural adaptations of a very special nature. In the present article I have endeavored to distinguish those features that represent a high degree of differentiation, from others that link *Chlamydoselachus* with the most primitive fishes.

Since the publication of Garman's (1885.2) description of a partly eviscerated specimen with a slightly mutilated tail, there has been no comprehensive account of the anatomy of *Chlamydoselachus*; but there have been many investigations dealing with particular organs or parts of the body of this rare fish. Some of these contributions were published in such form as to be readily accessible, but much information concerning the structure of *Chlamydoselachus* lies buried under titles of a somewhat general nature. In bringing together a digest of all these records I have endeavored to supplement them, wherever it seemed desirable and practicable, by original observations on all the material available.

This material includes three large female specimens (lengths 1350 mm., 1485 mm. and 1550 mm. respectively) brought from Japan by Dr. Bashford Dean, and now in the collections of the American Museum of Natural History; and a fourth large female specimen (1398 mm. long) kindly lent by Dr. E. Grace White. The first three specimens had been preserved in formalin and alcohol for about thirty years. The fourth shark had been preserved in formalin, then alcohol, for an unknown period. In all the specimens the viscera were in a more or less unsatisfactory condition for study, and from the fourth specimen the digestive organs had been entirely removed. Nevertheless, a careful exami-

EDITOR'S NOTE:—The first study of the anatomy of *Chlamydoselachus* was made by Samuel Garman at the Museum of Comparative Zoology, Cambridge, Mass., on the first specimen ever brought to America (1884). Garman's monograph was published in 1885 and is referred to herein as 1885.2. The original drawings and the woodcuts made from these have fortunately been preserved in Cambridge. They have been most kindly sent to me by Dr. Thomas Barbour, Director of the Museum of Comparative Zoology. Many of the woodcuts have become warped and split by drying during the past half century, but it is a great satisfaction to be able to use three of them (Text-figures 94, and 101A-B) in this paper, and to have new cuts made from certain of the original drawings—those representing the brain, which are reproduced here as Plate VI.

nation of this material has enabled me to fill in some of the most important gaps in the hitherto available knowledge of the gross structure of *Chlamydoselachus*. Our knowledge of this interesting fish is still incomplete, and one purpose of the present article is to direct attention to the opportunities for investigation that still exist for one who is able to secure favorable material.

Since the anatomy of the lower vertebrates is of interest chiefly from the comparative point of view, I have endeavored, within the limits imposed by practical considerations, to point out some of the resemblances and differences between *Chlamydoselachus* and other primitive sharks—particularly its nearest relatives, the Notidanidae. Fortunately for my purpose one of these, *Heptanchus maculatus*, forms the basis of Daniel's (1934) masterly treatise on the anatomy of the elasmobranch fishes—a volume which I have found very helpful.

For those who view this and similar undertakings from afar, it may be permissible to state that only anatomists and embryologists realize how much the study of elasmobranchs has contributed to our understanding of the present structure and past history of the human body.

EXTERNAL CHARACTERS OF *CHLAMYDOSELACHUS*

Since the external characters of the frilled shark have been described in detail by Gudger and Smith (1933), only a few of these features which are of particular significance for comparative anatomy need be considered here.

GENERAL FORM OF THE BODY

As compared with other sharks, *Chlamydoselachus* (Text-figure 1) is very slender. Therefore it is pertinent to inquire what an elongate form of body means in the evolutionary history of a group of vertebrates. In general, the most primitive members of any large and divergent group are only moderately elongate, while a high degree of speciali-



Text-figure 1.

Chlamydoselachus anguineus Garman, adult female, 1473 mm. long.

After Dean, 1895, Fig. 92; redrawn from Günther, 1887, Pl. LXIV.

zation may affect the body form in either of two ways: the body may become short and broad, as in skates, frogs and turtles; or it may become very slender, as in eels, coelilians and snakes. A consideration of the evidence upon which this generalization is based would take us too far afield, but it is a principle that appears to be accepted by most comparative anatomists.

In the case of *Chlamydoselachus*, the elongation of the body has proceeded far enough to remove it from the category of primitive characters. It serves, perhaps, as an adaptation to life on a rough sea bottom, where the animal is obliged, occasionally, to swim or crawl through crevices. In such situations, *Chlamydoselachus* may lie in hiding, or may even stalk its prey, then strike suddenly as does a snake. But there is another advantage to be gained from an elongate form of body. It may be observed that the

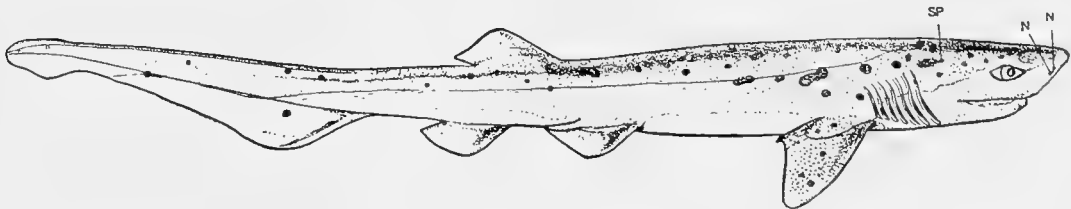
ectoparasitic cyclostomes have bodies that are very slender, and that *Echeneis*, the sucking fish, also is slender-bodied. These are creatures that fasten on to fishes larger than themselves and are towed along by the host. Owing to the slenderness of their bodies they are not readily shaken off. Because of the large mouth and the prehensile teeth (Text-figure 2), it has been surmised (Gudger and Smith, 1933) that *Chlamydoselachus* seizes and swallows living prey nearly as large as itself. The swallowing of a large fish struggling to escape is presumably not an easy matter, and were *Chlamydoselachus* a form that offered much resistance to being dragged through the water, it might not be able to maintain its initial hold.



Text-figure 2.

Front view of the widely-distended mouth of a specimen of *Chlamydoselachus* collected in Japanese waters by Dr. Bashford Dean and presented to Columbia University.

After Gudger and Smith, 1933, Fig. 3, pl. X.



Text-figure 3.

Heptanchus (*Heptabranhias*) *maculatus*, adult female.

NN, nares; SP, spiracle.

After Dean, 1895, Fig. 93.

More than in most sharks, the head of *Chlamydoselachus*, though not its body, is decidedly flattened in a dorsoventral direction when the jaws are closed. This, together with the fact that the creature is usually taken at great depths, suggests that the frilled shark is, at least partly, a bottom-dwelling form. We need not, however, conclude that the flattening of the head tends to remove *Chlamydoselachus* from the category of archaic fishes. "For various reasons it seems likely that the primitive chordates were not swift-swimming, pelagic types but partly depressed, partly bottom-living forms" (Gregory, 1933, p. 101).

Among living sharks the notidanid *Heptanchus maculatus* (Text-figure 3), though stouter-bodied than *Chlamydoselachus*, presents the greatest similarity in general form, position and shape of the fins, and in the shape of the tail. Throughout the present article I have made many comparisons between *Chlamydoselachus* and *Heptanchus*. Dean (1895) stated that "*Heptanchus*, of all living sharks, inherits possibly to the greatest extent the features of its remote ancestors." This is doubtless still a fair generalization when one considers only the external characters, but in many, perhaps most, of the internal structures described in the present article, *Chlamydoselachus* is less specialized than *Heptanchus*.

POSITION OF THE MOUTH

In *Chlamydoselachus* the mouth is sub-terminal (Text-figure 4, after Garman), but it approaches a terminal position to a degree found in no other shark, so far as I know, save only *Rhineodon*, the whale-shark. Sharks are pre-eminently surface-feeding forms, but the mouth is usually ventral. In skates and rays, which are bottom-feeding fishes, the mouth is decidedly ventral. In teleosts, with the exception of a few bottom-feeding forms, the mouth is terminal or subterminal. Thus in fishes the position of the mouth is decidedly variable. In linking the great groups of fishes, to assign phylogenetic value to such a character is hazardous. One cannot fail to note the resemblance, in the position of the mouth, between *Chlamydoselachus* and the teleosts, but their real relationship must be decided on the basis of more stable characters. Nevertheless, it may be pertinent to inquire, what is the primitive position of the mouth in the vertebrates?

Since in vertebrate embryos the mouth is ventrally situated, one might infer that this position is primitive for vertebrates. This inference is not supported by all the facts of development. The ventral position of the mouth of a vertebrate embryo is due, in part to a precocious enlargement of the anterior end of the brain, in part to the cephalic and cervical flexures which, in later development, tend to straighten out. If we consider only adult structures and accept the time-honored theory that the jaws represent a modified gill-arch, then the mouth is formed on the morphologically anterior side of this gill-arch. In its primitive position the mouth would naturally open forward, though situated at a lower level than the cranium and to this extent not fully terminal. The vertebrate mouth is, primarily, anteroventral or subterminal.

From its primitive position, the mouth may be displaced either ventrally or terminally. In elasmobranchs it is usually displaced ventrally by the thickening and forward elongation of the cranium to form a rostrum. In other words, when the cranium becomes extended anteriorly, the mouth of necessity becomes ventral. This may occur regardless of the size of the mouth. In the basking shark, *Cetorhinus*, the mouth is very large but is nevertheless ventral because of the elongate snout. In the sawfishes the prolongation of the rostrum is carried to an extreme that makes the mouth decidedly ventral. In teleosts the mouth tends more often to become terminal, though in some forms, as in the freshwater suckers, it is brought into a ventral position by an extensive development of the related soft parts.

I conclude that, in connection with its enormous enlargement, the mouth of *Chlamydoselachus* has departed only slightly from the primitive orientation, and that this departure has been in the direction of a more nearly terminal position. The anatomical basis for this condition is described more fully in the section on the skull. The position of the mouth is decidedly more primitive in *Chlamydoselachus* than it is in most elasmobranchs; it shows a closer parallel with the condition usually found in teleosts. But there is substantial evidence, which cannot be considered here, indicating that the line of cleavage between elasmobranchs and teleostomes extends back to forms more generalized than any living fish.

GILL-COVERS AND SPIRACLES

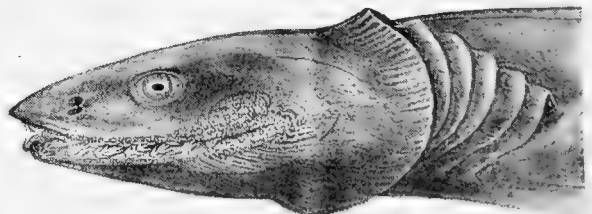
The presence, in *Chlamydoselachus*, of a sixth pair of gill-slits has usually been accounted a primitive character of considerable phylogenetic importance, linking *Chlamydoselachus* with the notidanids. But *Pliotrema*, a sawfish, has six pairs of gill-slits (Regan, 1906.1), differing in this respect from other sawfishes. While there is abundant ground for the conviction that *Chlamydoselachus* is related to the notidanids, one must not lean too heavily on the evidence afforded by the number of gill-slits. "In the existing elasmobranchs the normal number of gills is five and it may well be suspected that the six or seven gill-slits of the notidanids and the six of *Pliotrema* represent a secondary increase in number" (Gregory, 1933, p. 424).

In *Chlamydoselachus*, the unusually well developed first pair of gill-covers (Text-figure 4), continuous as the gular fold across the mid-ventral line, simulates an operculum such as is found in bony fishes. Garman (1884.2) suggested that this operculum-like fold or collar of *Chlamydoselachus* is a character indicating that the frilled shark lies near

Text-figure 4.

A side view of the head of *Chlamydoselachus* to show the position of the mouth, the length of the lower jaw, the position of the nostril and of the eye, and the position and form of the gill-covers; about one-fourth natural size.

After Garman, 1885.2, pl. I.



the primitive stock from which elasmobranchs and teleostomes diverged. On this point, Dr. W. K. Gregory, in a personal communication, commented as follows: "The idea that *Chlamydoselachus* stands nearer to the true fishes than do the sharks proper, is without a vestige of real evidence in its favor and with a mountain of evidence against it."

In *Chlamydoselachus* the external openings of the spiracles (Text-figures 70, p. 396; and 124, p. 489) are very small. In the notidanids the spiracles are said to be small. In some sharks that certainly bear no close resemblance to *Chlamydoselachus*, spiracles are absent altogether. In skates and rays, which are bottom-dwelling forms, the spiracles are proportionally large. It has been inferred that spiracles were developed in connection with a sea-bottom habitat; but this is true only of the valvular apparatus which, in skates and rays, enables the spiracle to function for the *intake* of water when the mouth is buried in sand or mud. In *Squatina*, a bottom-dwelling shark, the spiracles sometimes admit water to the oropharyngeal cavity. But sharks are characteristically free-swimming forms in which the spiracles, if present, serve merely for the *exit* of water from the pharyngeal cavity, thereby retaining their primitive function as gill-slits. This is the function of the spiracles even in *Chlamydoselachus*, as will appear from the description of the spiracular canal (p. 423) in the section on the respiratory organs.

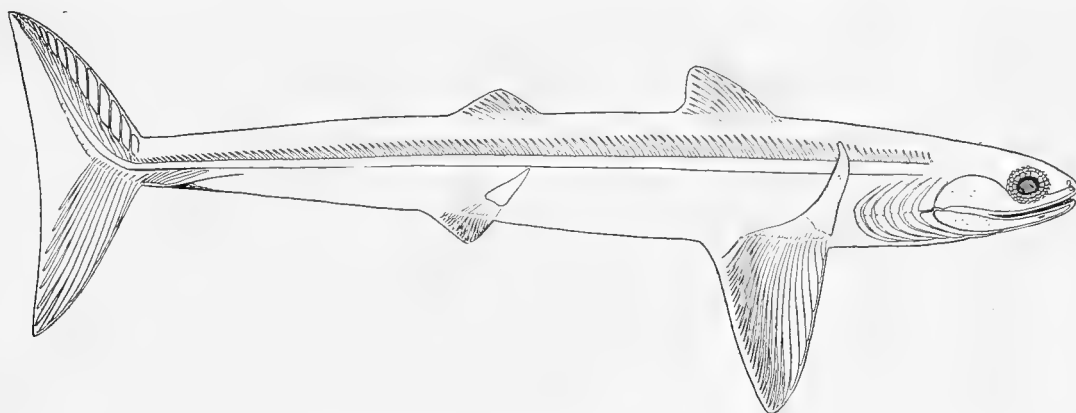
The small size of the external spiracular openings of *Chlamydoselachus* affords evidence that the spiracles are in a vestigial, not an incipient condition. Spiracles have not arisen *de novo*; they represent merely a modification, sometimes accompanied by a change in function, of a primitive pair of gill-slits situated between the mandibular and the hyoid arches. In the process of transformation of this primitive anterior pair of gill-slits into spiracles, the ventral portions of the openings close, while the dorsal portions persist—as is shown in Text-figure 62, p. 388. The internal aperture is much larger than the external. If one opens the mouth of any shark possessing spiracles, he will find a pair of large internal spiracular openings resembling gill-slits, in exact serial relation with the dorsal portions of the gill-slits. In *Chlamydoselachus*, whose external spiracular opening is a slit only 2 or 3 mm. long (Text-figures 70, p. 396; and 124, p. 489), the internal spiracular orifice is an elliptical aperture more than 20 mm. long and wide enough to admit easily the blunt end of a pencil. As in many other selachians, the spiracles of *Chlamydoselachus* possess vestigial gills, called pseudobranchs.

FINS, PAIRED AND UNPAIRED

The bunching of the pelvic, ventral and dorsal fins near the caudal (Text-figure 1) gives color to Garman's view (1884.1, .2) that these fins provide the creature with a fulcrum from which to strike. This arrangement of the fins is a very special feature. The pelvic fins, the anal fin and the ventral lobe of the caudal fin are sufficiently large to indicate that *Chlamydoselachus* is not closely confined to the sea bottom. The shape of the tail is much like that of *Heptanchus* (Text-figure 3).

The weakness of the fins of *Chlamydoselachus* is due not only to the softness and fineness of the dermal fin rays, which are exoskeletal structures, but also to the rudimen-

tary character of the cartilaginous rods, particularly the radials, that stiffen the basal portions of the fins. These rods belong to the endoskeleton and will be further considered in their proper place. In all the fins there is a wide expanse supported only by fine dermal fin rays. From the viewpoint of adaptation to environment, one may say that softness and flexibility of the fins is an advantage to a fish that must make its way through crevices in a rough sea bottom. In such a situation, stiff fins might be a decided impediment. Evidently *Chlamydoselachus* is not a rapid swimmer, since it must depend for locomotion partly upon serpentine movements of a slender body.



Text-figure 5.

Restoration of the Devonian shark, *Cladoselache*. Its fins were supported by simple parallel rods of cartilage extending nearly to the margin.

After Dean, 1909, Fig. 41.

In the earliest fossil remains of sharks that appear to have left modern descendants, the parallel rods of cartilage (radials) that support each fin extend almost to its margin, so that the entire fin must have been fairly rigid (e. g., as in *Cladoselache*, Text-figure 5). In living sharks there has been a reduction and modification of the radials and a correspondingly greater dependence on dermal rays for stiffening the fins. In *Chlamydoselachus* the reduction of the radials has proceeded to an unusual degree but without a compensating development of the dermal rays.

The shortness and breadth of base of the fins of *Chlamydoselachus* bring to mind the fin-fold theory (Thacher, 1877; Balfour, 1878; Mivart, 1879) for the origin of the fins of fishes; but fins that are broad and short are found in some of the most highly specialized sharks and more notably in the skates and rays. So this form of fin is not necessarily primitive. In *Chlamydoselachus*, the shortness and breadth of the fins are in strict harmony with the marked elongation of the body which we consider a departure from the norm for primitive fishes.

In discussing a series of elasmobranchs (*Cladoselache*, typically Devonian; *Pleuracanthus*, typically Permo-Carboniferous; *Hybodus*, typically Jurassic; and *Chlamydosela-*

chus, now existing but exemplifying the Cretaceous and Tertiary type) selected to illustrate the types prevailing in successive periods of time, Woodward (1921) says: "Very soon the remnants of lateral fin folds, which must have acted merely as two pairs of balancers in these fishes [the earliest known fossil elasmobranchs] concentrated into paddles, and these again passed into stout-based fins adapted for swimming." It is not explicitly stated, by the author quoted, that he regards this succession of types of paired fins as a phylogenetic series, but one may infer that he considers the breadth of base of the paired fins of *Hybodus* and *Chlamydoselachus* as something secondarily acquired.

It is known that Dean was an ardent advocate of the fin-fold theory for which he (1894 and 1895) obtained interesting evidence in the case of the fossil *Cladoseleache* (Text-figure 5). The question of the origin of paired fins was one of the problems Dean had in mind while he was searching in Japanese waters for embryos of *Chlamydoselachus*, *Cestracion* (*Heterodontus*) and other primitive fishes. Subsequently, Dean's material was studied by Osburn (1906 and 1907) who defended the fin-fold theory against the attacks of those who favored the opposing gill-arch theory originally proposed by Gegenbaur (1865).

ABDOMINAL OR TROPEIC FOLDS

The abdominal or tropeic folds are a pair of slender longitudinal thickenings of the ventral abdominal wall, situated close to the median line and separated by an external groove. They are figured and comprehensively described by Gudger and Smith (1933, pp. 283-284, Text-fig. 12), and are shown in transverse section in various figures inserted in my chapter on the muscular system (p. 381).

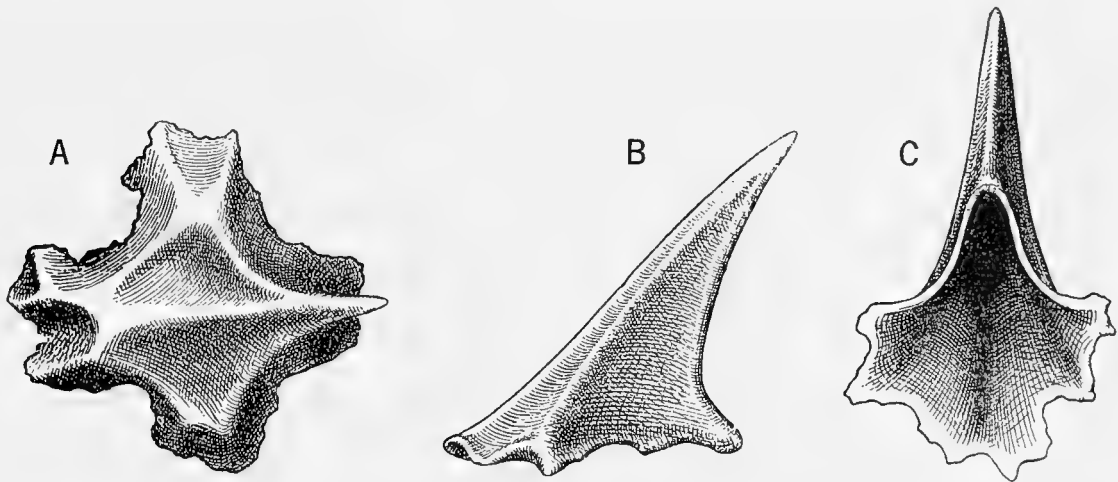
No satisfactory explanation has ever been advanced to account for the presence of the tropeic folds, which are structures peculiar to *Chlamydoselachus*. Concerning them Garman (1885.2, p. 3) wrote: "From their position, shape and extent, it is evident that the folds will furnish support to one of the theories regarding the origin of paired fins." I agree with Braus (1898) that "Der Kiel des *Chlamydoselachus* hat zur Genese der paarigen Gliedmassen *nicht* die geringste Beziehung." In my section on the muscular system there is given a fairly satisfactory explanation (illustrated by Text-figure 58, p. 386) as to the manner of embryonic development, but this does not answer the question as to the fitness of these peculiar structures for the needs of *Chlamydoselachus* in its particular environment. One can infer from their form and position that they may have some slight utility in locomotion similar to that afforded by the keel of a ship: but in some specimens they are too small to be of any appreciable use in this way.

SCALES AND TEETH

The variations in the form of the placoid scales or dermal denticles of *Chlamydoselachus* on different parts of the body, the form of the teeth, and the arrangement of the teeth in rows have been described by Garman (1885.2), Röse (1895), and by Gudger

and Smith (1933). We are here concerned chiefly with the structural and developmental relations between scales and teeth. The latter are not ordinarily considered as external structures, but are discussed here because of their morphological relationship to scales.

Some typical scales of *Chlamydoselachus* are shown in Text-figure 6. Each scale is, essentially, a hollow cone with ridges extending from the base to the apex. It is composed of dentine covered with a thin layer of enamel. In addition to the single prominent spine there are sometimes, as shown in Text-figure 6A, slight elevations near the margin of the base, formed by intersecting ridges. These elevations might easily develop into



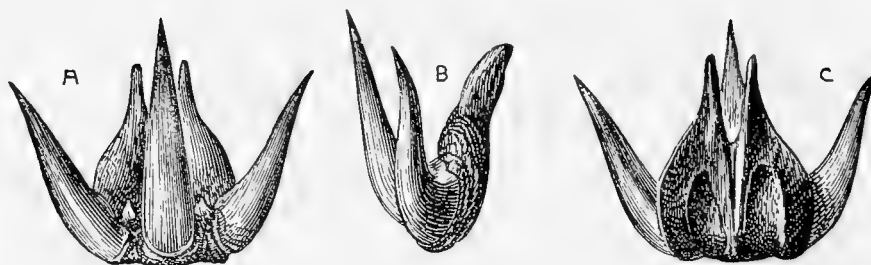
Text-figure 6.

Three different views of a placoid scale or dermal denticle (x 130) from a 340-mm. embryo of *Chlamydoselachus*: A, scale from the flank, viewed from above; B, lateral view of a scale from the region of the tail; C, scale from the region of the tail, seen from beneath.

After Röse, 1895, Abb. 1, 2, 3.

accessory spines. Of the atypical scales, those forming the "armature" on the anterior edge of the dorsal fin (Garman, 1885.2, p. 7; Gudger and Smith, 1933, p. 294) are interesting because, in form and arrangement, they resemble the "fulcral scales" of the Actinopterygii. The latter are described by Goodrich (1909, p. 304), and are said to be quite peculiar to this group.

A typical tooth, viewed from three aspects, is represented in Text-figure 7. It has three sharp, slender, curved cusps, and two rudimentary cusps or denticles. It is attached to the jaw in such fashion that the denticles project inward toward the mouth cavity. The broad base of the tooth is prolonged posteriorly (toward the interior of the mouth) and is forked so as to interlock with a paired excavation in the base of the succeeding tooth. In the illustrations the prongs of the base might readily be mistaken for cusps, but in the actual specimens the appearance is very different since the base is composed entirely of dentine while the cusps are covered with shiny white enamel.



Text-figure 7.

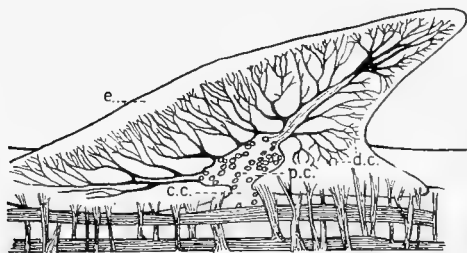
Three different views of a tooth of *Chlamydoselachus*, six times natural size:

A, seen from above; B, from the side; C, from beneath.

After Garman, 1885.2, Figs. 1, 3 and 4, pl. VI.

The essential similarity of the internal structure in scales and teeth of sharks is evident from a comparison of Text-figure 8 with Text-figure 9. Each has the form of a hollow cone, slightly recurved at the apex. Each is composed of dentine (*D.*, *D.2*) overlaid with enamel (*e.*, *S.*). The dentine is traversed by canals (*d. c.*) radiating from the pulp cavity (*p. c.* and *P.*).

Both scales and teeth are exoskeletal structures. Evidently teeth, which are the more complex, have developed from the same materials and in the same manner as scales. It would, perhaps, be a trifle crude to say that teeth are developed from scales, but it seems entirely proper to say that teeth are homologous with scales. This has long been admitted, but in *Chlamydoselachus* we have material exceptionally favorable for revealing the precise manner in which teeth correspond to scales. Superficially, the chief difference



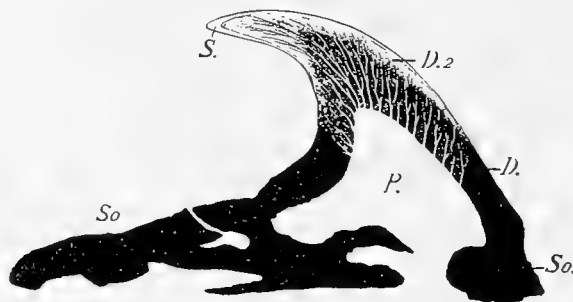
Text-figure 8.

Sagittal sections showing similarity of structure between scales and teeth of sharks.

Text-figure 8. Section showing finer structure of a placoid scale of *Scymnus lichia*.

c.c. central canal; *d.c.*, dentinal canal; *e.*, enamel; *p.c.*, pulp cavity.

After Daniel, 1934, Fig. 35; redrawn from Hertwig, 1874, Fig. 2, Taf. XII.



Text-figure 9.

Text-figure 9. Section of a single-cusped tooth (x 75) from the lower jaw of a 340-mm. embryo of *Chlamydoselachus*.

D., dentine; *D.2*, strongly calcified dentine; *P.*, pulp cavity; *S.*, enamel; *So.*, base.

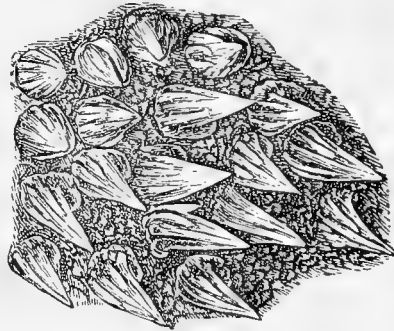
After R  se, 1895, Abb. 9,

between a scale and a tooth in *Chlamydoselachus* is that the scale has but one projection large enough to be called a spine, while the tooth usually has three large spines or cusps, and two rudimentary cusps. The question arises: does a single scale correspond to an entire tooth, or does a tooth develop as an aggregate of several scale-like rudiments?

Near the angles of the mouth of *Chlamydoselachus*, teeth sometimes grade into scales. In the four large specimens studied by Gudger and Smith (1933), the teeth of the last rows, as these approach the angles of the jaws, become very small, irregular and rudimentary until finally it is with great difficulty, even with the aid of a strong lens, that rows of teeth can be distinguished from groups of undoubted scales like those shown in Text-figure 10. The teeth are not comparable to individual scales, but each cusp

Text-figure 10.
Placoid scales or dermal denticles (x 5) from the angle of the mouth of *Chlamydoselachus*. Each scale resembles a single cusp of the rudimentary three-cusped teeth occurring in this region.

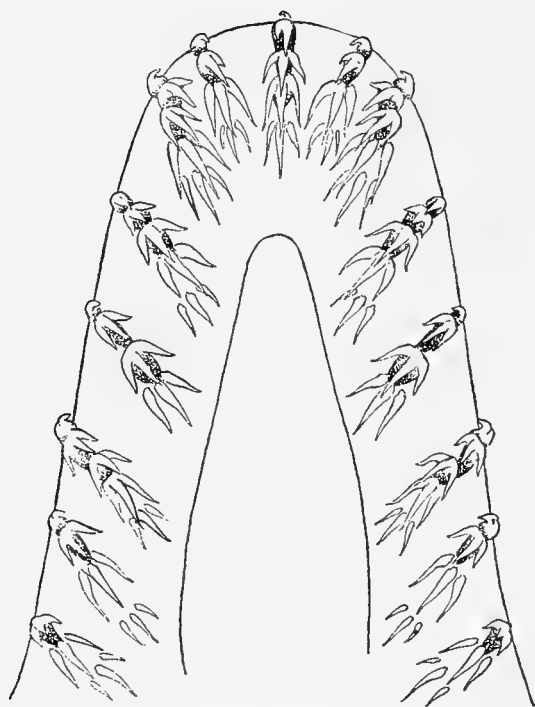
After Garman, 1885.2, Fig. 12, pl. VI.



resembles a scale, and the scales are sometimes arranged in columns of threes in series with the rows of teeth. In two specimens the border line between teeth and scales could be distinguished with considerable certainty, but in the other two specimens there was room for doubt. On the other hand, Garman (1885.2, p. 5) says of his single adult specimen: "the change from teeth with broad base, three cusps, and two buttons [rudimentary cusps] is sudden and decided; i.e., they do not grade into each other. A strong lens, however, is necessary to distinguish them, since in the hinder row each cusp looks much like a single scale." The last statement, together with the observations of Gudger and Smith, suggests a multiple origin for each tooth.

The development of a placoid scale has not been studied in *Chlamydoselachus*; but in the leopard shark, *Triakis semifasciatus*, a scale develops from a single primordium (Daniel, 1934, p. 26 and Fig. 29). It is of interest to inquire whether the multicusped teeth of *Chlamydoselachus* develop in the same manner.

The teeth of a 340 mm. embryo of *Chlamydoselachus* have been studied by Röse (1895). In this embryo, none of the teeth (Text-figure 11) had attained its final form, but some in the middle of each row were like those of the adult except that they lacked the two very small cusps. The innermost teeth of each row were represented, individually, by three distinct cusps not yet united at their bases; apparently each cusp had developed from a separate primordium. The evidence certainly indicates that, at the inner end of



Text-figure 11.

Teeth of the lower jaw (x 5) of a 340-mm. embryo of *Chlamydoselachus*, in their natural positions.

After Röse, 1895, Abb. 5.

of these teeth has but one cusp, the other has two cusps. Röse claims that this anomaly has a phylogenetic significance, since it indicates the manner in which a jawbone might arise through the fusion of teeth at their bases. Further, Röse asserts that the three- and especially the five-cusped teeth of an adult *Chlamydoselachus* furnish an excellent transition between a single-cusped shark tooth and the toothplates of an adult *Siren*, likewise of all urodele embryos. Also, he finds in his *Chlamydoselachus* embryo all possible forms intermediate between a simple placoid scale and a three-cusped tooth. The single-cusped tooth shown at the left in Text-figure 12 differs very little from a simple scale and is smaller than some of the scales found on the external surface of the body. Röse calls attention to the fact that in *Chlamydoselachus* the dentine (illustrated by his Fig. 10) develops in fundamentally the same way as in mammals.

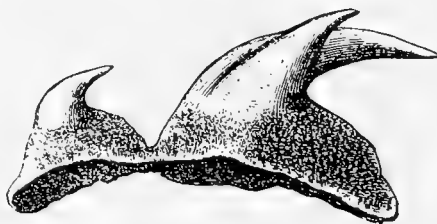
each row, teeth were being formed by the union of simple denticles homologous with placoid scales. At the outer ends of the rows, the teeth were small and rudimentary; each tooth had from one to three cusps. Those with a single cusp bore a strong resemblance to placoid scales. In the teeth with two or three cusps, the cusps were so closely fused at their bases that the enamel was continuous from one cusp to another. According to Röse, these teeth represent a stage transitional to the adult teeth of many teleosts. Possibly these teeth were anomalous, since in my four large specimens the outer teeth are only slightly different from those at the middle of each row: all have three cusps well developed and well separated. Röse thinks that all the two- and three-cusped teeth of his embryo developed through the fusion of simple cusps.

On one side of the upper jaw of his embryo, Röse found the first two teeth of the third row united at their bases, but delimited by a deep groove (Text-figure 12 herein). One

Text-figure 12.

The first two teeth (x 45) of the third row of the upper jaw of a 340-mm. embryo of *Chlamydoselachus*. These teeth are united at their bases.

After Röse, 1895, Abb. 6.





Text-figure 13.

Placoid scales from two species of the Devonian shark *Cladoselache*.

A—Scales (x 25) from various parts of the body of *C. fylleri*. From a specimen in the American Museum.

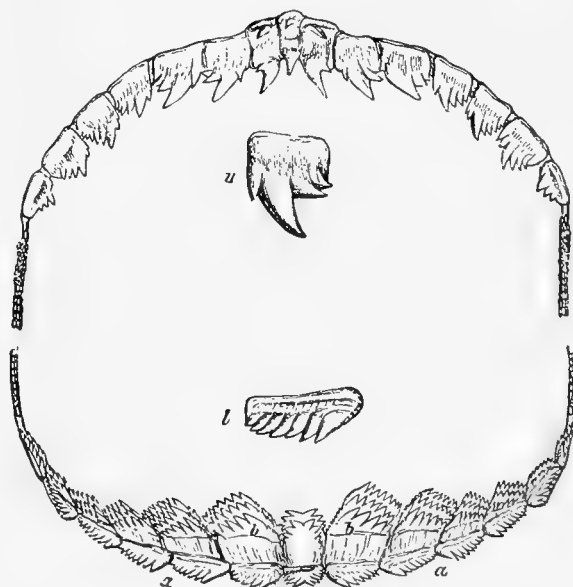
B—Trifid scale (x 20) from near margin of mouth of *C. fylleri*. From a specimen in the American Museum.

C—Larger scales (x 10) of *Cladoselache* (probably *clarki*). From a specimen in the British Museum.

After Dean, 1909, Figs. 1, 2, 3.

In *Chlamydoselachus* and in *Heptanchus* (Daniel, 1934, Fig. 27) the structure of the scales is simple and conforms to the same fundamental plan, though in both fishes the form of the scales varies considerably on different parts of the body. One should not attribute much phylogenetic importance to differences in the form of the scales of elasmobranchs. Some of the most specialized elasmobranchs (e.g., *Raja*) have simple scales, while the fossil *Cladoselache*, one of the most primitive sharks, has scales of various forms ranging from those only slightly indented or subdivided (Text-figures 13A and B) to those indented to such a degree that their exposed surfaces bristle with cusp-like points or ridges (Text-figure 13c.) In *Cladoselache* as in modern sharks, the scales vary in size and shape in different regions of the body (Dean, 1909, p. 214).

The teeth of *Chlamydoselachus* are barb-like, prehensile. In *Heptanchus* (Text-figure 14) the teeth are not alike on upper and lower jaws. The upper teeth seem adapted mainly for holding, the lower ones for cutting. The decided differences between the teeth of *Chlamydoselachus* and *Heptanchus*—forms which, in many important respects, seem closely related—serve to weaken one's faith in the validity



Text-figure 14.

Dentition of *Heptanchus* (*Notidanus*) *indicus*.
a, teeth in function; b, teeth in reserve; u and l, upper and lower single teeth (natural size).

From Goodrich, 1909, after Günther.



Text-figure 15.

Teeth of two fossil *Chlamydoselachids* from the Tertiary.

Text-figure 16.

Text-figure 15. Fossil teeth of *Chlamydoselachus lawleyi* from the Pliocene of Orciano, Tuscany, Italy. Note the lack of rudimentary cusps.

1 and 1b, teeth viewed from above; 1a, from below; 1c, from the side (1b, natural size; all others x 2).

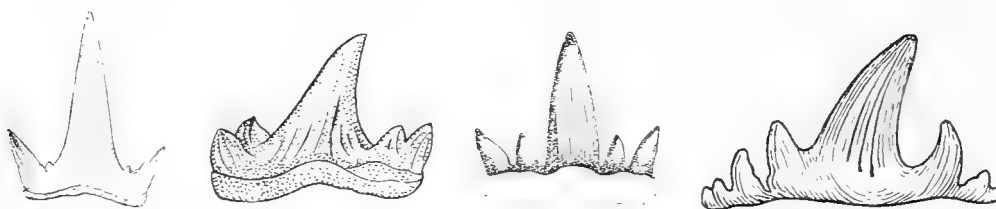
After Lawley, 1876, Figs. 1 to 1c, pl. I.

Text-figure 16. A fossil tooth (A, natural size; B, x 2) of *Chlamydoselachus tobleri* from Trinidad, British West Indies. Note presence of rudimentary cusps.

After Leriche, 1929.

of phylogenetic deductions based on a comparison of present-day fishes with fossil forms that are known only by their teeth.

In the fossil *Chlamydoselachus lawleyi* (Lawley, 1876), which is known only by its teeth (Text-figure 15), the resemblance to the teeth of *C. anguineus* is very close. Apart from their smaller size, the teeth of *C. lawleyi* differ from those of *C. anguineus* only in that they lack the pair of very small cusps. In *C. tobleri*, which is known only from a single fossil tooth (Leriche, 1929), the small cusps are present, but in some other respects the tooth (Text-figure 16) is so different that one may regard the inclusion of this form in the genus *Chlamydoselachus* as merely tentative.



Text-figure 17.

Text-figure 18.

Text-figure 19.

Text-figure 20.

Teeth somewhat resembling those of *Chlamydoselachus anguineus*, from various fossil sharks.

Text-figure 17. Tooth (x 5) of *Cladoselache fylleri* from the Devonian.

After Dean, 1909, Fig. 5.

Text-figure 18. Tooth of *Cladodus acutus* from the upper Devonian.

After Agassiz, 1843.

Text-figure 19. Tooth of *Ctenacanthus clarki* from the Carboniferous.

After Dean, 1909, Fig. 42.

Text-figure 20. Tooth of *Hybodus reticulatus* from the lower Jurassic.

After Zittel, 1923, Fig. 93.

Among fossil forms assigned to other genera, teeth more or less resembling those of *Chlamydoselachus anguineus* are found in *Cladoselache* (Text-figure 17), in *Cladodus* (Text-figure 18), in *Ctenacanthus* (Text-figure 19), and in *Hybodus* (Text-figure 20). In each of these fossil sharks the teeth vary in form, but those represented in the figures may be regarded as typical. In all these teeth the cusps are conical, and the central cusp is by far the most prominent. In *Hybodus* the lateral cusps (3 or 4 on each side) become smaller in proportion to their distance from the central cusp. In *Cladodus*, *Ctenacanthus* and *Cladoselache* there are two cusps on each side of the central cusp, and the marginal cusps are larger than the intermediate cusps. In *Cladoselache* the intermediate cusps are very small, as in the frilled shark. In *Hybodus* and in *Cladodus* most of the cusps are recurved at the tip. In *Ctenacanthus* and in *Cladoselache* the cusps are more slender and appear practically straight, though Dean (1909) states that in *Cladoselache clarki* there is a slight sigmoid flexure of the cusps. Of the four forms considered, *Cladoselache* possesses the sharpest cusps. In this, as in many other respects, the teeth of *Cladoselache* most nearly resemble those of the frilled shark, but in this connection I quote the following from Dean, 1909, p. 253:

When teeth of the type of *Cladodus* were discovered in different horizons from the Devonian well into the Mesozoic, it was naturally concluded that the sharks themselves would be found to correspond closely—to belong if not to the same genus at least to the same family. When, however, associated remains of the earlier forms were discovered, it became clear that these sharks were by no means closely allied. Instead of being proven to be cestracionts, one type of “*Cladodus*” (*Cladoselache kepleri*, *C. fylleri*; Upper Devonian), was found to be spineless, and quite different in essential structures from the modern cestraciont: another type of “*Cladodus*,” *Symmorium* Cope (Coal Measures), was then shown to be unlike both *Cestracion* and *Cladoselache*; and still another, “*Cladodus*” *neilsoni*, was demonstrated by Traquair to be quite different in fin characters from all the rest. And now a fourth cladodont, *Ctenacanthus*, is found notably discrepant. It is, then, only the mesozoic group of “cladodonts” typified by *Hybodus* which remains faithful to our preconceived notions as to what kind of a shark a cladodont tooth should predicate. The fact of the matter is that the cladodont type of tooth is as ancient as it has been useful in the subclass Elasmobranchii, and that it has appeared in many different lines, either as an heirloom from primitive sharks, or, less probably, as an independent acquisition. Certain it is that it appears with little variation in as many as seven families of sharks, and in at least three distinct orders.

When teeth are highly differentiated, resemblances amounting almost to identity (as between *Chlamydoselachus anguineus* and *C. lawleyi*) are probably significant. On the other hand, among living fishes we find instances where members of the same family have widely different teeth. On *a priori* grounds it seems likely that, where cusps are numerous and close together, development may proceed by the elimination of some of the cusps in order that the others may be better nourished; or, putting the matter in another way, some cusps may develop at the expense of the others. It seems probable that, in the long lapse of time, teeth like those of *Chlamydoselachus anguineus* could have evolved out of rather irregular and rudimentary structures, like the teeth of *Hybodus reticulatus*

(Text-figure 20), quite as readily as from teeth like those of *Ctenacanthus clarki* (Text-figure 19), *Cladodus acutus* Ag. (Text-figure 18) and *Cladoselache fylleri* (Text-figure 17), which they more nearly resemble.

THE ENDOSKELETON

The most comprehensive studies of the endoskeleton of *Chlamydoselachus* are those of Garman (1885.2), Deinema (1909 and 1923), and Goodey (1910.1). In addition, Günther (1887) described the skeleton of the claspers; Braus (1902) that of the paired fins; Fürbringer (1903) and Garman (1913) the visceral skeleton; while Allis (1923), using material supplied by Dr. Bashford Dean, described the skull. Deinema's first (1909) paper is in Russian, but his original figures are reproduced in his later (1923) paper which is in German.

As in selachians generally, the endoskeleton (excepting the notochord) of *Chlamydoselachus* is composed entirely of cartilage. In most elasmobranchs the cartilage is in many places hardened by deposits of calcareous material without, however, assuming the histological character of true bone. In *Chlamydoselachus*, it appears that such calcification is very limited in extent. Thus Garman (1885.2) writes that the cartilage of the skull is soft except in the parachordal region where it is hard and granular. Allis (1923) says of the skull of *Chlamydoselachus*: "The entire posteroventral region of the chondrocranium is extensively calcified in all my specimens, my observations thus differing from Goodey's" (1910.1, p. 553). Goodey does mention (p. 543) a calcification of the floor of the cranium in the region of its junction with the vertebral column, and elsewhere in the same article he describes local calcifications forming the rudimentary centra of the vertebrae, but he emphasizes (p. 553) "the small amount of calcification appearing in the skeleton at all."

In the softness of its cartilaginous endoskeleton, *Chlamydoselachus* agrees with *Heptanchus* which, according to Daniel (1934), has cartilage of the clear hyaline variety with very little in the nature of calcareous deposits. In both genera this is probably a primitive character.

THE SKULL OF CHLAMYDOSELACHUS

The vertebrate skull consists of the cranium and the visceral skeleton. The cranium serves to protect the brain and certain sense organs: the olfactory organs, the eyes and the membranous labyrinths. The visceral skeleton consists of a series of cartilaginous or bony arches which partly surround the mouth and the pharynx. These arches comprise the jaws or the mandibular arch, the hyoid arch, and the branchial arches or gill-arches. The term cranium is sometimes used as a synonym for skull. The cranium is then divisible into two portions, the cerebral cranium or neurocranium, and the visceral cranium or branchiocranium.

THE CRANIUM

To illustrate various aspects of the cranium and some closely associated parts of the endoskeleton of *Chlamydoselachus*, I have selected the excellent figures of Allis (1923) for reproduction in my Plates I, II and III. In connection with his very detailed description of the skull, Allis has critically reviewed the work of his predecessors, Garman (1885.2) and Goodey (1910.1). Of the work of Deinega (1909), Allis was probably unaware since he makes no reference to it.

Garman (1885.2, p. 8) writes thus of the "skull" (cranium) of his 1510-mm. specimen of *Chlamydoselachus*:

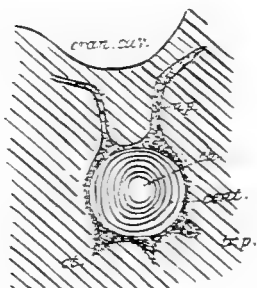
The skull of the frilled shark is suggestive of immaturity; the thin walls, soft cartilage, and large pores and foramina with thin edges around them, seem to be those of a young, rather than an adult specimen. Compared with that of *Heptabanchias* [*Heptanchus*] it agrees better with an embryo than an adult. Looking at it from above, its shape may be likened to that of the body of a guitar, the vertebral column answering to the neck of the instrument, and the narrow section between the orbits to the middle of its box . . . The walls are very thin. In longitudinal section the thickness of floor and roof is comparatively uniform. There is a marked contrast in this respect if compared with the skulls of *Hexanchus* and *Heptabanchias*, which in these portions are thick and irregular (see Gegenbaur, 1872, *Das Kopfskelett der Selachier*, Figs. 1 and 2, pl. IV) . . . The chamber is large, and the brain small.

Allis (1923), whose excellent figures showing dorsal, ventral and lateral aspects of the "neurocranium" of *Chlamydoselachus* are reproduced as my Plate I, says: "In dorsal view [my Figure 1] it greatly resembles the neurocranium of *Hexanchus* (Gegenbaur, 1872), but its dorsal surface is even flatter." Also, in dorsal view the cranium of *Chlamydoselachus* is much like that of *Heptanchus* (Daniel, 1934, Figs. 45 and 46). According to Allis the cranium of *Chlamydoselachus* differs from those of *Hexanchus* and *Heptanchus*, and resembles those of *Acanthias*, *Centrophorus* and *Scymnus* (Gegenbaur, 1872, p. 39) in that the ventral surfaces (Figure 2, plate I) of the occipital and labyrinthine regions lie in the same level, and in that the eminence of the bulla acustica is found on this ventral surface and not on the lateral surface (Figure 3, plate I) of the neurocranium. This ventral position was considered by Gegenbaur to be secondary, due largely to a greater development of the hyomandibular articular facet than is found in *Hexanchus* and *Heptanchus*, or indeed in any other selachian skull figured by him.

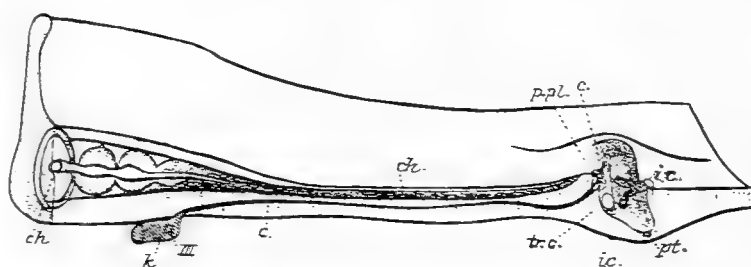
All who have studied the matter agree that the notochord of *Chlamydoselachus* is continued as a slender strand of tissue in the base of the cranium as far forward as the pituitary fossa. This is clearly shown in Garman's (1885.2) Fig. B, nc, pl. VII; also in my Text-figures 21 and 22 after Ayers, and in my Text-figure 30, p. 364, after Goodey. It is faintly indicated in Deinega's (1909 and 1924) Fig. 4, pl. II; in Goodey's (1910.1) Fig. 2, pl. XLII; and in my Figure 4, plate II (after Allis). This persistence of the anterior portion of the notochord in the region of the basis cranii is a very primitive character. To be sure, in all vertebrate embryos the notochord extends forward almost to the

infundibulum, but in the higher vertebrates it disappears from the basis cranii during later development.

In connection with his account of the persistence of the notochord of *Chlamydoselachus* in the region of the basis cranii, Goodey (1910.1, p. 543) makes the following interesting statement: "The cartilage of the floor of the cranium in the region of its junction with the vertebral column is thick and somewhat heavily calcified. It here shows some indications of its probable vertebral nature, by the slight resemblance which the calcification presents to the inverted V-formation found in the centra of the vertebral column." Ayers (1889) found more decided evidences (my Text-figures 21 and 22) of



Text-figure 21.



Text-figure 22.

Sections through the skull of the frilled shark, *Chlamydoselachus anguineus*.

Text-figure 21. A transection of the basis cranii near the vertebral articulation, to show the figure made by the calcareous sheath (and its processes) of the notochord, resembling a vertebra of the trunk region.

cent., vertebral centrum (sheath of notochord); ch., chorda dorsalis; cran.cav., cranial cavity; ct., cartilage of the basis cranii; n.p., neural process; tr.p., transverse process.

After Ayers, 1889, Fig. 8.

Text-figure 22. Left half of the hemisected cranium, to show the relations of the notochord and cranial aorta to the basis cranii and to the pituitary prominence and space.

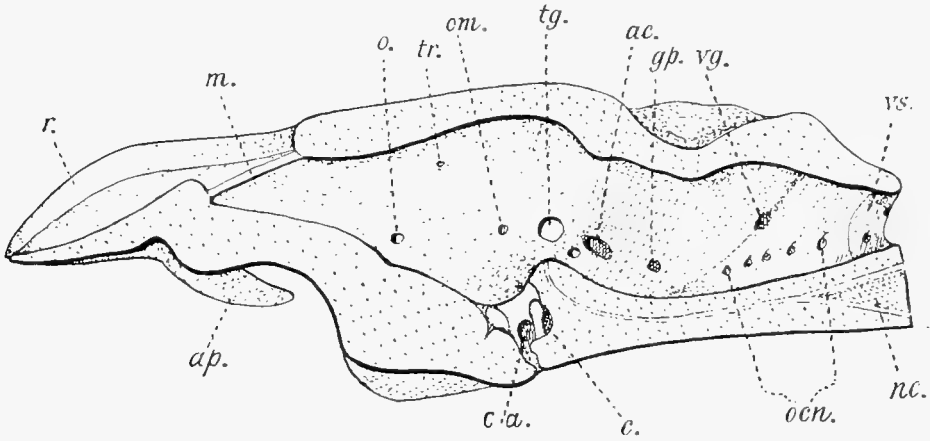
c., cranial aorta; ch., chorda dorsalis (notochord); i.c., internal carotid artery; k., cephalic aorta; p.pl., pituitary plexus; pt., pituitary space; tr.c., transverse canal; III, third pair of aortic arches.

After Ayers, 1889, Fig. 3.

the persistence of the notochord (ch) and the rudimentary vertebral column in the basis cranii of his specimen: but in view of the doubts that have been expressed concerning the accuracy of many of Ayers' observations on *Chlamydoselachus*, one should accept this description and the accompanying figures with some reserve. In *Hexanchus* the notochord (Text-figure 23, nc) persists in the posterior portion of the basis cranii, much as in *Chlamydoselachus*.

My Figure 4, plate II, showing a medial view of the cranium of *Chlamydoselachus*, should be compared with Text-figure 23, showing a similar view of the cranium of *Hexanchus*. The two figures are of interest chiefly because they show the foramina for the exit of the cranial and occipital nerve roots.

In *Chlamydoselachus*, any consideration of the cranium as a whole must take into account its relation to the upper jaw (palatoquadrate) and to the suspensory apparatus, on both of which it seems, to a considerable degree, to be molded. As one looks at the skull from the side (Figure 5, plate II) he is impressed by the extraordinary length of the jaws which begin posteriorly far behind the cranium and lie, when the mouth is closed, in a nearly horizontal position. The ectethmoidal process projects over the outer surface of the palatoquadrate, thus helping to hold it in place. The postorbital process of *Chlamydoselachus* is exceptionally large, but even when the mouth is closed it fails to reach the



Text-figure 23.

Inner view of the right half of the skull of *Hexanchus* to show the cranial portion of the notochord and the foramina for cranial nerves.

ac., foramen for auditory nerve; *a.p.*, antorbital process; *c.*, carotid foramen; *ca.*, interorbital canal; *gp.*, glossopharyngeal nerve; *m.*, membrane over fontanelle; *nc.*, notochord; *o.*, optic nerve; *ocn.*, spino-occipital nerve; *om.*, oculomotor nerve; *r.*, rostrum; *tg.*, trigeminal nerve; *tr.*, trochlear nerve; *vg.*, vagus nerve; *vs.*, occipitospinal nerve.

From Goodrich, 1909, Fig. 93, after Gegenbaur, 1872.

palatoquadrate. The nearly terminal position of the mouth is attained somewhat at the expense of the cranium, for the rostrum is short and thin, though broad, and the anterior third of the ventral surface of the cranium slants upward in such a way as to allow the anterior part of the upper jaw to lie on a level with the posterior part of the basis cranii. This is only one of several adjustments that make this creature, when viewed from in front with its enormous jaws spread apart (Text-figure 2), seem to be nearly all mouth. When this same specimen with the wide-open mouth is viewed from the side, it appears that, in the process of opening the mouth, the upper jaw (and of course, the cranium also) is elevated anteriorly, thus keeping the center of the mouth cavity in line with the body. The site of this flexure is not in the occipito-vertebral articulation, but in the vertebral column a few centimeters posterior to it. How this flexion is accomplished I do not know, since the vertebral column has no articulations

that seem to give any appreciable freedom of movement; but one should remember that even a solid rod of cartilage is flexible.

In most selachians, when the mouth is closed the hyomandibular is directed downward, outward or even forward; but in *Chlamydoselachus* it is directed posteriorly. As the mouth opens, its angles spread apart so that the entire oropharyngeal cavity broadens; this is made possible by the length and mobility of the hyomandibular. When the mouth is closed, the hyomandibular is neatly folded between the palatoquadrate and the vertebral column, its anterior end lying somewhat apart from the cranium and a little above the level of the anterior end of the dorsal border of the hyomandibular facet (*af* in Figure 3, plate I). This facet is a broad groove extending longitudinally for a considerable distance on the posterior part of the lateral surface of the cranium. When the jaws are opened, the anterior end of the hyomandibular must slide posteriorly along the facet, while the posterior end swings laterad and somewhat ventrad through an angle of about 45° (Garman, 1885.2). Thus the articulation of the hyomandibular with the cranium is a sliding joint of unusually loose construction, aiding greatly in the range of movement of the hyomandibular. This peculiar hyostylism of the skull, together with the nearly terminal position of the mouth, the long jaws and indeed the entire complex of adjustments that gives *Chlamydoselachus* its enormous gape, are to be viewed as comparatively recent adaptations of a highly specialized character. Goodey (1910.1, p. 550) says of the jaws of *Chlamydoselachus* that "their disposition relative to the cranium is quite different from that found in any Selachian whose skull I have been able to examine or see a figure of. It resembles nothing among the Vertebrates so much, perhaps, as the general disposition of the jaws in certain of the Ophidia."

Allis has described a palatal process of the palatoquadrate which serves as a support for the soft parts of the horizontal palatine shelf. "The palatine process of *Chlamydoselachus* . . . is a curved flat plate of cartilage, of nearly even width, that projects antero-mesially beneath the anterior end of the neurocranium" (Allis, 1914, p. 354). The horizontal palatine shelf, which is evidently a homologue of the maxillary breathing valve of certain teleosts, is fully described by Gudger and Smith (1933, p. 269).

The cartilaginous lateral wall of the suprapalatine recess is perforated, on either side, by the nasal fontanelle (*naf*, Figure 2, plate I). In its position and relations the nasal fontanelle is, apparently, the strict topographical homologue of the fenestra choanalis of Amphibia (Allis, 1913 and 1914). In its natural state the nasal fontanelle of *Chlamydoselachus* is closed by a tough membrane (Allis, 1923, p. 132) which appears to be a part of the cranium. This membrane is distinct from the mucous membranes lining the nasal capsule and the mouth. The membrane evidently represents unchondrified portions of the subnasal plate and the nasal capsule. "The nasal cavity of *Chlamydoselachus* is thus separated from the suprapalatine recess by membranous and mucous tissues only, and if these tissues were to be secondarily [sic] perforated . . . an internal nasal aperture would be formed which would lie directly above the horizontal palatine shelf" (Allis, 1914, p. 355).

The postorbital process closely approaches the palatoquadrate but does not articulate with it. The orbital process of the palatoquadrate is unusually large and projects far into the deeper portion of the orbit, where it articulates with a large facet on the ventral edge of the anterior wall of the orbit. The orbital process forces the eyeball away from the medial wall of the orbit. These relations must change considerably when the pharynx is expanded, on account of the spreading of the jaws posteriorly and the shifting of the angles of the jaws ventrad (note the space between palatoquadrate and cranium in Text-figure 84, p. 429). The only articulation of the palatoquadrate with the cranium is by way of the orbital process, which is very loosely attached to the cranium.

The eyestalk of *Chlamydoselachus* is a slender rod of cartilage which projects from the anterior edge of the trigemino-pituitary fossa and curves around the posterior surface of the capsular sheath of the orbital process of the palatoquadrate (Figure 2, plate I; Figures 5 and 6, plate II). Its distal end has a sliding articulation with the medial surface of the eyeball, without being attached to it. According to Gegenbaur (1872) the eyestalk of the plagiostomes does not belong genetically to the eye, neither does it, except in its basal portion, belong to the chondrocranium. In all the plagiostomes, the basal portion of the eyestalk is of firmer tissue than the remainder of the stalk, which is always of softer tissue than the chondrocranium. Gegenbaur suggested that the eyestalk (excepting its basal portion) might be a part of the visceral skeleton that had secondarily acquired relations with the eyeball. Allis (1923) cites Dohrn's suggestion that it might represent a part of a premandibular visceral arch, and recalls his own earlier suggestion (Allis, 1914, p. 365) that "the eyestalk is a modified branchial ray or rays, of a mandibular or premandibular arch, that has secondarily acquired relations to the eyeball." While such explanations are highly speculative, an origin from a branchial ray of the mandibular arch seems the most plausible. That the eyestalk originated from some pre-existing cartilaginous structure seems indicated by this statement from Allis (1914, p. 347):

The eyestalk is certainly a retrograding and archaic structure, as its varying importance and wide distribution clearly indicate, and it seems certain that it could not have been developed independently, merely as a support to the eyeball, a function it so inefficiently fulfils except in certain rays (Harman). And that it was developed as a point of attachment for the recti muscles seems improbable because it actually fulfils that function, so far as I can find, only in *Chlamydoselachus* (Hawkes, 1906) and possibly in *Zygaena*.

At the bottom of the endolymphatic fossa (*cf.* Figure 1, plate I) are four apertures, two on each side, described by Goodey (1910.1) and by Allis (1923, p. 155). Each anterior aperture is a foramen ductus endolymphaticus, or aqueductus vestibuli, and affords passage for the ductus endolymphaticus. Each posterior aperture leads directly into the perilymphatic cavity of an ear, and is the so-called fenestra ovalis of Scarpa, or the fenestra vestibuli cartilaginei of Weber. In the natural state this aperture is closed by a membrane. In *Chlamydoselachus* and in *Mustelus*, the fenestra vestibuli lies immediately above the apex of the posterior membranous semicircular canal of the ear.

A rear view of the skull (Figure 6, plate II) shows the foramen magnum (*fm*), and beneath it a small perforation, not labeled, for the extension of the notochord forward into the basis cranii. The figure shows also a posterior view of the hyomandibular articular facet (*af*), the postorbital process (*pop*), the ectethmoidal process (*ecp*), and the eyestalk (*es*).

As in other elasmobranchs, the brain does not fill the cranial cavity, which is shown from the dorsal aspect in Figure 7, plate III. This figure shows also the olfactory capsules, partly dissected, lying on each side of the broad rostrum.

THE VISCERAL SKELETON

In most elasmobranchs there are seven visceral arches: the mandibular, the hyoid, and five branchial arches. In *Chlamydoselachus* and the notidanids there are additional branchial arches making a total of eight visceral arches in *Chlamydoselachus* and *Hexanchus*, and nine in *Heptanchus*.

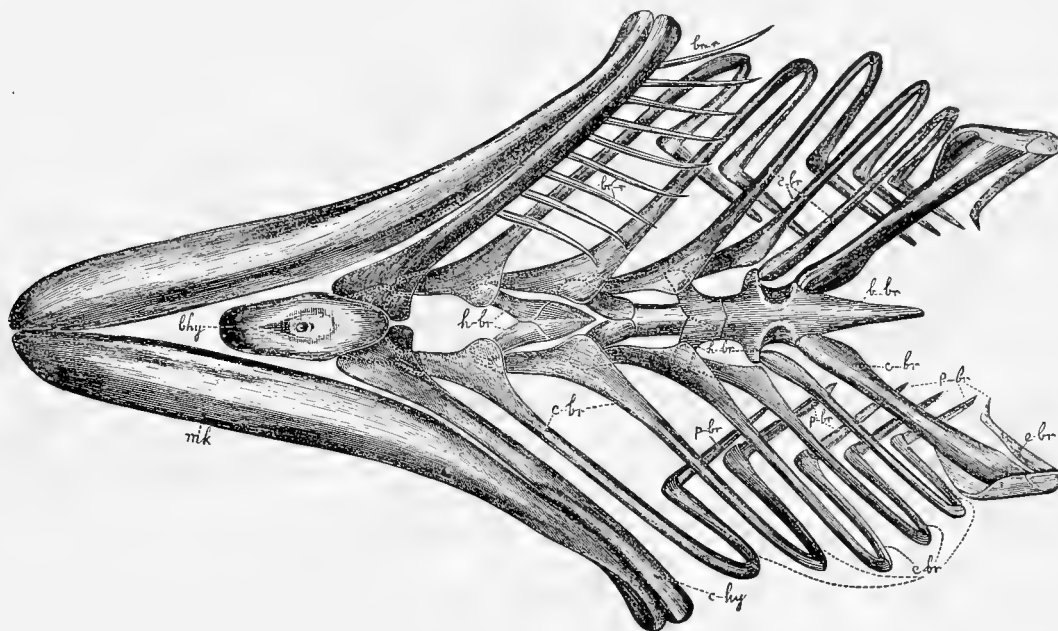
Since the mandibular arch and the hyoid arch are usually regarded as derivatives of primitive branchial arches, some embryologists use the term branchial arch for each member of the entire series of visceral arches, and number them consecutively. In comparative anatomy it is more common to designate the mandibular arch and the hyoid arch as such, and restrict the name branchial arch to the succeeding arches, which are numbered separately. Thus, the third visceral arch is the first branchial arch.

In *Chlamydoselachus*, as in other elasmobranchs, the mandibular arch (Figure 5, plate II) is divided into an upper palatoquadrate or pterygoquadrate segment, and a lower mandibular segment (Meckel's cartilage). The articulation between these two elements is of a simple type, figured by Allis (1923) in his Pl. XII. The ligaments connecting the palatoquadrate with the mandible, and the mandibular arch with the hyoid arch, are shown by Allis (1923) in his Pls. X and XI. Allis (1923, p. 149) states that the orbital process of the palatoquadrate has a capsular sheath, and (pp. 208 and 209) refers to a "somewhat ligamentous portion of the connective tissue that attaches the capsular sheath to the anterior wall of the orbit." Garman (1885.2, p. 10) writes: "Some of the most prominent differences between *Chlamydoselachus* and the notidanids are to be seen in the attachments and articulations of this cartilage [the palatoquadrate]."

As compared with the same structures in other sharks, the jaws of *Chlamydoselachus* (Text-figure 24; Figure 5, plate II) are slender. This slenderness stands in marked contrast with the condition found in *Heptanchus* (Daniel, 1934, Fig. 48), and is correlated with a decided difference in the character of the teeth. In *Chlamydoselachus*, much more than in *Heptanchus*, the jaws resemble branchial arches.

The anterior labial cartilage (Figure 5, plate II) gives insertion to a long and stout ligament attached to the cranium. From this ligament a series of ligamentous strings are sent off to the upper lip. The posterior upper labial has no direct supporting relations to the upper lip, but the posterior lower labial or mandibular labial gives attachment, at its posterior end, to the tendon of the protractor anguli oris, and from its point of artic-

ulation with the posterior upper labial it extends forward, along the ventral edge of the mouth, strongly attached to the inner surface of the dermis of the lower lip (Allis, 1923). The presence of a mechanism for strengthening and mobilizing the soft tissues at the angles of the mouth supports my contention that *Chlamydoselachus* seizes and swallows large prey.



Text-figure 24.

Ventral view of the visceral skeleton (three-fourths natural size) of Garman's first specimen of *Chlamydoselachus*. The branchial rays are omitted from all arches except the hyoid.

b-br, basibranchial; b-hy, basihyoid; br-r, branchial ray; c-br, ceratobranchial; c-hy, ceratohyal; e-br, epibranchial; h-br, hypobranchial; mk, mandible or Meckel's cartilage; p-br, pharyngobranchials.

After Garman, 1885.2, Pl. IX.

The homologies of the labial cartilages of elasmobranchs are obscure. Pollard (1895) considered the labial cartilages to be the remains of the skeletal supports of a set of primitive oral cirrhi such as are found still in *Amphioxus* and in myxinoids. Others, like Sewertzoff (1916), believe the labial cartilages to represent vestiges of the visceral arches of two segments in front of the mandibular. Concerning this view Goodrich (1930, p. 448) writes as follows: "Against the theory maintained by Sewertzoff it may be urged that there is no good evidence of the existence at any time of gill-pouches, arches, etc., anterior to the mandibular, that the labials are too superficial to be of visceral nature, and that the supposed vestiges of gill-pouches corresponding to them apparently occur anteriorly to the pharynx (endodermal gut). Possibly the labials are merely secondary in Gnathostomes and of no great morphological importance." The labials may be tentatively classified as extravisceral cartilages of the mandibular arch, in series with the extrahyoids and the extrabranchials.

Neither Garman (1885.2) nor Goodey (1910.1) found any spiracular cartilages in the specimens dissected by them, and Fürbringer (1903, p. 389) found only a single spiracular cartilage in his specimen. Allis (1923, Fig. 22, pl. XI) found three small nodules of cartilage situated in a loose prespiracular band of connective tissue which does not have the same relations as a spiracular ligament on each side of one specimen. The cartilages are described by Allis (1923, p. 169) as follows:

These cartilages present strikingly the appearance of being rudiments of the basal portions of three adjoining branchial rays related to the mandibular arch, and, like the single spiracular cartilage described by Fürbringer in the one specimen examined by him, they lie lateral, and hence morphologically anterior, to the artery of the arch. They lie posteroventral to that part of the spiracular canal that bears the pseudobranchial filaments and in no supporting relations whatever to them, and hence, while possibly representing persisting rudiments of mandibular rays, they may not be true spiracular cartilages, for Gegenbaur (1872, p. 198) says that in all the Plagiostomi in which it is found, the spiracular cartilage always lies in the anterior wall of the spiracular canal, and that, where there is a pseudobranch, the filaments of that organ lie directly upon the cartilage.

Evidently Daniel (1934, p. 63) considers that the dorsal segment of the second visceral arch of *Chlamydoselachus* is not a true hyomandibular, since he writes of it that "the dorsal segment is on its way to become a hyomandibula or suspensorium." According to Allis (1923) there is no ligament connecting the hyomandibular with the palatoquadrate; there are, however, ligaments connecting the hyomandibular with the mandible (Meckel's cartilage) in the region of the quadrato-mandibular articulation, and a broad capsular ligament binding the hyomandibular strongly to the cranium. The sliding articulation of the hyomandibular with the cranium has already been described. The homologies of the hyomandibular of fishes are discussed by Allis (1915) and by Gregory (1933, pp. 80-82). Woodward (1921, p. 39) regards the hyostylic suspension of the jaws, found in nearly all modern sharks and skates, as a condition secondarily attained, while the primitive mode of suspension of the jaws is amphistylic, as in *Cladoselache* and in the notidanids. One may well be puzzled to decide whether the peculiar mode of suspension of the jaws of *Chlamydoselachus* is amphistylic or hyostylic. It does not conform fully to either type, but comes nearer to being hyostylic. Goodey (1910.1, p. 544) states unreservedly that "the suspension of the jaws is hyostylic."

The hyomandibular of *Chlamydoselachus* bears nine Garman, 1885.2 or more cartilaginous branchial rays. Goodey (1910.1) shows, in his Fig. 1, pl. XLIII, ten branchial rays attached to the hyomandibular and one branchial ray slightly detached from it. Allis (1923), in his figure reproduced as my Figure 5, plate II, shows nine branchial rays attached to the hyomandibular and five or six others more or less detached but evidently related to it.

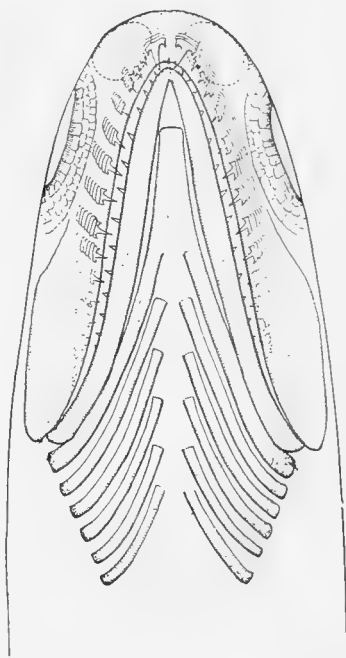
The ceratohyoids (Text-figure 24, *c-hy*) parallel the mandibular or Meckelian cartilages (*mk*) and are intermediate in size between these and the ceratobranchials (*c-br*). Viewed from below, as in Garman's figure, the visceral skeleton of *Chlamydoselachus*

presents a striking picture of gradation between jaws and gill-arches. A more nearly perfect gradation is exhibited in Dean's reconstruction of *Cladoselache fylleri*, shown in my Text-figure 25. Since the ceratohyoids, as well as the hyomandibulars, of *Chlamydoselachus* bear branchial rays (my Figure 5, plate II), the hyoid arch can scarcely be derived from the velum of an amphioxoid ancestor as alleged by Ayers (1931). In *Heptanchus* (Daniel, 1934) the hyoid segment possesses an extravisceral cartilage, not present in *Chlamydoselachus*.

All the branchial arches of *Chlamydoselachus*, excepting the sixth and the vestigial seventh, bear branchial rays (Text-figure 77; and Figure 8, plate III). These are very slender rods of cartilage, attached at one end to a branchial arch, and supporting the gill-septum. Goodey (1910.1) states that in his two specimens, male and female respectively, the greatest number of rays occurs on the hyoid arch, and as one proceeds posteriorly the number gradually decreases. His tables showing the number of rays on the right and left sides of each arch, from the hyoid to the fifth branchial arch inclusive, support his statement. The same trend is shown in Collett's (1897) table showing the number of rays for each branchial arch (one side only?), from the first to the sixth inclusive, in his large specimen; but it is probable that Collett's first arch, bearing nineteen rays, is really the hyoid arch, and his sixth branchial arch, bearing eight rays, is really the fifth.

In each of the first five branchial arches of *Chlamydoselachus* there is a dorsal extrabranchial cartilage, described by Fürbringer (1903) and by Allis (1923, Fig. 49. pl. XVIII). In Fürbringer's Figs. 31, 32, 33, Taf. XVIII, the extrabranchial cartilages appear like detached or fragmented branchial rays, usually small.

The basibranchials and hypobranchials constitute the most variable part of the visceral skeleton of *Chlamydoselachus*. Viewed as departures from an easily recognized type, these variations are interesting. In none of the specimens of *Chlamydoselachus* that have been described is there a distinct basibranchial associated with the first pair of ceratobranchials. To be sure, Garman (1885.2, p. 11) enumerates a first basibranchial in his series, but this would be a second if the series were complete. In order to make comparisons, one must revise his enumeration to correspond with that used by Goodey (1910.1) and others. With this change of labels, Garman describes and figures separate second and third basibranchials (my Text-figure 24). The fourth basibranchial is fused with the corresponding hypobranchials, is obliquely and indistinctly divided, and is closely joined with the fifth which is fused with the sixth and indistinguishable from it save by



Text-figure 25.

Reconstruction of the underside of the skull of a Devonian shark, *Cladoselache fylleri*, showing lower jaw in series with gill-arches.

After Dean, 1909, Fig. 6.

its position and relations. The hypobranchials of the first pair are small and are situated dorsal to the medial ends of the ceratohyoids. The second and third pairs of hypobranchials are distinct and well developed. The fifth and sixth pairs of hypobranchials are mere rudiments fused with the basibranchials.

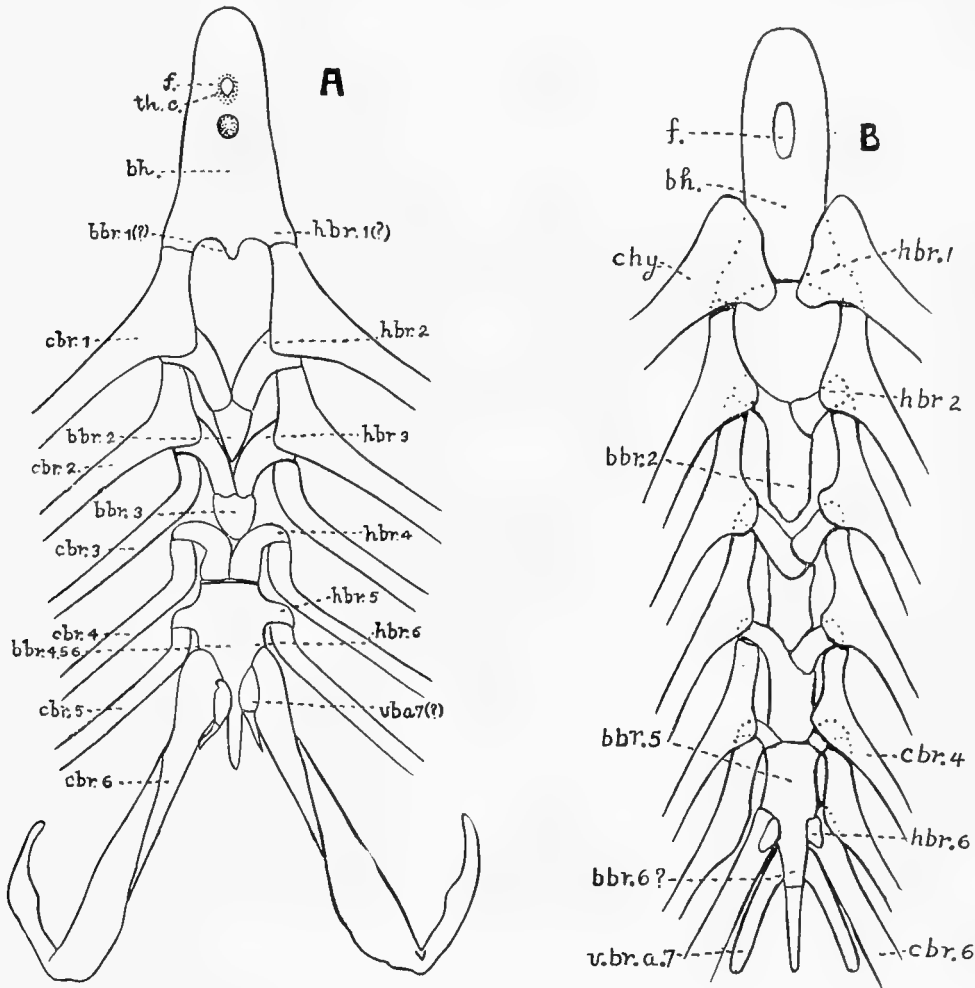
Fürbringer's specimen (1903, Fig. 18, Taf. XVII) presents several features that are different. A small median posteriorly directed prominence fused with the basihyoid may represent the first basibranchial, and a pair of posterolateral processes of the basihyoid probably represents the first pair of hypobranchials. The second basibranchial appears to be entirely absent, but there is a pair of second hypobranchials. The third basibranchial is distinct from the fourth basibranchial, but is fused with the fourth pair of hypobranchials. The fourth basibranchial is distinct from the fifth, but the fifth and sixth basibranchials are fused together. The fifth and sixth pairs of hypobranchials are not identified with certainty. There is a vestigial seventh branchial element. Some features of Fürbringer's drawing are obscure, so that it is not suitable for reproduction here.

Goodey (1910.1) described and figured (my Text-figure 26A) a small posteriorly projecting prominence (*bbr. 1?*) on the basihyoid which, as in Fürbringer's specimen, probably represents a fused first basibranchial. Otherwise, Goodey's drawing more closely resembles that of Garman (1885.2). There are, however, some differences. "The two lateral prominences [of the basihyoid], also at the posterior end, no doubt represent the hypobranchials of the first branchial arch" (Goodey, 1910.1, p. 545). In Garman's figure (my Text-figure 24) the hypobranchials of the first branchial arch appear to be separate elements overlapped by the ceratohyoids.

Garman (1913) described and figured (my Text-figure 26B) this region of the visceral skeleton in still another specimen. Here, there is no posterior projection of the middle part of the basihyoid to represent a vestigial first basibranchial, but the other basibranchials are more numerous and regular than in any other specimen that has been figured. There are five elements represented in this series, of which the fourth probably represents the combined fifth and sixth basibranchials, while the slender posterior element may belong to the vestigial seventh branchial arch discovered by Fürbringer (1903). The first pair of hypobranchials (*hbr. 1*) is represented by posterolateral processes of the basihyoid, while one member of both the second and the fourth pairs of hypobranchials is fused with the corresponding basibranchial. The hypobranchials of the sixth pair are small and are displaced somewhat posteriorly. The most posterior pair of cartilages (*v. br. a. 7*) presumably represent ceratohyoids of the seventh arch.

Allis (1923) agrees closely with Garman (1885.2) in his description and portrayal of the basibranchials, but in the fourth branchial arch of his specimen he finds one of the hypobranchials distinct and independent while the other is fused with the fourth basibranchial to form a single median cartilage with a lateral process on one side only. This fused hypobranchial is well shown in dorsal view (Figure 8, plate III), but is only partly shown in a ventral view (Figure 9, plate III). The former figure shows also a pair of rudimentary nodules representing the sixth hypobranchials, and both figures show a pair of rudimentary seventh hypobranchials.

Deinaga's otherwise excellent figure (1909 and 1923, Fig. 5, pl. II) of the visceral skeleton of *Chlamydoselachus* does not show clearly the limits and the relations of all the basibranchials and hypobranchials, hence it cannot be used for comparison.



Text-figure 26.

Ventral views of the median portions of the branchial skeletons of two specimens of *Chlamydoselachus* to show variations.

A—Dissection by Goodey (1910.1) of a specimen in the University of Birmingham.

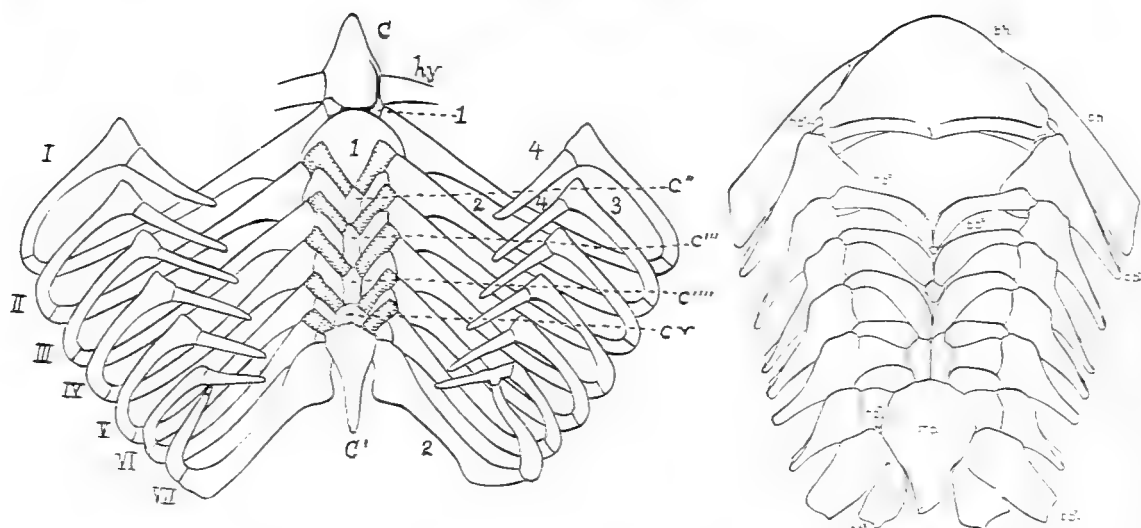
bbr.1(?)–6, basibranchials of the first (?) to the sixth arch; bh., basihyoid; cbr.1–6, ceratobranchials of the first to the sixth arch; f., foramen; hbr. (1) (?)–6, hypobranchials of the first to the sixth arches; th.c., thyroid concavity; vba7(?), vestigial seventh branchial arch.

Redrawn, with some changes in labels, after Goodey, 1910.1, Fig. 6, pl. XLIII.

B—Dissection by Garman (1913) of his second specimen in the Museum of Comparative Zoology. The original is without lettering.

bbr.2, 5 and 6 (?), basibranchials; bh., basihyoid; cbr.4 and 6, ceratobranchials; chy., ceratohyoid; f., foramen in basihyoid cartilage; hbr.1,2 and 6, hypobranchials; v.br.a.7, vestigial seventh branchial arch.

After Garman, 1913, Fig. 6, pl. 59.



Text-figure 27.

Dorsal and ventral views of the visceral skeleton of the notidanid shark, *Heptanchus*.

Text-figure 27. Branchial skeleton of *Heptanchus* sp., in dorsal view.

I-VII, first to seventh branchial arches; C, copula or basihyoid; CI, fused sixth and seventh basibranchials; c II—c V, second to fifth basibranchials; hy, ceratohyoid; 1, hypobranchials; 2, ceratobranchials; 3, epibranchials; 4, pharyngobranchials.

After Gegenbaur, 1872, Fig. 1, Taf. XVIII.

Text-figure 28. Visceral skeleton of *Heptanchus maculatus*, ventral aspect.

bb.2, second basibranchial; bh., basihyoid; cb., ceratobranchials; ch., ceratohyoid; hb., hypobranchials; mp., median piece.

After Daniel, 1934, Fig. 50A.

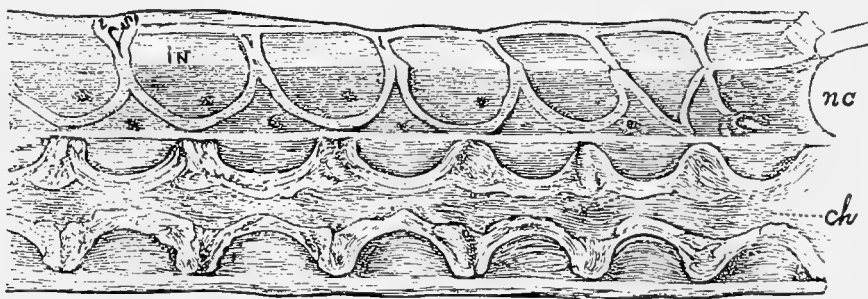
The vestigial seventh branchial arch in *Chlamydoselachus* was first described and figured by Fürbringer (1903, p. 409 and Fig. 18, pl. XVII). In his specimen it consisted of a single small rod of cartilage on each side. In a young specimen described by Hawkes (1907) it consisted of four small pieces on one side and two on the other. In another specimen, an adult, examined by Hawkes there were only two pieces "in a similar position," the larger one equal in length to the combined four pieces found in the smaller specimen. In a third specimen studied by Hawkes a seventh branchial arch was entirely lacking. Of two specimens examined by Goodey (1910.1), in one this arch was lacking, in the other it was represented (Text-figure 26A, *vba.* 7?) by "a pair of small, segmental tapering pieces lying on the ventral side of the last basibranchial at the bases of the sixth ceratobranchials." In a specimen described and figured by Garman (1913) the vestigial seventh arch (my Text-figure 26B) is represented by a pair of cartilages considerably larger than any described or figured in other specimens. The seventh branchial arch of a specimen studied by Allis is shown in my Figures 8 and 9, plate III, and is described by Allis (1923, p. 179) as follows:

From the left postero-lateral corner of the sixth basibranchial, a chain of small thin nodules of cartilage extends posteriorly and represents the vestigial seventh ceratobranchial . . . On the right side of the head this chain of nodules is represented by a process of the basibranchial. Wedged in between the base of this process and the distal end of the sixth ceratobranchial

there is a small nodule of cartilage, a similar nodule being found on the opposite side of the head wedged in between the basal one of the chain of three small nodules and the related ceratobranchial. These two little nodules are, in position and appearance, strict serial homologues of the two nodules that represent the proximal ends of the sixth hypobranchials, and they are accordingly quite probably the corresponding ends of the seventh hypobranchials, the posterior process of the large cardiobranchial then being the seventh basibranchial.

A comparison of all the available figures of the seventh branchial arch in *Chlamydoselachus* shows that this arch is extremely variable and is never fully developed. I am inclined to think that phylogenetically it is in process of disappearance rather than in process of development. A rudimentary ninth branchial arch is present in *Heptanchus* (Daniel, 1934, Fig. 50B).

It is in the ventral portion of the branchial skeleton of selachians that the greatest amount of variation takes place. A complete series of basibranchials and hypobranchials, without fusion, is presumably the primitive condition, but so far as I know this condition is not fully realized in any living fish. *Chlamydoselachus* and the notidanids probably come the nearest. Gegenbaur's drawing (1872, Fig. 1, pl. XVIII) of the branchial skeleton of *Heptanchus* is here reproduced as Text-figure 27. The first basibranchial is lacking and the sixth and seventh are fused together. If one compares Fürbringer's drawing of *Heptanchus* (1903, Fig. 29, Taf. XVIII), and Daniel's illustration (1934, Fig. 50A) reproduced as my Text-figure 28, one finds in the basibranchials of *Heptanchus* quite as much irregularity as I have noted for the same structures in *Chlamydoselachus*. On the other hand, in *Heptanchus* the hypobranchials form a more nearly perfect series, especially if one considers the vestigial first and seventh pairs figured by Daniel (my Text-figure 28). In *Hexanchus* (Gegenbaur, 1872, Fig. 2, Taf. XVIII; Fürbringer, 1903, Fig. 19, Taf. XVII), the basibranchials resemble those of *Chlamydoselachus* as figured by Goodey (my Text-figure 26A). In respect to both basibranchials and hypobranchials, *Chlamydoselachus* and the notidanids are primitive, yet so variable that they seem to possess the materials for a rapid evolutionary change.



Text-figure 29.

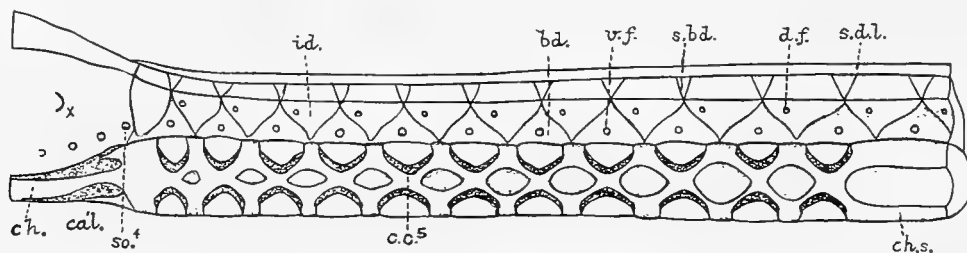
Longitudinal section of vertebral column and notochord in the cervical region of *Chlamydoselachus*.

ch, notochord; in, interdorsal; is, interspinous process; nc, neural canal.

After Garman, 1885.2, Fig. 3, pl. X.

NOTOCHORD AND VERTEBRAL COLUMN

In *Chlamydoselachus*, the notochord is persistent to a degree not found in the higher elasmobranchs. Perhaps in no other living shark does the notochord of the adult retain its primitive condition through so large a portion of its length. The notochord of *Chlamydoselachus* extends from the pituitary fossa of the basis cranii to the extreme tip of the tail. In the basis cranii it is very slender, but elsewhere it is a fairly stout rod.



Text-figure 30.

Vertical longitudinal section of the anterior end of the vertebral column in a large female *Chlamydoselachus*, showing calcified cyclospondylous centra.

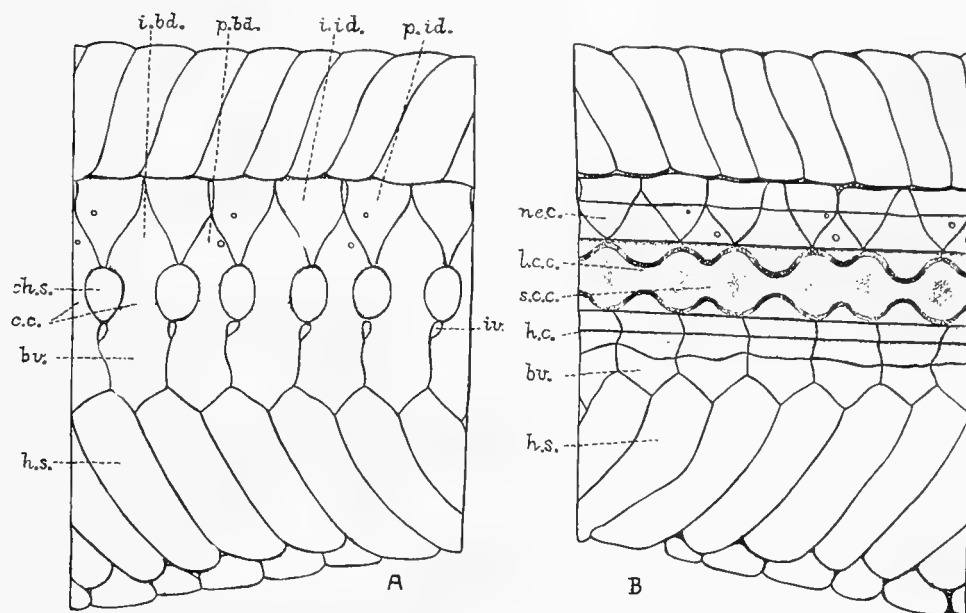
bd., basidorsal; cal., calcification; c.c.5, cyclospondylous centrum of the fifth cervical vertebra; ch., notochord; ch.s., chordal sheath; d.f., dorsal root foramen; i.d., inter-dorsal cartilaginous element; s.bd., suprabasidorsal; s.d.l., supradorsal ligament; so.4, spino-occipital foramen; v.f., ventral root foramen; X, foramen for tenth cranial nerve.

After Goodey, 1910.1, Fig. 10, pl. XLIII.

In the cervical (cephalic, according to Goodey's nomenclature) and main caudal regions the notochord of *Chlamydoselachus* shows pronounced metameric constrictions (Text-figures 29, 30 and 31) due to inward projecting thickenings of its sheath. In the trunk region and in the region of the dorsal and anal fins, the constrictions of the notochord are very slight (Text-figures 32 and 33); according to Garman (1885.2, Fig. 2, pl. X) they are limited to the ventral portion of the notochordal sheath and do not extend to the notochord proper. The metameric constrictions of the notochord are of interest because they occur in connection with the formation of rudimentary cyclospondylous centra. In *Chlamydoselachus* we find initial stages in the formation of these centra.

Similar constrictions of the notochord occur in *Heptanchus*. For the cervical region and near the base of the anal fin, these are illustrated by Text-figures 34 and 35. In the trunk region of *Heptanchus* the constrictions of the notochord are slight (Daniel, 1934, p. 48). In *Hexanchus* (Regan, 1906.2, p. 740) the notochord is constricted by annular thickenings of the cartilaginous sheath, without calcification such as occurs in *Heptabanchias* (*Heptanchus*) where the notochord is constricted vertebally by a series of calcified rings.

On page 351 I have described the continuity of the vertebral portion of the notochord with its more slender portion imbedded in the cranium. All observers agree in emphasizing the firmness of the attachment of the vertebral column to the cranium. Goodey



Text-figure 31.

Surface and sectional views of a portion of the vertebral column (x 1.25) from the main caudal region of *Chlamydoselachus*.

A—Surface view showing ridged extensions of the arcualia around the notochord.

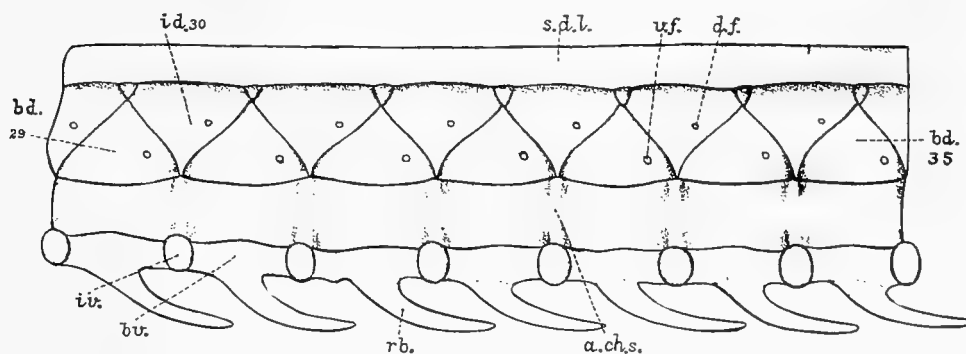
bv., basiventral; c.c., cyclospondylous centra; ch.s., chordal sheath; h.s., haemal spine; i.bd., imperforate basidorsal; i.id., imperforate interdorsal; iv., interventral; p.bd., perforate basidorsal; p.id., perforate interdorsal.

After Goodey, 1910.1, Fig. 15, pl. XLIV.

B—Vertical longitudinal section (with anterior and posterior ends reversed) showing calcified cyclospondylous centra of two sizes.

bv., basiventral; h.c., haemal canal; h.s., haemal spine; l.c.c., larger cyclospondylous centrum; nec., neural canal; s.c.c., smaller cyclospondylous centrum.

After Goodey, 1910.1, Fig. 16, pl. XLIV.



Text-figure 32.

A portion of the vertebral column (x 1.5) from the trunk region of *Chlamydoselachus*.

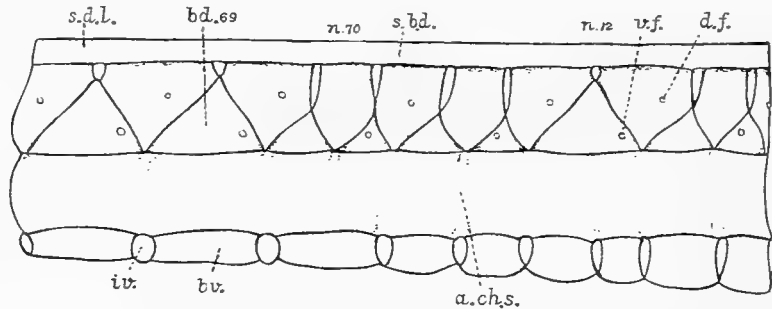
Note the rudimentary ribs.

a.ch.s., annulation in the chordal sheath; bd., basidorsal; bv., basiventral; d.f., dorsal foramen; id., interdorsal; i.v., interventral; rb., rib; s.d.l., supradorsal ligament.

After Goodey, 1910.1, Fig. 11, pl. XLIV.

(1910.1, p. 554) states: "The vertebral column is fused to the cranium quite firmly, so that but slight articulation is possible between the two." On this point Allis (1923, p. 161) writes:

In my specimens of *Chlamydoselachus* there is no continuity of the cartilage here, so far as I can determine from macroscopic examination. The opposing surfaces of the chondrocranium and first vertebra are closely applied to each other, and there is but little movement possible between them, but a certain amount of lateral movement is nevertheless possible, and the two articular surfaces can always be separated without breakage of the cartilage.



Text-figure 33.

A portion of the vertebral column ($\times 1.4$) of *Chlamydoselachus*, in the region of the dorsal and anal fins, showing the transition from monospondylous to diplospondylous vertebrae.

a.ch.s., annulation in the chordal sheath; bd.69, basidorsal no. 69; bv., basiventrals; d.f., dorsal foramen; iv., interventral; n.70 and n.72, neuromeres 70 and 72 respectively; s.bd., supra-basidorsal; s.d.l., supradorsal ligament; v.f., ventral foramen.

After Goodey, 1910.1, Fig. 12, pl. XLIV.

The vertebral column of *Chlamydoselachus* is of a very simple elasmobranch type. The best description is that of Goodey (1910.1), and I shall base my treatment mainly on his account. There is a long central cylinder, which comprises the notochord together with its enlarged sheath. Above the chordal sheath there is a series of cartilaginous vertebral elements arching over the spinal cord. These elements, comprising the neural arches or the dorsalia, are classified by Goodey, using Gadow's (1895) nomenclature, as follows: basidorsals, interdorsals and supra-basidorsals, the last-named being segmented off from the apices of the basidorsals. Below the chordal sheath there is another series of vertebral elements, the ventralia, consisting of basiventrals, interventrals, ribs, and haemal spines in the caudal region. These various elements making up the vertebral column are illustrated in Text-figures 30–33 inclusive. There is an elastic supradorsal ligament which extends from the cranium to a point just posterior to the dorsal fin. This must greatly strengthen the column.

There is no detailed account of the histological structure of the chordal sheath in *Chlamydoselachus*, but in *Heptanchus* (Daniel, 1934, p. 48, and Fig. 52 reproduced as my

Text-figure 34) it is composed of three concentric layers as follows: "The outermost of these layers is relatively thin and consists of cartilage; within this cartilage is a second and lighter broad area which appears to be made up of transverse fibers. Within this second layer and bounding the notochord is a third layer of a white tissue. At regular intervals the third layer forms septa which produce the regular constrictions in the central part of the notochord. It will be observed that the septa are more pronounced ventrally than dorsally, and that they pass intra-centrally." The development of the sheath is discussed by Daniel (1934, p. 70).

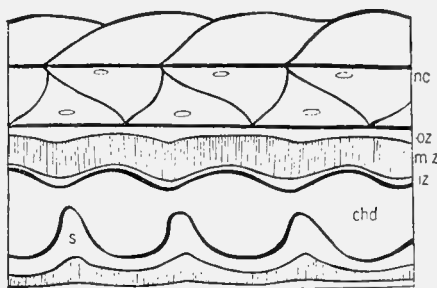
In a large female specimen of *Chlamydoselachus* described by Goodey (1910.1) the first eleven vertebrae possess ring-like thickenings of the chordal sheath, which project inward in such a manner as to constrict the notochord and make it appear somewhat

Text-figure 34.

Sagittal section through sixth to eighth segments of the vertebral column of *Heptanchus maculatus*, showing structure of the chordal sheath.

chd, notochord; iz, inner zone, mz, middle zone, and oz, outer zone, of the notochordal sheath; nc, neural canal; s, septum constricting notochord.

After Daniel, 1934, Fig. 52.



like a string of beads (Text-figure 30). The soft notochordal tissue gradually becomes obliterated from the intervertebral spaces as it approaches the skull, so that in the space between the first centrum and the cranium soft tissue is not present at all (Goodey, 1910.1, p. 555). This is apparently not true of Garman's large specimen (Text-figure 29) in which the notochord (ch) is nowhere completely interrupted by the constrictions of the chordal sheath. Continuing my account of the cervical region in Goodey's large specimen: Each constriction appears below a basidorsal, so that the constrictions are intravertebral. Each thickening of the chordal sheath possesses a calcification, as shown by the deeply shaded areas in Text-figure 30, c. c., and in a median vertical longitudinal section of a single vertebra these calcified areas appear like two Vs placed point-to-point. Thus each centrum has the form of a short cylinder constricted round its middle. There are no articular surfaces, nor even septa, separating any two successive centra; the notochordal sheath is continuous and the intervertebral spaces are filled in by successive bead-like segments of the notochord. The relations of the notochordal sheath are shown somewhat better in a smaller and presumably younger specimen studied by Goodey (1910.1, Fig. 9, pl. XLIII), in which some of the constrictions are not so well developed and the calcifications are not complete.

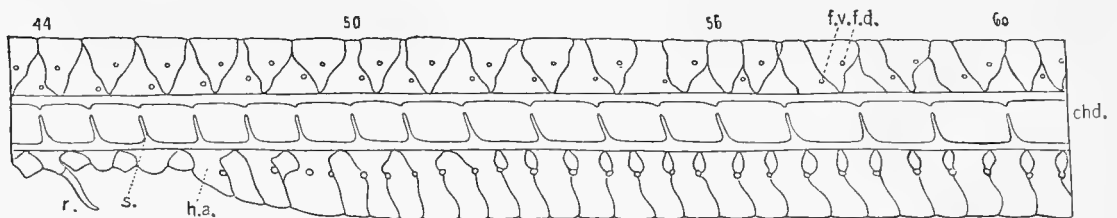
In the unusually long trunk region of *Chlamydoselachus*, the notochord (Text-figure 32) is almost uniform in diameter; nevertheless, according to Goodey, it shows slight but unmistakable signs of segmentation. This segmentation is described by Goodey as follows:

The segmentation is shown by a difference in the appearance of the chordal sheath along lines corresponding in position to the ends of the basidorsals. At these points there appear to be narrow rings or annulations of the notochord as shown in Fig. 11 [my Text-figure 32]. In a view of the cut surface of a vertical longitudinal section of a portion from this region, no apparent constrictions of the notochord are found to correspond with the external segmentation of the chordal sheath. The interior of the chord presents a fairly uniform appearance, as was noted by Garman. If, however, a horizontal longitudinal section be made of the notochord, a regular sequence of constrictions of the chordal sheath is at once apparent. Each of these occurs beneath a basidorsal, and extends between two consecutive segmentation marks on the exterior of the chordal sheath. Each takes the form of a bulging inward of the sheath, so that a slightly pinched-in cylinder is formed.

There are no calcifications of the notochordal sheath in the trunk region of *Chlamydoselachus*. Rudimentary ribs are shown in Text-figure 32.

The cervical and trunk regions are typically monospondylous, i. e., each "neuromere" (Goodey's terminology) is made up of one of each kind of vertebral element: basidorsal, interdorsal, supra-basidorsal, basiventral and interventral. The foramina for the spinal nerves do not occur between the dorsalia but are actual perforations of the basidorsals and interdorsals. In the monospondylous regions each basidorsal transmits a foramen for a ventral root, and each interdorsal, one for a dorsal root. At the seventieth neuromere, Goodey found an interesting transition from the monospondylous to the diplospondylous condition (my Text-figure 33). There is a doubling of the number of basidorsals, interdorsals and supra-basidorsals, but only the posterior interdorsals and basidorsals of each neuromere contain foramina for the exit of the roots of spinal nerves. In the seventy-second neuromere the monospondylous condition recurs dorsally, but the ventral elements are diplospondylous. The diplospondylous condition characteristic of the caudal portion of the vertebral column in sharks probably arises out of the monospondylous by a process of fragmentation of the primitive cartilaginous vertebral elements.

Goodey does not tell us precisely where, with reference to external features, the transition from the monospondylous to the diplospondylous condition in *Chlamydosela-*

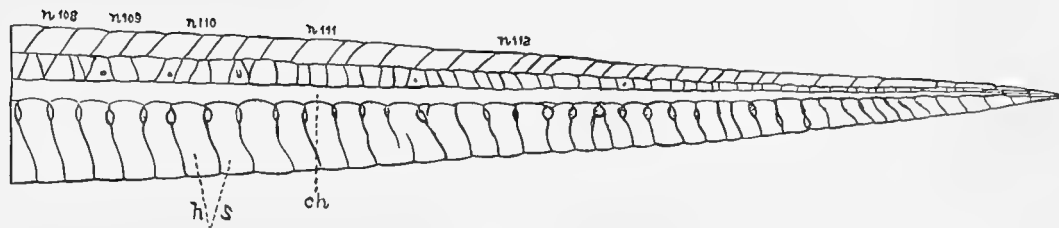


Text-figure 35.

Lateral view of the spinal column of *Heptanchus maculatus* in the region of transition from the monospondylous to the diplospondylous condition, near the base of the anal fin.

chd., notochord; f.d., foramen for dorsal nerve root; f.v., foramen for ventral nerve root; h.a., haemal arch; r., rib; s., septum constricting notochord; 44-60, vertebrae.

After Daniel, 1934, Fig. 53.



Text-figure 36.

Terminal caudal portion of the vertebral column of *Chlamydoselachus*, showing heterospondyly.

ch, notochord; hs, haemal spine; n 108—n 112, neuromeres.

After Goodey, 1910.1, Fig. 17, pl. XLV

chus occurs; but from a comparison of Text-figure 33, after Goodey, with Text-figure 48, p. 378, after Garman, it appears to be in the region of the dorsal and anal fins. Here, the condition of the notochord and of the chordal sheath (Text-figure 33) is similar to that in the trunk region (Text-figure 32). In *Heptanchus* (Daniel, 1934, p. 48) the transition occurs at about the fifty-sixth segment dorsally, and somewhat farther forward ventrally (my Text-figure 35); this region lies dorsal to the base of the anal fin.

In the main caudal region of a large female specimen of *Chlamydoselachus* described by Goodey (1910.1), the diplospondylous condition is well established (my Text-figure 31). The constrictions of the chordal sheath are of two sizes, the larger more calcified ones lying beneath the imperforate dorsals, and the smaller less calcified ones beneath the perforate dorsals. The segmented appearance of the notochord is due in part to constrictions by bands of cartilage. These bands are lateral extensions of the dorsal and ventral arcualia (basidorsals and basiventrals) round the chordal sheath, forming bridges that connect the dorsal and ventral cartilages from which they arise. These bridges alternate with spaces in which the chordal sheath is naked. In the trunk region, homologous bands of cartilage occur but they are so thin that they are recognizable only in microscopical sections.

Toward the tip of the tail the differences in the sizes of the cyclospondylous centra gradually become lost, the constrictions becoming equal in size along with the equalization in the size of the perforate and imperforate basidorsals. This stage marks a near approach to perfection in the expression of diplospondyly.

In the extreme tip of the tail the vertebral column is a gradually tapering structure (Text-figure 36) which remains segmented up to the very end. The arrangement of the nerve foramina with relation to the number of dorsalia is such that Goodey characterizes this region as "heterospondylic." In *Heptanchus* (Daniel, 1934, p. 49) the segments of the tail are said to show "an incomplete diplospondyly" in the arches both above and below the central column. No exception is made in regard to the extreme tip of the tail.

Concerning the occurrence of cyclospondylous centra, Goodey (1910.1) writes as follows:

The points at which the calcified centra occur are perhaps deserving of some mention. It seems that they are found where there are the greatest demands made for strength. At the anterior end, combined with the fusion of the vertebral column to the cranium, they give a rigidity to the supporting elements which is of service no doubt in enabling the fish to cleave the water. In the caudal region they meet the demand for increased strength caused by the purchase which the caudal fin obtains upon the water.

It might be added that in the caudal region the cartilaginous bridges across the lateral surfaces of the chordal sheath give greater strength to the vertebral column. On the other hand, the diplospondylous condition gives greater flexibility (Ridewood, 1899). In general, the vertebrae are best developed in the region that is subjected to the most severe stresses.

We have seen that the vertebral column of *Chlamydoselachus* is of interest in a number of ways. The notochord persists, in the adult, with so little modification that it is one of the most primitive known in living sharks. The cartilaginous elements of the vertebral column are of a very simple elasmobranch type and illustrate various stages in the formation of complete vertebrae. In the cervical and caudal regions one finds early stages in the formation of cyclospondylous centra; these arise as calcifications in the chordal sheath. In the main region of the tail the dorsal and ventral arcualia are connected by cartilaginous bridges, giving unity and completeness to the structure of each vertebra. In the region of transition from body to tail, monospondylous vertebrae gradually give way to diplospondylous vertebrae. Finally, at the extreme tip of the tail there is a condition of heterospondyly which is perhaps unique among selachians.

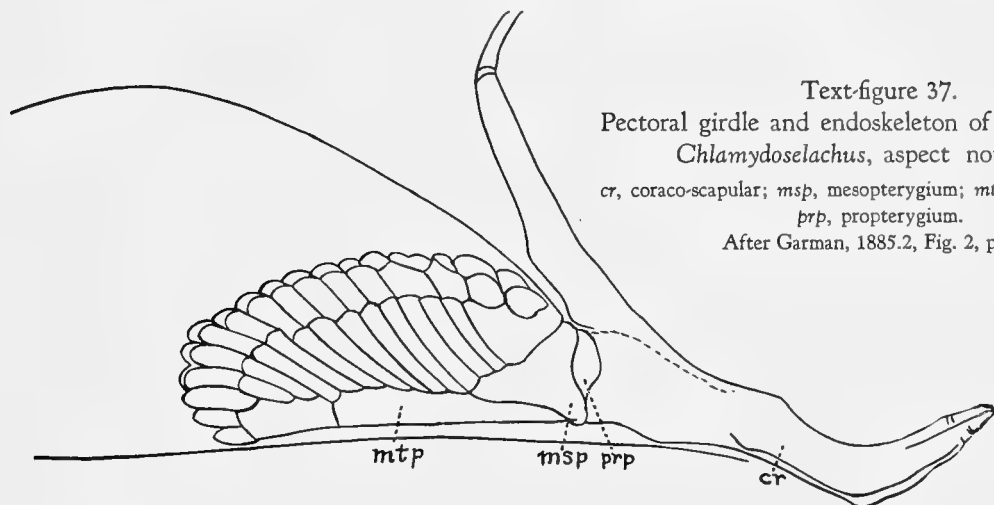
APPENDICULAR SKELETON

The appendicular skeleton of *Chlamydoselachus* includes the cartilaginous framework of the pectoral and pelvic fins, together with the pectoral and pelvic girdles; and the cartilaginous supports of the dorsal and anal fins. The endoskeletal supports of the tail fin belong mainly to the axial skeleton, but it is convenient to consider the framework of the caudal fin along with the skeletons of the other fins.

PECTORAL FINS AND GIRDLE

The skeleton of the pectoral fin of *Chlamydoselachus* has been described and figured by Garman (1885.2); Braus (1902); Deinema (1909 and 1923); and Goodey (1910.1). The pectoral girdle or coraco-scapular (Text-figures 37 and 38) bears a decided resemblance to that of *Heptanchus* (Daniel, 1934, Fig. 54); but in the fin proper the radials of *Chlamydoselachus* are relatively shorter, and are segmented to form typically three rows of cartilaginous elements while *Heptanchus* has about twice that number.

Braus's figure of the pectoral fin skeleton of *Chlamydoselachus* portrays a ventral view. It differs from Garman's figure (aspect not stated) in a number of details, as may



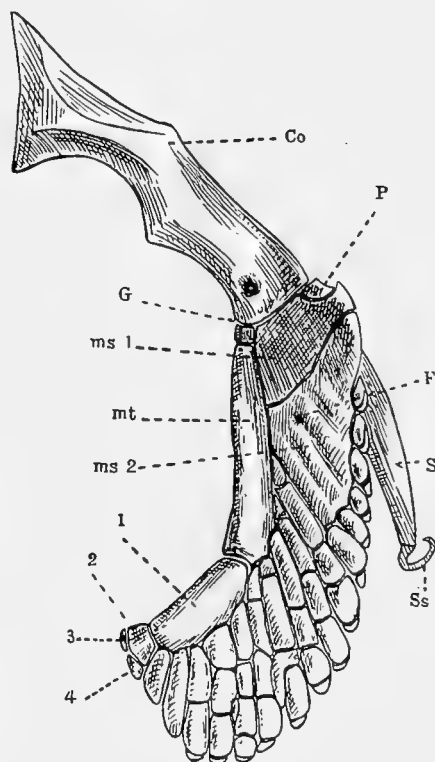
Text-figure 37.

Pectoral girdle and endoskeleton of pectoral fin of *Chlamydoselachus*, aspect not stated.

cr, coraco-scapular; msp, mesopterygium; mtp, metapterygium; prp, propterygium.

After Garman, 1885.2, Fig. 2, pl. XI.

be seen upon comparing Text-figures 37 and 38. There are differences in the number, sizes and shapes of the basal cartilages, particularly the mesopterygium. In Garman's figure this is triangular in outline, in Braus's figure it is more nearly quadrangular. The anterior radials are fused over a considerable area in Braus's figure, but exhibit a more limited amount of fusion in Garman's figure. In Braus's specimen, many of the radials posterior to the region of fusion have four or five segments; in Garman's specimen, there are nowhere more than three segments of a single radial. Deinega's Fig. 14, Taf. IV, portraying a pectoral fin (aspect not stated) of *Chlamydoselachus* closely resembles Garman's figure (my Text-figure 37) save that right and left are reversed. Deinega's Fig. 15, Taf. IV, representing an inner (ventral) view of a pectoral fin of *Chlamydoselachus*, more nearly resembles Braus's figure (my Text-figure 38) which is also a ventral view. The chief differences in the figures thus far considered are understandable on the assumption that Garman portrayed a dorsal view, and that Deinega's Fig. 14 is also a dorsal view. In Deinega's figures of the pectoral fin, some of the lines at the distal margin are so indistinct that one cannot determine the exact number of cartilaginous elements; but in his text he states that there are three rows of radial segments. Goodey's drawing (1910.1, Fig. 18, pl. XLV) of the left pectoral fin (aspect not stated) of



Text-figure 38.

Ventral (inner) view of a pectoral fin skeleton of *Chlamydoselachus*.

Co, coracoid; F, foramen for blood vessel; G, shoulder joint; ms 1, primary mesopterygium; ms 2, secondary mesopterygium; mt, metapterygium; P, propterygium; S, scapula; Ss, suprascapula; 1-4, cartilages in line with basals.

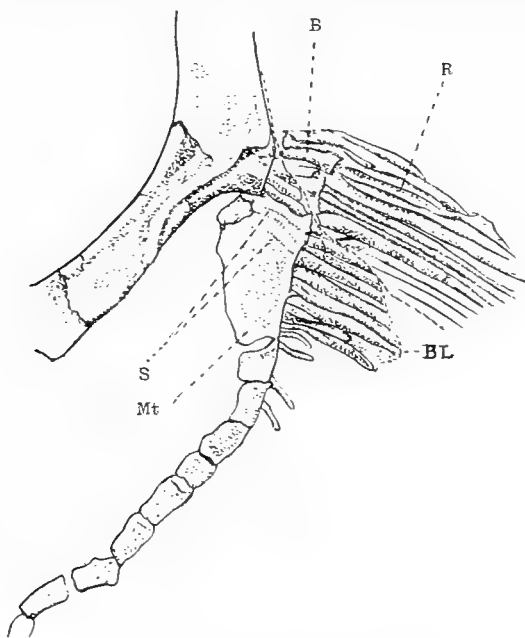
After Braus, 1902, Fig. 1.

Chlamydoselachus shows a large secondary mesopterygium, as in Braus's figure, and the primary mesopterygium also resembles that figured by Braus. The posterior radials are segmented to form no more than three rows of segments. At the extreme posterior ends of the fins shown in the various figures there are individual differences.

In connection with his study of the development of paired fins, Sewertzoff (1926, p. 547) states:

It is now generally accepted that the skeleton of the fins of the lowest cartilaginous fishes (Chondropterygii) has developed from metamerically disposed rays, and that the basal cartilage of the free parts of the fin, i.e., the pro-, meso-, and the metapterygium, as well as the girdles, were formed by the concrescence or fusion of the proximal segments of these rays. But this view may not be considered settled, and, looking over the literature of this question, we see that many writers, who accept the theory of the [metameric] origin of the paired fins, pass over in silence the question of the primitive structure of their skeletons or express themselves on that subject with considerable caution.

In the pectoral fin skeletons of both *Cladodus neilsoni* Traquair (Text-figure 39) and *Symmorium reniforme* Cope (Text-figure 40) there is only one basal that can be



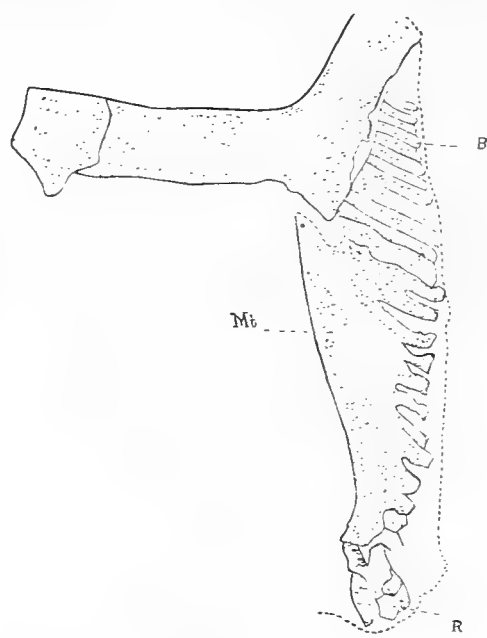
Text-figure 39.

Pectoral girdles and fin skeletons of two fossil sharks, *Cladodus* and *Symmorium*.

Text-figure 39. Endoskeleton of the pectoral fin of *Cladodus neilsoni* Traquair.

B, basal piece; BL, fracture line; Mt, metapterygium; R, radial; S, furrow in outer proximal margin of the metapterygium.

From Braus, 1902, Fig. 2; after Traquair, 1897, Fig. 1, pl. IV.

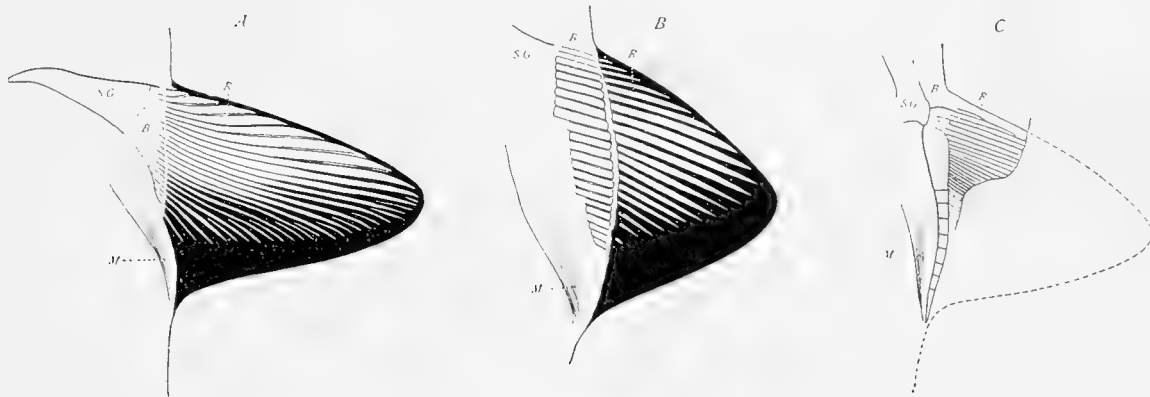


Text-figure 40.

Text-figure 40. Fragment of a pectoral fin skeleton of *Symmorium reniforme* Cope.

B, basal piece; Mt., metapterygium; R, some small radials at the distal end.

From Braus, 1902, Fig. 3; after Cope, 1895, Fig. 1, pl. VIII.



Text-figure 41.

Pectoral fins of the fossil sharks (A) *Cladoselache*, (B) *Ctenacanthus*, and (C) *Cladodus neilsoni*, indicating the mode of origin of the metapterygial axis.

B, basalia; M, muscle of hindmost region of the fin; R, radials; SG, shoulder girdle.

After Dean, 1909, Fig. 28.

homologized with a basal in recent fishes, and it is considered to be a metapterygium. In front of this element there is, apparently, a series of radials in direct articulation with the pectoral girdle. In *Symmorium* the metapterygium itself shows a segmentation, probably metameric, along its distal margin. If the above interpretations are correct, they afford evidence that basals are developed by the concrescence of proximal segments of radials. For comparison I have inserted Dean's (1909) figures (my Text-figure 41) of the pectoral fins of *Cladoselache*, *Ctenacanthus* and *Cladodus neilsoni*. The origin of the girdles (discussed on p. 376) is obscure, but there seem to be sufficient data to warrant an acceptance of the theory of the metameric origin of the basals of the paired fins.

PELVIC FINS AND PELVIS

Since the pelvic fins of the male *Chlamydoselachus* are highly modified to form copulatory organs (myxopterygia), it is necessary to describe the pelvic fins of the two sexes separately.

PELVIC FINS AND PELVIS OF THE FEMALE.—The pelvis and the pelvic fin skeleton of the female *Chlamydoselachus* have been described and figured by Garman (1885.2), Deinema (1909 and 1923), and Goodey (1910.1). The figures by Garman and by Goodey are reproduced as my Text-figures 42, 43, and 89 (p. 434).

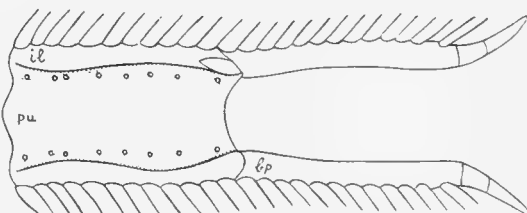
The pelvis of *Chlamydoselachus*, as compared with that of *Heptanchus*, is very long (i.e., in the direction of the principal axis of the body). Commenting on this fact, Garman

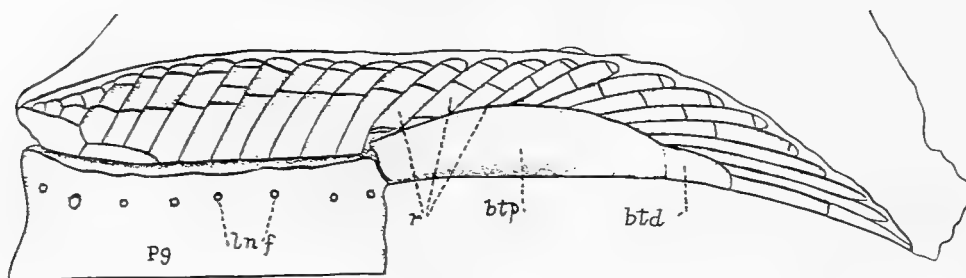
Text-figure 42.

Dorsal view of the pelvis (one-half natural size) of an adult female *Chlamydoselachus*.

bp, basipterygium; il, iliac ridge; pu, pubis.

Redrawn after Garman, 1885.2, Fig. 1, pl. XI.





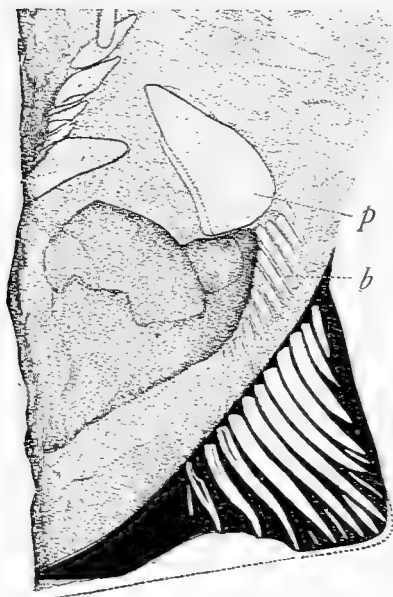
Text-figure 43.

Dorsal view of the right half of the pelvis, and of the right pelvic fin, of a female *Chlamydoselachus*.

btd, distal segment of the basipterygium; *btp*, proximal segment of the basipterygium; *lnf*, longitudinal row of foramina for nerves; *pg*, pelvic girdle; *r*, lateral radials.

Redrawn from Goodey, 1910.1, Fig. 19, pl. XLV.

(1885.2) writes: "The peculiar shape of the pelvis suggests an embryonic character of other sharks. In embryos the pelvis is longer than in the adult, in comparison with the transverse measurement. An embryo of *Heptabanchias* before me has it half as long as wide, proportions which are intermediate between those of the adult and an adult *Chlamydoselachus*." From another point of view one may say that an elongate pelvis is in keeping with the general body form of *Chlamydoselachus*.



Text-figure 44.

Pelvic fin and girdle of the fossil shark, *Cladoselache kepleri*.

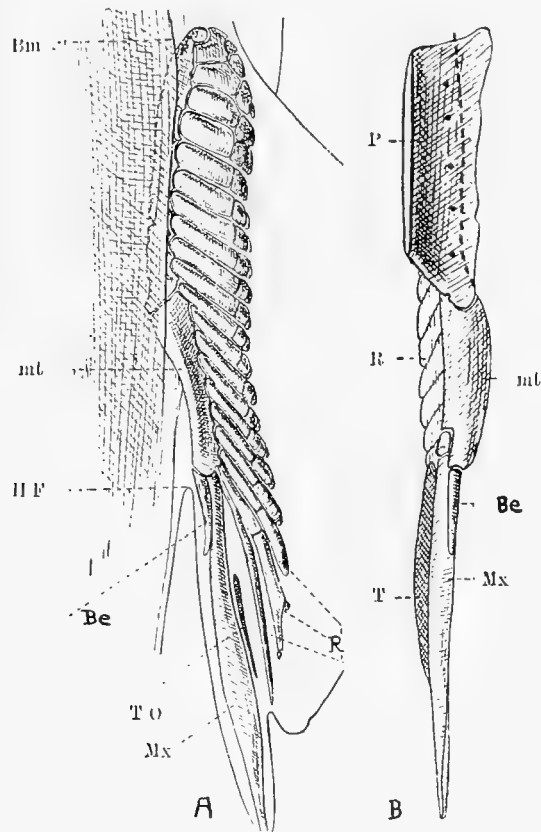
b, basals; *p*, pelvic arch.
After Dean, 1909, Fig. 18.

Garman's figure reproduced as my Text-figure 89 (p. 434) is a ventral view, and shows a wedge-shaped piece inserted, at the anterior margin, between the two paired portions of the pelvis. Thus the median suture becomes Y-shaped. This wedge-shaped cartilaginous element is not shown in Garman's figure reproduced as my Text-figure 42, which is a dorsal view of the pelvis, presumably of the same female; nor is it shown in any other published drawing of the pelvis of *Chlamydoselachus*, male or female, dorsal or ventral. Apparently, it is an individual variation. Deinega's drawing (1909, 1923) shows a median groove or suture extending the entire length of the pelvis.

Along the lateral margins of Deinega's drawing of the pelvis, at regular intervals, there are faint transverse grooves pierced by foramina, marking off segments in line with the radials. These transverse grooves indicate a metameric origin of this portion of the pelvis, presumably through the fusion of primitive radials to form basals which were later added to the pelvis. The manner in which basals of the pelvic fins may be derived from radials is illustrated by Dean's

figure of the fossil *Cladoselache* (my Text-figure 44).

In the female *Chlamydoselachus*, the skeleton of the pelvic fin proper (Text-figures 43 and 89, the latter on p. 434) is much like that of *Heptanchus* as figured by Gegenbaur (1870, Fig. 3, Taf. XV); and as shown in my Text-figure 45A, after Daniel. In *Chlamydoselachus* the basipterygium is shorter and more of the radials are attached directly to the pelvis. There is very little fusion of radials in the pelvic fins of either

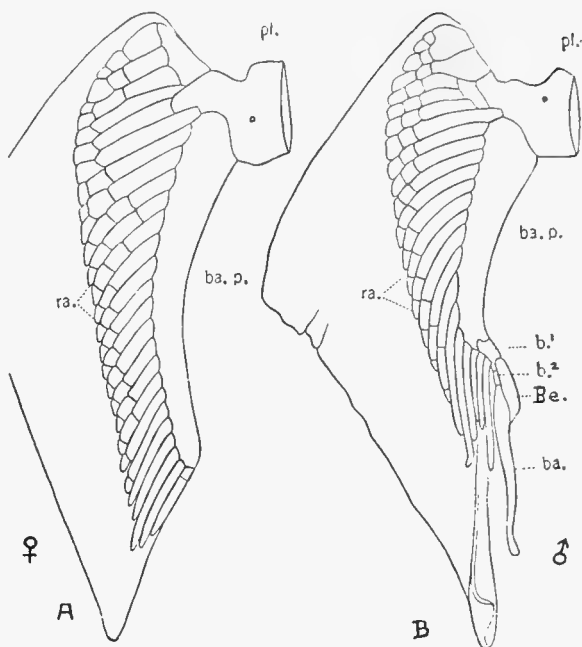


Text-figure 46.

Pelvic fin skeleton of a male *Chlamydoselachus*: A, viewed obliquely from above; B, viewed from the inner (ventral) side.

Be, medial radial belonging to the myxopterygium; Bm, abdominal musculature; mt, metapterygium; Mx, principal radial of the myxopterygium; P, pelvis; R, radials; T, pocket of the myxopterygium; TO, opening of the pocket.

After Braus, 1902, Abb. 7 and 8.



Text-figure 45.

Skeleton of the pelvic fin and girdle of *Heptanchus maculatus*: A, female; B, male.

Be, beta cartilage; b.1—2, first and second connecting segments ba., basal or axial cartilage; ba.p., basipterygium; pl., pelvis; ra., radials.

After Daniel, 1934, Fig. 55.

Chlamydoselachus or *Heptanchus*, and this fusion is confined to the anterior end of the fin skeleton where some plates of cartilage may be regarded as rudimentary basals. In Deinega's drawing (1909 and 1923) of the pelvic fin of *Chlamydoselachus*, it is difficult to determine the number of segments in the radials—the row of small distal segments is either not well shown or is absent.

PELVIC FINS AND PELVIS OF THE MALE.—In the male *Chlamydoselachus*, the skeleton of the pelvic fins, together with the pelvis, has been fully described and figured by Braus (1902) and by Goodey (1910.1). Their figures are reproduced as my Text-figure 46 and my Figure 21, plate V. By comparison with Text-figures 42, 43, and 89 (p. 434) it will

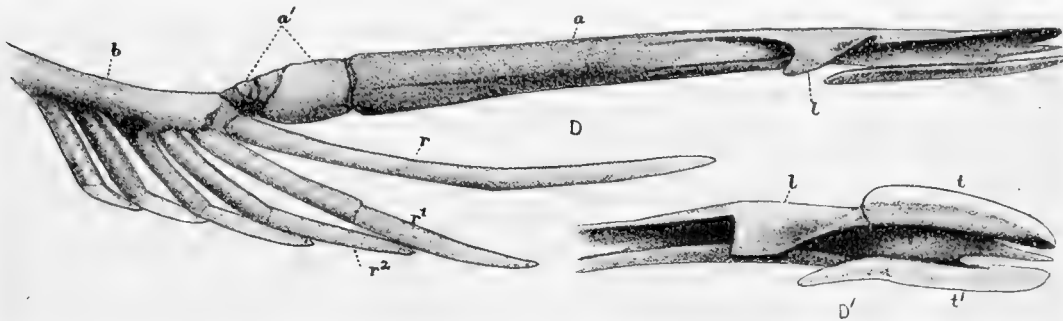
be seen that the pelvis is alike in the two sexes. In its basal, anterior and middle portions, the skeleton of the pelvic fin of the male is much like that of the female. In the specimen figured by Goodey there is a slight amount of fusion of radials at the extreme anterior end. This fusion of radials does not appear in Braus's figure.

Osburn (1907) described and figured the pelvis and the pelvic fin skeleton of a 225-mm. embryo of *Chlamydoselachus*. The sex is not stated, but the condition of the most posterior radials is intermediate between that characteristic of the adult female and that shown in the male figured by Braus. Osburn noted that each pelvic girdle (lateral half of the pelvis) is pierced by eight foramina for nerves, and serves as a basal for about half of the radials of the fin. In the mesenchyme stage, the two girdles fuse at the mid-line, and in the stage figured "the separation at the anterior end is not yet complete." This "separation" presumably refers to the presence of a suture between the two cartilaginous elements in the adult stage. In the fossil *Chladoselache* (according to Dean, 1909) there are two quite separate pelvic girdles forming a pair, and in the fin skeleton the basals consist of small rod-like elements like the radials (Text-figure 44).

After reviewing the literature on the embryological development of the paired fins of selachians, Regan (1906.2, p. 731) states: "The mode of development of the fin-girdles is in favor of the hypothesis that they are outgrowths of the basipterygia, and the latter may well have been formed from the coalescence of the originally separate basal segments of the supporting cartilages, since in the median fins also these are segmented off from continuous laminae." Osburn (1907, p. 188) also inclines to the view that the origin of the girdles may be traced to the supporting elements of the fin. He compares the pelvic girdle of *Chlamydoselachus* to the basals of unpaired fins.

THE MYXOPTERYGIA.—Posteriorly and medially, the skeleton of the pelvic fin in the male is decidedly different from that of the female since it is enlarged and modified to form the framework of the copulatory organ, the myxopterygium. The skeleton of the myxopterygium or "clasper" has been described and figured separately by Günther (1887) and by Leigh-Sharpe (1926), whose figures are reproduced as my Text-figures 47 and 115A (the latter on p. 472). It has also been described and figured as a part of the pelvic fin by Braus (1902) and by Goodey (1910.1) whose figures are reproduced as my Text-figure 46 and Figure 21, plate V. The endoskeletal elements involved in the formation of this organ are in line with the basals but are in serial relation with the radials. They appear to be radials that are enlarged, elongated and otherwise differentiated. In the several figures, there are minor differences in the radials associated with the one that is most highly developed, and in Braus's specimen the skeleton of the myxopterygium is not differentiated to the same degree as in the others. Possibly, Braus worked on a specimen that was not fully mature. Leigh-Sharpe's description (1926, p. 312) of the skeleton of the claspers, illustrated by his Fig. 5A (reproduced as my Text-figure 115A, p. 472), is as follows:

The skeleton consists of a main stout bar of supporting cartilages, the myxapterygium [sic], with three additional minor cartilages, of which a pair on either side stiffens the apical expansile valves, the remaining one acting as a foundation for the supposed rhipidion. Two of the radial cartilages attached to the basiptyergium, part of which is seen in the upper portion of the figure, come down to support the walls of the clasper cavity.



Text-figure 47.

Skeleton of a clasper (myxopterygium) of *Chlamydoselachus anguineus*.

a, principal cartilage; *a'*, intermediate cartilage; *b*, basals of pelvic fin; *l*, lobe-like expansion of cartilage *a*; *r*, *r1* and *r2*, rays of pelvic fin; *t*, *t1*, movable calcified terminal pieces by which the canal can be opened or closed.

After Günther, 1887, Figs. D and D1, pl. LXIV.

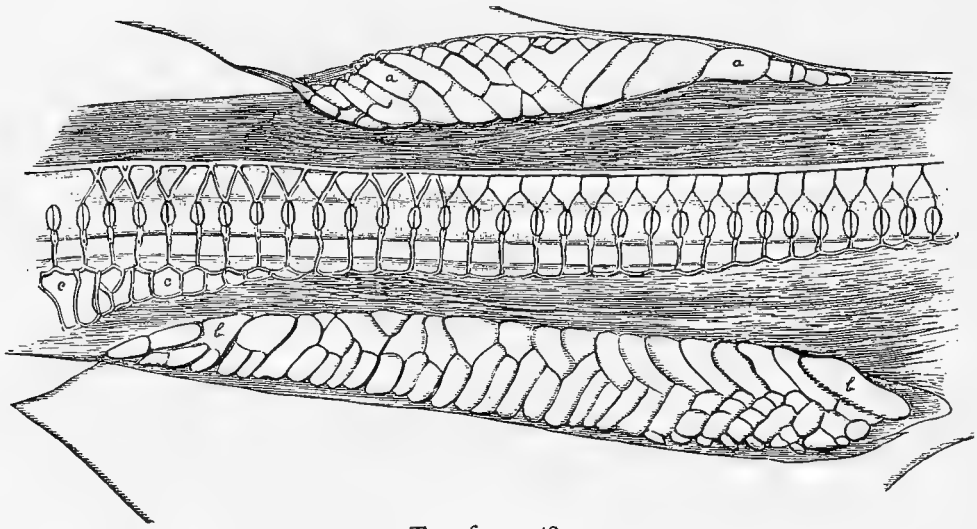
Günther (1887) states that, as compared with other elasmobranchs, the skeleton of the clasper of *Chlamydoselachus* (Text-figure 47) is extremely simple and is very similar to that of *Acanthias* as figured by Gegenbaur (1870, Fig. 15, Taf. XVI). Goodey (1910.1, p. 567) writes:

When the mixiptyergium [sic] of *Chlamydoselachus* is compared with that of *Hexanchus griseus*, described and figured by Huber, one is at once struck by the high degree of development presented by the organ in *Chlamydoselachus*. Whereas in *Hexanchus* the axial cartilage is represented by a comparatively short cartilage, scarcely distinguishable from a lateral radial, and bearing no accessory cartilages; the homologous part in *Chlamydoselachus* is a long, stout cartilage, furnished distally with three movable accessory cartilages.

As described by Daniel (1934) and as shown in my Text-figure 45B, the skeleton of the myxopterygium of *Heptanchus* is somewhat simpler than that of *Chlamydoselachus*. The skeleton of the pelvic fin of a male *Raja* (sp.?) figured by Gegenbaur (1870, Fig. 21, Taf. XVI) is simpler than any that I have mentioned. Evidently, differences in the form of the skeleton of the claspers are of little phylogenetic significance.

THE DORSAL FIN

In the single dorsal fin of *Chlamydoselachus*, the cartilaginous elements (radials) forming the endoskeleton are very irregular, as shown in my Text-figure 48. The tapering anterior portion extends a considerable distance in front of the small membranous portion of the fin. Garman (1885.2, p. 15) interprets this condition as follows:



Text-figure 48.

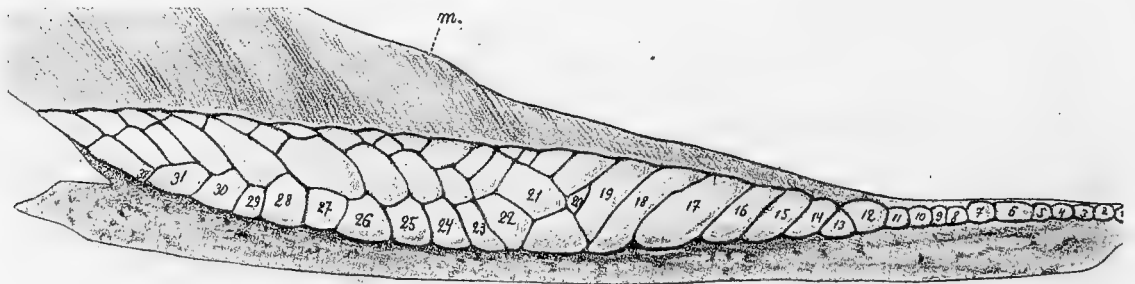
Endoskeleton of dorsal and anal fins of *Chlamydoselachus anguineus*.

a, radial of dorsal fin; b, radial of anal fin; c, anterior radial of caudal fin.

After Garman, 1885.2, pl. XIII.

The great extent of the band compared with the size of the fin, and the manner in which it dwindles toward the front, taken in connection with the fact of the continuation of the peculiar scales of the fin-border some two inches in front of the cartilages, show that in ancestral forms of this animal the dorsal fin was much longer, and corresponded more nearly in proportions with the anal.

The only additional figure of the adult dorsal fin skeleton that I have found is Deinega's (1909 and 1923), which is reproduced as my Text-figure 49. This figure is instructive in that it shows clearly a much greater number of cartilaginous elements than is shown in Garman's drawing (my Text-figure 48). Deinega distinguishes a series of thirty-two basal elements which he calls radials, whereas in Garman's figure there are scarcely half as many of these elements, which he also calls radials.



Text-figure 49.

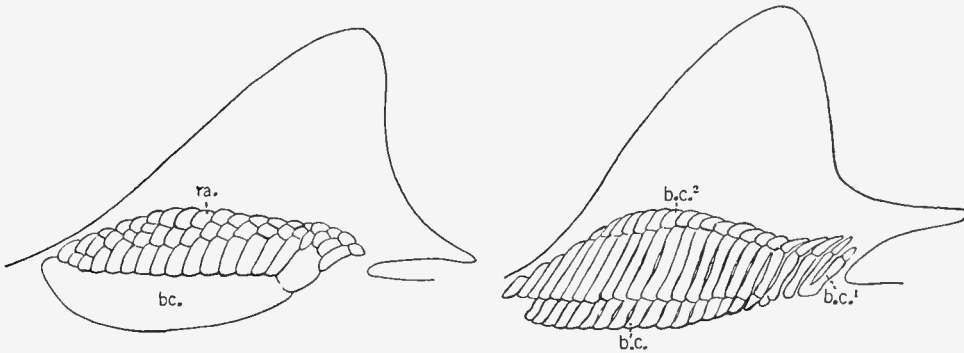
Endoskeleton of the dorsal fin of *Chlamydoselachus anguineus*.

m., fin membrane; 1-32, first row of radials (no. 1 not shown).

After Deinega, 1909, Fig. 12, pl. III.

Osburn has published a drawing (1907, Fig. 19, pl. V) of the dorsal fin skeleton of a 225-mm. embryo of *Chlamydoselachus*. The total number of cartilaginous elements (thirty-six) is smaller than in Garman's specimen (forty-five), and much smaller than in Deinega's specimen (sixty-one). The larger number in the adult may possibly be due to fragmentation. Osburn notes the wide separation of the dorsal fin skeleton from the axial skeleton.

In the absence of any further examples it appears that the entire endoskeleton of the dorsal fin of *Chlamydoselachus* is composed of radials. Some segments of these radials have undergone slight displacement, but there is little or no fusion. In *Heptanchus cinereus* (Text-figure 50) the radials (*ra.*) of the dorsal fin are much more regular and there



Text-figure 50.

Text-figure 51.

Endoskeletons of the dorsal fins of *Heptanchus* and *Mustelus*.

Text-figure 50. Cartilages of the dorsal fin of *Heptanchus cinereus*.

bc., basal; *ra.*, radial cartilage.

From Daniel, 1934, Fig. 56; after Mivart, 1879, Fig. 2, pl. LXXV.

Text-figure 51. Cartilaginous elements of dorsal fin of *Mustelus antarcticus*.

b.c., basal segments; *b.c.1*, median segments; *b.c.2*, distal segments.

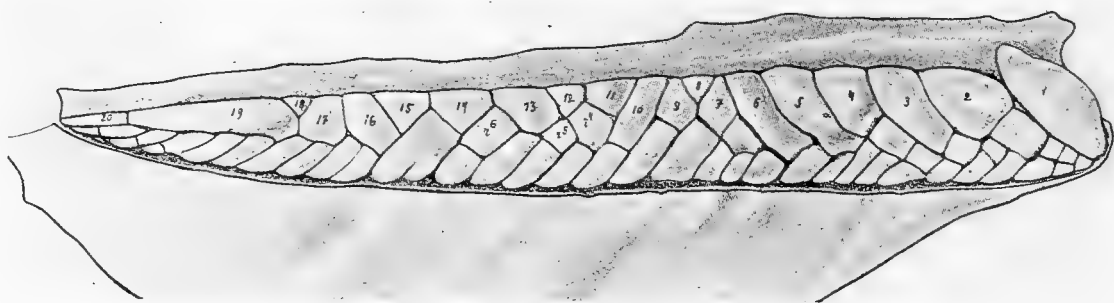
From Daniel, 1934, Fig. 89A, after Mivart.

is a large but thin basal cartilage (*bc.*). In *Mustelus* (Text-figure 51) there is a distinct row of basal cartilages (*b.c.*) that appear to have been segmented off from the radials, but there is no fusion.

There is no need of recourse to fossil forms to find evidence of the manner of origin of basal plates in the dorsal fin skeleton. Beginning with the condition exemplified by *Mustelus*, which I regard as primitive, there may be found in living forms all intermediate conditions leading to one in which fusion of basal segments of the radials has formed large basal plates. The literature pertaining to the fin skeletons of sharks abounds in figures which, upon comparison, illustrate the point, but it is sufficient to cite Mivart's (1879) well-known drawings. In *Chlamydoselachus* the endoskeleton of the dorsal fin, though primitive, seems to have suffered regression as evidenced by the irregular form and arrangement of many of the cartilaginous elements.

THE ANAL FIN

In the endoskeleton of the anal fin of *Chlamydoselachus* (Text-figures 48 and 52 after Garman and Deinega respectively) there is some fusion of proximal elements, and even a slight amount of fusion of distal elements. The elements of the basal series are usually oriented in a different direction from the distal elements. In the adult, this fin skeleton is very long and slender (in an anteroposterior direction). The same is true of the anal fin skeleton of a 225-mm. embryo figured by Osburn, 1907 (Fig. 6, pl. IV). In this embryonic specimen the fusion of basal elements is not so pronounced. The separation of the fin skeleton from the vertebral column is very marked. In *Heptanchus cinereus* (Daniel, 1934, Fig. 57 after Mivart) there is a fairly large basal element in series with some smaller basal elements, all apparently formed by the fusion of radials.



Text-figure 52.

Endoskeleton of the anal fin of *Chlamydoselachus anguineus* (showing basals 1-20).

After Deinega, 1909, Fig. 13, pl. IV.

THE CAUDAL FIN

The general appearance of the cartilaginous supports for the dorsal and ventral lobes of the greater part of the tail fin is shown in Deinega's (1909 and 1923) Fig. 9, pl. III, which is too large for satisfactory reproduction here; also in Garman's (1885.2) Pl. 14, which was drawn from a specimen in which the tip of the tail had been mutilated during life. Details are better shown in Goodey's (1910.1) drawings reproduced herein as Text-figures 31 and 36.

The cartilaginous supports for the ventral lobe of the caudal fin of *Chlamydoselachus* are supplied almost entirely by the haemal spines, which belong to the axial skeleton. The occurrence of small radials distinct from the haemal spines is confined to the anterior portion (Text-figures 31 and 48) of the ventral lobe, and these radials are possibly segmented off from the haemal spines.

The cartilaginous supports for the dorsal lobe of the caudal fin of *Chlamydoselachus* consist partly of neural spines, which belong to the axial skeleton; but there is an entire series of dorsal radial elements (Text-figures 31 and 36) distal to the neural spines. "For a short distance in front . . . the series is separated by a space from the neural

intercalaria, as if the radials had originated, like those of the dorsal and anal [fins] independently, and afterwards through downward growth had in the greater portion of the extent come in contact with the neural processes. These radials and interneurals are not fused like the radials and haemapophyses" (Garman, 1885.2, p. 16). With this interpretation Goodey (1910.1, p. 553) seems to agree, for he says: "The dorsal radial supports of the caudal fin I do not consider as dorso-spinalia, because at their commencement anteriorly they are not always continuous with the neural arches, and, moreover, there is as much evidence to show that in general they originate independently of the vertebral column as there is in favor of their being portions segmented off from the dorsalia below them."

In the section on external characters, attention has been called to the shortness of the cartilaginous fin rays of *Chlamydoselachus*, as compared with their condition in one of the most primitive of fossil sharks, *Cladoselache*. We are now in a position to ask, is there any evidence, in the patterns of the fin skeletons, to support the view that the somewhat rudimentary character of the appendicular skeleton in *Chlamydoselachus* is secondary, not primary? Along with the fusion of radials to form basals, radials are found breaking up into segments which do not always retain their original alignment. The shapes of these segments are sometimes irregular. As indicated by Woodward (1921), this fragmentation and displacement of typical parts seems to indicate retrogression. The shortness of the radials is presumably due to arrested development.

THE MUSCULAR SYSTEM

Only the skeletal or voluntary striated muscles are considered here. Little is known concerning smooth muscle and cardiac muscle, in *Chlamydoselachus*, and in any case these are best considered in connection with the organs of which they form a part. It is convenient to classify the skeletal muscles upon an embryological basis. In *Chlamydoselachus*, as in other vertebrates, most of these muscles may be assigned to two great groups, the metameric muscles and the branchiomic muscles. The great muscles of the body wall are metameric muscles. The branchiomic muscles are of visceral-arch origin, but they do not include all the muscles attached to the visceral skeleton.

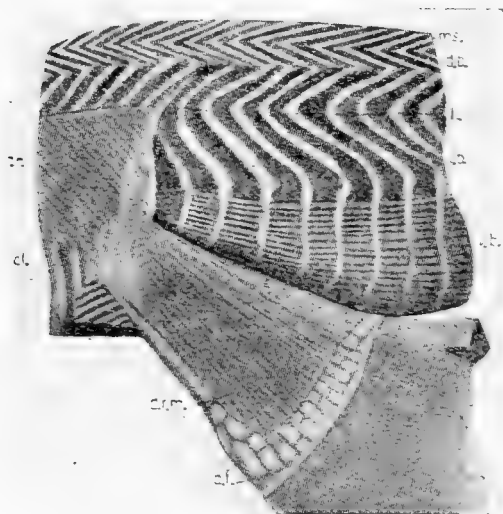
THE METAMERIC MUSCLES

The metameric muscles of fishes are divisible into two groups: the axial muscles, in which the metamerism is clearly expressed even in the adult; and the appendicular muscles or fin muscles. In the latter, the metameric condition is seldom recognizable in the adult; nevertheless, in primitive fishes the appendicular muscles arise from the metamerically arranged myotomes of the early embryo.

THE AXIAL MUSCLES

In fishes the axial muscles comprise (a) the great masses of muscle contributing to the formation of the body wall and tail; (b) a group of muscles in the hypobranchial region; and (c) the muscles that move the eyeballs.

MUSCLES OF THE TRUNK AND TAIL.—Metamerism is such a striking feature of the trunk muscles of fishes that it overshadows the longitudinal division into muscle bundles or layers and the incipient differentiation into individual muscles—a development that, in the higher vertebrates, quite reverses the picture.



Text-figure 53.

Lateral view of the body musculature in the pectoral region of *Heptanchus maculatus*.

cl., gill-cleft; d.b., dorsal bundle; d.f., dermal fin rays; d.r.m., dorsal radial muscles of pectoral fin; l.b., lateral bundle; ll., lateral line; ms., myoseptum; tr., trapezius muscle; v.b., ventral median muscle.

After Daniel, 1934, Fig. 90.

In surface views of the six large embryos of *Chlamydoselachus* in the American Museum, ranging from 190 mm. to 374 mm. in length, the myomeres are more or less sharply defined. Along the lateral surfaces of the trunk and tail they are clearly outlined, and in some specimens they may be traced ventrally as far as the tropeic folds. Dorsally, they are usually obscure and in this situation better views were obtained by removing patches of skin from one of these embryonic specimens. In the adult specimens, only slight indications of the body musculature could be seen until after the skin had been reflected; then the myosepta stood out boldly. It is apparent, even from a cursory study of our material, that the myomeres of the trunk region of *Chlamydoselachus* conform to the primitive elasmobranch type and bear a close resemblance to those of *Heptanchus* as described and figured by Maurer (1912) and Daniel (1934). From Daniel (1934, p. 89) I quote the following paragraph which is illustrated by my Text-figure 53:

In a side view, the muscles of the body of *Heptanchus maculatus* are divided at the lateral line (ll.) into dorsal bundles (d.b.) which attach to the cranium, and ventrolateral bundles which attach to the pectoral girdle. Both the dorsal and the ventrolateral muscles extend to the tip of the tail. In these bundles the myosepta (ms.) are bent into zigzag shape. Above the lateral line one of the columns has the apices of its myosepta directed forward, the other backward. Below the line there appears to be a single column with apex pointed posteriorly. Some of the anterior fibers of the ventral bundle are specialized as the pectoral muscles of the pectoral fin.

Howell (1933, p. 249) attaches considerable significance, from a developmental point of view, to the longitudinal division of the trunk musculature of fishes into dorsal and ventrolateral bundles. His account of the developmental processes leading to this condition follows:

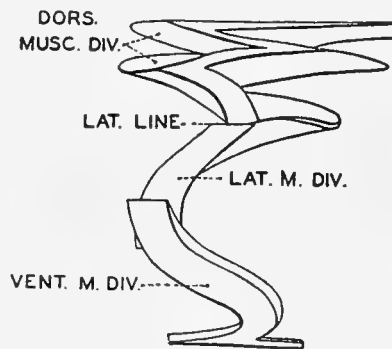
A frequent misconception regarding the development of the musculature is to the effect that the muscles ventral to the lateral line are formed by actual growth in that direction of the original, dorsally situated myotomes. Conditions vary in different parts of the body, but in the anterior trunk at least there appears to be a lateroventral muscle mass entirely distinct from the dorsal myotome. Between the two there is a connective tissue septum, and tending further to separate them at early stages of phylogeny are the pronephros and its duct, and the lateral line structures. The lateroventral musculature differentiates by condensations of mesoderm progressively in a ventral direction, forming a lateral somatopleure, giving rise to the somatic musculature, and a medial splanchnopleure, from which is derived the smooth musculature of the intestinal tract. Whether or not all the striated branchial muscles are also derived from this element is not entirely certain. Between the two plates is a coelomic cavity. In other parts of the body, or in vertebrates that have long since discarded all vestige of a lateral line system, the distinctiveness in origin of the dorsal from the lateroventral musculature tends to become obscured in the embryonic picture.

Text-figure 54.

Model of myomere of a selachian (*Squalus*), showing divisions into longitudinal muscle bundles.

DORS.MUSC.DIV., dorsal bundle; LAT. LINE, lateral line; LAT.M.DIV., lateral bundle; VENT.M.DIV., ventral bundle.

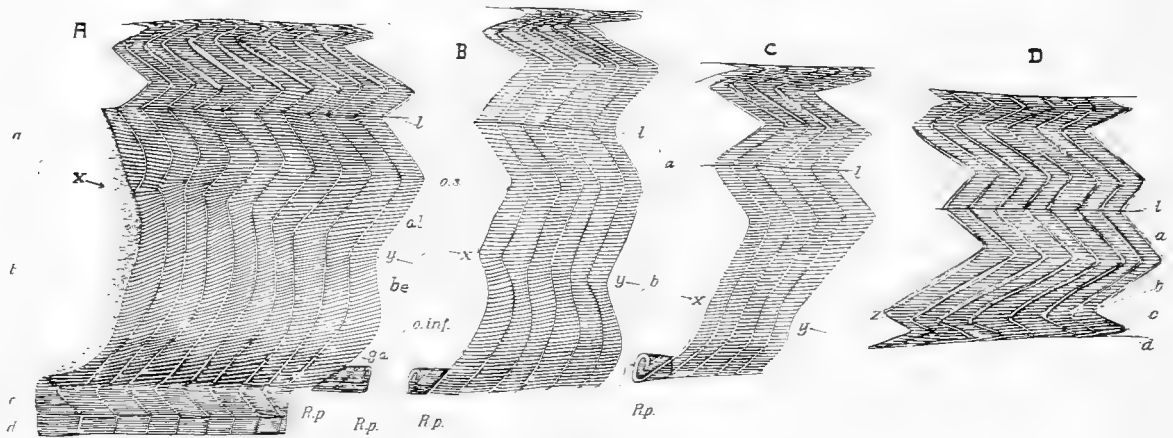
After Howell, 1933, Fig. 3, modified from Langelaan and Daniel.



A model of a single myomere of the trunk region of a selachian is illustrated by Text-figure 54. Regarding the basic segmental features of vertebrate trunk musculature, Howell (1933, pp. 255–256) writes:

The original plan of vertebrate trunk musculature, well illustrated by cyclostomes, involves a series of segmental muscles each of which is separated from the muscles of adjoining segments by myocommata or myosepta. The axially directed muscle fibers of each segment are basically divided into a dorsal division, above the lateral line on either side of the mid-line, and a continuous lateroventral division below; this constitutes the primary muscular plan. It is a primitive scheme, suited to a low vertebrate that can bend with equal facility in any direction—the essentially vermiform type of control.

In this plan the myosepta are virtually transverse and usually gently curved. Unlike the situation in mammals, most of whose muscles have one end solidly anchored on bone, in the primitive state the fibers at both ends are attached to yielding connective tissue. Accordingly there was originally a tendency for some of the groups of fibers to pull certain parts of the myosepta in a forward and others in a backward direction, as a result of specialized action of the groups concerned. This would have a contortional effect upon the myosepta, and in consequence some parts would have an anterior and others a posterior inclination, as suggested in the given diagram of a myomere of a shark (Fig. 3) [Text-figure 54 herein]. Presumably the swifter the fish (i.e., the stronger the muscle action) the more tortuous the pattern of the myosepta.



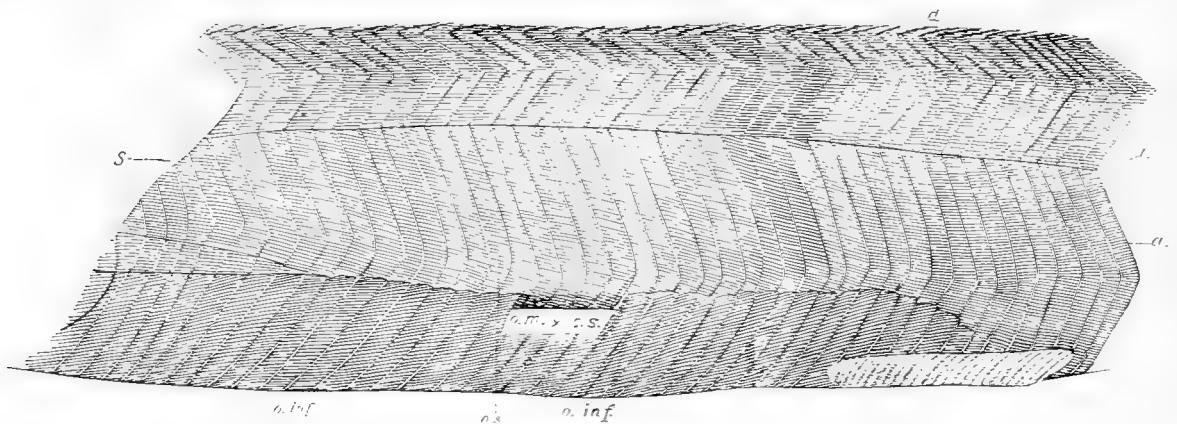
Text-figure 55.

Lateral view of the trunk musculature of *Chlamydoselachus* in four different regions: A, anterior part of the trunk; B, middle part; C, posterior part; and D, anterior portion of the tail.

a, b, c, d, the four longitudinal divisions of the ventral bundle (ventrolateral of other authors); al (alpha), be (beta), and ga (gamma), the three longitudinal regions into which the division b may be divided; l, lateral line; o. inf., musculus obliquus inferior; o. s., musculus obliquus superior; R. p., rectus profundus muscle—in A it is shown artificially spread out, as well as in its original position, inrolled. A line drawn from x to y, along each region, would separate, approximately, the inferior oblique from the superior oblique muscles.

After Maurer, 1912, Fig. 1, Taf. 1.

Maurer (1912) has given us detailed information concerning the trunk musculature of both *Chlamydoselachus* and *Heptanchus*. In *Chlamydoselachus* (Text-figure 55) the ventrolateral bundle has the same fundamental division into two columns (divided otherwise by Maurer) as is found in the dorsal bundle. This is best exemplified in the region of the base of the tail (Text-figure 55D) where the ventrolateral bundle is the



Text-figure 56.

Lateral view of the trunk musculature of *Heptanchus cinereus*.

a., dorsal region of ventral bundle (ventrolateral of other authors); d., dorsal bundle; l, lateral line; o. inf., inferior oblique; o. m. x o. s., portions of middle oblique and superior oblique overlapped by inferior oblique; o. s., superior oblique; S, shoulder girdle.

After Maurer, 1912, Fig. 4, Taf. 2.

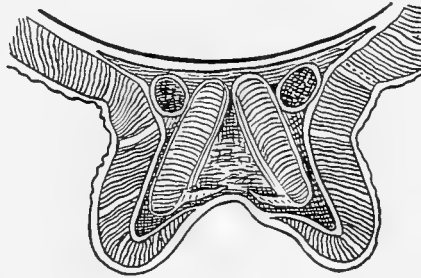
mirrored image of the dorsal bundle; but it is expressed, with some modifications, in the trunk region also. These modifications have to do with (a) the incipient separation of a superior oblique muscle from an inferior oblique, and (b) the inrolling of the ventral column of the ventrolateral bundle to form the muscles of the tropeic folds—structures peculiar to *Chlamydoselachus*. In *Heptanchus* (Text-figure 56) conditions are not so simple, for there is a small middle oblique muscle and there is considerable overlapping of the middle and superior oblique muscles by the inferior oblique. The figure for *Chlamydoselachus* is drawn from a rather small specimen, 1330 mm. long. The figure for *Heptanchus* is from a specimen 900 mm. long.

Since the abdominal or tropeic folds are structures peculiar to *Chlamydoselachus*, their musculature is entitled to further consideration. The superficial appearance of the tropeic folds has been described, in three adult specimens and six large embryos, by

Text-figure 57.

Transverse section showing the tropeic folds ($\times 1$) of an adult *Chlamydoselachus*. This section was taken eight inches in front of the pelvis.

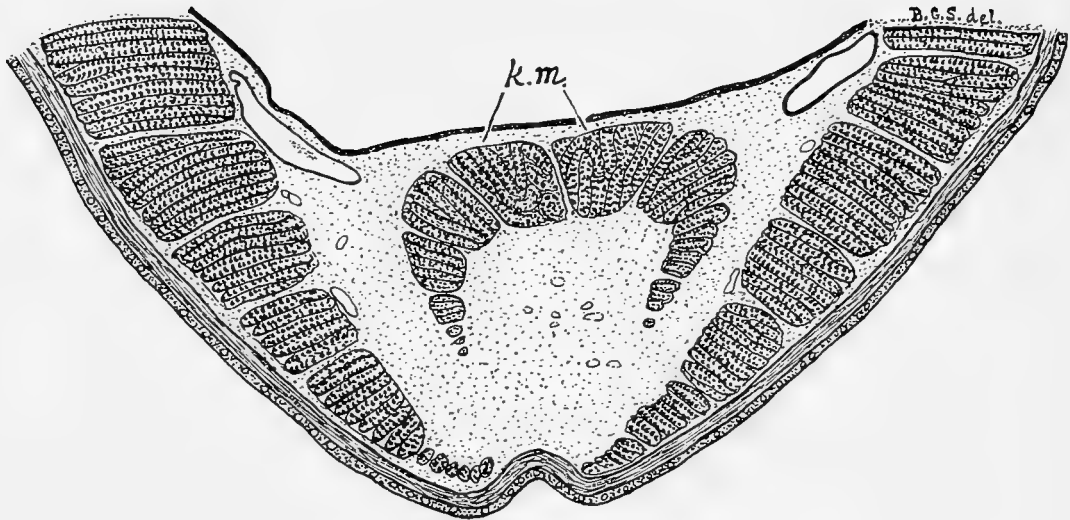
After Garman, 1885.2, Fig. B, pl. XX.



Gudger and Smith (1933). The internal structure of the abdominal folds in a single adult specimen has been figured by Garman (1885.2) in his Figs. A and B, pl. XX—the latter figure being reproduced as my Text-figure 57. Concerning these figures Garman (p. 21) says:

One of the folds is seen to hang below each of the large abdominal vessels. The vessels are parallel or nearly so. Between them are two muscular bands, one to each fold. Each band is nearly an inch in width, very thin at its lower edge, and near one-fifth of an inch thick toward the rounded upper edge, between the veins. The fiber in these tropeic . . . or keel muscles differs from that in the walls of the flank in being coarser in the bundles and plates, and more loosely put together. Apparently the keel muscle corresponds to the rectus abdominis of lower vertebrates.

Garman's figures readily suggest that the keel muscle is derived during development by an infolding of the musculature of the ventral body wall. In order to test this hypothesis I have prepared transverse serial sections from a segment of the ventral abdominal wall excised from a 210-mm. male embryo. In this specimen the distance from pectoral fin to pelvic girdle is 55 mm. The segment comprised the region extending from 10 mm. to 20 mm. in front of the pelvic fins. A drawing (Text-figure 58) was made from a section taken approximately 15 mm. from the pelvic fins—corresponding very nearly to the region (200 mm. in front of the pelvic girdle) figured by Garman for his large adult specimen. In my sections I have found some further indications of the manner of origin of the muscle



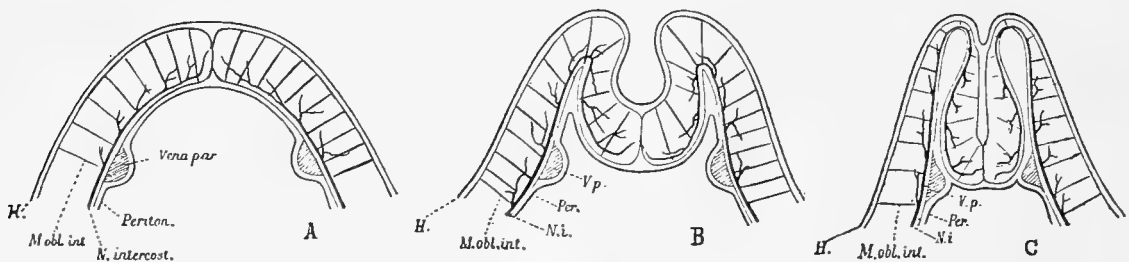
Text-figure 58.

Section through the trophic folds ($\times 25$) of a 210 mm. embryo of *Chlamydoselachus*, showing the keel muscle (*k.m.*). The section was taken about 15 mm. in front of the pelvis.

Drawn from a specimen collected in Japan by Dr. Bashford Dean, and now in the American Museum.

under consideration. It is clearly derived as a simple inpocketing of the ventral musculature of the body wall, in the region where the ventral bundles of the two sides of the body meet. Furthermore, it is segmented after the fashion of the metameric muscles of the body wall—a feature that is entirely lacking in Garman's drawings and is not mentioned in his text. Earlier stages would be required to show continuity of the musculature in this region.

Evidence regarding the manner of origin of the keel muscle was obtained by Braus (1898, Fig. 2, pl. XIII) in connection with his studies of the innervation. In this case the depth of the "keel" is remarkable. Braus applies the term *rectus* to the thin muscle of the body wall in the region of the ventral mid-line—a muscle which is interrupted by



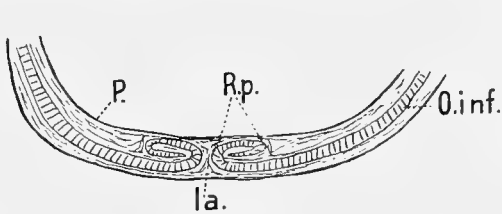
Text-figure 59.

Diagrams of sections (all inverted) showing the probable manner of origin of the keel muscle: A, absent in *Squalus*; B, hypothetical intermediate stage; C, as in adult *Chlamydoselachus*.

H, skin; M.obl.int., musculus obliquus internus; N.i., intercostal nerve; Per., peritoneum; V.p., vena parietalis.

After Braus, 1898, Text-fig. 3.

the tropeic groove. The deep muscle that Garman calls the rectus abdominis or keel muscle is called by Braus simply the keel muscle. Braus (1898, p. 337) states that the nerves that innervate the keel muscle lie on its lateral surface, and not on the medial surface as in the case of the musculus rectus abdominis and the oblique muscles of the body wall. He concludes, therefore, that an invagination, leading to inversion, of the ventral body wall has occurred at the mid-line; for it is well known that nerves ending in developing muscles tend to follow these muscles in their migrations. Braus has embodied these conclusions regarding the phylogenetic origin of this muscle in a diagram which I have reproduced as Text-figure 59.



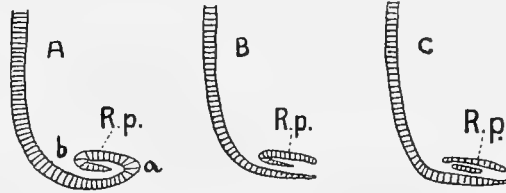
Text-figure 60.

Transverse sections of the ventral body wall of *Chlamydoselachus* showing the inrolling of the musculature in the region of the tropeic folds.

Text-figure 60. Transverse section of the ventral abdominal wall immediately behind the pectoral girdle.

la., linea alba; P., peritoneum; o.inf., musculus obliquus inferior; R.p., rectus profundus muscle, which is recognizable as an inrolled portion of the ordinary musculature of the body wall.

After Maurer, 1912, Text-fig. 1.



Text-figure 61.

Text-figure 61. Diagrams showing the condition of the ventral musculature on one side of the body in four different regions: A, just behind the pectoral and likewise immediately in front of the pelvic girdle; B, in the second quarter, and C, in the third quarter of the trunk.

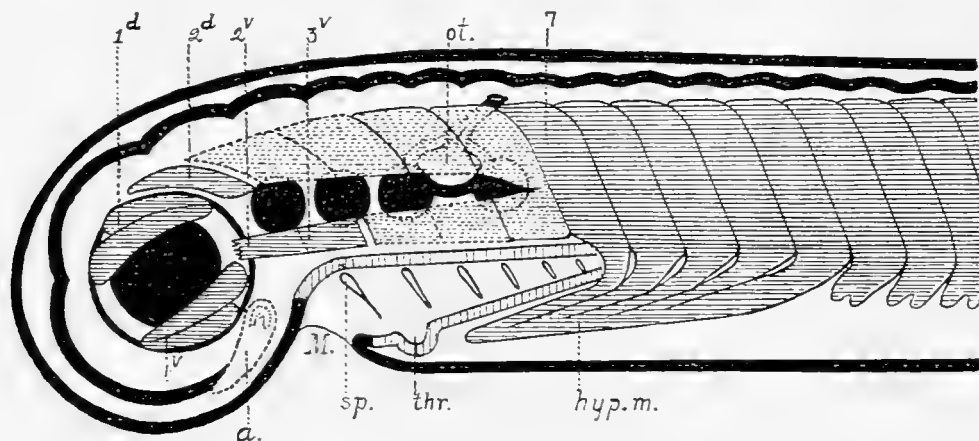
R.p., musculus rectus profundus; a, first; and b, second fold of the rectus profundus.

After Maurer, 1912, Text-fig. 3.

Maurer (1912) has given a somewhat different picture (Text-figures 60 and 61) of the manner of origin of the deeply situated ventral longitudinal muscle, which he calls the rectus profundus. These figures are based on sections taken from four different regions along the ventral body wall of his adult, or nearly adult, specimen. A connection between the rectus profundus and the ventrolateral bundle persists in the region immediately behind the pectoral girdle and immediately in front of the pelvic girdle, but is lost throughout the remaining extent of the tropeic folds. A curious feature of all Maurer's drawings of the ventral musculature of his specimens is that in none of them does he show any ventral protrusion of the body wall to form the keel which has been described by Garman (1885.2), Collett (1897), Braus (1898), and by Gudger and Smith (1933). But the most remarkable thing about Maurer's drawings of the musculature of the tropeic folds is that he represents the infolding process not as a simple invagination but as a parting of the musculature of the body wall along the mid-line, after which each edge becomes inrolled independently, like a scroll (Text-figures 55, 60 and 61). This

does not accord with the conditions portrayed by other authors in their drawings of transverse sections through the keel muscle.

As to the function of the deep muscle variously called the keel muscle, the rectus abdominis, and the rectus profundus, it clearly aids in a rapid ventral flexion of the body; but why it should be so uniquely set apart from the remaining musculature of the ventral body wall is problematical.



Text-figure 62.

Diagram showing the relation between head somites and body somites, and the origin of the hypobranchial or hypoglossal musculature from trunk myotomes, in a larval *Squalus acanthias*. The somites that degenerate in ontogeny are indicated by broken lines. The anlagen of the six eye muscles, which arise from the first three somites, are already differentiated.

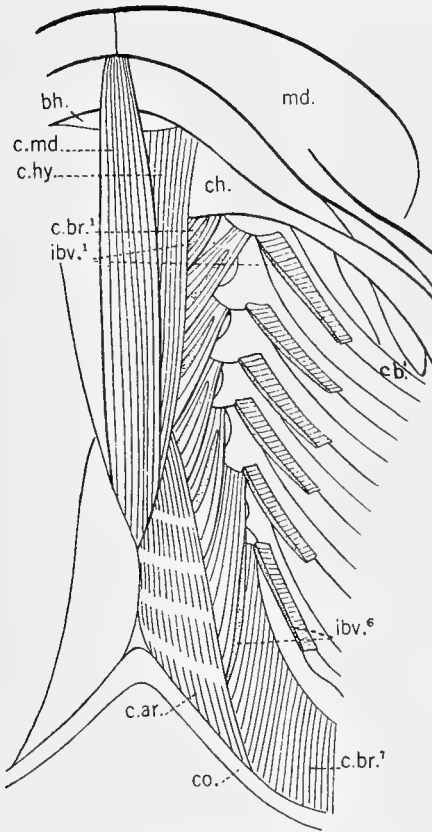
1d, dorsal moiety of the first myotome; 1v, ventral moiety of the first myotome; 2d, 2v, dorsal and ventral moieties of the second myotome; 3v, ventral moiety of the third myotome; 7, seventh myotome; a., anterior cavities; hyp.m., hypobranchial musculature; M., mouth; ot, otic capsule; sp., spiracle; thr., thyroid.

After Neal, 1918, Fig. 19.

Goodey (1910.1) studied the relations of the myomeres to neuromeres in the tail and posterior part of the trunk of *Chlamydoselachus*. In the trunk, he found the limits of a myomere corresponding in extent with a monospondylous neuromere. In the main caudal region each myomere is equal in extent with a diplospondylous neuromere. In the tip of the tail each irregularly divided or heterospondylous neuromere has its myomere. Thus the myomeres of the tail region are not particularly influenced by the secondary segmentation of the vertebral column in this region.

THE HYPOBRANCHIAL GROUP.—In fishes, as in other vertebrates, the hypobranchial region has a group of muscles that appear to be a continuation of the longitudinal musculature of the ventral body wall. The muscles of the hypobranchial group are attached posteriorly to the shoulder girdle and anteriorly to ventral portions of the visceral skeleton. This hypobranchial or hypoglossal musculature does in fact arise (Text-figure 62, hyp.m.) as a forward prolongation of some myotomes of the occipital and anterior trunk region which are in strict serial relationship with the myotomes that give rise to the segmental

muscles of the body and tail—as in *Scyllium* (Van Wijhe, 1883, p. 36 and Fig. 25, Taf. III); in *Lacerta* (Corning, 1895); in *Petromyzon* and *Squalus* (Neal, 1897); and in *Lepidosiren* and *Protopterus* (Agar, 1907).



Text-figure 63.

Hypobranchial muscles of the notidanid,
Heptanchus maculatus, ventral view.

bh., basihyoid cartilage; c.ar., musculus coracoarcales; cb.1, first ceratobranchial cartilage; c.br.1-7, first to seventh ceratobranchial muscles; ch., ceratohyoid cartilage; c.hy., musculus coracohyoideus; co., coracoid cartilage; c.md., musculus coracomandibularis; ibv.1-6, first to sixth ventral interbranchial muscles; md., mandibular cartilage.

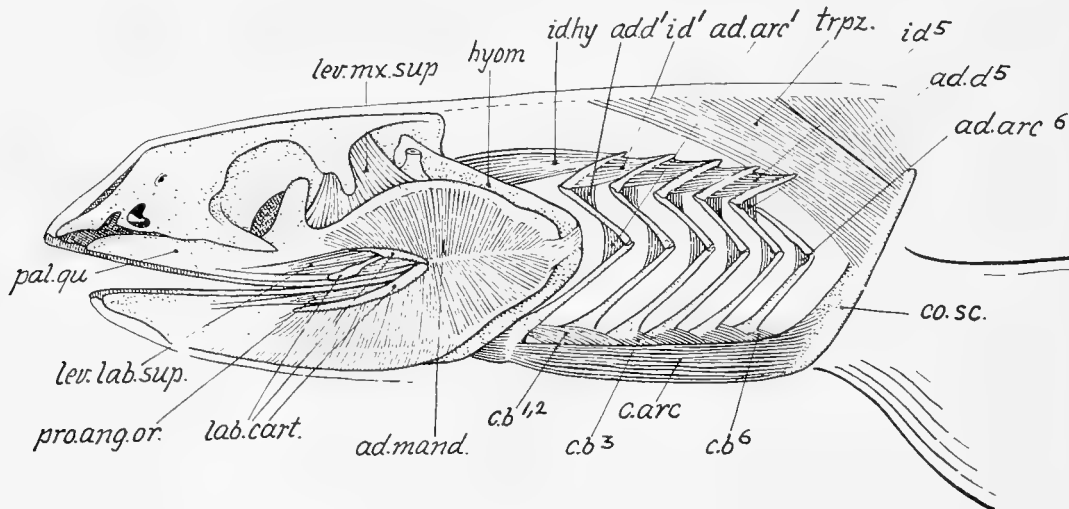
After Davidson, 1918, Fig. 4.

In *Heptanchus* (Davidson, 1918) the following muscles (Text-figure 63) are recognized as members of the hypobranchial group: the paired coracoarcales communes (c.ar.), the unpaired coracomandibularis (c.md.), the paired coracohyoidei (c.hy.), and seven pairs of coracobranchiales (c.br.1-7). In elasmobranchs generally, according to Daniel (1934, p. 108), all of these muscles excepting the coracobranchiales arise from the first five trunk myotomes. Edgeworth (1903) states that in *Scyllium* the coracobranchiales develop from head myotomes. In the adult *Heptanchus*, the metameric nature of the coracoarcales is attested by the presence of a series of four transverse or slightly oblique myosepta (Text-figure 63). In the coracoarcales of *Scymnus*, there are five such myosepta (Fürbringer, 1897, Fig. 3, Taf. VI). In *Heptanchus*, Vetter (1874, Fig. 9, pl. XV) shows a myoseptum in the coracohyoideus muscle also.

The hypobranchial group of muscles is often called the hypoglossal musculature because the muscles of this group are supplied, somewhat indirectly, by a nerve which, variously called the spino-occipital, occipital or hypoglossal nerve in fishes and amphibians, in the higher vertebrates is known as the hypoglossal (hypoglossus) or twelfth cranial nerve. This nerve is a composite structure, made up from a series of roots representing, perhaps, several neuromeres.

Allis (1917 and 1923) does not distinguish the hypobranchial muscles of *Chlamydoselachus* as a separate group. However, he describes the distribution of the branches of "a large nerve which was not traced upward to its origin, but which is either of spinal, or spinal and occipital origin" (Allis, 1923, p. 195). The muscles supplied by this nerve are identical with those included in Davidson's list of hypobranchial muscles in *Heptanchus*, with the addition of a muscle which Allis calls the "pharyngo-clavicularis." The hypobranchial muscles of *Chlamydoselachus* are shown, in color, by Allis (1923) in his Figs. 35 and 37-40, pls. XIII-XV; but nowhere are these muscles of *Chlamydoselachus*

figured as a complete and separate group. The coracoarcuales and coracobranchiales muscles of one side of the head are shown in Text-figure 64 after Gregory, and the first pair of coracobranchiales (*cb.1*) are shown in my Figure 8, plate III. Allis (1923, pp. 192–195) gives a detailed description of each of the muscles under consideration.



Text-figure 64.

Skull and visceral arches of *Chlamydoselachus* with the deep muscles of the branchiocranium. These muscles fall into two main groups: extensors of the oral and branchial arches, running anteroposteriorly; and flexors, running vertically.

ad.arc., muscoli adductores arcuales 1–6. *ad.d.*, muscoli adductores dorsales 1–5; *ad.mand.*, musculus adductor mandibulae; *carc.*, musculus coracoarcualis; *cb.*, muscoli coracobranchiales 1–6; *co.sc.*, coracoscapular arch; *hyom.*, hyomandibular; *id.*, muscoli interdorsales 1–5; *id.hy.*, interarcualis between hyal and first branchial arch; *lab.cart.*, labial cartilages; *lev.lab.sup.*, musculus levator labii superioris; *lev.mx.sup.*, musculus levator maxillae superioris; *pal.qu.*, palatoquadrate; *pro.ang.or.*, musculus protractor anguli oris; *trpz.*, musculus trapezius.

After Gregory, 1933, Fig. 4.

As one would expect from the similarity of their cartilaginous branchial frameworks, there is a marked likeness between the hypobranchial musculatures of *Chlamydoselachus* and *Heptanchus*. Only a few points call for special consideration here.

There are, to be sure, only six pairs of coracobranchiales in *Chlamydoselachus*, as compared with seven in *Heptanchus*, but this difference is correlated with the number of gill arches. Of these muscles in *Chlamydoselachus*, Allis (1923) says: "The more posterior coracobranchiales have no connection whatever with the muscoli coracoarcuales, *Chlamydoselachus* differing markedly in this respect from *Heptanchus* (Vetter, 1874) and closely resembling *Acanthias* (Vetter, l.c.)." In Vetter's figure of *Heptanchus* (his Fig. 9, pl. XV), the coracobranchiales of the region under consideration appear to arise directly from the muscoli coracoarcuales, while one gets a somewhat different impression from Davidson's figure reproduced as my Text-figure 63. Davidson (1918, p. 162) describes the origin of the coracobranchiales muscles of *Heptanchus* as follows:

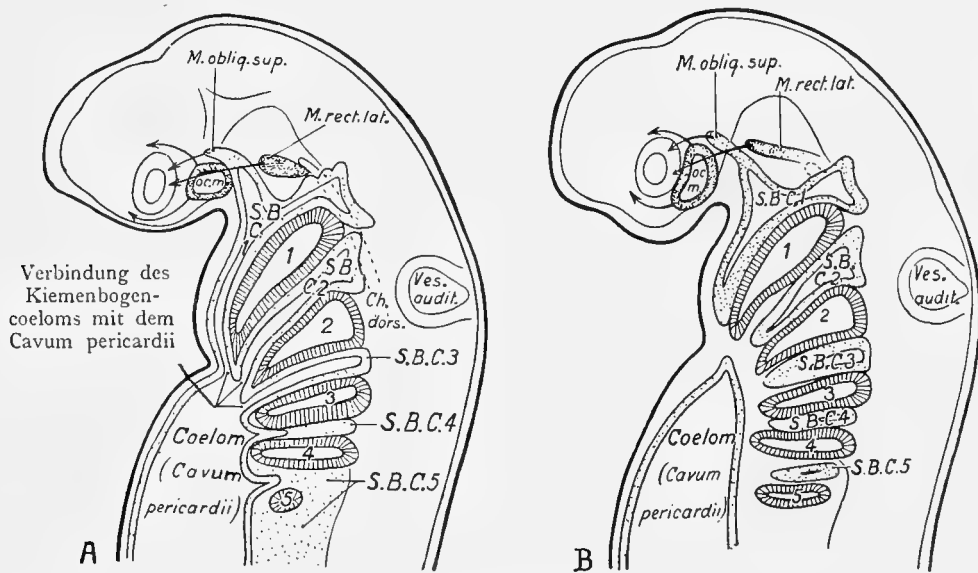
The first [coracobranchialis muscle] has its origin in the connective tissue directly over and attached to the coracohyoideus muscles. The origins of the second to the sixth coracobranchiales are in the strong connective tissue just dorsal to the coracoarcuales. The anterior part of the origin of the seventh is continuous with the origin of the sixth while the posterior part has its origin on the pectoral girdle, just lateral to the origin of the coracoarcuales.

Until we know more of the relations of the sheet of connective tissue that affords origin to the coracobranchiales of *Heptanchus* we cannot be sure that these muscles have any real connection with the coracoarcuales. Comparison should be made directly from dissections of the two forms.

The muscle which Allis calls the pharyngo-clavicularis is described by him (1893, p. 195) as follows:

Immediately dorsoposterior to the surface of insertion of the coracobranchialis VI on the sixth ceratobranchial, a broad muscle has its origin, and running ventromesially and contracting rapidly has its insertion on the clavicle dorsolateral to the coracoarcualis muscle of its side. This muscle would seem to be the homologue of the pharyngo-clavicularis of *Amia* (Allis, 1897), and it is not described by Vetter as a separate muscle in any of the selachians considered by him.

THE EYEBALL GROUP.—In elasmobranchs and perhaps in vertebrates generally, the muscles that move the eyeballs arise (Marshall, 1881; Van Wijhe, 1883; Neal, 1918)



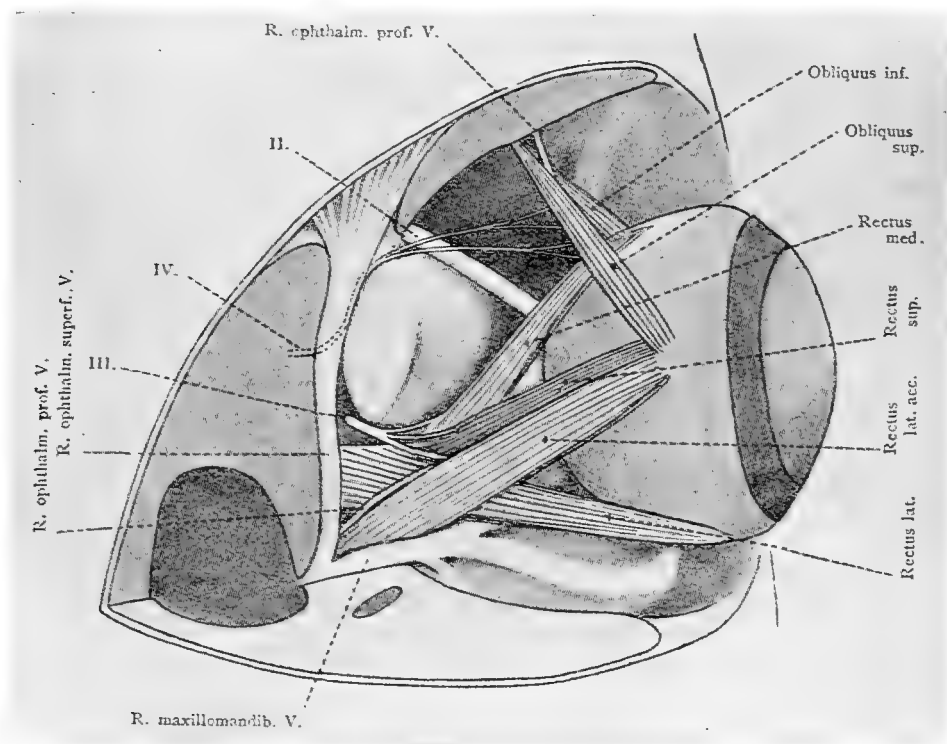
Text-figure 65.

Diagrams showing the origin of eye muscles, and the extensions of the primitive coelomic cavity into the gill-arches, in selachian embryos. In A, the cavities of the pharyngeal arches are shown communicating with the pericardial portion of the coelomic cavity; in B, which is a later stage, the connections of these cavities have been lost.

1, 2, 3, 4, gill-clefts; S.B.C.1—5, pharyngeal arch extensions of the coelomic cavity; *ch.dors.*, chorda dorsalis; *oc.m.*, anlagen of the oculomotor muscles; *M.obliq. sup.* and *M.rect.lat.*, anlagen of the superior oblique and lateral rectus muscles respectively; *ves.audit.*, otic vesicle.

After Corning, 1925, Figs. 222 and 223; based on Froriep's (1902) Figs. 4 and 5 (*Torpedo ocellatus*).

from mesodermal segments (head somites) which are serially homologous with those of the trunk (Text-figure 62). In primitive fishes, the head somites, like the trunk somites of vertebrates generally, are at first hollow and their cavities communicate with the primitive coelomic cavity. In other words, the coelomic cavity extends into the somites. In the head, this communication is by way of the mesoderm of the branchial arches, as shown (for *Torpedo*) in Text-figure 65 after Corning. Van Wijhe (1883, Figs. 1 and 2, Taf. I) gives more exact drawings showing the same features in *Scyllium canicula*. These channels quickly close, and the somites later become solid structures.



Text-figure 66.

Dorsal view of the eye muscles of *Chlamydoselachus* on the right side.

The Roman numerals distinguish the nerves supplying the eye: II, second cranial or optic nerve; III, third cranial or oculomotor nerve; IV, fourth cranial or trochlear nerve. Other abbreviations are self-explanatory.

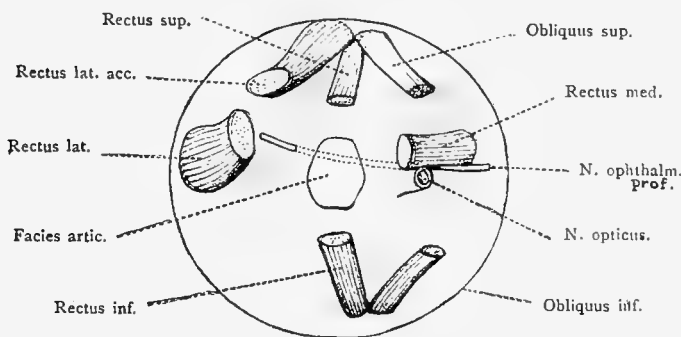
After Nishi, 1923, Fig. 1.

In *Chlamydoselachus*, the muscles of the eyeball and their innervation were described from two specimens by Hawkes (1906), and later by Nishi (1922) who used four adult specimens. They were considered briefly by Allis (1923), who merely supplemented the work of Hawkes by comparisons with his own specimens.

The disposition of the various eye muscles of *Chlamydoselachus* is shown in Figures 10, 11, and 12, Plate IV; also in Text-figures 66 and 67. It will be seen from Text-figure 67 that the dorsal side of the eyeball has three muscles, while only two muscles supply the

ventral side. The combined strength of the dorsal group is obviously greater than that of the ventral group. As figured and described by Hawkes the inequality in the strength of these two groups is more striking. The dorsal group is strengthened to turn the eye upward, not only to a moderate degree for the purpose of looking upward, but to a much greater extent when the cornea is turned well under cover of the socket, for protecting this most delicate part of the surface of the eyeball. The part of the eyeball (sclera) then left exposed is covered with shagreen. These devices for protecting the eyes in the absence of lids have been described by Gudger and Smith (1933).

Conditions are simpler in *Heptanchus* as described and figured by Davidson (1918, pp. 162-163 and Fig. 5). In this shark two groups of muscles (Text-figure 68) are present in the orbit. The first group is placed anteriorly and consists of the superior oblique



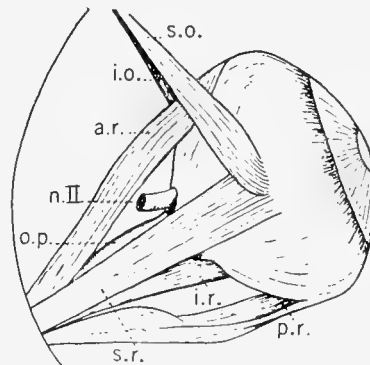
Text-figure 67.

Eye muscles of *Chlamydoselachus* and *Heptanchus* showing insertions on eyeballs.

Text-figure 67. Semidiagrammatic figure of left bulbus oculi of *Chlamydoselachus* in medial aspect.

The abbreviations are self-explanatory.

After Nishi, 1923, Fig. 2.



Text-figure 68.

Text-figure 68. Eye muscles of *Heptanchus maculatus* in dorsal view, right side.

a.r., anterior rectus; i.o., inferior oblique; i.r., inferior rectus; n.II, optic nerve; o.p., optic pedicel; p.r., posterior rectus; s.o., superior oblique; s.r., superior rectus.

After Davidson, 1918, Fig. 5.

(s.o.) and the inferior oblique (i.o.). These muscles extend from the anterior part of the orbit outward and caudad to be inserted on the eyeball. The second group consists of the four recti muscles, all of which arise from the posterior surface of the orbit around the base of the optic pedicel. The most dorsal member of this group is the superior rectus, the most ventral the inferior rectus, the most posterior the external or lateral rectus, and the most anterior the internal or medial rectus. They pass outward and forward to be inserted on the eyeball.

The chief peculiarity of the musculature of the eyeball of *Chlamydoselachus* is the fact that all the muscoli recti, save only a portion of an accessory rectus lateralis (externus), take origin from the eyestalk. In *Chlamydoselachus* the function of the eye-

stalk is twofold: it prevents the eye from sinking too far into the socket, and it supplies a more lateral basis for the origin of the recti muscles. The lateral rectus consists of two parts which have separate origins and insertions, although they are otherwise united by strong strands of muscle fibers. One division of this muscle takes origin from the outer part of the optic stalk, while its insertion is on the posterior surface of the eyeball. This is the normal insertion for an undivided rectus lateralis. The other division is said by Hawkes to be twice as large, though in Nishi's figures (reproduced here as Text-figures 66 and 67) it appears slightly smaller than it does in Hawkes' figures. Its origin is from the cranium as well as along the proximal portion of the optic stalk. The insertion is on the dorsal side of the eyeball, somewhat more external than that of the rectus superior which it partly overlaps. From the positions of its origin and insertion, this division must be considered as a secondary or derivative portion of the primitive rectus lateralis. This secondary muscle was probably split off from a typical rectus lateralis to aid the superior rectus and the superior oblique in tilting the eye upward. The recti superior, medialis (internus) and inferior are all attached to the top of the optic stalk, just below its flattened head.

THE APPENDICULAR MUSCLES

From embryological studies on certain elasmobranchs and primitive teleostomes it is clear that, in these fishes, buds from the myotomes grow into the embryonic fins and there break down into mesenchyme which is the source of the fin muscle: as in *Spinax* (Braus, 1899); *Scyllium* (Goodrich, 1906); *Cestracion* (Osburn, 1907); *Acanthias* (E. Müller, 1911); in *Amia* and *Lepidosteus* (Schmalhausen, 1912). Thus the muscles that move the fins are metameric in origin; this applies to both paired and unpaired fins. Some features of this developmental history have been interpreted in terms of the fin-fold theory of the origin of paired fins. Concerning this matter, Daniel (1934, p. 110) says:

It is evident that the number of segments that take part in the formation of buds for the pectoral fin is fewer in the sharks than in the rays. This fact is clear when we consider two types like *Mustelus* and *Torpedo*, in the former of which the fin is relatively narrow and in the latter is of great extent. According to Maurer (1912), in the embryo of *Mustelus* only 10 segments contribute to the formation of the musculature of the pectoral fin; while in *Torpedo* there are 26 such segments.

The further course of the development of these buds in two forms like the above has been studied in great detail because of the bearing which such development has on the lateral fin-fold theory. That, in a type like *Mustelus*, segments (myotomes) anterior to the pectoral fin and between the pectoral and the pelvic fins form buds which atrophy without entering the fin, is taken by those who accept the lateral fin-fold theory to mean that the fin previously had a much greater anteroposterior extent than at present; and it is hence in agreement with what would be expected from that theory.

In common with the notidanids, *Chlamydoselachus* seems to afford favorable material for the study of the origin and development of the fin muscles, but so far as I am aware, such studies have never been made on these forms.

Of the fins of *Chlamydoselachus*, only the pelvics of the male have received attention with respect to their musculature. The muscles of these fins have been described in

Text-figure 69.

Endoskeleton and musculature of male pelvic fins of *Heptanchus maculatus*.

A—Skeleton of male left pelvic fin in dorsal view.

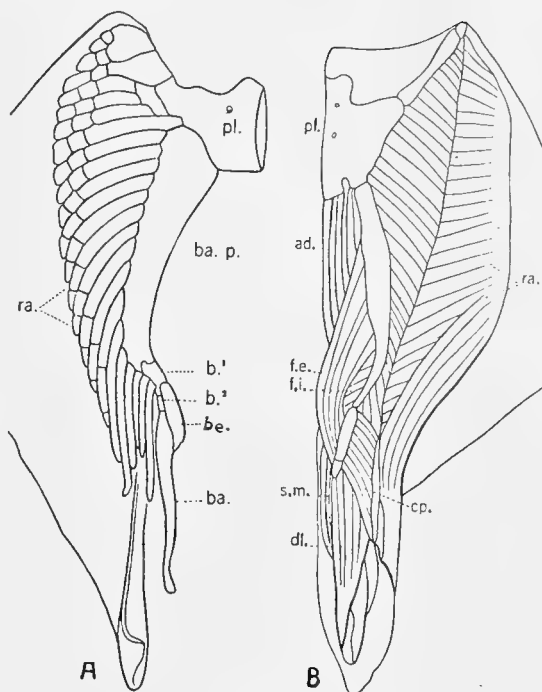
b.1 and b.2, connecting segments; ba., basal piece; ba.p., basipterygium; be., beta cartilage; pl., pelvic girdle; ra., radial cartilages.

After Davidson, 1918, Fig. 8.

B—Musculature of male right pelvic fin in dorsal view.

ad., adductor muscle; cp., compressor muscle; dl., dilator muscle; f.e., flexor externus; f.i., flexor internus; pl., pelvic girdle; ra., radial muscles; s.m., muscle of sac or pocket.

After Davidson, 1918, Fig. 9.



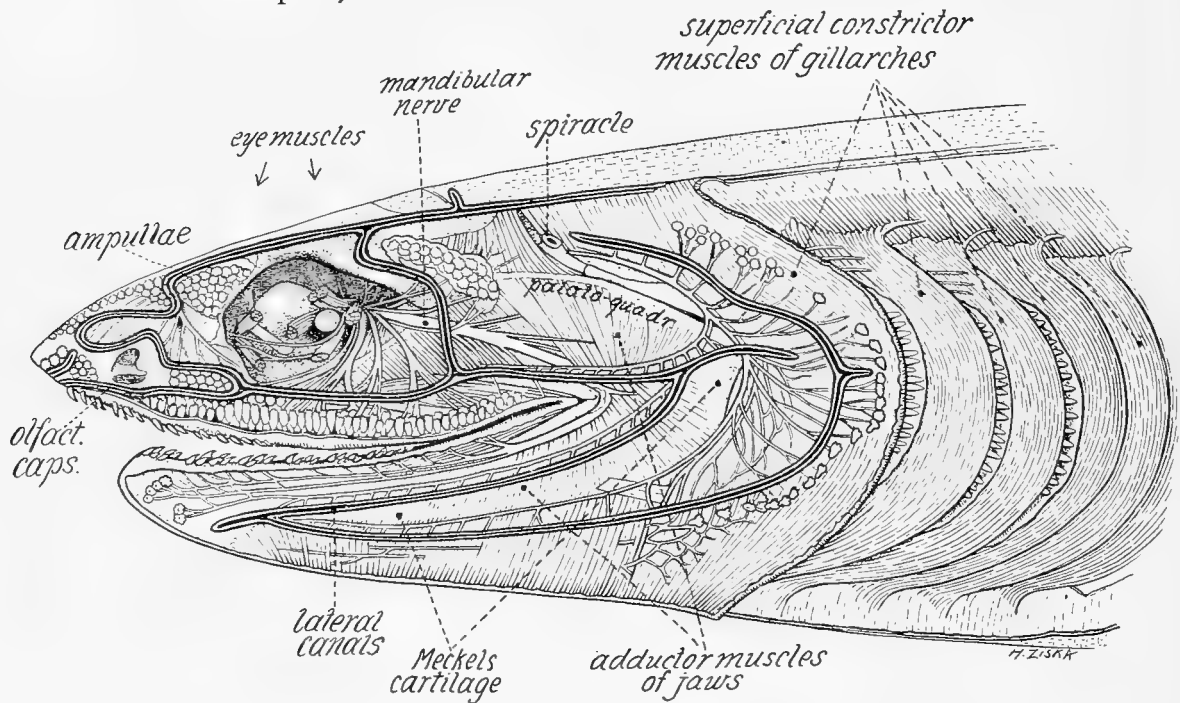
detail by Goodey (1910. 1, pp. 564–565) whose Figs. 20 and 21, pl. XLVI, are reproduced as my Figures 22 and 23, plate V, alongside Figure 21 which shows the endoskeleton. The radial muscles (*Ra.*, Figure 23, plate V) exhibit a division into bundles paralleling the radial cartilages. Concerning the ventral radial muscles Goodey says: “On the ventral side there are the radial muscles *Ra.*, which originate on the pelvic girdle close to the median line and extend outward to the horny fibers. Toward the anterior end the separate bundles have fused together, thus corresponding with the fusion of the radials above.”

The muscles of the clasper have been described in *Heptanchus* by Davidson (1918, pp. 165–167 and Fig. 9). Davidson’s figure of the musculature is here reproduced as Text-figure 69B alongside his figure of the endoskeleton (Text-figure 69A). In both *Chlamydoselachus* (Figures 22 and 23, plate V) and *Heptanchus* (Text-figure 69B), the musculature of the myxopterygium is simple as compared with that of most elasmobranchs. Few differences are found when *Chlamydoselachus* and *Heptanchus* are compared with each other. As pointed out by Daniel (1934, p. 110), the principal difference is in the adductors. In *Heptanchus* the adductor (*ad.* in Text-figure 69B) is a long muscle; in *Chlamydoselachus* it (A in Figure 22, plate V) is relatively broad and fan-shaped. Also, in *Heptanchus* the external and internal flexors are united at their origins, while in *Chlamydoselachus* the point of origin of the external flexor is far removed from that of the internal flexor.

From a functional point of view, certain muscles of the myxopterygia or claspers of *Chlamydoselachus* are described by Leigh-Sharpe (1926, p. 312) as follows: “The musculature is represented by the anteroflexor muscle, which anteroflexes the whole clasper for intromission, and the erector muscle which in this case causes expansion of the apical valves by pulling on a common tendon. The anteroflexor muscle is strongly developed in this genus.” These muscles are shown (p. 472) in Text-figure 115B, after Leigh-Sharpe.

THE BRANCHIOMERIC MUSCLES

The segmentation that gives rise to the branchial arches is of a different nature from that which carves out the somites. The term branchial arches is used by embryologists, in its widest sense, to include the mandibular and hyoid arches which are considered to be modified gill-arches. By comparative anatomists, the entire series is usually designated the visceral skeleton, and the arches are called visceral arches. It is common to speak of the branchiomeric muscles as the pharyngeal muscles, here also making no distinction between mouth and pharynx.



Text-figure 70.

A dissected head of *Chlamydoselachus anguineus* in lateral view.

From Gregory, 1933, Fig. 6; redrawn and slightly simplified after color figure in Allis, 1923, pl. IV.

While the metameric muscles are derived, at least in large part, from a dorsal zone of early mesoderm which has previously been cut up into somites, the muscles of the branchial (visceral) arches (excluding the hypobranchial group of muscles) do not arise from somites but from mesoderm that is commonly regarded as splanchnic. The nerves that supply these muscles are placed in a different category (visceral) from those (somatic) that supply metameric muscles.

Fürbringer (1903) described some of the muscles of gill-arch origin, particularly those of the mandibular arch, in *Chlamydoselachus*. Luther (1909) described the muscles innervated by the trigeminal nerve. Goodey (1910.1) described the muscles of the mandibular and hyoid arches. Allis (1923) has given a detailed, comprehensive and beautifully illustrated description of the pharyngeal muscles of *Chlamydoselachus*, which

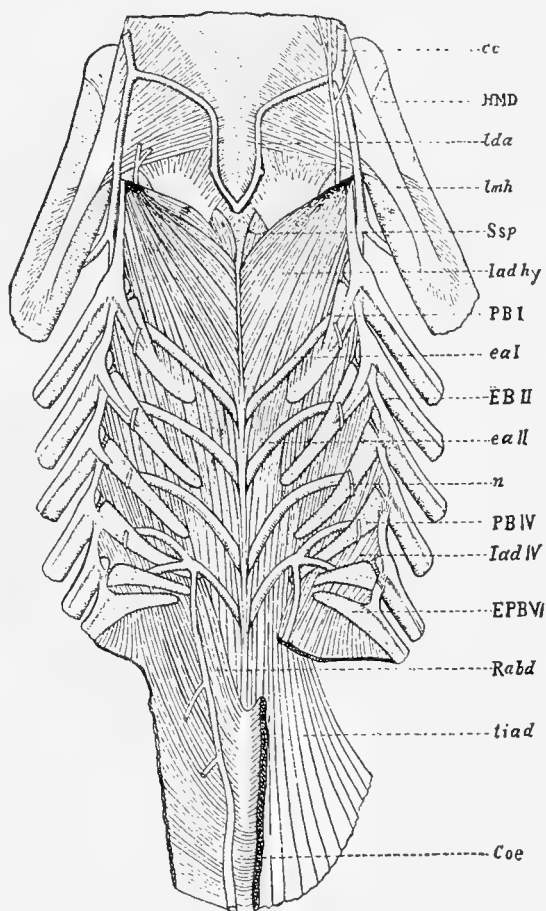
should be consulted by anyone wishing a more complete account than is given here. Most of the pharyngeal muscles are represented in Text-figures 64 and 70 after Gregory (1933). The interarcuales dorsales (*Iad.*) and subspinales (*S.sp.*) are shown in Text-figure 71, after Allis (1915), drawn from a specimen in which the interarcuales are somewhat atypical. In Text-figures 64 and 71 the methods of numbering the interarcuales differ, so that Allis's interarcualis IV corresponds to Grègory's interdorsalis V.

Text-figure 71.

Ventral view of the roof of the pharyngeal cavity of *Chlamydoselachus*, after the lining membrane has been removed, showing the pharyngo-branchial cartilages, efferent arteries and interarcuales dorsales muscles in natural position.

cc, common carotid artery; *Coe*, constrictor of the esophagus; *ea*I, efferent branchial artery of the first branchial arch; *ea*II, efferent branchial artery of the second branchial arch; *EB*II, epibranchial cartilage of the second branchial arch; *EPB*VI, epi-pharyngobranchial cartilage of sixth branchial arch; *HMD*, hyomandibular cartilage; *Iad*IV, musculus interarcualis dorsalis between arches IV-V; *Iad*hy, musculus interarcualis dorsalis between hyoid and first visceral arches; *lda*, lateral dorsal aorta; *lmh*, ligamentum mandibula-hyoideum; *n.*, cut ends of nerves to tissues of roof of branchial chamber; *PB*I, pharyngobranchial cartilage of first branchial arch; *PB*IV, pharyngobranchial cartilage of the fourth branchial arch; *Rabd*, musculus retractor arcuum branchialium dorsalis; *Ssp*, subspinalis muscle; *tia*d, ligamentous sheet formed by tendons of musculi interarcuales dorsales.

After Allis, 1915, Fig. 1.



Davidson (1918) classified the pharyngeal (branchiomic) muscles of *Heptanchus* as follows: (1) superficial circular [constrictor] muscles; (2) interarcuales; (3) subspinales; (4) adductors; and (5) the hypobranchials. For reasons concerned with the mode of development, the hypobranchials have already been considered under the category of metameric muscles, though it is more common to include them with the pharyngeal group, to which they functionally belong.

All observers agree that the adductor mandibulae of *Chlamydoselachus* is "a thick massive muscle, filling up the concavities on the outer side of the palatoquadrate and the mandible" (Goodey, 1910.1, p. 547). In all the illustrations (by various authors) of this

muscle, it appears surprisingly large considering the slenderness and flexibility of the jaws. This is well shown in Gregory's drawing (Text-figure 64 herein) and is perhaps exaggerated in Fürbringer's (1903) Fig. 1, pl. XVI. Consideration of the large size of this muscle strengthens the conviction that *Chlamydoselachus* is in the habit of seizing and swallowing fairly large prey. In this case the superficial constrictor muscles (Text-figure 70; also Allis, 1923, Fig. 46, pl. XVII, and Fig. 48, pl. XVIII) as well as practically every other muscle of the oral and branchial region, may be brought into play to assist in the act of swallowing which is finally completed by the constrictor of the esophagus. The superficial constrictor muscles that run in the gill-flaps are thin (Text-figure 78, p. 421) but they are broad and they overlap like the shingles on a roof, so that collectively they may exert considerable pressure. It has already been noted that the labial cartilages are held in place by strong ligaments and fascia; some of these cartilages serve for the attachment of special muscles. Thus an integumental muscle, the protractor anguli oris, has a tendon attached to the mandibular labial cartilage (Allis, 1923). The strong levator labii superioris (Allis, 1923, pp. 183-184 and Fig. 15, pl. X) may assist the creature in expanding the mouth opening while swallowing its prey. Of this muscle Allis says:

The levator labii superioris, in all my specimens, is wholly independent of the adductor mandibulae, my specimens apparently differing in this respect from those examined by Fürbringer (1903, p. 384) and Luther. The muscle arises by a relatively long tendon from the ventro-postero-lateral corner of the ectethmoidal process, and running almost directly posteriorly swells abruptly into a muscle body which is inserted on the anterior half of the posterior upper labial, some of the fibers apparently being inserted in the adjacent tissue of the upper lip. The muscle is innervated, as both Fürbringer and Luther have stated, by a branch of the mandibularis trigemini which arises from that nerve shortly after its separation from the maxillaris trigemini.

In many selachians there is a fairly strong adductor muscle, related to the mandible, which is usually referred to as the muscle *add. gamma* of Vetter's (1874) description. In *Chlamydoselachus*, the long tendinous portion of this muscle is apparently represented by a strong ligament, which has its origin on a little process of the anterior edge of the hyomandibular and its insertion on the posterior edge of the postorbital process of the cranium (Allis, 1923, p. 187 and Fig. 23, pl. XI). I quote the following from Allis, 1923, pp. 187-188:

Fürbringer and Luther both say that this muscle is not found in *Chlamydoselachus*. Fürbringer accordingly considers it to be a secondary arrangement, possibly the beginning of a differentiation of a superficial portion of the adductor mandibulae, such as is found in *Amia* and in many teleosts. Luther (1909, p. 54) thinks it is developed from the most posterior portion of the adductor, and he considers it to be an archaic feature (l.c., p. 64) notwithstanding that he did not find it in either *Chlamydoselachus*, *Echinorhynchus* or *Odontaspis*. In *Squatina*, it is to be noted, the muscle arises by a few fibers from the hyomandibula (Luther, 1909, p. 60).

One is especially impressed by the differences, with respect to this muscle *add. gamma*, between the closely related forms, *Heptanchus* and *Chlamydoselachus*. In

Heptanchus (Vetter, 1874, Fig. 1, pl. XIV) the muscle is well developed; in *Chlamydoselachus* it is apparently represented by a ligament which is attached, not to the mandible, but to the hyomandibular. It seems probable that the presence of this muscle, as in *Heptanchus*, is primitive for sharks while the related structure in *Chlamydoselachus* is a modification that has arisen in connection with the peculiar hyostylism of the jaws.

In attempting to identify homologous muscles in different species of vertebrates, considerable dependence is placed on their innervation. The motor nerves, growing outward from the central nervous system, establish connections with the muscles or pre-muscle masses quite early in their development. Should the muscle subsequently migrate in order to reach its definitive position, its nerve follows it. Thus in the branchial region, it is generally considered that all the muscles innervated by the fifth (trigeminal) nerve are derivatives of the first visceral (the mandibular) arch, while all the muscles innervated by the seventh (facial) nerve are derivatives of the second visceral (the hyoid) arch. In most sharks, the musculus intermandibularis is supplied by the mandibular branch of the trigeminal nerve; but in *Chlamydoselachus*, Furbringer (1903, Fig. 1, Taf. XVI) figures the musculus intermandibularis as supplied only by branches of the seventh (the facial) nerve, and Hawkes (1906) states that "the mandibular ramus [of the trigeminal nerve] does not supply the large median muscles which lie in the angle made by the two sides of the lower jaw." Luther (1909) was unable to trace any branches of the trigeminal nerve to the intermandibular muscles of *Chlamydoselachus*, *Hexanchus* and *Heptanchus*. In the notidanids and in *Chlamydoselachus*, the superficial muscles spanning the halves of the mandible are supplied by branches of the seventh or facial nerve (Luther, 1909). For *Chlamydoselachus* and *Heptanchus* the distribution of these branches is shown in Luther's (1909) Fig. 1, Taf. I, and Text-figs. 9 and 10; for *Chlamydoselachus* they are better shown by Allis (1923) in his Fig. 6, pl. VI, which is in color. Luther (1909) concluded that when the intermandibular muscle is innervated wholly by the nervus facialis, a muscle of mandibular-arch origin has simply been crowded out by one of hyoid arch origin; but in his later work (1913, p. 46) Luther decided that the trigeminus muscle here persisted, but had secondarily acquired innervation by the nervus facialis.

Allis (1917) gave particular attention to this matter of the innervation of the musculus intermandibularis in *Chlamydoselachus* and related forms. His conclusions appear to be embodied in the following statement (Allis, 1917, p. 389):

The interhyoideus and intermandibularis muscles of *Chlamydoselachus* could accordingly both be of facialis origin, so far as the relations of nerve and muscle are concerned, but in all probability only that portion of the intermandibularis that lies anterior to the point where the nervus facialis definitely disappears from its external surface could be of mandibular origin. And if this portion of the muscle be of mandibular origin, as several authors have maintained, I consider it certain that it is innervated by a branch of the nervus mandibularis trigemini, and that that branch has simply been missed in dissections, my own included.

In the introduction to his 1923 memoir, Allis states: "The investigation of the nervous system had only just begun, and . . . this part of the cranial anatomy is only

briefly noticed in the present memoir." This leaves us in doubt whether Allis made any further dissections before writing (1923, pp. 188-189):

The muscles innervated by the nervus facialis, all of which are here considered as belonging to the hyal arch, are represented by a single continuous muscle sheet, which is partially differentiated, by differences in the insertion of its fibers, into a constrictor superficialis, a levator hyomandibularis, an interhyoideus and an intermandibularis. . . . These several portions of the continuous muscle sheet are all apparently innervated exclusively by branches of the nervus facialis, and there is accordingly no musculus intermandibularis of mandibular origin in this fish. This has been fully discussed in an earlier work (Allis, 1917), the course of the ramus hyoideus facialis and its relations to the several muscles there also being given.

Whatever light future investigations may throw on the possible persistence of a vestigial musculus intermandibularis of mandibular arch origin, the fact remains that what appears to be the intermandibular muscle of *Chlamydoselachus*, *Hexanchus* and *Heptanchus* is innervated by a branch of the facial nerve, contrary to what has been found in all other sharks that have been investigated. This evidence, so far as it goes, tends to draw *Chlamydoselachus* and the notidanids closer together and at the same time to separate them further from other existing sharks.

Considering the small size of the external opening of the spiracle and the absence of an authentic spiracular cartilage, it is not surprising that we have found no mention of a special spiracular muscle in *Chlamydoselachus*. Luther (1909, p. 12) mentions a spiracular muscle in *Hexanchus*, and in his Fig. 1, Taf. I, it is clearly shown as a prominent sphincter; but there appears to be no special differentiation of the muscles adjoining the spiracle of *Heptanchus* (Luther, 1909, Fig. 2, Taf. I).

An interesting though probably anomalous condition of the muscoli interarcuales dorsales was found by Allis (1915 and 1923) in one of three specimens of *Chlamydoselachus* studied by him. In the specimen under consideration, the muscoli interarcuales dorsales form an almost continuous sheet of muscular and ligamentous tissue in the roof of the pharynx (Text-figure 71). These muscles are better shown in Allis's (1923) Fig. 56, pl. XXI, which is drawn from the same specimen but to a larger scale and in color. In the two other specimens of *Chlamydoselachus* studied by Allis, the individual muscles of the interarcuales dorsales group are better differentiated and there is no common sheet of muscular tissue mesial to the pharyngobranchials. Nevertheless, the related ligamentous sheet existed in the two specimens as in the other one, and "extended the full length of the branchial region" (Allis, 1915). From one of the two specimens thus described, Allis's (1923) Fig. 53, pl. XX, was drawn. The condition shown here is more like what is found in *Heptanchus* (Fürbringer, 1897, Fig. 1, Taf. V; Davidson, 1918, Fig. 3), where the muscle is broken up into segments between the respective pharyngobranchial cartilages. Thus we find, in the muscoli interarcuales dorsales of *Chlamydoselachus*, one more example of decided variability.

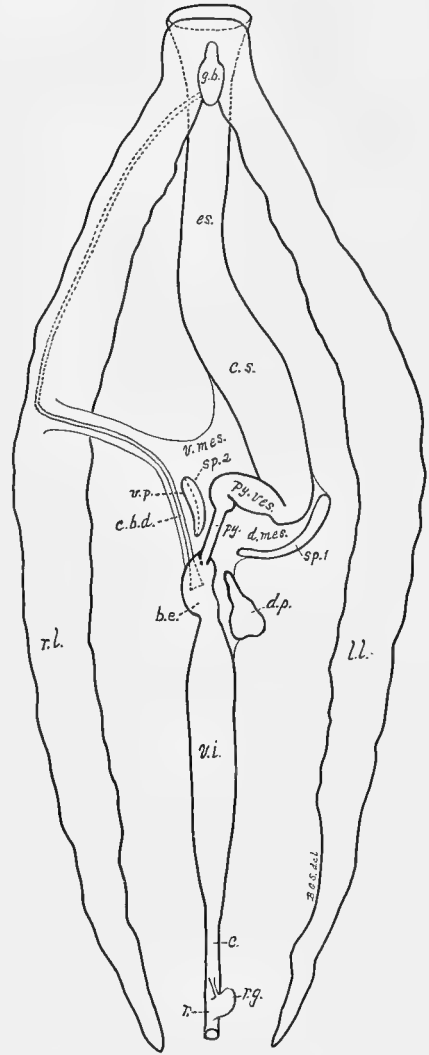
DIGESTIVE SYSTEM AND ASSOCIATED ORGANS

There are few published descriptions of the digestive organs of *Chlamydoselachus*, and these accounts are very brief. This situation may be due, in part, to the circumstance that most of the specimens that have come into the hands of anatomists had been eviscerated. The following account is based mainly on my studies and drawings of material in the collection of the American Museum of Natural History, but it includes a review of the work of other investigators.

My material includes the three large female specimens whose external characteristics have been fully described by Gudger and Smith (1933). In all these specimens, the body cavity had been opened by a ventral longitudinal incision and the digestive tube had been split open along its length. Thus it was not possible to view the digestive organs in an undisturbed condition. In two specimens, the liver was nearly all missing and the mesenteries had been much torn. The best-preserved specimen, No. I, had all the digestive organs, also the spleen, complete; but the mesenteries were considerably torn. Another large female specimen, kindly lent by Dr. E. Grace White, was used here only for the study of the thyroid, since the digestive organs had been removed. I shall call this specimen No. IV.

THE DIGESTIVE TUBE

Before proceeding with a description of the various parts of the digestive system, it is advisable to call attention to Text-figure 72, drawn from specimen No. I, wherein each part of the digestive system, excepting mouth and pharynx, is drawn to scale in its approximate relation to the whole. In order to display certain organs to the best advantage, the natural position has in some instances been altered. Thus the lobes of the liver have been drawn aside, the cardiac stomach has been turned to the left in order to bring



Text-figure 72.

The digestive system of *Chlamydoselachus*, ventral aspect, about one-fifth natural size.

b.e., bursa entiana; c., colon; c.b.d., common bile duct; c.s., cardiac stomach; d.mes., dorsal mesentery; d.p., dorsal pancreas; es., esophagus; g.b., gall bladder; l.l., left lobe of liver; py., pylorus; py.ves., pyloric vestibule; r., rectum; r.g., rectal gland; r.l., right lobe of liver; sp.1, spleen; sp.2, accessory spleen; v.i., valvular intestine; v.mes., ventral mesentery; v.p., ventral pancreas.

Drawn from specimen No. I in the collection of the American Museum of Natural History.

the pyloric vestibule and the pylorus into view, and the rectal gland has been turned to the left. In this paper, the terms right and left mean the right and left sides of the fish itself, regardless of its position with respect to the observer.

THE PHARYNX

The mouth, including the teeth, has been adequately described by Gudger and Smith (1933). The pharynx is of importance for respiration, but since it affords passage for food it must be briefly considered from this point of view.

The mouth and pharynx of *Chlamydoselachus* form one large cavity, the oropharyngeal cavity. For so slender a shark, the size of this cavity when fully distended is remarkable (Text-figure 2, p. 337). Although a large mouth does not necessarily imply that large objects are taken as food, in the case of *Chlamydoselachus* there is collateral evidence, such as the character of the teeth, indicating that the animal seizes and swallows living prey of considerable size. It seems likely that the elaborate pharyngeal musculature, already considered, assists in the act of swallowing the prey, snake-fashion.

Almost the entire oropharyngeal cavity is lined with close-set denticles. On the lining of the roof, the denticles are exceedingly small. On the floor, especially where this is upraised to form a structure superficially resembling a rudimentary tongue, the denticles are appreciably larger. Some of these denticles, in a region overlying the thyroid gland, are shown in Text-figures 75 and 76, p. 417. On the inner surfaces of the gill-arches, excepting only the hyoid arch and the dorsal portions of the most posterior branchial arch, they are particularly large, but are still smaller than those at the angles of the mouth (Text-figure 10, p. 345), described and figured by Gudger and Smith (1933). The larger denticles are of the same general character as those of the epidermis; but the central cusp is longer and sharper, and curves backward. The denticles of the gill-arches and the floor of the pharynx offer little resistance to a finger tip passed over them in a cephalocaudal direction, but pierce the epidermis and cling tenaciously when the finger tip is pulled over them in the opposite direction. Presumably, the pharyngeal denticles assist the animal in retaining its hold on slippery prey, partly swallowed. Garman (1885.2) shows denticles on the inner surfaces of the gill-arches of his specimen (my Text-figure 77, p. 421), but they appear larger than those found in a corresponding situation in my specimens.

ESOPHAGUS AND CARDIAC STOMACH

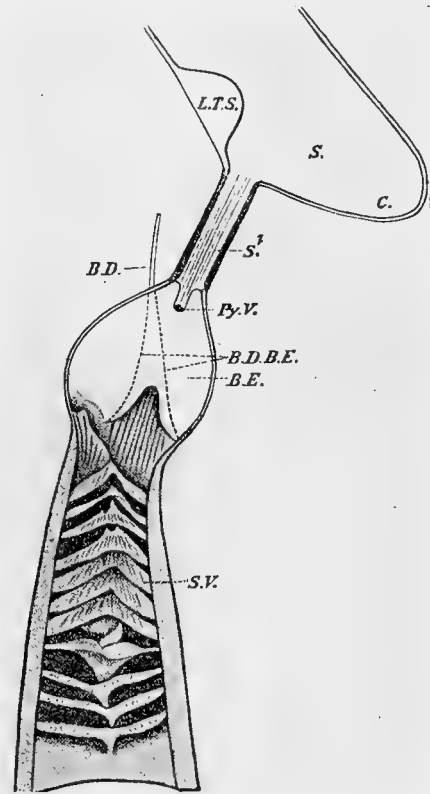
As in most elasmobranchs, the wide, distensible esophagus passes without abrupt demarcation into the large, thin-walled cardiac portion of the stomach. In *Chlamydoselachus* one cannot tell precisely where the esophagus leaves off and the stomach begins. The combined length of esophagus and cardiac stomach is remarkable (Text-figure 72; and Table I, p. 412), since together they form about half the total length of the digestive tube. In my best-preserved specimen, No. I, the collapsed and flattened esophagus is

about 55 mm. wide where it joins the pharynx, but it narrows rapidly to an almost uniform width of 30 mm. throughout most of its length. The diameter of the widest portion of the cardiac stomach is about 45 mm.

In all the specimens in the American Museum, a previous dissection had shown the stomachs to be practically empty. Nevertheless in specimen No. III the cardiac stomach had evidently been hardened while in a distended condition, since its lumen is unusually large and its walls are very thin. In this specimen, throughout a large portion of what is presumably cardiac stomach, the wall is only about 1 mm. thick; I suspect, however, that most of the mucosa is missing. The inner surface is smooth. In my other specimens the cardiac stomach is less distended and its wall is appreciably thicker; the inner surface is cast into slight longitudinal folds. In all three specimens the thickness of the wall of the cardiac stomach increases toward its caudal end, but it is nowhere more than 2 or 3 mm. thick.

On the right side near the caudal end of the cardiac stomach of *Chlamydoselachus*, Hawkes (1907) describes and figures (my Text-figure 73) a more decided thickening (*L.T.S.*) which she suggests may be a "lymphatic gland." Hawkes does not tell how many specimens she studied, nor whether this thickening occurred in more than one specimen. I have found no such structure in any of my three specimens. From specimens I and III, I have excised some segments of the slightly thickened wall near the caudal end of the cardiac stomach, and upon microscopical examination have found only the layers characteristic of a stomach, including an inner glandular layer in a poor state of preservation. Collett (1897) states that in his specimen of *Chlamydoselachus* measuring 1910 mm., the stomach proper is small and proportionally narrow; its length is 340 mm., its breadth is about 45 mm.

In *Heptanchus* (Daniel, 1934) the stomach is U-shaped or V-shaped, the larger left limb being the cardiac portion, and the smaller right limb, the pyloric division. In two of my specimens of *Chlamydoselachus* a small division, the pyloric vestibule, is inter-



Text-figure 73.

Digestive tube of *Chlamydoselachus*, from the middle of the stomach to the middle of the valvular intestine.

B.D., bile duct; *B.D.B.E.*, dotted line showing the position of the enlarged end of the bile duct in the wall of the bursa entiana; *B.E.*, bursa entiana; *C.*, caecum at the hinder end of the larger arm of the stomach; *L.T.S.*, thickening of the stomach wall, probably due to a lymph node; *Py.V.*, pyloric valve; *S.*, stomach; *S.I.*, short arm of stomach; *S.V.*, spiral valve.

After Hawkes, 1907, first text-figure.

posed between the cardiac stomach and the pylorus. It seems probable that, when present, this division in *Chlamydoselachus* is homologous with a part of the pyloric stomach of *Heptanchus*.

THE PYLORIC VESTIBULE

In my specimen No. I the cardiac stomach narrows considerably near its caudal end. It is marked off from the next division, which I shall call the pyloric vestibule, by a sharp constriction. The pyloric vestibule is cylindrical in form and is of smaller caliber than the cardiac stomach, though decidedly larger than the pylorus. The vestibule leads off from the dorsal surface of the cardiac stomach, beginning about 10 mm. from its caudal end, and extends somewhat cephalad, dorsal to the cardiac stomach, for a distance of about 25 mm., then makes an abrupt turn dorsad and caudad before joining the pylorus which extends obliquely to the right and caudad. Thus the pyloric vestibule, considered together with the adjoining portion of the cardiac stomach, is somewhat S-shaped. In Text-figure 72 the pyloric vestibule (*py.ves.*) has been exposed by turning the cardiac stomach to the left. Therefore the vestibule has been rotated through an angle of nearly 90° and appears almost as if viewed, in its natural position, from the right side. In the specimen under consideration, the pyloric vestibule is about 35 mm. long and (in a collapsed and flattened condition) about 22 mm. wide in its widest portion which is near its junction with the cardiac stomach. Its wall is about 1.5 mm. thick and is of the same general character as the wall of the cardiac stomach. The sharp constriction between the cardiac stomach and the pyloric vestibule is more marked internally since here the flattened lumen has a width of only 15 mm., which is 4 mm. less than the diameter of the lumen of the adjoining portion of the pyloric vestibule. At its pyloric end, the vestibule narrows abruptly to join the pylorus; here, the entrance has the same diameter as the lumen of the pylorus.

In specimen No. III, the pyloric vestibule is much smaller. It is situated on the dorsal side of the caudal end of the cardiac stomach. In life it was probably spherical, but it is now much flattened by pressure between the cardiac stomach and the dorsal body wall; it has been hardened in that condition. Externally, on its anterior border it is marked off from the cardiac stomach by a deep groove. Internally, its lumen is partially separated from that of the cardiac stomach by a crescentic valve-like flap almost completely encircling the residual lumen but leaving a circular aperture about 15 mm. in diameter. On the anterior side, where it is best developed, the width of this flap is about 5 mm. I am of the opinion that the flap, as such, is an artifact due to pressure, since by stretching the wall of the stomach longitudinally the flap may be reduced to a low fold. There remains, however, a very decided constriction marking off the pyloric vestibule from the cardiac stomach. An aperture about 4 mm. in diameter leads off from the anterodorsal side of the pyloric vestibule into the pylorus which extends obliquely to the right and caudad. The proximal third of the pylorus adheres firmly to the wall of the pyloric vestibule.

In specimen No. II there is nothing resembling a pyloric vestibule; the pylorus comes off abruptly from the caudal end of the cardiac stomach and leads directly backward. The aperture leading from the cardiac stomach to the pylorus is very small, but admits a probe without difficulty. The muscular wall surrounding this aperture is unusually thick; evidently it serves as a sphincter. In the specimen figured by Hawkes (1907) and reproduced as my Text-figure 73, there is no division of the stomach corresponding to what I have called the pyloric vestibule. I cannot reconcile this difference further than to say that here, as in many other structures, *Chlamydoselachus* shows remarkable variability.

THE PYLORUS

In all my specimens, the pylorus is a slender portion of the digestive tube which, from superficial appearances, might more appropriately be designated a part of the small intestine. However, the region under consideration undoubtedly corresponds to what is called pylorus in other sharks, as in *Galeus* (Daniel, 1934, Fig. 135, p. 136). In *Chlamydoselachus* (Text-figure 72) the caudal extremity of the pylorus (*py.*) projects into the next division of the digestive tube, the bursa entiana (*b.e.*), as a large conical papilla, the pyloric valve. The muscular layers of the pylorus appear to be continuous with similar layers in the valve. At the summit of the papilla there is an aperture which, in the hardened condition of the material, is still large enough to admit a probe easily. This opening is the passageway from the pylorus to the bursa entiana. The cone-shaped valve is asymmetrically placed and adheres, more or less, to one side of the bursa.

On account of the overlapping of the pylorus by the bursa, in recording their lengths for the purposes of Table I it was necessary to divide the region of overlapping equally between them. In specimen No. I (Text-figure 72) the overlapping occurs mainly on one side and is about 6 mm. in its greatest extent; the total length of the pylorus, including its valve, is 36 mm. The width of the pylorus, in its present collapsed and flattened condition, is about 8 mm. In specimen No. II the lumen of the bursa entiana overlaps the pyloric valve for a distance of 14 mm. on one side and 6 mm. on the other. The total length of the pylorus, including its valve, is 40 mm. In this specimen the pylorus is cylindrical and its diameter is only 6 mm. In specimen No. III the pylorus is unusually short. Its valve is overlapped, on one side only, by the lumen of the bursa entiana for a distance of 6 mm. and its total length is 28 mm. At its widest point, which is near its middle, the collapsed and flattened pylorus of this specimen measures 12 mm. across. In specimens I and III the wall of the pylorus is a scant millimeter in thickness; in No. II it is about 2 mm. thick. In all my specimens the inner surface of the pylorus is traversed by longitudinal folds. These are more prominent in No. II because of the contracted condition of the pylorus in this specimen.

Hawkes (1907) describes the division which I have called the pylorus, as follows: "The shorter arm of the stomach (*S. 1*) differs from the larger anatomically and functionally. It is a short, thick-walled tube incapable of distension, the lining mucosa of which is

raised into parallel ridges. This arm opens into the intestine by a protruding pyloric aperture (Py. V.) which is furnished with distinct sphincter muscles." The pyloric valve (Py. V.) figured by Hawkes (my Text-figure 73) appears symmetrical, thin-walled, slender and cylindrical—quite unlike any that I have observed, save that it protrudes into the bursa. Possibly the drawing is inaccurate, since the valve appears too thin to be provided with a sphincter muscle. In *Heptanchus* (Daniel, 1934, Fig. 123), as in *Chlamydoselachus*, the pyloric valve projects as a well-defined circular band into the bursa.

THE BURSA ENTIANA

In *Chlamydoselachus*, as in sharks generally, the middle intestine or duodenum is short; as in certain other elasmobranchs, it is expanded to form a thin-walled sac, the bursa entiana (Text-figure 72, *b. e.*). In *Chlamydoselachus* the bursa entiana is shaped somewhat like the human stomach, but the orientation is different. Superficially, it would resemble the human stomach if the latter were reversed end-for-end and rotated so that the greater curvature would lie to the right and dorsally. In my three specimens the amount of distention of the bursa varies greatly, so that the dimensions recorded here do not give any accurate information as to what the relative size would be if the structures were measured under identical conditions.

In my specimen No. I the bursa entiana is moderately distended and has moderately thick walls; its condition is probably typical. Measured from the first coil of the spiral valve to the apex of the pyloric valve, its length is 33 mm.; but after including the total extent to which the bursa overlaps the pylorus, the length is 39 mm. Its greatest transverse diameter is about 14 mm. Its walls are very thin (less than 1 mm.) at the cephalic end, but toward the caudal end the thickness increases gradually to almost 2 mm. at the junction with the valvular intestine.

In specimen No. II the bursa is greatly contracted. Measured from the villousities on the inner surface of the cephalic end of the valvular intestine, to the apex of the pyloric valve, its length is 20 mm. Since the bursa overlaps the pyloric valve for a distance of 14 mm. on one side, its total length is 34 mm. Its greatest transverse diameter is about 10 mm. The thickness of its walls ranges from 1 mm. at the cephalic end to 3 mm. at the caudal end.

In specimen No. III the bursa is greatly expanded. Its length, measured from the cephalic end of the spiral valve to the apex of the pyloric valve, is 40 mm. After including the extent to which the bursa overlaps the pyloric valve, the total length is 46 mm. The greatest transverse diameter, which is near the caudal end, is about 18 mm.; near the cephalic end the transverse diameter is about 10 mm. The wall is everywhere less than 1 mm. thick.

In the lining of the ventral side of the bursa entiana in specimen No. I there is a pocket (shown by a dotted outline in Text-figure 72) about 10 mm. long, opening caudad into the lumen of the bursa. The opening is about 8 mm. wide and is situated about

one-third of the distance from the apex of the pyloric valve to the beginning of the valvular intestine. A probe inserted into the pocket readily entered the common bile duct (c.b.d.) which extends anteriorly. A similar but slightly larger pocket occurs in specimen No. III; it is situated a little further caudad, rather more than halfway toward the valvular intestine. A probe passed into this pocket did not find the opening of the bile duct. A bile duct could not be found in the vicinity, but this was probably because the region had been mutilated. In specimen No. II the pocket, as such, could not be found, but a channel or canal leads from the cephalic end of the valvular intestine into the rather thick, contracted wall of the bursa entiana. This channel was probed. After proceeding for a distance of about 15 mm. cephalad within the wall of the bursa, the probe entered the bile duct which extends anteriorly. The channel is, therefore, an extension of the bile duct caudad within the wall of the bursa entiana.

In specimen No. I the inner surface of the bursa is fairly smooth save in a region extending caudad from the pocket which forms the opening of the bile duct. This area is traversed by longitudinal folds similar to those shown in Text-figure 73. In specimen No. I, these folds extend along the inner surface of the outer wall of the pocket and are visible through its thin inner wall. In specimen No. III, where the bursa is greatly expanded, its inner surface is smooth except that the area which in specimen No. I is cast into longitudinal folds, is here somewhat rough and flaccid. In specimen No. II, where the bursa is strongly contracted, its entire inner surface is cast into strong longitudinal folds. The longitudinal canal within the wall of the bursa, which communicates with the bile duct anteriorly and opens into the valvular intestine posteriorly, was opened by a longitudinal incision after it had been probed. Its inner surface is very rough, with many small papillae like those found in the upper end of the valvular intestine. Thus, in the character of its lining, this channel resembles the valvular intestine and differs from the bursa entiana. It constitutes a decided variation from the usual condition in which the bile duct enters the bursa entiana through a funnel-shaped pocket.

Hawkes (1907) described and figured (my Text-figure 73) a pocket situated nearer the valvular intestine than the pockets described in my specimens No. I and III. The flap forming the inner wall of the pocket figured by Hawkes is not so well developed as in my specimens I and III, where its free edge extends in a straight line transversely or somewhat obliquely. The condition that I have described in specimen No. II, whereby the bile is conveyed through a special channel in the wall of the bursa directly into the valvular intestine, apparently has not been observed by any other investigator.

In *Heptanchus* (Daniel, 1934, Figs. 120 and 123) the middle intestine or duodenum, corresponding to the bursa entiana of *Chlamydoselachus*, is not sharply marked off from the valvular intestine. Daniel (p. 124) states that "the valve of the spiral intestine extends forward throughout the length of the middle intestine and touches the pyloric valve." This contrasts strongly with the simpler condition in *Chlamydoselachus*, already described.

THE VALVULAR INTESTINE

In my three specimens the valvular portion of the digestive tube is spindle-shaped, but tapers much more rapidly in its caudal half; the cephalic end is almost truncate. Günther's (1887) figure (my Figure 15, plate IV) gives proportions similar to those found in my specimens save that in his dissection the valvular intestine is laid widely open after being slit longitudinally. In my specimens the external surface of the valvular intestine is either bluish-gray or brown, appearing much darker than the other portions of the digestive tube. The walls are very thick, ranging from 5 or 6 mm. near the cephalic end, to 1 or 2 mm. at the caudal end where it joins the colon. In two of these specimens the spiral valve extends to the extreme cephalic end of the thick-walled portion of the digestive tube, but in No. II the spiral valve stops at about 20 mm. from the cephalic end of the thick-walled portion. For the remaining distance the inner surface shows villousities similar to, but larger than, those found in the region of the spiral valve. On this account, and also because of the thickness of its walls, this part is assigned to the valvular intestine. For similar reasons I have included with the valvular intestine a short thick-walled portion, with a velvety lining, between the caudal end of the spiral valve and the thin-walled colon. In specimens I and III the length of this region is 15 mm.; in No. II it is 20 mm. The posterior four-fifths of the valvular intestine lacks a mesentery.

In my specimen No. I, the form of the valvular intestine seems perfectly preserved. The maximum diameter is only 26 mm., while the length is 190 mm. In No. II the valvular intestine is much larger; its maximum diameter is about 33 mm., while its length is 240 mm. In No. III the organ is about the same size as in No. II, but is so irregularly molded that its diameter cannot be accurately measured.

In *Chlamydoselachus* the spiral valve is a continuous ribbon-like structure attached by one edge to the inside of the wall of the intestine, while the other edge is either free, winding about a central cavity, or is attached to an axial strand. In specimen No. I the anterior third of the spiral valve has a central cavity large enough to admit a pencil; the posterior third has a much smaller central cavity, while the middle third has an axial strand. In specimen No. II a central cavity alternates with an axial strand at irregular intervals. In specimen No. III there is a central cavity of moderate size extending the entire length of the spiral valve except in its middle portion, where there is a short axial strand. In the specimen portrayed by Günther (my Figure 15, plate IV) it is clear that there is a central cavity in the caudal half and at the cephalic end, while the interval between has possibly an axial strand.

In its natural position, the spiral valve of *Chlamydoselachus* does not lie vertical to the wall of the intestine; it slants either forward or backward. Thus each coil has the form of an asymmetrical cone, of which the apex may be missing. When the intestine is contracted, the spiral valve makes an acute angle with the wall of the intestine; when it is expanded, the spiral valve may be drawn into a nearly transverse position.

In my best-preserved specimen, No. I, there are 44 coils of the spiral valve. In the nine anterior coils, the angle is very acute and the cones point cephalad; in the remaining coils the cones point acutely caudad. The transition between the two conditions is abrupt. In specimen No. II there are 45 coils; each of these makes an acute angle with the wall of the intestine, and points caudad. In specimen No. III there are 37 coils. In the anterior third, the coils or cones are obtuse but point definitely cephalad; those of the posterior third are acute and point caudad; while those in the middle third are apparently transverse, but this region is much distended and is poorly preserved. In this specimen the transitions between the regions described are gradual.

Günther's (1887) Fig. 5, pl. LXV (my Figure 15, plate IV) shows 35 coils in the spiral valve of *Chlamydoselachus*. Of these, the first 19 point forward, one is transverse, and the remaining 15 point backward. Collett (1897, p. 13) states that in his specimen "the intestine (colon) is cylindrical, very muscular, and contains 47 spiral valves." In a specimen described by Hawkes (1907) there are 43 coils: the first 7 (my Text-figure 73) point forward, one is contorted, and the remaining 35 are directed backward. Hawkes points out that the inclination of the spiral valve has a physiological significance: where the valve is directed forward the passage of the food is undoubtedly slower than where it is directed backward.

In *Heptanchus maculatus* (Daniel, 1934, Fig. 123 and pp. 124-125) the spiral valve makes 17 or 18 turns. The folds are far apart anteriorly and very much closer posteriorly. The valve is considerably broader than the diameter of the intestine and is thrown into a series of cones having their apices pointed anteriorly. The surface of the valve, viewed under the microscope, shows numerous finger-like villi.

It has been noted in *Chlamydoselachus* that the anterior coils of the spiral valve usually point forward, and the posterior coils usually point backward. This condition of the spiral valve seems to be exceptional among elasmobranchs. A similar condition has been found (Parker, 1885) in a single specimen of *Scyllium canicula*, and something like it occurs in *Zygaena* (Parker, 1885, Fig. 8, pl. XI). In most sharks the apices of practically all the coils point forward, as in *Scyllium* (Parker, 1885, Fig. 5, pl. XI); or backward, as in *Heptranchias perlo* (Garman, 1913, Fig. 1, pl. 58). In some specimens of *Raja* (Parker, 1885) the apices of all the coils point forward, while in other specimens all but the first coil are deflected backward. Moreover in some sharks, as in *Cephaloscyllium umbratile* (Garman, 1913, Fig. 2, pl. 58), and in some specimens of *Raja* (Parker, 1885), an axial cord extends the entire length of the valvular intestine. In other sharks, as in *Isurus punctatus* (Garman, 1913, Fig. 3, pl. 58), and in other specimens of *Raja* (Parker, 1885), there is instead an axial tube. Both axial cord and axial tube occur, in *Chlamydoselachus*, in each individual specimen, where they are restricted to different parts of the valvular intestine. Thus in the valvular intestine of *Chlamydoselachus* there are combinations of features that almost always occur separately in other elasmobranchs. This affords a striking example of the structural comprehensiveness usually considered characteristic of the more archaic members of a phylum or class.

RECTUM AND RECTAL GLAND

In most elasmobranchs the portion of the digestive tube extending from the valvular intestine to the anal opening is differentiated into two parts, colon and rectum. In conformity with the usual practice I have distinguished two regions, colon (c.) and rectum (r.), in Text-figure 72; but these parts are much alike and there is no definite boundary between them, therefore I shall here consider the two regions, combined, under the term rectum.

The lengths, in my three specimens, are given in Table I, p. 412. It will be noticed that in specimen No. II the rectum is unusually long. In each specimen, the width of the rectum is about the same throughout its length, so that in ventral view it appears to be of uniform diameter; but when viewed from the side, the rectum appears somewhat funnel-shaped since it enlarges toward the anus. In specimen No. I the rectum is 9 mm. wide and has a dorsoventral diameter of 13 mm. at its cephalic end, 16 mm. at its middle, and 20 mm. at the anal end. Similar proportions are found in my other specimens. In specimen No. II the rectum is 6 mm. wide; its dorsoventral diameter is 10 mm. at the cephalic end, and 16 mm. at the anal end. In specimen No. III the width is 8 mm.; the dorsoventral diameter is 10 mm. at the cephalic end, and 18 mm. at the anal end. From these dimensions it is evident that in each case the rectum is laterally compressed, and dorsoventrally enlarged toward the anus. The anal opening faces both ventrad and caudad, so that it leads directly to the exterior and also into the cloaca. The wall of the rectum is from 1 to 2 mm. thick. The lining is cast into slight longitudinal folds which are more pronounced in specimen No. I. There is no mesorectum save the very small mesentery supporting the rectal gland, at the extreme caudal end of the rectum.

The rectal gland is a laterally compressed, somewhat kidney-shaped body situated in the angle between the rectum and the cloaca. In Text-figure 72 the rectal gland (r.g.) is shown turned toward the left. The dimensions in my three specimens are: No. I, 20 x 13 x 6 mm.; No. II, 18 x 14 x 7 mm.; No. III, 17 x 12 x 9 mm. The duct leads anteriorly and ventrally to open into the dorsal side of the rectum. In all three specimens the duct is 13 mm. long. The opening is distinctly visible on the inner surface of the rectum; it is guarded by a valve-like flap and readily admits a probe which passes easily into the rectal gland. In specimen No. I the opening is situated 20 mm. from the valvular intestine, just midway in the length of the rectum. In specimen No. II the opening is situated 40 mm. from the valvular intestine, also at the middle of the rectum. In specimen No. III the opening is situated 15 mm. from the valvular intestine and 25 mm. from the anus.

The proximity of the rectal gland to the cloaca has led to its being figured with the reproductive system. Thus Garman (1885.2) shows in his Fig. 2, pl. XIX (reproduced as my Text-figure 92, p. 440) an organ labeled "caecal pouch" which corresponds with what I have called the rectal gland. He does not describe its duct, but in his Fig. 3, pl. XIX a duct appears to open from this gland into the rectum. Günther (1887) figures a gland (my Figure 19, plate V) in the position of a rectal gland, and asserts that it opens

into the cloaca. Hawkes (1907) states that, in two specimens studied by her, the rectal gland opens into the rectum. It is so shown in her diagrammatic figure of the female cloacal region reproduced as Text-figure 90A, p. 435). The function of the rectal gland is unknown.

In *Heptanchus* (Daniel, 1934) the portion of the digestive tube between the valvular intestine and the anus is divided into two parts, colon and rectum. The two parts are much alike, but the form of the colon is slightly bulbous. The duct of the rectal gland reaches the wall of the rectum at its cephalic end, but does not enter here; it courses cephalad in the wall of the colon to enter the lumen at the caudal end of the valvular intestine.

THE DIGESTIVE TUBE AS A WHOLE

We have seen that the digestive tube of *Chlamydoselachus* is but slightly longer than the body cavity, and that all its parts, save only the valvular intestine, are more or less flaccid when empty. This leaves some doubt as to the precise form of the tube in its natural position, both when empty and when distended with food. In all my specimens the digestive tube is empty. In specimen No. I, which has a well-developed pyloric vestibule, there is an abrupt S-shaped fold of the pyloric vestibule and related portion of the cardiac stomach, in what appears to be the natural position of these organs. In specimen No. II, which has a shorter pyloric vestibule, the smaller fold in the same region cannot be straightened out. There are no other folds that appear to be of a permanent nature, but in all my specimens there is considerable irregular folding in the walls of the cardiac stomach. The question arises whether the distention of this organ with food would be sufficient to take up whatever "slack" exists in this region.

Table I gives the total length of the digestive tube, also the length of the body cavity excluding the small portions along the sides of the cloaca, in my three specimens. In specimen No. I the digestive tube is 100 mm. longer than the body cavity; in No. II it is 105 mm. longer; in No. III it is 203 mm. longer. In No. I and in No. III the recurrent course of the pyloric vestibule takes care of a small part of the excess length. It is probable that, in specimens I and II, when the cardiac stomach was fully distended with food the digestive tube became approximately straight; but the same statement could hardly apply to specimen No. III.

Günther (1887) writes of *Chlamydoselachus*: "The stomach is an extremely long cylindrical sack with thin walls; the short and narrow intestine, after having made a short and incomplete convolution, passes into the dilated portion which contains the spiral valve." I have found no evidence of folding of the intestine in any of my specimens, and it seems possible that the "short and incomplete convolution" mentioned by Günther really belonged to a pyloric vestibule. Collett (1897) states that the intestinal canal of his specimen is almost straight throughout its length, only the short duodenum being turned aside between the pylorus and the dilated portion with the spiral valve. Deinega's half-tone reproduction (1925, Fig. 1) of a drawing of the viscera *in situ* is printed on

unsuitable paper and details are obscure. The digestive tube appears as a nearly straight tube in which three main regions are recognizable; there is possibly a small convolution in the region of transition from stomach to intestine.

A continuous median dorsal mesentery, more fully described in the section on the urogenital system, supports the digestive tube of *Chlamydoselachus* throughout its length excepting the posterior four-fifths of the valvular intestine and the entire rectum. The rectal gland has a special mesentery which is evidently an isolated division of the dorsal mesentery. The mesentery supporting the common bile duct appears to be a ventral mesentery, but in my specimens it is considerably mutilated and some of its relations are obscure.

TABLE I

Length (in millimeters) of the digestive tube and its divisions in comparison with the total body length and the length of the body cavity anterior to the cloacal aperture, in three adult female specimens of *Chlamydoselachus*.

Specimen Number	Total Body Length	Esophagus and Cardia	Pyloric Vestibule	Pylorus	Bursa Entiana	Valvular Intestine	Colon and Rectum	Total Digestive Tube	Body Cavity
I	1350	330	35	33	36	190	40	664	564
II	1485	365	Absent	33	27	240	80	745	640
III	1550	440	25	25	43	230	40	803	600

THE LIVER

In my specimens II and III the liver is nearly all missing; but in No. I the liver is intact and (macroscopically) in an excellent state of preservation. Therefore my description is based entirely on a study of specimen No. I.

The liver of *Chlamydoselachus* (Text-figure 72) is a very large organ. It consists mainly of two lobes (*r.l.* and *l.l.*), one on each side of the body, extending the entire length (about 600 mm.) of the body cavity including the portions lateral to the cloaca. At their anterior ends, these lobes are continuous with the short unpaired portion of the liver which is median in position. The lobes are of equal size and alike in form save that there is a slight excavation near the distal end of the left lobe. Thus the form of the liver is decidedly symmetrical. Each lobe is flattened; the greatest width of a lobe is about 50 mm., but the thickness does not exceed 12 mm. In Text-figure 72 the lobes are shown in broad view, but in their natural position they would probably appear in an edge view. The unpaired portion of the liver is about 60 mm. wide, 55 mm. long, and 8 mm. thick; it is wrapped about the ventral and lateral surfaces of the esophagus. The gall bladder (*g.b.*) is 42 mm. long and 16 mm. wide. It is attached to the ventral and median surface of the unpaired portion of the liver, and projects slightly beyond its caudal margin.

A large duct, the common bile duct (*c.b.d.*), leaves the right lobe of the liver about 260 mm. from its anterior end to course within the ventral mesentery. Its course is shown in Text-figure 72; it empties into the pocket of the bursa entiana (*b.e.*). From the point where it leaves the right lobe of the liver, the duct was traced by palpation and dissection cephalad to the gall bladder. Its opening was found on the inside of the gall bladder, and a probe was passed through this opening into the duct. There is no duct visible at the surface, or leaving the surface, of the left lobe of the liver.

Gunther (1887) states that the liver of *Chlamydoselachus* consists of two extremely long lobes which reach backward to the end of the abdominal cavity, and anteriorly receive the gall bladder between them. Hawkes (1907) writes that the liver consists of right, left and median lobes. The gall bladder is situated in the median lobe. The length of the lobes necessitates their being doubled upon themselves. Evidently these statements are based on more than one specimen, for she writes that in one specimen the end of the left lobe was found lying on the right side of the body.

Of his 1910-mm. specimen of *Chlamydoselachus*, one of the largest ever taken, Collett (1897) writes that the liver was enormous. Two and one-half months after the death of the fish, when it had presumably lost considerable oil, this liver weighed 4250 grams. It consisted of two parallel and symmetrical lobes, the symphysis being 140 mm. long. Its total length was 950 mm.—nearly one-half the total length of the fish. The lobes were of equal thickness, and without side lobes except toward the end, where there was a small side flap. The height of each lobe was 100 mm., and the thickness 55 mm.; their upper (dorsal) edges were somewhat flattened, almost lamellar, while their lower (ventral) edges were smooth and rounded.

Deinaga (1925, Fig. 1) shows, rather indistinctly, a liver of *Chlamydoselachus* similar to the one I have described, save that the gall bladder is larger. In *Heptanchus* (Daniel, 1934, Fig. 119) the liver is constructed on the same general plan, but the lobes are shorter and relatively thicker than in *Chlamydoselachus*.

THE PANCREAS

In *Chlamydoselachus*, as in other sharks and in the embryos of higher vertebrates, there are two pancreases, dorsal and ventral respectively (Text-figure 72, *d.p.* and *v.p.*). The ventral pancreas is closely related to what appears to be a ventral mesentery, while the dorsal pancreas is supported by a special mesentery which seems to be a part of the dorsal mesentery. But in each of my specimens these mesenteries are considerably mutilated and the digestive tube is free to rotate. The dorsal pancreas is present in all my three specimens. The ventral pancreas is present in only two; in the other specimen, the absence of the ventral pancreas is evidently the result of mutilation. In my two specimens possessing a ventral pancreas, it is combined with an accessory spleen.

The dorsal pancreas is a flattened organ, irregular but somewhat triangular in shape, situated near the anterior part of the valvular intestine which it slightly overlaps, and

very close to the bursa entiana. In its natural position the dorsal pancreas tends to curl around these organs, but in Text-figure 72 it (*d.p.*) is shown displaced to the left and spread out flat. In my best-preserved specimen (No. I) the dorsal pancreas measures 45 x 25 x 2 mm. In my other specimens it is of approximately the same size, but is mutilated so that precise measurements are impossible. A piece of the dorsal pancreas from specimen No. I was removed for sectioning. Under the microscope the sections show, on one side, alveoli characteristic of a pancreas, but I was unable to identify the ducts. Considering that the material had been preserved for thirty years, the structure of the alveoli is surprisingly well preserved. On the other side of each section I found areolar tissue, blood vessels, cords of epithelioid cells and scattered epithelioid cells. This portion may possibly represent an organ of internal secretion.

In my specimens, the ventral pancreas is easily distinguished from the accessory spleen, to which it is closely attached, by a difference in color: the ventral pancreas, like the dorsal pancreas, is pale yellow, while the accessory spleen, like the spleen proper, is very dark. Together, the ventral pancreas and the accessory spleen form a slender, somewhat crescentic, slightly-flattened body whose approximate position is shown in Text-figure 72 (*v.p.* and *sp.* 2). In specimen No. I this duplex organ is 40 mm. long by 8 mm. wide at its widest level; in specimen No. II it is 70 mm. long by 10 mm. wide. The ventral pancreas and the accessory spleen are of equal length and width, and are united side-by-side; thus they appear as a single organ divided into two longitudinal zones. From specimen No. I, segments were cut from the light zone and the dark zone separately, and sections were prepared for microscopical examination. The light zone was found to be in a very poor state of preservation, but is undoubtedly glandular. It contains cords of epithelial cells, groups of cells which may represent alveoli, and cells arranged so as to give the appearance of ducts; also scattered epithelioid cells and many small blood vessels. A fairly large artery runs along one side of each section. The dark zone is in a much better state of preservation. It consists mainly of dense lymphoid tissue containing a multitude of leucocytes and many extravascular erythrocytes. These observations seem sufficient to identify the organ as a spleen.

From specimen No. II a segment extending entirely across the duplex organ (ventral pancreas and accessory spleen) was cut into transverse serial sections. The material is in poor condition for histological study, but one side of each section is undoubtedly pancreas, the other, spleen. Each organ has a connective tissue capsule. In places the two organs are connected by their capsules, in other places the capsules are separated by a cleft.

So far as I know, this combination of a ventral pancreas with an accessory spleen has not been observed in any other elasmobranch. In the teleost, *Gambusia patruelis*, the mingling of spleen and pancreas is described by Potter and Medlen (1935) from whose paper I quote as follows: "The typical histological structure of this organ [the spleen] is modified by the presence of pancreatic tissue. The pancreas is located in the mesen-

teries of the organs in this region, and it penetrates the substance of the spleen by following the blood vessels which supply this organ."

I was unable to find, by dissection, any undoubted pancreatic ducts. Such ducts are presumably present, unless they have disintegrated through long preservation of the material. Hawkes (1907) does not mention any pancreas in *Chlamydoselachus*, but describes a pancreatic duct which probably belongs to the dorsal pancreas since it opens into the valvular intestine where the spiral valve begins.

Collett's (1897) description of the pancreas in his specimen of *Chlamydoselachus* is interesting in that he speaks of dark and light portions of the pancreas. His description is quoted in full:

The pancreas consists of two large lobes, of which each is subdivided into an upper and lower portion, so that it really is in four divisions, of which the two hinder portions are lighter in color than the front ones. On the right side it forms, first, a short light-colored lobe, about 80 mm. long and 35 mm. broad. Anteriorly, it is almost entirely separated from a curved front portion, which is of darker hue than the hinder part. Posteriorly there also exists a lower portion, of a length of about 100 mm.; above this lies a darker-colored portion whose length is about 48 mm., which adjoins the hinder lighter part, and is connected with it.

Although Collett does not mention a spleen, it seems likely that the dark organs described by him are accessory spleens.

Deinaga's (1925) drawing (his Fig. 1) of the digestive system of *Chlamydoselachus* does not show any organ labeled pancreas, but his Fig. 2 is a drawing of a section of some tissue said to have been taken near the pancreas. In it he distinguishes blood vessels, fibers and cells. He suggests that it may be splenic tissue. Evidently this material was in a very poor state of preservation for microscopical study.

In *Heptanchus* (Daniel, 1934, Fig. 119) both dorsal and ventral pancreases are present and well developed. Their relations, as shown in this figure, appear to be much the same as in *Chlamydoselachus*. In another figure by Daniel (1934, Fig. 120) the names of the two divisions of the pancreas appear to have been interchanged.

ORGANS ASSOCIATED WITH THE DIGESTIVE TRACT

For convenience there are included in this section brief descriptions of two organs that are topographically related to the digestive system, but are not a part of it: the thyroid gland, which develops from the distal portion of a diverticulum from the floor of the pharynx; and the spleen, which has no developmental relation to any part of the digestive system.

THE THYROID GLAND

The position of the thyroid, attached to the ventral surface of the basihyoid cartilage, is shown in my Text-figure 26A, p. 361, after Goodey, 1910.1; also by Goodey (1910.2) in his Fig. 1; and by Allis (1923) in his Fig. 38, pl. XIV.

The thyroid of *Chlamydoselachus* is especially interesting because, in the adult, it sometimes retains a primitive or embryonic feature. Phylogenetically, the thyroid is

regarded as a derivative of a median trough-like fold, the endostyle, such as is found in the floor of the pharynx in *Amphioxus* and the ascidians. In all vertebrates in which the ontogenetic development of the thyroid has been studied, it arises in the embryo (*thr.*, Text-figure 62, p. 388) as an outpocketing from the floor of the pharynx. The distal portion of the outpocketing becomes the thyroid gland. The slender stalk persists for a time either as a hollow tube, the so-called thyroglossal duct, or as a solid cord; but eventually it degenerates and disappears. Goodey (1910.2) made the remarkable discovery, in an adult *Chlamydoselachus*, of a persistent thyroid duct (my Text-figure 74, *v.t.*) opening into the pharynx through a perforation in the basihyoid cartilage, and ending blindly where it comes into contact with the thyroid. This, of course, is not a functional duct; but it is comparable to the "thyroglossal duct" found in the embryos of many vertebrates. The so-called duct is lined with pharyngeal mucous membrane in which are numerous incompletely developed pharyngeal denticles.



Text-figure 74.

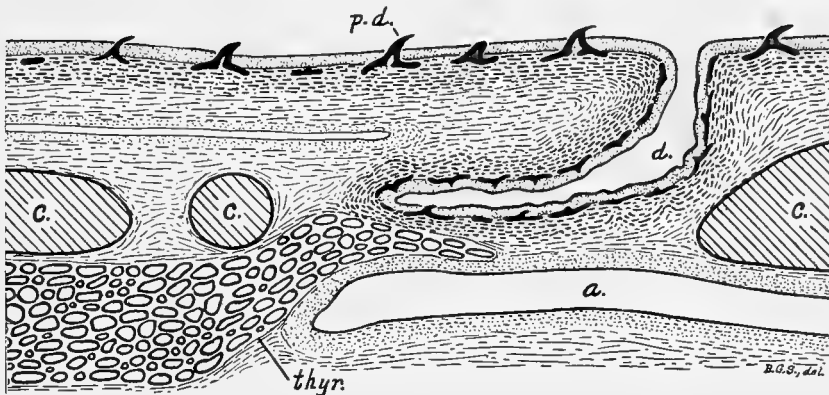
Sagittal section (x 15) through the thyroid gland and persistent thyroglossal duct of an adult *Chlamydoselachus*.

b.v., blood vessels; *d.*, denticles; *e.*, enamel organ; *fo.*, follicles; *l.t.*, lumen of tube; *v.t.*, vestigial tube (thyroglossal duct).

After Goodey, 1910.2, Fig. 2.

Since Goodey's account of the thyroglossal duct of *Chlamydoselachus* appears to be based on a single specimen, I have thought it worth while to investigate the possible occurrence of such a duct in the four large specimens at my disposal. From each specimen the thyroid was excised together with a large block of surrounding tissues including a portion of the basihyoid cartilage and the lining of the pharynx. The material was partially decalcified, then imbedded in celloidin and cut into serial sagittal sections. In each case the series extended completely through the large foramen in the basihyoid overlying the thyroid. In one case only (specimen No. I) there were two foramina; the anterior foramen is very small. This specimen, No. I, is the only one in which a thyroglossal duct was found (Text-figure 75, *d.*), and this duct lies within the posterior and larger foramen. In specimens III and IV, a thyroglossal duct is demonstrably absent. In specimen No. II the material is in such poor condition that neither the presence nor the absence of a duct could be determined.

In the series of sections from specimen No. I, the lumen of the thyroglossal duct is slightly tortuous, so that the continuity of the duct cannot be demonstrated in any single section. Text-figure 75, representing the thyroglossal duct, is a reconstruction from forty successive sections, each about 20 microns thick, and is slightly diagrammatic. The total thickness of the sections used in this reconstruction is about 800 microns

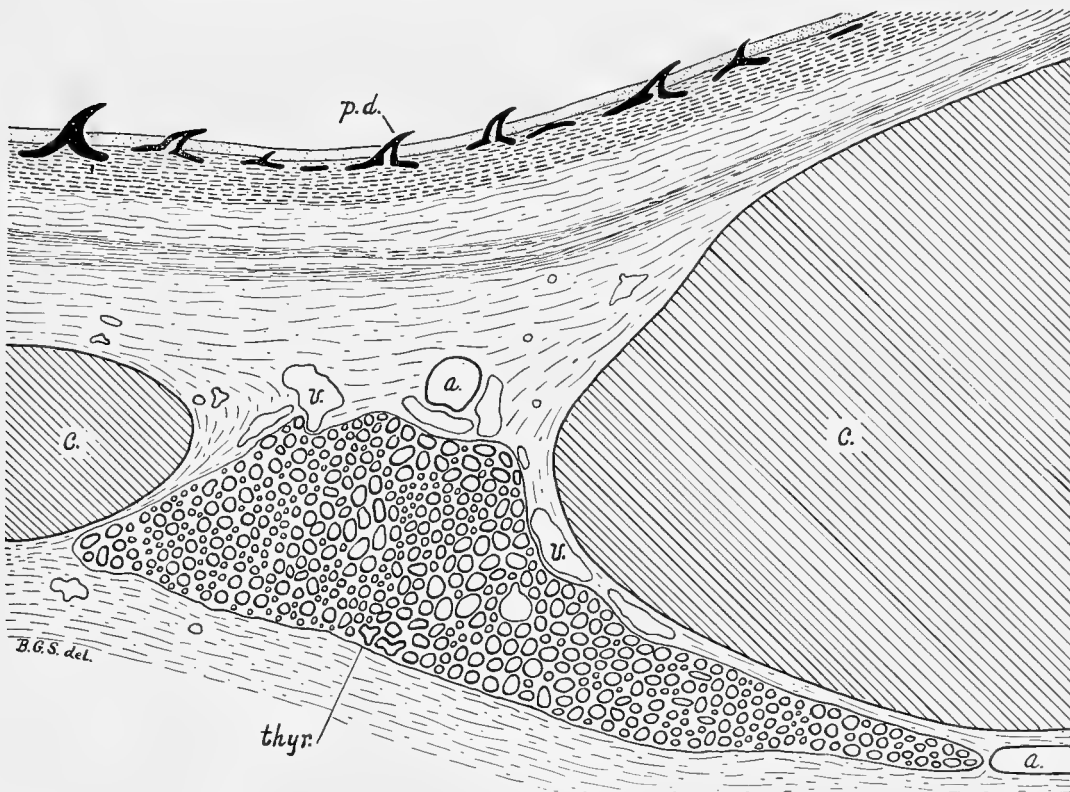


Text-figure 75.

Median sagittal section (x 12) showing thyroid gland and thyroglossal duct of an adult *Chlamydoselachus*.

a., artery; c., basihyoid cartilage; d., thyroglossal duct; p.d., pharyngeal denticle; thyr., thyroid gland.

Drawn from Specimen No. I in the collection of the American Museum of Natural History.



Text-figure 76.

Median sagittal section (x 10) showing thyroid gland of an adult *Chlamydoselachus* in which there was no thyroglossal duct.

a., artery; c., basihyoid cartilage; p. d., pharyngeal denticle; thyr., thyroid; v., vein.

Drawn from Specimen No. III in the collection of the American Museum of Natural History.

(less than a millimeter). The finer structure of this specimen is rather poorly preserved, but permits of the following observations. The duct (d.) is lined with stratified squamous epithelium continuous with the epithelial lining of the pharynx. The outer layer of the duct consists of a thick layer of dense connective tissue continuous with a similar layer comprising the deeper portion of the mucous membrane of the pharynx. Between the epithelium of the duct and its connective tissue layer, there are many calcifications having the form of rudimentary denticles. These are smaller than the fully developed denticles (p.d.) that occur in the lining of the pharynx. The distal end of the duct ends blindly in close contact with the thyroid (thyr.).

Text-figure 76 is a drawing of the thyroid of one of my specimens (No. III) in which a thyroglossal duct is absent. The histological condition of this material, also, is rather poor, but the topographical relations are well shown. Upon comparing Text-figures 76 and 75, it will be seen that in specimens I and III the position of the main mass of the thyroid (thyr.) with respect to the large foramen in the basihyoid cartilage (c.) is not quite the same.

In specimen No. IV a large part of the thyroid was cut away in trimming the block preparatory to imbedding, but in the remaining portion the finer structure is well preserved. While the simple cuboidal epithelium of the follicles is in good condition, the lumens of the follicles appear empty, as they do in the other specimens. In the sections of No. IV, the pharyngeal denticles are beautifully shown. In all the sections, the epithelial lining of the pharynx is very poorly preserved. Fundamentally, it is stratified epithelium, but it contains many unusually large pale cells, singly or in groups, which are probably mucous cells.

In *Heptanchus* (Daniel, 1934, p. 123) the thyroid gland is located "at the symphysis of the lower jaws between the coracomandibularis and coracohyoideus muscles." Ferguson (1911), after studying many species of elasmobranchs, states that "The [thyroid] gland rests upon the basihyal cartilage whose anterior margin forms an excellent guide to its location." His paper deals with the histological structure as well as the form and gross anatomical relations of the thyroid in elasmobranchs, and includes a description of the blood vessels supplying the thyroid. In *Scyllium catulus* and in *S. canicula* (Goodey, 1910.2), the thyroid gland is situated close to a foramen in the basihyoid cartilage. In both species of *Scyllium* the connective tissue investment of the thyroid extends into the foramen as a plug containing, in some instances, a small amount of thyroid tissue, and in one instance, a problematical duct. So far as our present knowledge extends, *Chlamydoselachus* is the only vertebrate possessing, at least occasionally, a persistent thyroglossal duct.

THE SPLEEN

In *Chlamydoselachus* the spleen proper (Text-figure 72, sp.1) is a very elongate, somewhat comma-shaped, flattened organ lying in the dorsal mesentery at the level of the pylorus, pyloric vestibule, and caudal end of the cardiac stomach. In its natural

position it is probably somewhat coiled about these portions of the digestive tube, but in Text-figure 72 it is shown displaced to the left. The color of the spleen, in my preserved specimens, is a very dark bluish-gray. In my specimen No. I the spleen measures 80 x 10 x 3 mm.; in No. II, 60 x 10 x 4 mm.; in No. III the spleen could not be found and had evidently been torn away.

From specimen No. I, a transverse segment of the spleen was removed for sectioning. Under the microscope the sections were found to consist mainly of lymphoid tissue containing an abundance of leucocytes and many extravascular erythrocytes; small arteries and veins were distinguishable. In its finer structure the spleen proper is very much like the accessory spleen already described in association with the ventral pancreas.

Hawkes (1907) states that the spleen of *Chlamydoselachus* is divided into two parts which are separated by a space of 40 mm. The additional "lobe" (which is apparently comparable to what I have called the accessory spleen) is situated to the right of the stomach and somewhat dorsally. It is an ovoid body, 30 mm. long and nearly 20 mm. broad in its widest part, and is situated between the stomach and a fold of mesentery which supports the latter. The other part or spleen proper lies in the usual place at the angle of the stomach. The spleen proper, when examined by a low-power lens, presents the usual appearance; but the additional "lobe" is much more compact. Hawkes does not mention a pancreas in association with the secondary spleen.

In *Chlamydoselachus*, Deinega (1925, Fig. 1) shows, indistinctly, an organ labeled spleen, which appears to be on the right side of the body since it is crossed by the common bile duct on its way from the right lobe of the liver to the intestine. In *Heptanchus*, the spleen (Daniel, 1934, Figs. 119 and 120) is much more extensive, and is broken up into several different parts or "lobes."

In concluding this section I note that the digestive system of *Chlamydoselachus* presents the following features of especial interest: (1) The great variability in the region of transition from stomach to intestine; (2) the differentiation of the coils of the spiral valve into two series, with apices facing in different directions; (3) the presence of an axial strand in the middle portion of the valvular intestine, along with an axial tube in both anterior and posterior portions; (4) the great length of the lobes of the liver, in adaptation to the form of the body; (5) variations in the position of the opening of the common bile duct into the intestine; and (6) the presence of an accessory spleen associated with the ventral pancreas. In some specimens, there is (7) a persistent thyroglossal duct which is lined with stratified squamous epithelium and which possesses rudimentary denticles.

THE RESPIRATORY ORGANS

In *Chlamydoselachus*, as in other fishes, the gill-filaments and their lamellae are the primary organs of respiration. Accessory structures such as the branchial skeleton and musculature, the oral breathing valve and the valvular gill-folds or gill-flaps, are concerned

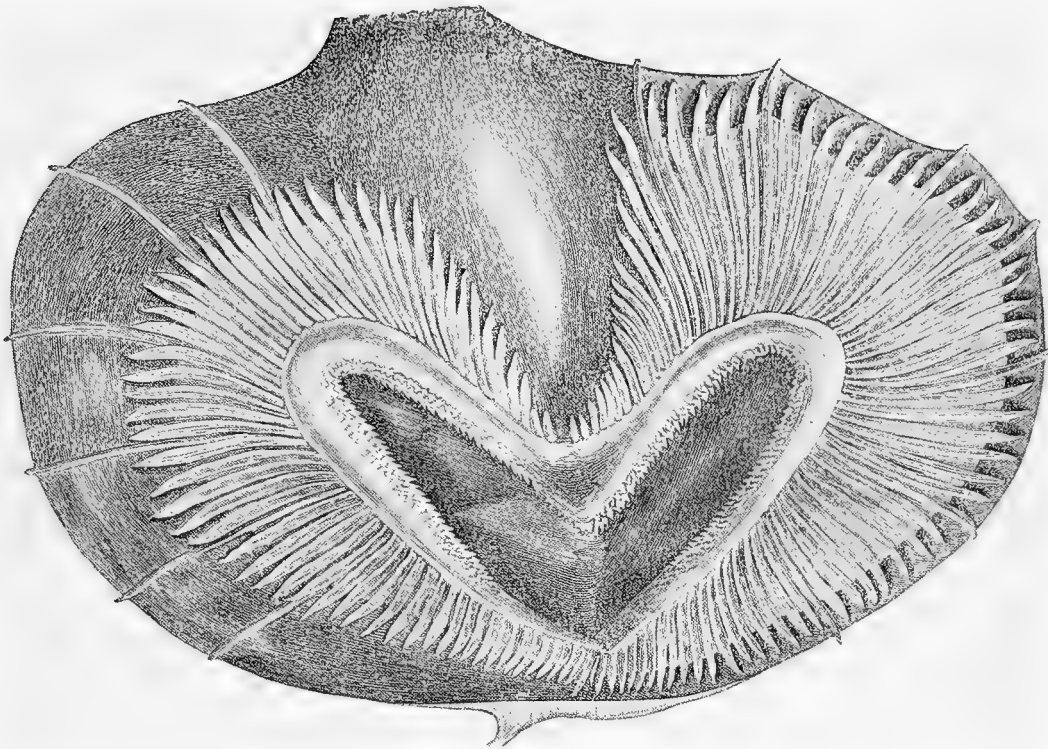
with regulating the passage of water, subservient to respiration, through the mouth into the pharynx and out through the gill-clefts. When the spiracular canal and external spiracular orifices of *Chlamydoselachus* are sufficiently large, doubtless a little water is expelled through the spiracles. The oral breathing valve, the external openings of the spiracles, and the gill-flaps have been described by Gudger and Smith (1933). In the present paper I have already described the skeleton and muscles of the oral and pharyngeal region, and have noted the absence of a true spiracular cartilage. It remains to describe the gill-filaments in relation to their supporting structures—in other words, the gills—and to complete the description of the spiracles. The blood vessels of the gills are described in the section on the blood-vascular system. My own observations and drawings of the respiratory system of *Chlamydoselachus* are based on the three large specimens in the collection of the American Museum of Natural History, and a fourth large specimen kindly lent by Dr. E. Grace White.

THE GILLS

From the descriptions and illustrations in the article by Gudger and Smith (1933) it is apparent that the gill-clefts of *Chlamydoselachus* are unusually large in proportion to the size of the body. Some idea of the size of these clefts may be obtained from Text-figures 4 (p. 339) and 77. Of his specimen Garman (1885.2) writes: "The gill-openings are large; the first, when extended, will admit an object of four inches or more, and the last will take one of two inches in width." In my specimen No. I, which is 1350 mm. long (rather small for an adult), I find that the first gill-cleft (the one between the hyoid arch and the first branchial arch) will admit the fingers and thumb of an entire hand; the second, the four fingers as far as the palm; the third, the tips of four fingers; the fourth, three fingers; the fifth, two large fingers; and the sixth, a thumb. These crude measurements are sufficient to show the approximate size of the gill-clefts and the rapid decrease in their size posteriorly.

Garman's (1885.2) drawing (my Text-figure 77) of a gill-cleft and related structures represents the fourth gill-opening on the right side. I have oriented the reproduction of Garman's figure with the dorsal side uppermost; this brings the anterior holobranch to the right.

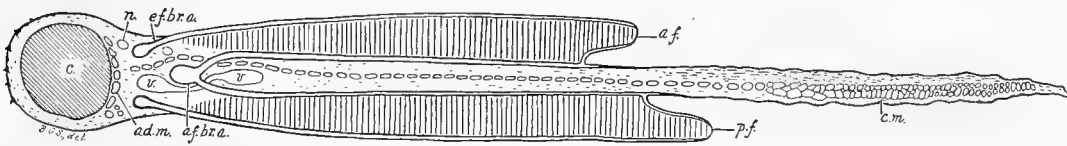
Each gill-arch of *Chlamydoselachus* affords attachment, distally, to one edge of a crescentic plate, the gill-septum. The framework of the gill-arches is supplied by the cartilaginous branchial arches, while the gill-septa are strengthened by very slender radially directed cartilaginous rods, the branchial rays. Each branchial ray begins in contact with the cartilaginous branchial arch and extends to the extreme edge of the gill-septum, where it may cause a slight projection of the overlying membrane. In places the margin of the gill-septum is strengthened by a delicate extrabranchial cartilage. On each side of a gill-septum there are long narrow primary folds, the gill-filaments, extending in a radial direction from the base of the gill-septum toward its margin (Text-figure 77; Text-figure 78, *a.f.* and *p.f.*). On each broad surface of a gill-filament there are



Text-figure 77.

The fourth gill-opening on the right side of a specimen of *Chlamydoselachus anguineus*, with the gills spread apart to display the gill-filaments and branchial rays. The uppermost side of the figure is dorsal, the right side anterior.

After Garman, 1885.2, Plate V.



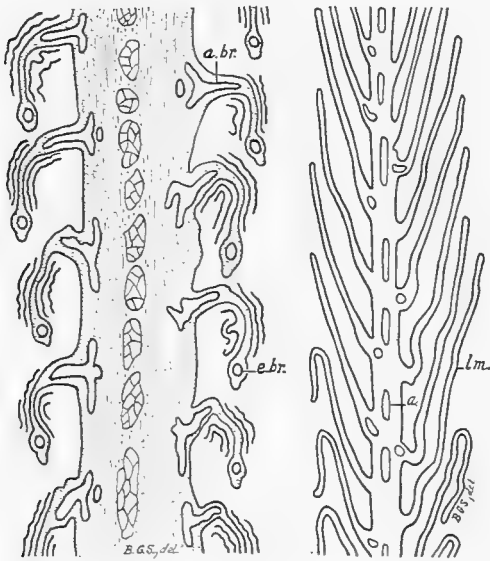
Text-figure 78.

Radial section (x4) of a gill of *Chlamydoselachus*, partly diagrammatic. The lines extending across each filament indicate the sites of attachment of the lamellae on one surface of the filament. The number of lamellae shown is approximately the actual number found in sections through the ventral portion of the gill of the first branchial arch on the right side of Specimen No. I.

ad.m., adductor branchialis muscle; *a.f.*, anterior filament; *af.br.a.*, afferent branchial artery; *c.*, cartilage of the gill-arch; *c.m.*, superficial constrictor muscle of the gill-flap, continuous with the thinner interbranchial muscle of the gill-septum; *ef.br.a.*, efferent branchial arteriole; *n.*, nerve; *p.f.*, posterior filament; *v.*, vein, presumably draining the small blood vessels of the gill-septum.

Based on drawings of serial sections from two specimens in the American Museum of Natural History.

transverse secondary folds or lamellae (Text-figures 78, 79, 80 *lm.*) too small for ordinary observation. Goodrich (1930) and some others apply the term lamella to the structure that I have called a filament, and designate as "secondary lamellae" the small leaf-like folds that I have called simply lamellae. In my specimens, the distal end of a gill-filament is free for a distance of from 3 to 8 mm.; the gill-filaments never reach the distal edge of the septum, but leave a smooth outer portion (from one-fourth to one-half of the entire surface of the septum) constituting the gill-flap or gill-fold. Successive gill-flaps overlap like the shingles on a roof. In addition to affording protection to the delicate gills, they function as respiratory valves.



Text-figure 79.

Text-figure 80.

Sections showing filaments and lamellae of a gill of *Chlamydoselachus*.

Text-figure 79. Portion of a section ($\times 12$) through the ventral part of the gill of the fourth arch on the right side, cut transversely to the filaments.

a.br., afferent branchial arteriole; *e.br.*, efferent branchial arteriole.

Drawn from a section of a gill from a specimen lent by Dr. E. Grace White.

Text-figure 80. Outline of a portion of a section ($\times 36$) taken lengthwise of a gill-filament, in the ventral part of the gill of the first arch on the right side. The upper end of the figure is distal.

a., arteriole; *lm.*, lamella.

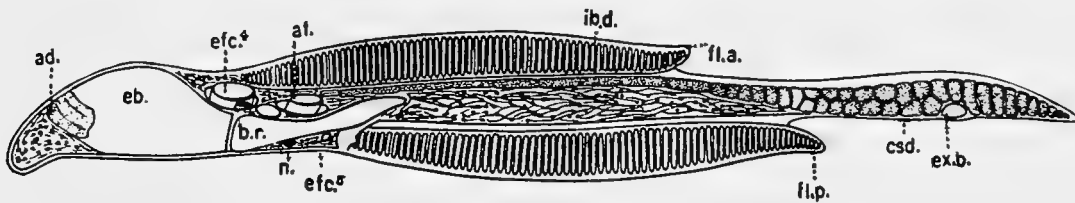
Drawn from a specimen in the American Museum of Natural History.

All the gill-filaments between two successive gill-clefts, together with the structures supporting these gill-filaments, constitute a holobranch or entire gill. One of these is shown, in a radial section cutting lengthwise of the filaments, in Text-figure 78. The filaments on one side of a gill-septum constitute a demibranch or half-gill. There is a demibranch on both sides of each gill-cleft of *Chlamydoselachus*, excepting the posterior side of the sixth or last gill-slit. In my specimens, as in Garman's figure, the filaments on the anterior side of a gill-cleft are always longer than those on the posterior side. In other words, the filaments of a posterior demibranch (posterior with reference to the septum, not to the gill-cleft) are always longer than those of the anterior demibranch of the same gill. Further, the filaments on both sides of the first gill-cleft are distinctly shorter than those in corresponding positions with reference to the other gill-clefts. Since the close-set filaments, all bearing numerous lamellae, of each demibranch are distributed along the entire length of each gill and extend, on the average, considerably more than halfway from the base of the septum to its free edge, it is apparent that the respiratory

surface is very large—perhaps larger, in proportion to body size, than in most elasmobranchs. The blood vessels of the gills are described in the section on the blood-vascular system, but it may be noted here that, thin as they are, the lamellae nevertheless contain exceedingly rich capillary plexuses.

The general plan of a gill of *Chlamydoselachus* is much like that of *Heptanchus* (Text-figure 81, which should be compared with Text-figure 78). Indeed, so far as the gills of elasmobranchs have been studied, there is a considerable degree of uniformity in their structure throughout the group.

From my observations I conclude that the gills of *Chlamydoselachus* are of the usual elasmobranch type. In proportion to body size, the gill-clefts are unusually long (Text-figure 4); they are separated by very slender branchial arches. The widely-distensible



Text-figure 81.

Section, cutting parallel to branchial filaments, through second holobranch of *Heptanchus maculatus*.

ad., adductor muscle; af., third afferent artery; b.r., branchial ray cut short; csd., fourth dorsal constrictor muscle; eb., epibranchial segment of cartilaginous branchial arch; efc.4-5, fourth and fifth efferent collector arteries; ex.b., extrabranchial cartilage; fl.a., anterior filament; fl.p., posterior filament; ib.d., dorsal interbranchial muscle; n., posterior division of the branchial nerve.

After Daniel, 1934, Fig. 143.

pharynx is adapted for the rapid expulsion of a large volume of water through the gill-clefts. This, in connection with the large respiratory surface afforded by the gill-filaments and particularly by their lamellae, makes an efficient mechanism for aerating the blood.

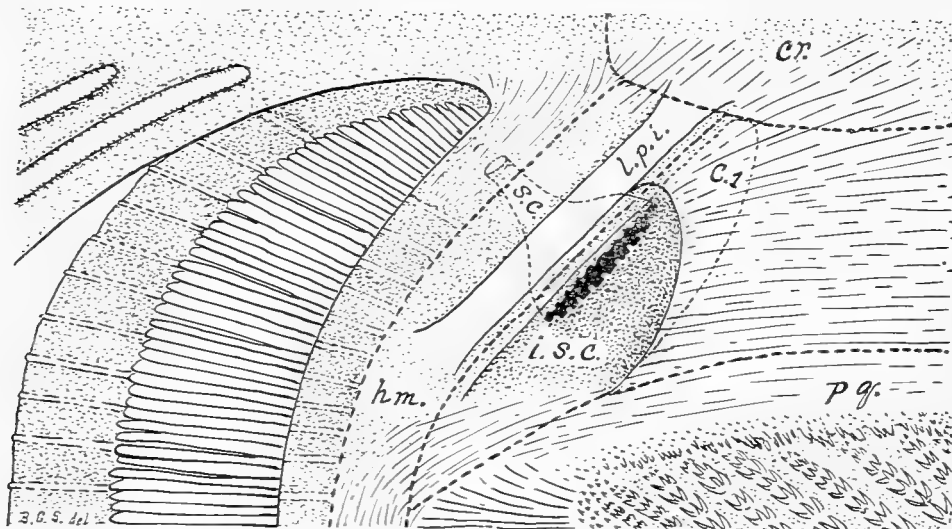
A discussion of the question as to the phylogenetic significance of the unusually large number of gill-clefts and gill-arches in *Chlamydoselachus* and the notidanids would lead us too far afield. Considerable data regarding the number of gill-clefts, from *Amphioxus* through the cyclostomes and fishes to the amphibian *Cryptobranchius*, is presented by Corrington (1930, pp. 246-251), together with a discussion of the subject from an evolutionary point of view.

THE SPIRACLES

The spiracles of elasmobranchs derive special interest from the fact that they arise through modifications of a primitive first pair of gill-slits (Text-figure 62, p. 388) which, in mammals, are represented by Eustachian tubes, tympanic cavities and external auditory meatuses. In elasmobranchs the modifications are almost entirely concerned with the regulation of the respiratory current, but the anatomical relations of certain parts presage their use in connection with organs of hearing.

The following description of the spiracles of *Chlamydoselachus* is based on my four adult specimens, numbered I to IV respectively, of which the first three were dissected by me and the fourth was studied without dissection.

The external spiracular apertures are ordinarily very small (Text-figures 70, p. 396; and 124, p. 489). With one exception to be described presently, they are mere slits, from 1 to 3 mm. long. In my four specimens each aperture is situated in line with the



Text-figure 82.

Left internal spiracular aperture and cavity ($\times 1.5$) of *Chlamydoselachus*. The boundaries of the cranium, hyomandibular, palatoquadrate, caecum and spiracular canal are indicated by broken lines.

c.1., caecum; cr., cranium; hm., hyomandibular cartilage; i.s.c., internal spiracular aperture and cavity; l.p.i., ligamentum postspiracular inferior; p.q., palatoquadrate cartilage (upper jaw); s.c., spiracular canal.

Drawn from specimen No. I in the collection of the American Museum of Natural History.

spiracular division of the sensory canal system (Text-figure 124, p. 489), about 8 mm. from its anterodorsal end. In each case, the direction of the long axis of the slit-like aperture coincides with that of the laterosensory canal. The lengths of the apertures in our four specimens are as follows: No. I, 3 mm. on each side; No. II, 2 mm. on the right side and 7 mm. on the left; No. III, 2 mm. on the right side and 1 mm. on the left; No. IV, 3 mm. on the right side and 2 mm. on the left. The exceptionally large aperture on the left side of No. II is not a slit, but an elliptical opening fully three millimeters wide. The unusually small opening on the left side of No. III could not be found until a bristle had been inserted by way of the internal opening. It was overlooked entirely by Gudger and Smith (1933) who also failed to identify as a spiracular opening the exceptionally large aperture on the left side of No. II, mistaking it for a perforation made by a hook.

Each internal spiracular aperture or cavity (i.s.c.) is situated, in series with the gill-slits, between the hyomandibular cartilage and the palatoquadrate (Text-figure 82,

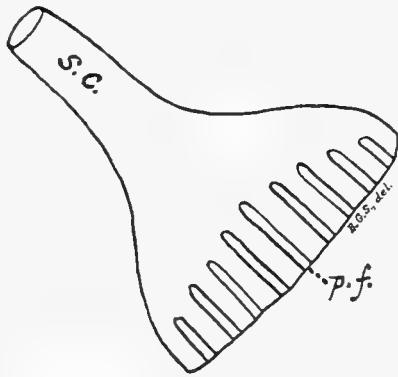
hm., pq.). In my four specimens these openings are very much alike. They measure about 20 to 25 mm. long and are about 12 mm. wide when the pharynx is fully expanded. Thus each internal spiracular aperture (i.s.c.) is large enough to admit a small finger. Its posteromedial and anterolateral margins are well defined; they converge toward the cranium and, when the pharynx is expanded, have the form of a furcula or "wishbone." The posteromedial margin is formed by a prominent ridge where a fold of the mucous membrane overlies a ligament (ligamentum postspiraculare inferior) extending along the ventral surface of the hyomandibular cartilage and connecting it with the cranium. The anterolateral margin is formed by a valve-like fold or flap of the mucous membrane. There is no very definite ventrolateral margin, for here the inner surface of the pharynx slopes gradually into the spiracular cavity. This side lies toward the palatoquadrate. When the pharynx contracts, the posteromedial and anterolateral margins of the internal spiracular aperture approximate until the opening is reduced to a mere slit compressed between the hyomandibular and palatoquadrate cartilages. No doubt the opening may be completely closed by the contraction of the pharynx, but this can occur only after most of the water has been expelled from the pharynx.

Each internal spiracular aperture leads into a broad cavity or sac, the internal spiracular cavity (Text-figure 82, i.s.c.), which is no wider than its internal opening and is about 7 mm. deep in its deepest portion. The roof of this cavity lies in close proximity to the integument. By palpation I found that the overlying plate of tissues, covering not only the deeper portion of the cavity but also its sloping side toward the palatoquadrate (Text-figure 82, p.q.), is decidedly thin. Evidently, it comprises little more than integument and mucous membrane which come almost into apposition. In its structure and in some of its relations this plate or membrane bears considerable resemblance to the tympanic membrane of an amphibian. However, this membrane is evidently not homologous with the structure described by Howes (1883) as the tympanic membrane in *Raja*. Forming the anteromedial end of the internal spiracular cavity, beneath a flap of mucous membrane, there is a pocket or caecum (c.1) which extends alongside the hyomandibular in an anteromedial direction for a distance of about 10 mm. Its distal end usually comes into contact with the auditory capsule of the cranium—a relation which is most interesting when we compare the internal spiracular cavity of *Chlamydoselachus* with the tympanic cavity of higher vertebrates. In three instances, I found in this caecum a large gelatinous mass, almost cartilaginous in consistency, which was easily removed.

Before proceeding with the further description of the spiracle in my specimens I quote the following from Goodey (1910.1, p. 550), who appears to be the only author who has given any special attention to the spiracles of *Chlamydoselachus*:

On removing the skin [of *Chlamydoselachus*] and carefully dissecting away the underlying spongy cutis which covers the jaw muscles, it is seen that the lumen of the spiracle passes down into the oral cavity between the hyomandibular and the mandibular [sic] cartilages. Just inside the external opening, the cavity becomes enlarged and a short caecal

diverticulum is given off anteriorly. This is overlaid by the levator maxillae muscle . . . The caecum extends as far forward as the anterior knob of the proximal end of the hyomandibular, which projects from the articular depression on the auditory capsule. It is not attached to the hyomandibular, but is separated from it by the hyoidean branch of the seventh nerve, which passes just internal and ventral to it. In all probability it is homologous with the more extensive caeca mentioned by Ridewood (1896) which have been described in other selachians by Müller and Van Bemmelen. In *Scyllium*, for example, the caecum extends inwards over the hyomandibular and becomes firmly attached to the wall of the auditory capsule, being in some way concerned with the function of hearing. A similar caecum is found in *Heptanchus*, so that here we have another point in which *Chlamydoselachus* differs from this member of the Notidanidae.



Text-figure 83.

Anterolateral wall of the left pseudobranchial chamber and peripheral wall of the spiracular canal (x 3) of *Chlamydoselachus*, represented in one plane.

p.f., pseudobranchial filament; s.c., spiracular canal.

Drawn from specimen No. I in the collection of the American Museum of Natural History.

Along the posteromedial side of the deeper portion of the internal spiracular cavity, close to the hyomandibular, there is a narrow cleft with tumid lips, about 13 mm. long and 5 mm. deep. This cleft (solidly black in Text-figure 82) is the pseudobranchial chamber. The anterolateral lip is decidedly serrate, the posteromedial lip is slightly serrate. The pseudobranchial chamber will be further described presently.

There is some variation in the manner in which the pseudobranchial chamber communicates with the external spiracular aperture. In specimen No. I, on the left side, a bristle inserted into the pseudobranchial chamber, anywhere along its length, passes posteromedially through a slit-like aperture into the spiracular canal (s.c. in Text-figures 82 and 83) which is compressed between the hyomandibular and the integument. The spiracular canal becomes narrower as it approaches the external spiracular aperture. On the right side, the pseudobranchial chamber communicates with the narrow spiracular canal only by way of a small round opening situated at the posterolateral end of the pseudobranchial chamber. In specimen No. II, on the left side, the external spiracular aperture is exceptionally large and leads directly into the pseudobranchial chamber. On the right side, the spiracular canal is like that on the left side of No. I. In specimen No. III, which has unusually small external spiracular apertures, each pseudobranchial chamber opens into the slender spiracular canal by means of a very small aperture situated as it is on the right side of No. I. Thus I find, in my specimens, decided differences in the size of the spiracular canal in the region where it communicates with the pseudo-

branchial chamber: and in one case, which I regard as anomalous since the external spiracular opening is very much larger than the others, the spiracular canal is absent.

In specimen No. I a bristle inserted into either external spiracular opening passes anterolaterally, within the spiracular canal, to enter the pseudobranchial chamber. The distance from the external spiracular aperture to the pseudobranchial chamber is about 10 mm., on each side. In specimen No. II, on the right side, a bristle inserted into the spiracular canal by way of the external spiracular aperture travels about the same distance and in a similar direction, before reaching the pseudobranchial chamber. In specimen No. III, on either side, only a very slender bristle could be inserted by way of the external spiracular aperture, and this passed directly forward for a distance of about 5 mm. before entering the pseudobranchial cavity. By dissection I have opened the spiracular canals of specimens I, II, and III without finding anything of interest save a confirmation of my description based on exploration with a bristle. Their walls are smooth.

The spiracular canal always lies just beneath the integument. Thus the external spiracular aperture is bordered, on the side toward the canal, by a somewhat flexible lip. In cases where the external opening is large enough to allow the passage of an appreciable amount of water, this lip may function as a valve preventing the intake of water through the spiracle while the pharynx is expanding. In my four preserved specimens the entire spiracular canal is very much flattened, since it is compressed between the hyomandibular cartilage and the integument.

In the free-swimming sharks, the spiracles are not so highly specialized for purposes of respiration as in the skates and rays, which are bottom-dwelling forms. Concerning the function of the spiracles, Daniel (1934, p. 156) writes as follows:

In the free-swimming sharks the current enters the mouth, from which it passes into the pharynx and into the gill-pockets, the external clefts, including the spiracle, at the same time remaining closed. The mouth then closes, the external clefts open, and the water is forced out.

In the rays, which spend most of their time at the bottom and hence often in mud or sand, there is an interesting change in the direction of the current. In these the greater part of the current enters through the [large] spiracles and but little through the mouth. The valves of the spiracles then close and the water is forced out ventrally through the external branchial clefts. At the expulsion of the water the mouth does not entirely close, but only a little of the water is able to gain exit through it because of valves which are located on its roof and floor.

In *Squatina*, a bottom-dwelling shark, the respiratory current is known to enter through the spiracles (Darbishire, 1907), though not exclusively (Daniel, 1934). From my observations on the structure of the spiracle in *Chlamydoselachus* it is obvious that this organ normally functions as in the free-swimming sharks and not as in *Squatina*. From the small size of the external spiracular openings in *Chlamydoselachus* it is evident that very little water passes through them.

In elasmobranchs the spiracle ordinarily differs from the gill-slits in never possessing gill-filaments, though it often has traces of these as a few small folds of the lining of its anterior wall, which constitute the pseudobranch or mandibular gill. Allis (1923, p. 169) mentions pseudobranchial filaments in the "spiracular canal" of *Chlamydoselachus*, but does not describe them. Goodey (1910.1, p. 550) writes of his specimens of *Chlamydoselachus*: "The pseudobranch in each spiracle consists of about ten short ridges, which lie on the anterior outer wall just inside the external aperture. In the Notidanidae the pseudobranchs are said to be better developed than in any of the [other] selachians, so that in this respect we find *Chlamydoselachus* presenting a small difference from *Heptanchus* and *Hexanchus*."

In my specimens I have distinguished a special chamber communicating with the internal spiracular cavity (i.s.c.) on the one hand and the spiracular canal (s.c.) on the other, which I call the pseudobranchial chamber (Text-figures 82 and 83). This chamber presents for examination two surfaces, anterolateral and posteromedial respectively. In specimen No. I each surface is about 13 mm. long (measured on the side toward the internal spiracular cavity) and 5 mm. wide (measured from the internal spiracular cavity to the beginning of the spiracular canal). Toward the internal spiracular cavity each of these surfaces is bounded by a distinct ridge or lip, decidedly serrate in the case of the anterolateral lip, only slightly so in the case of the posteromedial lip. The peripheral boundary is not so well defined, save in those cases where the two surfaces meet on the side toward the integument, leaving only a small round aperture leading from the posterolateral end of the pseudobranchial chamber into the spiracular canal. In cases where the passage into the spiracular canal is large (as shown in Text-figures 82 and 83) the boundary between this chamber and the spiracular canal may be defined as the line where an abrupt change in direction occurs—for the pseudobranchial chamber lies along the anterolateral surface of the hyomandibular, the spiracular canal along its peripheral surface.

On the anterolateral wall or surface of the pseudobranchial chamber, the pseudobranchial filaments (Text-figure 83, *p.f.*) begin at regular intervals along the serrate lip and extend peripherally for a distance varying from 2 to 5 mm. The serrations correspond to the filaments—that is, the projections, which appear tooth-like when the lips of the pseudobranchial chamber are approximated, are seen to be the proximal ends of the folds or filaments when the chamber is opened to view. The pseudobranchial filaments are little more than mere ridges; the height of these filaments seldom exceeds 1 mm. and is never more than 1.5 mm. The longest filaments are usually those near the middle of the row. Some of the filaments—particularly those of the left pseudobranchial chamber of specimen No. II, which has the largest filaments—are free at their peripheral ends, where they project as finger-shaped structures as in the case of ordinary gill-filaments. The number of filaments composing each pseudobranch varies from eight to sixteen.

So far as I know, a pseudobranch on the posteromedial surface of the pseudobranchial chamber has never been described in any elasmobranch. Nevertheless I find, on this

surface in some spiracles of my specimens, structures which may be vestiges of gill-filaments. These structures are low ridges, soft when palpated but not disappearing entirely when the mucous membrane is stretched at right angles to their long axes. They are spaced regularly, like gill-filaments. In number, position, length and direction they resemble the pseudobranchial filaments on the opposite side of the pseudobranchial chamber, but they are usually broader and are never so high. I suspect that if fresh specimens were available, the presence of vestigial gill-filaments on the posteromedial wall of the pseudobranchial chamber could be conclusively demonstrated.

A pit or depression representing the ventral end of a primitive gill-cleft extending between the hyoid and mandibular arches has been described by Ridewood (1896) in *Galeus*, *Carcharias*, *Zygaena*, *Triacis* and *Chiloscyllium*. It is faintly marked in *Mustelus*, but is absent in *Scyllium*, *Notidanus* and *Acanthias*. Concerning this pit or depression Ridewood writes as follows:

If a line be drawn joining the lower ends of the pharyngeal apertures of the branchial clefts, it will pass through the lower or anterior extremity of the pit, just as a curved line joining the upper ends of the branchial clefts will, if produced, pass through the inner or superior edge of the pharyngeal aperture of the spiracle. It is universally admitted that the spiracle of sharks represents only the upper part of the hyoid cleft, the middle and lower portions being obliterated. Hence, in this depression of the mucous membrane, is a structure which, in complete absence of evidence to the contrary, may be regarded as the internal or pharyngeal portion of the lower half of the hyoid cleft.

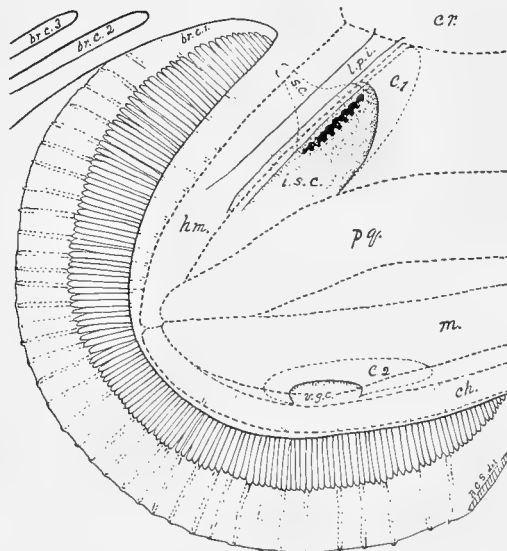
In my four adult specimens of *Chlamydoselachus* I found, on each side of the floor of the pharynx, between the ceratohyoid and mandibular cartilages and directly ventral to the internal spiracular aperture, a large opening (Text-figure 84, v.g.c.) leading into

Text-figure 84.

Left internal spiracular aperture and vestigial gill-cleft (x 0.86) of *Chlamydoselachus* in their relation to each other and to the adjoining cartilages.

br.c.1, first gill-cleft, showing the demibranch attached to the hyomandibular and ceratohyoid cartilages; *br.c.2-3*, second and third gill-clefts; *c.1*, caecum of the internal spiracular cavity; *c.2*, caecum of the vestigial gill-cleft; *ch*, ceratohyoid cartilage; *cr*, cranium; *i.s.c.*, internal spiracular aperture and cavity; *hm*, hyomandibular cartilage; *l.p.i.*, ligamentum postspiracular inferior; *m*, mandible or Meckel's cartilage; *pg*, palatoquadrate; *s.c.*, spiracular canal; *v.g.c.*, vestigial gill-cleft.

Drawn from specimen No. I in the collection of the American Museum of Natural History.



a pocket or caecum. This, like the pit or depression mentioned by Ridewood, is evidently a vestige of the ventral end of a primitive gill-cleft. Although Ridewood was careful to describe the relations of the pit or depression studied by him, he does not give any description of the pit itself further than that implied in the terms used. I infer that the pit or depression examined by Ridewood is so simple that it does not need any further description. In *Chlamydoselachus* the opening is in series with the ventral ends of the branchial clefts. In my four specimens it is from 8 to 15 mm. long and is bordered on the lateral side (toward the mandible) by a crescentic valve-like flap or fold of the mucous membrane. The medial side has no definite boundary. The opening leads into a shallow cavity or caecum (Text-figure 84, c.2) extending beneath the flap posteriorly and laterally for a distance of from 3 to 5 mm., anteriorly for a distance of from 5 to 20 mm. Its average extension anteriorly is about 12 mm., as shown in the figure. The structure and relations of this cavity leave no doubt that it is a persistent ventral portion of a primitive gill-cleft originally continuous with the dorsal portion now represented by the spiracle. This primitive gill-cleft was bordered on the anterior side by the elements comprising the jaw-cartilages, on the posterior side by the hyoid arch represented by the ceratohyoid and the hyomandibular cartilages.

Since writing the preceding paragraph and preparing the accompanying illustrations, (Text-figures 82 and 84), I have found in the midst of a description by Allis (1916, pp. 110-111) of the mandibular artery of *Chlamydoselachus*, the following account of a somewhat similar pocket in the lining of the oropharyngeal cavity of his specimen:

This latter branch [of the arteria mandibularis], on both sides of the head of this specimen, passes immediately anterior to a relatively deep tubular pocket, or recess, of the lining membrane of the mouth cavity which, beginning slightly posterior to the angle of the gape, extends dorsoposteriorly toward the quadrato-mandibular articulation. This pocket lies along the external surface of the hind end of the palatoquadrate, between that cartilage and those fibers of the musculus adductor mandibulae that pass uninterruptedly from the upper to the lower jaw. Posteriorly it ends blindly, its blind end being attached to ligamentous tissues which, continuing on in the line prolonged of the pocket, are attached to the hind (distal) end of the palatoquadrate. The pocket thus lies morphologically anterior to the palatoquadrate, in the relation to that cartilage that a persisting remnant either of the mandibular cleft or of a premandibular cleft would have, and its position, posterior to the musculus mandibulae, is not unfavorable to its being a remnant of either of those clefts, for the adductor muscle, if it be derived from the superficial constrictor of the mandibular arch, could readily, when it slipped from the external (actually posterior) edge of the arch on to its anterior (actually lateral) surface, have acquired a position superficial, and hence morphologically anterior, to the pocket. A branch of the artery is sent posteriorly, on either side of the pocket, to the adductor muscle.

It is evident, upon comparing this description with Text-figure 84, that the pocket described by Allis does not have the same anatomical relations as the one described and figured by me.

THE UROGENITAL SYSTEM

In *Chlamydoselachus*, as in other vertebrates, the urogenital system comprises two functionally distinct parts, the excretory system and the reproductive system; but these are so closely related developmentally and anatomically, especially in the male, that it is often convenient to refer to them collectively.

UROGENITAL SYSTEM OF THE FEMALE

Since the literature on the urogenital system of *Chlamydoselachus* is very meager, the following account is based mainly on my own observations and drawings which were made from four large specimens: Nos. I, II and III collected in Japan by Dr. Bashford Dean and now in the American Museum of Natural History, and another specimen (No. IV) kindly lent by Dr. E. Grace White. All four specimens are females. References to the work of other investigators are made throughout the text. Brohmer's (1908) account of the excretory system of an embryo of *Chlamydoselachus* deals with an early stage and need not be considered here.

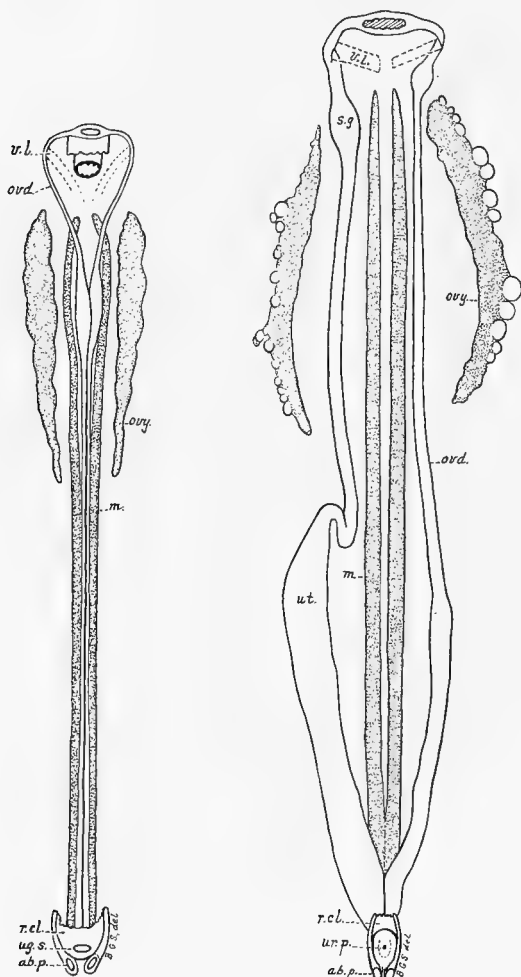
UROGENITAL SINUS IN THE FEMALE

In some elasmobranchs the expression "urogenital sinus" is hardly applicable to the female, but in the case of *Chlamydoselachus* I can see no reason for avoiding the use of this convenient term. In all my specimens the urogenital portion of the cloaca is quite plainly marked off from the rectal portion, though the distinction is most clear-cut in the decidedly immature specimen.

In this specimen (No. IV) a small aperture (Text-figure 85, *ug.s.*), situated on the dorsal surface of the rectal portion of the cloaca, leads into the urogenital sinus which extends in an anterodorsal direction for a distance of about 13 mm. The urogenital sinus must be examined by dissection. It is about 10 mm. wide, but its opening into the rectal portion of the cloaca has a width of only 5 mm. On each side of the sinus, near its anterior end, there is an opening from the uterine portion of an oviduct. The urinary papilla is a longitudinal fluted ridge, free at its posterior end, situated on the dorsal surface of the sinus a little to the left of the median line. The urethral aperture, a narrow slit not more than 3 mm. long, is located near the center of the papilla. No urethral orifice could be found on the right side of this specimen.

In specimen No. III, which is nearly mature, the urogenital sinus (shown without a label in Text-figure 86) is still sharply marked off from the rectal portion of the cloaca, though its opening is much larger than in specimen No. IV. The orifices of the uteri are not shown in the figure since they open into the anterior portion of the urogenital sinus, which lies dorsal to the rectal cloaca. The opening of the right uterus is large enough to admit a finger; the left is much smaller. The urinary papilla is a broad ridge, not well defined, on the dorsal surface of the urogenital sinus. The single urethral orifice is a round pore (*ur.p.*), readily admitting a probe. It is situated near the center of the dorsal surface of the urogenital sinus, but a trifle to the left.

In specimen No. I, which is fully mature, the urogenital sinus (Text-figure 87) is still slightly constricted where it joins the rectal portion of the cloaca, but the openings of the uteri are readily visible and are indicated by line-shading in the figure. The right uterus has a much larger opening than the left. There are two urethral pores (*ur.p.*), right and left, and these are situated close together near the posterior end of the dorsal



Text-figure 85.

Text-figure 86.

Urogenital system of the female *Chlamydoselachus*, ventral views, one-fifth natural size.

Text-figure 85. Urogenital organs of a specimen 1398 mm. long. The excretory ducts are concealed by the oviducts.

ab.p., abdominal pore; *m.*, mesonephros; *ovd.*, oviduct; *ovy.*, ovary; *r.cl.*, rectal portion of the cloaca; *ug.s.*, opening from the urogenital sinus; *v.l.*, ventral ligament of the oviduct.

Drawn from specimen No. IV in the American Museum of Natural History.

Text-figure 86. Urogenital organs of a specimen 1550 mm. long. The shell glands and the adjacent portions of the oviducts are displaced laterally, and the excretory ducts are not shown.

ab.p., abdominal pore; *m.*, mesonephros; *ovd.*, oviduct; *ovy.*, ovary; *r.cl.*, rectal portion of the cloaca; *s.g.*, shell gland; *ur.p.*, urethral pore; *ut.*, uterus; *v.l.*, ventral ligament of the oviduct.

Drawn from specimen No. III in the American Museum of Natural History.

surface of the urogenital sinus. The right urethral aperture is decidedly smaller than the left and is situated a little further posteriorly. There is no urinary papilla.

In specimen No. II, which is fully mature, almost the entire urogenital sinus (Text-figure 88) seems built around the very large opening of the right uterus, indicated by line-shading in the figure. In the hardened condition of the material, this opening is still large enough to admit a thumb. The opening of the left uterus is much smaller. There are two urethral orifices, right and left, situated about 4 mm. apart near the center of the dorsal surface of the urogenital sinus. The right urethral aperture (*ur.p.*) is somewhat

smaller than the left. There is no urinary papilla. The rectal portion of the cloaca is very short.

A ventral view of the cloaca of Garman's (1885.2) adult female specimen of *Chlamydoselachus* is shown in his Pl. XII, reproduced here as Text-figure 89. There is no line of demarcation between urogenital and rectal portions of the cloaca (cl.). There is only

Urogenital system of the female *Chlamydoselachus*, ventral views, one-fifth natural size. The shell-glands and the adjoining portions of the oviducts are displaced laterally.

Text-figure 87. Urogenital organs of a specimen 1350 mm. long. The right uterus and ovary are incomplete.

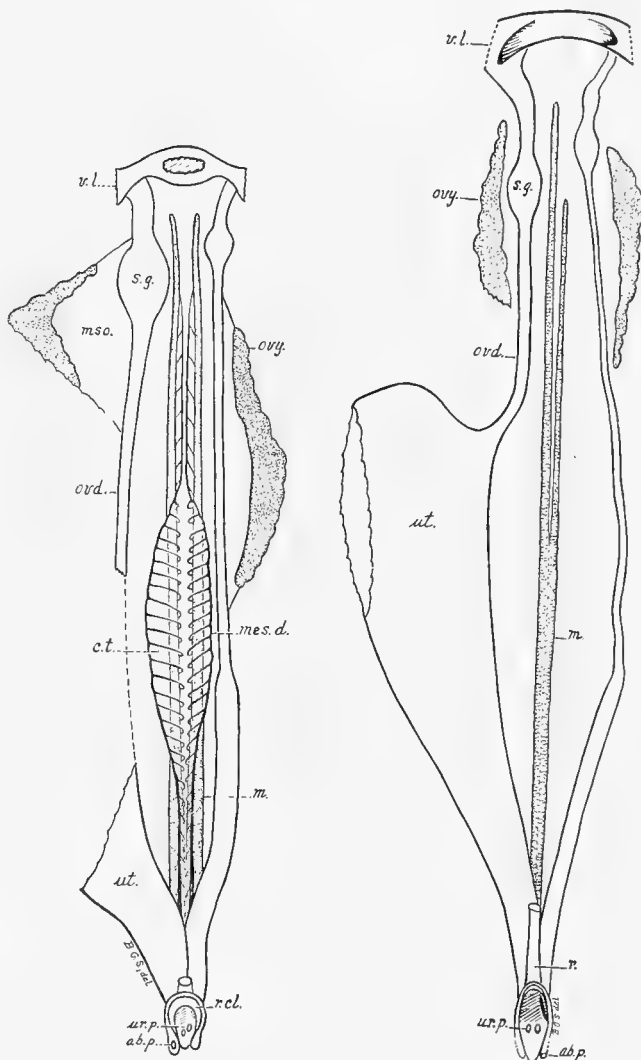
ab.p., right abdominal pore (the left is closed superficially); *c.t.*, collecting tubule; *m.*, mesonephros; *mes.d.*, mesonephric duct; *mso.*, mesovarium; *ovd.*, oviduct; *ovy.*, ovary; *r.cl.*, rectal portion of the cloaca; *s.g.*, shell gland; *ur.p.*, urethral pores; *ut.*, uterus; *v.l.*, ventral ligament of the oviduct.

Drawn from specimen No. I in the American Museum of Natural History.

Text-figure 88. Urogenital organs of a specimen 1485 mm. long. A segment has been excised from the right uterus, and the right ovary is incomplete. The excretory ducts are not shown.

ab.p., abdominal pore; *m.*, mesonephros; *ovd.*, oviduct; *ovy.*, ovary; *r.*, rectum; *s.g.*, shell gland; *ur.p.*, urethral pores; *ut.*, uterus; *v.l.*, ventral ligament of the oviduct.

Drawn from specimen No. II in the American Museum of Natural History



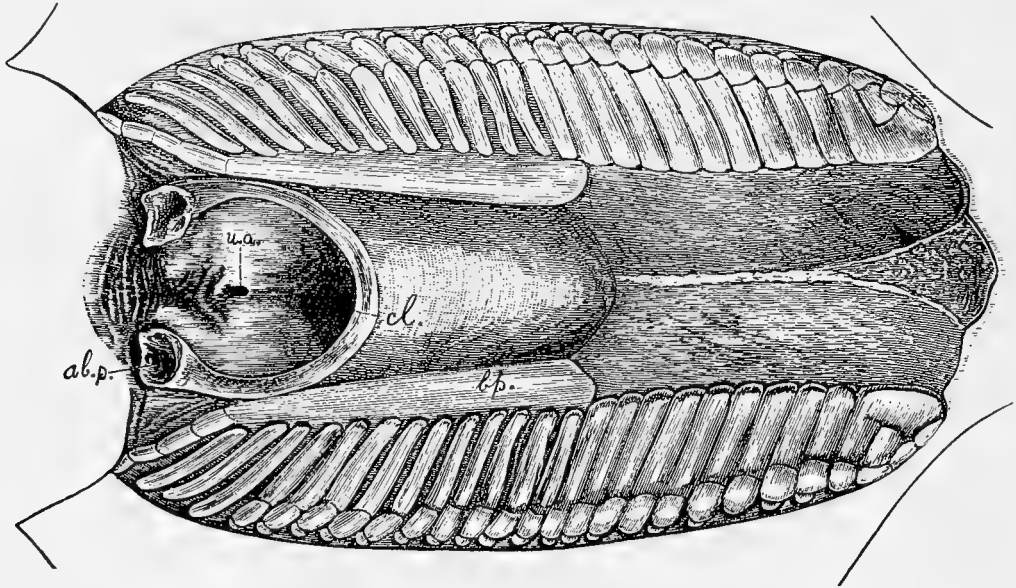
Text-figure 87.

Text-figure 88.

one urethral aperture; this (*u.a.*) is rather large and its position is median. Garman states that "there is no appearance of a urethral papilla; the anterior border of the opening is inflated into a flap or valve, which closes the opening against objects passing outward through the cloaca, or better, which is made to close it by the object themselves."

Hawkes (1907) has represented the cloaca of her female specimen of *Chlamydoselachus* by a diagram which is reproduced as my Text-figure 90A. She notes that there are two

small cloacal apertures (U.S.1) for the urinary sinuses (U.S.) of which only the one on the left side is shown. These apertures are situated close to the median line near the posterior border of the cloaca. She states further that in the female the rectal aperture (R.) is displaced to the right. The opening of the right oviduct (R.Ov.) is much larger than the left (L.Ov.), and appears to crowd the latter anteriorly. This, perhaps, explains the displacement of the rectal opening to the right.



Text-figure 89.

Ventral view of cloaca, pelvis and pelvic fin cartilages of a female *Chlamydoselachus*.

ab.p., abdominal pores; bp., basipterygium; cl., cloaca; u.a., urethral aperture.

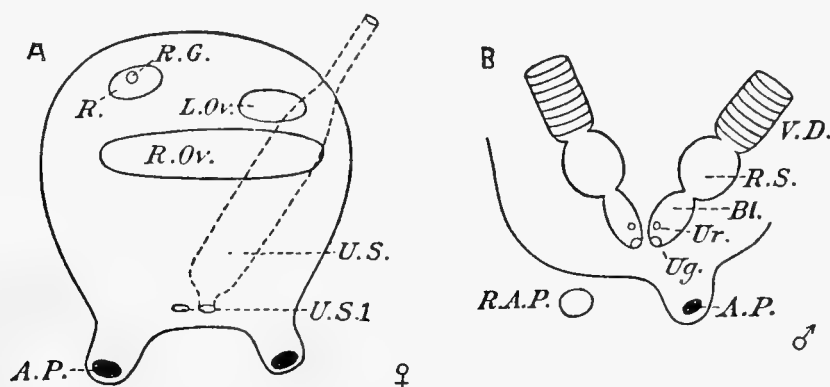
After Garman, 1885.2, Pl. XII.

ORGANS OF EXCRETION IN THE FEMALE

The organs of excretion in the female *Chlamydoselachus* consist of a pair of mesonephroi or functional kidneys, numerous collecting tubules, a pair of mesonephric ducts or Wolffian ducts, and a pair of urinary sinuses or functional bladders which are formed by the enlargement of the posterior portions of the mesonephric ducts. In each of my four specimens, the two urinary sinuses are entirely separate structures.

THE MESONEPHROI.—In my four female specimens, the mesonephroi are a pair of slender flattened organs (*m.* in Text-figures 85 to 88) extending through about 87 per cent of the total length of the body cavity (Tables II and III). Posteriorly, the mesonephroi begin dorsal to the posterior margin of the rectal portion of the cloaca, save in specimen No. IV where they begin as far back as the urethral orifice. Thus the mesonephroi do not begin at the extreme posterior limit of the body cavity, which extends farther caudad dorsally than it does ventrally. Dorsally, the body cavity extends as far back as the external openings of the abdominal pores, which are situated ventrally. The members of

a pair of mesonephroi are usually of equal length, but in specimen No. II (Text-figure 88) the left mesonephros is shorter than the right. In most cases the mesonephroi thin out so gradually at the anterior end that the anterior limit can be made out only after a careful examination.



Text-figure 90.

Diagrammatic figures of the cloaca in female (A) and male (B) specimens of *Chlamydoselachus*.

A.P., closed abdominal pore; Bl., so-called bladder (urogenital sinus); L.Ov., left oviducal opening; R., rectum; R.A.P., functional right abdominal pore; R.G., opening of rectal gland into the rectum; R.Ov., right oviducal opening; R.S., seminal vesicle; Ug., urogenital opening; Ur., opening of ureter into urogenital sinus; U.S., urinary sinus of female (one sinus is omitted from the drawing); U.S.1, openings of urinary sinuses into the cloaca; V.D., vas deferens (ductus deferens).

After Hawkes, 1907, second text-figure, p. 476.

In Table II are shown the lengths of the mesonephroi in my specimens, together with the "over-all" length of the body and the total length of the body cavity. In Table III the ratios of length of mesonephros to body length and to length of the body cavity are expressed in percentages. From an inspection of Text-figures 85 to 88 it will be seen that specimen No. IV is sexually immature, No. III is nearly mature, while Nos. I and II are fully mature. The variations shown in Tables II and III are too small to be signif-

TABLE II

Length in millimeters of the mesonephros of the female *Chlamydoselachus* compared with the total length of its body and the entire length of its body cavity. The specimens are arranged in the order of sexual maturity.

Specimen Number	IV.	III.	I.	II.
Total Length of Body	1398	1550	1350	1485
Length of Body Cavity	554	634	588	686
Length of Mesonephros	486	554	518	605*

*This applies to the right mesonephros only. In this specimen the left mesonephros is shorter; its length is 541 millimeters.

TABLE III.

Length of the mesonephros in proportion to the total body length and to the entire length of the body cavity, in four female specimens of *Chlamydoselachus*, shown in percentages. The specimens are arranged in the order of sexual maturity.

Specimen Number	IV.	III.	I.	II.
$\frac{\text{Length of Mesonephros}}{\text{Total Body Length}}$	34.7	35.7	38.3	40.7
$\frac{\text{Length of Mesonephros}}{\text{Length of Body Cavity}}$	87.7	87.3	88.0	88.1*

*Percentage computed from the right mesonephros only.

icant of either developmental or retrogressive changes. Therefore I conclude that there is no appreciable change in the length of the mesonephros proportional to body length or to the length of the body cavity, within the age limits represented by my specimens. From dissections, one gets the impression that the mesonephroi originally extended a little further forward, since vestiges of these organs appear in front of the unequivocal portions represented in the figures. In any event, the length of the mesonephros in the female *Chlamydoselachus* is remarkable. In many of the more highly differentiated elasmobranchs (e.g., the skates) only the posterior portion of the female mesonephros persists in the adult. In *Chlamydoselachus*, the presence of the mesonephros throughout almost the entire length of the body cavity of the female must be accounted a primitive character.

Throughout their entire extent, the mesonephroi lie against the dorsal body wall, close to the median line. At their posterior ends they are actually united, but they diverge a little anteriorly. Therefore, along the greater part of their course they lie along the low ridge formed by the vertebral column, but at their anterior ends they depart slightly from this ridge. In specimens IV, III and I, the mesonephroi lie almost flat against the dorsal body wall; therefore in Text-figures 85, 86 and 87, which are drawn from these specimens, the mesonephroi are shown very nearly in broad view. Variations in the width of the mesonephroi are fairly well shown in these figures. In specimen No. III, which has the largest mesonephroi, each mesonephros has a maximum width of 13 mm. In specimen No. II (Text-figure 88), within the posterior half of the body cavity the mesonephroi are approximated to such a degree that the surfaces ordinarily dorsal are medial. Hence, in a ventral view, the mesonephroi are seen almost on edge, so that their actual width is not fully represented in the figure. In the anterior half of the body cavity of No. II, the mesonephroi gradually become flattened against the body wall as they diverge anteriorly.

There is considerable variation in the extent of union of the mesonephroi at their posterior ends. In specimen No. IV the two mesonephroi are united across the median plane for a distance of about 80 mm. measured from their posterior ends; in No. III,

for a distance of 70 mm.; in No. I, for about 100 mm.; while in No. II they are united for a distance of 296 mm. In this respect, as in some others already noted, the mesonephroi of specimen No. II are atypical.

In general, the mesonephroi are thickest at their posterior ends, where each mesonephros (considered as a separate entity) has a maximum thickness equal to about one-third its width. Anteriorly, the mesonephroi become thinner very gradually. No. IV is exceptional in that the caudal portion of each mesonephros, for a distance of 15 mm. measured from its posterior end, is abruptly thicker than the part immediately in front of it. This caudal portion has a thickness equal to about two-thirds its width.

Since the mesonephroi are entirely retroperitoneal, they come into actual contact with the peritoneum only by their broad ventral or ventrolateral surfaces. Wherever the mesonephroi are approximated, they lie close to the base of the dorsal mesentery, which extends along the dorsal median line for the entire length of the body cavity. The dorsal mesentery gives rise, laterally, to special mesenteries supporting the oviducal organs and the ovaries; ventrally, to a continuous median mesentery supporting the digestive tube excepting the posterior four-fifths of the valvular intestine and the entire rectum. The mesenteries related to the mesonephroi and to the oviducal organs are particularly important, since these mesenteries contain the collecting tubules and the mesonephric ducts.

In order to investigate the microscopic structure of the mesonephros and the relations of the right and left mesonephroi to each other, transverse serial sections were cut from segments taken at intervals along the length of these organs in all my specimens. In every case the material was found to be in very poor condition for histological study, but mesonephric tubules and glomeruli were readily identified. In the region of union, the two mesonephroi are sometimes connected by renal tissue, but more often by what appears to be lymphoid tissue.

Since the mesonephroi are seldom, if ever, disturbed when newly-captured specimens are eviscerated by fishermen, it seems strange that there is so little recorded concerning them. Collett (1897) describes the mesonephroi of his large female specimen as follows: "The kidneys were also very long, the right being the longer (length 780 mm.) and rather flat, the left being more cylindrical, and of a length of 770 mm. Posteriorly, both kidneys form a club-shaped, thickened, coalescent portion terminating somewhat abruptly toward the anus. The length of the coalescent portion is 120 mm." The only additional description of the "kidney" of *Chlamydoselachus* that I have found is that of Hawkes (1907, p. 477), which reads as follows:

The kidney in the female [*Chlamydoselachus*] is thin dorsoventrally and of irregular breadth. It extends from the region of the oviducal gland to the end of the body cavity, gradually widening as it passes backward in a sinuous line. The sinuosity is due to the arrangement of some of the dorsal muscles. Cephalad to the kidney and apparently unconnected with it, there is an irregular body (1.5 cm.) which extends somewhat beyond the end of the abdominal cavity. This is probably the head kidney (pronephros?) which in the adult has retained its position in the region to which the coelome extended in the embryo.

In the absence of any statements to the contrary, it may be assumed that the "kidney" of Hawkes' specimen was a paired structure, and that the two, more or less separate, members were of equal length. As already noted, in one of my specimens (and less significantly in Collett's large specimen) the left mesonephros is shorter than the right. This does not necessarily mean a decrease in function of the left mesonephros, since a shortening of the thin anterior end might readily be compensated by a hardly noticeable increase in thickness posteriorly. A concentration of the adult female mesonephros into a compact organ situated in the posterior part of the body cavity is characteristic of the highly specialized elasmobranchs.

Concerning the mesonephroi of the female *Heptanchus*, Daniel (1934, p. 287) writes as follows: "Each kidney extends as a narrow ribbon of tissue from the pericardio-peritoneal septum posteriorly one-half the length of the body cavity; back of this it broadens out and becomes much thicker so that the main mass of the tissue lies posterior to the region of the superior mesenteric artery." From an inspection of Daniel's figures it appears that the broadening of the posterior part of the "kidney" is rather abrupt, not gradual as in the case of *Chlamydoselachus*. The assertion that the kidney of the female *Heptanchus* extends from the pericardio-peritoneal septum is hardly understandable in view of Daniel's statement (p. 289) that the kidney of the male extends farther forward than that of the female.

THE URINARY SINUSES.—In specimen No. IV, which is immature, a probe inserted through the urethral orifice passes in one direction (anterodorsally) only, for a distance of about 10 mm. The slender cavity thus explored is the rudimentary left urinary sinus. Its posterior half is imbedded in the thick dorsal wall of the urogenital sinus, while its anterior half lies in a thick portion of the dorsal mesentery supporting the two uteri which are joined by their medial walls for a distance of 50 mm. anterior to the urogenital sinus. The left mesonephric duct, too small to be probed but clearly visible with a hand lens, extends anteriorly from the left urinary sinus along the base of the dorsal mesentery close to the left mesonephros. There is a right urinary sinus, of the same size as the left and in a corresponding position. Anteriorly, it is continuous with the right mesonephric duct which lies alongside the left; but I could not find any opening from the right urinary sinus into the urogenital sinus, either by way of the urethral orifice which serves as an outlet for the left mesonephric duct, or otherwise. The right urinary sinus was found by dissection, using the right mesonephric duct as a guide. I could not find any aperture connecting the two urinary sinuses, which are separated by a thick septum.

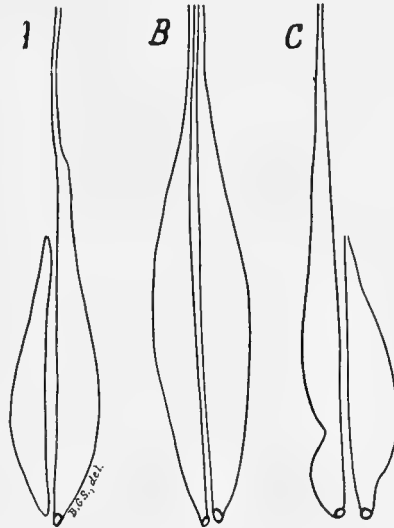
In specimen No. III the two urinary sinuses (Text-figure 91A), right and left, lie close to the median plane. The left urinary sinus extends 75 mm. anterior to the urethral orifice. Near its posterior end this sinus is broad but shallow; its greatest width is 9 mm. For a distance of 25 mm. from the urethral orifice, the expanded posterior portion of the left urinary sinus lies within the dorsal and left lateral wall of the urogenital sinus. Here, only the medial border of the left urinary sinus comes into relation with the dorsal mesentery which connects the urogenital sinus with the dorsal body wall and with the

mesonephroi. Anteriorly, the left urinary sinus gradually diminishes in caliber as it extends within the dorsal mesentery close to the uteri which are united by their medial walls for a distance of 40 mm. in front of the urogenital sinus. At 75 mm. from the urogenital orifice, the left urinary sinus tapers rather abruptly to become continuous with the left mesonephric duct which extends forward in the dorsal mesentery. The right urinary sinus is apparently cystic, and was found by dissection. It begins as far posteriorly as the left urinary sinus, but is only 60 mm. long and 8 mm. wide in its widest portion. Its relations to the wall of the urogenital sinus and to the dorsal mesentery are

Text-figure 91.

Urinary sinuses (ventral views, three-fifths natural size) of three female specimens of *Chlamydoselachus*: A, specimen No. III; B, No. I; C, No. II. In order to show the correct proportions, the outlines are drawn as if the sinuses were spread in a horizontal plane.

Drawn from specimens in the American Museum of Natural History.



similar to those of the left urinary sinus. While the left urinary sinus readily admits a probe by way of the urethral pore, and the probe continues into the left mesonephric duct, no opening for the right urinary sinus could be found in any direction.

Specimen No. I has a pair of well-developed urinary sinuses (Text-figure 91B) situated close to the median plane but lacking any direct communication with each other. In this specimen the two uteri are united by their medial walls for a distance of 50 mm. in front of the urinary sinuses, hence are supported, in this region, directly by the dorsal mesentery. The relations of the urinary sinuses to the wall of the urogenital sinus and to the dorsal mesentery are the same as in specimen No. III, save that here the urinary sinus of the right side is confined to the dorsal mesentery. Each urinary sinus connects posteriorly with its short urethral pore, through which it may be probed. The urinary sinus of the left side is larger than the corresponding sinus of No. III; it is about 90 mm. long, and 10 mm. wide throughout more than half its length. The posterior end narrows abruptly, the anterior end so gradually that its limit must be determined somewhat arbitrarily. The sinus is continuous anteriorly with the left mesonephric duct which was probed more easily than that of No. III. The right urinary sinus is slightly smaller than the left. It is 85 mm. long, and 8 mm. wide throughout its middle third;

it tapers gradually both anteriorly and posteriorly. Anteriorly, the right urinary sinus is continuous with the right mesonephric duct which was easily probed.

In Specimen No. II the urinary sinuses (Text-figure 91c) are well developed and are situated close to the median plane. As in the other specimens, they are not united to form a single functional bladder. Each urinary sinus connects posteriorly with a short urethral pore, through which it may be probed. The two uteri are united by their medial walls for a distance of 50 mm. in front of the urogenital sinus, and so have a common dorsal mesentery. The relations of the urinary sinuses to the urogenital sinus and to the



Text-figure 92.

Longitudinal section through cloaca and right oviduct of *Chlamydoselachus*, three-fourths natural size. The dorsal side is uppermost.

ab-p, abdominal pore; *cl*, cloaca; *int*, intestine; *ov*, oviduct; *p*, caecal pouch, or rectal gland; *ua*, urethral aperture.

After Garman, 1885.2, Fig. 2, pl. XIX.

dorsal mesentery are much the same as in specimen No. III. The left urinary sinus is only 50 mm. long, but it is comparatively broad, having a maximum width of 10 mm. The left mesonephric duct could not be probed. The right urinary sinus is about 100 mm. long. It has a maximum width of 7 mm., but there is an abrupt constriction in its posterior third. In its anterior half it tapers very gradually to become continuous with the right mesonephric duct, which was probed for a distance of 20 mm. in front of the urinary sinus.

In the well-developed urinary sinuses of specimens III, I, and II, the direction of greatest width is determined by the relations to the urogenital sinus and to the dorsal mesentery. In most cases by far the greater portion of the urinary sinus is imbedded in the dorsal mesentery, and the direction of greatest width of the sinus is therefore mainly dorsoventral. In Text-figure 91 some liberties have been taken with the anatomical relations in order to show the full width of the urinary sinuses.

Garman (1885.2) states that in his (female) specimen of *Chlamydoselachus* the "ureters" unite before reaching the cloaca, into which they empty by means of a single aperture. From an inspection of his figure reproduced as my Text-figure 92, it appears probable that the so-called ureters are large mesonephric ducts which unite before reaching the single urethral opening. The fused portion may be considered a rudimentary urinary sinus.

Concerning the urinary sinuses of *Chlamydoselachus*, Hawkes (1907, p. 477), whose observations were apparently made on a single specimen, writes:

Each [urethral] aperture passes into an expanded chamber [U.S., my Text-figure 90A, after Hawkes] with laminated walls, the lumen of which has a diameter of 5 mm. in the cloacal region. The first portion of the sinus is imbedded in the thick cloacal walls. Each sinus extends forward for a distance of 6 cm. beyond the cloaca along the inner side of the kidney, but in front of this point it lies near the oviduct, at a distance from the kidney varying from 1 to 2 cm.

A survey of the specimens described to date indicates that paired urinary sinuses, opening into the urogenital sinus by separate urethral apertures, are typical for the female *Chlamydoselachus*. Nevertheless, there is marked variability. The rudimentary median urinary sinus, or posterior fused portion of the mesonephric ducts, described by Garman, is anomalous. It illustrates one method by which a single median bladder, opening by a single urethral aperture, might be evolved. In my specimens, I find two instances (Text-figures 91A and B) where the right urinary sinus is smaller than the left, and one instance (Text-figure 91C) where the right urinary sinus is irregular in shape. In two instances (specimens IV and III) a right urethral aperture could not be found, while in two others (Nos. I and II) the right urethral aperture is smaller than the left. In No. III no connection of the right urinary sinus with a mesonephric duct could be found. To offset these deficiencies of the right urinary sinus and its openings there is but one instance of similar deficiency on the left side: in No. II a probe could not be passed from the left urinary sinus into the left mesonephric duct, though the latter is of normal size. It is evident that the urinary sinus and also the urethral pore of the right side are much more likely to be defective. That genetic factors are involved is probable from the condition in specimen No. IV, which is quite immature, and in No. III, which is not fully mature.

In *Heptanchus maculatus* (Daniel, 1934) there is ordinarily a single median urinary sinus, but in one specimen two urinary sinuses, right and left respectively, were found. I have been unable to find any other instances, except in *Chlamydoselachus*, of a pair of urinary sinuses opening separately into the urogenital sinus of an elasmobranch. In the Myxinidae, the mesonephric ducts are said (Sedgwick, 1905) to open separately into the urogenital sinus, but in *Petromyzon* these ducts join to discharge their fluid through a single pore. In vertebrate embryos, the mesonephric ducts open separately. The condition found in *Chlamydoselachus* is probably primitive in a phylogenetic sense, but may be due to arrested development.

MESONEPHRIC DUCTS AND COLLECTING TUBULES.—In specimen No. IV, which is immature, the mesonephric ducts are so slender that they are barely visible to the naked eye, but with the aid of a dissecting lens they were easily recognized. They were identified also in transverse serial sections of the urogenital system taken at distances of approximately 25 mm., 140 mm. and 400 mm. from the posterior ends of the mesonephroi. In all three regions the mesonephric ducts lie side by side—at 25 mm. and 140 mm., close together within the dorsal mesentery; and at 400 mm., some little distance apart, within the very narrow special mesenteries supporting the oviducts. The mesonephric ducts are of equal size. Collecting tubules were not positively identified.

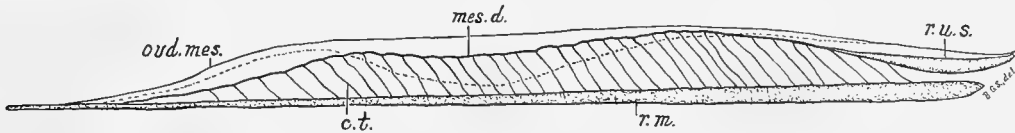
In specimen No. III the left mesonephric duct was probed for a distance of 25 mm. from the left urinary sinus, and was bristled for an equal distance further. Throughout this posterior 50 mm. of its course, it runs in the narrow dorsal mesentery. Due, perhaps, to the poor preservation of the material, the duct could not be satisfactorily traced further. No duct connected with the right urinary sinus could be found by dissection. Collecting tubules could not be identified. A segment of the dorsal mesentery taken about 100 mm. in front of the urethral pore was sectioned transversely. The sections show two mesonephric ducts, side by side, but of unequal size. The right duct is the smaller, and in places is almost obliterated.

Of my four specimens, No. I (Text-figures 87 and 93) is most favorable for the study of the duct system. The left mesonephric duct (*mes.d.*) was easily probed, by way of the left urinary sinus, for a distance of about 80 mm. in front of the urinary sinus. Throughout this distance it runs in the dorsal mesentery; but just where the probe fails to penetrate, the duct leaves the dorsal mesentery to enter the special mesentery supporting the left uterus. In its further course the duct is quite conspicuous and it was easily traced almost to the anterior end of the mesonephros. In the anterior third of the body cavity, the duct again courses in the basal portion of the dorsal mesentery. The right mesonephric duct has a similar distribution. It was probed for 80 mm. from the right urinary sinus, but in general it is not quite so well developed as the left duct. Where the two ducts course together in the dorsal mesentery they do not lie side by side. Posteriorly, the left duct is immediately dorsal to the right; anteriorly, the left duct is some little distance ventral to the right. Collecting tubules (*c.t.*) entering the right duct are about as numerous as those entering the left duct. All the tubules incline forward as they course ventrad from the mesonephroi to the ducts. In the dorsal mesentery the tubules leading to right and left ducts respectively are roughly alternate in position.

Since the mesonephroi extend posteriorly much farther than the mesonephric ducts, the question arises whether any collecting tubules from the posterior end of a mesonephros enter the urinary sinus directly instead of by way of the mesonephric ducts. In the vicinity of the urinary sinus the dorsal mesentery is rather thick and quite opaque, so that it is difficult to determine whether collecting ducts are present. Nevertheless, two or three collecting tubules were found entering the anterior end of each urinary sinus, as shown for the right side in Text-figure 93.

Transverse serial sections of the excretory system of specimen No. I were taken from a region near the center of the body cavity, where the mesonephric ducts course in the oviducal mesenteries; also from a region just posterior to the shell glands, where the ducts run in the dorsal mesentery. In each case the right duct is decidedly smaller than the left. In these sections of the mesenteries, the collecting tubules have much thicker walls than the arteries and veins; so it is unlikely that, in dissections, any blood vessels were mistaken for collecting tubules.

In specimen No. II, due to poor preservation and excessive mutilation of the mesenteries, only fragmentary portions of the mesonephric ducts and collecting tubules could be found. In their size and distribution these portions conform to the general plan revealed in my other specimens, particularly in No. I.



Text-figure 93.

Excretory organs of the right side of a female *Chlamydoselachus* in right lateral view, one-fourth natural size. The broken line indicates the junction of the dorsal mesentery with the oviducal mesenteries. The ventral region is uppermost.

c.t., collecting tubule; mes.d., mesonephric duct; ovd.mes., line of attachment of the right oviducal mesentery to the right oviduct; r.m., right mesonephros; r.u.s., right urinary sinus.

Drawn from specimen No. I in the American Museum of Natural History.

The posterior portions of the mesonephric ducts of Garman's specimen (1885.2) are illustrated in my Text-figure 92. In this figure, as already noted in my account of the urinary sinuses, the mesonephric ducts are shown uniting to form a single large duct posteriorly. Hawkes (1907) states that in the female *Chlamydoselachus*: "The same mesentery which supports the oviduct also supports the urinary sinus and the mesonephric ducts. The latter pass from the kidney at regular distances, there being approximately one to each myotome." This description of the mesonephric ducts is doubtless intended for the collecting tubules.

In the account of the urethral apertures and urinary sinuses of my four specimens, I have noted occasional deficiencies in these features on the right side. It remains to call attention to some observed instances of deficiency in the duct system on the right side. In specimen No. I the mesonephric ducts and collecting tubules, though well developed on both sides, are slightly smaller on the right. In specimen No. III the right mesonephric duct is of microscopic size, though the left duct is well developed for at least 50 mm. in front of the urinary sinus. We might attribute these defects to pressure from the right uterus, which is enormously enlarged while the young are being carried, were it not for the fact that the most extensive defects occur in No. III, which is evidently not quite mature. It seems more likely that the tendency to shift the burden of excretion on to the left side is due to germinal variations which, however, are adaptive in view of the unbalanced development of the reproductive organs of the right side.

Among related forms, the female *Heptanchus* (Daniel, 1934) presents a much more highly differentiated condition of the duct system. Only those collecting tubules from a little more than the anterior halves of the mesonephroi drain into the mesonephric ducts which, at the level of the ovaries, are coiled somewhat like the corresponding portions in the male. This coiling is correlated with the presence of a rudimentary testis. The remaining tubules, which lead from the broad and thick posterior portions of the mesonephroi, open into a pair of very large tubular "ureters" which, in this region, lie dorsal and lateral to the mesonephric ducts. Usually, each ureter joins a mesonephric duct, posteriorly, before the combined vessels enter the single urinary sinus. In an anomalous specimen with two urinary sinuses, right and left respectively, the mesonephric duct and the ureter of each side open separately into the urinary sinus.

The convergence and union of collecting tubules from the posterior portions of the mesonephroi, to form "ureters" which enter the urinary sinus directly, are features more characteristic of the highly differentiated elasmobranchs, especially the skates and rays. Daniel (1934) states that the Wolffian duct (mesonephric duct) decreases in importance as we approach the rays. In the female *Squalus sucklii* (Daniel, 1934, p. 295 and Fig. 253A) the condition is essentially the same as in *Chlamydoselachus*: the mesonephric duct receives the collecting tubules from practically the whole of the mesonephros. This is probably the primitive condition. It seems extraordinary that *Heptanchus*, in many respects one of the most primitive of living sharks, should have departed so far from this archaic type of duct system.

GENITAL ORGANS OF THE FEMALE

From an inspection of Text-figures 85 to 88, it will be seen that my four specimens display various degrees of development of the genital organs. Some of these differences are certainly associated with age, others may possibly be concerned with a sexual cycle. Though specimen No. IV is almost as large as the largest, its reproductive system retains strict bilateral symmetry, and is obviously immature. In all the other specimens the reproductive organs are better developed on the right side save that in No. III, which is probably not quite mature, the left ovary shows a slightly more advanced stage of development than the right. Specimens I and II are fully mature. Some structures seem better developed in No. II than in No. I, but since it is probable that there is a definite breeding season (Gudger and Smith, 1933, p. 302) these differences may be correlated with a sexual cycle.

The largest known female, collected in Japan by Dr. Bashford Dean, had a total length of 1960 mm. The average length for 35 females, comprising all known post-natal female specimens for which the length has been recorded, is 1532 mm. (Gudger and Smith, 1933, Table V, p. 263). We do not know how many of these were sexually mature, but only two of them had a length of less than 1220 mm. My two fully mature female specimens, Nos. I and II, measure 1350 mm. and 1485 mm. respectively. My largest specimen, No. III, has a total length of 1550 mm., yet it seems not quite mature. My

quite immature specimen, No. IV, has a total length of 1398 mm. It is evident that, allowing for individual variations, the female *Chlamydoselachus* reaches almost or quite full size before attaining sexual maturity.

THE OVARIES.—In *Chlamydoselachus*, the ovaries (Text-figures 85 to 88) are a pair of elongate, more or less flattened organs situated in the anterior part of the body cavity and attached, rather indirectly, to the dorsal body wall by means of broad mesenteries. In specimens I and II, throughout their entire length the ovaries are attached by their special mesenteries (mesovaria) to the ventrolateral surfaces of the oviducts including the shell glands. In my immature specimen, No. IV, the ovarian mesenteries are attached to the median dorsal mesentery just ventral to the attachments of the oviducts. In No. III the ovarian mesenteries are attached as in No. IV, save that where these mesenteries pass along the ventral surfaces of the shell glands they are fused to the latter organs. In Text-figures 85 to 88 the ovaries are displaced laterally as far as their attachments allow.

In specimen No. IV the two ovaries (Text-figure 85) are much alike. The length of each ovary is about 180 mm., the maximum width (near the anterior end) is 20 mm., and the maximum thickness is 6 mm. The largest follicles, which are in a collapsed and flattened condition, measure only 10 mm. in their greater diameter. Since the mature egg may be 100 mm. long and 60 mm. wide—measurements based on Nishikawa's (1898) Fig. 1, pl. IV—it is evident that, in the ovaries under consideration, the ovocytes are very incompletely developed. There are no ruptured follicles indicating that ova have been liberated. Only the largest follicles are represented on the ventral surface. The dorsal surface shows, in addition to the large follicles, many smaller ones.

In specimen No. III the ovaries (Text-figure 86) are of almost equal size but the left is slightly better developed. In each ovary, the largest follicles are situated along the lateral margin. Since the largest follicle has a diameter of only 17 mm., it is evident that the ovocytes are decidedly immature.

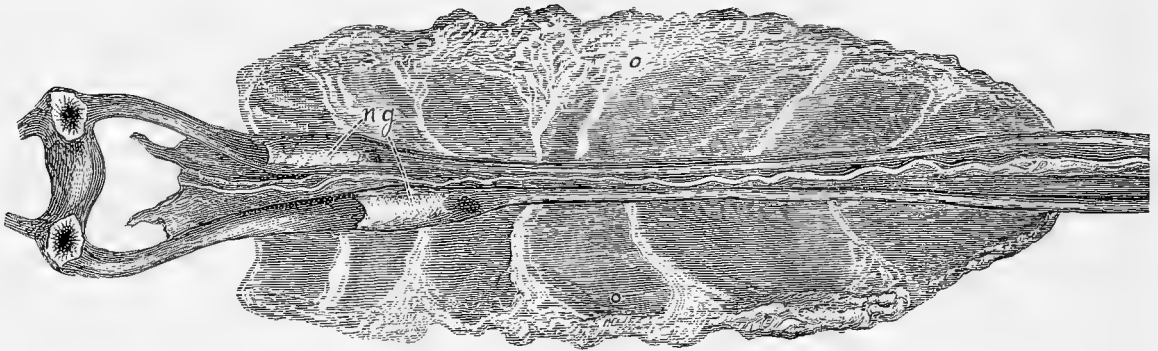
In specimen No. I the posterior part of the right ovary (Text-figure 87) is missing, and has apparently been cut away. From the shape of the remaining portion, I infer that this ovary was originally much larger than the left one which is intact. No follicles are represented on the ventral surface of either ovary, but on the dorsal side of the left ovary some small follicles, none more than 2 or 3 mm. in diameter, were found.

In specimen No. II the posterior part of the right ovary (Text-figure 88) is missing. The preservation of this organ is very poor, so that it is difficult to distinguish a cut edge from a mutilation produced by handling. Doubtless the rupture of large follicles has played a part in the disintegration or contraction of this ovary. No follicles are recognizable from the ventral surface. On the dorsal surface are protuberances due to the presence of many small follicles, none exceeding 4 mm. in diameter; there is also a concavity, 15 mm. in diameter, which represents the persisting half of a follicle. It is not likely that this follicle has ruptured naturally. In the left ovary no follicles are recog-

nizable from the ventral surface, and the largest follicles represented on the dorsal surface measure only 6 mm. in diameter.

Garman's (1885.2) figure, reproduced as my Text-figure 94, portrays the ovaries of his specimen. He states that the ovaries had been badly preserved and that they were much torn. Hawkes (1907) writes that the ovaries of *Chlamydoselachus* are diffuse bodies attached by broad mesenteries to the line of attachment of the "stomach" mesentery. The right ovary is placed somewhat more anteriorly than the left.

In *Heptanchus* (Daniel, 1934) and in *Hexanchus* (Semper, 1875, Fig. 1, pl. XIV), a rudimentary testis is associated with each ovary. In *Heptanchus maculatus* this testis lies in the mesovarium, at the base of the ovary, and runs parallel with the ovary. The



Text-figure 94.

Ovaries and oviducts of *Chlamydoselachus*, drawn one-half natural size.

ng, nidamental gland; o, ovary.

Printed from the original wood-cut after the drawing by Paulus Roetter for Garman, 1885.2, Fig. 1, pl. XIX.

rudimentary testis consists of an anterior larger portion, and a marked swelling or ridge which extends practically the entire length of the ovary.

THE OVIDUCTS.—The oviducts of my four specimens are shown, in ventral view, in Text-figures 85 to 88 inclusive. In specimen No. IV there is but slight differentiation in the regions of the future uteri (*ut.*) and shell glands (*s.g.*); all parts of the oviducal system show strict bilateral symmetry save that the rudiment of the right shell gland is slightly larger than the rudiment of the left, and the right ventral ligament is quite noticeably larger than the left. In specimen No. III, all the oviducal organs of the right side are decidedly larger than those of the left. The discrepancy is even greater in my specimens I and II. To be sure, in specimen No. I a large part of the uterus has been cut away, but the form of the remaining portion gives evidence of the original size. I conclude that, so far as one can judge from the specimens at hand, only the right oviduct is ordinarily functional, but the degree of development attained by the left oviduct is such that it might possibly become functional. In any case, the oviduct proper must become greatly distended while an egg (60 x 100 mm.) is passing through it, and some idea of the size of the uterus after it has contained developing embryos may be obtained from Text-figures 87 and 88.

The common opening (ostium abdominale tubae uterinae) from the body cavity into the oviducts is situated in the region of junction of the oviducts at the extreme anterior end of the body cavity, ventral to the root of the liver. In specimen No. II (Text-figure 88) this opening is almost divided into two, one for each oviduct, which face somewhat medially. It seems almost incredible that so large an egg as that of *Chlamydoselachus* can find its way into one of these openings, though the fluted, funnel-shaped ostium is evidently capable of distention.

Throughout almost their entire lengths the oviducts are supported by special mesenteries attached to the median dorsal mesentery. The only exceptions are found anteriorly, where in front of the shell glands the oviducts diverge to course along the dorsal, lateral and ventral walls of the body cavity, and then unite ventral to the root of the liver. In specimen No. IV each oviduct, where it traverses the lateral wall of the body cavity, is attached to this wall by a narrow mesentery. This mesentery, which we may call the dorsolateral mesentery of the oviduct, is not shown in Text-figure 85. It is not present in my older specimens where the corresponding part of the oviduct is closely applied to the body wall and is merely covered by the peritoneum. In all my specimens, special provision is made for the support of the ventral portions of the oviducts. In specimens IV and III this support is furnished by a pair of ventral ligaments (Text-figures 85 and 86), which are strong special mesenteries. Each has one end fastened to the ventrolateral portion of the oviduct and the other end attached to the ventral body wall near the mid-line. In my older specimens, Nos. I and II, these ligaments (Text-figures 87 and 88) are shorter and broader; they differ, too, in their histological structure, since they blend with the substance of the oviducts.

In its enlarged state, on the right sides of my adult specimens, the so-called uterus has thin walls, a velvety inner surface and a fairly rich blood supply. The mucous membrane is not sufficiently well preserved to permit a study of the finer structure.

The anterior portions of the oviducts ("some twelve inches in length") of Garman's specimen (1885.2) are represented in my Text-figure 94. It is interesting to note that there are two ostia, entirely separate from one another (compare my Text-figures 85 to 88 inclusive). Of his specimen Garman says: "Three inches from the anterior end of one of the oviducts it bore a nidamental gland; the gland of the other tube was an inch farther back. A piece left at the cloaca showed one of the ducts greatly distended, possibly with young that had hatched within it. Only one of the tubes had been in use." In Text-figure 92 the opening of the oviduct that had not been expanded is shown on the left side, the other (right side) having been cut open to show the internal arrangement. Garman's intricate description, illustrated by his Fig. C, pl. XX, of the internal structure of the nidamental gland (shell gland) is too involved for consideration here. It should be compared with Borc a's account (1905, pp. 419-427, Text-figs. 93, 94 and 95) of the structure of the nidamental gland of *Scyllium*.

Collett's (1897) puzzling description of the oviducts and "uteri" of his large female

specimen is quoted here with the comment that nowhere in his paper do I find any mention of the ovaries:

The oviducts were extremely long, both being of about equal length. Towards their upper ends [sic] each expands to a uterus-like sack, of which the right is somewhat larger than the left; both contained immature eggs. Below this expansion the oviducts are quite narrow, but subsequently expand slightly downwards towards the abdominal pores. The total length of each oviduct is about 900 mm.

The right "uterus" was 240 mm. in length, and contained 10 large eggs, about the size of the yolk of a small hen's egg, but some varied in size. There were, besides, about 30 lesser yolks of the size of large and small peas, as well as a few bigger ones about the size of the yolk of a pigeon's egg. The length of the left uterus was 220 mm., and it contained 5 large yolks, and about 20 small ones.

Nishikawa (1898) states that the left oviduct of *Chlamydoselachus* is always rudimentary, and the nidamental gland of the right side is better developed than that of the opposite side. The right oviduct is much distended when it contains from 3 to 12 eggs, these numbers being the limits observed in 7 specimens. Each egg is 110 to 120 mm. long (transverse diameter not stated), while the oviduct is only 600 mm. long. As already stated, measurements based on Nishikawa's Fig. 1, pl. IV, representing an egg within its envelopes, give a length of 100 mm. and a transverse diameter of 60 mm. Doubtless changes in the form of the egg occur, since it must be compressed while passing through the oviduct proper. In a foot-note to Nishikawa's paper, S. Goto, who prepared the manuscript for publication, states that when no eggs are contained there is no perceptible difference in size between the two oviducts. In another foot-note Goto writes: "Mr. Nishikawa tells me . . . that the female genital organs of *Chlamydoselachus* are essentially like those of other sharks, and I can confirm his statement from a passing examination of a specimen brought some time ago to my laboratory. Collett's description of these organs appears to me irrelevant."

Hawkes' (1907, pp. 475-476) description of the oviducts of the female *Chlamydoselachus* is so instructive that it is quoted entire:

The oviducts have large funnels which open ventrad to the stomach, instead of dorsad as is usually the case. The edges of the funnels are irregular and spreading, and are united in the median ventral line to one another, thus forming one large funnel. The anterior edges of the funnels become united to the anterior wall of the body cavity, whilst the posterior edges of the united fimbriae hang free. A triangular dorsal pouch is thus made between the wall of the abdominal cavity and the funnel. As this pouch is in the usual position of the coelomic openings of the oviduct, the eggs would tend to pass into it instead of into the latter, if this were not prevented by the unusual position of the ovaries which are ventral to the oviducts. For the first 6 cm. the oviduct is a straight tube, the walls of which are lined with numerous laminae. This region passes into the oviducal gland, the walls of which are much thickened, except along two longitudinal lines which are approximately dorsal and ventral. The length of the gland is 3 cm. Its interior is covered by fine laminae continuous with those in the preceding and succeeding portions of the oviduct. The laminae run spirally, and are very close together, instead of longitudinally and somewhat separated, as is the case throughout the remainder of the oviduct. The transverse deeper groove in the oviducal

gland mentioned by Garman [1885.2] was found in the specimen examined. Passing from the oviducal glands, the oviducts regain their original diameter, but the walls are smoother, the laminae being reduced to slight striae. When the oviduct reaches the level of the anterior end of the colon, it enlarges. The enlargement is gradual and only increased in diameter about fourfold on the left side, but on the right the enlargement is sudden and very apparent, the diameter increasing 14 to 15 times. This region in addition to being enlarged has folded walls, in which occur one large and several small areas of dilated blood-vessels. The largest blood plexus occupies about one-third of the right side of the oviduct. In connection with each plexus, on its dorsal side, the oviducal wall is thickened over an area which equals the plexus in length and breadth. The enlarged vessels apparently supplied these thickened areas. The condition of the oviduct thus described suggests that this portion of the oviduct acts as a functional uterus, and that therefore *Chlamydoselachus* produces the young alive, as suggested by Garman. The final portion of the oviduct, which succeeds the uterine, has smooth walls and a large diameter, the latter gradually diminishing towards the cloaca. This region divides the functional uterus from the cloaca, thus functionally representing the the vagina of higher types. The opening of the right enlarged oviduct [Text-figure 90A, R.Ov.] has acquired a median position, the left oviducal opening [L.Ov.] lying cephalad to it.

Deinega's (1925) small half-tone figure of the abdominal viscera of a female *Chlamydoselachus* is printed on unsuitable paper, so that details are obscure. It is chiefly remarkable in that it shows a complete right uterus which is even larger than that of my specimen No. II. Its length, including the part bulging anteriorly, is equal to about five-sevenths of the length of the body cavity. It is somewhat kidney-shaped, with a maximum width of more than one-fourth its length. The left oviduct is not conspicuously enlarged in its uterine portion.

Hawkes's observations on the presence of vascular plexuses in thickened portions of the uterine wall suggest a physiological relation between the maternal tissues and the young. I do not know whether the young are carried after the exhaustion of their store of yolk. It seems likely, however, that the young sharks are born as soon as, or even before, the yolk is entirely utilized. The largest known intra-uterine specimen, taken by Dr. Bashford Dean, was a well-formed shark, 390 mm. (15.35 in.) long, yet its yolk sac measured 100 x 70 mm. Additional data are given by Gudger and Smith (1933, pp. 298-301).

It is unnecessary to review the evidence that the genital organs of the right side alone are functional in the female *Chlamydoselachus*. There is not a single known instance of complete development of the reproductive organs of the left side. Yet it must be borne in mind that the number of specimens that have been described is still very small. The organs of the left side are developed to such a degree that they can scarcely be called rudimentary. In view of the great variability found in many other organs of *Chlamydoselachus*, one should not be surprised if the examination of additional material should reveal cases in which the genital organs of the left side, or of both sides, are functional.

In the adult female *Heptanchus* as described by Daniel (1934), the general plan of the oviducts is much the same as in the immature female *Chlamydoselachus*. According to Daniel "the oviduct . . . is not so greatly enlarged in *Heptanchus* as in many other Elasmobranchs in which it forms the conspicuous uterus." In the absence of any definite state-

ment to the contrary, one might assume that the two oviducts of *Heptanchus* are of equal size; but if I interpret Daniel's fig. 251A correctly, the right oviduct is considerably larger than the left.

UROGENITAL SYSTEM OF THE MALE

I have no adult male specimens of *Chlamydoselachus*, and the literature on the male reproductive organs is very fragmentary. No description of the mesonephroi in the male has been found. It seems best to present the observations of each author in chronological order, reserving for special treatment the myxopterygia or "claspers."

EXCRETORY AND INTERNAL GENITAL ORGANS

Günther's (1887) material consisted of two males, the larger 1473 mm. long. Both specimens seemed to be sexually mature. The testes are narrow elongate bodies of nearly equal size, about 127 mm. long and 13 mm. broad at the broadest part. They reach close to the anterior end of the abdominal cavity. In one of the males the arrangement of the urogenital organs and ducts, as well as of the external openings, is perfectly symmetrical (Figure 17, plate V), while in the other (Figures 18 and 19, plate V) the left side shows a much more highly developed condition than the right. In the former (bilaterally symmetrical) specimen, the urogenital organs are not further described. In the latter specimen the left ductus deferens is much wider than the right, and its interior contains low, circular, close-set septa (Figure 16, plate IV). Only faint traces of septa can be seen in the right duct. They are limited to the lower three or four inches of the duct. The left ductus deferens opens into "the urinary bladder, if a bottle-shaped dilatation which terminates externally in a single small conical papilla may be so called." The right ductus deferens opens by a slit at the side of the papilla directly into the cloaca.

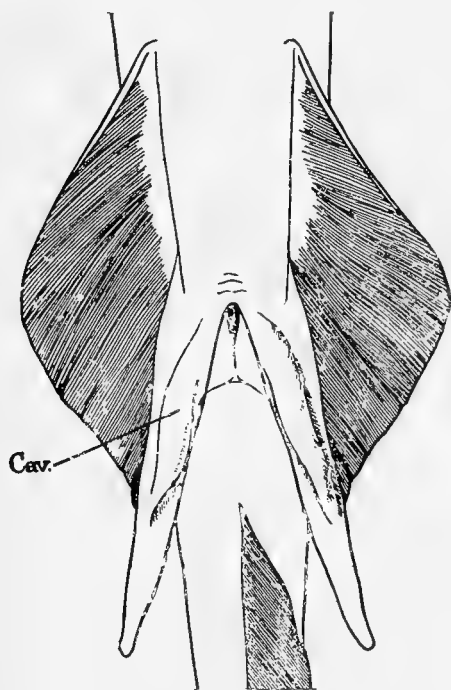
It is not clear how many male specimens Hawkes (1907) examined. In describing the urogenital system of the male, she refers to "my specimen," but in her description of the abdominal pores she writes concerning "one of the males examined." She states that in the male there are two urogenital apertures (Text-figure 90B, after Hawkes), each being the outlet of an oval urogenital sinus (*Bl.*) which Günther described as a urinary bladder. Anteriorly, the sinus communicates by a very small aperture with a second and larger chamber (*R.S.*), which is continuous with the ductus deferens (*V.D.*) or mesonephric duct, and possibly functions as a seminal vesicle. The ductus deferens has (presumably on its inner surface) one or more projecting spiral folds which run from one end of the duct to the other. In the posterior 100 mm. of the length of the duct, the folds are very obvious, but from this point forward they become almost invisible to the naked eye. In the posterior part of the duct the folds are very close together (Günther describes them as "circular" folds). Hawkes further states that the lumen of the left ductus deferens (which Günther found, in one of his specimens, to be better developed than the right) is very irregular in diameter "in my specimen." At its widest, the duct measures about 5 mm., but where narrowest it allows only the passage of a bristle.

Since the excretory and the internal genital organs of the male *Chlamydoselachus* are so imperfectly known, a comparison with other elasmobranchs would be unprofitable.

MYXOPTERYGIA OR CLASPERS

The superficial appearance of the intromittent organs or so-called claspers of the male *Chlamydoselachus* is illustrated in Figure 20, plate V, after Günther; Text-figures 95 to 97, after Leigh-Sharpe. The skeletal anatomy has been discussed in the section on the endoskeleton, and is illustrated by Text-figure 46, p. 375, after Braus; Text-figure 47, p. 377, after Günther; Figure 21, plate V, after Goodey; and Text-figure 115A (p. 472), after Leigh-Sharpe. The muscles of the claspers have been considered in the section on the muscular system, and are illustrated by Figures 22 and 23, plate V, after Goodey; also by Text-figure 115B (p. 472), after Leigh-Sharpe. The peculiar blood vessels of the claspers are described in the section on the blood-vascular system. The present account deals with the general form and structure of the claspers, together with some inferences as to the manner in which they function.

As an introduction to the study of the claspers I can do no better than to quote the following from Leigh-Sharpe (1920, pp. 245-246):

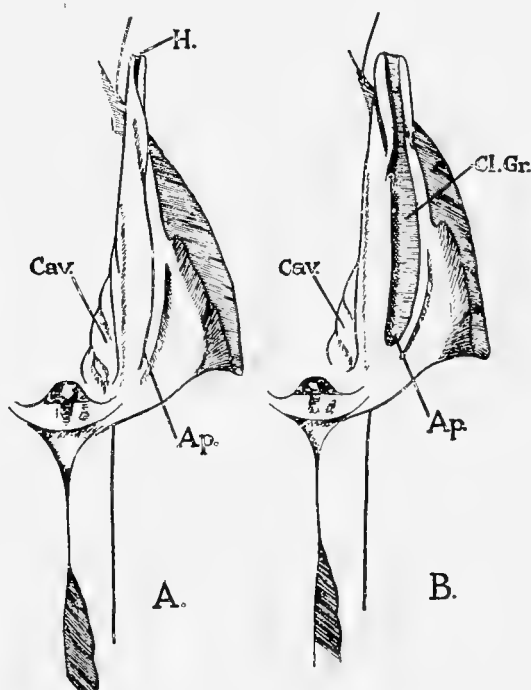


Text-figure 95.

Ventral view of the pelvic region of a male *Chlamydoselachus*, showing myxopterygia or claspers.

Cav., projection of cavity.

After Leigh-Sharpe, 1926, Fig. 1, p. 308.



Text-figure 96.

Ventral view of the pelvic region of a male *Chlamydoselachus* with claspers anteroflexed as in copula: A, with the clasper groove closed; B, with the clasper groove forced open.

Ap., apopyle; Cav., cavity; Cl.Gr., clasper groove; H., hypopyle.

After Leigh-Sharpe, 1926, Fig. 2, p. 309.

In the male elasmobranchs, where fertilization is internal, the basal element of each pelvic fin (basipterygium) is prolonged to form a stout backwardly directed skeletal rod supporting a portion of the fin which is demarcated from the remainder and especially modified to form a copulatory organ, the clasper.

The clasper is rolled up in a manner resembling a scroll, so that instead of being a groove, as it is usually described, it is a sufficiently closed tube along the greater portion of its length, though the edges may not be and usually are not completely fused but overlapping. This

tube is one along which spermatozoa pass, injected by an apparatus, the siphon, which has not hitherto been sufficiently well known and investigated.

The anterior proximal opening into this scroll-like clasper groove or tube will be hereafter known as the apopyle, the posterior, distal exit from the same as the hypopyle. In the sharks and dogfish the apopyle is close to the cloacal aperture, while in the skates it is some considerable distance posterior to it, an inch or more in a moderately sized adult.

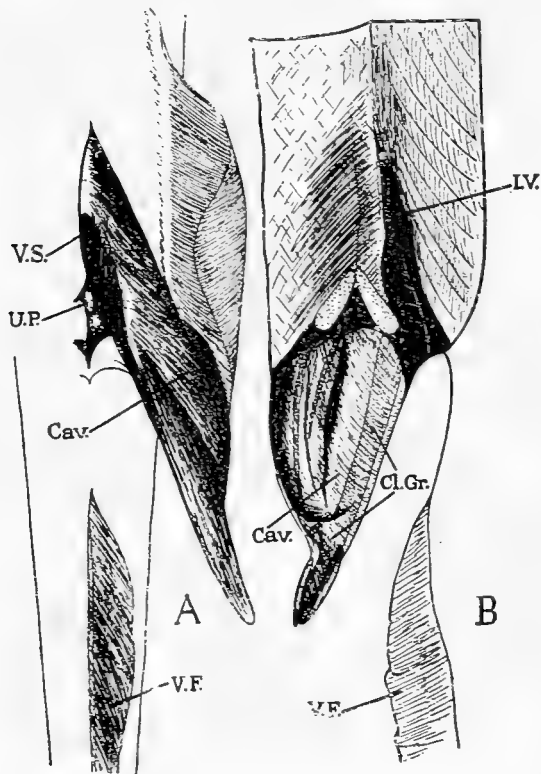
Leading into the apopyle by a narrow aperture, so as to communicate with the clasper tube on either side, is a large cavity, the siphon, a sac with extremely muscular walls, situated immediately below the corium of the ventral surface of the abdomen, frequently several inches in length, close to the median line, and ending blindly, having no communication with the coelom, and whose function and significance it will be my endeavor to elucidate.

In the skates, on the other hand, no such hollow sac is found, but its place is taken by the clasper gland, contained in a sac which it completely fills. This gland has long been recognized, but its containing sac does not appear up to the present to have been demonstrated to be homologous with the clasper siphon of the sharks and dogfish, which is but little known.

Other accessory structures may be present on the claspers, such as the spurs and the like

in *Acanthias*, but of these none attains such importance and is more frequently present than a fan-like expansion at the distal end of the clasper, the rhipidion, whose function is to spray the spermatozoa in all directions in a radiating manner. . . . The rhipidion attains a greater development in the skates than in the sharks.

The manner in which the various parts of a myxopterygium, particularly the siphon, function is described at length by Leigh-Sharpe (1920, pp. 247-251) in the case of *Scyllium catulus*.



Text-figure 97.

Pelvic fin region of a male *Chlamydoselachus*:
A, ventral aspect; B, left lateral aspect.

Cav., cavity; Cl.Gr., clasper groove; I.V., iliac vein; U.P., urogenital papilla; V.F., ventral fin; V.S., venous sinus.

After Leigh-Sharpe, 1926, Fig. 4, p. 311.

Concerning the external anatomy of the myxopterygium of *Chlamydoselachus*, Goodey (1910.1, p. 564) states that:

On the dorsal side of each appendage, bounded by muscles, is the channel, which, toward its posterior end, becomes somewhat lateral in position and is bounded here by the knife-edged, movable terminal cartilages *T.d.* and *T.v.* [my Figure 22, plate V]. In a ventral aspect [my Figure 23, plate V] the most prominent feature of the appendage is the glandular sac [S] and compressor muscle, covered with loosely fitting, soft skin. The skin covering the sac and the termina l parts of the appendages is very soft and is entirely free from dermal spines.

For a more comprehensive description of the claspers of *Chlamydoselachus*, we are indebted to Leigh-Sharpe (1926) whose account is illustrated by my Text-figures 95 to 97, and 115 (p. 472). From Leigh-Sharpe (pp. 308–311) I quote as follows:

This genus [*Chlamydoselachus*], though included from other characters in the Proto-selachii, does not show any affinities with *Notidanus* in its copulatory organs. The claspers, far from being primitive, are long, tapering, and somewhat slender, though possessing strong skeletal supports, 13 cm. in length in this specimen, and devoid of dermal denticles (Fig. 1) [my Text-figure 95]. The clasper groove is long and closed for the greater part of its length (Fig. 2) [my Text-figure 96A], and the apophyle is small. The apex of the clasper is capable of expansion or erection, like a bivalve shell, the larger valve acting as a cover rhipidion. The true rhipidion may be represented by a small protuberance, not far from the apex, which contains a separate cartilage, and is discernible in figure 5 [my Text-figure 115A, p. 472]. On this occasion the animal's left clasper has been dissected instead of the right as heretofore.

There is no siphon present, but situate on the inner ventral aspect of the proximal end of the clasper is a large cavity which opens dorsally by the clasper groove of which it forms an expansion. In these two characters a startling similarity is shown to the Holocephali, more especially to *Rhinochimaera*, and, as I was unable to dissect the latter, the details of the present type are portrayed more fully.

The cavity, which occupies roughly three-quarters of the length of the clasper parallel with the clasper groove, is much distended, with powerful muscular walls, supported by two radial cartilages outspread in a fan-wise manner (Figs. 4 and 5A) [my Text-figures 97 and 115A]. I have no doubt that it can be used for pumping spermatozoa, being, therefore, analogous with a siphon; and in this it agrees with the cavity of *Callorhynchus* and *Rhinochimaera*, though not with that of *Cestracion* (which possesses a siphon) and some species of *Chimaera*. When the claspers are antero flexed as in copula (Fig. 2) [my Text-figure 96], the cavity collapses and is compressed. By a comparison of measurements, it seems certain that the posterior part of the cavity must be included in that part of the clasper which is introduced into the oviduct of the female.

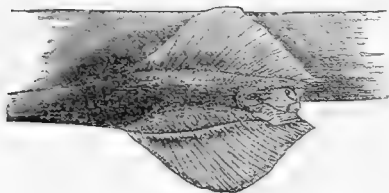
The simplicity of the clasper has prompted a more detailed account of its anatomy.

Regan (1906.2, p. 740) states that the myxopterygium of *Chlamydoselachus* and the notidanids is a more primitive structure than that of the galeoid sharks.

THE ABDOMINAL PORES

Although there is no immediate evidence that the abdominal pores have anything to do with the urogenital system, it is convenient to consider them here, since they are situated near the urogenital sinus and are often figured with it.

The abdominal pores of my female specimens of *Chlamydoselachus* are a pair of short canals leading from the ventral portion of the body cavity, by the most direct route, to their external openings on each side of the ventral surface of the body just posterior to the cloaca. The body cavity extends along each side of the cloaca, but not so far caudad in its ventral as in its dorsal portion. The difference (about 15 mm.) is approximately equal to the length of the abdominal pores. The distal or superficial half of each canal lies just beneath the integument which is usually upraised to form a low ridge. The inner opening is somewhat funnel-shaped and is large enough to admit a pencil. The canals, when probed from the body cavity, are found to be quite uniform in caliber, well-rounded and about 5 mm. in diameter. The external openings (*ab.p.* in Text-figures 85 to 88) vary considerably in size. When well developed, as in specimens IV and III (Text-figures 85 and 86) they are elliptical, about 8 mm. long, and face obliquely ventrad, laterad and caudad. In specimens I and II (Text-figures 87 and 88) they are usually



Text-figure 98.

Pelvic fins, abdominal pores and
cloacal aperture of a 1220-mm.
female *Chlamydoselachus*.

After Garman, 1885.2, Pl. I.

round and comparatively small, but one is absent. On the right side of No. II the external opening is so small that it barely admits a probe. In the single case (specimen No. I) where an external opening is absent, the canal is fully developed internally but is closed externally by the integument.

The external openings of the abdominal pores in Garman's (1885.2) specimen, a large female, are shown in his plates, reproduced as my Text-figures 98 and 89. Garman states that the mouth of each abdominal pore is inflated into a broad flap, by which the pores are hidden. Hawkes (1907), in a figure reproduced as my Text-figure 90A, shows the cloacal region of a female with two closed abdominal pores.

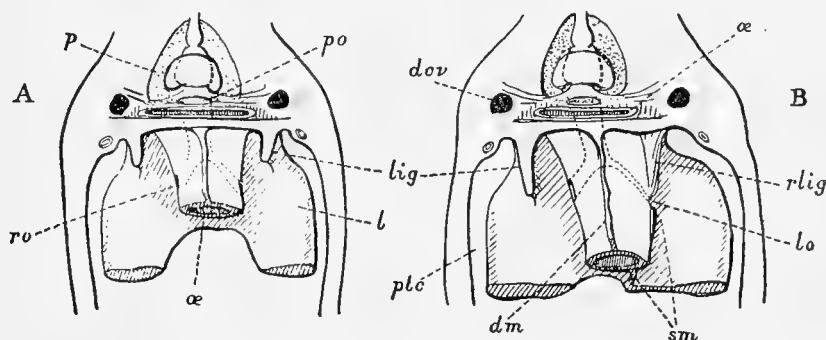
The specimens thus far considered are all females. It remains to describe the condition of the abdominal pores in the male. Günther's (1887) illustrations include two figures (my Figures 17 and 18, plate V) showing the abdominal pores of his male specimens. One is normal, showing two open pores similar to those of the typical female; the other is anomalous, possessing only a single abdominal pore, which is unusually large. In his text, Günther states that this single abdominal pore is situated immediately behind the cloaca and "in the median line (or very slightly to the left of it)" but his figure shows it definitely on the left side. Hawkes (1907) writes: "One of the males examined has two abdominal pores of which the right is the better developed." In the explanation of her diagrammatic text-figure (my Text-figure 90B) the left pore is said to be closed.

From the meager evidence at hand it does not appear that there is any important difference between the abdominal pores of the male and the female, but it is clear that

both are decidedly variable. That they are not essential for the life of the fish is indicated by Hawkes' observation of an adult female with both abdominal pores closed.

PERICARDIO-PERITONEAL CANALS

In the embryonic development of higher vertebrates, the primitive coelomic cavity becomes divided into three cavities, pericardial, pleural and peritoneal respectively. In the adult elasmobranch there are only two coelomic cavities, pericardial and peritoneal, and their separation is not quite complete. A pair of slender thin-walled canals, joined



Text-figure 99.

Diagrams showing the pericardio-peritoneal canals (dorsal views) in: A, an adult *Squalus*; and B, an adult *Scyllium*. Dorsal parts removed by a horizontal cut. The canals below the esophagus are represented by dotted lines. *dcv*, ductus Cuvieri; *dm*, dorsal mesentery; *lig*, lateral suspensory ligament of *l*, the liver; *lo, ro*, left and right openings of the pericardio-peritoneal canals; *oe*, esophagus; *p*, pericardial coelom; *po*, median opening of the pericardio-peritoneal canal into the pericardial coelom; *rlig*, right lateral suspensory fold; *sm*, sub-esophageal lesser mesentery (hepato-enteric mesentery).

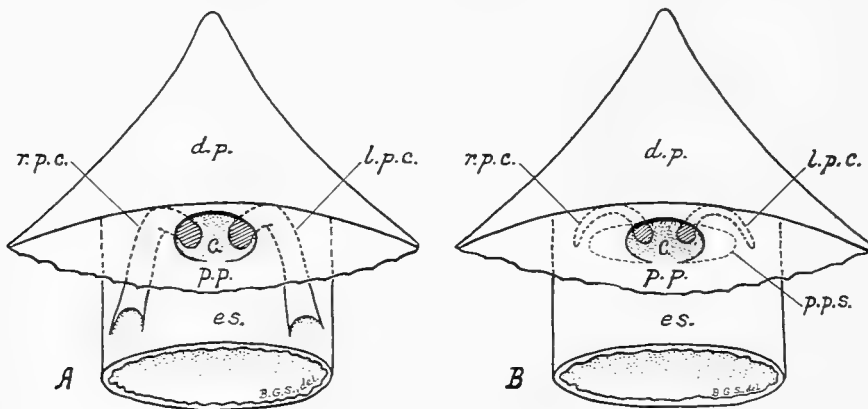
After Goodrich, 1918.1, Fig. 18.

at their pericardial ends to form a single large canal opening into the pericardial cavity (Text-fig. 99), course posteriorly along the ventral wall of the esophagus to open by wide apertures, thus placing the pericardial cavity in communication with the peritoneal cavity—as in *Squalus* and *Scyllium* (Goodrich, 1918.1, Fig. 18); and *Raja* (Monro, 1785).

Pericardio-peritoneal canals of selachians were first described and figured by Monro in the skate. Balfour (1876–78) interpreted these canals as developmental arrests, but Hochstetter (1900) claimed that in *Acanthias* the early communication between the pericardial and peritoneal cavities became completely closed, and that the canal opening from one to the other in the adult is a new formation. Goodrich (1918.1) investigated the development of these canals not only in *Squalus* (*Acanthias*) but also in *Scyllium*, concluding that Hochstetter was mistaken in his interpretation and that Balfour's view is essentially correct.

In each of my four large specimens of *Chlamydoselachus*, pericardio-peritoneal canals were found. Since there is considerable variation in the structure and relations of these canals, each specimen will be described separately.

In specimen No. II the condition of the canals (Text-figure 100A) is most like that described for other elasmobranchs, though some differences are obvious. On the anterior surface of the posterior pericardium (*p.p.*), close to its dorsal border, there is a large opening (*c.*) leading into a shallow cavity. The width of the cavity (and of its opening) is about 12 mm.; its depth is only about 3 mm. This cavity, which I shall call the pericardio-peritoneal sac, represents the fused portion of the two canals (*r.p.c.* and *l.p.c.*), which open into it by apertures about 4 mm. in diameter. The canals were probed. Each is about 4 mm. wide when collapsed, and is about 20 mm. long; the walls are very thin.



Text-figure 100.

Pericardio-peritoneal canals of *Chlamydoselachus*, leading from the pericardial cavity (above) to the peritoneal cavity (below); ventral views, natural size.

c., common opening of the canals into the peritoneal cavity; *d.p.*, dorsal pericardium; *l.p.c.*, left pericardio-peritoneal canal; *es.*, esophagus; *p.p.*, posterior pericardium; *p.p.s.*, pericardio-peritoneal sac formed by the fusion of right and left canals; *r.p.c.*, right pericardio-peritoneal canal.

A is drawn from specimen No. II in the collection of the American Museum of Natural History;

B, from a specimen (No. IV) lent by Dr. E. Grace White.

The canals pass dorsad along the posterior surface of the pericardial wall to reach the esophagus (*es.*), then caudad along the ventral surface of the esophagus, dorsal to the liver, to open by wide crescentic apertures into the peritoneal cavity (Text-figure 100A).

In my specimen No. I, conditions are practically the same as in No. II save that the pericardio-peritoneal sac is about 6 mm. wider than its opening into the pericardial cavity, and that the right pericardio-peritoneal canal is closed at its posterior end.

In specimen No. III the common aperture and the pericardio-peritoneal sac are much the same as in specimen No. II, but their situation on the posterior wall of the pericardial cavity is a little further ventrad—not so close to the dorsal border as in the preceding specimens. Thus the paired canals must pass a little further dorsad in order to reach the esophagus. The canal on the right side is only 5 mm. long and does not reach the esophagus. The canal on the left side is 10 mm. long and turns posteriorly upon reaching the esophagus. Both canals are closed at their posterior ends.

In specimen No. IV (Text-figure 100B) the common aperture (c.) of the pericardio-peritoneal canal is situated as in No. III, a few millimeters from the dorsal border of the posterior pericardial wall. This opening has about the same size (12 mm. wide) as the corresponding openings in the other specimens; but it is bordered laterally by thin lips due to an extension of the pericardio-peritoneal sac (p. p. s.) which is about 22 mm. wide though no deeper than in the other specimens. The openings into the paired canals are smaller, and the canals are more slender. Each canal is about 13 mm. long and ends in contact with the esophagus at the extreme anterior end of the peritoneal cavity. Both canals end blindly.

In two respects the pericardio-peritoneal canals of *Chlamydoselachus* differ from the condition typical for elasmobranchs: the anterior unpaired portion is extremely short and broad, forming a shallow sac; and the paired canals often end blindly. Of the eight canals in my four specimens, five are closed at their posterior ends. It is noteworthy that the closed canals are usually smaller than the open ones. It is apparent that there is a tendency toward obliteration of the canals, and this may be interpreted as a departure from primitive conditions.

BLOOD-VASCULAR SYSTEM

Studies of the blood-vascular system of *Chlamydoselachus* have been almost entirely limited to (1) the heart; (2) the arteries anterior to the heart; (3) the large venous trunks; and (4) the venous sinuses of the claspers. These comprise, however, the most interesting and complex portions of this system. In my own material, only a few portions of the blood-vascular system are in a condition favorable for investigation. I have therefore studied only the heart and the blood vessels of the gills.

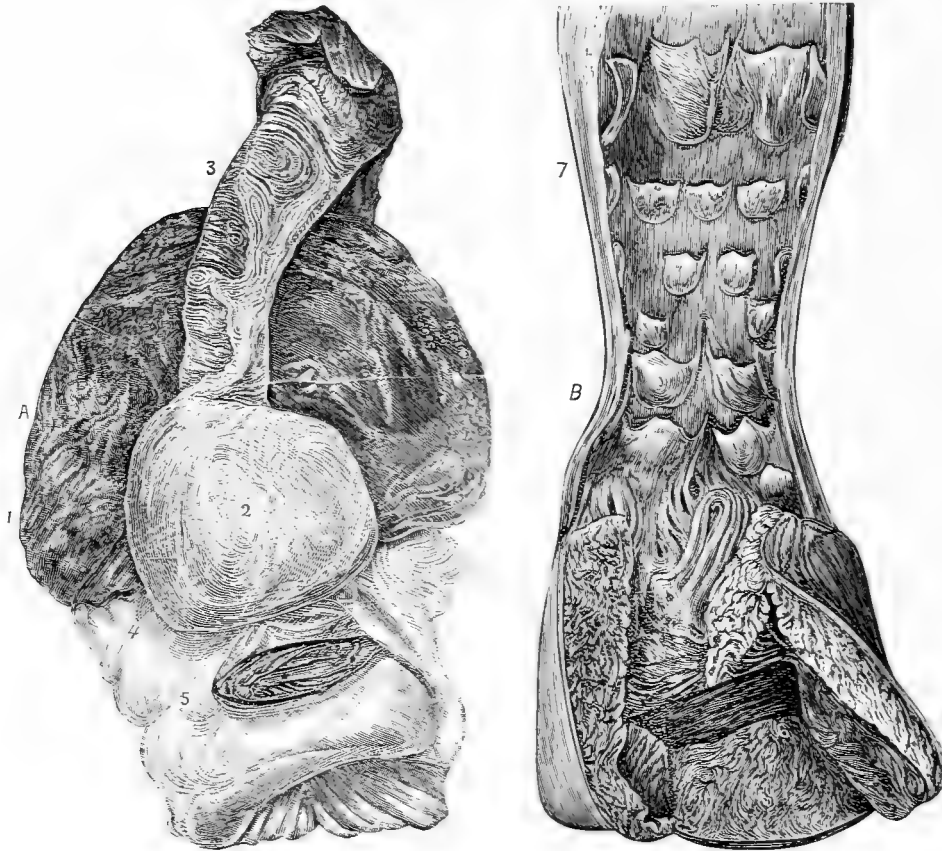
THE HEART

Since there is much variation in the names that have been applied, by different authors, to the anterior division of the elasmobranch heart, it is desirable to justify my choice of the term *conus arteriosus*, which is used throughout this section. The present status of our knowledge of the homologies of this portion of the heart is set forth by Goodrich (1930, p. 538) in the following words:

There has been considerable confusion in the nomenclature of the anterior region of the heart. *Bulbus cordis* is the name now generally applied by embryologists to the anterior chamber. But the name *conus arteriosus*, introduced by Gegenbaur to designate the anterior muscular region of the Selachian heart, is often given to it. Moreover, the Selachian *conus* does not [precisely?] correspond to that part of the heart so called in human anatomy. It is best, then, to apply the name *bulbus cordis*, introduced by A. Langer, to the embryonic structure throughout the Craniata, and keep the name *conus arteriosus* for the adult muscular contractile chamber derived from it in Pisces and Amphibia.

Garman's figures of the heart of *Chlamydoselachus* are reproduced as my Text-figures 101A and 101B. Of his specimen Garman (1885.2, pp. 18 and 19) writes:

Departing considerably from the conventional form of heart, this genus presents a shape that is somewhat peculiar. Seen from below, it has a small subquadrangular ventricle, a large auricle, and a long bulbus arteriosus. The ventricle measures nearly three-quarters of an inch in either width or length. When filled, the auricle is subtriangular, and measures on each side an inch and a half. The bulbus is almost twice as long as the ventricle. Behind the auricle, and above and behind the ventricle, lies the sinus, which has a capacity that nearly



Text-figure 101.

Heart of *Chlamydoselachus*: A, in ventral view; B, longitudinal section showing cavity in ventricle, also valves of the bulbus (conus) arteriosus.

1, auricle (atrium); 2, ventricle; 3, bulbus (conus) arteriosus; 4, sinus venosus; 5, dark tissue between cardiac and abdominal chambers; 6, cavity in ventricle; 7, valves in bulbus (conus).

Printed from original wood-cuts after drawings by Paulus Roetter for Garman, 1885.2, Pls. XVII and XVIII.

equals the bulk of the ventricle. From it the opening into the auricle is guarded by a pair of valves that are without chordae. The auriculo-ventricular opening is furnished with a pair of valves provided with chordae tendineae. In the ventricle the cavity or chamber is small; its outlines in longitudinal section resemble those of a pipe with a short stem, the stem being directed toward the left upper side and the bowl toward the bulbus. Along the inside of the passage (Fig. B, pl. XVIII) [my Text-figure 101b], the muscles lie in bands (columnae)

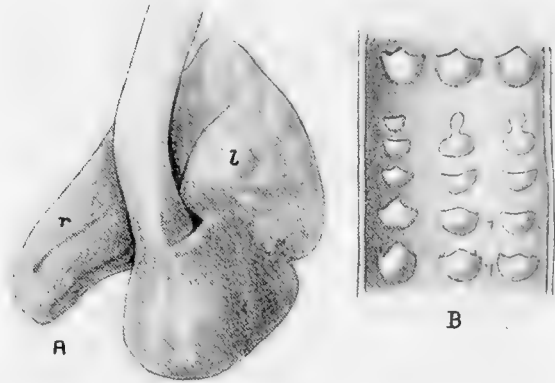
loosely laid one upon another, those in the posterior section, or stem of the pipe, running transversely, and those of the anterior section being longitudinal.

Behind the ventricle, in the partition, between the peritoneum and the pericardium, there is a spongy mass of dark tissue an eighth of an inch in thickness.

Günther (1887) had available for examination three well-preserved specimens of *Chlamydoselachus*. His drawings, illustrating the external form of the heart and the configuration of the valves of the conus, are reproduced as my Text-figures 102A and 102B. Günther gives no general description of the heart, but it will be noticed that his figure confirms Garman's (1885.2) statement concerning its form.

Ayers' (1889) Fig. 2 (reproduced as my Text-figure 105, p. 462) portrays the heart of *Chlamydoselachus* in sectional view, and the drawing appears to be semi-diagrammatic. Therefore this figure does not give us much information concerning the form of the heart in his specimen. His description (p. 194) of the conus arteriosus follows:

The conus arteriosus forms a thick spindle-shaped trunk about an inch long and one-fourth of an inch in diameter. It is provided with six rows of valves, all of which are quite small, except the anterior set of three, which are large, tridentate, and formed of a white tough tissue of a cartilaginous consistency.



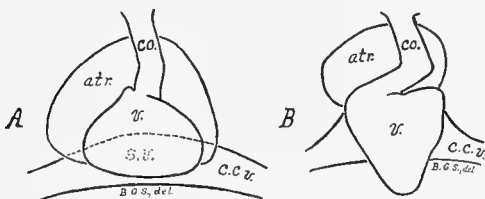
Text-figure 102.

Heart of *Chlamydoselachus*: A, in ventral view; B, conus arteriosus opened longitudinally to show the arrangement of the valves.

r, right atrium; l, left atrium.

After Günther, 1887, Figs. 7 and 8, pl. LXV.

My observations do not entirely agree with those of Garman and Günther regarding the proportions of certain parts of the heart. In my three specimens (from the fourth specimen the heart had been removed) the conus arteriosus is indeed long, as in Garman's, Günther's, and Ayers' specimens; but the ventricle, even when empty, is larger than it appears in the figures by Garman and Günther, and the size of the atrium is variable. Text-figure 103A is drawn from my specimen No. III in which the ventricle (v.) is moderately distended with blood. The atrium (atr.) is empty, but in its flattened condition it retains a smoothly rounded outline, as shown in the figure. The size of the atrium is somewhat exaggerated due to its flattened condition; nevertheless, the atrium of this



Text-figure 103.

Hearts of two specimens of *Chlamydoselachus*, in ventral view, one-half natural size:

A, drawn from No. III; B, from No. II.

atr., atrium; c.c.v., common cardinal vein; co., conus arteriosus; s.v., sinus venosus; v., ventricle.

Drawn from specimens in the American Museum.

specimen is certainly large. In specimen No. II (Text-figure 103B) the ventricle (*v.*) is partially distended with blood. Its size equals that of No. I but its form is quite different, more nearly resembling that of the human ventricles. The conus (*co.*) is so long that proximal and distal halves, when at rest, are bent almost at right angles to each other in order to find room within the pericardial cavity. In specimen No. I the proportions are much the same as in No. III, but the ventricle, which is empty, is kidney-shaped with its long axis extending transversely and its lesser curvature facing anteriorly. In the undisturbed condition, the left half of the ventricle was folded dorsal to the right half. In this condition, when viewed from the ventral aspect, the ventricle of No. I has much the same appearance as in Günther's figure. Thus in my three specimens, even after allowing for differences due to expansion and contraction of its chambers, the form of the heart as viewed from the ventral aspect varies considerably, but the ventricles are uniformly larger than those shown in Garman's and Günther's figures.

In my three specimens, the sinus venosus (*s.v.* in Text-figure 103A) and the common cardinal veins or ducts of Cuvier (*c.c.*) are of the usual elasmobranch type, but seem rather large. Of the mass of spongy tissue in the posterior pericardial wall, mentioned by Garman, I can find no trace.

Concerning the valves of the conus (*bulbus*) arteriosus in the specimen illustrated by my Text-figure 101B, Garman (1885.2, p. 18) writes: "The bulbus contains six rows of valves, or seven if we count the single valve nearest the ventricle as a row. Two or three of the posterior series have chordae tendineae." Günther's (1887, p. 4) description of the conus arteriosus in his specimen follows:

The conus arteriosus (Figs. 7 and 8) [my Text-figure 102] is of considerable length, slightly bent towards the right, and of nearly the same diameter throughout. No special valve separates it from the ventricle. I find the valves much more regularly arranged than would appear from the figure given by Garman. They form three longitudinal and six transverse rows (Fig. 8). The largest are those of the distal transverse row, placed close to the end of the conus, and somewhat more distant from the next row than the five other rows are from each other. The next largest valves are those of the proximal row, those of the second and third being smaller, and those of the fourth still smaller, with only partially free anterior margins; the valves of the fifth row are quite rudimentary, and two of them merely indicated as raised papillae, which are confluent with those of the fourth row. Finally, a fourth intermediate longitudinal series is indicated by two minute valves, belonging to the first and second transverse rows. The larger valves are provided with tendinous chordae.

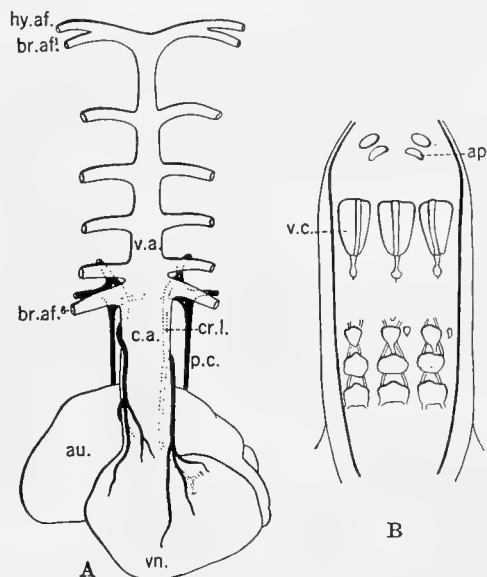
The valves of the conus in my three specimens are regularly arranged in transverse rows, but the arrangement in longitudinal rows is not always perfect. In specimen No. III the valves are the largest, but this may be due to the fact that they are best preserved. In this specimen there are five transverse rows, with a space of double the usual extent between the fourth and fifth rows counting from the proximal end of the conus. The valves of the distal row are much the largest, as in Garman's specimen; the valves of the two proximal rows rank next in size. The numbers of valves in each row, reckoning from the proximal end of the conus, are 3, 4, 4, 5, and 3 respectively. In specimen No. II there

are four transverse rows with at least three valves in each row—the precise number is uncertain. The same may be said of No. I.

As stated by Garman (1885.2), generally among sharks the conus is shorter and the transverse rows of valves less numerous, than in *Chlamydoselachus*. In Garman's Pls. 56 and 57 (1913) we find illustrated (without text) the external form of the heart, and the form and arrangement of the valves of the conus arteriosus, in many different species of elasmobranchs. The heart of *Heptanchus maculatus* (Text-figure 104A) has a fairly long conus arteriosus—longer than that of *Heptranchias* (*Heptanchus*) *perlo* (Garman, 1913, Fig. 1, pl. 56) but shorter than that of *Chlamydoselachus*. In *Heptanchus* (Text-figure 104B) the valves of the conus arteriosus show partial suppression of the second row counting from the distal end of the conus, and complete suppression of the third row.

THE BLOOD VESSELS

For descriptions of the blood vessels of *Chlamydoselachus*, we must rely almost entirely on the work of Ayers (1889) and Allis (1908, 1911, 1912 and 1923). In several respects, the condition of the arteries as described and portrayed by Ayers is not typical for *Chlamydoselachus*. His work has been severely criticised, but in view of the marked variability that has been found in other organs and parts of *Chlamydoselachus*, it seems possible that he worked on an anomalous specimen. I have included two of his figures (Text-figures 105 and 106), because of their historical importance and because they are more comprehensive than those of other authors.



Text-figure 104.

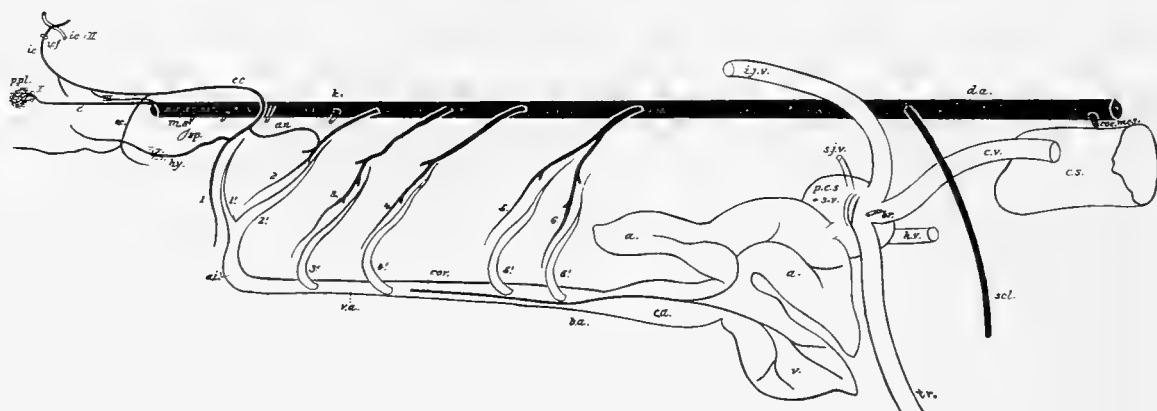
Ventral views of (A) heart and ventral aorta, (B) valves of the conus arteriosus, in *Heptanchus maculatus*.

ap., aperture of last afferent artery; au., auricle (atrium); br.af.1-6, first to sixth afferent branchial arteries; c.a., conus arteriosus; cr.l., left coronary artery; hy.af., afferent hyoidean artery; p.c., pericardial artery; v.a., ventral aorta; v.c., valves of the conus; vn., ventricle. From Daniel, 1934, Fig. 150A and B; the latter redrawn after Garman, 1913, Fig. 1, pl. 59.

THE ARTERIES

In *Chlamydoselachus*, particular interest attaches to the study of the dorsal aorta (anterior portion), the branchial arteries, and the circulation within the gills.

THE DORSAL AORTA.—Ayers (1889) described a slender median artery, coursing in the basis cranii, which he called the cranial aorta (c in Text-figures 105, 106, and 22 p. 352) since he regarded it as a direct continuation of the dorsal aorta. "Unlike all other gnathostomous vertebrates, *Chlamydoselachus* has a dorsal aorta (dorsal vessel) running the entire length of the notochord, to which it is intimately attached throughout

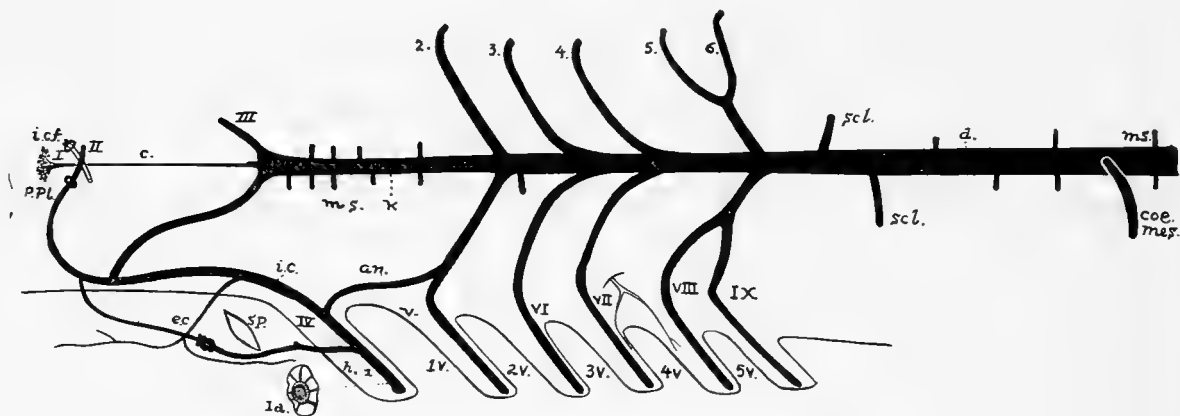


Text-figure 105.

Semidiagrammatic figure of heart and anterior blood vessels (anomalous?) of a specimen of *Chlamydoselachus* viewed from the left side.

a., auricle (atrium); a.i., anterior innominate artery; an., anastomotic branch of first efferent branchial artery; b.a., bulbus arteriosus; br., brachial vein; c., cranial aorta; c. a., conus arteriosus; c.c., anterior carotid commissure; coe.mes., coeliaco-mesenteric artery; cor., coronary artery (plus hypobranchial trunk); c.s., cardinal sinus; c.v., cardinal vein; d.a., dorsal aorta (posterior to *k*); e.c., external carotid artery; h.v., hepatic vein; hy., hypophysis; i.c., internal carotid artery; i.c.f., internal carotid foramen; i.j.v., internal jugular vein; k., cephalic aorta; m.s., arteriae musculo-spinales; p.c.s., precaval sinus; p.pl., pituitary plexus; scl., subclavian artery; s.j.v., superior jugular vein; sp., spiracle; s.v., sinus venosus; tr., tropeic (lateral abdominal) vein; v., ventricle; v.a., ventral aorta; I-III, first to third pairs of aortic roots (arches); 1-6, first to sixth pairs of efferent branchial arteries; 1-6!, first to sixth pairs of afferent branchial arteries.

After Ayers, 1889, Fig. 2.



Text-figure 106.

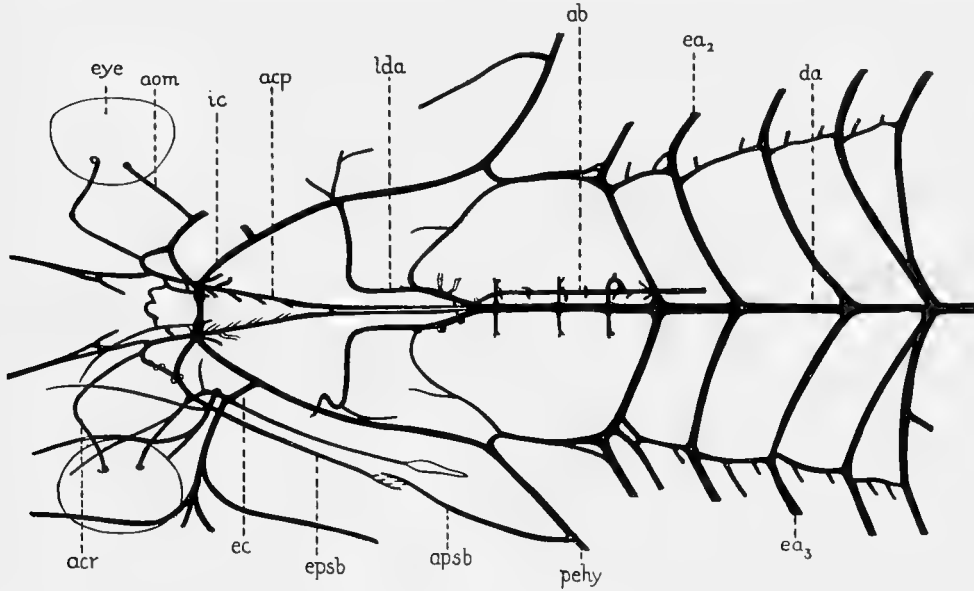
Efferent branchial vessels and dorsal aorta (anomalous?) of a specimen of *Chlamydoselachus*.

an., anastomotic branch of first efferent branchial artery; c., cranial aorta; coe.mes., coeliaco-mesenteric artery; d., dorsal aorta (posterior to *k*); e.c., external carotid artery; h., hyoid arch; i.c., internal carotid artery; i.c.f., internal carotid foramen; k., cephalic aorta; m.s., arteriae musculo-spinales; p.pl., pituitary plexus; scl., subclavian artery; sp., spiracle. I-IX, first to ninth pairs of aortic roots (arches); 1-6, first to sixth pairs of efferent branchial arteries; 1v-5v, first to fifth branchial arches.

After Ayers, 1889, Fig. 1.

the greater part of its course" (Ayers, 1889, p. 195). Concerning the part of this vessel which Ayers calls the cranial aorta, Allis (1908, pp. 111–112) comments as follows:

Ayers shows and describes, in *Chlamydoselachus*, a small median vessel, which runs directly forward from the point where, according to his nomenclature, the dorsal aorta is joined by the third pair of aortic roots; that is, in the nomenclature employed by me, from the point where the lateral dorsal aortae unite to form a single median trunk. This vessel



Text-figure 107.

The dorsal aorta and its branches in *Chlamydoselachus*, ventral view. The myelonic (basilar) artery is displaced slightly to one side so as to be seen.

ab, arteria basilaris; *acp*, a. cerebialis posterior; *acr*, a. centralis retinae; *aom*, a. ophthalmica magna; *apsb*, afferent pseudobranchial artery; *da*, dorsal aorta; *ea* 2–3, efferent arteries of second and third branchial arches; *ec*, external carotid artery; *epsb*, efferent pseudobranchial artery; *ic*, internal carotid artery; *lda*, lateral dorsal aorta; *pehy*, posterior efferent hyal artery.

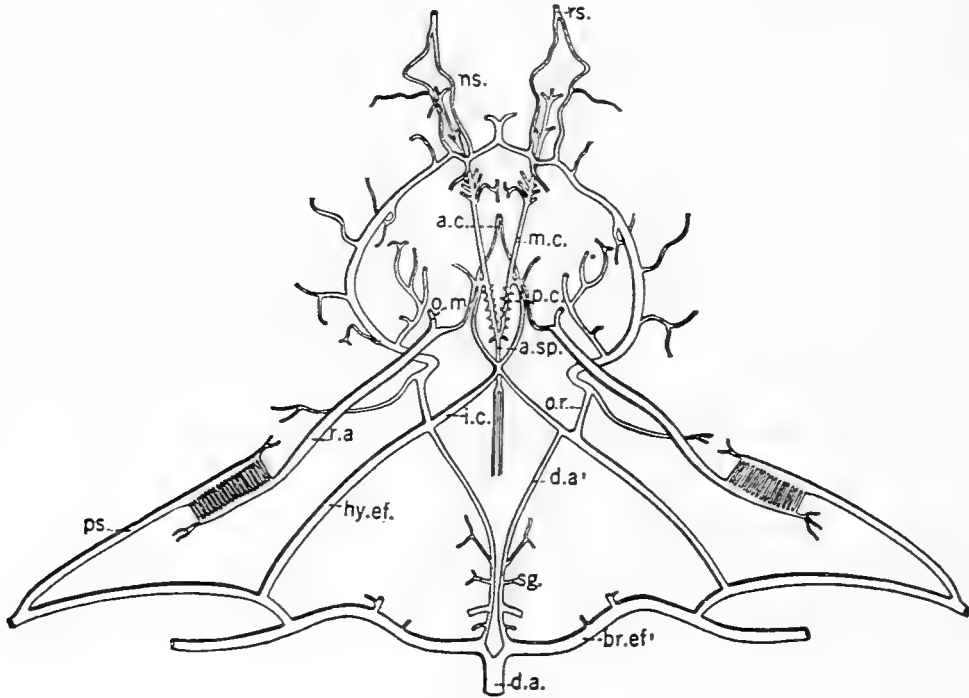
After Allis, 1923, Fig. 60, pl. XXIII.

is said by Ayers to extend forward to the pituitary body, and it is called by him the cranial aorta, that being the name given by Hyrtl to a similar vessel said to have been found by him in *Scyllium*. This median vessel, described in these two fishes, has been discussed by both Dohrn and Carazzi, and there seems some doubt as to its existence; or, if it exists, as to its being an artery. I have accordingly not given any consideration to it in my diagrams.

Further, Allis (1911, p. 516) states concerning the "cranial aorta" of *Chlamydoselachus*: "No trace whatever of such a vessel could be found in either of my two specimens, notwithstanding that it was most carefully and particularly looked for."

Since the discredited concept of a cephalic or cranial aorta existing as a median unpaired structure is of some historical importance, I append a further consideration of it by quoting the following from Corrington (1930, pp. 227–228):

This imaginary artery has been one of the causes operating to delay recognition of the paired dorsal aortae. First described by Hyrtl (1872) in *Catulus*, its status and importance were established by the author's prestige. Later Ayers (1899) reported the same vessel in *Chlamydoselachus*, seemingly to place this artery on a firm basis. But many other workers have since been unable to find any trace of it whatever in any species, either in embryo or adult. Dohrn attempted to explain Ayers's paper but only confused matters the more, and



Text-figure 108.

The dorsal aorta (anterior portion) and its branches, also the first efferent branchial artery and its branches, in *Heptanchus maculatus*.

ac., anterior cerebral; *a.sp.*, arteria spinalis; *br.ef.1*, first branchial efferent; *d.a.1*, paired dorsal aorta; *d.a.*, dorsal aorta; *hy.ef.*, hyoidean efferent; *i.c.*, internal carotid; *m.c.*, median cerebral; *ns.*, nasal artery; *o.m.*, ophthalmica magna; *or.*, orbital artery; *p.c.*, posterior cerebral; *ps.*, pseudobranchial artery; *r.a.*, ramus anastomoticus; *rs.*, rostral artery; *sg.*, segmental artery.

After Daniel, 1934, Fig. 152.

it remained for Allis (1911.2) to re-examine the same species and to expose so many other glaring errors in the previous work that Ayers's description has been entirely discredited.

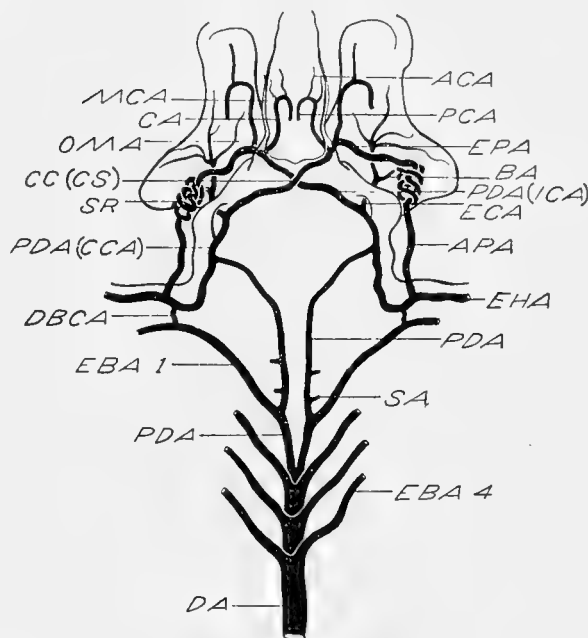
These paragraphs furnish the most striking case encountered in this investigation illustrating the danger of (1) erecting specific types from the dissection of a single specimen; (2) not making adequate allowance for a possible high degree of variability; and (3) attempting to establish adult homologies without thorough embryological preparation.

The bifurcation of the dorsal aorta anteriorly, as portrayed in Text-figures 107, 108 and 109, of *Chlamydoselachus*, *Heptanchus* and *Squalus* respectively, is a feature common to all elasmobranchs, so far as known. From an embryological point of view this is

a primitive condition since, in the early embryo, the dorsal aorta is paired throughout its entire length. As students of embryology know, the members of this pair of vessels meet in the median line, throughout the greater part of their length, to form the single dorsal aorta of adult anatomy. In gnathostomous vertebrates generally, the common carotid and the internal carotid arteries are regarded as anterior portions of the primitive dorsal aortae, which persist in the paired condition throughout life. These considerations lend interest to the study of these arteries in *Chlamydoselachus*. My Text-figures 107 and 110, after Allis, will enable the reader to follow the description of these arteries which I quote from Allis (1911, pp. 516-518) as follows:

Running forward and slightly laterally, immediately beneath the broad and rounded base of the chondrocranium, the lateral aorta [*lda*] of each side is joined by the corresponding efferent hyoidean artery and then soon turns sharply laterally and, at the edge of the base of the chondrocranium, receives the commissural vessel . . . from the efferent hyoidean artery; this commissural vessel being considerably larger than the lateral aorta. The latter vessel, now becoming the common carotid, turns sharply forward, at an acute angle, in the direction prolonged of the commissural vessel, runs forward and slightly mesially along the lateral edge of the ventral surface of the chondrocranium, and soon gives off its external branch. . . .

The internal carotid, which is the anterior prolongation of the lateral dorsal aorta beyond the point of origin of the external carotid, runs forward and mesially along the base of the chondrocranium and, not far from the median line, traverses a foramen in the base of the skull and enters the cranial cavity. . . . Having entered the cranial cavity, the internal carotid meets in the median line and anastomoses with, or is connected by a short commissure with its fellow of the opposite side, and then immediately turns directly laterally, and then forward and laterally in the cavity. There it is soon joined by the efferent pseudobranchial artery, which artery enters the cranial cavity by traversing a foramen in the orbital wall immediately anteroventral to the base of the eye-stalk. . . . Having been joined by the efferent pseudobranchial artery, the internal carotid soon gives off an optic branch and then separates into anterior and posterior cerebral branches, the latter of which



Text-figure 109.

The carotid system of arteries in *Squalus acanthias*, ventral aspect.

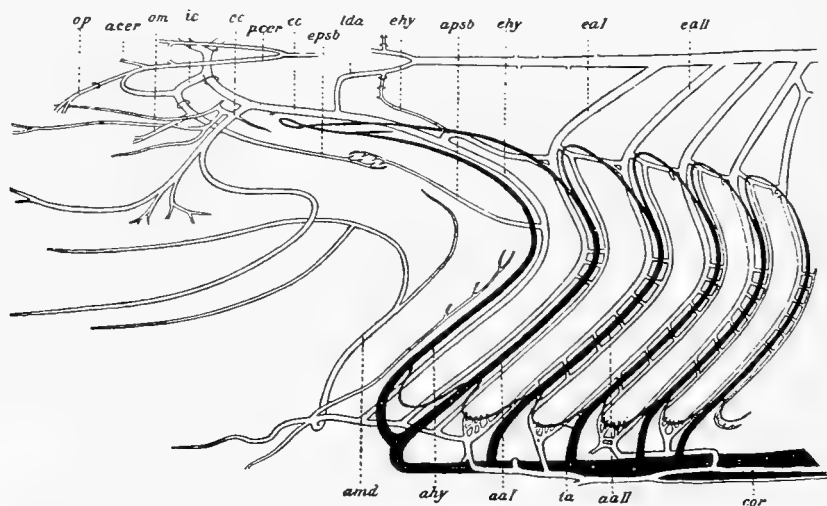
ACA, anterior cerebral artery; APA, afferent pseudobranchial artery; BA, buccal artery; CA, cerebral artery; CC, carotid crossing; CCA, common carotid artery; CS, cephalic sinus; DA, dorsal aorta; DBCA, dorsal branchial commissural artery; EBA, efferent branchial artery; ECA, external carotid artery; EHA, efferent hyal artery; EPA, efferent pseudobranchial artery; ICA, internal carotid artery; MCA, middle cerebral artery; OMA, ophthalmic artery; PCA, posterior cerebral artery; PDA, paired dorsal aorta; SA, segmental artery; SR, spiracular retia.

From Corrington, 1930, Text-fig. 22; after Hyrtl, 1872.

fuses posteriorly, in the median line, with its fellow of the opposite side, to form a single median myelonie artery. The optic artery issues from the cranial cavity with the nervus opticus and penetrates the eyeball with or near that nerve.

My Text-figure 107 of *Chlamydoselachus* (after Allis) should be compared with Text-figures 108 (after Daniel), and 109 (from Corrington, after Hyrtl), showing the corresponding arteries for *Heptanchus* and *Squalus* respectively.

THE BRANCHIAL ARTERIES.—Either Ayers' (1889) figures (reproduced as my Text-figures 105 and 106) are inaccurate, or his specimen of *Chlamydoselachus* was anomalous



Text-figure 110.

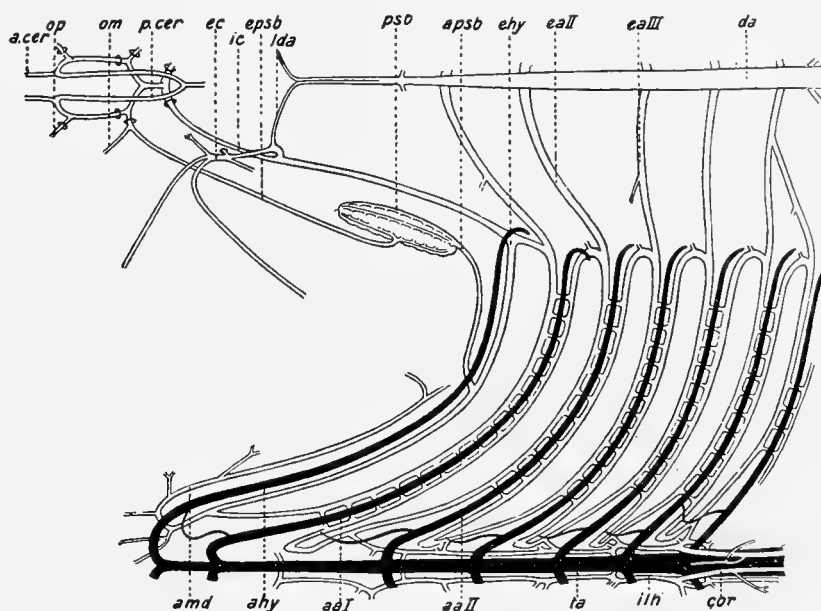
Branchial, pseudobranchial and carotid arteries of *Chlamydoselachus*.

aaI, II, etc., afferent arteries in the 1st, 2nd etc. branchial arches; acer, anterior cerebral artery; ahy, afferent hyoidean artery; amd, afferent mandibular artery; apsb, afferent pseudobranchial artery; cc, common carotid; cor., coronary; da, dorsal aorta; eaI, II etc., efferent arteries in 1st, 2nd etc. branchial arches; ec, external carotid; ehy, efferent hyoidean artery; epsb, efferent pseudobranchial artery; ic, internal carotid; lda, lateral dorsal aorta; om, arteria ophthalmica magna; op, optic artery; pcer, posterior cerebral artery; psb, pseudobranch; ta, truncus arteriosus.

After Allis, 1911, Fig. 1.

in this respect: only one efferent-collector artery is shown in each gill-arch, whereas in all other specimens of *Chlamydoselachus* that have been examined, my own specimens included, there are two such arteries. To be sure, Goodrich (1909, p. 137) wrote: "Except in *Chlamydoselachus*, the branchial arches of the Selachii, like those of the Dipnoi, have two efferent arteries;" but it is probable that Goodrich merely accepted Ayers' account without verifying it. In his later (1930) text, Goodrich figures *Chlamydoselachus* with two efferent arteries in each gill-arch. Allis (1908) at first accepted Ayers' description of the efferent branchial arteries, but later (1911) he prepared a figure (my Text-figure 110) based on dissections of his own material, and commented (pp. 511-512) on the results as follows:

In 1889 Ayers, in a work entitled "The Morphology of the Carotids," described the branchial and carotid arteries in *Chlamydoselachus*, and these arteries, as described by him, were in certain respects quite unusual. Ayers himself called especial attention to this fact, and on the conditions, as described by him, he based certain quite important conclusions. In 1908 I had occasion to consult this work by Ayers, and I then published (Allis, 1908) a diagrammatic representation of the carotid and related arteries in this fish, as described by Ayers but as interpreted by myself. The diagram was, however, most unsatisfactory, and



Text-figure 111.

Branchial, pseudobranchial and carotid arteries of *Heptanchus cinereus*.

aaI, II, etc., afferent arteries in the 1st, 2nd etc. branchial arches; acer., anterior cerebral artery; ahy, afferent hyoidean artery; amd, afferent mandibular artery; apsb, afferent pseudobranchial artery; cor, coronary artery; da, dorsal aorta; ea.I.II. etc., efferent arteries in the 1st, 2nd, etc. branchial arches; ec, external carotid; ehy, efferent hyoidean artery; epsb, efferent pseudobranchial artery; ic, internal carotid; ilh, internal lateral hypobranchial artery; lda, lateral dorsal aorta; om, ophthalmica magna artery; op, optic artery; p.cer, posterior cerebral artery; psb, pseudobranch; ta, truncus arteriosus.

After Allis, 1912, Fig. 1.

having since received several heads of this fish, most kindly sent me by Prof. Bashford Dean, I have had dissections made of the arteries concerned, in two of them, the dissections being prepared by my assistant, Mr. Jujiro Nomura. The arteries, as I find them, are shown in the accompanying Figure 1 [my Text-figure 110]. . . .

The arteries in *Chlamydoselachus* . . . differ in no important particular from those in the Scylliidae and in *Mustelus* (Allis, 1908), excepting in that the dorsal end of the efferent hyoidean artery has, in *Chlamydoselachus*, a double connection with the lateral dorsal aorta.

In *Chlamydoselachus*, as in elasmobranchs generally, the efferent-collector arteries (Text-figure 110) form complete loops around each gill-cleft excepting the last one. To be

sure, Ayers notes the absence of such loops in his specimen, but they are shown in various figures by Allis (1911 and 1923). In *Chlamydoselachus* a posterior efferent-collector may retain a dorsal connection with the anterior efferent-collector of the same gill (Text-figure 110), an arrangement not usually found in adult elasmobranchs though commonly present in their early embryos.

As portrayed in Text-figure 110, the afferent branchial arteries of *Chlamydoselachus*, excepting the hyoidean and the last branchial, bifurcate dorsally, one branch passing over the cleft anteriorly to join the afferent in front, the other passing posteriorly over the succeeding cleft to join the following afferent. Thus the afferents, like the efferents, are connected into a series of loops around all the clefts. Complete afferent loops are not found in other sharks. Basing his opinion upon what is known concerning the manner of development of the branchial arteries in other sharks (particularly in *Squalus* as described by Scammon, 1911), Corrington (1930) concluded that the anastomoses which complete the afferent loops around the gill-clefts in *Chlamydoselachus* could arise only late in embryonic development, after the arterial pattern had been nearly completed; therefore they are among the most recent acquisitions of the branchial arches. They represent a secondary and specialized condition—an interpolation—in *Chlamydoselachus*, and are probably incipient in *Heptanchus* (Text-figure 111).

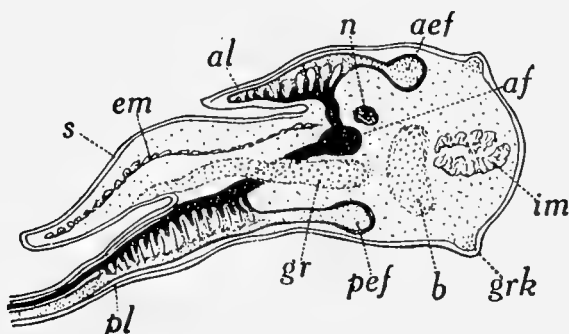
In elasmobranchs generally, each epibranchial artery of the early embryo is situated dorsal to a gill-arch; but in later development these arteries become shifted to positions dorsal to the respective gill-slits (Goodrich, 1930, Figs. 531A-D and 532). In *Chlamydoselachus*, the epibranchial arteries of the adult (Text-figure 110) are situated dorsal to the respective gill-arches—that is, they retain what is presumably their embryonic position. According to Allis (1912) they are very nearly in the same position in *Heptanchus* (my Text-figure 111).

Corrington (1930, p. 198) suggests that, since Daniel has given us the apt designation of efferent-collector artery for the lower forks that gather up the oxygenated blood from the gills, we may restrict the name efferent branchial artery to the upper and single trunk, thus expressing its revehent correspondence to the afferent branchial artery in their relationships to the gills. Epibranchial thus becomes a synonym for efferent branchial. Concerning the efferent branchial (epibranchial) arteries in elasmobranchs, Corrington (pp. 198–199) writes as follows:

The first of the series is the efferent hyal artery which courses forward and has been . . . long identified with the carotid system. . . . Then follow 4, 5 or 6 efferent branchials, depending on the species, and conforming to the number of gills and of afferents, as previously noted. Usually these are all separate, but in *Notorhynchus*, *Heptanchias* [*Heptanchus*], *Chlamydoselachus* and doubtless in other notidanids, the last efferent joins the penultimate midway of its course so that the two have a common stem thence to the aorta. The condition indicates the approaching loss of the last gill in each case, and is a parallel circumstance to the fusion of the pharyngobranchials of the last two skeletal arches, so commonly seen in sharks.

ARTERIOLES WITHIN THE GILLS.—In searching the literature on *Chlamydoselachus*, I have found nothing on the blood-vascular system within a gill proper. In order to study this I have been obliged to prepare serial sections of gill-arches and holobranchs excised from my specimens.

The general plan of the blood-vascular system within a gill is indicated in my Text-figures 78, 79 and 80 (see pages 421 and 422), which do not, however, show any capil-



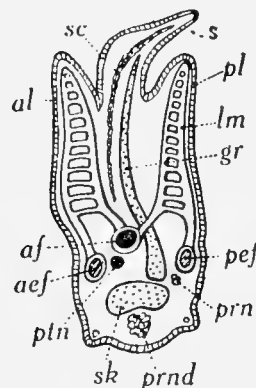
Text-figure 112.

Sections through gills of elasmobranchs, showing afferent and efferent vessels.

Text-figure 112. Section across gill-bar of *Scyllium canicula*, late embryo 32 mm. long, showing blood supply to lamellae.

aef, anterior efferent artery; *af*, afferent artery; *al*, anterior lamella (filament); *b*, branchial bar; *em*, external constrictor muscle; *gr*, gill-ray; *grk*, gill-raker; *im*, adductor branchialis muscle; *n*, nerve; *pef*, posterior efferent artery; *pl*, posterior lamella (filament) continued into external filament (not present in adult); *s*, gill-septum.

After Goodrich, 1930, Fig. 516.



Text-figure 113.

Text-figure 113. Diagram illustrating the structure of a gill of a selachian.

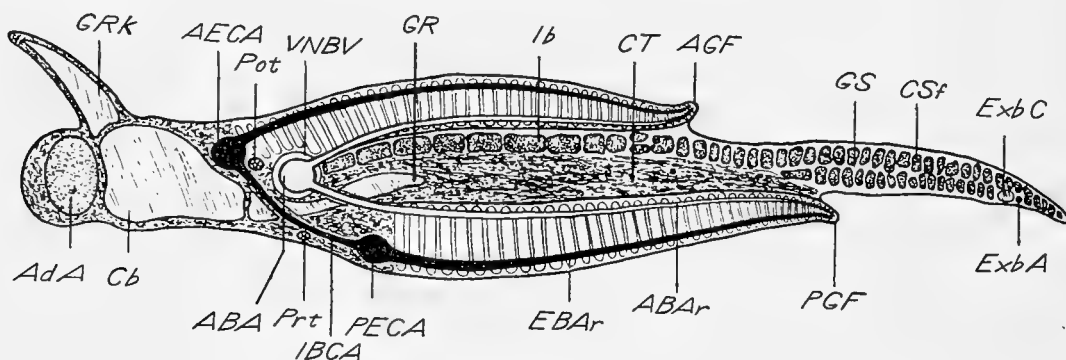
aef, anterior efferent artery of arch; *af*, afferent artery of lamella (filament); *al*, anterior lamella (filament); *gr*, gill-ray; *lm*, capillary network; *pef*, posterior efferent artery; *pl*, posterior lamella (filament); *prn*, pretrematic nerve; *prnd*, branchial muscle; *ptn*, post-trematic nerve; *s*, outer region of septum; *sc*, superficial constrictor muscle; *sk*, skeletal arch.

After Goodrich, 1930, Fig. 517b.

laries. An afferent artery, (*af. br. a.* in Text-figure 78), coursing along the outer side of the gill-arch, gives off a branch (afferent branchial arteriole) to each filament. Each afferent arteriole passes along the base of the corresponding filament (Text-figure 78), giving off numerous branches to it (Text-figures 79) and also to the septum. The precise manner of this branching has not been fully worked out, since the task requires an elaborate reconstruction, but it is evident that many of the arterioles are here somewhat lacunar in character. An efferent branchial arteriole (*ef. br. a.* in Text-figure 78) courses along the outer edge of each filament, returning the blood from the capillaries of the filament to an efferent-collector artery of the gill-arch. A fairly large vein, (*v.* in Text-

figure 78), presumably draining the blood from smaller vessels in the gill-septum, was found in the proximal portion of the septum. Just proximal to the main afferent artery of the gill-arch, in the location where an extension of the coelomic cavity presumably occurs in the early embryo, there is a fairly large space which probably represents a lymphatic vessel whose thin wall is incompletely preserved.

The distribution of arteries within a gill of *Chlamydoselachus* is essentially the same as in other elasmobranchs, e. g., as in *Heptanchus* (Text-figure 81, p. 423); in *Scyllium* (Text-figure 112); and in selachians generally (Text-figures 113 and 114). Of these figures, Corrington's (my No. 114) is the only one showing an intermediate branchial



Text-figure 114.

Frontal section through a shark-gill, drawn semidiagrammatically.

ABA, afferent branchial artery; ABAr, afferent branchial arteriole; AdA, adductor arcus; AECA, anterior efferent-collector artery; AGF, anterior gill-filament; Cb, ceratobranchial; CSf, constrictor superficialis; CT, connective tissue; EBAr, efferent branchial arteriole; ExbA, extrabranchial artery; ExbC, extrabranchial cartilage; GR, gill-ray, distal portion not shown; GRK, gill-raker; GS, gill-septum; Ib, intrabranchialis; IBCA, intermediate branchial commissural artery; PECA, posterior efferent collector artery; PGF, posterior gill-filament; Pot, post-trematic ramus, branchial nerve; PRt, pretrematic ramus, branchial nerve; VNBV, ventral nutrient branchial vein.

After Corrington, 1930, Fig. 10, p. 200.

commissural artery (IBCA) connecting the two efferent-collector arteries of a single gill. Such arteries exist in *Chlamydoselachus* (Text-figure 110) as well as in many other elasmobranchs. In some of my sections, I have observed a small artery in the appropriate location for an intermediate commissural artery but was unable to trace its connections due to the lack of a sufficient number of sections in the series.

The gill-filaments of *Chlamydoselachus* contain few capillaries; they consist chiefly of connective tissue traversed by arterioles and bounded by a very thin integument. They serve, therefore, mainly as supports for the lamellae which are the essential organs of respiration. The lamellae are exceedingly rich in capillaries. In a section, such as that shown in outline in my Text-figure 80 (p. 422), most of the capillaries are cut transversely. Since the lamellae are only slightly thicker than the capillaries when the latter are distended with blood (as they usually are in my sections), each capillary comes in contact with the integument on two sides. So rich is the capillary plexus that there is scarcely any space between capillaries; in sections where the capillaries are cut transversely they look somewhat like a string of beads.

In studying the blood-vascular system of the gills of *Chlamydoselachus*, one is impressed by the enormous increase in the cross-sectional area of the blood stream as it leaves the gill-arch, as it enters the filaments, and again as it reaches the plexus of capillaries in the lamellae. There is a corresponding decrease as the blood returns to the main efferent branchial arteries. The total arrangement functions to reduce the velocity of the blood as it passes through a multitude of tiny capillaries.

In the section on the respiratory system I have pointed out that in proportion to body size the respiratory surface in *Chlamydoselachus* is very large—perhaps larger than in most sharks. It seems likely that in fishes that live in the deeper waters of the ocean, where it is always cold and where oxygen is not so plentiful as at the surface, there is need for more efficient organs of respiration; but adequate data for comparison are not available.

In his well-organized treatise on the anterior arteries of sharks, Corrington (1930) gives a refreshingly clear presentation of the essential data, illuminated by discussions of its significance from a comparative point of view. His synonymy for these arteries will be found very useful. Some remarks by Corrington (p. 205) on the hypobranchial system of arteries will perhaps explain why I have not included a comparison of these vessels in *Chlamydoselachus* with those of the same region in other sharks:

These [hypobranchial arteries] are the last arteries of the head to be formed before assumption of the adult condition. This lateness of development and also absence in lower groups argue that this system was one of the last vascular acquisitions of the immediate shark ancestor. Increased bulk and muscular specialization of the subpharyngeal, interbranchial area demanded an extra mechanism for nutritive supply, and this was hence derived from the nearest source. No homologies involving the alteration of any elements previously present are necessary or possible, and none have been suggested as far as I am aware. . . . There is no type arrangement for these arteries in either the Class or Order, or even in various species, so that description must be of a somewhat general nature.

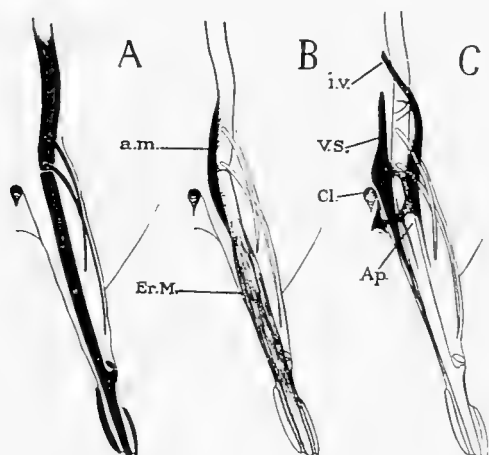
The most elaborate figures of the arteries of the head of *Chlamydoselachus* are those of Allis (1923). These (which are in color) should be consulted by any one wishing a more comprehensive account than is given here.

THE VEINS

Very little work has been done on the venous system of *Chlamydoselachus*. Ayers (1889) states that extensive venous sinuses, always simple in character, are developed in the course of the large venous trunks. Portions of the principal venous trunks are shown in Text-figure 105, copied from Ayers. These vessels are the internal jugular vein (*i.j.v.*), the cardinal vein (*c.v.*), the hepatic vein (*h.v.*), and the tropeic or lateral abdominal vein (*tr.*). The cardinal sinus (*c.s.*) seems unusually large, as in my own specimens. The marked development of the venous sinuses is regarded by Ayers as a primitive character.

Hawkes (1906, p. 983) states that in *Chlamydoselachus* the anterior cardinal vein lies in the vicinity of the vanished seventh gill-cleft, though in most elasmobranchs it is in the position of the missing sixth gill-cleft.

The claspers of *Chlamydoselachus* have been studied comprehensively by Leigh-Sharpe (1926). His Fig. 5A-C (my Text-figure 115A-C) shows the endoskeleton, certain muscles, and the venous sinuses of the claspers. His Figures 5A and B have been referred to in the sections on the endoskeleton (p. 376) and muscular system (p. 395) respectively. The venous sinuses of the claspers of *Chlamydoselachus* are described by Leigh-Sharpe (1926, pp. 312-313) as follows:



Text-figure 115.

Claspers of *Chlamydoselachus* in ventral aspect: A, the cartilages; B, the musculature; and C, the venous system of the clasper.

a.m., antero-flexor muscle; Ap., position of apophysis; Cl., cloaca; Er.M., erector or expansor muscle; i.v., iliac vein; V.S., venous sinus.

After Leigh-Sharpe, 1926, Fig. 5.

The main blood-vascular system is composed of two venous sinuses, parallel to, and on either side of, the myxapterygium (Fig. 5c) [Text-figure 115c], in connection with which no erectile tissue could be discovered.

The inner [sinus], which is the longer and more superficial (Figs. 4A [my Text-figure 97A, p. 452] and 5c [my Text-figure 115c]), arises posteriorly in the distal third of the clasper, and, surrounding the clasper muscles, ends blindly in the middle line anterior and ventral to the cloaca. Dorsal to the myxapterygial articulation it communicates with the other, more lateral, deep-seated sinus; the latter drains blood from the extra-cloacal region and from the edges of the clasper and, continuing forward, empties its contents into the iliac vein dorsal to the basipterygium. Five nerves, proceeding to the pelvic fin and clasper, traverse this sinus, and also a space (apparently lymphatic) between it and the abdominal muscles. These structures are seen displayed in Fig. 4b [my Text-figure 97b, p. 452], and the entire venous system in Fig. 5c [my Text-figure 115c]. As stated above, the function of the blood-

vascular system in *Chlamydoselachus* does not appear to be that of erection, nor would the metabolism of the muscles supplied by it warrant so extensive a system of vessels. Possibly the sinuses are required to provide easy play for the muscles in the position of antero-flexion.

THE NERVOUS SYSTEM

Although some careful work has been done on the nervous system of *Chlamydoselachus*, much remains to be accomplished before a satisfactory account can be written. The brain has never been adequately described, even superficially, and the spinal cord has been ignored. The functional analysis of the cranial and spinal nerves is incomplete. Save for some references to the ciliary ganglion, the sympathetic system has been wholly neglected. Lack of time and suitable material prevents my attempting to remedy any of these deficiencies.

THE BRAIN

Garman's brief description (1885.2, pp. 16–17) of the brain of *Chlamydoselachus*, illustrated by his Pls. XV and XVI (my Plate VI) is the first, and remains the most comprehensive account of the form and structure of this organ. This comparative neglect may be partly explained by the fact that it appears to be very difficult to obtain specimens in which proper attention has been given to the preservation of the brain. Garman states that the brain of his specimen was very soft. When removed from the skull, it collapsed and spread out, so that the figures sketched are a trifle more broad and flattened than is natural. His entire description follows:

The brain is very small. Comparatively the amount of forebrain is much smaller than in the higher sharks, *Carcharias*, *Zygaena*, and others. In outlines and proportions there is great similarity between this brain and that of the Notidanidae. In both of the genera of that family the brain is equally elongate and the disposition of the nerves is not greatly different; the differences are mainly in details rather than in general build. . . . The olfactory lobe is shorter than that of *Hexanchus* (compare Maclay, *Das Gehirn der Selachier*, Plate II). The olfactory bulb is similar in shape in these genera; it is a club-shaped expansion with lobules at the end from which the nerve distribution takes place. Being broader in front, the hemispheres taper more toward the hypophysis than is the case in *Hexanchus*. As in the latter, the optic lobes are rounded above and in front, and are—when viewed from above—about half exposed.

The cerebellum is of medium size, rather smooth on its upper surface, rounded in front, and presents an acute angle—with blunted apex—between the corpora restiformia. On the upper surface the longitudinal depressions are partly due to the uneven floor of the ventricle, on which the upper walls rest. There are three moderate transverse depressions. In the cerebellum the amount of plication is greater than that in *Hexanchus* as figured by Maclay. There is some likelihood that his figure is taken from a young specimen, and that a large one will be marked by greater complication. In Maclay's figure of *Hexanchus* the folds are represented by a simple upward line with a transverse bar on the top, like a letter T. To represent the same section in the new shark, we shall have to place another T on each end of the transverse bar. Maclay figures a longitudinal section of the cerebellum of a young *Mustelus*, which shows a pretty close agreement. An adult *Mustelus*, which is a great deal more complex, is also figured.

The corpora restiformia are comparatively large; they approach each other behind the cerebellum till there is but a small space between them.

The medulla is large, somewhat larger than the same portion in the Notidanidae. The waved appearance in the sinus rhomboidalis, fourth ventricle, is caused by the transverse bands of fibers in its membranous roof. . . .

The close similarity existing between the brains of *Chlamydoselachus* and the Notidanidae is a strong point in favor of genetic relationship.

From the report on an address by Wilder (1905) before the American Philosophical Society, I quote the following:

Here [in *Chlamydoselachus*] the walls of the forebrain are thinner and less differentiated [than in *Scymnus*], and in the lateral extensions toward the olfactory cups ('nostrils') the so-called cerebral portion expands nearly equally in every direction from the axis represented by the olfactory crus; in most other sharks and in rays or skates the special cerebral extension is

toward the meson or middle line, so as to meet the corresponding part of the other side; in the lamprey the cerebral extensions are away from the meson; in the Dipnoi, as shown by the speaker in 1887, they are downward, while in the ordinary and higher air-breathing vertebrates, reptiles, birds and mammals, the cerebral hemispheres expand mostly upward. It is as if nature had experimented in the four directions at right angles with one another from the primitive condition, nearly as in *Chlamydoselachus*, where the extension is almost uniformly in all directions from the olfactory axis. . . . In this connection the speaker reiterated his previously expressed conviction that in evolution the olfactory portion of the brain had preceded the cerebral; that the ancestral vertebrates needed to smell rather than to think; that the organ of forethought had been, so to speak, an afterthought, and that the cerebral region, so preponderant in man, was rather an offshoot from the olfactory region, and had been interpolated between that and the hinder portions of the brain.

Hawkes' (1906) figures (my Figures 13 and 14, Plate IV) representing dorsal and ventral views of the brain of *Chlamydoselachus* are not well adapted for showing the form of the brain, since each figure shows only a lateral half and some parts have been cut away. In general, the brain appears broader and shorter than in the other figures, and the breadth is particularly noticeable in the region of the medulla. Hawkes' description (p. 987) of the brain follows:

The external features of the brain [of *Chlamydoselachus*] having a typical arrangement, need not be described. . . . Two points only may be noticed: (1) there is a large rhinocoel extending to the end of the olfactory stalk; (2) the dorsal roof of both prosencephalon and rhinocoel is non-nervous. This second point is of considerable interest, as it recalls the condition of *Ammocoetes* and of the teleosts. The non-nervous roof may be regarded as primitive when compared with that of *Ammocoetes*, but as specialized when compared with that of the Teleosts. That a non-nervous roof should be found among the Elasmobranchs is a point of considerable interest, although its significance is as yet undetermined.

It is not clear whether Hawkes made a microscopical examination of the roof described as non-nervous; she states merely that this observation was made on an immature specimen.

Allis's (1923) artistic portrait of the brain of *Chlamydoselachus* is reproduced as my Figure 7, plate III. This figure gives the impression of being accurately drawn from a well-preserved specimen, and is evidently not in any sense a diagram. It should be explained that the membranes enclosing the brain had not been removed. Allis states that this dissection had not been completed nor controlled when work was stopped by the death of his assistant, Mr. Nomura. Comparison of this figure with Daniel's (1934) figure representing a dorsal view of the brain of *Heptanchus* (reproduced as my Figure 28, plate VII), gives point to Garman's remark that the brain of *Chlamydoselachus* closely resembles that of a notidanid. In Allis's figure, the optic lobes seem considerably smaller, and the cerebellum larger, than in *Heptanchus*. The olfactory lobes are longer than those of *Heptanchus*, though Garman says that they are shorter than those of *Hexanchus*. These comparisons are of course based on the proportional size of each part in relation to the total size of the brain. The olfactory tracts diverge more strongly in *Chlamydoselachus* than they do in *Heptanchus*.

Concerning the source of his material for study of the cranial anatomy of *Chlamydoselachus*, Allis (1923, p. 123) wrote as follows:

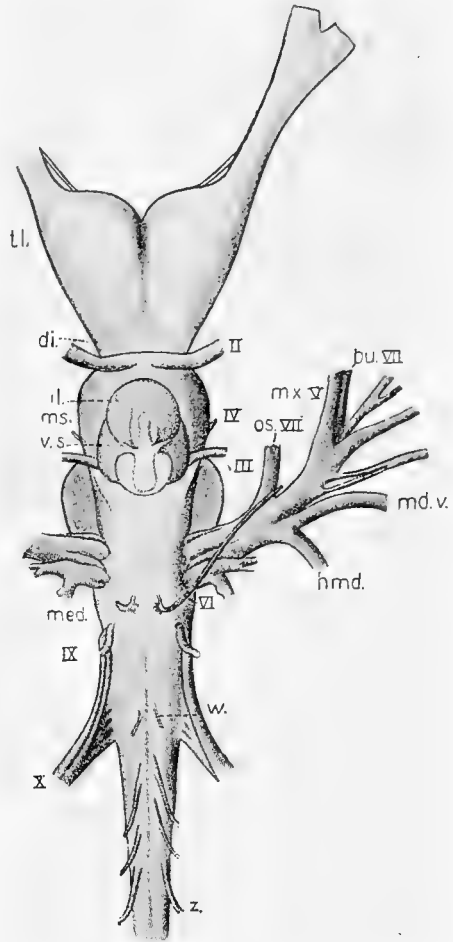
In 1902, Professor Bashford Dean, of Columbia University, New York City, most kindly sent me a single head of *Chlamydoselachus*, and it was given to my assistant, Mr. Jujiro Nomura, for dissection. It was, however, soon found that this one head would not suffice for the work contemplated, and, at my request, Professor Dean had several other heads sent me from Japan.

In all the figures of the brain of *Chlamydoselachus*, the divisions are very incompletely labeled. To one familiar with the structures of the elasmobranch brain, the parts are readily recognizable. In any event they may be identified by reference to my Figure 28, plate VII, and to Text-figure 116, after Daniel, representing dorsal and ventral views of the brain of *Heptanchus*, which is very similar to that of *Chlamydoselachus*.

Today, there are available for comparison a wealth of figures of the elasmobranch brain that were not in existence when Garman wrote his description of the brain of *Chlamydoselachus*. Particular mention should be made of the many fine drawings of selachian brains published, much later, by Garman (1913) himself. These, buried in his great systematic monograph on "The Plagiostomia," have probably never received the attention that they deserve. They do not, however, include figures of the brain of *Chlamydoselachus* nor of any notidanid.

THE CRANIAL NERVES

Garman's (1885.2) account of the cranial nerves of *Chlamydoselachus* is limited to naming them and to describing, in a very general way, the superficial origin of their roots. Hawkes (1906) has given us the only comprehensive and detailed account of the entire series of cranial nerves; her illustrations of these nerves are reproduced herein.



Text-figure 116.

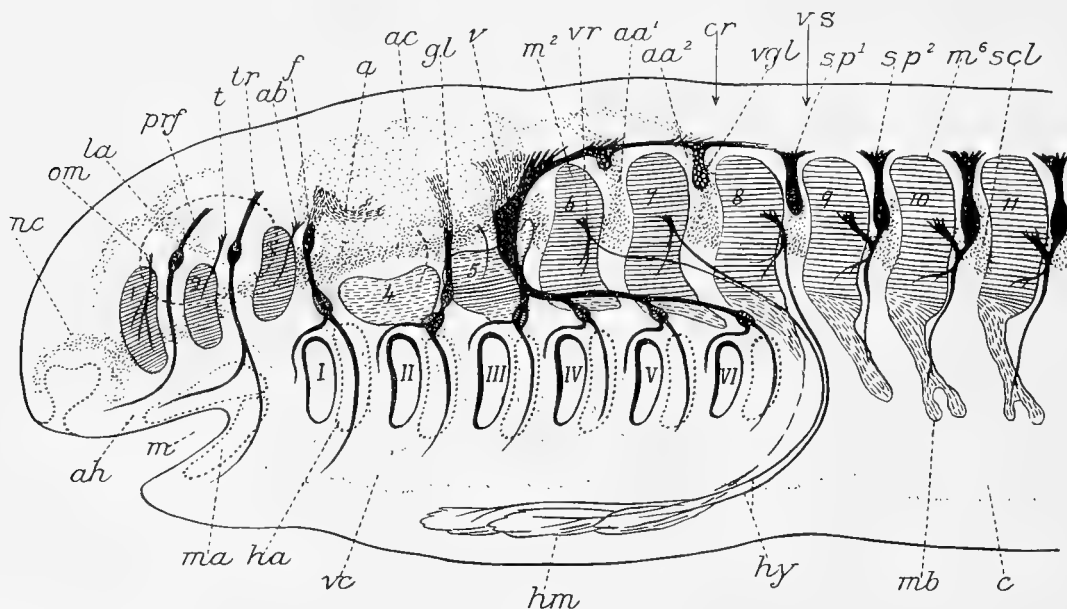
The brain and cranial nerves of *Heptanchus maculatus* in ventral view.

bu. VII, buccal branch of facial nerve; di., diencephalon; hmd., hyomandibular division of the facial nerve; il., inferior lobe; med., medulla; ms., mesencephalon; md. V, mandibular division of the fifth or trigeminal nerve; mx. V, maxillary division of the trigeminal; os. VII, ophthalmic superficialis division of the facial nerve; tl., telencephalon; v.s., vascular sac; w. to z., occipitospinal nerves; II, III, IV, VI, IX and X, cranial nerves.

After Daniel, 1934, Fig. 200b.

Brohmer (1909) described briefly the cranial nerves of a 25-mm. embryo. The account of the cranial nerves by Allis (1923) is, as the author states, incomplete.

The general plan of the cranial nerves of vertebrates is best revealed in their embryos. For the embryo of *Scyllium*, this plan is set forth diagrammatically in Text-figure 117. A somewhat comparable figure for *Chlamydoselachus*, based on a single embryo, is supplied by Text-figure 118, after Brohmer.



Text-figure 117.

Diagram of the segmentation of the head in an embryo of *Scyllium canicula*. The myotomes are longitudinally striated, the nerves black, and the scleromeres dotted. The cartilaginous visceral arches, also the optic capsule and the nasal sac, are represented by dotted outlines.

I-VI, gill-slits; 1-11, somites, prootic from 3 forwards, and metaotic from 4 backwards; a, auditory nerve; ab, abducens nerve; ac, auditory capsule; ah, anterior head cavity; c, coelom in lateral plate mesoblast; cr, limit of cranial region; f, facial nerve; gl, glossopharyngeal nerve; ha, hyoid cartilaginous arch; hm, hypoglossal muscles from myotomes of somites 6, 7, 8; hy, hypoglossal complex nerve; la, lamina antotica; m, mouth; m2, second metaotic myotome; m6, sixth metaotic myotome; ma, mandibular cartilaginous arch; mb, muscle bud to pectoral fin; nc, nasal capsule, continuous with trabecula behind; aa1 and aa2, first and second occipital arches of segments 6 and 7; om, oculomotor nerve; prf, profundus nerve; scl, sclerotome of segment 10; sp1, vestigial dorsal root and ganglion of first spinal nerve; sp2, second spinal; t, trochlear nerve; tr, trigeminal nerve; v, complex root of vagus nerve; vgl, vestigial dorsal root and ganglion of segment 7; vc, ventral coelom extending up each visceral bar; vr, ventral nerve root of segment 6, supplying second metaotic myotome and hypoglossal muscle; vs, limit of visceral region.

After Goodrich, 1918.2, Text-fig. 1.

For the adult *Chlamydoselachus*, the chief cranial nerves are represented in my Figure 29, plate VII. The roots of the cranial nerves are shown in Figures 13 and 14, plate IV, and in Text-figure 119. For comparison, I have inserted a figure showing the cranial nerves of *Squalus* (Text-figure 120). My principal illustration of the cranial nerves of *Chlamydoselachus* (Figure 29, plate VII) is complicated by a diagram of the lateral line system of sensory canals. Hawkes, throughout her work on *Chlamydoselachus*,

devoted much attention to the innervation of the lateral line system, renaming most of the divisions of that system in accordance with their nerve supply—a method first employed by Cole (1896) in his work on *Chimaera*, and which has since been generally adopted.

The reader who is not familiar with the terms employed in the classification, on a functional basis, of the cranial nerve components of fishes should consult Herrick, 1899, pp. 7–19; Johnston, 1905.1, pp. 176–184 and Pl. IV; Norris and Hughes, 1920, Fig. 51, showing the cranial nerve components of *Squalus* in color; and Goodrich, 1930, pp. 725–755.

A complete *résumé* of the rather lengthy descriptions, by Hawkes (1906) and Allis (1923), of the cranial nerves of *Chlamydoselachus* seems unnecessary since, for the most part, these nerves are much like those of other elasmobranchs (e.g., *Heptanchus*, briefly described by Daniel, 1934; and *Squalus*, elaborately described by Norris and Hughes, 1920). It seems sufficient to mention some respects in which the cranial nerves of *Chlamydoselachus* are more or less unique, or in which the descriptions of authors differ. The following account is based primarily on Hawkes' description.

A *nervus terminalis* is not mentioned by Garman, nor is it shown in any of his figures of the brain. It is, however, described by Hawkes (who calls it Locy's nerve, *L.N.*, Figure 13, plate IV) as large and well-defined. Originating near the median line, somewhat to the ventral side of the forebrain, it passes outward, curving upward along the anterior and upper side of the olfactory stalk to be distributed between the end of the stalk and the beginning of the olfactory capsule. On reaching this point, the nerve becomes somewhat enlarged by flattening, then breaks up into a number of fine branches which pass toward the olfactory epithelium but could not be traced to their endings.

Allis (1923) writes that in his specimen a small *nervus terminalis* runs outward along the anterior surface of each tractus olfactorius, and then turns upward onto its dorsal surface, as stated by Hawkes. The terminal portion of the nerve of the left side is shown (without a label) in Figure 7, plate III.

The olfactory nerve of *Chlamydoselachus* is neither figured nor mentioned by any author. From this we may surmise that it is essentially the same as in other elasmobranchs, developing from neuroblasts in the epithelium of the olfactory capsule and extending as a double nerve backward to the olfactory bulb. In *Heptanchus*, as in some other forms, the nerve is so short as to be hardly recognizable without microscopical examination.

The optic nerve (2, Figures 25, 26 and 27, plate VI, after Garman) does not take the most direct route to reach the eyeball. As described by Allis (1923) and as shown in his Figs. 52 and 59 (the latter reproduced as my Figure 7, plate III) this nerve runs antero-laterally. Having issued through its foramen, it turns ventro-latero-posteriorly around the anterior end of the capsular sheath that encloses the orbital process of the palato-quadrates, and reaches the eyeball, passing ventral to the somewhat ligamentous portion of the connective tissue that attaches the capsular sheath to the anterior wall of the orbit.

The innervation of the muscles that move the eyeball is shown (with the exception of the abducens or sixth nerve, which innervates the external rectus) in my Figures 10, 11 and 12, plate IV. The chief peculiarities of the muscles (p. 392, Text-figures 66 and 67) are: (1) the external rectus is divided, as in some other elasmobranchs, into two parts; and (2) all the recti muscles are attached to the top of the eyestalk, near its flattened head. Allowing for these peculiarities of the muscles, the distribution of the third (oculomotor), fourth (trochlear), and sixth (abducens) nerves is the same as in vertebrates generally. The relations of these nerves are described by Allis (1923).

Hawkes states that only one root of the trigeminal nerve (*R.V.* in Text-figure 119A and B) is recognizable macroscopically, though presumably both sensory and motor components are present as in other forms. The single root is broad, but in a side view it is almost completely hidden by the ganglion buccalis (*VII* in Text-figure 119A and B).

The ophthalmicus profundus nerve (*Pro.*), together with the ophthalmicus superficialis *V* (*S.Op.V.*), originates from a small enlargement (presumably ganglionic) on the inner side of the Gasserian ganglion (*V* in Text-figure 119B). Thus, as in *Chimaera* (Cole, 1896) and in *Petromyzon* (Johnston, 1905.2), there is evidence that, at the present time, the profundus (*prf.*) is a branch of the trigeminal, although in origin it belongs to a more anterior segment (Johnston, 1905.1), as shown for *Scyllium* in Text-figure 117. In both *Chimaera* and *Petromyzon*, the profundus nerve has an undoubted ganglion. The distribution of this nerve is described by Hawkes (1906, p. 971) as follows:

On entering the orbit the [profundus] nerve passes between the large rectus externus muscle and the cranial wall, sending dorsally a long ciliary nerve which ends around the upper part of the eyeball. The main nerve then passes outward, parallel with the oculomotor nerve, to which it sends or from which it receives an anastomosing branch. Five mm. beyond the origin of the ciliary branch the profundus passes somewhat ventrally between the eyeball and the external rectus muscle to disappear in the eyeball, near the point of insertion of the ventral part of the external rectus muscle. The profundus passes for about 1 cm. under the covering membrane of the eyeball, emerging near the point where the optic nerve originates from the eyeball. The nerve then passes anteriorly and out of the orbit immediately to the outer side of the attachment of the inferior oblique muscle. Almost at once the nerve divides into a number of branches, which spread over the olfactory capsules immediately below the skin.

The course of the profundus nerve in the region of the eyeball is illustrated in Figures 10 and 12, plate IV, after Hawkes, who suggests that the anastomosis (*A.B.*) between the profundus and the oculomotor nerve may comprise the fibers that connect the ciliary ganglion and the oculomotor nerve, which here pass not directly to the ciliary ganglion, but by way of the profundus. The distribution and relations of the profundus nerve in the region of the eyeball are described in more detail by Allis (1923).

Brohmer (1909) states that in his 25-mm. embryo of *Chlamydoselachus* the ciliary ganglion occurs in the course of the nervus ophthalmicus profundus, which sends a branch to the "nerve knot" on the wall of the premandibular cavity (Text-figure 118). From the nerve knot a branch, which Brohmer calls the oculomotorius (*Oc.*), extends forward.

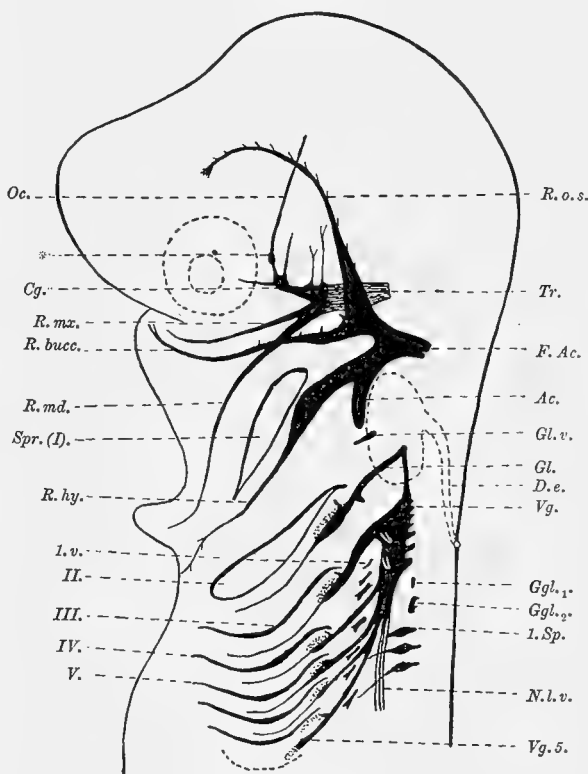
He was unable to trace this nerve to the brain. In his summary (p. 677) he writes: "Der Oculomotorius steht mit dem Trigeminus in Verbindung."

Ziegler (1908) remarks that the 25-mm. embryo of *Chlamydoselachus* studied by his pupil, Brohmer, was cut in "eine lückenlose Schnittserie." Ziegler's account of the cranial nerves of *Chlamydoselachus*, which is based on Brohmer's studies and some observations of his own, is largely a confirmation of Brohmer's results. Ziegler evidently believes that, in elasmobranchs generally, the ciliary ganglion is closely associated with the profundus nerve, though many authors have emphasized its relation to the oculomotor.

In various selachians, one or more small (ciliary) ganglia are related to the oculomotor nerve (Daniel, 1934). These ganglia give rise to nonmedullated fibers which make up the short ciliary nerve. In *Squalus* (Norris and Hughes, 1920) the ciliary ganglion is connected by fibers with the oculomotorius, the ophthalmicus profundus V, and the palatinus VII nerves. A review of the literature on the relations of the ciliary ganglion in elasmobranchs is given by Norris and Hughes (1920).

In *Chlamydoselachus* the superficial ophthalmic V, according to Hawkes, passes from the Gasserian ganglion side by side with the profundus nerve, which it equals in size. It at once passes dorsally and enters the same groove as the ophthalmicus superficialis VII, with which, however, it does not unite. About as far forward as the external nares, but nearer the median line, it spreads out into many branches which lie immediately under the skin. This nerve apparently contains only cutaneous elements. A somewhat different account of the same nerve is given by Allis (1923, pp. 210-211) as follows:

The ramus ophthalmicus superficialis trigemini, as I define this nerve, includes the similarly named nerve of Merritt Hawkes' descriptions and her ramus ophthalmicus superficialis facialis, and these two nerves were completely fused with each other in the two specimens examined, instead of



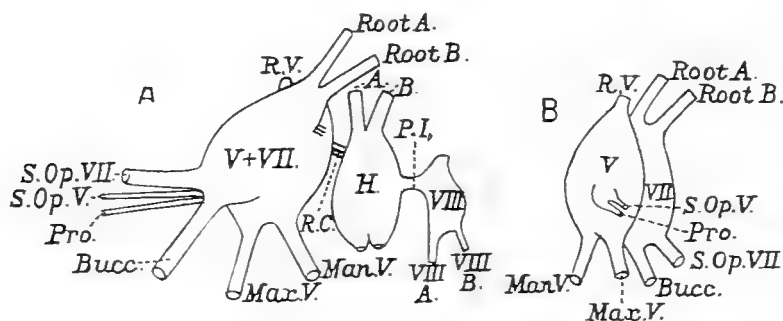
Text-figure 118.

Reconstruction of the cranial nerves in a 25-mm. embryo of *Chlamydoselachus*.

Ac., nervus acusticus; Cg., ciliary ganglion; D.e., ductus endolymphaticus; F.Ac., n. facialis acusticus; Ggl.1, Ggl.2, remnants of the ganglionic crest; Gl., n. glossopharyngeus; Gl.v., ventral root of the glossopharyngeal nerve; N.l.v., n. lateralis vagi; Oc., n. oculomotorius; *, nerve knot in the premandibular cavity; R.bucc., ramus buccalis; R.hy., ramus hyoideus; R.md., ramus mandibularis; R.mx., ramus maxillaris; R.o.s., ramus ophthalmicus profundus; Spr. (I), spiracle (first gill-cleft); Tr., n. trigeminus; Vg., roots of the vagus nerve; Vg.5., the last branch of the vagus; I.Sp., first spinal ganglion; I.v., first ventral root (of the occipitospinal nerves); II, III, IV, V, second to fifth gill-clefts.

After Brohmer, 1909. Text-fig. 10.

being wholly independent, as Merritt Hawkes describes and shows them. Furthermore, it is to be noted that the origin of her ophthalmicus superficialis trigemini from that small swelling on the inner side of the Gasserian ganglion from which the ophthalmicus profundus has its origin, would seem to indicate that it is a portio ophthalmici profundus and not a trigeminus nerve, and its origin in *Squalus*, as given by Landacre (1916), and its distribution in the same fish, as given by Norris and Hughes (1920), are not unfavourable to this interpretation of it. The nerve is, however, said by Norris and Hughes to arise from ganglionic cells in the Gasserian ganglion, while the fibers of the ophthalmicus profundus simply traverse that ganglion. The nerve, as I find and define it in *Chlamydoselachus*, is large, and running forward dorsal to all the nerves and muscles of the orbit, traverses the



Text-figure 119.

Gangliated roots of fifth, seventh and eighth cranial nerves of *Chlamydoselachus*: A, lateral view; B, medial (inner) view.

Bucc., ramus buccalis VII; *H.*, ganglion of the truncus hyomandibularis (i.e., the true ganglion of the facialis, combined with the acustico-lateralis ganglion); *Man.V* and *Max.V*, mandibular and maxillary divisions of the facial nerve; *P.I.*, pars intermedia; *Pro.*, profundus branch of the facial; *R.C.*, ramus communicans; *R.V.*, root of trigeminal nerve; *S.Op.V* and *S.Op.VII*, superficial ophthalmic divisions of the fifth and seventh cranial nerves.

After Hawkes, 1906, Figs. 2 and 3, pl. LXVIII.

preorbital foramen and reaches the dorsal surface of the nasal capsule, where it immediately breaks up into numerous branches which spread out, fan-shaped, and innervate the sensory organs of the supraorbital laterosensory canal and the supraorbital ampullae, as shown in the figures. As the nerve traverses the orbit a number of branches are sent upward through the foramina supraorbitalia to the related portion of the supraorbital canal.

The maxillary and the mandibular rami of the trigeminal nerve (*Max. V.* and *Man. V.* in Text-figure 119) come off separately from the Gasserian ganglion; there is no common maxillo-mandibular trunk. This condition is somewhat exceptional among elasmobranchs. Since, in *Chlamydoselachus*, the angle of the jaw is situated far posteriorly, the mandibular nerve leaves the maxillary early in its course and passes over the posterior wall of the orbit to reach the angle of the mouth, as in *Acanthias*. The mandibular nerve does not supply the large median transverse muscle bridging the halves of the lower jaw in the gular region (Fürbringer, 1903; Hawkes, 1906; Luther, 1909; Allis, 1917 and 1923). This unique feature has been fully discussed (p. 399) in the section on the muscular system.

Hawkes finds many small branches of the maxillary nerve which terminate in the mucosa of the roof of the mouth and are therefore visceral, but she thinks it probable that these visceral components belong to the facial nerve and are only secondarily united with the trigeminal.

Every student of comparative anatomy is familiar with the difficulty of separating the fifth and the seventh nerves where parts of different nerves are interwoven or run in the same sheath. Hawkes (1906, pp. 968 and 969) states that in *Chlamydoselachus*:

No complete union between the [fifth and seventh] nerves has been found, except for a distance of about 1 cm. on the left side, where a branch of the ramus buccalis and of the ramus maxillaris are inseparable. The appearance of union occurs chiefly in the region just beyond the orbit, where there are plexiform connections between the buccalis VII, mandibularis V, maxillaris V, and their branches. Here, when two or more nerves come into close contact, they are loosely or tightly bound together by connective tissue, but, in all cases except the one mentioned above, in such a way that a separation can be effected by careful dissection. The smaller branches and these pseudo-unions vary considerably on the two sides of the same specimen and in different specimens. The variability, which is met with in every system of *Chlamydoselachus*, suggests that the species has considerable anatomical instability.

There is considerable difference of opinion as to what parts, in the region of the gangliated roots, belong to the fifth and seventh nerves respectively. In most elasmobranchs the ganglion of the buccal division of the seventh or facial nerve is intimately associated with the Gasserian ganglion, and the two are often inseparable. In *Chlamydoselachus* the two ganglia are distinct medially, as shown in Text-figure 119B, after Hawkes. Concerning some interrelations of the fifth and seventh nerves Allis (1923, pp. 209 and 210) writes:

The nervi profundus and trigeminus, as I interpret these nerves, arise by two main roots, the anteroventral one of which is formed by the combined roots of the profundus and that part of the trigeminus that is currently considered to form the entire nerve. The other root arises by two rootlets, in close connection with the root of the nervus facialis, the two rootlets being the facialis roots A and B of Merritt Hawkes' descriptions. This root joins the anteroventral root inside the cranial cavity, and, in the specimen used for the accompanying Fig. 58, the two roots traverse the membrane that forms the mesial wall of the acustico-trigemino-facialis recess through a single foramen which lies anterior to the foramen for the root of the nervus facialis and wholly separate from it. In the acustico-trigemino-facialis recess these two roots enter a ganglionic complex, but this complex was not particularly examined. According to Merritt Hawkes a ganglion forms on each of the two roots, one of which she calls the Gasserian ganglion and the other the buccalis ganglion, the latter ganglion lying dorsal to the former and wholly [?] separate from it. On the "inner side" of the Gasserian ganglion there is said to be a small swelling, from which the rami profundus and superficial ophthalmic V arise, side by side and of equal size. Comparison of these conditions, as thus described, with those in *Squalus acanthias* and *Mustelus californicus*, as described by Norris and Hughes (1920), would seem to establish beyond question that the anterior root of *Chlamydoselachus* is composed entirely of motor and general sensory (spinal V) fibers, that the little swelling on the inner side of the so-called Gasserian ganglion is the ganglion of the nervus profundus, and that the posterior root of the complex derives

its fibers both from the lateral line lobe and the acusticum. Whether these latter fibers are all strictly laterosensory ones, as Norris and Hughes conclude, or are in part to be compared to the communis fibers that enter into the trigeminus in the Teleostomi, seems to me still an open question. The three fine nerve strands said by Merritt Hawkes to be sent from the Gasserian ganglion to the facialis ganglion are evidently general sensory ones, as Merritt Hawkes suggests.

In one respect, according to Hawkes (1906), the facial nerve is in an unusually primitive condition, in that it has a remnant of the post-trematic ramus quite separate from the truncus hyomandibularis. Hawkes states that a chorda tympani, as defined by Cole (1896) and by Herrick (1899), is present; but Allis (1923) writes that the so-called chorda tympani described by Hawkes seems to be a ramus pretrematicus internus and hence, according to recent opinion, not the chorda. Further, the ramus mandibularis internus passes internal to the ligamentum mandibulo-hyoideum and then forward along the internal surface of the mandible, supplying the tissues of that region. This nerve, according to Allis, is a ramus post-trematicus internus facialis and is the one now generally considered to represent the chorda tympani.

Hawkes describes, in *Chlamydoselachus*, a small branch of the glossopharyngeal nerve innervating neuromasts. A branch similar in function has been described in *Squalus acanthias* by Norris and Hughes (1920), but they state that in *Raja radiata* there are no lateral line elements in the ninth nerve.

Brohmer (1909) finds, between the facialis acusticus and the glossopharyngeal nerves of his 25-mm. embryo, a small ventral root (Text-figure 118, *Gl.v.*) which he interprets as belonging to the glossopharyngeal. He thinks it likely that this ventral root disappears in later stages, and names it "the rudimentary ventral root of the glossopharyngeal nerve." Goodrich (1918.2) represents (by a dotted line in front of *gl.*) this root in his schematic Text-fig. 1, reproduced as Text-figure 117 herein.

Garman (1885.2) states that in his specimen "The tenth pair (vagus) is somewhat asymmetrical, having eight roots on one side and twelve on the other. There are also four pairs of ventral roots near the median line." Hawkes (1906) states that the vagus arises by from nine to twelve roots from the hinder end of the medulla. The lateralis root, which is the most cephalad, is invariably large, the remainder are small. These small roots are not symmetrical in number and arrangement even in the same fish, much less do they agree in different fishes. The roots arise at the same level, being arranged in an arc which extends along the side of the medulla to the beginning of the spinal cord. The roots cannot be assigned to the separate rami, and the ganglia of the vagus cannot be separated completely by gross methods. The ramus lateralis vagi unites closely with the true vagus in the ganglionic region. There is a sixth ramus branchialis vagi which passes toward the remnants of the seventh branchial arch. Hawkes found no trace of any median ventral roots uniting with the vagal complex. Commenting on Garman's statement concerning the presence of ventral roots in his specimen, Hawkes writes: "If Garman were right, his specimen suggests the retention of the somatic motor compo-

ment of the vagus, whereas, in all cases, so far as is known, the remains of that component have passed [as ventral occipitospinal roots] into the hypoglossal. . . . This would indeed be a primitive condition." Garman (1885.2) does not mention any occipitospinal nerves, but the ventral roots labeled "10" in his Fig. A, pl. XVI (my Figure 26, plate VI) are probably occipitospinales.

Hawkes found, in *Chlamydoselachus*, four (pairs?) of spino-occipital (occipitospinal) nerves, which pass out of the cranium by four separate foramina. Three of these roots are shown in Figure 13, plate IV, after Hawkes. No ventral occipitospinal roots are shown in Hawkes' figure of the ventral surface of the brain. She records that two of the occipitospinal roots were placed completely under, the third partly under, the cover of the vagal roots. Immediately outside the cranium the occipitospinal nerves unite into a flattened strand, the hypoglossal nerve. Hawkes states that the third and fourth occipitospinales of *Chlamydoselachus* have each a dorsal branch, which, like the dorsal branches of the succeeding spinal nerves, passes upward and backward. No dorsal branches were found on the first two occipitospinal nerves.

Johnston (1905.1, p. 231) interprets the occipitospinal nerves as follows: "The dorsal and ventral 'hypoglossal' roots need not be considered as *spinalartige* nerves. They probably are not equivalent to spinal nerves at all, but are only the general cutaneous and somatic motor components of nerves of the vagus region, the visceral sensory and motor components of which have been collected into a single large vagus root."

In his 25-mm. embryo, Brohmer (1909) describes and figures (my Text-figure 118) a series of ventral roots lying between the main branches of the vagus. The first of these (1.v.) is present on only one side, and is very small; the others are paired. Brohmer states that six of these ventral roots are occipitospinal nerves, but it seems possible that only four or five of the most anterior ones are really occipitospinales, the remaining posterior ones being ventral roots of spinal nerves. (Daniel, 1934, states that "as many as five" of the ventral occipitospinales have been located on each side in the young of *Heptanchus* and *Chlamydoselachus*). Dorsal to the third and fourth ventral roots, Brohmer found two ganglionic masses (Ggl.1., Ggl.2.), which he interprets as remains of the ganglionic crest. The more posterior of the two masses has two rootlets.

In *Heptanchus* (Fürbringer, 1897; Daniel, 1934) there are four pairs of ventral occipitospinal nerves or roots (Text-figure 116, *w-z*), but only two pairs of dorsal roots (Figure 28, plate VII). The members of the first dorsal pair join the corresponding members of the third ventral pair to form a pair of nerve trunks resembling spinal nerves in that they have both dorsal and ventral roots. The first roots to arise ventrally are near the median line and in origin are not unlike the sixth or abducens nerves.

In a 26-mm. embryo of *Spinax* described by Braus (1899) there were four pairs of ventral roots representing occipitospinal nerves. Of these, one on the left and two on the right were joined by dorsal roots bearing ganglia, thus increasing the resemblance to spinal nerves.

dency toward unification of the system. The trigemino-facial complex is less primitive than that of *Chimaera*, but more so than that of most elasmobranchs. Hawkes' general conclusion is that the cranial nerves of *Chlamydoselachus* are not in so primitive a condition as would be expected from the low position of the species in the taxonomic series, especially as regards the vagus and the lateralis nerves.

THE SPINAL NERVES

Hawkes' description (1906, pp. 985-987) of the spinal nerves of *Chlamydoselachus* is concerned mainly with the spinal nerve roots. I quote her account almost entire:

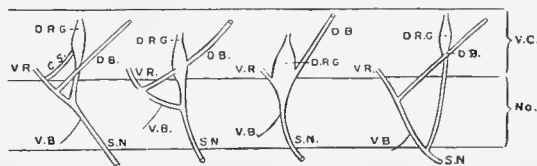
The ventral root of the first true or complete spinal nerve originates between the first and second vertebrae. Spinal nerves 1, 2, 3, 4, 5 (Fig. 1, pl. LXVIII) [my Figure 29, plate VII] unite with the spino-occipital nerves into a strand, which passes backwards, then out-

Text-figure 121.

Diagram of spinal nerves from anterior, middle and tail regions of *Chlamydoselachus*.

C.S., connecting strands between dorsal and ventral roots;
D.B., dorsal branch; D.R.G., dorsal root with its ganglion;
No., notochord; S.N., spinal nerve; V.B., ventral branch;
V. C., vertebral column; V. R., ventral root.

After Hawkes, 1906, Text-fig. 141.

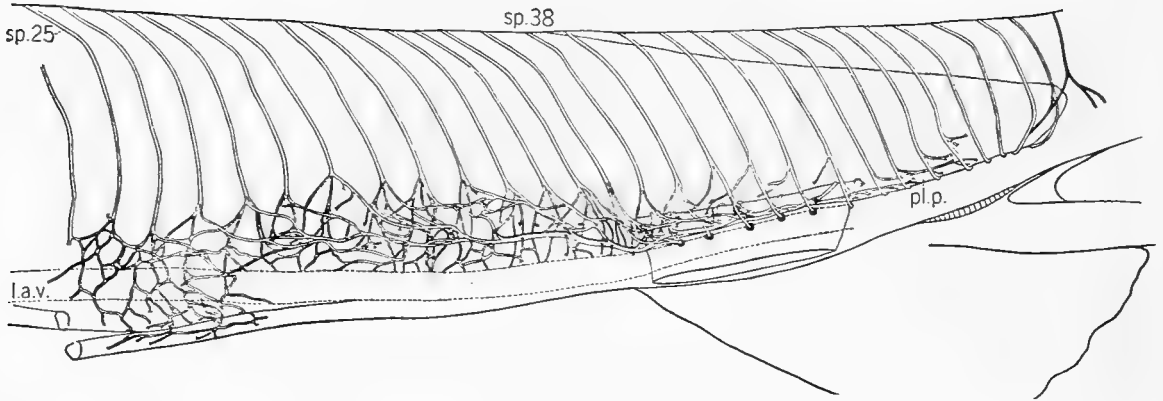


wards towards the pectoral girdle. Spinal nerves 6 and 7 unite with one another before joining this plexus. Spinal nerve 8 runs by its side, but does not actually join. The spinal plexus gives off anteriorly two branches (S.h.1 and S.h.2). Branch S.h.1, which is connected with vagus 6, passes forwards and downwards to join branch S.h.2. The resulting compound nerve passes forward near the median ventral line to supply a portion of the median mandibular or hypoglossal musculature. It is probable that this nerve consists only of fibers from the spino-occipital nerves, and would therefore be the homologue of the hypoglossal nerve of higher forms.

The brachial plexus consists of the remaining parts of the composite strand, i.e., the first eight complete spinal nerves of which the last remains distinct. The brachial plexus is here in a simple condition, for it consists of but few nerves, and those are not intimately united. . . .

Each spinal nerve arises by two alternate roots, a dorsal and a ventral. The ventral root [V.R.] arises by three rootlets, then, after emerging from the vertebral column, gives off a large dorsal branch (Text-fig. 141, D.B.) [my Text-figure 121] before uniting with the dorsal, ganglionated root [D.R.G.]. In the anterior and middle regions of the vertebral column, this union takes place at a level with the top of the notochord, but in the tail region at a level with the base of the notochord, immediately to the inner side of the ramus lateralis vagi. The ventral branch (V.B.) is given off at varying points (Text-fig. 141) [my Text-figure 121].

The dorsal branch (D.B.) of the ventral root runs caudad and upwards, passing over the ganglion of the dorsal root (D.R.G.) to be distributed to the muscles of the middle region of the back. A similar root (ventral-dorsal) has been described by Ewart and Cole in *Raia*. No dorsal branch was found for the complete spinal nerve or for the dorsal root, as it is probable that the dorsal branch of the ventral root receives fibres from the dorsal root as it passes over the latter on its backward course. In one segment (Text-fig. 141) [my Text-figure 121]



Text-figure 122.

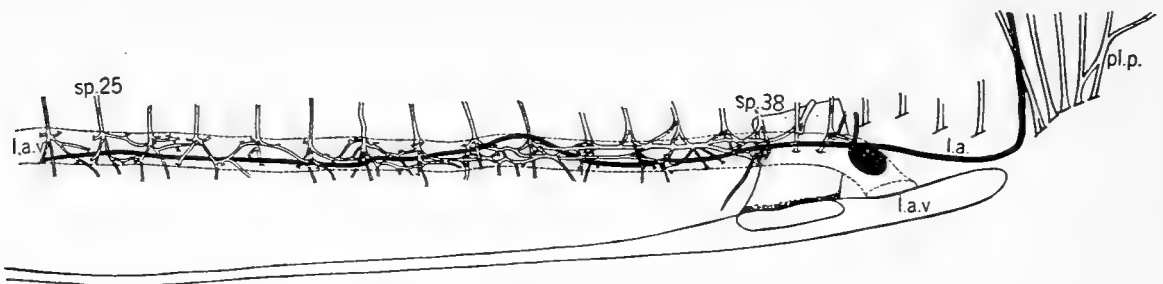
Nervus collector, consisting of longitudinal strands connecting the ventral rami of certain of the spinal nerves, in *Chlamydoselachus*.

l.a.v., lateral abdominal vein; *pl.p.*, pelvic plexus; *sp.25,38*, twenty-fifth and thirty-eight spinal nerves.

From Daniel, 1934, Fig. 224; after Braus, 1898, Fig. 1, Taf. XIII.

the dorsal branch of the ventral root could be seen, by the naked eye, running over the dorsal root ganglion, from which it could not be separated; in the succeeding segment the dorsal and ventral roots were joined in the region of the sensory ganglion, and the dorsal branch appeared to arise from the ganglion itself. The spinal nerves here recall the condition of *Laemargus*, of *Bdellostoma*, and of *Myxine*, in that all three have (1) several rootlets for the ventral root, (2) a dorsal branch from the ventral root which unites with the dorsal root ganglion or with some portion of the dorsal root.

The "nervus collector" studied by Braus (1898) in *Chlamydoselachus* and in a number of other elasmobranchs, consists of one or more longitudinal strands connecting the ventral rami of some of the spinal nerves situated posterior to the pectoral fin and in the region of the lateral abdominal vein. The principal collector nerve of *Chlamydoselachus* (Text-figure 122) is plexiform, and consists of a multitude of anastomosing strands together with some branches that end freely. The nervus collector, though variable, appears to be best developed in primitive forms like *Chlamydoselachus* and *Heptanchus* (Text-figure 123), in both of which the twenty-fifth to the thirty-eight spinal nerves take part. The



Text-figure 123.

Nervus collector, connecting the ventral rami of certain of the spinal nerves, in *Heptanchus cinereus*.

l.a., lateral artery; *l.a.v.*, lateral abdominal vein; *pl.p.*, pelvic plexus; *sp. 25,38*, twenty-fifth and thirty-eighth spinal nerves.

From Daniel, 1934, Fig. 205; after Braus, 1898, Fig. 1, Taf. XI.

collector is much more complex in *Chlamydoselachus* than it is in *Heptanchus*. In other forms few nerves take part (as in *Spinax*), or the collector may be absent (as in *Squatina* and in *Raja*).

The nervus collector has been studied minutely by Braus and others (cited by Osburn, 1906 and 1907) because of its possible relation to the origin of the paired fins, with results that have been interpreted differently by exponents of the gill-arch and fin-fold theories respectively.

From a functional point of view, the nervus collector is somewhat comparable to the caudal longitudinal collecting nerve trunks described by Speidel (1923) in *Squalus acanthias* and in *Raja laevis*. In both cases, the longitudinal trunks and accompanying nervous network provide a conducting system which may be effective in the coordination of muscular action.

The innervation of the trophic folds, described by Braus (1898), has been considered in the section on the muscular system and is illustrated by my Text-figure 59, p. 386.

THE SENSE ORGANS

This account of the sense organs of *Chlamydoselachus* is necessarily very incomplete. None of these organs has been described histologically, and my material is unfit for study in serial sections.

The external openings of the olfactory sacs have been described by Gudger and Smith (1933), whose account is based on the descriptions of various authors, supplemented by their own observations; but the internal structure of the olfactory organs of *Chlamydoselachus* has never been described.

The external appearance of the eye and the peculiar mechanism by which the cornea may be protected in the absence of lids have been described by Gudger and Smith (1933). In the present paper I have described the muscles of the eye and their innervation, in the sections on the muscular system and the nervous system respectively. The internal structure of the eye has never been described.

Of the various sense organs of *Chlamydoselachus*, the lateral line or sensory canal system and associated organs have received the most attention, but even here the various authors (Garman, 1888; Hawkes, 1906; and Allis, 1923) are concerned only with gross structure and distribution. The ear (membranous labyrinth) has been studied and described by Goodey (1910.1).

THE MEMBRANOUS LABYRINTH

Goodey's (1910.1) Figs. 7 and 8, pl. XLIII, illustrating medial and lateral views of the membranous labyrinth of *Chlamydoselachus*, are reproduced as my Figures 30 and 31, Plate VII. His description (pp. 551 and 552) of this organ is best given in his own words:

On removing the skin from the dorsal surface of the cranium it is seen that the parietal fossa is rather deep and possesses four apertures, two on either side of the median longitudinal line. One of these apertures, the anterior, is small, and transmits the ductus endolymphaticus.

The posterior is larger and is closed with soft subcutaneous tissue. It is an opening into the perilymph cavity surrounding the posterior vertical canal, and seems to correspond to the tympanic aperture which Howes (1883) described in *Raia*. Before proceeding further, I may mention that in this account I am following the nomenclature used by Stewart (1906), which differs somewhat from that used by Retzius (1881) in his great monograph.

The ductus endolymphaticus, on emerging from its cranial foramen, soon expands into the saccus endolymphaticus. The latter lies partly in the parietal fossa and is partly attached to the under surface of the skin covering this region. It is fairly regular in shape, somewhat rounded on its anterior surface, and extends posteriorly in a slightly outward direction, gradually becoming attenuated until it reaches its external aperture, which is quite small. Internally the ductus endolymphaticus leads into the sacculus. This is not rounded, but is laterally flattened, and gives off at its postero-inferior end the lagena in the form of a simple caecum.

The utriculus in this species is like that in other Elasmobranchs, being divided into two portions, anterior and posterior, which do not communicate directly with each other, but indirectly through the sacculus.

The anterior utricle is rather laterally compressed and gives off the anterior canal dorsally. The latter curves forward and slightly outward, and describes almost a semicircle in its course, expanding at its lower end into the anterior ampulla, which then opens by a wide portion into the lower end of the utricle again.

The recessus utriculi is a somewhat spherical structure on the inferior and outer border of the anterior utricle. It communicates with the latter by means of a slit-like aperture just below that leading into the ampulla externus. The anterior utricle does not open directly into the sacculus, but communicates indirectly with it through the recessus utriculi, which opens into the sacculus by means of a rounded aperture on the posterodorsal side of the recessus.

Arising from the dorsal end of the anterior utricle, and proceeding in a posterior and outward direction, is the external canal, which bends downward and comes to lie in an almost horizontal position. At its anterior end it is slightly elevated and expands into the ampulla externus, which communicates with the anterior utricle again by means of a short canal which rests on the upper side of the recessus utriculi, but does not open directly into it.

The posterior utricle, which is situated more internally than the rest of the labyrinth, is somewhat cylindrical in shape and is slightly curved upon itself. It communicates directly with the sacculus by means of a short, almost vertical canal, the ductus utriculo-saccularis posterior. Arising from its dorsal end is the posterior canal, which curves outward and downward, and then expands into the posterior ampulla, which opens into the lower end of the utricle again.

All three canals, anterior and posterior vertical, and external horizontal, are not rounded in section, but are markedly flattened, so that their height is equal to about twice their width. The external canal in its almost horizontal position lies with its compressed sides in the horizontal plane.

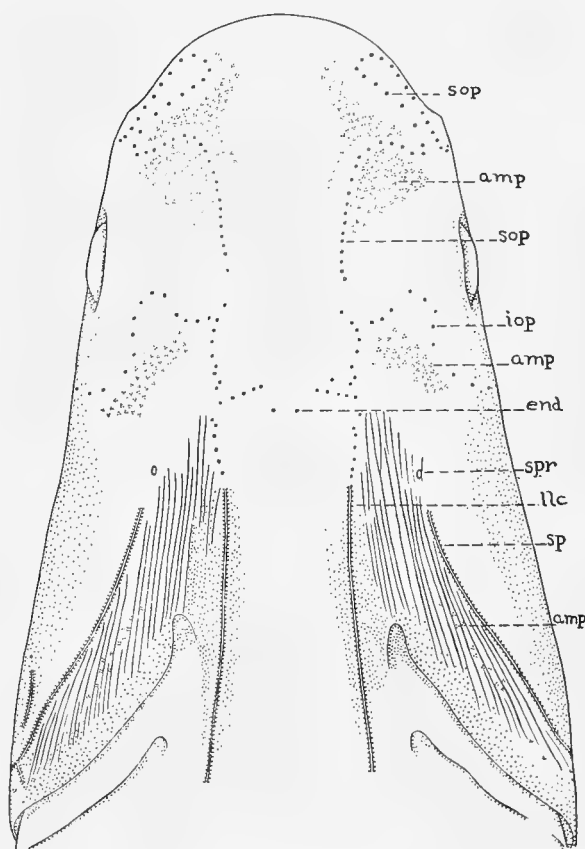
Goodey then continues with an account of the nerve supply of the membranous labyrinth. In conclusion, he states that in structure and in the distribution of the nerve supply the membranous labyrinth of *Chlamydoselachus* resembles rather closely that of *Notidanus* (*Hexanchus*) *griseus* figured by Stewart, 1906. The membranous labyrinth of *Heptanchus* is described and figured by Daniel (1934).

THE SENSORY CANAL SYSTEM

The distribution of the sensory canals of *Chlamydoselachus* has been described by Garman (1888), Hawkes (1906) and Allis (1923 and 1934). Their descriptions have been briefly reviewed by Gudger and Smith (1933), who added some observations on the specimens in the American Museum of Natural History. This account, which is fairly well illustrated, need not be repeated here. Some of the sensory canals of the head are shown in my Text-figure 70, page 396; and in Text-figure 124. The innervation of the sensory canals of the head has been worked out by Hawkes (1906), whose drawing is reproduced as my Figure 29, plate VII. For comparison, I have inserted a similar figure (Text-figure 125) representing the sensory canals of the head in *Squalus*. It remains to consider the sensory canal system of *Chlamydoselachus* briefly from a comparative point of view.

In all adult elasmobranchs, the sensory canals are fairly similar in their distribution. A pair of these canals extend in or under the skin, from the tip of the tail to the vicinity of the ear, where they connect with other canals branching over the various regions of the head. At intervals, the canals open to the exterior by means of pores, so that their approximate distribution can usually be traced without dissection.

Among living elasmobranchs it is very unusual for the sensory canals to be present as open grooves through so great a portion of their extent as is the case in *Chlamydoselachus*. The lateral line of *Chlamydoselachus* is an open groove from the tip of the tail almost as far forward as the spiracle (Garman, 1888). The anterior portion of the lateral line (llc.) is shown in Text-figure 124. Several of the longest sensory canals of the head are open—in particular, the spiracular (sp. in Text-figure 124), the gular and the oral. The latter are shown in Gudger and Smith's (1933) Figure 7, plate II, after Allis; they appear, without labels, in my Text-figure 70, page 396. In Figure 29, plate VII, after

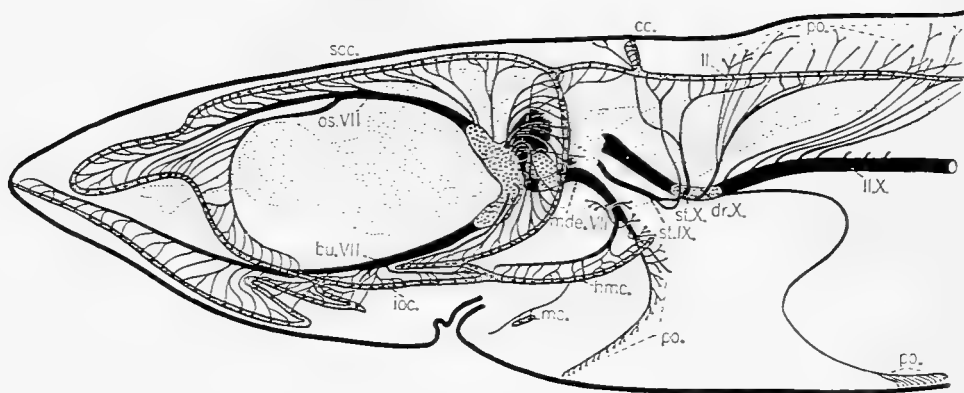


Text-figure 124.

Dorsal view of the head of *Chlamydoselachus*, showing the external openings of the ampullae of Lorenzini and of the laterosensory canals.

amp, ampullary pores; end, pore of the endolymphatic duct; iop, infraorbital laterosensory pores; llc, lateral line canal of body; sop, supraorbital laterosensory pores; sp, spiracular laterosensory canal; spr, spiracle.

Redrawn after Allis, 1923, Pl. II.



Text-figure 125.

Innervation of the sensory canal system and certain of the pit organs in *Squalus acanthias*. bu.VII, buccalis nerve; cc., supratemporal canal; dr.X, ramus dorsalis of tenth nerve; hmc., hyomandibular canal; ioc., infraorbital canal; ll., lateral line canal; ll.X, lateral line nerve; mc., mandibular canal; mde.VII, external mandibular nerve; os.VII, ophthalmicus superficialis of seventh nerve; po., pit organs; soc., supraorbital canal; st.IX, supratemporalis of ninth nerve; st.X, supratemporalis of tenth nerve.

From Daniel, 1934, Fig. 245; after Norris and Hughes, 1920, Fig. 50.

Hawkes, the oral, gular and spiracular are labeled *HLA*, *HLB* and *HLC* respectively. The preceding statements concerning the open condition of the canals hold for my four large specimens, save that on the right side of No. I the groove is lacking for a distance of about 30 mm. from the tip of the tail.

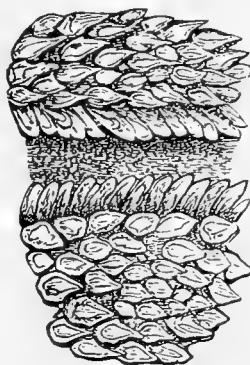
A more extensive occurrence of sensory canals as open grooves is found in the Holocephali, where most of the canals, including those of the head, are open; but in the Selachii, *Chlamydoselachus* appears to be unique in the extent to which its sensory canals are open. The nearest approach to its condition in this respect is found in the notidanids (Daniel, 1934), where the lateral line is an open groove as far forward as the pectoral fin. In *Heptanchus* the canals of the head are all closed tubes, as far back as the fifth gill-cleft. Posterior to this, the lateral lines are represented by a pair of open grooves extending almost to the tip of the tail. In *Squalus* (Text-figure 125) the canals are closed excepting in the region toward the tip of the tail. In higher elasmobranchs, the canals are usually closed throughout their entire length.

The open condition of the sensory canals found by Garman in *Chlamydoselachus* (Text-figure 126) is probably primitive, and in the light of all the evidence can scarcely be explained as due to arrested development in the embryonic sense. Lateral line canals as open grooves were found by Dean (1909, p. 252) in the Devonian fossil shark *Ctenacanthus clarkii* (Text-figure 127) as well as in many acanthodians. In all these forms the dermal denticles terminate abruptly at the margins of the groove, and the marginal denticles are, in most instances, unusually large, precisely as they are in *Chlamydoselachus*.

Most of the terms used by Garman in describing the sensory canals of the head in his specimen have been abandoned, and in their places are names for the various divisions

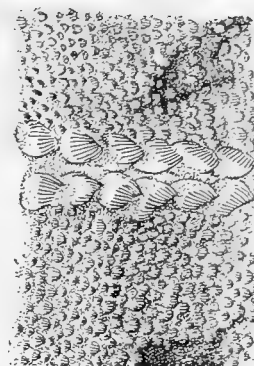
based on their innervation. Concerning certain sensory canals of *Chlamydoselachus* Garman (1888, pp. 82 and 83) writes:

The aural [supratemporal] canal is closed. It has no tubules. Contrary to what obtains in other Galei, it lies in front of the so-called ear openings [endolymphatic ducts]. These openings, however, are at the ends of tubes the inner extremities of which are in front of the [supratemporal] canal. The canal is nearly straight, bending slightly forward in the middle and a little backward near each end. . . . At the end of the jugular, near the middle of the first branchial aperture, there are two branches not found in any other of the sharks examined: a *spiracular* [HLC in Figure 29, plate VII], turning upward and forward toward the spiracle; and a *gular* [HLB in Figure 29, plate VII], turning down and forward near the median line, and finally uniting with the oral [HLA in Figure 29, plate VII] a short distance from the inner end. . . . Apparently the pre-nasal is reversed in direction, meeting the nasal in front and running backward to join the sub-rostral. . . . Like the corporals, the oral, gular



Text-figure 126.

Portions of open lateral line canals in a living and in an extinct shark.



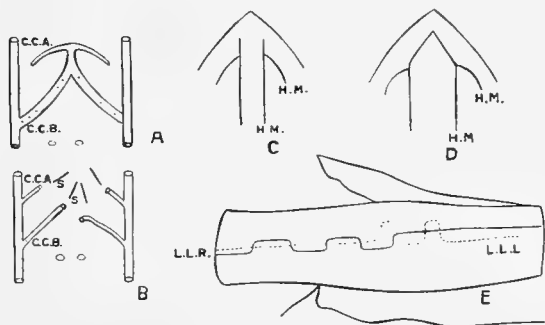
Text-figure 127.

Text-figure 126. The open lateral line canal in the tail region of *Chlamydoselachus*. Note the elongate scales (x 5) which partially cover the open canal.

After Garman, 1885.2, Fig. 10, pl. VI.

Text-figure 127. Lateral line canal of the fossil shark *Ctenacanthus clarki*, showing the enlarged denticles at the margin of the groove.

After Dean, 1909, Fig. 44.



Text-figure 128.

Variations in lateral line canals of *Chlamydoselachus*: A and B, supratemporal or commissural canal; C and D, ventral view of hyomandibular canal under the lower jaw; E, lateral line canal in the region of the dorsal fin.

C.C.A. and C.C.B., anterior and posterior portions of commissural canal; H.M., parts of the hyomandibular canal; L.L.R. and L.L.L., lateral canal on right and left sides.

S., vestigial canals (?).

After Hawkes, 1906, Text-fig. 140.

and spiracular [canals] are open grooves. In the spiraculars and gulars of this shark are found the nearest approach to the pleurals of the Batoidei.

Hawkes (1906) states that the lateral line system of the head of *Chlamydoselachus* is much more complicated than is usual among elasmobranchs (excepting rays and skates). Evidently, she refers merely to the gross pattern or topographical relations of these canals. The supratemporal or commissural canal in *Chlamydoselachus* is placed anterior to the openings of the ductus endolymphaticus, and is never the usual straight, transverse line connecting the right and left lateral canals. It varies greatly, as shown in her Text-fig. 140 (my Text-figure 128A and B). There are indications of two instead of one com-

missural canal, but it is impossible to state whether the present condition of these canals is vestigial or rudimentary. It is certain, however, that the condition of all the canals, but especially those in this region, is very unstable. Some variations in the hyomandibular region are shown in Text-figure 128c and d; other variations, in the pelvic and caudal portions of the lateral line, are represented in Text-figure 128e. Additional examples of variation in the posterior course of the lateral line are described by Gudger and Smith (1933, pp. 288-9) in three adult specimens.

Hawkes concludes that the lateral line system of *Chlamydoselachus* is primitive as regards: (1) the open condition of a portion of the canals; (2) the cutaneous rather than subcutaneous position of the canals; and (3) the entire absence of tubules in many places. In the occipital and hyomandibular region, however, the system tends to a considerable topographical complexity. Again there are indications, in the occipital and lateral canals, of either a vestigial or a rudimentary complexity.

In *Heptanchus* (Daniel, 1934), anterior to the spiracle and just posterior to the endolymphatic duct, a small transverse or supratemporal canal passes off from the lateral canal toward the median line. This, however, does not meet and fuse with the similar canal from the opposite side. In *Heptanchus maculatus* there may be two supratemporal canals on a side, one posterior to the endolymphatic duct, the other anterior to it. Thus we find evidence, in this region, of a variability somewhat comparable to that described in *Chlamydoselachus*. In *Heptanchus*, Daniel describes a "gular line" of pit organs corresponding in position to Garman's gular division of the sensory canal system in *Chlamydoselachus*. Allis (1923; 1934), like Garman, describes and figures the gular line as a part of the canal system. "The spiracular and gular canals [of *Chlamydoselachus*] form a continuous open groove" (Allis, 1923). This statement holds, without exception, for both right and left sides of my four large specimens. Norris (1929) writes: "The mandibular series of pit organs in *Squalus* (Norris and Hughes, 1920) and *Mustelus* (Johnson, 1917) evidently correspond to the gular canal organs in *Chlamydoselachus* (Hawkes, Allis)".

Many other comparisons of the sensory canal, ampullary and pit organs of *Chlamydoselachus* with those of other elasmobranchs are elaborated in the works of some of the authors cited, but these involve details that cannot be considered here.

DISCUSSION

The present section is concerned with the phylogenetic significance of the anatomical characters described on the preceding pages. In every section of this article, comparisons have been made between *Chlamydoselachus* and other vertebrates, so that it is not necessary to enter into details here.

My own interest in *Chlamydoselachus* relates chiefly to the evolution of organs and organ systems as such. Nevertheless, while studying this shark I have been impressed by certain things that have a bearing on the question of its phylogenetic affinities: first,

in some features it seems more primitive than any other living shark; second, in certain other respects it is highly specialized; third, it possesses some characters that are unique; fourth, it combines (as in the spiral intestine) some characters that are ordinarily segregated in different species; and fifth, it is highly variable. Within obvious limits, the frilled shark is a comprehensive type, and this constitutes one of the difficulties in the way of determining its affinities.

It is recognized that we are here on treacherous ground. Opinions will differ concerning the evaluation of the anatomical characters of *Chlamydoselachus*, and concerning the status of the animal as a whole. Nevertheless, to give point to the discussion I have summarized the most important data (Tables IV and V, pp. 496-497) in two lists of characters: one palingenetic or primitive, the other cenogenetic or of relatively recent origin, with reference to comparable structures in other living sharks. Some very obvious features, such as the unusual number of gill-slits and the dorsoventral flattening of the head, are excluded because of insufficient evidence as to their status. It is not expected that anyone will accept either list in its entirety. Each list might be greatly extended, affording endless opportunities for debate.

The more striking peculiarities of *Chlamydoselachus*, such as the very elongate form of the body and the peculiar hyostylism of the skull, are obviously cenogenetic. The real difficulty lies in the disguises which may conceal other cenogenetic characters. Apparent primitiveness is frequently the result of degeneration or retrogression, in a phylogenetic sense; this, as applied to the individual, is usually a matter of arrested development. In *Chlamydoselachus* there are evidences of retrogression in the skeletons of the fins, in the mesonephric duct and urinary sinus of the right side, and in the vestigial seventh gill-arch. In each case there are decided irregularities. It seems to be a fairly general rule that, when the development of an organ is arrested, it does not merely fail to attain the ancestral condition, but exhibits a vestigial complexity.

In *Chlamydoselachus* there are features, such as the thin walls and large foramina of the cranium, the incipient cyclospondylous vertebral centra, and the paired condition of the urinary sinuses in the adult, that appear more characteristic of an immature than of an adult shark. The position of the epibranchial arteries is that found in the embryos of other sharks. In all these cases there is no evidence that development has ever gone further. The alternative is to accept these features as primitive characters. The persistent thyroglossal duct may be anomalous, since it is not found in all specimens. Since the so-called duct differentiates like the wall of the pharynx, from which it is derived, it is obviously something more than an embryonic rudiment.

I have said that, within obvious limits, *Chlamydoselachus* is a comprehensive type. This is true mainly with respect to features that may be found in other sharks, but some of the resemblances to higher vertebrates are striking. Of these, it is sufficient to mention the extreme length and mobility of the jaws, suggestive of the Ophidia; the gular fold, simulating a condition found in many of the Teleostomi; and the armature of scales on

the anterior border of the dorsal fin, resembling in form and arrangement the "fulcral scales" of the Actinopterygii. It is scarcely necessary to add that these resemblances to higher vertebrates have no phylogenetic significance.

The expression "oldest living type of vertebrate" used by Garman (1884.3 and 1884.4) and by Gill (1884.1 and 1884.2) with reference to *Chlamydoselachus*, quite ignores the cyclostomes. While the cyclostomes are in some respects degenerate, in others highly organized, they retain, to a greater degree than any other vertebrates, the fundamental chordate structures. The view that skeletal degeneration has been a major trend in fish history has its limitations, particularly when one considers the endoskeleton rather than the external armor. Cartilaginous, calcified and bony vertebral centra develop largely at the expense of the notochord, and it seems unlikely that degeneration of the harder structures would result in the notochord being restored to its primitive condition as an effective organ in the adult. In Cyclostomata, as in Holocephali, the notochord is unimpaired. The ammocoetes larva of the lamprey links this form with the lower chordates rather than with the fishes. If phylogeny be defined as the succession of adult forms in the line of evolution, this latter evidence is not admissible, but if organisms are genetically related in the adult stage, then they must be related at all stages of their development. The cyclostomes have long been regarded as the lowest group of living vertebrates (craniates), and the evidence in support of this view should not be lightly set aside.

The very interesting question of the relationship of *Chlamydoselachus* to fossil forms is one that I am quite willing to leave to paleontologists. Such studies must remain under the handicap that, in fossils, little knowledge is available concerning organs that are quite as important as the more enduring skeleton. Since the "hard parts" of *Chlamydoselachus*, upon which we must depend for comparison with fossils, have long been known, it can scarcely be expected that the present paper will add much that will be of value to paleontologists. What has been added concerning the "soft parts" serves to confirm the generally accepted systematic relationship of *Chlamydoselachus* to the notidanids without, however, bringing them any nearer together. While *Chlamydoselachus* and the notidanids must be assigned to different families, the relationship is closer than that between *Chlamydoselachus* and any other existing sharks. In this connection the following quotation from Woodward (1921) seems pertinent:

The Hybodonts, which for the most part exhibit the primitive notochordal condition until the Lower Cretaceous Period, are especially interesting because, while their dentition and their general appearance resemble those of the existing Cestraciontidae, their skull is very different and more closely agrees with that of the Notidanidae. They are indeed a generalized group from which several later families appear to have arisen, and they are the dominant sharks of the Jurassic and early Cretaceous periods.

Previous discussions of the affinities of the frilled shark to fossil forms have been reviewed at length by Gudger and Smith (1933). Garman (1885.2) was particularly impressed by the resemblance of the teeth of *Chlamydoselachus* (Text-figure 7, p. 344)

to those of *Cladodus*, and went so far as to say that "*Chlamydoselachus* is a cladodont." In the present paper (p. 349) I have compared the teeth of the frilled shark with those of two cladodonts, *Cladoselache* and *Cladodus*, and two hybodonts, *Ctenacanthus* and *Hybodus* (Text-figures 17, 18, 19, 20, on p. 348). The resemblance between the teeth of *Chlamydoselachus* and the cladodonts is indeed striking, but the paleontological history of *Chlamydoselachus* goes back no further than the Tertiary, while the cladodonts are generally considered to be extinct since the Carboniferous. The teeth of hybodonts are more generalized and variable; nevertheless, out of such structures, teeth like those of *Chlamydoselachus* might readily have been evolved. The presence, in the hybodonts, of a large spine at the anterior border of each dorsal fin does not exclude this family from relationship with the Chlamydoselachidae. In the Spinacidae, some genera possess spines similarly located, while other genera lack them.

Throughout this article I have recorded and emphasized the great variability of *Chlamydoselachus* in most of its structures. The significance of this variability is not self-evident. "As a paleontologist knows . . . variability is a special characteristic of the struggling end of a disappearing race quite as frequently as it is a mark of the beginning of a new race" (Woodward, 1933). There are reasons why, in the case of *Chlamydoselachus*, one may favor the former interpretation. The frilled shark has been taken only in Japanese waters and off the western coast of Europe. If it were a new species, one would not expect it to occur in waters so widely separated, particularly since it is not gifted with extraordinary powers of locomotion. Since it is quite rare even in these restricted localities, it seems to have a precarious hold on existence. It may be significant, in this connection, that *Chlamydoselachus anguineus* is somewhat isolated in its systematic position. The genus stands far enough from the Notidanidae to be placed in a separate family, the Chlamydoselachidae, containing no other genera. There are no other species save the fossil *C. lawleyi* and *C. tobleri*, both known only by their teeth (Text-figures 15 and 16, p. 348), and one may question whether the latter really belongs to the genus *Chlamydoselachus*. The frilled shark appears to be a form that has long been differentiated in adaptation for a particular habitat and mode of life, in which it has not been altogether successful since it now seems to be facing extinction.

My outstanding impression of the frilled shark is that it presents a strange assemblage of characters ranging from very primitive to highly differentiated. In this, it is comparable to *Chimaera*, though the latter is specialized in a decidedly different way. *Chlamydoselachus* is a deep-sea adaptation of some rather ancient type of shark, and is now waging a losing battle in the struggle for existence.¹

¹Since writing these pages I have found in Deinega's (1925) English abstract of his Russian text the following statement: "We may still consider *Chlamydoselachus* as one of the most ancient representatives of the vertebrates, having survived to our day and now undergoing extinction" (italics mine). I do not know of any other author who has expressed the view that *Chlamydoselachus* is threatened with extinction. In my opinion, *Chlamydoselachus* is not "one of the most ancient representatives of the vertebrates." It is, however, one of the most primitive of existing sharks.

TABLE IV.

PALINGENETIC CHARACTERS OF *CHLAMYDOSELACHUS*

Teeth, of "cladodont" type, are formed by the fusion of simple denticles.

At the angles of the mouth, scales grade into teeth.

The notochord persists with very little constriction.

Calcification of the endoskeleton is very limited in amount.

Cyclospondylous vertebral centra are incipient or rudimentary.

The visceral skeleton shows a striking gradation between jaws and gill-arches.

Nearly complete series of basibranchials and hypobranchials, with little fusion.

In the trunk musculature, longitudinal divisions are few and simple.

The digestive tube is relatively simple and is nearly straight.

The bursa entiana is not invaded by the spiral intestine.

In the valvular intestine, the apices of the anterior and posterior coils point in different directions.

In the middle portion of the spiral intestine, there is an axial strand; in both anterior and posterior portions, there is an axial tube.

The liver is bilaterally symmetrical.

In some specimens, there is a persistent thyroglossal duct lined with pharyngeal mucosa.

Pouch-like vestige of the ventral end of the spiracular gill cleft.

In the female, the mesonephroi persist through almost the entire length of the body cavity.

In females, there is a pair of urinary sinuses which open separately into the urogenital sinus.

In females, nearly all the collecting tubules enter the mesonephric duct. So-called ureters are absent.

Epibranchial (efferent branchial) arteries are situated dorsal to the respective gill-arches, as in the embryos of other sharks.

Posterior efferent collector arteries may retain a dorsal connection with the anterior efferent collector of the same gill.

The brain is very small; the forebrain is small proportionally.

The roof of the definitive forebrain is said to be non-nervous.

In a 25-mm. embryo, the glossopharyngeal nerve has a ventral root.

The "nervus collector" is unusually well developed.

The lateral line sensory canal is an open groove from the tip of the tail as far forward as the spiracle. Several of the longer sensory canals of the head are open.

Whether open or closed, the sensory canals of the lateral line system are cutaneous rather than subcutaneous.

The gular division of the sensory canal system corresponds to the "gular line" of pit organs in *Heptanchus*, *Squalus* and *Mustelus*.

TABLE V.
CENOGENETIC CHARACTERS OF *CHLAMYDOSELACHUS*

Unusually elongate form of the body.

Weakness of the dermal fin rays.

Bunching of the pelvic, dorsal and anal fins near the caudal.

Unusually large mouth, and very distensible oropharyngeal cavity.

First pair of gill-covers enlarged, loose-fitting and frilled. They are continuous with a gular fold, unique among sharks.

Abdominal or tropeic folds, unique among vertebrates.

Peculiar and imperfect hyostylism of the skull. The hyomandibular articular facet is very long, permitting a gliding action.

Jaws are unusually long, and begin far posterior to the cranium.

Heterospondyly of the extreme caudal end of the vertebral column.

Shortness and irregularity (fragmentation, displacement, fusion) of cartilaginous fin rays (radials).

Infolding of the musculature of the ventral body wall in connection with the tropeic folds.

Alleged absence of an intermandibular muscle innervated by a branch of the trigeminal nerve.

Dorsal group of eye muscles much stronger than the ventral group.

Presence of an accessory musculus rectus lateralis.

All the recti muscles, save only a portion of the accessory rectus lateralis, take origin from the eyestalk.

Pyloric vestibule sometimes a sharply defined division of the digestive tube.

The middle intestine is expanded to form a bursa entiana.

Right and left lobes of the liver extend the entire length of the body cavity.

The gill-clefts are unusually large, and the respiratory surface afforded by the gills is great.

The external spiracular openings are very small.

Mesonephric duct, urinary sinus and urethral pore of the right side are often defective.

In adult females, the genital organs of the right side are much better developed than those of the left side; the latter are probably not functional.

The young are retained in the uterus until they reach an advanced stage of development.

The anterior unpaired portion of the pericardio-peritoneal canal is very short and broad. The paired canals often end blindly.

Afferent branchial arteries are connected by a series of loops over the gill-slits.

The connections between the acustico-lateralis elements of the fifth, seventh and eighth cranial nerves show a tendency toward unification of the system.

Peculiar mechanism by which the eyes may be protected in the absence of lids,

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PLATE I
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE I

THE CRANIUM OF *CHLAMYDOSELACHUS*, WITH THE ANTERIOR END OF THE VERTEBRAL COLUMN ATTACHED

Fig. 1. Dorsal view of the cranium, natural size.

af, articular facet for hyomandibular; *an*, ala nasalis; *cp*, cavum precerebrale; *ecp*, ectethmoidal process; *ef*, endolymphatic fossa; *es*, eyestalk; *fp*, foramen for nervus profundus; *id*, interdorsal; *pc*, preorbital canal or foramen; *pop*, postorbital process.

After Allis, 1923, Fig. 9, pl. VIII.

Fig. 2. Ventral view of the cranium, natural size.

aop, antorbital process; *ba*, bulla acustica; *fic*, foramen for internal carotid artery; *fso*, foramina supraorbitalia; *naf*, nasal fontanelle; *pb*, palatobasal ridge.

After Allis, 1923, Fig. 11, pl. IX.

Fig. 3. Lateral view of the cranium, natural size.

af, articular facet for hyomandibular; *bd*, basidorsals; *fe*, foramen for efferent pseudobranchial artery; *ff*, foramen for nervus facialis; *fic*, foramen for internal carotid artery; *fo*, foramen for nervus opticus; *foc*, foramina for occipital nerves; *fom*, foramen for nervus oculomotorius; *fp*, foramen for nervus profundus; *ftr*, foramen for nervus trochlearis; *id*, interdorsals; *n*, nodule of cartilage; *naf*, nasal fontanelle; *onc*, orbitonasal canal; *pb*, palatobasal ridge; *pc*, preorbital canal, or foramen; *r*, rostrum; *sbd*, supra-basidorsals; *tpf*, trigemino-pituitary fossa.

After Allis, 1923, Fig. 8, pl. VIII.

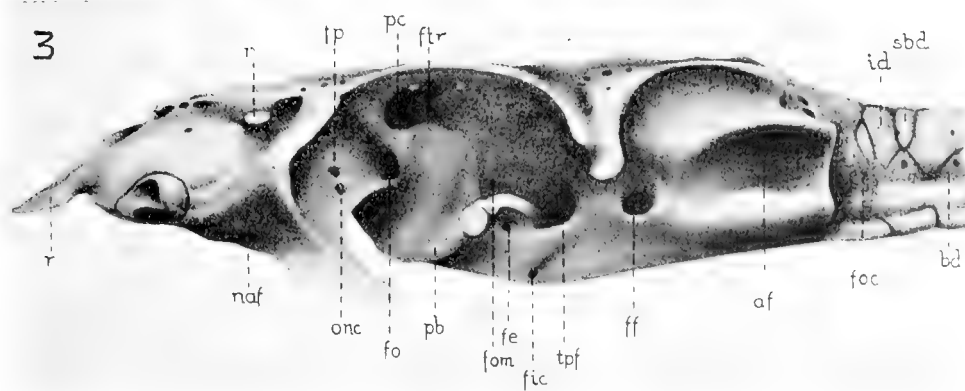
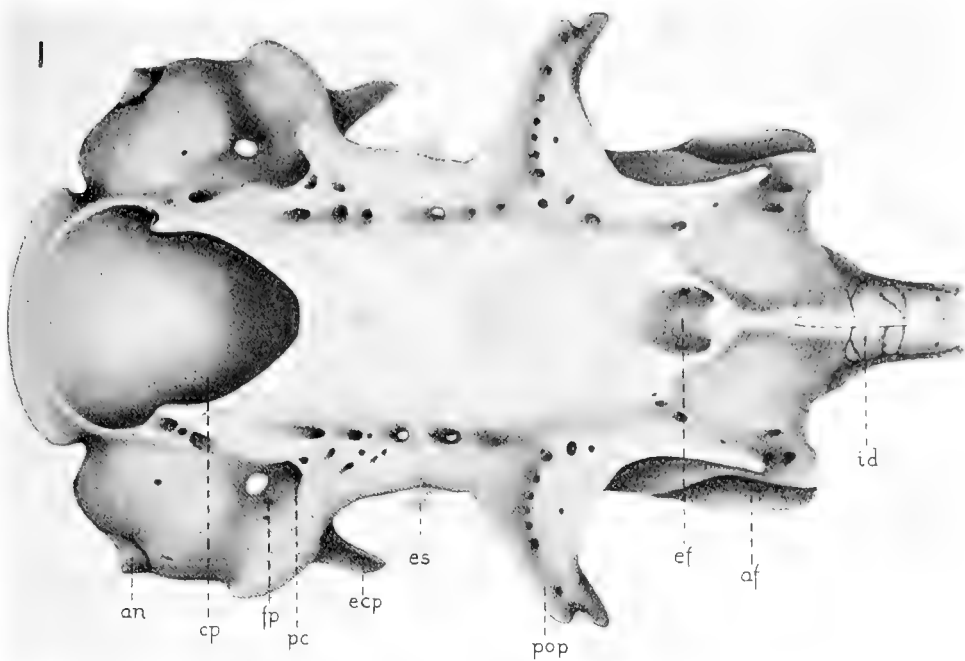


PLATE II
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE II

THE CRANIUM AND PORTIONS OF THE VISCERAL SKELETON OF CHLAMYDOSELACHUS

Fig. 4. Medial view of cranium and anterior end of the vertebral column, natural size.

an, ala nasalis; *bd*, basidorsals; *ef*, endolymphatic fossa; *fe*, foramen for efferent pseudobranchial artery; *fgl*, foramen for nervus glossopharyngeus; *fic*, foramen for internal carotid artery; *fo*, foramen for nervus opticus; *foc*, foramina for occipital nerves; *fol*, foramen for nervus olfactorius; *fom*, foramen for nervus oculomotorius; *ftr*, foramen for nervus trochlearis; *fv*, foramen for nervus vagus; *id*, interdorsal; *nc*, notochord; *pb*, palatobasal ridge; *pv*, canal, or foramen, for pituitary vein; *r*, rostrum; *tf*, acustico-trigemino-facialis recess.

After Allis, 1923, Fig. 12, pl. IX.

Fig. 5. Lateral view of cranium, with jaw cartilages and hyoid cartilages attached, natural size.

al, anterior upper labial cartilage; *an*, ala nasalis; *aop*, antorbital process; *ch*, ceratohyoid; *ecp*, ectethmoidal process; *es*, eyestalk; *g* (= gamma), the process corresponding to Addy of Vetter's (1874) description in other selachians; *hmd*, hyomandibular; *lmh*, ligamentum mandibulo-hyoideum; *md*, mandibular; *ml*, mandibular labial cartilage; *n*, nodule of cartilage; *naf*, nasal fontanelle; *orp*, orbital process of palatoquadrate; *pl*, posterior upper labial cartilage; *pop*, postorbital process; *pq*, palatoquadrate.

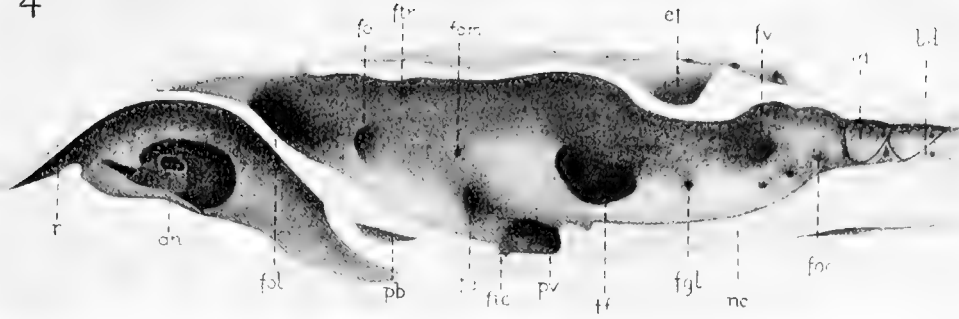
After Allis, 1923, Fig. 7, pl. VII.

Fig. 6. Posterior view of the cranium, natural size.

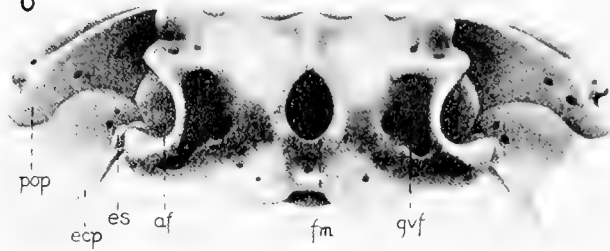
af, articular facet for hyomandibular; *ecp*, ectethmoidal process; *es*, eyestalk; *fm*, foramen magnum; *gvf*, glossopharyngo-vagus fossa; *pop*, postorbital process.

After Allis, 1923, Fig. 10, pl. VIII.

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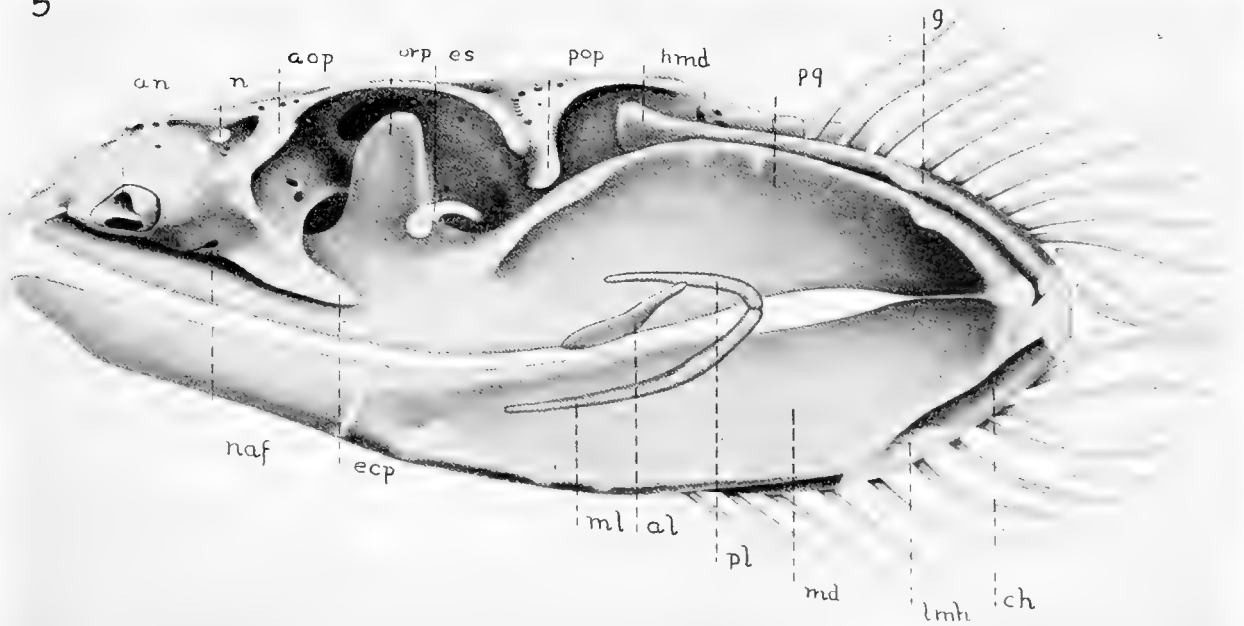


PLATE III
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE III

THE BRAIN AND PORTIONS OF THE VISCERAL SKELETON OF *CHLAMYDOSELACHUS*

Fig. 7. Dorsal view of the brain and cranial cavity, natural size.

a, artery; *o*, nervus opticus; *ocm*, n. oculomotorius; *ol*, tractus olfactorius; *tr*, n. trochlearis; *v*, vein.

After Allis, 1923, Fig. 59, pl. XXII.

Fig. 8. Dorsal view of the branchial arches, natural size. The branchial rays related to the ceratobranchials have been removed.

bbr2, second basibranchial; *bbr5-6*, fused fifth and sixth basibranchials; *bh*, basihyoid; *cb1*, musculus coracobranchialis of the first arch; *cbr1*, ceratobranchial of the first arch; *cbr6*, ceratobranchial of the sixth arch; *ch*, ceratohyoid; *ebr1*, epibranchial of the first arch; *ebr6*, epibranchial of the sixth arch; *hbr2*, hypobranchial of the second arch; *pbr5*, pharyngobranchial of the fifth arch.

After Allis, 1923, Fig. 35, pl. XIII.

Fig. 9. Ventral view of the median portion of the branchial skeleton, natural size.

bbr3, basibranchial of the third arch; *cbr6*, ceratobranchial of the sixth arch; *ch*, ceratohyoid; *hbr2*, hypobranchial of the second arch.

After Allis, 1923, Fig. 36, pl. XIII.

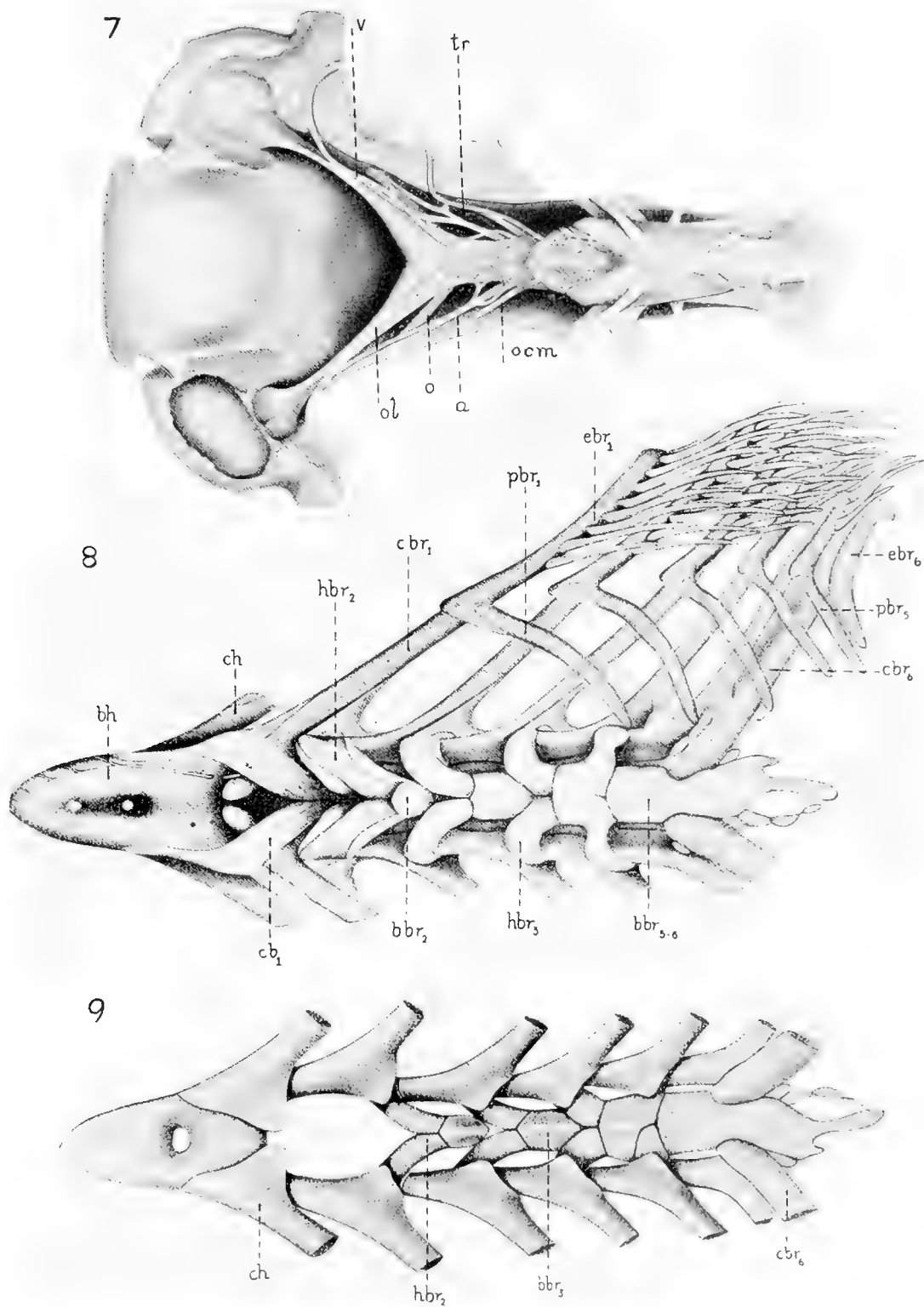


PLATE IV
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE IV

EYE MUSCLES, BRAIN, VALVULAR INTESTINE AND DUCTUS DEFERENS OF *CHLAMYDOSELACHUS*

Figs. 10, 11 and 12. The eye muscles and their nerves, excepting the nervus abducens which innervates the external rectus muscle.

The explanation of the labels is combined with that for the next two figures.

After Hawkes, 1906, Figs. 4-6, pl. LXIX.

Figs. 13 and 14. Dorsal and ventral views of lateral halves of the brain, showing roots of cranial nerves.

II, optic nerve; *III*, oculomotor nerve; *IV*, trochlear nerve; *V*, *VII*, the united Gasserian and buccalis ganglia; *VI*, nervus abducens; *VII b.*, ramus buccalis; *VII h.*, truncus hyomandibularis; *VIII*, the ganglion of the eighth nerve; *IX*, glossopharyngeal nerve; *X*, vagus nerve.

A.B., anastomosing branch between the oculomotor and profundus nerves; *C.*, ciliary branch of the profundus; *Cer.*, cerebellum; *Hy.*, hypophysis; *I.O.*, inferior oblique muscle; *L.I.*, lobi inferiores; *Lin.Lat.*, lineae laterales or restiform bodies; *L.N.*, Locy's nerve (nervus terminalis); *Oc.1,2,3*, first three spino-occipital nerves; *Op.S.*, optic stalk (cartilago sustentaculum oculi); *Op.L.*, optic lobes; *O.S.*, olfactory stalk; *Pro.*, profundus branch of fifth or trigeminal nerve; *Pros.*, prosencephalon; *R.Ext.*, *A* and *B*, two parts of the rectus externus muscle; *R.In.*, rectus internus muscle; *R.Inf.*, rectus inferior muscle; *R.S.*, rectus superior muscle; *S.Ob.*, superior oblique muscle; *S.V.*, saccus vasculosus.

After Hawkes, 1906, Figs. 7 and 8, pl. LXIX.

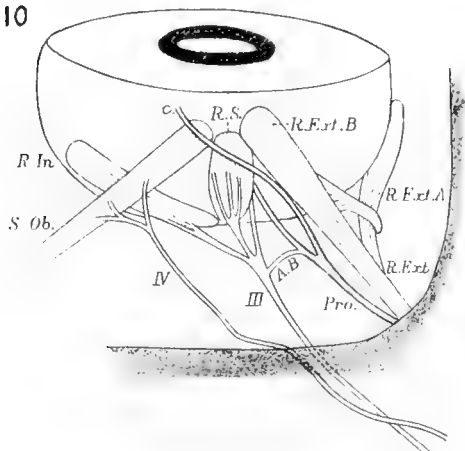
Fig. 15. Valvular intestine slit open to show the spiral valve and the thick muscular wall.

After Günther, 1887, Fig. 5, pl. LXV.

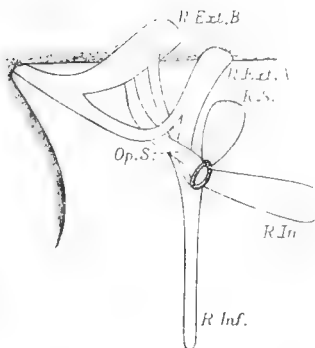
Fig. 16. Lower part of left ductus deferens (vas deferens) opened longitudinally to show "annular" folds.

After Günther, 1887, Fig. 4, pl. LXV.

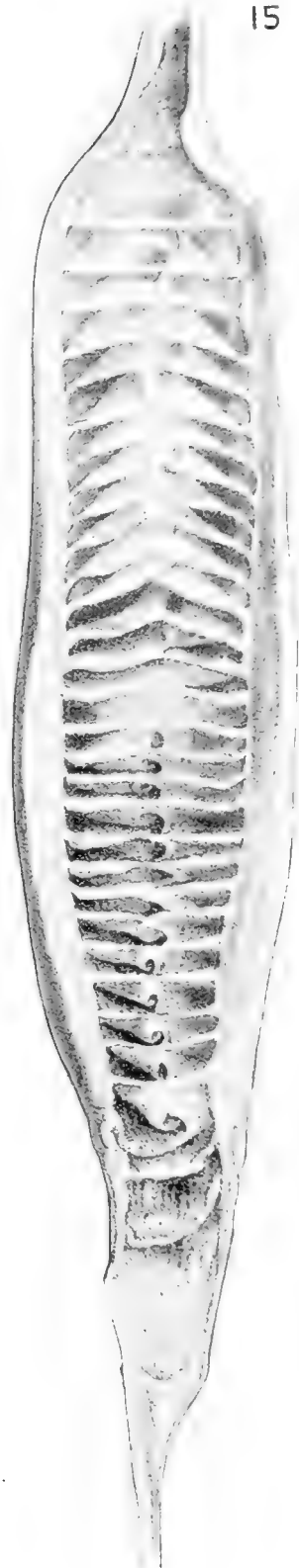
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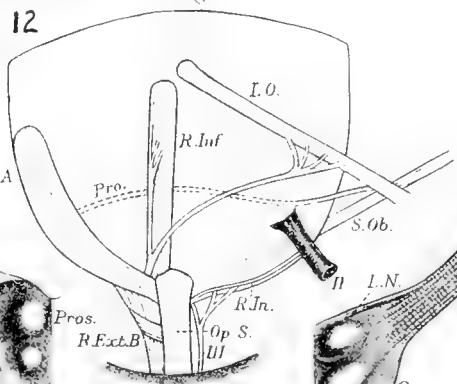
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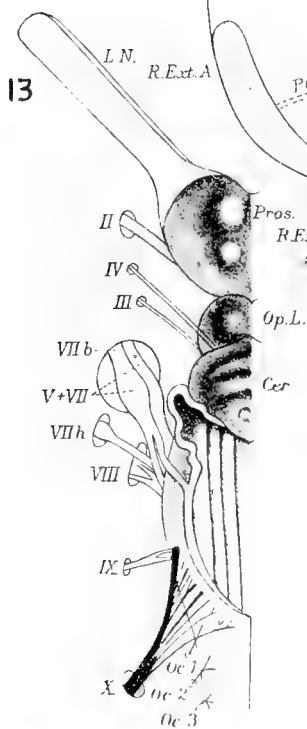
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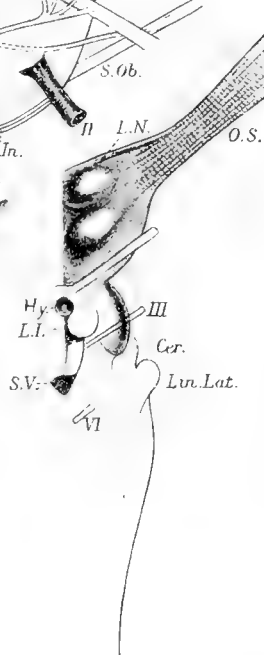
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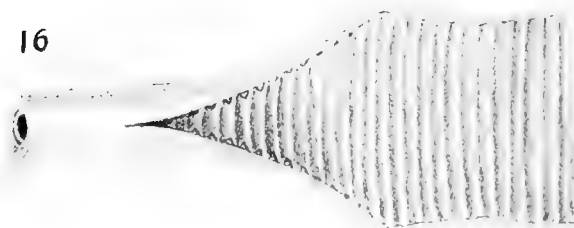


PLATE V
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE V

THE UROGENITAL ORGANS OF *CHLAMYDOSELACHUS*

Fig. 17. External (ventral) view of the cloaca and abdominal apertures in a normally developed male.

cl, cloaca; po, porus abdominalis; ug, urogenital openings; v, vent.

After Günther, 1887, Fig. 1, pl. LXV.

Fig. 18. External (ventral) view of the cloaca and abdominal apertures in an asymmetrically developed male. The ducts of the right side are not so well developed as those of the left.

cl, cloaca; po, porus abdominalis; ug, urogenital openings; v, vent.

After Günther, 1887, Fig. 2, pl. LXV.

Fig. 19. Side view of the ductus deferentia (vasa deferentia) of a specimen with unequal development of the genital ducts. Compare preceding figure, drawn from the same specimen.

gl, gland; i, rectum opened; po, porus abdominalis; r, kidney; u, urinary bladder; ug, right, and ugl, left urogenital opening; vd, left, and vdl, right ductus deferens.

After Günther, 1887, Fig. 3, pl. LXV.

Fig. 20. Ventral view of pelvic fins, myxopterygia and cloacal aperture of a 1474-mm. male.

After Günther, 1887, Fig. C, pl. LXIV.

Fig. 21. Dorsal view of the right half of the pelvic girdle and endoskeleton of the right pelvic fin of a male.

B., basipterygium; b., axial cartilage; bl, intercalary cartilage; Be. [beta], modified radial; l.n.f., longitudinal nerve foramen; p.g., pelvic girdle; r., lateral radials; R.v., marginal ventral cartilage; T.d., terminal dorsal cartilage; T.v., terminal ventral cartilage.

After Goodey, 1910.1, Fig. 22, pl. XLVI.

Fig. 22. Dorsal view of the pelvic fin and the right half of the pelvic girdle of a male, showing musculature.

A., adductor muscle; B., basipterygium; Be. [beta], modified radial; c.n., collector nerve; D., dilator muscle; Fl.e., musculus flexor externus; Fl.i., musculus flexor internus; l.r., last lateral radial; O., dorsal radial muscles; p.g., pelvic girdle; R.v., marginal ventral cartilage; S., compressor muscle; T.d., terminal dorsal cartilage; T.v., terminal ventral cartilage.

After Goodey, 1910.1, Fig. 20, plate XLVI.

Fig. 23. Ventral view of the pelvic fin represented in Figs. 21 and 22, showing muscles.

Fl.e., musculus flexor externus; Ra., ventral radial muscles; S., compressor muscle; T.v., terminal ventral cartilage.

After Goodey, 1910.1, Fig. 21, pl. XLVI.

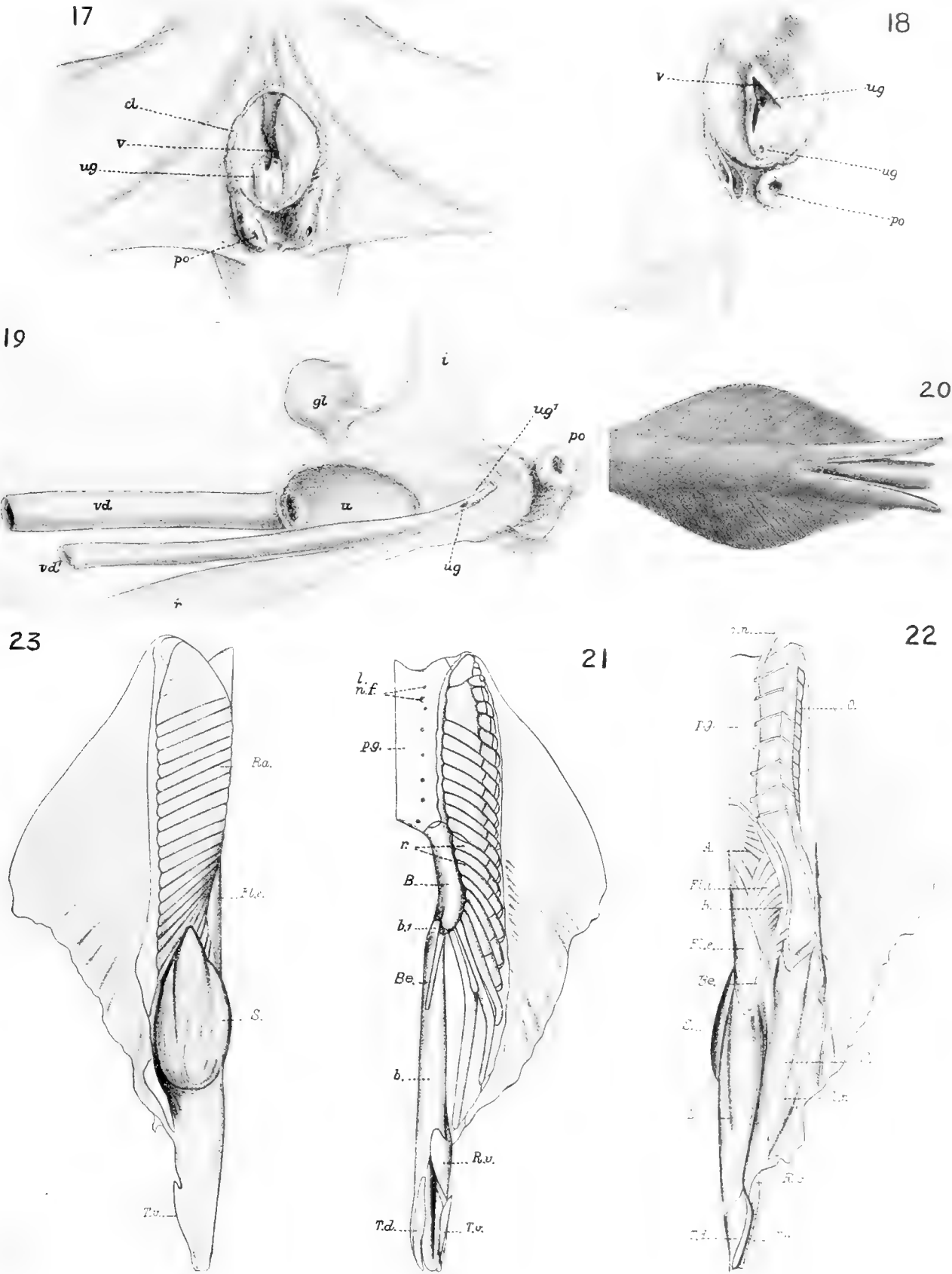




PLATE VI
THE ANATOMY OF *CHLAMYDOSELACHUS ANGIUNEUS*

PLATE VI
THE BRAIN OF *CHLAMDOSELACHUS*

Fig. 24. The brain in dorsal view and in transverse sections taken at various levels.

Fig. 25. Ventral view of the brain of the frilled shark.

Fig. 26. The brain of *Chlamydoselachus* in lateral view.

Fig. 27. Vertical longitudinal section of the brain of *Chlamydoselachus*.

1, olfactory lobe; 2, nervus opticus; 3, oculomotorius; 4, trochlearis; 5, trigeminus; 6, abducens; 7, facialis; 8, acusticus; 9, glossopharyngeus; 10, vagus.

These figures are reproduced from the original drawings by Paulus Roetter for Garman, 1885.2, Pls. XV and XVI.

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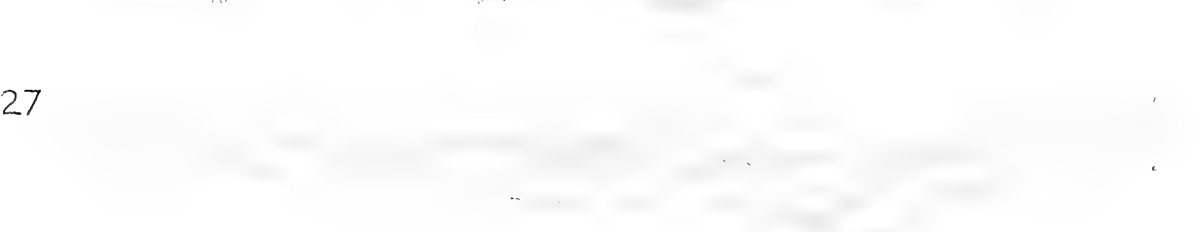


PLATE VII
THE ANATOMY OF *CHLAMYDOSELACHUS ANGUINEUS*

PLATE VII NERVOUS SYSTEM AND CERTAIN SENSE ORGANS OF *HEPTANCHUS* AND *CHLAMYDOSELACHUS*

Fig. 28. Brain, cranial nerves and associated sense organs of *Heptanchus maculatus*, dorsal view.

bu.VII, buccal branch of facial nerve; *cb.*, cerebellum; *cl.*, ciliary nerve; *c.r.*, restiform body; *hmd.*, hyomandibular division of the facial nerve; *md.V*, mandibular division of the fifth nerve; *m.n.*, median olfactory nucleus; *med.*, medulla; *mx.V*, maxillary division of trigeminal nerve; *ol.b.*, olfactory bulb; *ol.l.*, olfactory lobe; *ol.t.*, olfactory tract; *op.l.*, optic lobe; *op.V*, ophthalmicus profundus division of the trigeminal nerve; *os.V* and *VII*, ophthalmicus superficialis of trigeminal and facial nerves; *tl.*, telencephalon; *tn.*, terminal nerve; *y-z*, occipitospinal nerves: I, olfactory nerve; II, optic; III, oculomotor; IV, trochlearis; VI, abducens; VIII, auditory; IX, glossopharyngeal; X, vagus.

After Daniel, 1934, Fig. 200A.

Fig. 29. Diagrammatic drawing of the cranial nerves and lateral line canals of *Chlamydoselachius*.

B.A., buccal ampullae; *Bucc.*, ramus buccalis VII; *C.F.*, general cutaneous fibres going to skin; *Con.V5*, nerve strand connecting the pre- and post-trematic rami of vagus 5; *Con.V6*, nerve strand connecting vagus 6 with a spinal nerve; *D.G.*, dorsal branch of the glossopharyngeus, dividing into a cephalad branch which passes to the neuromasts, and a caudal branch whose distribution is undetermined; *E.M. (VII)(A,B,C,D,E)*, the five parts of the externus mandibularis VII; *H.*, the ganglion of the truncus hyomandibularis, i.e., the true ganglion of the facialis, combined with one of the acustico-lateralis ganglia; *H.A.*, hyoid ampullae; *H.L.(A,B,C)*, the hyomandibular lateral line canal and its three main branches; *H.M.*, the common trunk of the ramus hyoideus and ramus internus mandibularis VII; *I.(A,B,C)*, the three principal rami intestinales; *I.H.*, the cardiac branch of the ramus intestinalis; *I.M.VII*, ramus internus mandibularis VII; *I.O.L.*, infraorbital lateral line canal; *L.L.*, main lateral line canal; *Mxb.*, branch of the maxillaris which becomes united with a branch of the buccalis; *Mxb.b.*, two fine nerves which appear to originate from a branch of the buccalis, but which are composed of general cutaneous fibers which have come from *Mxb.*; *P.*, palatine branches of the facialis; *P.B.A.*, posterobuccal ampullae; *Pr.F.(ch.)*, the chorda tympani; *Pr.* and *Pt.*, the pre- and post-trematic rami of IX and of the vagus; *Pro.*, profundus branch of V; *Pt.F.*, post-trematic facialis; *R.H.*, ramus hyoideus VII; *R.Man.V*, ramus mandibularis V; *R.Max.*, ramus maxillaris V; *R.O.*, ramus oticus with cutaneous branches *R.O.C.*; *S.(1,2,3,4,5,6,7,8)*, the first eight spinal nerves; *s.h.(1,2)*, the two branches which make up the hypoglossal nerve; *S.O.*, occipitospinal riband; *S.O.A.*, supraorbital ampullae; *S.O.L.*, supraorbital lateral line canal; *S.Op.V*, superficialis ophthalmicus V; *S.Op.VII*, superficialis ophthalmicus VII; *T.H.*, truncus hyomandibularis; *V(1,2,3,4,5,6)*, the six branchial branches of the vagus; *V.G.*, visceralis branch of IX; *Vis.*, visceralis branches of the vagus; *V.VII*, the united Gasserian and buccalis ganglia; *IX*, *IXg.*, the glossopharyngeal nerve and its ganglion; *X*, *Xg.*, the vagus nerve and its composite ganglion; *X.A* and *X.B*, dorsal branches of the vagus to neuromasts. The remaining abbreviations are not explained by the author.

After Hawkes, 1906, Fig. 1, pl. LXVIII (in color).

Fig. 30. Right membranous labyrinth (x 2) of *Chlamydoselachius*, medial aspect.

The explanation of the labels is combined with that for the next figure.

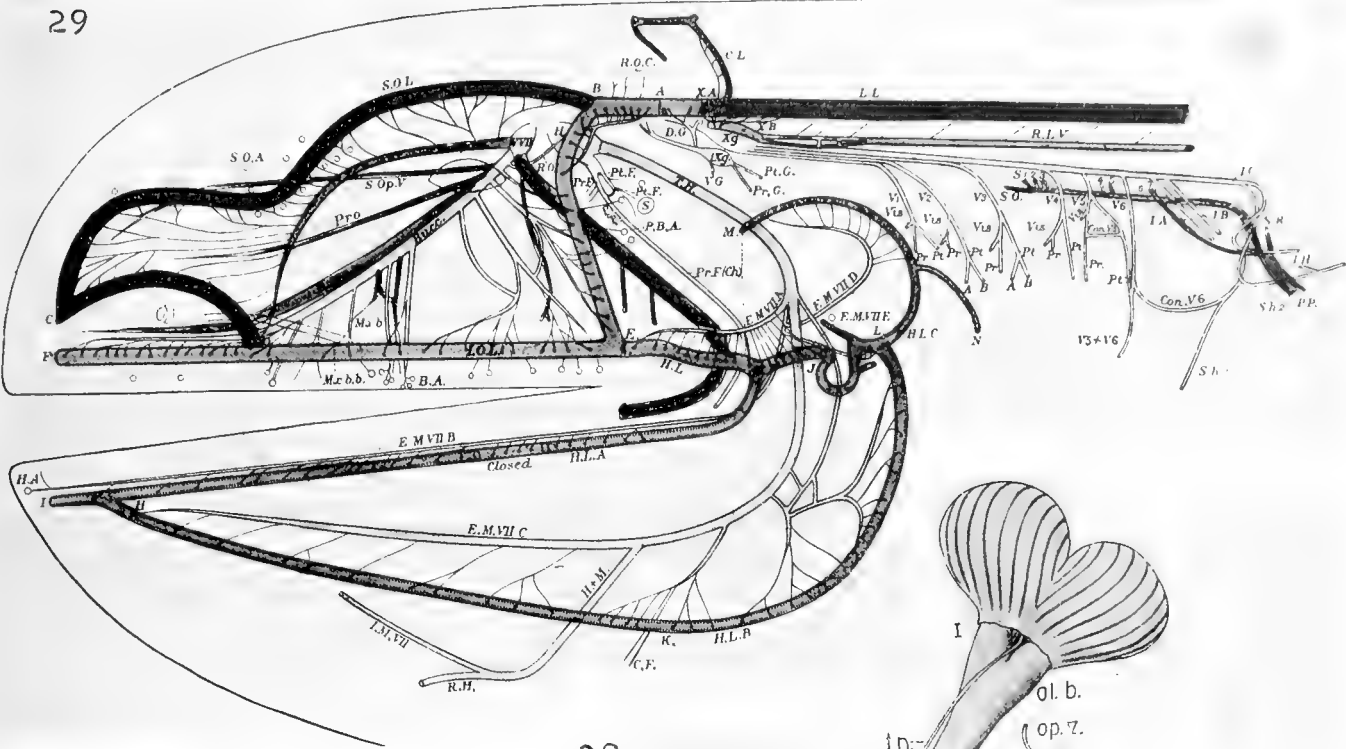
After Goodey, 1910.1, Fig. 7, pl. XLIII.

Fig. 31. Right membranous labyrinth (x 2) of *Chlamydoselachius*, lateral aspect.

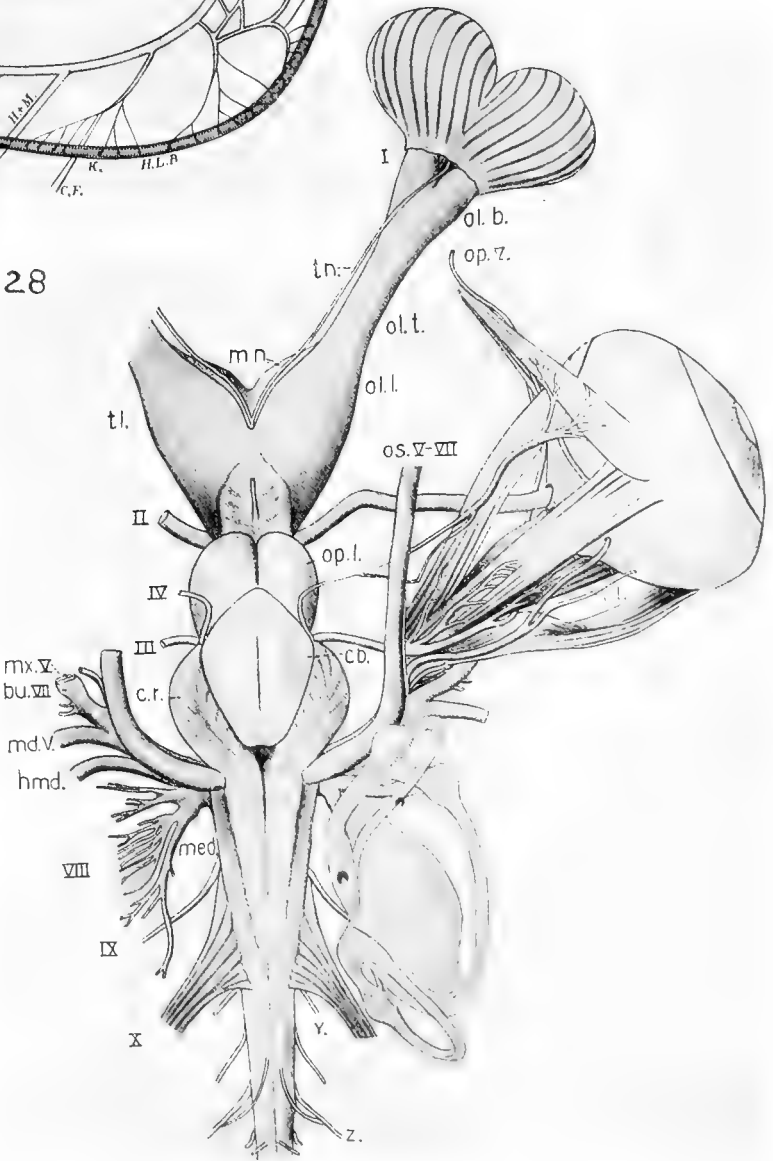
a.a., ampulla anterior; *a.d.e.*, apertura ductus endolymphaticus externus; *a.e.*, ampulla externus; *a.p.*, ampulla posterior; *c.a.*, canalis anterior; *c.e.*, canalis externus; *c.p.*, canalis posterior; *d.e.*, ductus endolymphaticus; *d.u.s.p.*, ductus utriculo-sacculus posterior; *l.*, lagena; *p.f.*, parietal fossa; *r.a.a.*, ramus of eighth nerve to ampulla of anterior canal; *r.a.e.*, ramus to ampulla externus; *r.a.p.*, ramus to ampulla posterior; *rec.*, recessus utriculi; *r.l.*, ramus to lagena; *r.n.*, ramus to macula neglecta; *r.s.*, ramus to sacculus; *r.u.*, ramus to utriculus; *s.*, sacculus; *s.e.*, saccus endolymphaticus; *t.*, tympanic aperture; *u.a.*, utriculus anterior; *u.p.*, utriculus posterior; VIII, eighth cranial nerve.

After Goodey, 1910.1, Fig. 8, pl. XLIII.

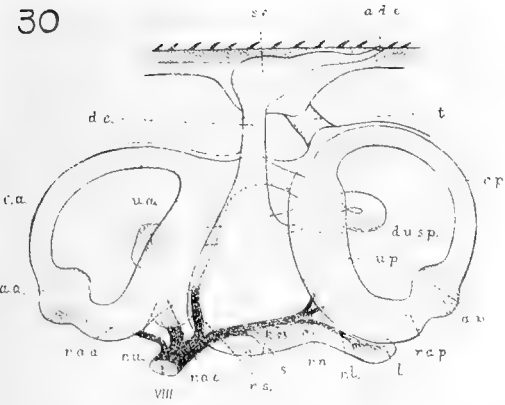
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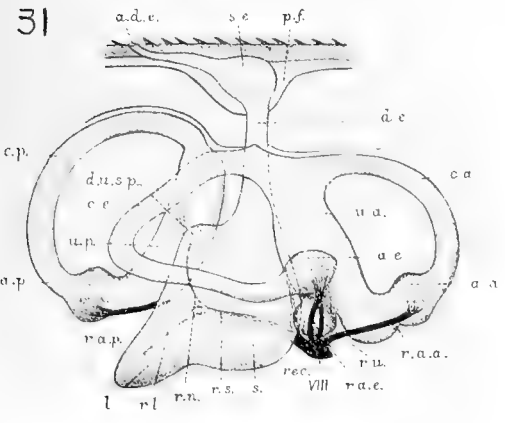
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THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE VII

THE BREEDING HABITS, REPRODUCTIVE ORGANS
AND EXTERNAL EMBRYONIC DEVELOPMENT
OF *CHLAMYDOSELACHUS*, BASED ON NOTES
AND DRAWINGS BY BASHFORD DEAN

By E. W. GUDGER
Honorary Associate in Ichthyology
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By E. W. Gudger

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THE BREEDING HABITS, REPRODUCTIVE ORGANS, AND
EXTERNAL EMBRYONIC DEVELOPMENT OF *CHLAMYDOSELACHUS*,
BASED ON NOTES AND DRAWINGS LEFT
BY BASHFORD DEAN

By E. W. GUDGER
Honorary Associate in Ichthyology
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INTRODUCTION

While on a leave of absence from Columbia University, Prof. Bashford Dean spent parts of 1900 and 1901 in Japan. There he collected and studied many rare and little-known marine animals—particularly certain archaic fishes and their eggs and embryos. That these collections were extensive, we know since there is a letter by him stating that when shipped to America by freight they filled seven cases. In this shipment were several adult frilled sharks, and others were sent to him later. Of the disposition of these and of Dean's generosity in sending specimens of this fish to various European investigators, Gudger and Smith have written (1933, pp. 250–252).

Dean's embryological materials were collected to enable him to follow and to illustrate the early life histories of two primitive elasmobranchs—the frilled shark, *Chlamydoselachus anguineus*, and the Port Jackson shark, *Heterodontus (Cestracion) philippi*. Back in America, Dean found gaps in his materials and figures, so he returned to Japan and did further work on these fishes during the months from May to October, 1906. Furthermore, other frilled-shark material was still later collected in Japan and sent to him in America. I have records of specimens received by Dean on February 10, 1911, and on January 13, 1912. I have been unable to trace these specimens, but other lots came to him and were deposited in the Dean collection in the zoological museum of Columbia University. Among the specimens loaned from Columbia are four lots of young embryos without yolk sacs labelled "Bought in Tokyo Market, February 4, 1913; April 4, 1913; January 22, 1914; April 23, 1917". His Japanese collectors evidently found the fresh-caught adult sharks in the Tokyo market, opened the fish, cut the embryos from the uterine eggs, and sent these embryos to Dean.

Since the above was written, I have learned that in 1917 Dr. Dean paid a flying visit to Japan to collect armor and objects of art for the Metropolitan Museum of Art, in which he was at that time curator of arms and armor. He reached Japan on March 28 and embarked for the U. S. on May 19. This I have from a member of the party and from his letters to Mrs. Dean. Hence he was in Japan when five embryos (to be referred to later) were collected on April 23. These and the ones referred to above, were obtained by his friends (whom he names in these letters), and preserved for him. The specimens collected in 1917 (and possibly the others listed with them) were brought back by him in May-June of that year.

Among the embryological records accumulated by Dr. Dean during these two trips and left unpublished at his death, are numerous drawings showing various stages in the development of the primitive shark, *Chlamydoselachus*. In keeping with the plan and purpose of this volume, as briefly set forth by Gudger and Smith on page 49 of Article II, the present contribution has been prepared in order to preserve for science these excellent drawings.

This article (No. VII) forms the third and last of a series dealing with this rare shark. In the first, Gudger and Smith (1933) brought together from widespread sources everything then known concerning the natural history of the fish, to form a background for work on the anatomy and the embryology. Next came Dr. B. G. Smith's monograph on the anatomy. This includes a review of the results of many investigators, but to these studies, Dr. Smith added the results of his own investigations on certain organ systems either wholly or partly omitted by other writers. Smith's dissections, it is interesting to note, were done on specimens obtained in Japan by Dean.

And now there are set before me two tasks. The first is to make a study of Dean's notes on the breeding habits and seasons and on the structure and functioning of the reproductive organs of the frilled shark. These notes are few, fragmentary and scattered throughout a notebook marked *CHLAMYDOSELACHUS* and in various loose notes, sketches and photographs. However, I have been able to piece together from Dean's notes, from the specimens loaned from Columbia University, and from the scanty literature, sufficient data to extend considerably our knowledge of these subjects. I am fortunately able to bring forward for comparison data from my observations on the breeding habits and genital organs of various sharks and rays, and particularly of the nurse shark, *Ginglymostoma cirratum*, whose reproductive habits and large shelled eggs are remarkably like those of *Chlamydoselachus*.

My second task is to prepare descriptions and explanations of the admirably drawn figures of the eggs and embryos of this shark left unpublished by Dr. Dean at his untimely death. For reasons to be given later, it will be clear why these figures do not portray a completely graded series of embryos but only such stages as were procurable with great difficulty. But before beginning the consideration of these drawings, other and introductory studies of the fish must be made.

Almost nothing has been published about the breeding seasons and breeding habits of the frilled shark and equally little concerning the functioning of the reproductive organs. Even less is known about the development of *Chlamydoselachus*. But when the breeding habits and seasons and the reproductive organs have been studied and the figures of the embryos described, the reader will have a fair idea of the life history of the frilled shark.

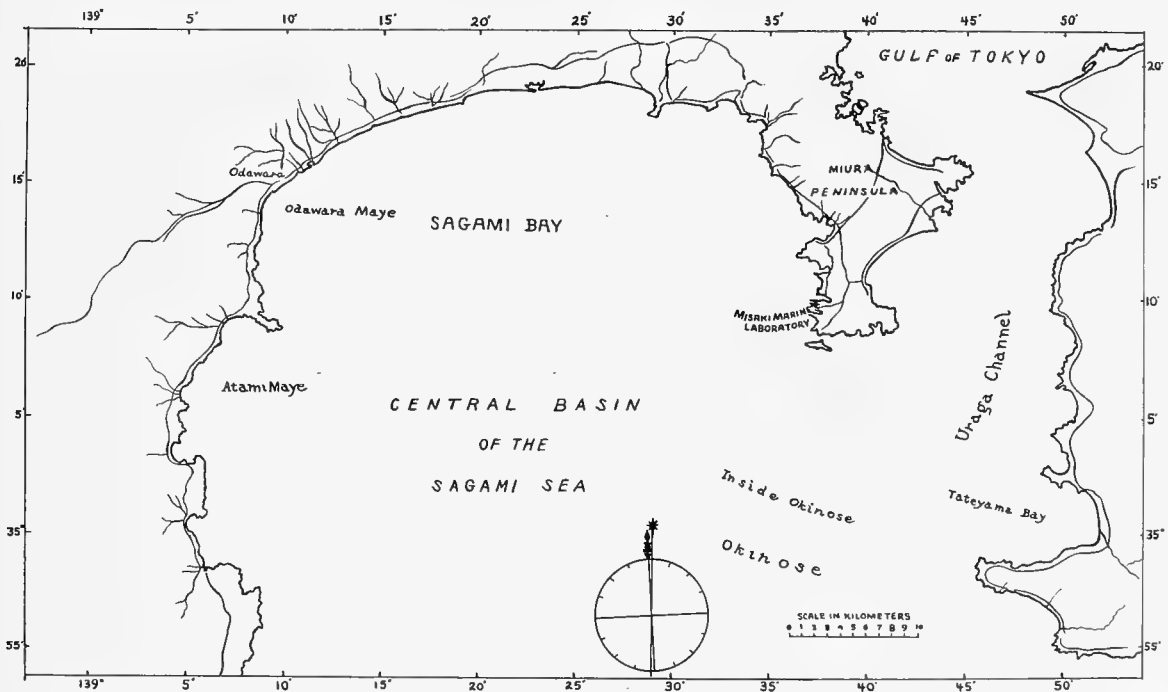
Some years before his death in 1928, Dr. Dean asked me to collaborate with him in preparing an article such as this. But having much work planned for years ahead, I presented my case, and, Dean, generous as always, withdrew his request and urged me to proceed with my own studies. And now that he is gone, I am trying to do what could have been done long ago so much better in collaboration with him, since his memory

would have supplied details not recorded among the very few notes available.

In this difficult task, I have been fortunate in having the active help and cooperation of Dr. B. G. Smith. It is a pleasure to acknowledge my large obligation to him.

THE SPECIMENS AND THEIR SOURCE

That the collecting of eggs and embryos of *Chlamydoselachus* was not the main object of Dean's first visit to Japan, and that the finding of these eggs was somewhat unexpected, is attested by this statement (Dean, 1901.1)—“My first object in visiting Japan [in 1900] was to secure the eggs and embryos of the Port Jackson shark [*Heterodontus* = *Cestracion*].” The eggs of *Heterodontus* were found among rocks and seaweed in shallow water, and were easily collected by divers and maintained without difficulty in aquaria of running water or in floats in the sea. Hence it is not surprising that Dean procured a fairly complete series of early stages of the embryos of this shark and that he devoted most of his time to their study. The drawings of the eggs and embryos of *Heterodontus*, which are more numerous than those of *Chlamydoselachus*, will form the basis of the final article in this Memorial Volume.



Text-figure 1

A map of the Sagami Sea, the Miura Peninsula, and part of the Gulf of Tokyo, showing the position of the Misaki Laboratory in which Doctor Dean worked, and the waters from which his specimens of *Chlamydoselachus* were obtained.

From an old chart compiled by Prof. I. Ijama.

Dean knew of Garman's monograph on the anatomy of *Chlamydoselachus* (1885) and of Nishikawa's pioneer work (1898) on the breeding habits and embryology. But in 1901 he wrote: "I hardly had hopes . . . of obtaining [at Misaki] a series of embryos [of *Chlamydoselachus*] . . . on account of its great rarity; for one could easily count on his fingers all of even the adult specimens which had hitherto been brought from Japan. . . I found, however, that . . . if one could secure many adult specimens there was a fair chance of obtaining embryos, since this shark was known to be viviparous."

During his twelve months in Japan (1900–1901), an intensive search for *Chlamydoselachus* was carried on. During his temporary absence from Misaki, this search was prosecuted by his assistants, and, even after his departure for the United States, the hunt was kept up—certainly as late as 1917. But so rare was the fish that in 1904, Dean wrote that ". . . in the course of a year, the neighborhood [the Sagami Sea] yields about a dozen specimens [of both sexes]". And in his notebook under the heading "Abundance" is this statement "1904. About 6—1 gravid". In another place is this notation—"1905. Kuma fished for about 5 weeks in the best ground off Odowara—special tackle—squid bait, depth from 300–600 fathoms, took 3 fish"—one male and two females. The scarcity of specimens and the difficulty of procuring them, it may be noted, is due to the fact that they have to be fished for with trawl hooks at depths averaging from 1200 to 3600 feet.

Although 10 adult specimens of *Chlamydoselachus* have been taken in the seas of western Europe, the only region where embryos have been obtained is still the Sagami Sea, more particularly the waters around the Miura Peninsula on which the Misaki Biological Station is situated. Dean states that he had females with young from Sagami Bay (and particularly from the Odowara Maye); while other materials came from the Gulf of Tokyo—another arm of the Sagami Sea. For these localities see Text-figure 1.

The chief collector at the Misaki Station in Dean's day and for long afterwards was Kuma Aoki, an ex-fisherman, who had a remarkable knowledge of all the specific localities where *Chlamydoselachus* might be found. In addition to fishing directly for Dean, Kuma made arrangements with other fishermen in Sagami Bay that all frilled sharks taken by them should be brought to the laboratory. Also Prof. Mitsukuri of the Imperial University of Tokyo arranged with the market people in Tokyo that all specimens brought there from any source whatever should at once be sent to the station at Misaki. From all these sources, material slowly came to Dean at the laboratory on the Miura Peninsula.

In the fragmentary entries in various handwritings in Dean's notebook, a total of 42 adults are listed—16 males and 26 females. These cover the years 1900–1906 inclusive. In Dean's own handwriting, there are listed with measurements 21 adult fishes—7 males and 14 females. I surmise that these were the results of Dean's collecting for the 12 months of 1900–1901. It is probable that the grand total of 42 adults, from all records in various handwritings in his notebook, contains a number of duplications. Of the 26 females listed, 10 are credited with producing 56 eggs. For 24 of these eggs it is stated that two were in the blastula stage, two in the gastrula, while 20 had on them embryos varying from 11.5 to 390 mm. in length.

The difficulty of arriving at a total for these eggs and embryos is due to the fact that these notes were made by at least two other persons besides Dean. The table in Dean's handwriting recording 21 adults must have been compiled from various other entries in the notebook labelled *CHLAMYDOSELACHUS*. Finally, the matter is complicated by the fact that the entries cover the catches of the years 1901–1906 inclusive. Here it must be noted that between Dean's departure from Japan in 1901 and his return in 1905, specimens of adults and embryos were collected and sent to him in America. Some of these are listed separately in the notebook referred to.

There was another small but valuable lot of material made available to Dean. A young Japanese student, T. Nishikawa by name, had in May, 1896, collected eggs and embryos of *Chlamydoselachus*. By June, 1897, he had finished a brief but interesting paper ("Notes on some embryos of *Chlamydoselachus anguineus* Garman"). This was published in 1898. In 1900, Dean at Misaki began to get eggs and embryos of the same shark. Nishikawa, having finished with his materials and having published his article, turned over to Dean all his specimens and slides to further Dean's researches. Evidence of this will be adduced in various sections of this article to follow.

Of the embryological material brought back by Dean in 1901 and 1905, or sent from Japan to him at various times, I have had access to certain embryos of *Chlamydoselachus* as follows. In the American Museum are six specimens ranging from 190 to 370 mm. in length. In the zoological collection of Columbia University, and loaned to me by Prof. J. H. McGregor, are 13 embryos of various sizes (but none so large as ours), some with and some without yolk sacs; and five eggs without embryos; then in addition there are four lots of embryos (mainly very young) collected in 1913, 1914 and 1917. Lastly from the Museum of Comparative Zoology, Cambridge, Massachusetts, there have come through the courtesy of Dr. Thomas Barbour, one small embryo brought from Japan in 1907; and an egg with a larger embryo presented by Dr. Dean in 1912.

THE DRAWINGS AND THEIR AUTHORSHIP

Found among Dean's records are 55 finished drawings reproduced herein as plates I to VI. These drawings range from a representation of what is evidently an ovarian egg to figures of specimens, male and female, in which the yolk sacs are no longer present. Of the 55 drawings, three are in color and the others are in grey (pencil), but all were prepared for reproduction by lithography. These figures were assembled on eleven unnumbered sheets of heavy cardboard, each plate comprising from one to nine figures. I could not make out any graded arrangement of these drawings as affixed to the sheets which have come to me. With the help of Dr. B. G. Smith, I have endeavored to consolidate the drawings of eggs and embryos and arrange them in sequence so far as is practicable—except that the colored figures have been grouped on one plate. All the drawings of adults have been grouped on the final plate.

The matter of the execution of the drawings, which form the basis for this article, was at first a puzzle. It seemed probable that some of them were made by Dean, but

there was reason to believe that most of them were done by Japanese artists under his direction. No one, who is familiar with Dean's skill as an artist, will doubt that he was capable of making drawings like those reproduced in this article. But his time at Misaki must have been fully occupied with pushing the collection and preparation not only of the embryological material of his archaic fishes (particularly the more abundant eggs and embryos of *Heterodontus*) but of the other rare zoological materials which he brought back to Columbia University.

As will be shown later, *Chlamydoselachus* is an ovoviviparous shark. The embryos with their huge yolk sacs, enclosed in egg capsules, were obtained from the uteri of the female fish newly caught in Sagami Bay. Brought up from depths of from 300–600 fathoms, these embryos presumably could not be kept alive in aquaria. They would be subjected to two greatly changed conditions—a lower pressure and a higher temperature. Further, there is probably a difference in the chemical composition of the surrounding medium when eggs and embryos are transferred from the uterine fluid to sea water. However, in the light of some personal observations, I cannot be sure of this. While a guest-investigator at the Tortugas (Florida) Station of the Carnegie Institution of Washington (1912–15), I found that when the similar thick-shelled intra-oviducal eggs of the nurse shark, *Ginglymostoma cirratum* (a shallow-water form), were removed from the uterus, opened, and the perivitelline fluid tasted, this was found to be salt. It may be noted here that the cloaca of the nurse shark has a wide external opening and that the common opening into it of the two gravid uteri will often admit three or four fingers. A similar testing of the perivitelline fluid of the uterine egg of a just-caught *Chlamydoselachus* would be very instructive.

Even if the factor of chemical composition of the surrounding medium is ruled out, still, because of the great alterations of pressure and temperature, the embryos of *Chlamydoselachus* would die quickly. Hence if they were to be drawn alive, the assistance of several skilled artists would be required. In this connection and in corroboration of the idea expressed above, Mrs. Dean states that she clearly remembers that Dr. Dean, while at Misaki in 1900–1901, had the assistance of six artists and that on the second visit (1905) he had four artists making drawings. Mrs. Dean is fortunately able from her diary to give the names of the six artists—one of them being a man named Kuwabara.

Furthermore, Dean was, at the time of the collection of embryos of *Chlamydoselachus*, also studying the much more abundant eggs and embryos of *Heterodontus* which were comparatively easy to procure from shallow water with the aid of divers.

Since there are many drawings of the young stages of this shark, it is probable that the artists devoted more time to these than to the embryos of *Chlamydoselachus*. Because of the abundance of valuable *Heterodontus* material and because the less viable embryos of *Chlamydoselachus* must be preserved immediately, it seems probable that figures of the embryos of the frilled shark were drawn at a later date from preserved specimens. I surmise that the colored figures and probably some of the uncolored ones were made at once from fresh specimens at Misaki, or that rough color sketches were made there, and

that later the finished sketches were made from these and from preserved specimens.

Finally, I have received from Dr. Naohide Yatsu, of Tokyo Imperial University, information which confirms the conjectures above and adds further to our knowledge of the authorship of these excellent drawings. Dr. Yatsu was associated with Dr. Dean on the first visit to Japan, and afterwards at Columbia University, where he was a student of Dean's and later an assistant in the Department of Zoology.

On the matter in question, Yatsu writes that at Misaki, Dean made sketches in pencil and in color from living embryos of *Chlamydoselachus*. Indeed among Dean's relictia is such a color sketch of the internal organs of a female *Chlamydoselachus*. As to the finished drawings, Yatsu is sure that the color figures were made from Dean's color sketches and the pencil drawings from Dean's sketches and also from preserved material. These were done in Tokyo in 1905 under Dean's supervision at the Zoological Institute of the University by Isaburo Kuwabara, the Institute draftsman. This is also the testimony of Yatsu's colleague, Dr. Tanaka.

VIVIPARITY (OVOVIVIPARITY) IN *CHLAMYDOSELACHUS*

All elasmobranchs (sharks and rays), whether oviparous or viviparous, have internal impregnation and fertilization. To effectuate this, the male is provided with intromittent organs, the claspers. These are modified portions of the hinder and inner part of each pelvic fin, which are inserted into the cloaca of the female and served to hold her fast and to transmit the seminal fluid.

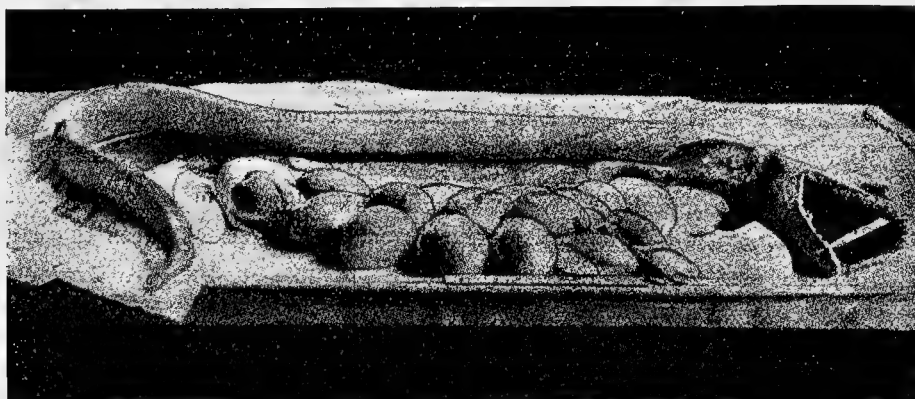
The preponderant evidence is that oviparity was the original method of reproduction in elasmobranchs. It persists today in certain sharks and skates, which extrude eggs enclosed in horny envelopes provided with tendrils by means of which they become attached to marine objects. In *Chlamydoselachus* the large egg is enclosed in a keratinoid capsule provided at each end with a process which varies greatly in form and structure. It is sometimes blunt but in many instances it is long, curved, and frayed at the apex into tendrils (Figures 2, 7 and 13, plate I). If these encapsuled eggs were found outside the body of the fish, one would surmise that these curved processes serve as organs of attachment. But egg and capsule are retained within the uterus even after the developing embryo has burst the shell, as will be shown later.

Thus in this shark, the presence of the egg shell with curved horns or frayed processes plainly indicates that the ancestors of *Chlamydoselachus* practiced oviparity. Yet in the frilled shark, possessing so many primitive characters, there prevails the most highly specialized form of reproduction—viviparity, or more properly ovoviviparity as will be explained later. This is another instance of the strange admixture of primitive and specialized characters found in *Chlamydoselachus* as pointed out by Smith in his study of the anatomy (1937).

That the fish is viviparous must have been known to Ludwig Döderlein, who, in the years 1879–1881, made an extensive collection of Japanese fishes. These were brought in 1881 to Vienna, and among them were two specimens of *Chlamydoselachus* taken in

Tokyo Bay in 1881. At least one of these was a female. For the scanty history of these two sharks see Gudger and Smith (1933, p. 248). As may be read therein, Döderlein described the two specimens of *Chlamydoselachus* but his paper was lost. It is plain, however, that he recognized that this shark is viviparous. For this see Röse's statement in a later paragraph in this section.

In 1884, the Museum of Comparative Zoology, Cambridge, Massachusetts, purchased a slender snake-like shark from Prof. H. A. Ward, who had obtained it from Japan. Samuel Garman, curator of fishes, seeing that it was a new form, at once published preliminary descriptions of it and named it *Chlamydoselachus anguineus* (the snake-like cloak-gilled shark). In 1885 Garman described the anatomy of this partially eviscerated female specimen. He found the badly preserved ovaries and oviducts much torn, but of



Text-figure 2

A female *Chlamydoselachus* with the eggs which have been cut out of her body.

This figure has been carefully retouched to make the outlines clearer.

After Nishikawa, 1898, Fig., p. 95.

one of the oviducal tubes he says that "A piece left at the cloaca showed one of the [ovi] ducts greatly distended, possible with young that had hatched within it".

That this was a sound deduction is shown by Röse's statement (1895, p. 194) that "One of the animals [a female *Chlamydoselachus* brought from Japan by Döderlein] had 'im Leibe' an embryo about 340 mm. [13.4 in.] long, which Professor Döderlein had the kindness to turn over to me for study". With this statement of Röse's, it became almost certainly established that *Chlamydoselachus* brings forth its young alive.

However, the man who personally first definitely demonstrated that the frilled shark is viviparous was the Japanese student, Nishikawa. In 1898, he wrote "*Chlamydoselachus anguineus* is viviparous, and the breeding season is spring, extending from about the end of March to the beginning of June". Furthermore, he figured a female shark and a number of eggs (Text-figure 2) taken from her body. This photograph was poorly reproduced on soft paper and is without any explanatory legend. It is plain, however, that these eggs are enormous in proportion to the size of the body of the fish.

It is impossible to determine with certainty how many eggs are represented in this figure. There seem to be about a dozen and in addition there are various objects not clearly recognizable. There is no date given for the capture of this fish, but from a female taken May 26, 1896, Nishikawa obtained six embryos ranging from 32–60 mm. in length. "Each embryo was attached to its large yolk-sac by means of an umbilical cord, which allowed considerable movement to the embryo".

Thus Nishikawa in 1898 was the first to demonstrate by dissection and publication that *Chlamydoselachus* is viviparous. He had dissected seven specimens in 1896. Since Dean kept closely in touch with the literature on the archaic fishes, it is likely that he knew of Nishikawa's article (1898) as is evidenced by his statement (Dean, 1901.1): "I found . . . that if one could secure [at Misaki] many adult [female] specimens [of *Chlamydoselachus*] there was a fair chance of obtaining embryos, since this shark was known to be viviparous".

Dean's extensive experience in collecting eggs and embryos at Misaki abundantly confirmed the conclusion that *Chlamydoselachus* is viviparous. His stages ranged from blastulae to embryos varying in length from 11.5 mm. to 390 mm. (15.35 in.)—all attached to yolk sacs.

The spawning habits of the frilled shark are unknown to this day. It seems to me that this fish must properly be called not viviparous but ovoviviparous, because it carries in its uterus not eggs in very thin-walled capsules as do some viviparous sharks and rays, but eggs with rather heavy keratinoid shells fit to be expelled into the water (Figures 2 to 10, plate I).

I have found that the tropical littoral nurse shark, *Ginglymostoma cirratum*, carries in its uteri very large eggs enclosed in very heavy keratinoid shells. Evidence (to be adduced later) leads to the belief that, when the embryo has attained some size the shell is burst and is expelled through the cloaca into the sea, while the egg and embryo are retained in the uterus for a considerable time. For these reasons, it seems to me that such a shark ought to be designated as ovoviviparous rather than viviparous. I have studied the nurse shark extensively and since its reproductive organs and breeding habits are very similar to those of the frilled shark, comparisons will frequently be made in order to clear up many puzzling questions about the reproduction of *Chlamydoselachus*.

The young frilled shark certainly breaks its egg shell long before it is old enough to be extruded from the uterus into the water (Figure 11, plate I). But we do not know at what stage in the development of the embryo the insoluble keratinoid egg capsule is cast off into the uterus nor when it is extruded into the sea. Nor is it known whether the embryo is expelled into the water before all the yolk is absorbed as occurs in the dogfish, but it seems improbable. If the young *Chlamydoselachus* or *Ginglymostoma* were extruded early, it would swim poorly because of its great yolk mass (Figure 49, plate V) and would be an easy prey for any marauding fish. One must conjecture that the young of both sharks are retained in the uterus until, when passed out into the sea, they are able

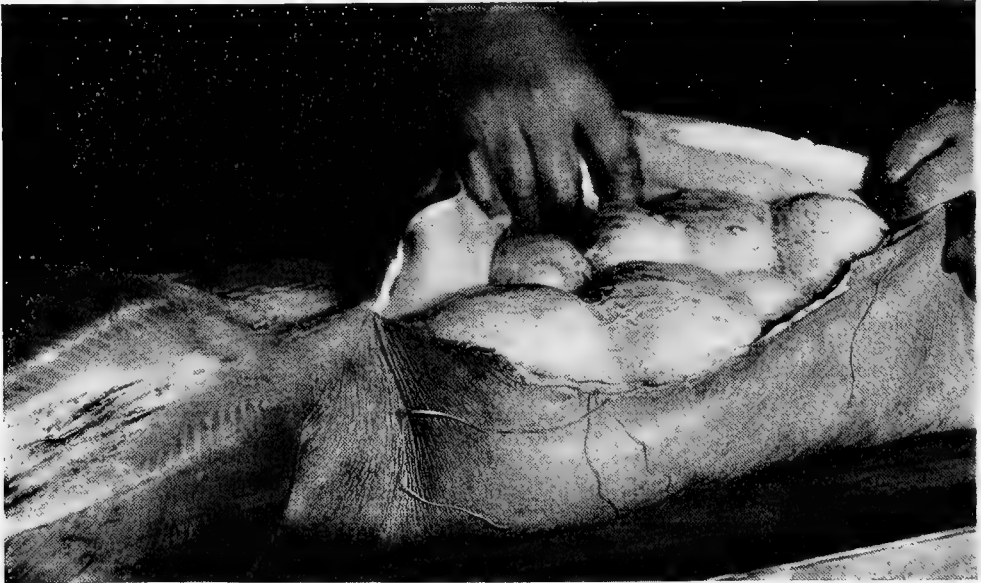
to fend for themselves. In support of this I have found (Gudger, 1918) that the 20-mm. eggs of the marine gaff-topsail catfish (*Felichthys felis*), which are orally incubated, are retained in the mouth of the male not only until the egg shell is thrown off but until all the large yolk mass is taken into the body of the young fish. Thus the little three- or four-inch fish when set free in the ocean is better equipped to escape its enemies and capture its food.

BREEDING SEASON OF THE FRILLED SHARK

Because of its deep-sea habitat, no direct observations on the breeding behavior and season of this shark have ever been made. Consequently we are confined to a study of the records indicating the stages of development of ovarian eggs and of uterine embryos on the dates of capture of the females. The evidence from the ovaries, since it does not include accounts of eggs ready to be discharged, is not of great value. Of prime importance, however, are the data as to stages of development of embryos in the oviducts. The all too scanty evidence from both sources will now be presented.

EVIDENCE FROM THE OVARIES

With one exception, the only available evidence from this source as to the breeding season of *Chlamydoselachus* is contained in the entries in Dean's notebook concerning eggs found in these organs. These fragmentary statements, being dated, do throw some light on the matter.



Text-figure 3

The partially opened abdomen of a 1510-mm. female frilled shark taken November 28, 1938, in the Sagami Sea. Five eggs, each measuring 80—83 mm., were contained in each ovary.

Photograph by courtesy of Fumio Momose.

In the handwriting of Dean's unnamed Japanese collector—possibly Kuma—are two records. In the ovary of a 1500-mm. *Chlamydoselachus* taken February 8, 1905, six "immature" eggs were found. And on April 30, 1903, he found in a female, 1670 mm. in length, three "immature" eggs in one ovary and nine in the other. Unfortunately the sizes of these eggs were not noted. However, under date of April 27 (1902?), Dean diagrammatically figured and also photographed the ovaries with eleven large eggs in a female measuring 1960 mm.—the largest *Chlamydoselachus* on record. In the left ovary were five eggs, size 70 x 30 mm., and in the right nine of the same size and two measuring 60 x 30 mm. As will be seen later, these eggs, though large, were not mature, but one may conjecture that they would have reached maturity later in the calendar year. Thus Dean recorded on October 1, 1905, "female, no eggs [in oviducts?], large ovar."

Since the above was written, Momose (1938) has described the visceral anatomy of a nearly ripe female taken in Sagami Bay, November 28, 1938. Each ovary contained five eggs measuring from 80 to 83 mm. in diameter. Momose has kindly sent me two photographs showing this fish opened along the mid-ventral line to reveal the ovaries. The better of these photographs is reproduced herein as Text-figure 3. Since ripe ovarian eggs and newly fertilized eggs (Figures 1, and 4, plate I) average about 95 mm. in diameter, it is clear that these 80–83-mm. eggs were almost mature.

The evidence from the ovaries is scanty but nevertheless significant. To recapitulate, ovarian eggs taken February 8 and April 30 were noted as "immature" but no sizes were recorded. However, on April 27 some eggs were measured and found to be 70 x 30 mm. On October 1 a "large ovar." was noted, and on November 28, several eggs measuring about 83 x 80 mm. were photographed (Text-figure 3)—eggs almost "ripe". These data indicate strongly that eggs in the ovaries of *Chlamydoselachus* ripen at any season throughout the year. But better evidence of a long breeding season will now be introduced.

STAGES OF EMBRYOS IN THE UTERI

The evidence as to the surprising range of the breeding season of the frilled shark, based on the ages of embryos obtained from the uteri, at various times in the year, will now be set out in chronological order.

Nishikawa (1898) gives the first intimation of a definite breeding season for the frilled shark. He states that "... the breeding season is spring, extending from about the end of March to the beginning of June". He had eggs in early and late blastula stages but he does not give the dates when these were obtained. Of his seven gravid female fish, he gives date of collection for but one. His youngest batch of embryos (from a 1700-mm. female) came to him on May 26, 1896. These embryos were six in number and measured 32, 35, 43, 48, 50 and 60 mm. long respectively.

Dean's notes give a far greater range of dates when uterine eggs and embryos were collected, and ordinarily he gives measurements for one or both. Thus he notes "1905, Early Jan. [not June]" eggs with embryos 11.5, 15.5, and 20 mm." Furthermore, in the jar of material from Columbia University referred to above there are two embryos of

about 20 and 45 mm. in length, without yolk sacs, bought in the Tokyo market January 22, 1914. These and other embryos from this jar are badly crumpled, hence the "about" for this and the three other lots. In this same jar are four embryos about 15, 18, 20 and 25 mm. "over all", "from Tokyo market February 4, 1913". In the same receptacle are seven embryos ranging from about 60–130 mm. in length "Bought Tokyo Market April 4, 1913". In his notebook Dean states that he got three blastulae on April 10 (year not noted). Next and last of the four Columbia University lots are five embryos measuring about 23, 25, 30, 43 and 47 mm. bought on April 23, 1917.

The remainder of the available data is also from Dean's notebook. On April 25 he records seven eggs with embryos—165, 175, 185, 195, 205, 210 and 250 mm. in length. Then in the writing of his unknown note-taker and correspondent, judged to be a Japanese, are recorded eggs from the oviducts of three females each measuring 1770 mm. The first taken April 25 had seven eggs with embryos (not measured), the second (of the same date) had five "broken eggs" in the oviduct; the third, taken April 27, had in the oviduct three "mature" eggs (two broken). Next in Dean's writing is this record "4 embs. large, taken about May 1, 1905". These measured in millimeters 317, 331 (yolk sac 111 x 100), 352, 390 (yolk 100 x 70). Then I find in Dean's writing a record, "? May 23, 1906," of five embryos (no measurements) from a 1390-mm. female. The next records come from late in the calendar year and are so important that they must be given in a separate paragraph.

Four eggs were taken from the uteri of a female captured in the Odowara Bank on or about October 1, 1905. This record is based on three separate notes in Dean's writing on three separate pages of his notebook. No one of these, no two would establish this fact; but when all three are studied together, date, place, and number of eggs all tie up into this definite record. Three of these eggs are noted as "oblong eggs, 2 drawn, in r. oviduct, small wind egg (drawn) in opposite [l.] oviduct, stage early [small pencil sketch] probably gastrula". For the two "oblong eggs", see Figures 2 and 3, plate I. Apparently the oblong egg with the probable gastrula, shown in the pencil sketch (Text-figure 26), was not drawn. For the "small wind egg" see Figure 51, plate V.

Among Dean's loose papers, I have found a rough sketch in water color of an egg and embryo labelled (in a hand other than Dean's) "*Chlamydoselachus anguineus*. Egg taken at out of Okinose, Sagami Sea. (Depth 360 fms.) December '06". The egg and embryo were presumably drawn natural size. The ellipsoidal yolk measured 122 x 69 mm., and the embryo 55 mm.—when taken in December!

Here let us recapitulate the dates throughout the whole calendar year on which embryos of the sizes noted have been taken: "Early Jan.", six specimens measuring 11.5 to 20 mm.; April 4, seven—60 to 130 mm.; April 10, three blastulae; April 23, five embryos—23 to 47 mm.; April 25, seven, 165 to 250 mm.; April 25 and April 27, fifteen eggs and embryos in three uteri; May 1, four embryos—317 to 390 mm.; May 23, five—no measurements; October 1, three eggs—probably blastulae; December '06, one embryo 55 mm.—in length.

The evidence from the ovaries is fairly strong, that from the uteri cumulative and overwhelming, that *Chlamydoselachus* ripens eggs in batches in its ovaries, and broods and hatches embryos in its uteri throughout the whole calendar year and probably in every month of the year.

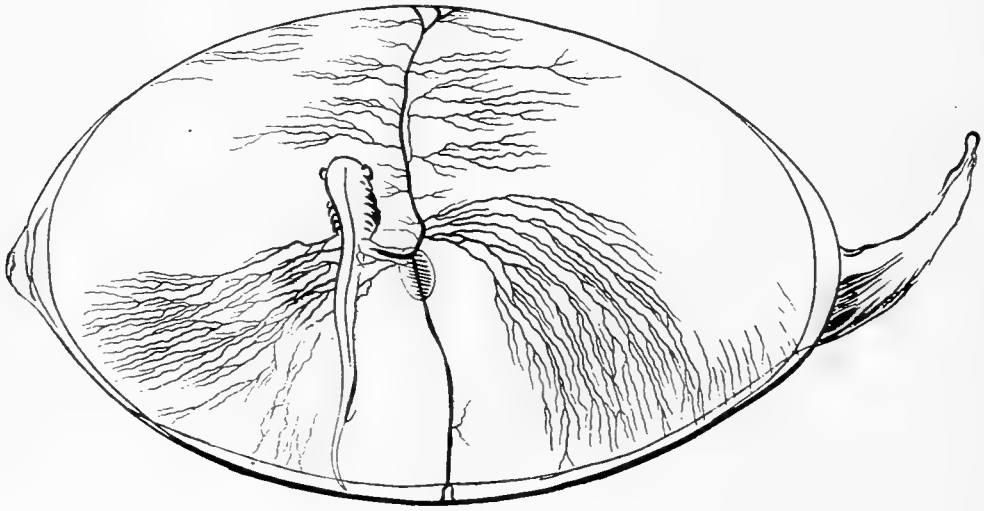
When one thinks the matter out, this does not seem so extraordinary as at first blush. *Chlamydoselachus* lives at the bottom of the Sagami Sea under uniform conditions of darkness, great pressure, low temperature, with a restricted oxygen supply, and on food with presumably little change in kind and quality. The maximum depth of the habitat of the frilled shark is about 3600 feet, the average 1500 to 1800. At 1800 feet the pressure is 814 lbs. to the square inch, the temperature about 43° F. and the human eye would find total darkness. Under the prevailing and unvarying conditions at these depths, the frilled shark would presumably have no special breeding season such as is found in surface-dwelling sharks in the Sagami Sea. In these, in contrast, breeding might be expected to take place in late spring or early summer due to the lengthening daylight period, the rising temperature, and the more abundant food consequent upon the return of the sun. In *Chlamydoselachus*, on the contrary, it is to be expected that eggs would ripen in the ovaries at any time during the year as indicated above and that breeding would take place during any month. Thus the findings of eggs with blastulae in October and of embryos 10–20 mm. long in January, and others measuring 317–390 mm. in May—as recorded by Dean—are understandable.

Before leaving this subject, it is pertinent to call attention to the notes above, which show that not all the eggs in a single uterus are in precisely the same stage of development. Even as the eggs break out of the ovary one at time as they ripen, so they make their way into the oviduct one at a time. Hence there must be a continuous process of fertilization, shell formation, and early development going on within a single female during a limited period of time. This I have found to take place in the shallow-water nurse shark of Florida. Likewise, there will be much later, in the uterus of each individual female *Chlamydoselachus*, a serial process of breaking and throwing off of egg capsules by the growing embryos, and finally a succession of young sharks being extruded into the sea.

It should be noted that ovarian eggs are matured in batches or clutches (a small number of approximately the same large size) and that, when nearly mature eggs are present in the ovary, there are no other eggs in the ovaries of the same individual at all comparable in size. Also, there are limits to the range of variation in sizes of embryos obtained from a single female at the same time. One does not find very early and very late embryos developing in a single individual at the same time. These observations indicate that in each individual *Chlamydoselachus* there is a definite cycle of reproductive activity, but one quite independent of seasonal influences, hence any single phase of reproduction and development may occur in different individuals at different seasons of the year. In this, *Chlamydoselachus* is unlike most vertebrates, but a comparable condition is found in civilized man.

DURATION OF GESTATION

The duration of the period of gestation in the frilled shark is not known, and, because of the habitat of the breeding fish and of the absence of any definite breeding season, it cannot be ascertained by direct observation. However, it will be of interest to set forth some facts that indicate that the period is protracted. The same factors of constant low temperature, great pressure, and restricted oxygen supply, that lead to an extension of the breeding season to cover the calendar year, would also be conducive to slow development of the embryos and a lengthened period of gestation.



Text-figure 4

Egg shell (measuring 128 mm.), egg (100 x 65 mm.), and embryo (43 mm.) of *Chlamydoselachus*, reproduced in natural size.

After Nishikawa, 1898, Fig. 1, pl. IV.

An idea of the duration of this period may be gained by studying a series of growing embryos and noting the relative diminution of their yolk sacs. But first one must endeavor to establish the normal size of the yolk mass at, or shortly following fertilization. The matter of the varying sizes of the eggs of *Chlamydoselachus* will be taken up later. Here we are interested in the size of the eggs in blastula or gastrula stages or in early stages of embryonic development. Only two investigators have studied such eggs. The first of these, Nishikawa (1898), states that the eggs (in early stages of development, probably segmentation), range from 65 to 75 mm. in short and from 102 to 124 mm. in long diameter. He writes of other eggs ranging from 110 to 120 mm. in long diameter. These measurements are probably made over the egg shell. Thus Text-figure 4 (his Fig. 1, tab. IV) is 128 mm. long in a straight line over the horns of the shell, whereas the egg itself measures 100 x 65 mm., and the embryo 43 mm. in length. The egg shown in Text-figure 4 is in natural size.

Dean portrays three eggs in blastula or gastrula stages in Figures 4, 5, and 6, plate I. The yolks measure: A, 97 x 88 mm.; B, 96 x 87; C, 90 x 87. Of eggs and early embryos in stages of development comparable to Nishikawa's 43-mm. embryo, Dean had three drawn. Figure 7, plate I shows a yolk 100 x 65 mm. with an embryo of 43 mm.; (as will be seen later, this is a copy of Nishikawa's Fig. 1, plate IV); in Figure 9, plate I, the yolk measures 108 x 68, the embryo 50 mm.; and lastly there is the drawing in color, Figure 50, plate V, with a yolk 95 x 69 and an embryo of 39 mm. In these early stages there is practically no diminution of yolk size.

To illustrate the slow rate of absorption of yolk, we may consider three large embryos listed by Dean. Thus in Figure 11, plate I, an embryo of 175 mm. (magnified to 205 mm.) sits on a yolk measuring 92 x 89 mm. This was collected April 25. Then "taken about May 1, 1905" were two still larger embryos. The smaller measured 331 mm. in length and had a huge yolk sac measuring 110 x 100 mm. The other is the largest embryo of which there is record. This fish, shown in color in Figure 49, plate V, was 390 mm. (15.35 in.) long and its yolk sac was 100 x 70 mm. in its transverse diameters.

To recapitulate, Dean's notes will be quoted. The specimens of Oct. 1, 1905, "stage early, probably gastrula", might possibly have grown by "early January" into embryos measuring 11.5, 15.5, and 20 mm. on yolk sacs undiminished in size. But it does not seem likely that by "Apr. 25" one of these could have attained the size of the 175-mm. embryo of Figure 11, plate I. Nor could the 175-mm. fishlet by "May 1" have grown to an embryo of 390 mm. (yolk 100 x 70), which is represented in Figure 49, plate V. From the above data it is clear that the fish grows much faster than the yolk decreases.

It is evident that all the yolk must be resorbed before the little shark is thrown out. into the sea to fend for itself. The 15.35-in. fish portrayed in Figure 49, plate V, would be so encumbered in swimming, and the large yolk covered with blood vessels would be so conspicuous and attractive to marauders, that the free life span of the fish would probably be but a few hours at most. But how large would the young shark be when it has used up all the food yolk? Surely it would be much larger—perhaps 20–24 in. (508–610 mm.) long. The latter size is that of a free-swimming *Chlamydoselachus* taken by the Prince of Monaco at Madeira (Collett, 1910). But would the uterus of the average-sized female contain such a large "baby" without its being folded or curled up? And could it contain several embryos of this size?

All the evidence points to a very long period of gestation in *Chlamydoselachus*. But how long? Because of its habitat and its breeding throughout the year, it is of course impossible to find the answer in the body or in the habits of the frilled shark. It is practically impossible to ascertain the length of time for the hatching of any shark's egg save in the oviparous forms—and only in those species small enough to be kept in aquaria, where the date of egg-extrusion and of egg-hatching can be recorded. This has been done in terms of "about so many days" for two species of dogfish. One must say "about" for one cannot know how far in development an internally-fertilized oviparous egg has gone when it is "laid". Here are all the facts, so far as known to me.

As early as 1867, Coste described how a pair of spotted dogfish, *Squalus* (*Scyllium*?) *catulus* were introduced into the vivarium at Concarneau (a rock-encircled arm of the sea shut off by gratings). The female extruded 18 eggs during the month of April, and the young were hatched out during the month of December. Thus the period between laying and hatching was about 8 months—not "about 9" as stated by Coste.

Bolau (1881) is more exact. On April 12, 1877, the Hamburg Aquarium received from the Brighton Aquarium a number of eggs of the European dogfish, *Scyllium canicula*, (how long after extrusion is not stated). Four of these hatched as follows—December 3, 1877, and January 1, 4, 17, 1878. Their periods were 235, 264, 267, 280 days—from 7 months and 21 days to 9 months and 10 days. Seven eggs of the catshark, *Scyllium catulus* (also from Brighton), hatched from August 19 to October 16—a time space of 129–187 days or 4 months and 9 days to 6 months 7 days. That same season an egg laid in the aquarium hatched in 180 days. During 1878 a number of catshark eggs were deposited in the same aquarium and 10 of them hatched in periods varying from 157 to 178 days or from 5 months and 7 days to 5 months and 28 days.

These are the known facts, but more data are needed. In comparison there is reason to believe that, while incubation is going on, the female frilled shark is living in water of probably not over 43°F. (at a depth of 1800 feet.). But what were the ranges of temperature to which the dogfish eggs were exposed at Concarneau and at Hamburg? We have already noted the great size of the egg of *Chlamydoselachus*. Bolau tells us that the barrow- or stretcher-shaped eggs of *Scyllium canicula* were 110 mm. long (over the horns) by 41 mm. broad (over the case). The corresponding measurements of the similar eggs of *S. catulus* are 60–55 mm. long by 24–22 wide. The sizes of the yolk masses in these eggs are not given, but they are undoubtedly far smaller than those of *Chlamydoselachus*—probably not more than one-third to one-fourth as large.

If it takes these relatively small eggs of the European dogfishes from 5.5 to 9.5 months to hatch at the spring, summer and autumn temperatures of the English Channel and the North Sea, how much longer must it take for the huge eggs of the frilled shark to hatch at the uniformly low temperatures of 1800 to 3600 feet down in the Sagami Sea? At first I was inclined to think that the incubation period lasted at least one year. But since Kyle (*Biology of Fishes*, p. 66) says that the embryo of *Acanthias* takes about a year to develop, it seems probable that it will take at least two years for the embryo of *Chlamydoselachus* to attain its full development.

It is unfortunate that Dean did not get large frilled-shark embryos later than May 1, and larger than the longest of that date (390 mm., yolk 100 x 70 mm.), with yolks either gone or nearing resorption. Such data would be of great value not only for the question under consideration, but for giving an idea of the amount of distention of the uterus "at term", and as indicating the size of the young shark at the time of birth. It is also unfortunate that no young free-swimming sharks were taken in the intensive deep-sea hook-trawl fishing carried on in the Sagami Sea by Kuma and the market fishermen. The smallest free-swimming specimen (a female) recorded by Dean measured 1240 mm. (48.8

in.), and the smallest ever put on record was taken by the Prince of Monaco at Funchal, Madeira, in 1889. Collett (1890) found this to be a female only 610 mm. (24 in.) long. He notes that it differed from typical adults from Japan only in insignificant details. He gives no figure.

THE REPRODUCTIVE ORGANS OF THE MALE *CHLAMYDOSELACHUS*

In general, the internal reproductive organs of the male frilled shark are like those of the other elasmobranchs. They have been figured and described by Smith in the preceding article of this volume. Here it is necessary to present only a brief account of the external organs of reproduction in the male.

MYXOPTERYGIA—EXTERNAL ORGANS OF THE MALE

The male shark has the curious intromittent organs, peculiar to the elasmobranchs, called the myxopterygia or claspers. They are modifications of the hinder inner parts of the pelvic fins of the male shark or ray. These secondary sex organs, as Text-figure 5



Text-figure 5.

A 1500-mm. (?) male frilled shark from the Odowara Bank, Sea of Sagami, Japan. Note the large myxopterygia or claspers. These are developed from the inner parts of the pelvic fins. The claspers help the male shark to hold the female during copulation.

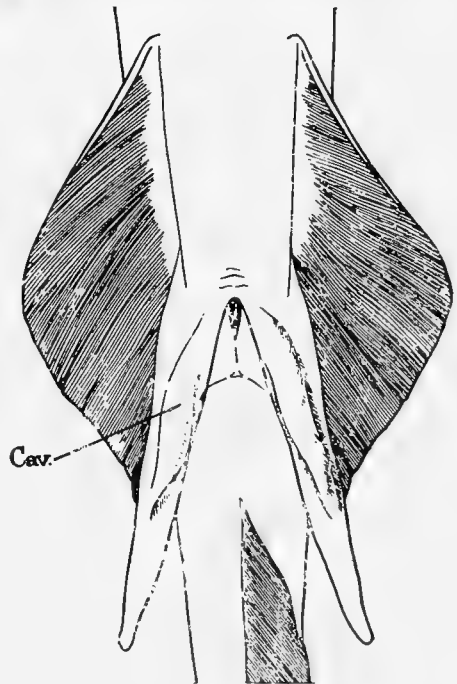
After Doflein, 1906, p. 257.

Text-figure 6

Ventral view of the pelvic region of a male *Chlamydoselachus*, showing myxopterygia or claspers. Through the tubular claspers, the seminal fluid is introduced into the cloaca of the female. This is necessary since in all sharks impregnation of the eggs is internal. The cloacal aperture may be seen between the bases of the myxopterygia.

Cav., projection of cavity.

After Leigh-Sharpe, 1926, Fig. 1, p. 308.



shows, enable one at a glance to distinguish the male. The claspers are necessary because impregnation in all sharks is internal. These myxopterygia are the only reproductive structures of the male that we need consider here. For elasmobranchs in general, they have been admirably described by Leigh-Sharpe, (1920, p. 245) from whose article I quote the following:

... the basal element of each pelvic fin (basipterygium) is prolonged to form a stout backwardly directed skeletal rod supporting a portion of the fin which is demarcated from the remainder and specially modified to form a copulatory organ, the clasper or myxopterygium ... The clasper is rolled up in a manner resembling a scroll [Text-figure 6] so that instead of being a groove, as it is usually described, it is a sufficiently closed tube along the greater portion of its length, though the edges may not be and usually are not completely fused but overlapping. This tube is one along which spermatozoa pass.

Not only do the claspers serve as intromittent organs, but inserted into the cloaca of a female they help hold her fast during copulation. Their appearance in lateral view of a male *Chlamydoselachus* is shown in Text-figure 5 and of another in Figure 53, plate VI. In Text-figure 6, we see these rolled-up organs in ventral aspect with the cloaca between their bases. No further description is necessary here.



Text-figure 7

A 1510-mm. female *Chlamydoselachus*, whose enlarged abdomen is due to the presence in her ovaries of 10 eggs measuring 80—83 mm. in diameter, as seen in Text-figures 3 and 9. Note the absence of any external secondary sex characters.

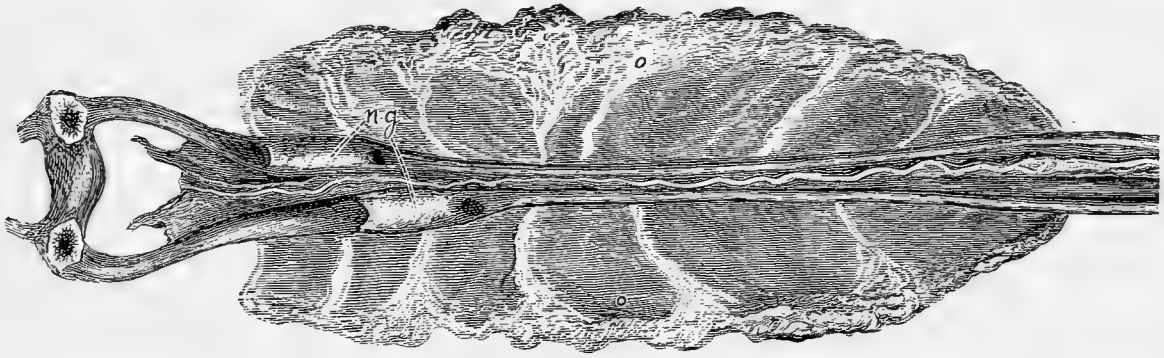
Photograph by courtesy of Fumio Momose.

REPRODUCTIVE ORGANS OF THE FEMALE *CHLAMYDOSELACHUS*

The female frilled shark (Text-figure 7) has no external secondary sex characters, but when the ovarian eggs approach ripeness or particularly when the uteri are filled with huge eggs undergoing development, the distended abdomen indicates pretty clearly the sex of the fish even though the pelvic fins are not distinctly visible. Thus all the reproductive organs of the female, the ovaries and the oviducts (with their various subdivisions), are internal. They have been thoroughly described by Smith (1937) in the article dealing with the anatomy of *Chlamydoselachus*, but it will be necessary to consider here certain features having to do with viviparous reproduction in this fish. These are: first, the enormous size attained by the eggs while still in the ovary; second, the great distention

of the uterine portion of the right, and rarely the left oviduct, which is necessary to accommodate the huge eggs and later the yolk sacs and the developing embryos in this viviparous shark.

In going through Dr. Dean's few scattered notes—literally with a magnifying glass because they are at times written in a minute hand—I have been able to correlate certain widely separated records and to find certain data either overlooked or not clearly evaluated before. These have to do mainly with the reproductive organs of the female and with the question as to whether those of both sides are functional or whether those of only one side are used in reproduction. These data are so interesting and so valuable that they deserve careful study. However, we will first take up the literature dealing with each set of organs—ovaries and oviducts—and then consider Dean's notes which will throw much light on both structure and function.



Text-figure 8

Ovaries and oviducts of *Chlamydoselachus*, drawn one-half natural size.

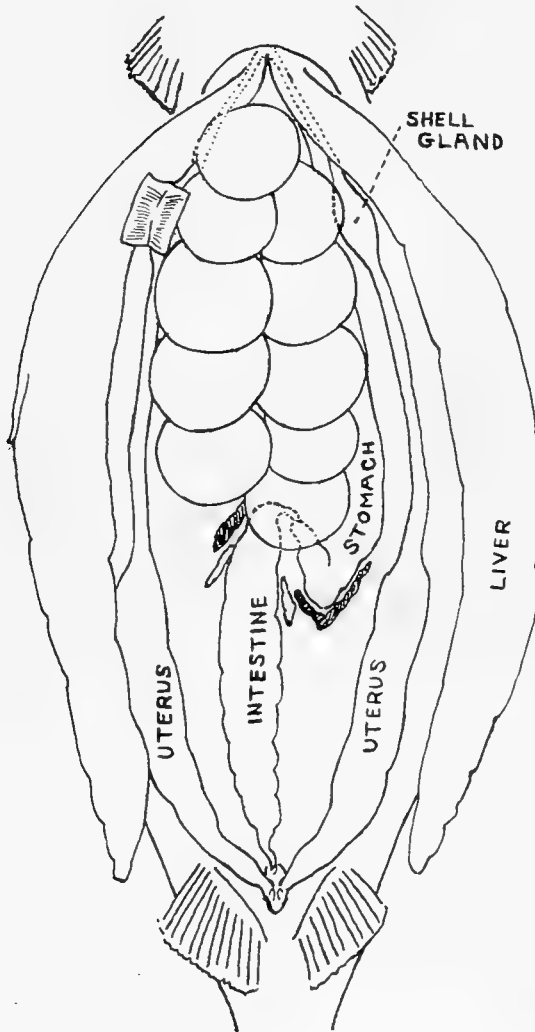
n. g., nidamental glands.

Printed from the original woodcut after the drawing by Paulus Roetter for Garman, 1885, Fig. 1, pl. XIX.

The ovaries and the anterior portions of the oviducts of *Chlamydoselachus* were first figured by Garman (1885). Because of its historic interest, his drawing is reproduced from the original woodcut (Text-figure 8 herein). Garman merely says of these organs "A section some 12 inches in length of the ovaries and oviducts is represented in the sketch". It is a long jump from Garman's figure (1885) to Deinega's representation (1925) of the genital organs of our fish. His small figure printed on poor paper is not easy to understand. However, Smith's admirable drawings, made from his dissections of four specimens from Japan in the Museum collection, give a clear picture of the form and the relative sizes of the female reproductive organs in various stages of development. They will be referred to later for positions and structures of both ovaries and oviducts.

And last of all Momose (1938) has figured the abdominal viscera of a 1510-mm. female *Chlamydoselachus* with the huge ovaries removed. This figure is reproduced in his article in small size on soft paper and is not suitable for reproduction. However, Momose has been good enough to send me the original drawing with the huge ovaries

(with their 10 eggs, each measuring 80–83 mm. in diameter) sketched in. This is reproduced herein as Text-figure 9. Being labelled, it needs no explanation here beyond the remark that the non-gravid uteri are of approximately the same size.



Text-figure 9

Semi-diagrammatic sketch to show the reproductive organs of a 1510-mm. female *Chlamydoselachus*. Note the five huge eggs (80–83 mm.) in each ovary, and the paired oviducts with their subdivisions. One shell gland is opened to show its structure, and both uteri are somewhat dilated.

Sketch by courtesy of F. Momose.

THE OVARIES

In *Chlamydoselachus*, the ovaries are paired, elongate, and in the non-breeding female, more or less flattened organs situated in the anterior part of the body cavity and attached, rather indirectly, to the dorsal body wall by means of broad mesenteries. These organs like others in this fish are subject to some interesting variations which will be pointed out further on.

Before Smith's studies (1937), but three investigators had published observations on the ovaries of *Chlamydoselachus*. Garman (1885) merely remarks—"The ovaries [Text-figure 8] had been badly preserved and were much torn". Collett (1897) describes the oviducts and then continues as follows: "The right uterus [ovary?] was 240 mm. in length, and contained 10 large eggs about the size of the yolk of a small hen's egg, but some varied in size. There were, besides, about 30 lesser yolks of the size of large and small peas, as well as a few bigger ones about the size of the yolk of a pigeon's egg. The length of the left uterus [ovary] was 220 mm., and it contained five large yolks, and about 20 small ones."

This is understandable only on the supposition that Collett used the word "uterus" but meant *ovary*. In the paragraph preceding the one quoted, he crudely described the oviducts—stating that they were 900 mm. long and that each expanded into "a uterus-like sack". His description of the "uterus" in the above quotation, if "uterus" is replaced by *ovary*, absolutely fits the structure of the immature elasmobranch ovary having in it

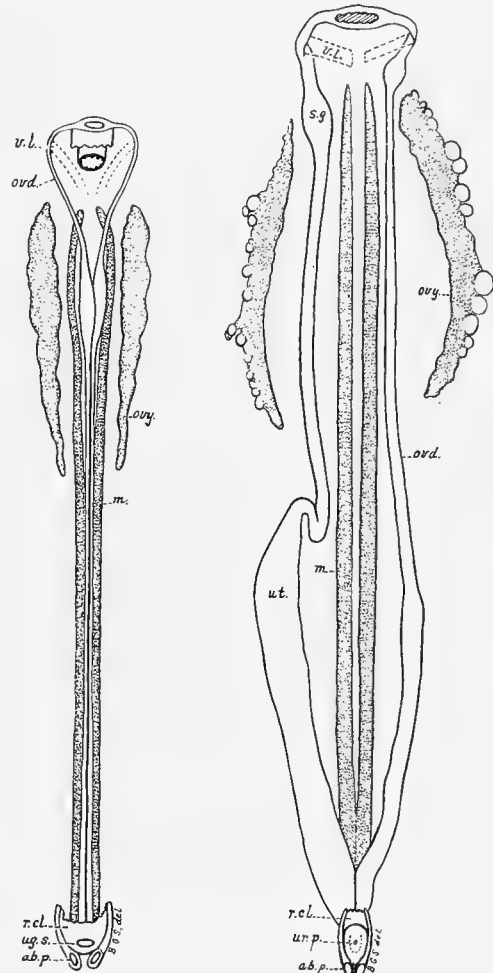
eggs of various sizes and of various degrees of "ripeness" such as I have found in the ovaries in scores of dissected sharks and rays. Furthermore, although, as I have found, all the eggs in the uterus of a viviparous shark or ray may vary somewhat in size, the limits are fairly close. They do not vary from "the size of the yolk of a small hen's egg" to that "of large and small peas". Then too when a wind egg is found, it, though smaller in size,

Urogenital system of the female *Chlamydoselachus*, ventral views, one-fifth natural size.

Text-figure 10. Urogenital organs of a specimen 1398 mm. long. The excretory ducts are concealed by the oviducts.

ab.p., abdominal pore; *m.*, mesonephros; *ovd.*, oviduct; *ovy.*, ovary; *r.cl.*, rectal portion of the cloaca; *ug.s.*, opening from the urogenital sinus; *v.l.*, ventral ligament of the oviduct. Drawn from specimen No. IV in the American Museum of Natural History.

After Smith, 1937, p. 432.



Text-figure 10.

Text-figure 11.

is plainly recognizable as being a shell without embryo and yolk. To settle the matter effectively, attention is called to the fact that Collett does not speak of egg shells. He wrote uterus but he surely meant ovary.

It seems that this misidentification of the genital organs may be due to the possibility that Collett wrote in Norwegian and that his thesis was translated into English by another hand and that it was published without his seeing the proofs.

Hawkes (1907) had several specimens, but, of the organs under consideration, she briefly states that "The ovaries are diffuse bodies attached by broad mesenteries to the

line of attachment of the stomach mesentery". From this, one may judge that her specimens were either immature or with ovaries spent. Deinega's specimen (1925) had had the ovaries removed. Smith (1937), however, gives definite data, particularly in that he records the sizes of eggs found in the ovaries of two of his fish. Unfortunately, there are no dates of capture of any of his specimens.

In a sexually immature female specimen, 1398 mm. long (Text-figure 10), Smith found that the ovaries were small and exhibited perfect bilateral symmetry. The largest follicles measured only 10 mm. in their greatest diameter. In a larger and nearly mature fish, 1550 mm. long, he found that both ovaries were well developed and contained follicles ranging in size up to 17 mm. in diameter as shown in Text-figure 11. Of the follicles large enough to be easily distinguished macroscopically, there were 13 on the left and 15 on the right. Some of those in the left ovary were larger than any in the right organ. In sexually mature specimens, 1350 and 1485 mm. long respectively, he found the ovaries of the right sides were spent and that those of the left sides were intact but small and contained only very small ovocytes, none more than 6 mm. in diameter (Text-figures 14 and 15).

In Dean's notebook on a pasted-in sheet (from its phraseology evidently from one of his Japanese collectors) are two records concerning the ovaries. The first is dated February 8, 1905, and reads "Six immature eggs in left ovary" of a 1500-mm. female. Under date of April 30, 1903, this entry occurs: "Three immature eggs were in the left ovary and nine immature eggs were in the right ovary" of a female 1670 mm. long. How large these eggs were cannot be stated, but at least they were of considerable size. Nevertheless, for another fish, we do have measurements of the eggs.

There is in this same notebook a rough pencil sketch and some notes in Dean's own writing, showing that on April 27th he dissected a 1960-mm. female (the largest *Chlamydoselachus* on record). This fish had in the right ovary 11 eggs in two rows (nine measuring 70 x 30 mm. and two 60 x 30 mm.), and 5 (70 x 30 mm.) in the left ovary. These large eggs are found on the margin of the genital fold precisely as they are shown in Text-figure 11 (Smith's 1550-mm. specimen), and as I have found them in mature ovaries in sharks of southern Florida. These eggs were surely approaching maturity.

Among Dean's *Chlamydoselachus* records is a faded photograph of the viscera of this same female. This shows the 5 large eggs on the left side, but on the right only 6 or 7 can be counted—the precise number is uncertain because some are covered by the other viscera. Lastly there is an incomplete water-color sketch of this same dissected fish. The photograph and the color sketch were evidently intended to furnish the basis for a finished figure in color. This, unfortunately, was either never made or has been lost. Dean's photograph is faded and the ovaries with their eggs are too much obscured by other viscera to permit its use. The wash drawing and pencil sketch are plainly unfinished. But fortunately other photographs are at hand to show these organs.

Momose in 1938 procured from Sagami Bay a 1510-mm. female having 10 nearly ripe eggs (size 80–83 mm.) in the ovaries—5 on each side. His figure is poorly printed on soft paper and is not suitable for reproduction. But, in answer to a request conveyed

through Dr. N. Yatsu, he has sent me two photographs showing the body cavity opened along the mid-ventral line. The better of the photographs, and the one which he reproduced, is shown herein as Text-figure 3. Momose also kindly sent me his drawing of the abdominal viscera of his *Chlamydoselachus* with the two huge ovaries sketched in, as seen in Text-figure 9. Each ovary contains five great eggs, measuring 80–83 mm. in diameter. It is interesting to find in Momose's photograph (Text-figure 3) and sketch (Text-figure 9) absolute corroboration of what is seen in Dean's 35-year-old photograph, in his rough colored wash drawing, and in his rougher pencil sketch.

So far as all this evidence goes, it strongly indicates that more eggs ripen in the right than in the left ovary—a total of 25 in the right and 19 in the left ovary in the four cases cited above. In Dean's specimen, having 5 eggs in the left and 11 (in two rows) in the right, and in Momose's fish having 5 eggs in each ovary are found the only cases on record in which the left ovary contained eggs approaching maturity. Smith's 1550-mm. specimen contained young eggs in both ovaries, but the larger ovocytes (up to 17 mm. in diameter) were found in the left ovary. Even with these bilateral ovaries considered, the weight of evidence is that the right ovary is the predominant egg-producer.

It is interesting to note the relative positions of the ovaries with regard to each other. Garman's drawing (1885) shows the two ovaries on the same level (Text-figure 8 herein). Hawkes (1907) says of her specimens (number not noted) that "The right ovary is placed somewhat more anteriorly than the left". Dean's rough sketch shows the two organs on the same level. Smith's young and sexually immature fish (1398 mm. long) had the two ovaries on the same level (Text-figure 10 herein). Another, measuring 1550 mm. with eggs up to 17 mm. in the left ovary, had this ovary somewhat further forward than the right (Text-figure 11). In each of his two other mature specimens (1350 and 1585 mm. long) the right ovary was placed markedly forward of the left (Text-figures 14 and 15). Momose's sketch shows the relative positions of the ovaries in his specimen. The right ovary is placed forward of the left by about two-thirds the diameter of one of the huge eggs (Text-figure 9).

Of the eight females for which we have data, three had the ovaries on the same level (one being sexually immature), one had the left anterior to the right, and four had the right placed further forward. This difference in position brings the right ovary nearer to the entrance funnel to the oviducts.

The matter of the one-sidedness of elasmobranchs in their reproductive organs—particularly that in *Chlamydoselachus* the right ovary only tends to be functional—is of very great interest and deserves some study. Fortunately I have made some firsthand observations as to unilaterality of the functioning of both ovaries and oviducts in various sharks and rays. It seems best to postpone the consideration of these data for ovaries until the oviducts of *Chlamydoselachus* have been studied, since in them also a tendency to unilaterality will be found, and since the functioning of the two are interdependent. But before going into the matter of oviducts, it seems well to consider here the question of the size attained by the egg before it is discharged from the ovary.

IMMATURE OVARIAN EGGS

Among the frilled-shark material loaned by the Department of Zoology of Columbia University are five ovarian eggs of different sizes. No. 1 (42 x 34 x 34 mm.) is greatly flattened on one side and is devoid of follicular membranes. No. 2 (45 x 38 x 38 mm.) is shaped like a hen's egg and is surrounded with fragments of the follicular membranes. No. 3 (46 x 46 x 35 mm.) is without follicular membranes. No. 4 (58 x 50 x 44 mm.) is

enclosed in follicular membranes. No. 5—also enclosed in follicular membranes—measures 60 x 49 x 49 mm. These are all immature eggs, probably about half-grown.

Other sizable (and in this case larger) ovarian eggs are those noted and sketched by Dean and taken from his huge 1960-mm. shark captured April 27. Of the 16 eggs in question in the two ovaries, 14 measured 70 x 30 mm. and 2 were 60 x 30 mm. They approached maturity much more than the smaller eggs just listed above. Last of all are the huge ovarian eggs reported by Momose (1938) from his 1510-mm. specimen taken November 28. These, measuring 80–83 mm. in diameter (Text-figures 3 and 9), were almost mature as will be seen from the data in the following paragraphs.



Text-figure 12

A ripe ovarian egg in its ovarian and follicular membranes. The circular area on top is probably a thin place in the membranes where the follicle will rupture to set the egg free into the coelom. This is probably the same egg as that shown in Figure 1, plate I. It is presumably figured in natural size.

Photograph by Bashford Dean.

A MATURE OVARIAN EGG

Such an egg is shown in Figure 1, plate I. In the original drawing, it measures 90 x 96 mm., and it was presumably drawn in natural size. It is of approximately the same size as the eggs in round capsules shown in plate I. Its measurements are close to those of eggs with gastrulae or very young embryos described by Nishikawa and by Dean as found in the uteri.

This egg (Figure 1, plate I) is enclosed in the egg follicle and is covered by the thin peripheral membranes of the ovary. These membranes are folded into ridges shown as

light streaks in the figure. Follicular blood vessels are shown as a dark network. This rich vascular network is concerned with the nutrition, development and growth of the huge egg. The circular area in the upper part of the figure is presumably a thin region of the ovarian membranes where the follicle will rupture to allow the egg to escape into the body cavity. It would seem that this egg is practically mature.

Among Dean's records I find a photograph (Text-figure 12) of an ovarian egg. Study of the detailed markings in drawing and photograph shows both to have been made from the same egg. The drawing was probably made first, the photograph possibly after the egg had been hardened and when a portion of the yolk had been torn away as shown in the photograph. The text-figure is reproduced in the size of the original drawing so that an accurate idea may be had of the natural size of this mature ovarian egg.

In this photograph the limits of the circular area shown in the upper part of Figure 1, plate I, are more sharply defined. Similar areas are visible in five of the large but immature eggs in the ovary shown in situ in Dean's photograph referred to above. On ovarian eggs Nos. 4 and 5, recorded in the list from Columbia University and mentioned in a preceding paragraph, are found similar areas. Upon dissecting off the follicular membranes from the circular area in one of these ovarian eggs, there was found a whitish region of corresponding shape and size, which presumably represents the germinal area. This area is surrounded by a shallow depression—a circular groove. The remainder of the egg is a dark yellow and appears to be composed entirely of yolk. I therefore conclude that the circular area, represented in Figure 1, plate I, and in Text-figure 12, overlies the germinal area and is of about the same size. It would be very desirable to study this egg but it cannot be found among the specimens from Columbia University at my command.

When the ovarian follicles break, the ripe eggs in some way, as yet not clearly understood, find their way into the funnel of an oviduct, and begin their descent into this tubular organ in which fertilization, shell formation and gestation take place.

THE OVIDUCTS

As in other sharks, the oviducts are elongate paired organs joined at their anterior ends where they communicate with the abdominal cavity through wide funnel-shaped openings or sometimes through a single median aperture. Posteriorly each opens separately into the cloaca. When an egg gains entrance into an oviduct through the funnel, it is fertilized by a spermatozoon, passes into and remains in the shell gland while the keratinoid shell is being formed around it and then it descends into the uterine enlargement where segmentation, gastrulation, and the formation and growth of the embryo take place. There will now be considered some interesting features relating to these divisions of the oviduct.

THE ABDOMINAL OPENINGS.

In *Chlamydoselachus* the abdominal openings of the oviducts are of particular interest because of their variability. These variations will now be pointed out.

In Garman's specimen (1885), each oviduct (Text-figure 8) has its own opening widely separated from the other. Hawkes (1907, p. 475) does not state how many female

specimens she examined, but she describes the funnels as follows: "The oviducts have large funnels, which open ventrad to the stomach. . . . The edges of the funnels are irregular and spreading, and are united in the median ventral line to one another, thus forming one large funnel. The anterior edges of the funnels become united to the anterior wall of the body cavity, whilst the posterior edges of the united fimbriae hang free."

Deinega's one specimen had a single unpaired opening. So also in three of Smith's specimens (including one that is sexually immature), the oviducts communicate with the body cavity through a single opening (Text figures 10, 11 and 14). In a fourth fish (which is mature), the abdominal opening has become transversely elongated until it functions as two separate openings—one for each oviduct (Text-figure 15). Momose's specimen (1938) had a single oviducal funnel.

In Dean's notebook is a good outline drawing, in pencil, evidently intended to form the basis of a complete drawing. This shows a single large common abdominal opening of both oviducts. In this respect, his specimen resembled those described by Hawkes (1907) and by Smith (1937).

THE SHELL GLAND

The uterine egg of *Chlamydoselachus* is enclosed in a keratinoid shell. This is secreted by a gland, the shell or nidamental gland, which is an enlargement of an anterior portion of the oviduct. The glands of the two oviducts may be at the same level, as in Smith's immature specimen seen in Text-figure 10 and in Dean's rough sketch showing the oviducts and the two ovaries with large eggs.

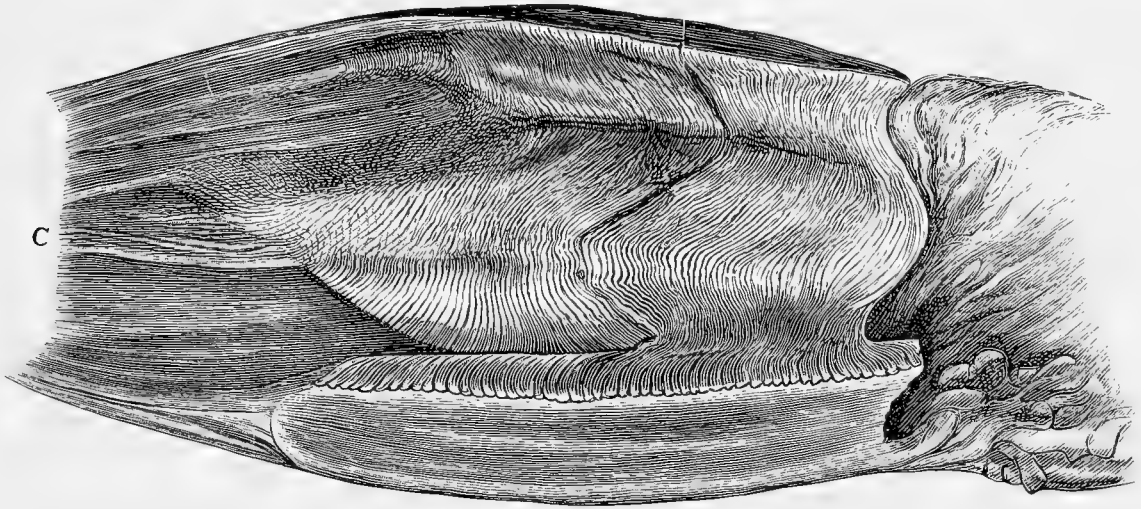
In contrast, in Garman's specimen (Text-figure 8), the left gland was anterior to the right. So also was it in Smith's three sexually mature fish as portrayed in Text-figures 11, 14 and 15. Deinega (1925) merely states that the shell gland of the right oviduct of his specimen was placed somewhat further back than the left. This asymmetric position of the shell glands (the left further forward) appears to be an adaptation to the slender form of the body of *Chlamydoselachus*, and is probably correlated with the fact that the right uterus is always functional and occupies much of the hinder abdominal cavity.

In Garman's fish (1885) the shell glands were of about equal size (Text-figure 8), as they are in Dean's sketch showing them and the ovaries with large eggs. Concerning this matter, Nishikawa says, "... the nidamental gland of the right side is better developed than that of the opposite side", but he does not say how many specimens he examined. Smith graphically shows (Text-figures 11, 14 and 15) that in three sexually mature females the right gland was noticeably better developed, and Deinega (1925) states this for his one fish. Why the right gland is the better developed will be understood when the uterus has been considered.

Garman (1885) figured and first described the internal structure of the nidamental gland (Text-figure 13 herein). Here is his description.

The gland consists, in appearance, of two thick plates of laminated structure. The plates are longer and thicker in the middle, and shorter and thinner at each side. The short sides have been applied and united; this leaves an acute point descending from the thicker

portion on the inside of the tube. The insides of the walls are crossed by minute striae, between the laminae, which appear transverse, but in reality are spiral and ultimately—following the outlines of the anterior or posterior borders—terminate, forward and backward, in the longitudinal folds of the tube itself. The inner edges of the laminae are set with minute pores. Near the middle of its length there is a deeper transverse groove. This is crossed by the laminae without change in their directions on its account. The plates are not distinct from each other through the whole of their length; branches frequently cross obliquely from one to the other. The bottoms of the grooves between them have closely-set transverse partitions. The walls of the gland are thicker anteriorly; they begin abruptly or even extend a little in front of their points of attachment to the tube. The appearance is such as would result from twisting the inside walls of the duct very closely for a short distance. In this we have a hint as to the origin of the gland.



Text-figure 13

Interior of the shell gland of the frilled shark, *Chlamydoselachus anguineus*. Note the laminated structure.

Printed from the original woodcut after the drawing by Paulus Roetter for Garman, 1885, Fig. C, pl. XX.

This is not very clear nor does Garman's figure (Text-figure 13 herein), devoid as it is of explanatory lettering, help matters much. However, both must be reproduced here; the text because it is the only full description ever published, and the figure because it is the only one on record.

This gland has also been studied and described by Hawkes (1905) and it seems well to quote her brief description. She gives no figure.

For the first 6 cm. the oviduct is a straight tube, the walls of which are lined with numerous laminae. This region passes into the oviducal gland, the walls of which are much thickened, except along two longitudinal lines which are approximately dorsal and ventral. The length of the gland is 3 cm. Its interior is covered by fine laminae continuous with those in the preceding and succeeding portions of the oviduct. The laminae run spirally, and are very close together, instead of longitudinally and somewhat separated, as is the case throughout the remainder of the oviduct. The transverse deeper groove in the oviducal gland mentioned by Garman was found in the specimen examined. Passing from the oviducal glands, the oviducts regain their original diameter, but the walls are smoother, the laminae being reduced to slight striae.

Unfortunately, after more than 30 years in preservative, the condition of the specimens in the American Museum is such that the internal structure of the shell glands cannot be studied advantageously.

THE UTERUS

In all viviparous sharks, the hinder part of the oviduct is enlarged into a more or less capacious sac in which are received the fertilized ova when they pass downward from the shell gland. Here the embryos undergo their development and here they are retained until the shells are cast off and until the young are so far developed that they may be passed out into the sea to fend for themselves. To fit the uteri for these purposes, they are much modified in various sharks and rays, and marked differences arise in the functioning of the right and left organs. This asymmetrical functioning we shall now study in *Chlamydoselachus*.

RIGHT UTERUS FUNCTIONAL

Since the oviducal apparatus of a shark is bilateral, one might expect to find the two oviducts equally developed in *Chlamydoselachus*. And so they are in sexually immature females such as Smith's 1398-mm. fish (Text-figure 10). In a footnote to Nishikawa's article (1898), Goto says, "When no eggs are contained there is no perceptible difference in size between the two oviducts." Such also is the condition shown in Momose's figure (1938) and much more clearly in the sketch sent me (Text-figure 9). This condition is rather unexpected in this fish when one views the 80-mm. eggs contained in both ovaries (Text-figure 9). That this condition is not always and necessarily true when eggs are absent from the oviducts is seen in Smith's drawing (my Text-figure 11) of the oviducts of his 1550-mm. specimen. This fish was almost sexually mature but like Goto's specimen was nonbreeding. The right oviduct (Text-figure 11) was noticeably larger than the left, and the ovaries contained growing eggs up to 17 mm. in diameter. Presumably the right uterus only in this fish was destined to be functional.

Our earliest information concerning the inequality of development of right and left oviducts in the frilled shark comes from Samuel Garman (1885), the man who first dissected *Chlamydoselachus*. In his specimen, which had been partially eviscerated, the anterior portions of the oviducts (about 12 in. long) remained as shown in his drawing (Text-figure 8 herein). But of the hinder end he was fortunately able to say—"A piece left at the cloaca showed one of the ducts greatly distended, possibly with young that had hatched within it [or which had been removed before the specimen came to him]. Only one of these tubes had been in use".

Next comes Collett (1897) who states that in his 1910-mm. fish each oviduct was 900 mm. long, and that "Towards their upper [lower ?] ends each expands to a uterus-like sack of which the right is somewhat larger than the left; both contained immature eggs". As noted above in the section on the ovaries, Collett or his translator got his identification of organs mixed, and here as there I have supplied the correction in brackets. His statement that both oviducts (the right being better developed) contained eggs, even if immature, is significant. It will be referred to later.

In 1898, Nishikawa gave us our first definite data on the inequality in structure and function of the oviducts. He states that the left one is always rudimentary but that "The right oviduct is very much distended and contains from 3 to 12 eggs, these numbers being the limits observed in 7 specimens".

Hawkes (1907) notes that the right oviduct in her specimens was much larger than the left. So Smith found and graphically shows for three fish in Text-figures 11, 14 and 15 herein. The uteri of Hawkes's specimens contained no embryos; nor did Smith's. Since Smith's specimens were brought from Japan by Dean, it is probable that, when the two gravid fish were caught, the uteri (Text-figures 14 and 15) were opened to get the eggs and embryos for him.

Deinega (1925) was evidently under the impression that *Chlamydoselachus*, like most other sharks, should carry eggs and embryos in both uteri. He states that in his specimen "the left oviduct, in its exterior form, produces the impression of being underdeveloped or of being in a temporarily non-functioning condition". However, the right oviduct, a short distance behind its large shell gland, "suddenly expands into a rather capacious sac". It contained no eggs.

Dean's notes afford both negative and positive evidence of the differential functioning of the oviducts. Thus of a 1565-mm. fish he says, "left ovid. greatly reduced, eggs fr. r."; of a 1575-mm. female he notes "left ovid. greatly reduced, no dilat. uterus"; another 1565-mm. fish had "l. ovid. small, small uterus". On the other hand Dean records the taking of various eggs and embryos from the right oviducts of specimens of *Chlamydoselachus* captured in the Sagami Sea. From one fish he got two eggs and from another three. Then he notes "8 in female"—oviduct not recorded but presumably the right. As seen above, and as will be noted later, had it been the left he would pretty surely have so stated. In the records of his Japanese collector are listed three eggs from right oviduct of one fish, five from another, and seven from the right oviduct of each of two other females. These last eggs were all in early stages and had egg shells.

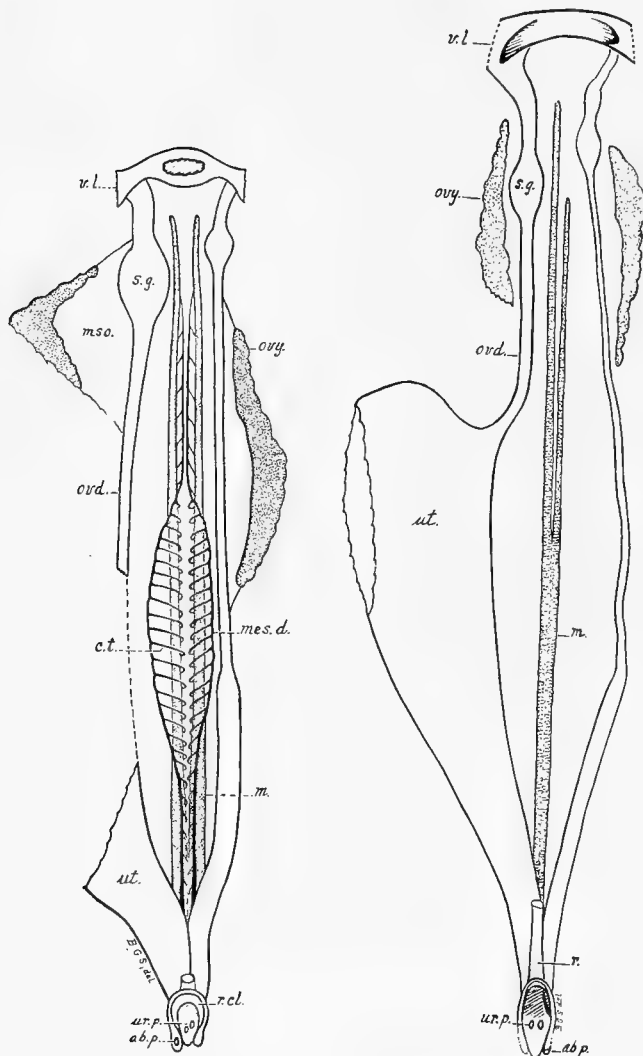
DISTENTION OF GRAVID RIGHT UTERUS.—Unfortunately there are little data available as to the size attained by the right uterus as gestation goes forward to birth. However, there are two ways of studying the problem: one by bringing together the few scattered measurements of the organ, the second by setting forth the number of eggs and embryos (with their measurements) found in the uterus. These compilations will now be made.

Measurements of Gravid Right Uterus.—Hawkes (1907) states that the oviducts begin to enlarge when they reach the level of the anterior end of the colon. On the left the diameter is increased gradually and only about four-fold, but "on the right, the enlargement is sudden and very apparent, the diameter increasing 14 to 15 times". She nowhere speaks of finding embryos in the uterus.

Deinega's description (1925) of the reproductive system is very brief. But the two things that the reader gets from it are that the left oviduct "produces the impression of an underdeveloped oviduct or a temporarily non-functioning one". While the right one in its posterior part "suddenly expands in the form of a rather capacious sac about 130 mm. in

diameter". This very great expansion is clear in his figure which, however, is so poorly printed on soft paper that it cannot be reproduced here.

Smith dissected and figured the reproductive organs of two sexually mature frilled sharks measuring 1350 and 1485 mm. respectively. He does not give measurements of the oviducts but Text-figures 14 and 15 give the relative sizes of the oviducts and other organs.



Text-figure 14.

Text-figure 15.

Urogenital system of the female *Chlamydoselachus*, ventral views, one-fifth natural size. The shell glands and the adjoining portions of the oviducts are displaced laterally.

Text-figure 14. Urogenital organs of a specimen 1350 mm. long. The right uterus and ovary are incomplete.

ab.p., right abdominal pore (the left is closed superficially); c.t., collecting tubule; m., mesonephros; mes.d., mesonephric duct; mso., mesovarium; ovd., oviduct; ovy., ovary; r.cl., rectal portion of the cloaca; s.g., shell gland; ur.p., urethral pores; ut., uterus; v.l., ventral ligament of the oviduct.

Drawn from specimen No. I in the American Museum of Natural History.

After Smith, 1937, p. 433.

Text-figure 15. Urogenital organs of a specimen 1485 mm. long. A segment has been excised from the right uterus, and the right ovary is incomplete. The excretory ducts are not shown.

ab.p., abdominal pore; m., mesonephros; ovd., oviduct; ovy., ovary; r., rectum; s.g., shell gland; ur.p., urethral pores; ut., uterus; v.l., ventral ligament of the oviduct. Drawn from specimen No. II in the American Museum of Natural History.

After Smith, 1937, p. 433.

These fish had evidently been gravid and the enlarged right uterus of each had been opened and the eggs removed. These adults (and probably the eggs also) came to Dean—presumably at Misaki, or were later sent to him in America.

In Dean's notebook is a rough sketch of the reproductive apparatus of his huge 1960-mm. female. This shows the two ovaries with many eggs (elsewhere referred to) and two empty uteri—the right twice as large as left. (Here recall Smith's drawing, my Text-

figure 11, showing similar organs). On this page, above Dean's sketch, is the statement "Ovid. [uterus?] of r. [side] dilated [through a length of] 340 mm.". Two pages away is another and more elaborate sketch of a non-gravid right oviduct (previously referred to) in which the uterus is labelled 25 mm. wide and 280 mm. long.

None of these specimens (except Nishikawa's) had ova in their uteri, and none of these uteri save those figured by Deinega and by Smith give us any clear idea of the size and the degree of distention attained before the young are born. However, some understanding of the degree of this dilation may be had by considering the number of eggs and embryos (with their measurements) that have been found in some gravid uteri. Earlier in this article some of these data have been used for other purposes but for completeness they will have to be repeated here.

Number of Eggs and Embryos in Gravid Right Uterus.—From two men only do we get firsthand data as to uterine embryos and their yolk sacs. Nishikawa introduces us to the subject briefly. But from Dean's notebook and from specimens brought back from Japan or sent thence to him, we get a good idea of the great size of eggs and embryos and of the uterine distention to which they give rise.

Nishikawa (1898) says "The right oviduct [600 mm. in total length] is very much distended . . . when as many as 12 eggs [his upper limit] each 110–120 mm. long are contained in it". Some of his eggs had embryos—the largest only 60 mm. long. He also speaks of having other eggs 65 to 75 mm. in shortest diameter and from 102 to 124 mm. in longest measurement. He figures in natural size an egg (Text-figure 4 herein) 67 x 100 mm. in an egg shell measuring 137 mm. including the processes.

Of large uterine embryos, Dean lists 14 specimens ranging from 165 to 390 mm. (6.6 to 15.35 in.). Of these only two have measurements of the yolk sacs set down. However, Dean brought from Japan and deposited in the zoological museum of Columbia University three embryos with yolk sacs, and in the American Museum six embryos with yolk sacs. From the Museum of Comparative Zoology, there has been loaned a large embryo on its yolk sac. This was presented by Dr. Dean in 1912. The measurements of these embryos with yolk sacs give one a full conception of the distention they would produce. They will be considered later, but it may be well first merely to list the embryos without yolks.

Dean's notebook records 12 such fishlets. To these I have added a specimen (190 mm.), in the collection here, from which the yolk has been removed. The measurements of these little fishes are from snout to tail-tip. These 13 range from 165 to 352 mm. (6.5 to 13.8 in.) as follows—165, 175 (2 specimens), 185 (2), 190, 195, 205, 210, 240, 250, 317, 352 mm.

To get a better idea of the distention of the gravid right uterus one must consult table I wherein are listed embryos ranging from 170 to 390 mm. (6.7 to 15.35 in.). These sit on yolk sacs whose diameters (measured in the lines of length and depth of the fish) vary from 67 x 55 mm. (fish, 327 mm.), to 111 x 100 (fish, 331 mm.), to 73 x 51 (fish, 374 mm.). With from 8 to 12 of these contained in the slender body of this snake-like (*anguineus*) shark, one can judge the enormous enlargement of uterus and abdomen.

TABLE I
SIZES IN MILLIMETERS OF UTERINE EMBRYOS AND EGGS

No.	Embryo	Yolk Sac	Where
1	170	72x68	Columbia University
2	175	92x90	Figure 11, plate I
3	180	77x75	Columbia University
4	210	75x57	Am. Mus. of Nat. Hist.
5	210	85x66	Mus. of Comp. Zool.
6	245	74x60	Am. Mus. of Nat. Hist.
7	305	83x57	" " " " "
8	320	76x64	" " " " "
9	327	67x55	Columbia University
10	331	111x100	Dean's Notebook
11	374	73x51	Am. Mus. of Nat. Hist.
12	390	100x70	Figure 49, plate V.

Just here it should be recorded that in Dean's notebook on the page of his list of specimens to be drawn is this entry. "Bt. in Tokyo June 20: 317; 331, yolk sac 111 x 100; 352; 390, yolk sac 100 x 70; 4 embs. large taken about May 1, 1905. 8 in female". I judge that the "4 embs. large" refer to the four for which he gives sizes, that they were taken from the female captured May 1, that they were preserved, and that he purchased them June 20 in Tokyo. This seems pretty certain. Possibly they were 4 of the "8 in female" as noted. Judging by their close gradation in size, I conjecture that they came from one uterus. If so, one can judge the tremendous distention of this. But what if one uterus contained "8" such embryos and eggs! It seems almost unthinkable, yet Nishikawa (1898) says "The right oviduct is very much distended and contains from 8-12 eggs. . . . The limits observed in seven specimens."

Two of the specimens recorded in the table were drawn for Dean and are reproduced in the plates. In Figure 11, plate I, the embryo measured 175 mm. and the yolk 92 x 90 mm. Still more striking is the colored Figure 49, plate V of a fish 390 mm. (15.35 in.) long on a yolk sac which measured 100 x 70 mm. Let the reader imagine (if he can) 8 to 12 embryos and yolk sacs of this size in the uterus of even a 1960-mm. female (the largest *Chlamydoselachus* on record). The egg and embryo of the colored figure are in our collection here, and the fish in its jar of alcohol looks even larger than it does when portrayed in its natural colors.

As one studies this table, three things attract attention. The first is that there are several discrepancies in the sizes of the yolk sacs in proportion to the sizes of the little fish found thereon. Surely some of the discrepancies date back to the varying sizes of eggs in the ovary. There must be more variability in the size of mature eggs in the oviduct than has heretofore been thought. The next idea is that the period of gestation must be very long to give time for the resorption of these great yolks, and then that the young fish when ready for extrusion must be from 20 to 25 in. long. The matter of the long period of gestation (surely at least 2 years) has been treated earlier.

The third matter is also based on the great disparity between the slight diminution of the yolk sac and the considerable growth of the embryo. It comes to me in this form - Does the embryo of this viviparous or ovoviviparous shark receive any nutriment from the uterine wall of the mother? The shallow water littoral tropical nurse shark, *Ginglymostoma cirratum*, is also ovoviviparous. It carries in its uteri huge (c. 145 mm. long) blunt-ended, thick-shelled eggs (Text-figure 16) entirely comparable to those of *Chlamydoselachus*. I have had the good fortune to make extensive studies on *Ginglymostoma*, the nurse shark, and from these I hope further on to throw light on this question.

All these data (save those from Deinega's article) were known to Smith when his monograph on the anatomy of *Chlamydoselachus* was published in 1937. But in the matter of the reputed unilaterality of the functioning of the oviducal apparatus of *Chlamydoselachus*, he showed sound judgment in his concluding remarks on the reproductive organs of the female of this shark. Here is his matured statement published before I had made my minute study of Dean's notes presently to be referred to. Smith (1937, p. 449) wrote as follows:

There is not a single known instance of complete development of the reproductive organs on the left side. Yet it must be borne in mind that the number of specimens that have been described is still very small. The organs on the left side are developed to such a degree that they can scarcely be called rudimentary. In view of the great variability found in many other organs of *Chlamydoselachus*, one should not be surprised if the examination of additional material should reveal cases in which the genital organs of the left side, or of both sides, are functional.

In the light of the data given above as to the functioning of the right oviduct only in *Chlamydoselachus*, there are now to be presented certain data showing that the left oviduct also is sometimes functional in this shark. In these data will be found the verification of Smith's prognosis.

THE LEFT UTERUS SOMETIMES FUNCTIONAL

It has already been seen that in the adult, while the right ovary is the predominant one, the left ovary does sometimes contain large eggs; i.e., is functional. Evidence that the left uterus is occasionally functional will now be presented. This is a matter of exceptional interest.

The earliest intimation, that the left oviduct may contain eggs, comes from Collett (1897). In his short and not always clear description of the oviducts of a 1910-mm. specimen, he says that "each expands to a uterus-like sack, of which the right is somewhat larger than the left; both contained immature eggs". There is no doubt that he was referring to the oviducts, but what he meant by "immature eggs" is very obscure. I can only conjecture them to have been wind eggs like that figured by Dean (Figure 51, plate V). In many years' dissections of viviparous sharks and rays, I do not recall ever having found in a uterus an "immature" egg, meaning an undeveloped or unripe or shell-less egg, but I have in the nurse shark found what my notes record as "infertile eggs". I do not recall that I opened one to get at its contents. I did not then know of the term "wind

eggs", but that is what these eggs were. I measured a number of these capsules from *Ginglymostoma* and found them always smaller than normal (fertile) eggs such as that shown in Text-figure 16.

The only other evidence of bilateral functioning of the oviducts in *Chlamydoselachus* is found in Dean's notebook. In one place he says of a 1620-mm. specimen "both ovid. same size", but he does not say that both were functioning. They may have been found in a sexually immature fish such as Smith had (Text-figure 10). However, from a 1392-mm. female taken about October 1, 1905, Dean records "3 oblong eggs, 135 mm. and larger in r. ovd." and a "small wind egg in l.". He states that two oblong eggs and the wind egg were drawn. The two oblong eggs I identify with the drawings shown in Figures 2 and 3, plate I; and the wind egg as that portrayed in color in Figure 51, plate V. From another female taken May 25, 1906, Dean records eggs "l. ovid. 3, 2 in r." but unfortunately he gives no description of these eggs.

It is very interesting and possibly significant that, so far as we have data, when eggs are found in both oviducts of *Chlamydoselachus*, there is something wrong with them. According to Collett both sets of eggs from his fish were "immature"—whatever that may mean. In Dean's first case, the egg from the left uterus was abnormal—an empty dwarf shell—while the eggs from the right side were at least unusual if not abnormal. All three were "oblong"—two of them in varying degrees, (Figure 2 and 3, plate I). One (Figure 2) is oblong but symmetrical, the other (Figure 3) is not only oblong but unsymmetrical, and is possessed of a most unusual process. Of the eggs from the two oviducts of his specimen taken May 25, 1906, Dean unfortunately gives neither figures nor descriptions.

As bearing on this matter, it may be noted here that the nurse shark has the *right* ovary only fertile but both uteri functional. Infertile wind eggs, always smaller than fertile ones (size about 105 mm. long by 120 in circumference) are found in both uteri of this shark, but are apparently more abundant in the left.

One wishes much for definite data here about *Chlamydoselachus*. What were Collett's "immature eggs?" What kind of eggs were those noted by Dean in the "l. ovid. 3"? Were they defective? The predominance of the right oviduct is of course correlated with the narrow abdomen of this "snake-like" shark—there is not room in the crowded abdominal cavity for two gravid uteri. Yet Dean states that he found such in two specimens. Here is a problem for someone in Japan to solve.

These data from Collett and from Dean show us that the commonly accepted dictum, that the right oviduct only in *Chlamydoselachus* is functional, is not always true, even though all other investigators have so found or thought. Since Dean's notes show that the "l. ovid." is sometimes functional, they have been quoted carefully and in full. Into Dean's hands there undoubtedly came more female specimens (26 in number) than have been had by all other students of *Chlamydoselachus* taken together. This of course made possible his discovery of the functioning of the left oviduct in his two specimens. Undoubtedly this functioning is very unusual and apparently it is not wholly normal.

But in any case, we are sure that, in some few instances, *Chlamydoselachus* does have both oviducts functional.

Here then is confirmation of Smith's statement (1937) —“In view of the great variability found in many other organs of *Chlamydoselachus*, one should not be surprised if examination of additional material [Dean's 26 female specimens] should reveal cases in which the genital organs of the left side, or both sides, are functional”. And all through his work, Smith points out generalized or primitive structures in *Chlamydoselachus* in consonance with the lowly position assigned it in the scale of shark life. Then again he finds highly specialized structures.

Chlamydoselachus is in process of becoming viviparous by getting rid of its primitive keratinoid egg shell—it has almost gotten rid of the hold-fast processes. Then further to make possible this viviparity in a small and narrow body cavity, it has almost achieved unilaterality in the functioning of its reproductive organs.

For comparison, evidence will later be presented to demonstrate that in certain higher viviparous sharks and in certain rays (highly specialized elasmobranchs) the unilaterality found imperfectly expressed in *Chlamydoselachus* has come to full fruition.

There is now to be considered certain indefinite evidence referred to above—the question whether the embryos of *Chlamydoselachus* are nourished by secretions from the wall of the maternal uterus.

DO EMBRYOS RECEIVE NUTRIMENT FROM THE UTERINE WALL?

On this point Hawkes (1907) writes of the enlarged (uterine) portion of the right oviduct as follows:

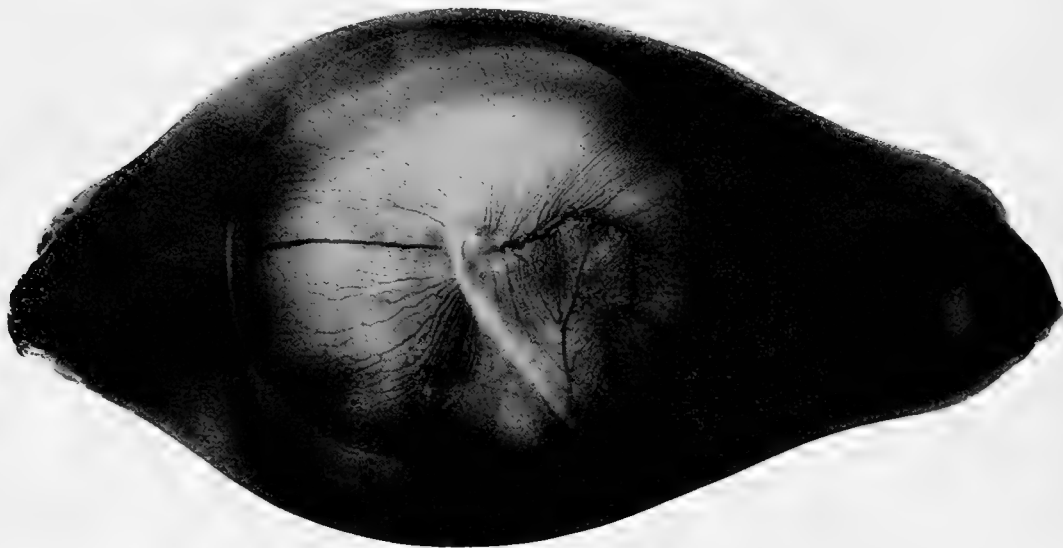
This region in addition to being enlarged has folded walls, in which occur one large and several small areas of dilated blood vessels. The largest blood plexus occupies about one-third of the right side of the oviduct. In connection with each plexus, on its dorsal side the oviducal wall is thickened over an area which equals the plexus in length and breadth. The enlarged vessels apparently supplied these thickened areas. The condition of the oviduct thus described suggests that this portion of the oviduct acts as a functional uterus.

Smith had hoped by study of our specimens to throw more light upon the internal structure of the uterus as described by Hawkes. But he had little success. He notes, however, (1937, p. 447) that—“In its enlarged state, on the right sides of my adult specimens, the so-called uterus has thin walls, a velvety inner surface and a fairly rich blood supply. The mucous membrane is not sufficiently well preserved to permit a study of the finer structure”.

To anyone with a firsthand knowledge of the structure and functioning of the uterine wall of viviparous sharks and rays, these findings are very significant. From a mere glance at Figure 49, plate V, it is apparent that there will never be a yolk-sac placenta connection between embryo and mother in *Chlamydoselachus*. If the uterus nourishes the embryo, this must be accomplished in some other way. In the hope of getting some

light on this obscure problem, let us now examine the uterus of that ovoviviparous shark whose reproduction most nearly parallels that of *Chlamydoselachus*.

The tropical shallow-water nurse shark, *Ginglymostoma cirratum*, carries in each greatly dilated uterus as many as 21 huge thick-shelled eggs like that shown in natural size in Text-figure 16. The inner wall of each uterus is made up of circumferential bands of hems or plaits overlapping like the shingles on a roof. The plaits are 5 or 6 mm. wide and are highly vascularized—"as red as a piece of fresh-cut beefsteak" my notes read.



Text-figure 16

The egg case (140 mm. long), egg, and embryo of the ovoviviparous nurse shark, *Ginglymostoma cirratum*—in natural size. Note the left, older, more finished looking end of the capsule and the larger, blunter, younger right end. The yolk blastopore is seen just to the right of the tail of the embryo.

Photograph by Alfred Goldsborough Mayor.

We have no statement of the collectors that embryos and their yolks are found in the uteri of *Chlamydoselachus* free of their shells, but it is evident that an embryo even as relatively young as that shown in Figure 11, plate I, or as old a one as that shown in color in Figure 49, plate V, has thrown off its heavy egg capsule. These large broken capsules could not be carried in the uterus without hurt to the delicate embryos. They must be thrown out into the sea. Similar reasoning must be applied to similar conditions in the nurse shark and its embryos enclosed in a larger and thicker egg shell.

The boatmen at the laboratory of the Carnegie Institution of Washington at Tortugas, Florida, where my studies were made, were all Florida and Bahama men, well acquainted with the nurse shark. They all told me that when the young are pretty well developed, they break out of the shells, and these latter are cast out while the embryos are

retained in the uteri during further development. I was told by the director, Dr. A. G. Mayor, that this was his understanding, but after these years I cannot recall if this was his personal observation. I was never fortunate in procuring large embryos nor small free-swimming young. Development is slow and the advent of the hurricane season led to the closing of the laboratory late in July of each year before the slow-developing eggs had gone far enough for the embryos to break out of their shells.

The young and growing fishes in the uteri of these two viviparous sharks must have oxygen. If sea water could penetrate the cloaca and into the uteri, it might provide this need. The nurse shark has a wide cloaca and the oviducal opening into it will sometimes admit "three or four fingers bunched into one mass", as my notes read in one case, and in them it is also recorded that a female *Ginglymostoma* hung up by the tail had the common oviducal opening measuring 1.5 in. in diameter. The opening must be this large to admit the outward passage of the large empty egg shells even if crumpled. Furthermore, I have opened a uterine egg of the nurse shark and on tasting the perivitelline fluid have found this salty. The embryo was very young.

I unwittingly performed another experiment which demonstrated that the egg capsule of *Ginglymostoma* is permeable to sea water. I took an egg capsule with its lively embryo out of the uterus of a just-killed female, cut a window in the capsule over the embryo, cleared out all the perivitelline fluid that I could and replaced it with molecular magnesium sulfate in order to anesthetize the embryo. The egg was then unthinkingly placed in a dish of sea water which did not cover the window. Twenty-two hours later the little shark was about as lively as ever. The sea water had penetrated the egg shell by osmosis and had so diluted the anesthetic solution that the embryo still lived.

There seems to be little doubt that the embryos of *Ginglymostoma* may get oxygen from the sea water which may come into the uterus through the dilated cloaca and the large oviducal openings. No experiments such as those above have been performed on *Chlamydoselachus*, but Dr. Smith tells me that the cloaca is open in his preserved specimens and that the right oviducal opening even when hardened in formalin will sometimes admit a man's thumb. So one may conjecture that sea water invades the uterine cavity of *Chlamydoselachus* and bathes the eggs. Thus the embryo could get oxygen from this water.

On the whole it seems quite probable that the young of both sharks may receive some oxygen by diffusion from the uterine wall into the fluids surrounding the embryo. Furthermore, from my knowledge of uterine gestation in other sharks and in various rays, I am strongly of the opinion that the uterine wall in both *Chlamydoselachus* and *Ginglymostoma* secretes liquid food materials to nourish the young after they are freed from the egg capsules. As shown in Figure 34, plate III, and Figure 43, plate IV, the embryos of *Chlamydoselachus* have short external gills, gills far shorter than I have found in the young of some viviparous sharks and particularly of various rays. Presumably the young of *Ginglymostoma* also have such gills. The long external gills of embryos of rays and of other sharks, when bathed in the uterine fluid, may take in not only oxygen but mineral

salts and possibly other food substances as well. The rich plexus of vitelline capillaries will also be bathed in the fluid of the uterine cavity and they may absorb some food and oxygen from it. If this takes place in *Chlamydoselachus*, it must go on for a long time, until and even after the yolk, shown in the colored Figure 49, plate V, is resorbed, and this yolk must be used up before the fish is born, else the free oceanic life of this little shark would be very brief.

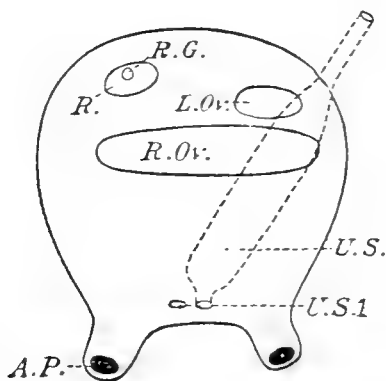
THE CLOACAL OPENINGS

As has been shown, the oviducts at their anterior ends have openings into the abdomen to receive the eggs set free from the ovaries. So, posteriorly the oviducts have openings into the cloaca through which the embryos, having used up their yolk masses in development, pass out to take up their free life in the sea. The lower end of the uterus progressively diminishes in size until, as a tube considerably reduced in cross-section, it opens out on the dorsal side of the cloaca. But even here, as everywhere else in this primitive shark, are found some surprising and interesting variations.

RIGHT CLOACAL OVIDUCAL OPENING PREDOMINANT

Since the right oviduct is predominant, since its uterine portion carries the developing young, and since these must pass out through its opening into the cloaca, one would expect to find that the right opening is larger and is possibly somewhat centrally placed.

Hawkes (1907) first and very briefly refers to the relative sizes of the oviducal openings into the cloaca thus: "The opening of the right enlarged oviduct . . . has acquired a median position, the left oviducal opening . . . lying cephalad to it". Only this, but she gives a diagrammatic figure to make these relative positions clear—Text-figure 17 herein. Deinega (1925) confirms Hawkes and writes at length. Thus he says "The right oviduct opens out by a large orifice in the middle of the cloaca"—as is shown in Hawkes's figure. Of the opening of the left oviduct he writes more fully "The left oviduct opens in the dorsal wall of the cloaca, rather far in front, so that it makes an impression as though it opens into the posterior section of the right oviduct; this orifice appears in the form of a cross fissure".



Text-figure 17

Diagrammatic figure of the cloaca of a female *Chlamydoselachus*.

A.P. closed abdominal pore; L.Or., left oviducal opening; R., rectum; R.G., opening of rectal gland into rectum; R.Or., right oviducal opening; U.S., urinary sinus (the other sinus is omitted); U.S. 1, openings of urinary sinuses into cloaca.

After Hawkes, 1907, p. 476.



Text-figure 18

Longitudinal section through cloaca and right oviduct of *Chlamydoselachus*, three-fourths natural size. The dorsal side is uppermost.

ab-p, abdominal pore; cl, cloaca; int, intestine; ov, oviduct; p, caecal pouch or rectal gland; ua, urethral aperture.

After Garman, 1885, Fig. 2, pl. XIX.

The relative positions of the two openings as stated by Deinega make somewhat clearer these openings as portrayed in Garman's drawing (Text-figure 18) of the cloaca of his specimen. If one holds the page in the vertical plane in the line of vision with the dorsal side of the figure uppermost and the cloacal end toward the observer, the relations will become clearer. The right lateral wall of the right oviduct (ov in the light area) has been cut away near the point of junction of the left oviduct (ov in center in dark area). The figure shows a common tube leading into the cloaca. From this, it is seen that the left oviducal opening is situated in the wall of the right aperture.

Smith found the two openings in all his specimens, but, excepting in the youngest, the right opening was predominant. This was markedly true in his two sexually mature females as shown in Text-figures 14 and 15. In the cloaca in each figure the large shaded area on the (fish's) right side is the opening of the right oviduct, the smaller shaded area on the left the opening of the left tube. Note how very predominant the right opening is in Text-figure 15. Here is Smith's statement on this condition in the fully mature specimen referred to: "... almost the entire urogenital sinus seems built around the very large opening of the right uterus indicated by line-shading in the figure [No. 15 herein]. In the hardened condition of the material, this opening is still large enough to admit a thumb. The opening of the left uterus is much smaller".

Here again is further proof of the unilaterality of functioning of the right oviduct of the frilled shark. Shell gland, uterine enlargement, posterior opening into cloaca, each overshadows its fellow on the left.

FEMALE REPRODUCTIVE ORGANS OF CERTAIN HIGHER SHARKS
AND VARIOUS RAYS

For the frilled shark, *Chlamydoselachus*, it has been shown that unilateral functioning of the reproductive organs is the general rule, that the right ovary and oviduct are uniformly fertile, but that rarely are both organs on the left side also functional. I have made some studies on this subject of unilateral functioning of reproductive organs based on dissections of sharks and rays at the U. S. Fisheries Laboratory at Beaufort, N. C., and in the reports on these (Gudger, 1912, 1913) I have given references to a number of articles bearing on this subject. To all these the interested reader is referred.

The records of my studies on the reproductive organs of sharks and rays dissected at Key West and at Dry Tortugas, Florida, while a guest-investigator at the marine laboratory of the Carnegie Institution of Washington, have never been published. Since some of these notes bear directly on the subject in hand, and particularly since one of the sharks (*Ginglymostoma cirratum*) in its eggs and reproductive apparatus shows certain marked likenesses to these structures in *Chlamydoselachus*, it seems well to quote from these notes here.

OVARIES AND OVIDUCTS OF SOME FLORIDA SHARKS

Since the sharks examined in southern Florida show the least departure from their early ancestors in the bilaterality of their reproductive organs, they will be studied first. The first departure from bilaterality like that noted in *Chlamydoselachus* has to do with the ovary.

The Nurse Shark, *Ginglymostoma cirratum*.—In eight dissected female specimens of this large, flat-bodied, sluggish, shallow-water shark with a large abdomen, both oviducts were always functional, but in each fish the right ovary only was functional. The fish were adults about 8 ft. in length, "over all". One had in the right ovary "30 eggs the size of small oranges (equatorial diameter=60–65 mm.)". Another had 33 ripe eggs in the right ovary. Still another had "right ovary enormously enlarged with 40 eggs size of billiard balls, some about 6 in. in circumference. These would have filled a peck measure or an ordinary water bucket". Three had "right ovary full of gaping pits from which ripe eggs had been erupted". Nearly all these enlarged right organs were median in position, while of the left ovary my notes say "insignificant in size", "hardly recognizable", "had to be hunted for". Not one left ovary had any eggs. It is to be regretted that none of these huge right ovaries was measured.

Various Other Florida Sharks.—The large, active, voracious tiger shark, *Galeocerdo tigrinus*, has the oviducts bilateral and functional. In four fish the left ovary was generally small and always non-functional, the right large, and functional with eggs in the anterior part. I have notes for three species of the requin shark, *Carcharhinus*. In four specimens of *C. obscurus* with bilateral functional oviducts, the left ovary was "small", "very small", "reduced"; while the right was always large and functional. In one 8-ft. fish, it was 2 ft. 10 in. long with 12 eggs, .5 to 1 in. in diameter. In one specimen of *C. falciformis*, my

notes read "l. ovar. very small, r. nearly twice as large". A solitary *C. platyodon* had the left ovary small and the right large with eggs in the anterior part. Both these sharks had both oviducts well developed and functional.

Of the genus *Hypoprion*, I dissected two species—*H. brevirostris* and *H. signatus*. In each, the oviducts were bilateral and functional, but the left ovary was small and without eggs; the right ovary was large and functional with eggs in the anterior end. The same condition of oviducts and ovaries was also found in *Scoliodon terranova*.

From these data on some of the tropical sharks of the eastern Gulf of Mexico, it is plain that they are on the way toward unilateral functioning of the reproductive organs. They have not gone so far in this matter as has *Chlamydoselachus*, since both oviducts are functional while only one ovary (the right) produces eggs. No reason for this can now be given, since they are sizable sharks with large abdominal cavities. This is especially true of the flat-bodied *Ginglymostoma*, in whose roomy abdomen are contained large uteri which when gravid much resemble in size and shape a pair of old-fashioned saddlebags. This size and form make it possible for each to contain, or are conditioned upon its containing, 20–21 eggs c. 140 mm. long x 185 in circumference. From these sharks with partial unilaterality of genital organs, we now pass to the rays in some of which complete unilaterality has been attained.

OVARIES AND OVIDUCTS OF VARIOUS RAYS

The rays are elasmobranchs flattened in the dorsoventral or vertical plane to fit them for bottom-living. They comprise the most specialized group of the Elasmobranchii. They are referred to here because there are found in these viviparous fishes the same variations in the reproductive organs that are found in *Chlamydoselachus*, the reputedly lowest form of the strap-gilled fishes. There is an extensive literature on this subject but I shall confine myself to my own researches.

Pteroplatea maclura.—The butterfly ray is abundant at Beaufort, N. C. In 1912 (Gudger, 1913) I dissected four female specimens. The reproductive organs of both sides were functional, but in every fish the left ovary was better developed than the right (in fish No. II, 25 per cent larger). Furthermore, in each case the left uterus was better developed and contained more eggs. Fish No. I had three eggs in the left uterus and an empty shell (wind egg) in the right; No. II had one egg (but with two yolks) in l. and an imperfect egg in r.; No. III had two eggs in l. (one with a malformed shell) and one in r.; No. IV had both uteri gravid but left twice as large as right. Unfortunately these two uteri were not dissected.

It is significant that in this ray the reproductive organs of the left side are better developed and more functional than those of the right. This is just the reverse of conditions in *Chlamydoselachus*. Another notable point is that imperfect eggs are found in both uteri of the ray. Parenthetically it may be noted that this same condition seems to prevail in the nurse shark. From all these data, I draw the conclusion that *Pteroplatea maclura* is in an intermediate stage between those rays having perfect bilaterality of the

reproductive organs and those having only one side functional as in *Dasyatis say* now to be briefly considered.

Dasyatis say.—The common stingray or “stingaree” also abounds at Beaufort, and in 1912 I reported the results of my dissections over a number of years. Sixteen non-breeding females (uteri showing no signs of having eggs in them) ranging from 13 to 35 in. in width had the left ovary from two to three times the size of the right. Thirteen breeding females (13 to 35 in. wide) had the left ovary functional (with eggs 12–18 mm. in diameter) and the left uterus greatly dilated—some with embryos, and some awaiting the coming of eggs. In the course of several summers’ work, no right ovary was found with any eggs in it and no right uterus was ever functional. These facts were paralleled by my studies of another species of the same genus.

Dasyatis hastata.—This is the common stingray of southern Florida. At Key West and at Tortugas, I dissected 10 specimens. Five were adults ranging from 3 to 4.5 ft. wide. In these, the left uterus only was enlarged and functional (some with embryos). In all, the right ovary was “insignificant” but the left was large and in many cases had large eggs in it. I also dissected five half-grown to adult specimens from 13 to 26 in. wide. Even in these, the left uterus was large and seemingly ready to receive eggs, the right reduced and indistinct. In all five the right ovary was small and non-functional. The left was always larger (in the 26-in. ray ten times larger) and filled with growing eggs.

Here is described a progressive gradation from partial to complete unilaterality in the functioning of the reproductive organs of elasmobranchs. In the butterfly ray, *Pteroplatea machura*, both ovaries and both uteri are functional, but in all dissections the left organs were invariably better developed—i.e., the right ones are beginning to degenerate. The sharks described (*Chlamydoselachus* excepted) all have bilaterally functioning oviducts, but unilaterality in the ovaries in that the right ones only are functional. Finally in the stingrays, *Dasyatis say* and *hastata*, complete unilaterality is found—left ovaries and left oviducts only are functional. Here then are those specializations in the functioning of the reproductive organs which are adumbrated in *Chlamydoselachus*, the lowest ranking shark and lowest elasmobranch. In the rays as in the frilled shark, there is found the same correlation of unilateral genital organs with a restricted body cavity. In *Chlamydoselachus*, the body cavity is narrow but is somewhat long to contain the closely-packed embryos; in the rays the cavity is both short and narrow and in the single uterus the few embryos are rolled up scroll-fashion.

From other notes made from my dissections and from a rather extensive but widely scattered literature, other similar unilateral functionings of ovaries and oviducts in other elasmobranchs might be given if it seemed necessary to go into the matter further.

THE ENCAPSULED EGG OF *CHLAMYDOSELACHUS*

The encapsuled egg of *Chlamydoselachus*, as it emerges from the shell gland and passes into the uterus, consists of a large yolk mass with a protoplasmic germinal area.

Shortly after the egg enters the oviduct, fertilization, encapsulation, and segmentation take place, followed later by gastrulation and the formation of the embryo. It is not known at what stage in the development of the growing embryo the capsule is burst, thrown off the yolk sac, and expelled from the uterus into the sea. But it must be long before the embryo attains the stage shown in Figure 11, plate I. However, we are here concerned with the early stages in which the egg is still encapsuled. These eggs occur in two distinct forms—as ellipsoidal and as round eggs.

ELLIPSOIDAL EGGS OF THE FRILLED SHARK

This form and shape of the encapsuled egg of *Chlamydoselachus* seems to be the typical one. At least, save for four round eggs portrayed by Dean, all eggs figured by all authors are ellipsoidal. This is true even of eggs freed from their capsules. Thus Brohmer (1909) figured without capsule an ellipsoidal egg 110 mm. long with an embryo of 75 mm. As drawn the yolk mass is 108 x 60 mm. And Garman (1913) portrayed a shell-less egg 98 x 56 mm. with a 59-mm. embryo on it. Neither figure will be reproduced here since, lacking details, they are of no particular value in this study.

Dean figured in color (Figure 50, plate V) a shell-less ellipsoidal egg 95 x 56 mm. with an embryo 39 mm. long. Then, among his miscellaneous *Chlamydoselachus* records, I have found a water-color sketch of a 55-mm. embryo on a yolk sac measuring 122 x 69 mm. This sketch, which is rather crude, was not made by Dean and was not intended for reproduction. The egg, from which the capsule had been removed, was taken off Okinose (Sagami Sea) in December, 1906. The references to these eggs without capsules are merely to show that the ellipsoidal form is the predominant one. Attention will now be directed to the capsules of these great eggs.

As portrayed by Dean, ellipsoidal encapsuled eggs seem to be of two kinds—normal and abnormal or at least unusual. These, as figured by him and by other investigators, will now be studied.

NORMAL ELLIPSOIDAL ENCAPSULED EGGS

The first encapsuled egg of *Chlamydoselachus* ever figured may be taken as an example of the normal egg of this type. The description and figure are from Nishikawa (1898). His material came from seven female specimens from the Sagami Sea. These fish contained from 3 to 12 eggs each—all ellipsoidal in form. His statement follows and evidently has to do with eggs in very early stages since he speaks of their having blastoderms on them. He also had eggs of the same type with early embryos as will be now shown. Here is Nishikawa's description:

The egg is ellipsoidal, and varies between 65–75 mm. in its shorter diameter and 102–124 mm. in its longer diameter, the measurements being made in physiological solution of salt (Figs. 1 & 2) [Fig. 1=Text-figure 4 herein]. It bears a stumpy excrescence at one end and a slightly recurved flattened process, about 35 mm. long, at the other. The capsule is light brown and transparent. The space between the capsule and the yolk sac is, in earlier stages, very insignificant, being confined mostly to the two poles of the eggs, and is filled with the white, which is very fluid. The yolk is of a pinkish color, and the yolk-sac is very delicate.

This description is of a live egg just taken from the body of the mother. I have found a very similar condition in the encapsulated intra-uterine egg of the nurse shark, *Ginglymostoma cirratum* (Text-figure 16). Here is a thick heavy capsule enclosing the huge round yolk with its embryo surrounded by a clear glairy fluid—evidently the counterpart of Nishikawa's "white". Lining the interior of the shell and particularly noticeable at the ends is a thicker jelly-like material which cushions the yolk as the egg rolls about in the saddle-bag-shaped uterus of the female *Ginglymostoma* as she twists and turns in avoiding enemies.

Nishikawa's drawing (Text-figure 4) shows an ellipsoidal egg in a capsule (natural size) 135 mm. over the processes (following the curve of the long one). The egg proper is 100 mm. long by 65 deep, with an embryo 43 mm. long on it. Attention is called to the blunt nipple-shaped process on the left, while on the right, the capsule terminates in a finger-like curved process about 40 mm. long over its outer curve. The capsule is transparent and here drawn to show the embryo and its circulatory system, but on the lower side just inside the heavy line representing the capsule is a light line portraying the raphe of the capsule. This extends from the end of the short blunt process along the shell and out on the long curved process. This raphe is bilateral—the other half being found on the side of the egg away from the observer.

Dean's drawings of encapsulated eggs number eight, including the wind egg previously referred to. These figures portray ellipsoidal eggs of two kinds: normal eggs with a blunt nipple-shaped process at one end and a long curved finger-like process at the other; and abnormal or at least unusually long eggs having at one end a long process with tendrils. There are also four drawings of round eggs. The normal ellipsoidal eggs will be studied first, the unusual types will later be considered in series.

Dean has figured two ellipsoidal eggs of the normal type. The first is shown in both dorsal and ventral aspects in Figures 7 and 8, plate I. Careful comparison of Figure 7, plate I, with Text-figure 4, a reproduction of Nishikawa's Fig. 1. pl. IV, shows that Dean's figure is a copy of Nishikawa's. The embryo measures 43 mm. in both; the yolk in Dean's figure is 65 x 100, in Nishikawa's the same. Likewise the eggs in ventral aspect (Figure 8, plate I, and Nishikawa's Fig. 2, pl. IV) are identical. Nishikawa also had an egg with a 50-mm. embryo on it, but he had no drawing made of it. This however, Dean had drawn in both dorsal and ventral aspects as may be seen in Figures 9 and 10, plate I.

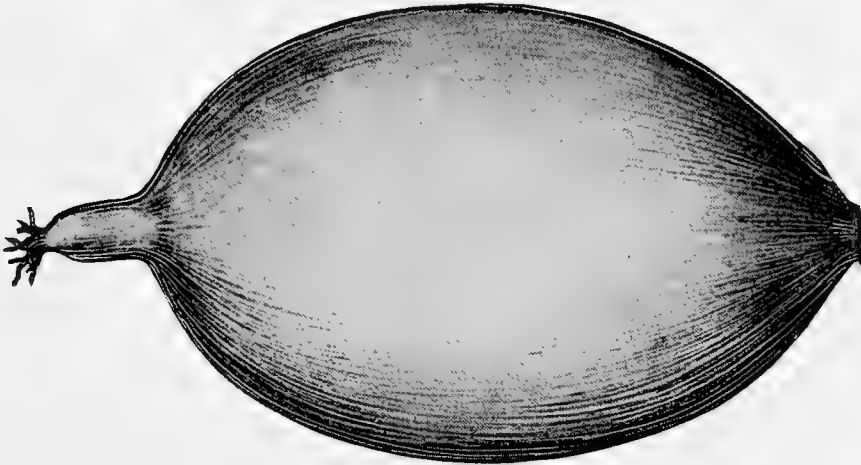
Having cleared up these points, let us now return to a study of the ellipsoidal capsules, which have been designated as normal. But first let it be said that no one else has ever obtained or at any rate portrayed capsules such as these. Each of the capsules, shown in Figures 7 and 9, plate I, has at the left end a rounded, blunt, nipple-shaped process or eminence. On the right, each capsule terminates in a curved, finger-like stumpy process, about 30 mm. long, and each curved in the same direction. In the drawing, each egg has on its lower side a distinct raphe, whose relation to the blunt process is obscure but which extends out onto the long curved process. The capsule of the younger egg measures 128 mm. in a straight line, that of the older egg 143 mm.

UNUSUAL ELLIPSOIDAL EGGS WITH TENDRILIFORM PROCESSES

There are now to be considered certain eggs whose capsules may generally be designated as ellipsoidal but which depart rather widely from the forms studied. All bear tendriform processes. One is unusual in form but is by no means abnormal. However, it does bear tendrils. Of all the unusual eggs, it departs so little from the normal that it will be considered first in this category.

AN ELLIPTICAL EGG

This egg is elliptical rather than ellipsoidal in outline and bears tendrils at one end (Text-figure 19). It is the only encapsuled egg, other than Nishikawa's (Text-figure 4)



Text-figure 19

An elliptical encapsuled egg (in natural size—112 mm.) in the Museum of Comparative Zoology, Cambridge, Mass. Note the striae on the capsule and the tendril-bearing process on the left. The stump on the right looks as if a similar process had been cut off.

After Garman, 1913, Fig. 4, pl. 59.

that has ever before been portrayed as a published figure. In 1906, this egg was brought from Japan by Dr. Thomas Barbour and deposited in the Museum of Comparative Zoology at Cambridge, Mass. In 1913 it was figured but not described by Samuel Garman. As my Text-figure 19 shows, the outline of this capsule is an almost perfect ellipse. The egg measures about 90 x 70 mm. The total length of the capsule is 112 mm. and of this the long process accounts for about 18 mm. At the left, the long seemingly round process breaks up into three short unequal-sized stumps and each of these into a number of smaller processes, of which the finer outer parts (see Figure 13, plate I) have broken away. At the right end is the stump of a process, apparently the product of an amputation by means of a dull knife of such a process as is still present on the left. The shell is covered with parallel striations. The egg is so drawn that the raphe forms both upper and lower edges or limits of the figure. Garman also figures the egg yolk with its 59-mm. embryo removed from the capsule as has been noted.

Next for study are three ellipsoidal tendril-bearing eggs found portrayed in Dean's portfolio of drawings of *Chlamydoselachus*. These eggs are not merely ellipsoidal but are decidedly oblong. Two of them were fertile, while the third, the wind egg previously referred to, was infertile.

SOME OBLONG FERTILE EGGS

In Dean's notes, as already referred to herein, the small wind egg is recorded as coming from the left oviduct of a female *Chlamydoselachus* taken off Misaki in 1905. From the right oviduct of this same fish were obtained "3 oblong eggs" of which two were "drawn". The one of the oblong eggs, not drawn, was roughly sketched in pencil in the notebook with the caption "stage early, probably gastrula". This sketch is reproduced as number C in my Text-figure 26. Note that the capsule has a tendril-bearing process at one end. This is very like the process in one of the "drawn" eggs now to be studied.

Symmetrical Oblong Eggs.—With the notes just quoted is the cryptic statement "135 mm. x 70 and longer". I identify the two oblong eggs "drawn" with Figures 2 and 3, plate I. The smaller egg (Figure 3) is symmetrical and measures (in the original drawing) 116 mm. excluding the processes and 140 mm. over them; it is 78 mm. deep. At the right end is a very short process, apparently the remains of a longer one. At the left end is a slightly curved stumpy process, 20 mm. long. Apparently the tip of this has been broken off leaving some splinter-like fragments. Along one side is a raphe which extends out on the long process. Its relation to the fragment of the process at the right is not clear. The capsule is everywhere covered with close-set parallel striations. At the left many of these striations are gathered together and extend out on the long process.

Among the *Chlamydoselachus* material deposited in the zoological collection of Columbia University and loaned by Prof. McGregor for this study, is an oblong encapsuled egg. This measures 108 x 71 mm.; is not only oblong but slightly asymmetrical, and has a large raphe similar to that on the egg figured. The raphe extends from a rudimentary blunt process at one pole of the egg over the yolk mass and out onto a short process ending in tendriliform fragments. This tendriliform process is somewhat shorter than that in Figure 3, plate I, and the egg is somewhat smaller. I believe, however, that this egg is the one figured, and that the slight differences are due to shrinking after 33 years in alcohol.

In the 108-mm. oblong egg, and in two others of about the same size from Columbia University (both having embryos), the raphes are complete. They entirely encircle the eggs, but are better developed on one side than on the other. Their function is not known. The color of the capsules of these preserved eggs is a light brown. A crumpled capsule, from which egg and embryo have been removed, appears decidedly browner than those capsules enclosing yolk masses. Possibly this difference in color between these capsules and that of the wind egg (Figure 51, plate V) is due to their long immersion in alcohol.

Asymmetrical Oblong Eggs.—The larger of the two oblong eggs, referred to in Dean's notes, is decidedly asymmetrical (Figure 2, plate I). Its length (excluding its one process—the other, if present, is hidden) is 135 mm. and its width 87 mm. It is pre-

sumably the "larger" of the two oblong eggs recorded in Dean's notebook. Its asymmetry is probably not the result of handling, as might be surmised, but was impressed upon the egg while the capsule was being formed. The long curved process measures about 30 mm. to the fork of the tendrils and these extend out about 15 mm. further. The capsule is everywhere traversed by fine longitudinal striations which converge at the left end and run out onto the long tendril-bearing process. The raphe, seen on the side of the egg next the observer, is very large and heavy. It runs out on the process which is plainly twisted to the left.

In the Dean collection of frilled-shark material in the Department of Zoology at Columbia University is a large somewhat asymmetrical ellipsoidal egg which deserves description. It measure 90 mm. long x 57 deep and has on it an embryo 71 mm. long. The large yolk mass has become split open by the action of the preservative and the resulting expansion has split the capsule along that raphe near to and somewhat parallel with the body of the embryo. At the end of the egg near the tail of the little fish I can find no evidence of a process. At the other end near the head of the fish is a process (broken off from the capsule) which, as hardened by the preservative, is quite flattened.

This process is shown in Figure 13, plate I. In nature, the basal part is about 17 mm. long and about 8 mm. wide. Each of its outer edges is constituted of the end of a raphe. Between these raphe-formed edges, in the flat body of the process, about seven horny strands can be made out with the aid of a magnifying glass. This process is very like that on the egg shown in Figure 2, plate I. The outer end of the process is split in two and each half breaks up into a twisted mass of fine tendrils. Here as in Figure 2, plate I, the raphes form a part of the tendril mass, exactly as they do in the egg cases of certain skates and European small sharks ("dogfishes").

In the first plate of Dean's figures is a separate drawing (Figure 14, plate I) which shows such a very much frayed-out process. This process seems also to be flat and to have the raphes forming its outer edges. It breaks up into one large and three small tendril masses. The larger at the base seems to be constituted of about 10 string-like bodies. The other three tendrils are separate and grade in size from outside in, the innermost being the smallest. The larger tendril mass seems to have had a filament cut off at the second bend, one tendril only remaining. Of the three others the median one seems to be broken up into two. The outer and inner tendrils are of about the same length. All are much crumpled. It seems not improbable that this drawing was made from such a process as that described in the preceding paragraph. Since the striae run onto the processes, one wonders what part they play in the formation of the strands in the process and of the tendrils. One wishes for fresh material here.

AN ELONGATE INFERTILE (WIND) EGG

Last of all of Dean's drawings of elongate eggs is the wind egg portrayed in color in Figure 51, plate V. It is hardly ellipsoidal but it is elongate and it has a long tendril-bearing process as may be seen in the figure. It was presumably drawn in natural size.

Its width is 23 mm. and its length over the processes (but excluding the tendrils) is 102 mm. At the larger end is a conical process. The long pointed end of the capsule breaks up into a group of tendrils measuring about 10 mm. The surface of the capsule exhibits very fine striations. Very clear is the longitudinal ridge or raphe extending from the tendrils along the small end of the egg capsule to and across the base of the conical process. Not visible is the corresponding one on the other side. At the lower side of the larger end of the capsule is a clearly delimited pale area. What it is I do not know. This egg apparently contained no yolk whatever and hence it is called "wind egg". The color as shown in the figure is presumably that common to all egg capsules.

ROUND EGGS OF THE FRILLED SHARK

Last among Dean's materials for the study of encapsuled eggs are three drawings of round eggs reproduced as Figures 4, 5, and 6 of plate I. These are labelled C, B, and A on the drawings, and are listed in this order in Dean's notebook in his writing, as indicating their progressive stages of development. Each egg capsule is round and has short curved processes. These eggs will be considered here in the order of size.

Egg A (Figure 6, plate I) in the original drawing measures 129 mm. over the processes, and the diameters of its yolk mass are c. 88 mm. in the line of the processes x 87 wide. Of the three eggs, its processes are the longest and slenderest, are of about the same size and length, and are curved in the same direction. Egg B (Figure 5) is 115 mm. over the processes, and its diameters are c. 87 x 96. Its processes are short and stumpy, are of about equal size, but are twisted in opposite directions. Egg C (Figure 4) is 116 mm. over the processes, and its diameters are c. 90 x 89. Its stumpy processes are short, of unequal size—one more than double the size of the other—but are curved in the same direction. All these processes appear to be "stumpy", but it may be that they were sharply curved away from the artist's line of sight and were longer than they appear in the drawings. Those of Egg A (Figure 6) certainly recall the longer process portrayed by Nishikawa in my Text-figure 4, and by Dean in his Figures 7 and 9, plate I. In this respect this capsule approaches what has been taken as the normal type.

In the capsule of each egg the raphe extends across the germinal region, where it is drawn much wider. It runs out onto and helps form each process. The striae are not visible over the egg but show faintly at the poles, where they converge and extend out on the processes. The formation of these processes is not easy to understand and so far as I know has never been explained. The anterior process of the capsule must be formed in the lower outlet of the shell gland while the egg in the shell gland is having its capsule laid down. As I shall show later the posterior process is formed as and when the encapsuled egg passes out of the gland on its way to the uterus. The exit orifice of the shell gland is small and its sphincter muscle evidently constricts the ends of the shell while they are still soft and gelatinous. While the processes are being formed, the striae on them are laid down in a way not as yet understood.

These encapsuled round eggs have been designated "unusual" since no one save Dean seems ever to have seen such, but they cannot be termed abnormal. Each seems to have a late blastula on it (these will be considered later) and there is undisputable proof that these round eggs go on to full development. This is admirably shown in Figure 11, plate I. The young fish was 175 mm. long and it is fast to a round yolk sac which in the original drawing measures 92 x 90 mm. and which is now freed of its capsule. Thus this yolk, bearing this advanced embryo, has still the almost perfectly round form of the three eggs shown in Figures 4, 5 and 6, plate I, and, judging by the sizes of these three other round eggs, it has decreased but little in bulk.

SIZES OF EGGS OF *CHLAMYDOSELACHUS* COMPARED WITH THOSE OF OTHER SHARKS

From his studies of all these extraordinarily large encapsuled eggs of *Chlamydoselachus*, Dean drew certain general conclusions as to their size and phylogenetic origin. These conclusions are contained in the only description (a single paragraph) of the eggs of the frilled shark which he ever published (1903). From this, I excerpt the following: "*Chlamydoselachus* has specialized in the line of producing large eggs, the largest indeed among recent animals, ostrich hardly excepted [egg 150 mm., 5.9 in., in long diameter]; that it was, however, until recently an egg-depositing shark is apparent from the character of the horn-like capsule (with rudimentary tendrilform processes) which the egg still retains".

At the time that Dean wrote, the egg of *Chlamydoselachus* was the largest egg known to him save only that of the ostrich, but since his day larger shark eggs have been discovered. Larger eggs are now known to be carried by various sharks of the family Isuridae, and by the ovoviviparous nurse shark, *Ginglymostoma cirratum*, often referred to earlier in this article. The eggs of these sharks will now be described that the reader by comparisons may see how large the eggs of *Chlamydoselachus* really are.

SIZES OF EGGS AND EMBRYOS OF THE FRILLED SHARK

As a basis for comparing the size of the egg of the frilled shark with that of other sharks, it will be necessary to establish the size of this egg. Our earliest information comes from Nishikawa (1898) who had eggs ranging from 102 to 124 mm. in long and from 65 to 75 mm. in short diameter. He also speaks of eggs "110–120 mm. long". These measurements were presumably made over the egg capsule and its processes. His one figured egg (Text-figure 4) thus measured is 128 x 65 mm., but the yolk mass is only 100 x 65 mm. natural size.

Let us now turn to Dean's materials. The three round eggs (yolks only) measure 90 x 87 mm., 96 x 87, and 97 x 88 in the original drawings. His two oblong eggs (yolks only) measure 119 x 80, and 138 x 90. Of his other material, Figure 9, plate I, portrays a 50-mm. embryo on a yolk measuring 108 x 68 mm. Then his Figure 11, plate I shows a large embryo on a yolk sac 92 x 90 mm. Also Dean records an embryo of 331 mm. on a yolk 111 x 100 mm. And finally there is the huge embryo of 390 mm. (15.35 in.)

on a yolk measuring 100 x 70 mm. This is portrayed in color in Figure 49, plate V. All these measurements are of the original drawings.

When one considers these measurements of such huge eggs as had never before been recorded of any animal marine or terrestrial (save only the ostrich), it is no wonder that Dean wrote (1903, p. 487) that "*Chlamydoselachus* has specialized in the line of producing large eggs, the largest indeed among recent animals, ostrich hardly excepted". But we will consider some eggs that exceed even the very large ones of *Chlamydoselachus*.

SIZES OF EGGS AND EMBRYOS OF ISURID SHARKS

Interestingly enough at about the very time that Dean was collecting adult specimens of *Chlamydoselachus* and studying their eggs in the Sagami Sea, Franz Doflein was also making very extensive collections of marine fauna from the same waters. He either collected or at any rate saw specimens of the frilled shark, for in his book (1906, p. 257) he figures a male specimen—the best portrayal (Text-figure 5 herein) yet published of the male fish. He also obtained a huge shark egg and later described it in the following terms:

The eggs of a giant shark were to me one of my most surprising discoveries. I had often gotten these eggs from the fishermen but I never obtained the mother fish. They were, however, taken from the mother fish, which evidently belongs to the viviparous sharks. With their enormous yolks, they seem to be the largest eggs yet known from the animals of that region. They were considerably larger than ostrich eggs [150 mm. long]. One could tell them from the eggs of other sharks by the fact that the embryo was not connected with the yolk sac by a long, ribbon-like umbilical cord, but grew directly from it.

When I had read thus far, I strongly conjectured that these were eggs of *Chlamydoselachus*, particularly since they came from a viviparous shark and since Doflein knew and figured *Chlamydoselachus* in his book. But fortunately, on the page following the paragraph quoted, Doflein figured one of these eggs and embryos. It is plainly a young Isurid shark, and the statement is added that the yolk sac has a (long?) diameter of 220 mm. No size is recorded for the little shark, but it is still comparatively young, probably not more than one-quarter grown.

Doflein brought back to Germany two of these huge Isurid uterine eggs along with his other Japanese fish collections. These eggs and embryos were turned over to Johannes Lohberger who made a thorough study of their external morphology and internal anatomy (1910). He found that the larger and older embryo (Text-figure 20 herein), after being in preservative for four years, was 553 mm. long (21.8 in.) and 63 mm. wide where it rested on the yolk mass. The length of the yolk mass was 211 mm. (8.3 in.) and its transverse diameter 123 mm. (4.85 in.). The weight of embryo and yolk was 2.68 kg.=5.9 lbs. The size of the female *Lamna* from which embryo and eggs were taken is not given and probably was not obtained.

In the same year that Lohberger published on his Lamnid embryos from Japan, Shann (1910) described embryos of *Lamna cornubica* from Scottish waters. He quotes H. C. Williamson that the largest porbeagle embryo he had ever seen was "19 inches in total length . . . the yolk measuring 9.25 inches in length". Shann's description

and table of measurements of his own four embryos are so involved that I can make out little about them. He had four embryos measuring 10.25, 18, 18.5 and 24 inches respectively and all in about the same stage of development. His detailed yolk-sac measurements are unintelligible to me—one wishes for diameters such as those given above. Shann states that one of the largest embryos he examined “was a female measuring 21.75 inches and the yolk sac was still of enormous bulk”. This is confirmed by his roughly-drawn



Text-figure 20

Egg and embryo of an Isurid shark (*Lamna* sp.) obtained in the Sagami Bay by Franz Doflein c.1905. The embryo was 553 mm. (21.8 in.) long. The yolk sac measured 211 mm. (8.3 in.) x 123 mm. (4.8 in). The whole weighed 2.68 kg. = 5.9 lbs.

After Lohberger, 1910, Fig. 1, pl. I.

figure which shows that the word “enormous” is correctly used. The yolk reaches almost from the angle of the jaw to the base of the caudal fin. He judges that at birth the young fish would be approximately 30 inches from tip to tip.

Other Isurids have large embryos on huge yolk sacs. Two cases will be indicated. Sanzo (1912) figures and describes from the Mediterranean the intra-uterine embryo of *Carcharodon rondeletii*, the great white shark or “man-eater”. The embryo was 361 mm.

(14.2 in.) long but no dimensions of the elongate yolk sac are given. The specimen weighed 800 g. (28.2 oz.) of which the yolk alone weighed 500 g. (17.9 oz.) In his figure the long yolk mass extends from the pectorals to beyond the cloaca.

Since the above was written, I find that, unknown to Dean, Lohberger, Shann, Sanzo and myself, a far larger egg and embryo of another Isurid shark had been recorded by Vaillant in 1889. He described but unfortunately did not figure an embryo of *Oxyrhina spallanzanii* whose total length was "50 cmt." (500 mm., 19.65 in.) on a yolk sac measuring 235 x 140 mm. (9.25 x 5.5 in.). Fish and yolk had been more than 50 years in alcohol. Yet, "Le poids total de cette pièce, qui représente en somme un oeuf gigantesque de Selacien, est, dans état actuel de conservation, de 3 kil. 250 gr." This weight (3250 g., 114.6 oz., 7.2 lbs.) seems incredible hence I have quoted Vaillant verbatim. So far as I know this is the largest egg and embryo of any shark ever described.

I can not find that the egg capsule of an Isurid shark has ever been figured. Not only does one wish to see an embryo and yolk sac of one of these sharks for comparison with a like stage of *Chlamydoselachus*, but also for comparison one wishes to see and examine the capsules which enclose the largest eggs in the animal kingdom—eggs much larger than those of the ostrich.

There is in the Museum collection an egg and embryo of *Chlamydoselachus* mounted for display on a sheet of glass in a rectangular jar of alcohol. The embryo measures 370 mm. (14.55 in.) and the yolk sac 78 x 60 mm. Dismounted, and with the excess of alcohol drained off, egg and embryo weigh 213 g. (7.5 oz.) Another yolk sac of about the same size (74 x 60) detached from its embryo weighed 142 g. (5 oz.) The little fish, drawn when fresh (Figure 49, plate V), measured 390 mm. and the unhardened yolk 100 x 70 mm., but after being in alcohol for at least 33 years it has shrunk to the dimensions noted above. The weight has also decreased somewhat. There is much yellow oil in the yolk. This soaks out into the alcohol, which has periodically to be replaced by fresh alcohol. This automatically reduces the weight of the yolk.

The young frilled shark is a little longer (370 vs. 361 mm.) but much more slightly built, especially in the forward parts, than Sanzo's *Carcharodon*. The total weights are very different—213 vs. 800 g.; but after all the greatest difference is in the weight of the yolk sac—142 vs. 500 g. Here contrast Dean's *Chlamydoselachus* (Figure 49, plate V) with Lohberger's *Lamna* (Text-figure 20).

SIZES OF EGGS OF THE NURSE SHARK

I have unfortunately never seen the eggs and embryos of *Lamna* nor *Carcharodon* but I have studied the encapsuled eggs and early embryos of the nurse shark, *Ginglymostoma*. And since these heavy-shelled intra-oviducal eggs are in many ways similar to those of *Chlamydoselachus*, some data concerning them in the encapsuled stage will be valuable here for comparison. My figures give lengths and unfortunately girths instead of widths of the capsules. Furthermore since it was not easy to measure the horizontal diameter of the yolk mass through the thick and oftentimes scarcely transparent capsule,

I mistakenly did not record the measurements of the yolks. Since the capsules are not round but flattened dorsoventrally, it would have been difficult to get measurements in this dimension.

In my notes I have measurements of 5 wind eggs recorded as "infertile". These are 105 mm. long x 120 in circumference; 105 x 145, 116 x 110, 122 x 145; and 130 x 146 mm. I noted the measurements of 6 average-sized fertile eggs as follows: 133 mm. long x 185 in circumference; 134 x 192; 141 x 185 (2 capsules); 142 x 193; 150 x 190—average 140 long x 187 in girth. From this it is seen that there is considerable variation in size—less in girth than in length. The girth of the capsule is pretty constant because the size of the contained yolk mass is fairly uniform. The variation in length is mainly due to variations in form and shape in the posterior or last-formed end of the capsule. This is sometimes pointed and sometimes blunt but always seemingly "pinched together". The anterior or first-formed end looks "finished", the posterior end, the last to emerge from the shell gland, looks unfinished. For these points see Text-figure 16. This matter of the posterior or unfinished end of the capsule will be referred to later.

It was difficult to get the weight of the yolk. This is surrounded by a clear glairy fluid which slowly flows like thick syrup. Next to the shell this becomes a thick jelly which adheres to the shell. At the ends of the shell this jelly forms the "plugs" already noted—see Text-figure 16. These substances—glairy fluid and jelly—probably correspond to the "white" of Nishikawa. To get at the weight of the yolk, shell and contents were weighed. Then a window was cut in the upper part of the shell, and the yolk and some of the surrounding glairy matter were poured out. The shell, the jelly and the remaining glairy material were then weighed. The data for my two largest eggs are as follows. Egg 1, 180 mm. long x 220 mm. in girth, weighed 318 g. The shell and jelly weighed 64 g. and the yolk 254 g. Egg. no. 2 was about the same size (no figures recorded) and weighed 311 g. The shell and jelly weighed 56 g. and the yolk 255 g.

From the data set out above, and from the eggs and capsules shown in Text-figures 16 and 21 it is manifest that, while the encapsuled egg of *Ginglymostoma* is very large, it is not so large as that of *Lamna* or *Carcharodon*. The average for the 6 normal-sized eggs of *Ginglymostoma* is 140 mm. (5.5 in.) long x 187 (7.4 in.) in girth. These eggs are somewhat flattened and have thick heavy raphes on each side. These help increase the girth measurements. Text-figure 16 was made from a large and entirely normal encapsuled egg. Its life size was unfortunately not noted, but as shown in the text-figure, it has been reproduced 140 mm. in length—the average as worked out above. This is just slightly more than the natural size of the encapsuled egg of *Ginglymostoma* figured by Garman (1913, Fig. 3, pl. 59). From these data it is seen that in size of their eggs these sharks rank thus; *Chlamydoselachus* has the smallest, *Ginglymostoma* the intermediate-sized, and the Isurids the largest eggs.

Again must comparison be drawn between the body size of *Chlamydoselachus* and that of these other sharks. The frilled shark has an elongate slender body averaging c.

5.1 ft. (largest 6.4 ft.)—with a correspondingly small abdomen (Text-figures 5 and 7). Yet in its right uterus it may carry as many as 7–12 large eggs and embryos. On the other hand, the nurse shark is large (average adult about 8 ft. long), broad and somewhat flat, and has a large abdominal cavity. Both of its uteri are functional and at breeding season become enlarged into a pair of saddlebag-like organs each of which may contain as many as 21 of the large eggs portrayed in Text-figure 16. The porbeagle is a fairly large shark. Shann notes females from 5–9 ft. long—more of the smaller size being recorded. I have no data for the size of the body cavity, but it must be large to accommodate the eggs and embryos noted above. Both uteri of *Lamna* are functional. Three and occasionally four young are produced, but one on each side, or one on one side and two on the other are more common. The young at birth are probably 28–31 in. long, and, since these young sharks are very large forward, they must fill the uteri and the abdominal cavity quite full. But to sum up, it can be said with assurance that the evidence points to the belief that *in proportion to the size of its body cavity*, the frilled shark ripens and incubates the largest eggs known at this writing.

With the making of these historical notes a part of the record dealing with the size of the encapsuled eggs of *Chlamydoselachus*, we will now turn to the study of the formation of the capsule.

FORMATION OF THE EGG CAPSULES OF *CHLAMYDOSELACHUS* AND OF *GINGLYMOSTOMA*

The presence of the thick keratinoid shell about the egg of an ovoviviparous shark is surely an archaic feature. As Dean long ago (1903) pointed out, this is a heritage from its egg-laying ancestors. Now all egg-laying elasmobranchs known to me have on their shells tendrils or holdfasts which catch on seaweed, stones, and other objects. Thus anchored, shell and egg escape being rolled about and injured or covered with sand or silt, and are assured of fresh water and oxygen.

As in other sharks, so in *Chlamydoselachus* these capsules are secreted by the shell gland, the interior of which is shown in Text-figure 13. For a description of this gland see page 550. As I have pointed out earlier, the egg shell exhibits minute striae, which sometimes have a faint spiral arrangement, and which in all cases are gathered up and extend out on the processes. For these see Figures 2 and 3, plate I. These striae are undoubtedly impressed on the capsule during its formation. The peculiar internal structure of the shell gland seen in Text-figure 13 must be responsible for these. The shell gland is somewhat flattened in form and I judge that the raphes are formed at the sides where the dorsal and ventral inner surfaces of the gland are united. The structure of the shell gland in *Chlamydoselachus* has yet to be thoroughly described and the details of its function explained.

Excepting only the round eggs portrayed by Dean, all egg capsules of the frilled shark figured have a long functional process at one end of the capsule. In most of the other eggs portrayed, the other end of the capsule has a low conical blunt nipple-like

process—as figured by Nishikawa (my Text-figure 4); and by Dean, Figures 7 and 9, plate I. Or this is very blunt and looks cut off as shown by Garman in Text-figure 19. Or, at this end of the capsule, the process is almost or entirely lacking as seen in Figures 2 and 3, plate I, and as found in eggs deposited by Dean in the zoological museum of Columbia University. Thus one end of the capsule looks “finished” and the other—especially when the process breaks up into tendrils—looks decidedly unfinished. However, the practical disappearance of the process at one end of the capsule, taken in connection with the fact of uterine gestation of the egg, is surely indicative of an evolutionary movement to get rid of the capsule around the egg of *Chlamydoselachus*.

Nothing is known as to the method of formation of the capsule and its processes in *Chlamydoselachus*. This could only be had by dissection of females immediately after capture in the hope of finding capsules still in the glands. How improbable is such an opportunity, the reader will readily realize from considering the habitat of the fish and the difficulty of its capture. However, I have fortunately been able to make such dissections and observations on the nurse shark, *Ginglymostoma cirratum*, which, as noted, carries in each uterus eggs with large thick-walled blunt-ended capsules. In this capsule, one end is likely to be smaller and seemingly pinched together, more “finished”, like that of *Chlamydoselachus*, while the other is larger, somewhat drawn out and blunter, unfinished looking—this end being presumably that last formed. In Text-figure 16 one cannot make this distinction very readily, because the ends are very much alike. But since I have examined scores of these eggs, I am satisfied that the longer and broader end of the capsule is the younger. Furthermore, the blunter end is plainly the younger in the eggs shown in Text-figure 21. Then there is another criterion on which to base judgment. The egg (yolk mass) is placed excentrically in the shell (Text-figures 16 and 21). This results from the fact that the jelly-like substance lining the shell forms a larger plug in one end of the capsule. In these unequal-ended capsules of the nurse shark, this larger amount of jelly is in the “unfinished” or younger end as may be seen in the figures referred to.

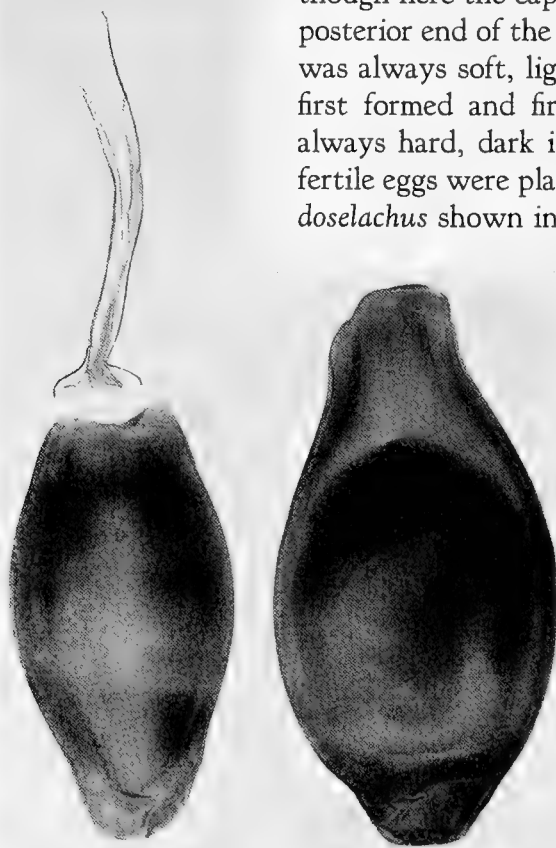
Now it is clear that *Ginglymostoma* is the last of a line of oviparous sharks, and that like *Chlamydoselachus*, it is an ovoviviparous selachian well on the way toward a viviparous mode of reproduction. As such, *Ginglymostoma* like *Chlamydoselachus* might be expected occasionally to retain tendrils at the larger, blunter, younger, or “unfinished” end of its capsule. That it does this is shown in Text-figure 21. Furthermore, while at Tortugas in 1912, I fortunately by dissection learned how and when these tendrils are formed. The facts as ascertained will now be given from my notes.

FORMATION OF TENDRILIFORM PROCESSES

On June 16, 1913, I dissected several female specimens of *Ginglymostoma* and found that “No. 1 fish had in the section of the left oviduct just behind the shell gland an egg whose backward [really its anterior] end was covered with a hard tough shell (like any of the eggs in the uterus) with the short blunted base of the absent horns drawn toward each other, as may be seen in Garman’s drawing (1913, Fig. 5, pl. 59). The posterior end of the

shell, however, still projected into the hinder part of the shell gland, and when drawn out this was found to be soft and gelatinous with prolongations which were evidently tendrils in the process of making. These were broken off in removing the egg, but they were placed in their normal position as shown in the photograph reproduced as Text-figure 21. This egg was "non-fertile".

From another female dissected on this day, I got an egg capsule with a pair of processes 55 mm. long, and on another capsule one process 120 mm. long. These eggs were undersized and probably infertile—though this unfortunately was not specifically noted as it was for other eggs below standard limits of size. My notes record five other cases from specimens dissected June 19. Some shells had processes on the posterior (i.e. last formed) end, a few had them on the anterior (first-formed) end, though here the capsule was generally "blunt" or rounded. The posterior end of the capsule still in the shell gland or just out of it was always soft, light in color and often translucent. That end first formed and first out of the gland, the anterior end, was always hard, dark in color, and noted as "finished". These infertile eggs were plainly wind eggs comparable to that of *Chlamydoselachus* shown in Figure 51, plate V.



Text-figure 21

Two typical egg capsules of the nurse shark *Ginglymostoma cirratum*. The first, a wind egg, has the rudiments of tendrils at the hinder end. The second, a fertile egg, has the normal, blunt, unfinished hinder end to its capsule.

Photograph by E. W. Gudger.

From these facts the only conclusion that can be drawn is that in *Ginglymostoma* the formation of these rudimentary and very variable processes indicates that they are vestigial structures inherited from oviparous ancestors whose egg shells had tendrils for holdfasts. Everything points to the face that the ovoviviparous shark *Ginglymostoma* is on its way toward becoming a truly viviparous one.

No dissections and no direct observations of the formation of the egg capsule of *Chlamydoselachus* have ever been made. But several scientific men on being asked which end of the egg capsule of the frilled shark was finished first (was the older) have unhesitatingly answered "the blunt end", and when asked why have answered that "It looks finished"—and so it does, while the end having the process looks "unfinished". For these points contrast the two ends of the capsule in Nishikawa's egg (my Text-figure 4) and in Deans'

drawings (Figures 7 and 9, plate I). More markedly does this contrast appear in Garman's drawing (Text-figure 19 herein) and in Dean's two oblong eggs (Figures 2 and 3, plate I).

Not being able to decide by observation which is the anterior or older end of the egg capsule in *Chlamydoselachus*, let us turn for comparison and explanation to the very similar egg shell of the nurse shark, *Ginglymostoma*, in which I have settled the matter by dissection and direct study. My observations on the formation of the process of the egg shell of *Ginglymostoma* make clear when and how the long processes seen on the capsule of *Chlamydoselachus* are formed. Here let the reader note the twisted processes in the figures just referred to, and the tendriform holdfast organs seen on Garman's egg and on Dean's oblong specimens. The bluntly conical, the "finished" end, is the anterior, the older, the first formed; the twisted and the tendriform ends are the younger, posterior, or later formed. So also one can understand the formation of the very much frayed-out tendrill-bearing tips shown in Figures 13 and 14, plate I. The finished ends of the capsules plainly came through the shell gland first and quickly, while the tendriform ends came last of all, lingered and were then formed.

It is difficult to explain the formation of the three round egg cases and their short blunt processes at each end as portrayed in Plate I. However, the smaller process of the egg in Figure 6 was probably formed last. It seems likely that, in some way not clearly understood, each end of a round capsule, as it passed through the sphincter at the hinder part of the shell gland, remained in the orifice the same length of time and received the same treatment. And as a result the two processes of each capsule are practically identical. It would seem that had these eggs at the close of shell formation lingered in passing through the sphincter the posterior process would have become long-drawn-out as seen in the oblong capsules and as observed by me in process of formation in the nurse shark.

Thus the structure of the posterior or last-formed end of the egg capsule of *Ginglymostoma* with its abortive tendrill-like processes, affords a clue to and explanation of the formation not only of the curved finger-like process on the normal egg capsules of *Chlamydoselachus* but also of the aberrant tendriform ones of the atypical egg shells.

EXTERNAL EMBRYONIC DEVELOPMENT OF *CHLAMYDOSELACHUS*

In earlier parts of this paper I have discussed the breeding habits and have described the reproductive organs of the frilled shark. These sections are based on Dean's scattered but invaluable notes and upon the scanty literature. These studies have considerably extended our knowledge of the reproductive activities of this shark and have laid a foundation for a study of its external embryonic development. For this there is at hand practically nothing but the excellent drawings reproduced in the plates. In the almost complete absence of notes, all that can be done is to arrange the drawings in the order of development of the embryos and to describe these as accurately as possible, always comparing

each stage with the one just preceding it and noting the progress in development of various organs. Here I must acknowledge my indebtedness to Scammon's excellent work published in 1911.

EARLY DEVELOPMENT

Since the total number of gravid females (26) obtained by Dean was not large, it is not surprising that he secured very few fertilized eggs in early stages of development. None of these has been preserved intact, nor do I find among Dean's materials any blastoderms excised from the eggs and preserved in toto—either mounted or unmounted. My only information concerning this material has been derived from a few scattered notes, a small number of serial sections, and a few drawings—some in a more or less finished condition, others mere sketches.

BLASTULAE

Nishikawa (1898) is the only student of the frilled shark who has published any observations on eggs with early blastoderms. He states that "The blastoderm has a yellowish red color, as in other sharks. The earliest stage that I have been able to obtain was nearly circular in form and had a diameter of 1.3 mm". This is confirmed by my observations on the eggs of *Ginglymostoma*. The blastoderms were noted in 1912 as "yellow spots", always placed "asymmetrically on the egg, generally in the corners so to speak". In 1914 my notes read—"Blastoderms very small, even minute [unfortunately they were not measured], placed excentrically; in one lot of eggs from one female, 7 at one end, and one on one side of egg". These blastoderms in *Ginglymostoma* were so small that I found them only by their color. But when removed and placed under the microscope I could make out the cells.

This colored spot seems to be a characteristic feature of the eggs of the Elasmobranchii. Leydig (1852) was, so far as I know, the first to figure and describe the "orange-yellow spot" on an elasmobranch egg. On the egg of *Pristiurus melanostomum*, he found it at the end of the egg next to the rounded end of the capsule—i.e., that with short horns, the finished or older end of the egg shell of this oviparous fish. It measured c. 3.2 mm. in diameter. Balfour (1885, p. 222) also found this spot on the eggs of *Pristiurus*, on the ova of two species of *Scyllium*, and on the eggs of *Raja* sp. He states that these blastoderms were asymmetrically placed on the eggs of *Pristiurus* and *Scyllium*. Haswell (1897, p. 97) found the yellow spot at the broader (older) end of the egg shell of *Heterodontus philippi* of Australia. Dean shows this spot in his plates of the development of *Heterodontus japonicus*, which will illustrate Article VIII of this Volume. Haswell, in his preliminary report on the development of *Heterodontus philippi* (1897), says "The blastoderm in its earlier stages, appears to the naked eye, as in other Elasmobranchs, as a circular reddish orange spot around which is a narrow light yellow band. When this orange spot has attained a diameter of about 2 mm. it assumes an oval shape". Then Haswell generalized about this spot thus—"There can be little doubt . . . that the 'orange spot', which forms such a striking feature of the egg of an Elasmobranch in its early stages, has been handed

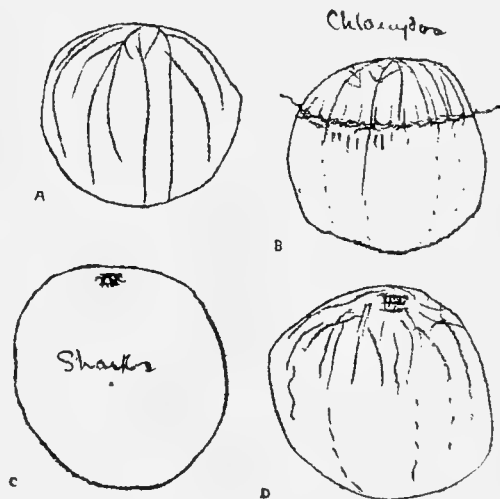
down with little change from Palaeozoic times". It is interesting to note the occurrence of this spot on the egg of that shark (*Chlamydoselachus*) to which systematists have assigned the lowest rank among recent elasmobranchs.

Nishikawa (1898) also had older blastoderms of *Chlamydoselachus*. He says "The next stage was a blastula, with a distinct segmentation cavity, whose floor was bounded by what has been termed 'periblast' with fine granular yolk, and merocytes with vacuolated protoplasm, due perhaps to the dissolution of the contained oil drops, and many nuclei. One end of the blastula was thicker than the other, and is evidently the 'embryonic end' of Balfour, and the 'anterior end' of Rückert". Unfortunately Nishikawa does not figure the blastoderm on the yolk, nor the entire blastoderm either in surface or sectional view, nor does he give the size to which it has grown. It is greatly to be regretted that Nishikawa did so little with this precious early material.

Text-figure 22

Diagrammatic sketches representing the cleavage pattern in four different types of vertebrate eggs: A, probably a hypothetical type ancestral to elasmobranchs; B, *Chlamydoselachus*; C, sharks; and D, a type reverting from the meroblastic to the holoblastic condition.

Sketches by Bashford Dean.



In Dean's notebook labelled *CHLAMYDOSELACHUS* there are in various places notes on eggs and embryos obtained during his two visits to Japan, or collected after each visit and sent to him in America. One paragraph is labelled "Material and List of Figures". Here I find "? Blastula", and on another page "Apr 10, 3 blastulae". He makes no specific mention of early blastulae—i.e., of early segmentation stages. Whether the alleged "blastulae" were in early or late stages is not known since Dean had no surface drawings made and since no preserved specimens can be found among his materials. If he had live eggs of *Chlamydoselachus*, perhaps he had the same trouble in finding early blastoderms that I had with live eggs of *Ginglymostoma*—i.e., that they were so small that he overlooked them, since these yellow spots would be obscured by the brownish-yellow capsules, as they were in *Ginglymostoma* by its thicker and darker capsules. This difficulty would be increased in preserved eggs since the "white" (a thin layer of glairy fluid) would be coagulated and some of the color of the germinal area would be destroyed by the preservative.

However, on still another page of his notebook, Dean lists and briefly describes two "Blastulae" one of which he states measured "44 mm." in diameter. These were "drawn" (Figures 4, and 6, plate I), but, since in the original drawings they measure 44 and 48 mm. in diameter, it seems to me that they were surely not blastulae but gastrulae. As such they will be discussed later.

As has been noted above, Dean went to Japan in 1900 particularly to get material for the embryology of the bull-head shark, *Heterodontus*. He obtained a large number of its eggs and embryos in various stages of development (including segmentation). On the egg of this shark, Dean published a short paper (1901.2) entitled "Reminiscences of Holoblastic Cleavage in the Egg of . . . *Heterodontus japonicus*". When he unexpectedly began to get embryological material of *Chlamydoselachus*, the shark assigned by systematists to the lowest position among the Elasmobranchii, Dean not unnaturally looked for similar reminiscences in its eggs. But, neither among his notes nor finished drawings is there any indication that he obtained eggs in early cleavage stages.

However, there is some slight evidence that Dean found something that made him suspect the possibility of holoblastic cleavage in the eggs of *Chlamydoselachus*. Among his rough pencil sketches I find a series of four diagrams comparing, in equatorial view, the cleavage patterns in eggs of four different types (Text-figure 22). The first (A) is moderately telolecithal but clearly holoblastic. This probably represents a hypothetical ancestral type. The second drawing (B) is labelled "*Chlamydoselachus*". It represents an egg with a large blastoderm (here defined as a mass of completely formed blastomeres) from which meridional furrows extend without interruption to an imaginary line drawn parallel to the equator and about 35° above it. If this line represents the margin of the germinal area, as it appears to do, then the size of this area is considerably exaggerated. Some of the meridional lines continue further, but are more or less broken. A few reach nearly to the vegetal pole. The third drawing (C) is labelled "Sharks"—evidently meaning typical sharks. It represents an egg with a very small blastoderm and no radial cleavage furrows extending beyond the margin of the mass of completely formed blastomeres. The fourth drawing (D), like the first, is not labelled. It portrays an egg with a small blastoderm from which many meridional furrows extend to the equator and some beyond it. Those that extend into the lower hemisphere are represented by broken lines. A few of these broken lines reach nearly to the vegetal pole. This drawing evidently represents a type of cleavage reverting from the meroblastic to the holoblastic condition. The cleavage pattern of *Chlamydoselachus*, as portrayed in the second drawing, bears some resemblance to that of *Cestracion* as figured by Dean (1901.2).

But are the lines crossing the margin of the germinal area really cleavage furrows? Among Dean's records I find three pencil drawings representing in greater detail the circular grooves shown in eggs C, B, and A (Figures 4, 5, and 6, plate I). These pencil drawings show very numerous fine lines crossing the groove in a radial direction. Because of the delicacy of these lines, these drawings are not suitable for reproduction. I have found similar lines at the margins of the germinal area in the nearly mature ovarian eggs.

Here, they are merely wrinkles in the very delicate vitelline membrane, probably due to shrinkage of the yolk mass during preservation in the mixture of formalin and alcohol. Unless examined with a lens, they might readily be mistaken for radial cleavage furrows. Some of the lines extend halfway to the equator of the egg. I find that Scammon (1911, Figs. 6 and 7, pl. I) shows similar radial wrinkles outside the blastoderm in early gastrula stages of *Squalus acanthias*. These I take to be identical with the very fine lines in Dean's sketches.

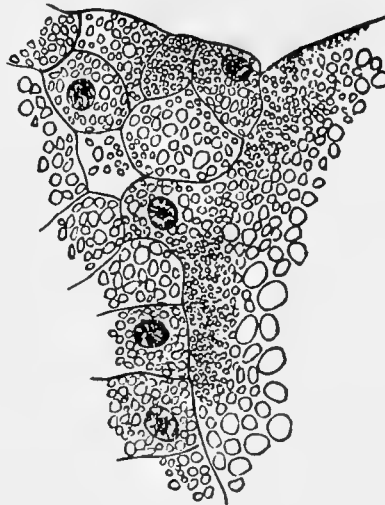
The germinal area of the egg of *Chlamydoselachus* (as outlined by the circles in Figures 4, 5, and 6, plate I) is unusually large. The question arises, how much of this area is occupied by the mass of completely formed blastomeres in the late blastula or early gastrula stages. In his description of egg C, a "blastula", Dean states that it (the germinal area?) shows segmentation over its entire extent. This segmentation might include radial furrows extending beyond the limits of the blastoderm proper. The only drawing which gives a comprehensive picture of the cleavage pattern is the one in the phylogenetic series (Text-figure 22), an equatorial view. In this, the blastoderm proper is not sharply defined. It is evidently larger than that of most elasmobranchs, but decidedly smaller than the germinal area in which it lies. Nishikawa (1898) states that the earliest stage (a blastoderm) that he was able to obtain was nearly circular in form and had a diameter of 1.3 mm. He mentions a later blastula, but does not give its size.

It is therefore clear that the blastoderm, in the narrow sense, occupies only a small central portion of the germinal area. If, during cleavage, the radial furrows extend to, or beyond, the margin of the germinal area, they must be extraordinarily long. I have mentioned the presence, in late ovarian eggs, of fine parallel wrinkles in the vitelline membrane, extending in a meridional direction and simulating cleavage furrows. My observations were made on eggs in preservative for more than thirty years and I have had no opportunity to examine eggs in the blastula stage. I do not know of any other shark, save only *Cestracion* (Dean, 1901.2), in which the radial cleavage furrows extend so far from the region of completed blastomeres.

Text-figure 23

Section through the margin of the blastoderm of an egg of *Chlamydoselachus* in a late blastula stage. This drawing probably represents the thicker end of the blastoderm in the same series used by Dean for the drawing reproduced in my Text-figure 24.

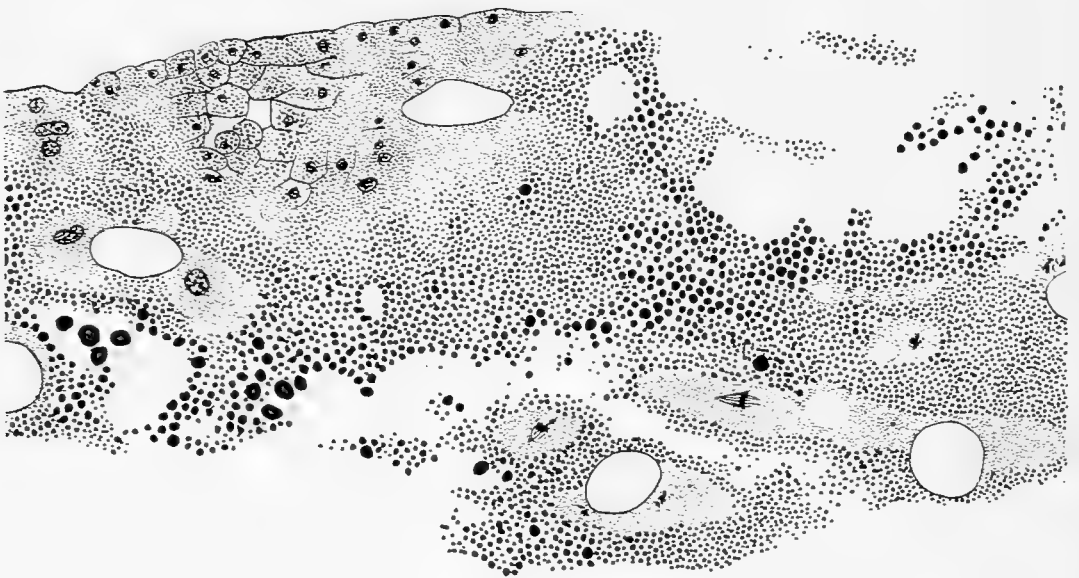
After Nishikawa, 1898, p. 97.



Nishikawa (1898) states that the yolk has a pinkish color. Presumably his observations were made on fresh material. In our specimens, in various stages of development but not including blastula and gastrula stages, the yolk is usually pale yellow but occasionally some portions are very pale pink. That Dean had live eggs with pink yolk is evidenced by his two drawings in color—Figures 49 and 50, plate V.

Among Dean's few *Chlamydoselachus* slides there are none of either whole mounts or sections of the blastula stage. However, there is evidence that, along with the other materials turned over to him by Nishikawa, there were sections of segmenting blastoderms. In one paragraph of his notebook are a number of rough outline sketches of sections of blastulae labelled "Nishikawa's Slides Early". Nishikawa (1898, p. 97) portrayed (Text-figure 23) without caption one edge of a segmenting blastoderm but never carried his studies further. Dean had these slides and drew a number of the sections.

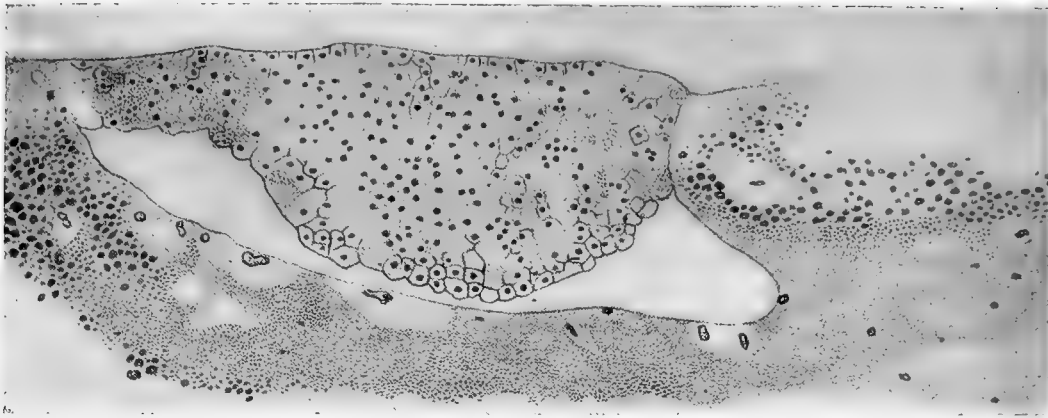
Among Dean's finished drawings are two, labelled *Chlamydoselachus*, which show sections through an early cleavage stage and a late blastula stage respectively. These are reproduced as Text-figures 24 and 25. The magnifications are not given, and the slides from which the drawings were made have been lost. There is nothing very striking about the mode of development portrayed, since it is typically elasmobranch; but Dean in his only publication (1903) dealing with the development of *Chlamydoselachus*—a brief note—calls attention to "the great depth of the zone of yolk nuclei". This is well shown



Text-figure 24

A section through the germinal area of a segmenting egg of *Chlamydoselachus* in an early blastula stage, showing the blastoderm (at left, above) and the broad and deep zone of periblast. At the left, about four-fifths of the lateral extent of the periblast has been trimmed off from the original drawing; at the right, one-fourth.

Drawing by Bashford Dean.



Text-figure 25

Median sagittal section (?) through the blastoderm, subgerminal cavity, and periblast of an egg of *Chlamydoselachus* in a late blastula stage. The zone of periblast is evidently not shown in its entirety.

Drawing by Bashford Dean.

in the early cleavage stage represented by Text-figure 24. Judging from Text-figure 25, the late blastula also is remarkable for the depth and breadth of the zone of yolk nuclei, which is evidently shown incompletely. Two other drawings of a late blastula, not reproduced, are very similar to the one shown in Text-figure 25, and were probably made from the same set of sections. These drawings all studied together indicate that in these early stages the extent of the germinal area is greater than the portion of it which is cut up into blastomeres.

It is my belief that all these drawings were made by Dean. On the boards on which they are mounted are notes in Dean's handwriting. The minute details in which the drawings abound are executed in Dean's characteristic style—according to his former students to whose attention they have been called.

The internal structure of the late blastula described by Nishikawa (1898, pp. 96-97) is evidently similar to the one studied by Dean and portrayed in my Text-figure 25. Indeed Dean's drawing was probably made from Nishikawa's blastoderm and from a section near the one shown in Text-figure 23. Nishikawa's description is as follows:

The next stage was a blastula, with a distinct segmentation cavity, whose floor was bounded by what has been termed "periblast" with finely granular yolk, and merocytes, with vacuolated cytoplasm, due perhaps to the dissolution of the contained oil drops, and many nuclei. One end of the blastula was thicker than the other, and is evidently the "embryonic end" of Balfour, and the "anterior end" of Rückert. On the surface of the blastoderm the cells are arranged epithelially. Most cells of the blastoderm are rich in yolk granules, but at the bottom of the blastoderm they have only a coarsely granular cytoplasm. The blastodermic cells are added from the periphery by the merocytes with fine yolk granules, as may be seen from cut 1 [Text-figure 23 herein] which has been composed from two consecutive sections. I have also found a cell simply resting on the floor of the segmentation cavity; but I cannot say for certain whether it originated from the periblast or from the blastoderm.

Dean's drawing (Text-figure 25) is made from a section cut parallel to the long axis of the future embryo. I wish to call attention particularly to the slight difference in the portrayal of the thicker margin by Dean and by Nishikawa. Dean represents the limit of the thickened end by a smoothly curved unbroken nearly vertical line separating the blastomeres from the region of pericytes. Nishikawa, whose drawing was made with a higher magnification, shows one of the embryonic cells incompletely cut off from the yolk mass (Text-figure 23). If this cell had gone on to complete separation, then the margins of the two figures would have been almost identical.

GASTRULAE

Earliest of all, Nishikawa collected but failed to figure and describe a gastrula of the frilled shark. Of his one egg he states—"I have also obtained a gastrula, which was oval in form and 3 mm. in length. I have nothing special to add about it as it was like the gastrula of any other shark". But was it? There is so much variability about *Chlamydo-*

Text-figure 26

Sketches from Dean's notebook. A and B—"Gastrulae 2 stages;" C one of "3 oblong eggs." For "2 drawn"—no gastrulae shown—see Figures 2 and 3, plate I. C was never "drawn," though labelled "probably gastrula."



Sketches by Bashford Dean.

selachus that one wishes for surface views and sections. To me this seemed very small for a gastrula and at first I was inclined to think that Nishikawa was in error, that no shark gastrula could be so small as 3 mm. in greatest diameter. But on looking up the literature I found that Ziegler (1902, p. 117) figures a gastrula of *Torpedo* 2 mm. long. And Scammon (1911) portrays gastrulae of *Squalus acanthias* 4.2 and 4.4 mm. long. Thus both Ziegler and Scammon give presumptive evidence that Nishikawa was correct.

On the page of Dean's notebook headed "Material and List of Figures", one finds this notation, "Gastrulae 2 stages", followed by two pencil sketches showing eggs with relatively large circles on them like those in Figures 4, 5, and 6, plate I. I have thought it well to reproduce these pencil sketches as Text-figure 26. Then on the page of the notebook on which Dean described the "3 oblong eggs", referred to later, there is a pencil sketch of an oblong egg with an incomplete ring placed asymmetrically (Text-figure 26), and having at the opposite end a tendril-bearing process. This egg is labelled "stage early, probably gastrula". Two of these "oblong eggs" were drawn and are identified and reproduced as Figures 2 and 3, plate I. Of the oblong egg with the gastrula, unfortunately no finished drawing was ever made.

On still another page of the notebook referred to is the heading, "Earlier stages, 3 eggs C. B. & A." Then follows brief descriptions of two which he thought were blastulae and of a third which he believed to be a gastrula. Here follow his descriptions:

[Egg] C [Figure 4, plate I]. Blastula shown in drawing (44. mm.) round. Shows segtn. over entire surface [of germinal area ?]—margin not good but at several places good transition from marginal blastomeres into central bl'ms. Not possible to trace furrows far down side of egg.

[Egg] B [Figure 5, plate I]. Bl. somewhat later than C, [germinal area 38 x 39 mm.]. Margl. blast. fine—surface blast. smaller and less conspicuous. At several points of marg. there are certain irregular folds of which none are (surely) gastrulation *erscheinungen* [manifestations].

[Egg] A [Figure 6, plate I]. Gastrula 44 x 48 mm.—drawn. No surface markings—except at margins as shn. in fig. [a pencil sketch in outline sectional view accompanies this note]—these continued sometimes over the marg. of yolk.

This is what Dean wrote and what is portrayed (half the original size) in Figures 4, 5, and 6, plate I. Egg A (the circle measuring 44 x 48 mm.), Dean thought to be a gastrula. Eggs B (circle 38 x 39 mm.) and C (circle, 44 x 44 mm.), he calls blastulae. If A, having the largest circle, is a gastrula, then, for all that I can see from the evidence at hand, B and C are not blastulae but gastrulae. Just here note that in C the germinal area (delimited by a shallow circular groove) is asymmetrically placed on the yolk. This asymmetry is like that noted for the third egg shown in Text-figure 26. Furthermore, it may be well to recall here that this is what I have found to be the general rule in the large eggs of *Ginglymostoma*.

Each egg, as represented in Figures 4, 5, and 6, plate I, has the germinal area marked off by a faint ring apparently representing a shallow circular groove. A similar groove bounds the margin of the germinal area in the preserved, half mature ovarian eggs examined and described earlier in this article. It is quite likely that this groove, if present in the living egg, would persist through cleavage and gastrula stages; or, if it is a fixation artifact, the same conditions would produce it in these stages. Balfour (1885, p. 222) found such grooves in living and sectioned elasmobranch eggs studied by him.

In these drawings (Figures 4, 5, and 6, plate I), the presence of the germinal area is indicated by faint circles only slightly darker than the remainder of the upper surfaces of the eggs. Indeed in eggs B and C, on one side the circle, as drawn, is so faint that it disappears into the general upper surface of each egg (especially B). Take away the circles and there would be nothing to indicate any germinal area. For another reason it must be noted here that one side of the ring is drawn more heavily shaded than the other. Balfour (1885, p. 225) noted this on his preserved material—"In sections of the germinal disc [of *Pristiurus*], the groove which separates it from the yolk is well marked on one side, but hardly visible at the other extremity of the section". What then did Dean's artist draw and how did he see anything to draw? If he drew preserved eggs, as is most likely, he drew the thickened edges of the blastoderms in early gastrula stages, more thickened on one edge than the other. This Balfour found as cited above and shows in a cross section of the blastoderm. These dark parts of the circles (Figures 4, 5, 6, plate I), I take to be the edges of the blastoderms wherein the embryos will be found later. In fixed eggs the thickened edges of the late blastoderms would show up more opaque than the inner and thinner regions.

But suppose that the artist had before him living eggs, would not the whole germinal area have the same color? The answer to this question is I believe to be found in my observations of living gastrula stages in the large thick-shelled intra-oviducal eggs of the nurse shark, *Ginglymostoma cirratum*. On some eggs examined on July 21, 1912, I found an orange-colored ring enclosing an area which covered one-fourth to one-third of the upper (or visible) side of the egg. This object was more plainly seen by cutting a window in the capsule over this colored ring and removing some of the glairy liquid surrounding the egg. Then, when a little sublimate-acetic was dropped on it, the whole blastoderm became visible with the beginning embryo in it. This was again seen on July 22, on an egg from another female. From another egg I got a "Blastoderm about the size of a silver dollar", and on another egg "Large blastoderm partly on top and partly on side of yolk". Another had "Blastoderm covering a little more than half the upper side of yolk, with one edge dipping over the side". On an egg examined on July 23, the "edge of the blastoderm was a rusty orange; embryo transparent and colorless, only visible when in motion". In the plates of the next article of this volume—that on the embryology of *Heterodontus*—will be seen the same orange-colored ring of a blastodisc embracing an area covering one-fourth to the whole of the upper visible surface of the 55-mm. egg with an embryo so small and transparent as to be almost invisible.

Thus the early gastrula stages of eggs of *Chlamydoselachus*, eggs alive or dead, were presumably seen as drawn in Figures 4, 5, and 6, plate I. If drawn alive at Misaki then the artist saw and drew the colored edges of the late blastodiscs. If the eggs had been "fixed", then it must be concluded that they were in early gastrula stages before embryos had been formed, but that as Balfour puts it "The embryonic rim is represented by a darker shading at the edge". Lastly it should be noted that these blastoderms in the gastrula (?) stages shown in the figure cited cover a substantial part of the upper surface of the eggs.

Finally, it must be said that if the eggs shown in Text-figure 26 are in the gastrula stage as Dean expressly states, then the three eggs portrayed in greater size and detail in Figures 4, 5, and 6, plate I, are also presumably in the gastrula stage. To me the sketches all show eggs in the same stage. Nothing in drawings or text differentiates them.

As noted at the beginning of this section, Nishikawa (1898) states that he obtained an early gastrula. This was sectioned and the sections were in 1901 or 1902 turned over to Dean. Among Dean's slides in my possession are five of serial sections of an early gastrula of *Chlamydoselachus*. I presume that these were sections prepared by Nishikawa and presented to Dean. In Dean's notebook are outline sketches made from these sections. The plane of the sections is oblique to the axis of the forming embryo and consequently these sections are not very favorable for study. In general the mode of development is like that found in other elasmobranchs.

LATER DEVELOPMENT

In this study of the frilled shark, my readers and I have now come to that part which perhaps holds the most interest since it is the most concrete—the study of the embry-

ology as portrayed in Dean's drawings. This perforce must be a study of the external development of the embryos from the smallest figured (11.5 mm.—Figure 15, plate II) to the largest (390 mm.)—shown in its life colors in Figure 49, plate V.

It does not lie within the scope of this article, as indicated by its title, to attempt any consideration of the internal development. To be sure, in my account of the blastula and gastrula stages I have included the meager information available concerning their internal structure. But Dean left neither notes nor drawings dealing with the early formation of the embryo and the development of organs. I have found a few serial sections of advanced embryos, but these are in poor condition. Therefore any consideration of the internal development would necessarily be limited to a review of previous contributions. In his article on the anatomy of *Chlamydoselachus*, Smith (1937) has included references to the scanty literature concerned with the development of organs, and has reviewed certain topics. It will suffice here to indicate briefly, for the convenience of future investigators, the contents of the few publications dealing with the organogeny of *Chlamydoselachus*.

RÉSUMÉ OF RESEARCHES ON THE INTERNAL DEVELOPMENT

Röse (1895) studied the teeth of a 340-mm. embryo. These teeth were not all in the same stage of development; therefore they afforded a graded series. Röse's observations indicate that the three large cusps of a typical tooth develop from separate anlagen; teeth are formed by the union of simple denticles homologous with placoid scales. None of the teeth studied by Röse had attained its final form.

Nishikawa (1898) figured four transverse sections through the head of a 32-mm. embryo in the region of Rathke's and Seessel's pouches; also a section through the "growing point" of a lateral line of the same embryo. He states that throughout the greater part of the lateral line there is a lumen, which is slit-shaped in transverse sections, but at the posterior extremity it is absent. In the anterior part, where the lateral nerve is in close contact with the anlage of the lateral line, the lumen opens to the exterior at several points. In this connection it should be stated that, as noted by various authors (Smith, 1937), in the adult the lateral line is open throughout almost its entire length.

Dean (1903) published a preliminary report on the embryology of *Chlamydoselachus*. The date of this paper comes after Dean's first visit to Japan, but before his second visit. Since this article is very brief, and constitutes Dean's only publication on the embryology of *Chlamydoselachus*, it is here quoted in full:

In view of the archaic features in the adult, he [Dean] noted as significant in the development of this form the great depth of the zone of yolk nuclei, the absence of external gills, the more nearly terminal position of the anus, the relatively smaller size of the head, the enormous spiracular cleft and the almost typically fin-fold type of limb. *Chlamydoselachus* has specialized in the line of producing large eggs, the largest indeed among recent animals, ostrich hardly excepted; that it was, however, until recently an egg-depositing shark is apparent from the character of the horn-like capsule (with rudimentary tendriform processes) which the egg still retains.

One may query Dean's statement concerning the absence of external gills. In Dean's own drawings, gill-filaments are shown projecting beyond the gill-flaps throughout the

advanced stages of embryonic development. It is probable that what Dean meant is that these external gill-filaments are merely temporary modifications of the gill-filaments that persist in the adult; also that they are not so long as they are in other embryonic sharks. This matter of external gills in both embryos and adults of *Chlamydoselachus* will be taken up fully in a later section of this paper. Hence it need not detain us here.

In his earlier article on the origin of vertebrate limbs, Osburn (1906) briefly mentions some features in the development of the skeleton of *Chlamydoselachus*. His later article (1907) on the same subject includes a more detailed consideration of the fin skeletons and pelvis, accompanied by some figures of these structures in a 225-mm. embryo.

Brohmer (1908) studied the excretory system of a 25-mm. young embryo of *Chlamydoselachus*. In the stage described, the pronephros is vestigial and the mesonephros is in an early stage of development.

Ziegler (1908) studied two embryos in the same stage, each 25-mm. long. His paper deals with the organogeny, particularly in the head region, with special attention to the "head cavities." These are cavities which, in elasmobranch embryos, occur in connection with mesodermal structures called "head somites," and are regarded as detached portions of the primitive coelomic cavity. For a further discussion see Smith, 1937, pp. 391-392. Ziegler was unable to find the anterior head cavity discovered by Platt in 1891 in certain other selachians, although he did find an anomalous cavity which he believed to be constricted off from the mandibular head cavity. Ziegler described also the infundibulum, Rathke's pouch, and the cranial nerves (reconstructed by his pupil, Brohmer).

Brohmer (1909) described in more detail the head somites in a 25-mm. embryo of *Chlamydoselachus*. Like Ziegler, he was unable to find the anterior head cavity described by Platt. Brohmer and Ziegler agree that there is but a single premandibular head cavity in *Chlamydoselachus*. Brohmer's contribution, like Ziegler's, includes a description of the cranial nerves of a 25-mm. embryo.

DESCRIPTIONS OF EMBRYOS FIGURED

On that page of Dean's notebook labelled "Material & List of Figures" is a list of embryos to be drawn. This list has been a partial guide for this section of the present article—partial only, because not all the embryos there listed were drawn, or if drawn some of the figures have in the long years since been lost. Then again the list is only partial because I find in the plates a number of figures not included in the list. Almost every drawing has noted on it the length of the embryo drawn, but some do not. These latter figures are rather difficult to locate in the series. Again other drawings with lengths indicated are not on the list. In addition to Dean's drawings of eggs and embryos, there have been introduced in their proper places, but as text-figures, a few illustrations of embryos described in external aspect by other authors. These fill in gaps in Dean's series and enable me better to show the progressive development of the external form of the embryos.

Owing to the complete absence of descriptive notes and the almost entire absence of material, the stages of development must be described as they are shown in the individual

drawings. Each figure will be compared point by point with the next younger in order to show the relative progress in development. Then so far as possible, comparisons will be made with embryos of *Squalus acanthias* of about similar size as portrayed so well in Scammon's "Normal Plates" (1911).

AN EMBRYO OF 11.5 MILLIMETERS

This is the smallest embryo listed and figured. It and two other small embryos (15.5 and 20 mm.) were taken "1905 Early January." Presumably all came from the same mother. If so, this shows that the embryos and eggs in a given uterus may be of different but closely related ages. This is to be expected since the eggs presumably ripen one at a time and are discharged from the ovary singly; certainly they pass one at a time into the oviducal funnel, are fertilized and encapsuled as they pass down into the uterus. Fertilization of these shelled eggs must take place before the capsule is formed. In *Ginglymostoma* I have taken segmenting eggs from the oviduct *above* the shell gland.

This embryo, seen in right lateral aspect, is labelled in the original drawing "Emb. C 11.5 mm.", and is shown in Figures 15 and 16, plate II. Figure 15 bears the notation " $\times 10+$ ", and in the original drawing it measures 121 mm. Figure 16 is drawn to larger scale. In length this embryo corresponds to Scammon's (1911) Fig. 24 of an 11.5-mm. *Squalus acanthias* shown in his pl. II. In development the two embryos are in about the same stage. As my Figure 15, plate II, shows, the frilled-shark embryo is attached to the large yolk sac by a short yolk stalk. In the original drawing this has an antero-posterior diameter of 10 mm. but in life of about 1 mm., which is the measurement for the cord of the 11.5-mm. *Squalus*. This is the "umbilical cord" of Nishikawa (1898). However, this is not an umbilical cord but merely a yolk stalk.

On the dorsum of this frilled-shark embryo (Figure 15, plate II), there is a convexity over the gill-arch region, a concavity over and behind the vertical of the yolk stalk, a slight convexity behind this, and a marked downward bend of the tail. The forebrain and midbrain make an angle of approximately 90° with the main axis of the body. The forebrain looks downward. The midbrain is delimited from the forebrain by a groove and superficially is sharply marked off from the hindbrain. The nasal groove, having its greatest invagination in front, is placed just below the eye. The optic cup is circular and without trace of optic fissure. The lens is prominent and circular in outline. The mouth is widely distended. The gill-plate is prominent, showing seven branchial grooves—the first indistinctly. Not all the grooves appearing in this region are branchial grooves. The second branchial groove appears to be forked, but the anterior limb is not a branchial groove as may be seen by comparing this drawing with Figure 16 where the gill-clefts are shown in larger scale.

The pectoral-fin rudiment is well-outlined for this early stage, and extends backward and downward, reaching some distance back of the hinder edge of the yolk cord. The cloacal elevation is quite prominent and in front of it is a slight swelling which I take to be the anlage of the pelvic fin. The tail ends in a point bent sharply downward. The V-shaped myomeres show faintly in the upper half of the trunk.

This same specimen was stained, cleared and drawn somewhat enlarged (to 161 mm.—x 14), apparently in order that the neuromeres and myomeres might be studied and counted. In this Figure 16, plate II, there is plainly seen between fore- and midbrain a small rounded body which I take to be the rudiment of the epiphysis. The neuromeres are divided into two sets of three each by a very short neuromere (?) which I do not understand. The auditory vesicle is prominent, standing over the bar between the second and third gill-clefts. From this vesicle to the end of the tail are 102 myomeres. This was noted in pencil on the original drawing. Plainly visible are six gill-clefts, the seventh being very faint. The heart is prominent—as is a large blood vessel, the vitelline artery, branching off from the dorsal aorta. The cloacal eminence is very prominent, and in front of it is a thickening which is presumably the rudiment of the pelvic fin. The fine line bounding the entire figure represents the superficial ectoderm.

AN EMBRYO 15.5 MM. IN LENGTH

The next drawing called for in Dean's "Material & List of Figures" portrays an embryo of this size in lateral aspect (Figure 17, plate II). This drawing is labelled "Emb. B 15.5 mm." on the drawing. This embryo agrees in length and in development very closely with Scammon's stage No. 26 (his pl. II), a 15-mm. *Squalus*. Dean's figure is marked "×10+" but in the original drawing it measures 177 mm. From the head, the back line slopes down to a point about over the yolk-stalk junction. Thence it runs backward almost straight to a point over the cloaca, from which region the tail bends down sharply. The forebrain together with the olfactory rudiment is prominent and is slightly upturned. The midbrain is large and bulges forward strongly. Thus the profile of the head of this embryo has a striking resemblance to that of a bulldog—though the parts do not correspond. The epiphysis is indicated by a slight swelling above the forebrain and in front of the eye. The optic cup and lens show some enlargement. The mouth still gapes widely.

The prominent bulge in front of the yolk is due to the presence of the heart. The pectoral fin is larger than that of the 11.5-mm. embryo. On the ventral surface of the body is a ridge, probably an evidence of the beginning of the gut. The cloacal swelling is very marked. In front of this is a thickening, presumably the anlage of the pelvic fin. Above the cloacal eminence, the straight dorsum slants downward as the tail. This ends in a curious upward hook like that found on the caudal extremity of a Boston terrier whose tail has been bobbed and the point bent upward.

In this 15.5-mm. *Chlamydoselachus* (Figure 17, plate II) the gill-arch region is very prominent. Some of the gill-arches appear crumpled. This crumpling is, I judge, an artifact due to shrinkage. In the dorsal portion of the branchial region, there appear three ridges that resemble incomplete gill-arches. Of these, the two anterior ones are probably not gill-arches but parts of the cranium, while the third is a portion of the first visceral arch. One notable difference between the 15.5-mm. embryonic *Chlamydoselachus* (Figure 15, plate II) and the 15-mm. embryonic *Squalus*, shown in Scammon's Fig. 26, pl. II, is that the little *Squalus* has at least one gill-filament projecting from each first, second and third slit, whereas these are entirely lacking in our embryo.

AN EMBRYO MEASURING 20 MILLIMETERS

The next drawing called for on the "List" is of this size. It bears the notation "Emb. A 20 mm." The original drawing is marked $\times 10+$ but it measures 222 mm. The drawing represents the embryo (in lateral view) as pulling forward on the yolk sac (Figure 18, plate II). There is fair correspondence between this embryonic *Chlamydoselachus* and Scammon's 20.6-mm. *Squalus* (his Fig. 28, pl. III). Compared with the 15.5-mm. embryonic frilled shark, the forebrain of the 20-mm. specimen is more prominent, the midbrain has become swollen laterally and is separated from the hindbrain by a constriction of its lateral and (morphologically) ventral surface. The dorsal line of this embryo, in contrast with the younger ones, runs almost straight to what is evidently the anlage of the dorsal fin—located just behind the vertical through the cloaca. The tail bends down sharply without, however, any upturned point as in the preceding stage. It is more like that in the 11.5-mm. specimen (Figure 15, plate II).

Returning to the head region, attention is called to the changed olfactory anlage and to the much enlarged eye. The mouth is somewhat less widely open than in the preceding stage. The gill-arch region is more prominent than ever. As in the preceding stage, some of the arches are in their lower halves sharply angled forward. There are eight distinct gill-arches with seven gill-clefts. The first visceral (the mandibular) arch forms the upper and lower jaws (palatoquadrate and Meckel's cartilage respectively). In the stage shown, with wide-open mouth, the jaws are open at an angle of about 90° . The ridge immediately behind the eye is probably not a branchial arch but a part of the cranium; likewise the two short ridges dorsal to the one just mentioned are presumably also eminences of the cranium.

The arch immediately behind the mandibular arch is the second visceral or the hyoid arch. Its dorsal half, lying immediately behind the protuberance of the skull previously mentioned, will give rise to the hyomandibular cartilage. This, in the adult, articulates with Meckel's cartilage at the angle of the jaw, thus helping to support the jaw. The first branchial cleft appears to be closed ventrally. Its dorsal portion, lying immediately in front of the dorsal segment of the hyoid arch, will become the spiracle. For the position and relations of the spiracular canal in the adult, see Smith (1937, Text-figs. 82 and 84). The other visceral arches (the gill-arches of the adult) are quite regular in form save for the crumpling already mentioned.

The bulge on the ventral surface of the embryo, immediately in front of the yolk stalk, is caused by the heart. The pectoral fin has become much broader and looks to be almost functional in a rudimentary fashion. The pelvic fin now shows clearly. The wart-like cloacal eminence is but little larger than that shown in the 15.5-mm. embryo. In front of it, the pelvic fin is clearly outlined. Back of it is the rudiment of the anal fin. The tail ends in a point sharply hooked downward. The somites are far advanced and now have the perfected zig zag shape faintly foreshadowed in the preceding stage—15.5 mm. (Figure 17, plate II).

Scammon's Fig. 28, pl. II, of his 20.6-mm. *Squalus* is further developed than Dean's 20-mm. *Chlamydoselachus*. The dogfish has all the fins, the pectoral being better de-

veloped. But most noticeable in the dogfish is a profusion of long gill-filaments coming out of slits 1-2-3, while shorter ones are to be seen in the spiracular cleft and the fifth slit. There is no indication of such filaments in the 20-mm. *Chlamydoselachus*, although the slits have apparently broken through.

TWO 25-MM. SPECIMENS—HEADS ONLY—DESCRIBED BY ZIEGLER AND BROHMER

In 1908, Paul von Rautenfeld brought to Germany from Japan a collection of zoological material, among which were three embryos of the frilled shark—two of 25 mm. without yolk sacs and one of 70 mm. with a yolk sac. These presently came to H. E. Ziegler for study. He figured and described (1908) one 25-mm. head in both lateral and ventral aspect. Then he cut sections of this and studied them as noted above. The other 25-mm. embryo and the 70-mm. specimen on its yolk sac, briefly referred to elsewhere, were turned over to his student, Brohmer. The latter deposited the larger embryo in the museum at Jena, but figured and described the head of the 25-mm specimen in dorsal aspect (1909). Then he sectioned it and studied it in comparison with like embryonic material from other sharks..

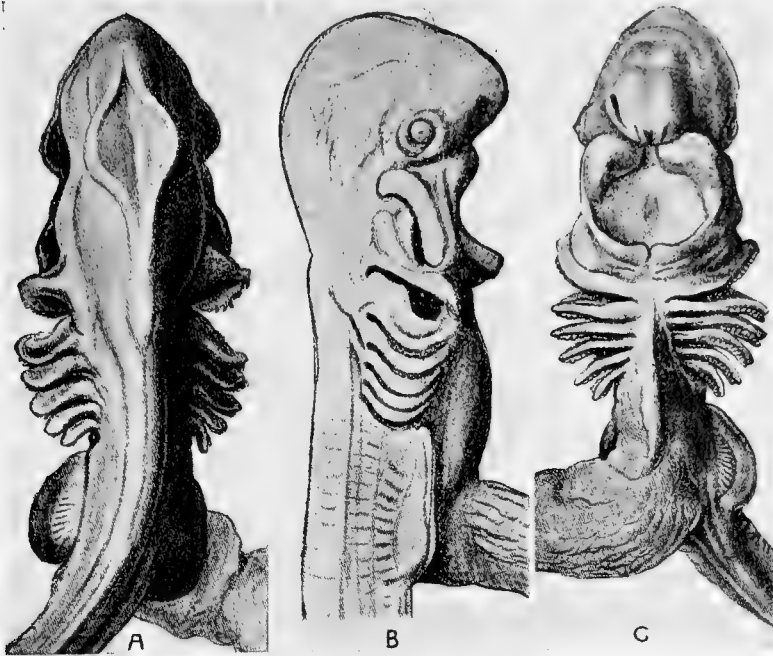
Dean's embryos above were all portrayed in lateral aspect only. The head of Ziegler's embryo was figured in lateral and ventral views and Brohmer's of the same size was portrayed in dorsal view. Since nearly all Dean's embryos figured are shown in all three aspects dorsal, lateral and ventral—these figures will be studied in that order. For this reason it has seemed well to begin consideration of the 25-mm. specimens by properly combining and studying the figures of Brohmer and Ziegler.

Head in Dorsal Aspect.—First let us consider Brohmer's figure (1909) of the head of the 25-mm. embryo seen from above reproduced herein as Text-figure 27A. Here the head seems to be pointed. The eyes are prominent, as are the spiracles. The gill-arches stand out widely—the first at about right angles to the body, the other five being directed obliquely backward. All have very short external gill-filaments. The pectoral fins show the beginnings of the basal cartilages. The most striking thing shown in this embryo is the transparent roof of the hindbrain—through which can be seen the floor with its median groove.

Ziegler (1908) figured the head of one of the 25-mm. embryos in both lateral and ventral aspects (my Text-figure 27). I will first give Ziegler's descriptions of his figures, and will then call attention to particular points. Ziegler wrote as follows:

Der weit geöffnete Mund ist jederseits von dem Kieferbogen begrenzt. Die Oberkieferwülste sind gross und lassen vorn median zwischen sich noch eine Lücke, an welche sich eine kleine mediane Rinne an der Unterseite des Vorderkopfes anschliesst. Auffallend ist die Grösse des Spritzloches und die ausserordentliche Weite der ersten echten Kiemenspalte. Die folgenden Kiemenspalten sind schmal und unter einander nicht viel verschieden. Bekanntlich gleicht *Chlamydoselachus* insofern dem *Hexanchus*, als 6 Kiemenspalten auf das Spritzloch folgen.

Hinter der letzten Kiemenspalte liegt noch ein kleiner Wulst, welcher die Kiemenregion abschliesst; an Fig. 1 wird er durch die letzte Kiemenplatte verdeckt. Dann folgt die vorder Extremität, sowie ventral der Nabelstrang.



Text-figure 27

Heads in three aspects (dorsal, lateral, and ventral) of two 25-mm. embryos of *Chlamydoselachus*.

A after Brohmer, 1909, Text-fig. 2; B and C after Ziegler, 1908, Text-figs. 1 and 2.

Head in Lateral View.—In addition to Ziegler's brief general description of the head of his 25-mm. embryo, comparison of it in this aspect (Text-figure 27B) should be made with the head of the 20-mm. specimen in lateral view (Figure 18, plate II). The head of the 25-mm. embryo is filled out and rounded with the forebrain pointing downward. The mouth still gapes widely. Brohmer (1909, Text-fig. 3) had a drawing made of his 25-mm. embryo in lateral aspect. This in its portrayal of the anterior visceral arches differs somewhat from Ziegler's figure of his specimen of the same size. It is difficult to understand the mode of development of the anterior visceral arches as portrayed in lateral view by these two investigators. Possibly their embryos were abnormal. However, in some ways they are related to what we shall find in Nishikawa's 32-mm. specimen.

In Ventral Aspect.—There is no like view of the head of the 20-mm. embryo available for comparison. This is our first description of the head of an embryonic *Chlamydoselachus* seen from below (Text-figure 27C). The snout-like forebrain stands out against the background of the larger rounded midbrain. The eyes and nasal capsules show faintly. The opening of the expanded mouth is about as broad as long. The halves of both upper and lower jaws are separated by fossae—the upper fossa is the wider. The gill-arches are distended, and short filaments are seen on their hinder sides. The pectoral-fin fundament shows traces of the basal cartilages. The yolk cord is large in comparison with the size of the body.

Scammon's drawing of his 24.7-mm. *Squalus* is in full-length lateral aspect only. When Ziegler's drawing of the lateral head of his 25-mm. specimen is compared with the head only of Scammon's *Squalus*, it is at once seen that the latter is more developed. Its gill-arches are more finished and are filled with a profusion of long external filaments. The spiracle is closed off and is also filled with filaments. Its pectoral fin, however, is in about the same stage of development as that of *Chlamydoselachus*.

NISHIKAWA'S 32-MM. EMBRYO—HEAD ONLY

The next stage called for in Dean's "List of Figures" for the development of *Chlamydoselachus*, is noted thus "Emb. of mm. 32—general view 2 figs.; head 3 pos'ns." No "general view 2 figs." can be found, but there are views of the head only, in dorsal, lateral, and ventral positions. These are reproduced as Figures 19, 20 and 21, plate II. But before describing them, I wish to set forth here a very interesting matter. Earlier in this article, I have expressed the belief that all Nishikawa's materials were turned over to Dean while he was working at Misaki and Tokyo. Nishikawa's brief article had been published in 1898 and in it he had figured the head of a 32-mm. embryo (his smallest specimen) in dorsal, lateral and ventral aspects. Dean had no specimens of his own between 20 and 34 mm. To lessen this gap in Dean's series of drawings showing the progressive development of the frilled shark, the figures of the head of Nishikawa's 32-mm. embryo were redrawn at the University (by Kuwabara ?) for reproduction by lithography. I have compared the two sets of three figures minutely and can affirm that they are identical.

But the reader may be wondering why Dean had Nishikawa's figures copied instead of having drawings made *de novo*. and why no full-length drawings are available as called for. The answer is to be found in Nishikawa's article (1898, pp. 98-99) wherein he figures diagrammatically and describes sections of the head of this embryo—it had been cut into sections in 1896.

Head in Dorsal Aspect.—The head of the 32-mm. embryo is seen from above in Figure 19, plate II. This head must be contrasted with that of the 25-mm. embryo portrayed in Text-figure 27A. The head in each figure is pointed. The curious outline on the head in Figure 19, plate II, is probably caused by the shrinking of the skin on the embryonic skull. In the 25-mm. head as drawn, the tissues are transparent and allow one to see the floor of the brain cavity. The 32-mm. head has the openings of the endolymphatic ducts which are lacking in the 25-mm. head. The former has the large spiracles seemingly placed higher on the head than those of the younger embryo. There are short filaments on both sides of the widely spread gill-arches of each head. The rudimentary pectoral fins are about in like stages of development in each embryo. On the whole the head of the 32-mm. specimen looks older and more perfected.

Head in Lateral View.—It is to be regretted that no full-length drawing of the 32-mm. embryo in lateral aspect is available for comparison with that of the 20-mm. specimen (Figure 18, plate II). One wishes to see what differentiation has taken place in body and tail as well as in the head. However, Figure 20, plate II, shows some interesting struc-

tures absent in the head of the 20-mm. specimen but found in the beginning stage in the 25-mm. embryo as seen in Text-figure 27B.

As Figure 20, plate II, shows, this 32-mm. specimen differs markedly in the head region from the 20-mm. embryo portrayed in Figure 18. The smoothly rounded fore- and midbrain vesicles are separated from each other by a cleft. The olfactory organ is well established, as is the eye which on the ventral side shows a trace of the optic cleft. The mouth is still widely open but far less so than in the 20-mm. embryo (Figure 18, plate II). The seven pairs of visceral clefts are open to the exterior and to the pharyngeal cavity, the second being the largest and the seventh (the sixth branchial cleft) the smallest. The first, the spiracular cleft, is almost closed off ventrally.

Further comparison of the 20- and 32-mm. specimens shows that the crumpled gill-slits of the 20-mm. embryo are in the 32-mm. head replaced by the more normal straight ones. All the clefts (including the spiracular) have external filaments in the 32-mm. head. It is interesting to note that the ridge immediately posterior to the eye in the 20-mm. specimen together with the hinder region of the upper jaw have here developed into a very prominent cheek-like process. The growth of this process apparently assists in the formation of the hinder part of the upper jaw and of the cheek region while at the same time superficially closing off the spiracle on its ventral side. It also assists in bringing the posterior end of the upper jaw in closer proximity to the hyomandibular element of the hyoid arch.

Let us now contrast the lateral view of the 25-mm. head shown in Text-figure 27B with that of the 32-mm. specimen portrayed in Figure 20, plate II. The 25-mm. head is more smoothly rounded. The eye has a fissure at its hinder edge whereas the other head has it in a ventral position. The mouth of the younger fish is more widely open. But most unusual of all are the curious structures around the spiracular opening. These I do not understand—possibly this specimen was abnormal. In any case these objects seem to be forerunners of the cheek pieces of the 32-mm. specimen shown so prominently in Figure 20, plate II. There is nothing unusual about the gill-arches and clefts of the 25-mm. fish save that the first is more widely open than that of the older specimen. Behind the seventh cleft on each head and almost over the yolk-stalk are the stubby pectoral fins. Faint traces of the lateral line are seen on each specimen.

Head in Ventral Aspect.—The drawing of the ventral aspect (Figure 21, plate II) gives one a clearer idea of the morphology of the organs on the sides and lower surface of the head. Note the head, blunt-pointed in this aspect, the prominent eyes, and also the kidney-shaped outlines of the nasal pits. The cartilages of the lower jaw have united, but between those of the upper there is still a gap. In the mouth behind this gap is a structure which Nishikawa, by sectioning this head, identified as Rathke's pouch extending back toward the infundibulum. In contrasting the 32-mm. head with that of the 25-mm. specimen in ventral aspect, it is seen at once that the former is much older and more "finished". Contrast the widely gaping round mouth of the younger fish, with its two median fossae, with the far more normal mouth of the older specimen. No further comment

is necessary. Note that in both heads, the isthmus grows progressively narrower from back to front. Short external filaments are found on each side of each arch.

Scammon's stage of *Squalus* nearest to this 32-mm. *Chlamydoselachus* is one of 28-mm. portrayed in full-length lateral, dorsal and ventral aspects (his Fig. 30a, b and c, pl. III). Since there is no full-length drawing of the 32-mm. *Chlamydoselachus*, comparisons are difficult. But comparisons of heads only show that this 28-mm. *Squalus* is much farther developed than the 32-mm. *Chlamydoselachus*. This is particularly true in the gill-region. The spiracular cleft of the dogfish is finished, and from it and the other clefts a profusion of long external gill-filaments protrude.

DEAN'S EMBRYO 34 MM. IN LENGTH

The "List of Figures" calls for "Embr. of 34 mm. Entire: head 2 other positions". And fortunately there are of this embryo a full-length drawing in lateral aspect (223 mm. long in the original) shown in Figure 23, plate II, and also dorsal and ventral figures of the head. Comparisons will be made of the head of this specimen in three aspects with the drawings of the head of the 32-mm. embryo. In addition comparison of the figure of the 34-mm. specimen in full lateral view will be made with the similar figure of the 20-mm. embryo.

Head in Dorsal View.—As may be seen in Figure 22, plate II, the head of this embryo contrasts strongly with that of the 32-mm. specimen. It is bluntly rounded and the eyes are less prominent. Let the reader contrast the markings on the head over the brain in the two figures. I do not understand them unless they are due to shrinkage of the soft tissues on the embryonic skull. Let the observer particularly note that the openings of the endolymphatic ducts are no longer visible. The spiracular openings are smaller. The gill-covers are less widely spread and in this aspect no filaments are seen in them. The pectorals are about as they were in the 32-mm. embryo.

Lateral Aspect, Head Only.—The head in this view (Figure 23, plate II) should be compared with the lateral view of the head of the 32-mm. embryo (Figure 20, plate II). The head of the 34-mm. embryo is more rounded. The eye still shows the choroid fissure. The greatest progress however is to be noted in the mouth and spiracle. The mouth begins to look somewhat like that of a shark. Most noticeable is the fact that the cheek-piece so conspicuous in the 32-mm. embryo (Figure 20, plate II) has here grown fast to the hyoid arch. The external opening of the spiracle is much smaller and is in line with the medial borders of the gill-slits. The first gill-slit is very large, and its arch and all the other arches show backward folds where they join the body above and the isthmus below.

Head in Ventral View.—In this aspect (Figure 24, plate II) it is noticeable that the nasal pits are smaller. The fossa between the cartilages of the upper jaw is much reduced, the mouth itself is less widely open than in the 32-mm. specimen (Figure 21, plate II), and is more adult in appearance. The reduction in width of the isthmus from the region of the sixth flap forward to the first is very noticeable. The distended first gill-covers

nearly meet across the isthmus, presaging the condition that suggested the name of our fish—the cloak-gilled shark.

Lateral Aspect, Full Length.—Comparison from this viewpoint of the 34-mm. embryo (Figure 23, plate II) with that of the 20-mm. specimen (Figure 18, plate II) shows clearly that both differentiation and growth have taken place. The head has rounded out and is almost protuberant, the mouth is almost closed and looks like a mouth. The gill-slits have lost the embryonic look even though short filaments are present. The paired fins show progress. The pectoral-fin base has some of the radial cartilages faintly shown. The pelvic fin is well differentiated. Even more differentiation is seen in the tail parts. Noticeable is the development of the dorsal and anal fins and of the dorsal and ventral lobes of the caudal (the latter lobe being better developed). This caudal, however, has an even more marked downward swing than that of the 20-mm. embryo. The original drawing of this figure measured 223 mm.

Comparison of this 34-mm. frilled shark in lateral aspect (Figure 23, plate II) with Scammon's 34-mm. dogfish in like aspect (his Fig. 31, pl. IV) shows that the dogfish is further advanced in development than the frilled shark. The fins (both median and paired) of *Squalus* are much better developed, and from its spiracles and gill-arches extend a great profusion of long external gills. Its lateral-line system is more prominent. The mouth of *Chlamydoselachus*, however, is far better developed than that of *Squalus*.

AN EMBRYO OF 39 MILLIMETERS

Of this specimen, Dean's "List" calls for drawings, "Entire in three positions". This is the first embryo of which there are three full-length portraits. There are four other embryos each drawn full-length in three aspects—dorsal, lateral, and ventral. For all five embryos, these full-length drawings will be studied in the order just noted, and the embryo in each aspect will be compared with the next younger embryo in the like aspect. Studied in such order one will get the most comprehensive view possible of each stage.

Dorsal Aspect.—The original drawing of this embryo measures 258 mm. and the magnification is 6.6. As seen in Figure 26, plate III, this is a trim-built embryo. The head is much rounder in front than that of the 34-mm. embryo shown in Figure 22, plate II, but it is still wide between the eyes. Forward of the first gill-flaps, are found the large spiracular clefts. The gill-folds are all well developed—the first markedly so. The pectoral fins are still in about the same stage of development as was found in the 34-mm. specimen. The pelvics, however, show up plainly alongside the slender body. The dorsal fin and the upper lobe of the caudal are faintly outlined.

Lateral Aspect.—In making this drawing of the 39-mm. embryo (Figure 25, plate II), the artist availed himself of artistic license to the amount of 10 mm. over the preceding figure—the original drawing measuring 268 mm. This specimen will now be compared with the 34-mm. fish in similar aspect (Figure 23, plate II). In the drawing it is seen that the head in front of the eyes has elongated somewhat. The olfactory organ has moved forward with reference to the eye—which no longer shows the choroid fissure. The

upper jaw has elongated beyond the vertical of the eye. The spiracle also has moved forward and slightly upward, and is now in the vertical of the angle of the jaw. The gill-straps are still angulate backward at their dorsal and ventral extremities. The first has the free edge irregular, as though it had been bitten. External filaments are found in gill-openings 1-4, but are still lacking in the spiracle. The pectoral and pelvic fins show little progress. The dorsal and anal fins, however, have grown larger. Contrary to what was found in the 34-mm. embryo (Figure 23, plate II) the caudal fin is bent upward but the soft parts of the fin seem little larger than they were in the 34-mm. fishlet.

Ventral View.—The original drawing of the 39-mm. embryo in this aspect is also 268 mm. long. This portrayal (Figure 27, plate III) is very instructive when compared with that of the head only of the 34-mm. fish in like aspect (Figure 24, plate II). The forehead is decidedly round. The edges of the olfactory pits are thickened, as if the valves are beginning to form. The eyes in this aspect are still prominent. The mouth is stretching forward toward the snout. The lower jaw has taken on something of the form found in the adult, and the upper jaw no longer has a fossa in the symphyseal region. The anterior part of the isthmus is broader in this embryo than in the 34-mm. embryo. The gill-arches all bear external filaments, those of the first slit being especially long—longer than they are shown in the lateral view (Figure 25), and longer than they are in the stages immediately following. The hindmost right gill-strap is curiously twisted. The stumpy pectoral fins show no progress, but the pelvics are well developed and the cloacal eminence appears between their hinder ends. Faintly outlined in the drawing is the ventral lobe of the caudal fin.

Brief comparison of the 39-mm. *Chlamydoselachus* may be made with Scammon's 37-mm. *Squalus*. In the latter, the fins are better developed. On the head the nasal pits are much more developed, and the latero-sensory canal system shows plainly. If present on *Chlamydoselachus* is it not shown in the drawings. The mouth of the frilled shark, however, is better developed. The embryonic gill-filaments of *Squalus* are profuse and long, some still coming from the spiracles. In *Chlamydoselachus* they are present in the gill-slits only, but are short and inconspicuous.

The figures of the 37-mm. *Squalus* are the last of Scammon's drawings made of specimens in the flesh. His other figures (text-figures) are reconstructions of serial sections of these embryos (portrayed in his plates I-IV). Comparisons with the drawings in his plates have been very instructive and helpful, and it is regretted that his series of plate drawings does not extend to older and larger embryos.

THE 39-MM. EMBRYO AND ITS YOLK SAC IN COLOR

Colored drawings were made of but three of Dean's *Chlamydoselachus* specimens—all shown on Plate V. Fortunately one of these is of the identical egg of which detailed figures have just been studied. This embryo and its yolk sac are beautifully portrayed in Figure 50, plate V. The embryo measures 39 mm. in length and the yolk sac 95 x 65 mm. The yolk stalk averages about 2.5 mm. in width and is about 7 mm. long. This long

and slender yolk stalk allows the embryo considerable freedom of motion. Embryo and egg are undoubtedly drawn in natural size. No mention of this figure is to be found in Dean's notebook.

Proceeding out from under the head of the embryo is the single vitelline artery, which, after traversing about 90° of the circumference of the yolk sac, divides into two. Coming in under the tail of the embryo is the vitelline vein which receives at right angles many tributaries. These are abundant in the proximal portion of the vein even to the point where it enters the yolk stalk. The complete circulatory pattern will be considered later when older stages are described. Note should be made of the pale pink color of the surface of the yolk mass. This drawing confirms Nishikawa's statement that "The yolk is of a pinkish color".

NISHIKAWA'S 43-MM. EMBRYO ON ITS YOLK-SAC.

There is no specimen of this size called for in Dean's list, but such an embryo is shown in his Figure 7, plate I. Here is the history of this egg as I have reconstructed it.

The egg with the 43-mm. embryo on it which Nishikawa figured in an outline pen and ink drawing (my Text-figure 4) was redrawn for Dean in pencil for lithographic reproduction, as may be seen by comparing the outline text-figure with Figure 7, plate I. This, I conjecture, was done not so much to fill in a gap in the series (there are no large drawings showing details of the morphology of this embryo) as to show the egg capsule and the yolk-sac circulation. Here it may merely be noted that the large unbranched vessel on the yolk is an artery, the much-branched one a vein. This specimen has already been studied for the structure of the capsule in the section on "The Encapsuled Egg". The yolk-sac circulation will be described later. Both original figures—text and plate—show egg and embryo in natural size. Even in figure 4 (reproduced natural size), the little fish is too small to show any details.

DEAN'S EMBRYO OF 46 MILLIMETERS

The "List" does not call for a specimen or figures of an embryo of this size, but I find carefully executed drawings in dorsal, ventral and lateral views. Moreover, two of these drawings are labelled in Dean's writing. Grouped with the three drawings, of the 46-mm. embryo are three each for embryos of 54, 66, and 103 mm. These drawings, all done in one technique by the same hand and mounted on a different kind of board, look to me to have been made more recently than any drawings thus far studied and more recently than single drawings of larger and older specimens to be studied later. All the older drawings of embryos both smaller and larger than these four are mounted on a poor quality of yellow cardboard, old, dog-eared, soft and crumbling. The drawings themselves are yellow with age and often spotted and dirty. These drawings are years older than the four sets referred to. The most tangible evidence of the technique of the newer drawings is found in the "window" in the eyes of the figures of these four sets of embryos. There is no evidence as to where and when they were made.

Dorsal Aspect.—The original drawing of this 46-mm. embryo seen from above measures 257 mm. (i.e., x 5.6). It is reproduced in Figure 28, plate III. When this drawing

of this embryo is compared with that of the 39-mm. specimen in the same view, it is seen that the larger embryo has a rounder and shorter snout with eyes somewhat less prominent and more normal. There are faint traces of the sensory canal system on the head. The spiracles are smaller, and are more dorsally situated—higher on the head. The gill-flaps are more widely distended than those of the smaller specimen. The external gill-filaments, lacking in this view in the 39-mm. embryo, are very noticeable especially in the first, second and third slits, and a few short ones are even found projecting from the spiracles. Both paired and median fins are better differentiated than in the 39-mm. embryo, and the artist has been able to portray in outline the dorsal fin and the soft dorsal part of the tail fin.

Lateral View.—Comparison and contrast will now be made of the 46- and 39-mm. embryos as seen in side view in Figure 29, plate III, and Figure 25, plate II. Where the 39-mm. fish is almost straight from head to dorsal fin, the 46-mm. fish has a depression in the vertical of the spiracle and angle of the mouth. Back of this the little fish is very sway-backed clear to the dorsal fin. The head of the 46-mm. specimen is shorter and more flatly rounded. The depth of the head is noticeably less than that of the 39-mm. fish. The nasal aperture is greatly reduced. Eye and mouth are both closer to the end of the snout, and the eye is very large. The spiracle is now a narrow slit seemingly not placed so high as it is shown in the dorsal view of this 46-mm. embryo. The first gill-cover seems either distorted or anomalous, unduly exposing the filaments of the first demibranch. The 39-mm. embryo has only short gill-filaments but in the 46-mm. specimen all the slits, but especially the first, have a profusion of slender external filaments—there are two projecting even from the spiracle. The paired fins are better developed than those of the younger specimen. Likewise dorsal and anal fins show much growth. Note that they look cut off squarely behind. The caudal fin is sharply bent down but the soft parts are developing well.

Ventral Aspect.—Seen from below (Figure 30, plate III), the 46-mm. embryo is very much like the 39-mm. one (Figure 27, plate III). The head is narrower and more rounded. This brings the nasal capsules and eyes closer to each other. The mouth has elongated somewhat. There is a remnant of a fossa in the median part of the upper jaw. This jaw is more heavily built and more sharply outlined than that of the younger fish. The mouth is still widely open and the lower jaw noticeably approaches the form of that of the adult. The gill-arches are widely distended and bear a profusion of external filaments. The isthmus is very narrow and the first pair of gill-covers is confluent over it. Thus first of all this embryo of 46-mm. justifies the name assigned this shark—*Chlamydoselachus*, the cloak-gilled shark. Lastly, the paired fins are much more developed than those of the 39-mm. specimen, and the cloaca shows conspicuously between the tips of the pelvics. The artist has also been able to show the anal fin and the lower lobe of the caudal.

The head of this 46-mm. embryo in both dorsal (Figure 28, plate III) and ventral (Figure 30, plate III) aspects seems entirely normal. But portrayal from the side shows a head which seems abnormal in every respect (Figure 29, plate III). One almost doubts if the three drawings were made from the same embryo.

HEAD OF A 48-MM. SPECIMEN IN VENTRAL VIEW

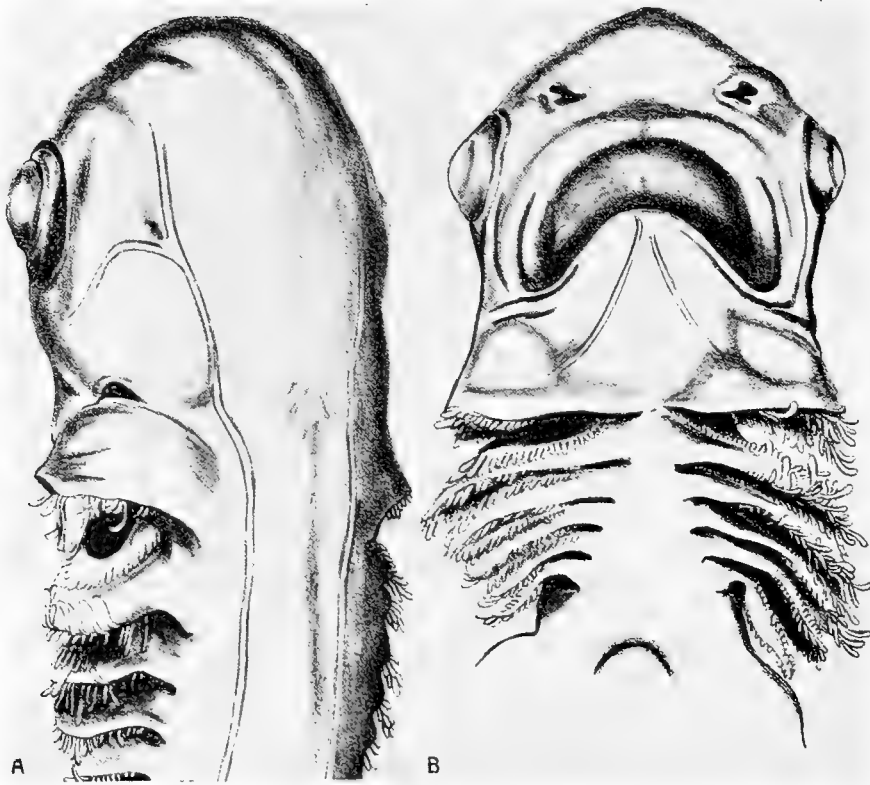
We now return to Dean's "List", which calls for "Embr. of 48 mm. ventral (head)" and on the opposite page is "48? Another, head only stained". Among the older drawings I find one without the figures "48" but with the significant label "head only stained". Moreover the drawing (Figure 31, plate III) shows this head in ventral view. From these data, and despite the fact that this "head . . . stained" in ventral view looks somewhat younger than the head of the 46-mm. embryo in ventral aspect and decidedly younger than that of the 54-mm. specimen (Figure 34, plate III), I believe that this head shown in ventral view is that of the 48-mm. embryo. Nishikawa had a 49-mm. specimen, and I believe that the "head only, stained" shown in Figure 31, plate III, is Nishikawa's specimen stained in toto (as was the practice in those days) but never sectioned.

Compared with the 46-mm. embryo (Figure 30, plate III), the head looks wider and more rounded, the eyes less prominent and the nasal organs better developed. The mouth is less advanced than that of the 46-mm. specimen. The upper jaw still has a definite median gap between the two halves, but the lower seems to be about normal for this stage. The gill-flaps are widely spread, especially the first pair—which are not continuous across the isthmus. Filaments seem to be absent, save in the first and second gill-slits on the right side. The pectoral fins are hardly so well developed as those in the 46-mm. embryo. The gular fold is lacking. That the 48-mm. embryo seems younger than the 46-mm. specimen is probably an individual variation.

NISHIKAWA'S 50-MM. EMBRYO ON ITS YOLK SAC

Nishikawa (1898) had a 50-mm. embryo of *Chlamydoselachus* on its yolk sac. He did not have either yolk sac or embryo drawn, but he does portray the head only in both dorsal and ventral aspects (Text-figure 28A and B). Whether Dean got a specimen of this size, through the help of Kuma or the commercial fishermen, cannot be said. But I suspect that Dean's drawings of egg and embryo (Figures 9 and 10, plate I) were made from Nishikawa's specimen. I have shown that Dean's Figures 7 and 8, plate I, are duplicates of Nishikawa's Figs. 1 and 2 of his pl. I. Here compare my Text-figure 4 with Figure 7, plate I. Now the capsules of the egg seen in Figures 7 and 9 plate I, are of the same type. Dean may have had eggs with capsules such as these, but, since no others of this kind are figured by him, I doubt it. In my judgment, the egg with the 50-mm embryo is the one listed by Nishikawa, and, since it had not been drawn for Nishikawa's article (1898), it was turned over with other specimens for Dean's studies.

On its Yolk Sac.—This 50-mm. embryo (shown in half size in Figure 9, plate I) is of course too small (even in Dean's drawing in natural size) to show any morphological details. It was probably drawn to show the capsule and the circulation over the yolk sac. The capsule has already been studied. It is a counterpart of that around the 43-mm. embryo and its yolk sac. The yolk circulation is somewhat more advanced than that on the yolk of the younger specimen. It will be discussed shortly. Fortunately the details lacking in Figure 9, plate I, may be found in Nishikawa's line drawings of the head (his Figs. 7 and 8, plate IV) which will now be considered.



Text-figure 28

Head of a 50-mm. *Chlamydoselachus anguineus* in two aspects; A in left-oblique dorsal view, B as seen from below.

After Nishikawa, 1898, Figs. 7 and 8, pl. IV.

Head Only, Dorsal View.—Nishikawa's drawing (my Text-figure 28A) was made in oblique-dorsal view. In it the front head is bluntly rounded. Being drawn in large scale, it shows the sensory canal system on the head with the lateral line extending backward onto the body. The small spiracular cleft is devoid of filaments. The gill-covers are distended (the first very widely) and abound in external gill-filaments—some of which appear to be longer than any thus far noted. It is difficult to compare this head with that shown in Figure 28, plate III.

Head Only, Ventral Aspect.—The 50-mm. head (Text-figure 28B) must be compared with that of the 48-mm. in the same view. The heads seem (as might be expected) to be in practically the same stage of development. The 50-mm. head is slightly more pointed. Eyes and nostrils show no perceptible divergence in the two specimens. Mouths are alike save that the upper jaw of this specimen has no fossa in the symphyseal region. The gill-arches are shown widely distended and, unlike those of the 48-mm. head, are filled with protruding filaments—those on the left side being the more abundant and certainly the longer. They are found on both sides of the five hinder arches. The gular fold is barely continuous across the isthmus.

AN EMBRYO OF 54 MILLIMETERS

In Dean's "List", the next call is for "Embryo of mm. 55. Entire—draw dorsal and ventral views [of head]". These drawings I find. But, in the plates of newer drawings of later origin (as noted above), I find three full-length drawings—in dorsal, lateral and ventral aspects—of an embryo labelled "54 mm." in Dean's writing. The full-length figures of the 54-mm. specimen will now be contrasted with those of the 46-mm. embryo. The figures of the 55-mm. fish (belonging to the older set of drawings) will be studied next. Each of the original drawings of the 54-mm. embryo measures 257 mm.—i. e. is multiplied by 4.7.

Dorsal Aspect.—When comparison of this drawing (Figure 32, plate III) is made with a similar one (Figure 28, plate III) of the 46-mm. specimen, the head and trunk are found to be notably larger. The fish is decidedly like an elongate tadpole. The latero-sensory canal system on the head is clearly seen. The first gill-covers are not so widely spread. From all the gill-slits profuse elongate filaments contrast with the shorter ones of the younger embryo. Then, too, from the spiracle protrude more and longer filaments. The pectoral and pelvic fins show decided growth, but in this aspect one cannot say about the dorsal fin and the upper lobe of the caudal. The body between pectorals and pelvics is relatively shorter than in the 46-mm. embryo.

Lateral View.—Marked contrasts may be drawn between the 54- and the 46-mm. embryos seen in lateral aspect (Figure 33, plate III, and Figure 29 on the same plate III). The 46-mm. fish is very sway-backed, the 54-mm specimen has a marked concavity in the neck region but behind this it is moderately hump-backed and has something of the look of the adult fish. The head is rounder and better developed than in any previous stage. The pits of the latero-sensory canal system are well developed over head and first gill-cover. The lower jaw has become greatly elongated and faintly recalls that of the adult. The almost vertical hinder edge of the first gill-cover contrasts markedly with the open U-shaped structure of the 46-mm. specimen—which is probably anomalous. The external gill-filaments are well developed. Some are found in the spiracle, which is much higher up on the side of the head than that of the 46-mm. fish. Both paired and unpaired fins of the 54-mm. fish are somewhat better developed than those in the younger one. The tail of the present fishlet is as much bent up as that of the 46-mm. specimen is bent down. Other than this, the tail regions are much alike.

Ventral Aspect.—Considerable contrast is to be noted when the two fish are compared in ventral view (the 54-mm. in Figure 34, plate III, and the 46-mm. fish in Figure 30 of the same plate. The head of the 54-mm. specimen is much broader as was noted in dorsal aspect. The eyes are larger, the openings of the olfactory slits smaller. The pits of the latero-sensory canal system show clearly. The mouth shows marked development—it resembles that of the adult but is still ventral in position. The first gill-covers form a wide cloak covering the isthmus. The gill-arches—standing out fairly at right angles in the younger specimen—are here bent somewhat backward. Every gill-slit is crowded with external filaments which reach their maximum development here. Trunk

and paired fins show some development, and anal fin and lower lobe of caudal are shown in wavy outline. As one would expect by referring to Figure 33, plate III (the lateral view), the dorsal and anal fins and lobes of the caudal are practically continuous. Along the mid-ventral line is a ridge which I take to be the beginning of the trophic folds. Note how much like a tadpole the little fish appears.

AN EMBRYO MEASURING 55 MILLIMETERS

As noted above, Dean's "List" calls for drawings of the entire embryo and dorsal and ventral views (presumably of the head) of an embryo of this size. These three drawings I find, but, since they look old and are mounted on discolored cardboard, I conjecture that they were made in Japan in 1901-02. They will be compared with the later-made drawings of the 54-mm. specimen. The full-length drawing of the 55-mm. embryo in lateral aspect measures 238 mm. ($= \times 4.3+$).

Head Only, Dorsal View.—It is now in order to contrast the head (Figure 35, plate III) of the 55-mm. embryo with the head of the 54-mm. specimen shown in full view in Figure 32, plate III. The 55-mm. head seems narrower but is rounded like the other, the eyes are a little further forward, and the sensory-canal system shows very indistinctly. The spiracles seem larger but show no gill-filaments. Nor are any filaments visible in the widely separated gill-arches. One queries why the 54-mm. embryo has and the 55-mm. one lacks these external filaments. Note that the pectoral fins of the 54-mm. fish have little hook-like spaces between fin and body, while these are lacking in the older embryo. In general it can be said that, contrasting the heads of two specimens, one gets the impression that the 55-mm. head looks more finished—i.e., older.

Full-length, Lateral Aspect.—The full-length lateral-view drawing of the 55-mm. specimen (Figure 36, plate III) will be contrasted with the like drawing (Figure 33, plate III) of the embryo of 54-mm. Naturally the differences between them are individual rather than of stages of development. The original drawing of the 55-mm. fish measures 238 mm. (i.e., $\times 4.3+$), that of the 54-mm. one measures 257 mm. (i.e., $\times 4.7+$). In the 55-mm. embryo, head and trunk are straight above and the head rounds off forwardly to a rather distinct snout. The nasal apertures are situated well forward almost in their definitive position. The lower jaw is not so long as that of the 54-mm. embryo. The lateral-line system shows plainly on the trunk but on the head is hardly so well-developed. The gill-covers (especially the first) are also hardly so well developed and the external filaments are not nearly so long as those in the 54-mm. fish. The spiracle of the 55-mm. specimen is higher on the head and contains several short gill-filaments. Of the fins, pectorals, pelvics and dorsal are about equally developed in both embryos. The anal fin is better developed and more sharply marked off from the lower lobe of the caudal in the 55-mm. embryo. The caudal fin droops, whereas that of the 54-mm. fish swings upward. Unfortunately the artist has used dark lines to indicate some grooves between somites, which thus appear like branches of the lateral-line canal.

Head Only, Ventral View.—Perhaps most instructive will be a comparison of the under surfaces of the two heads—the 55-mm. specimen in Figure 37, plate III, and

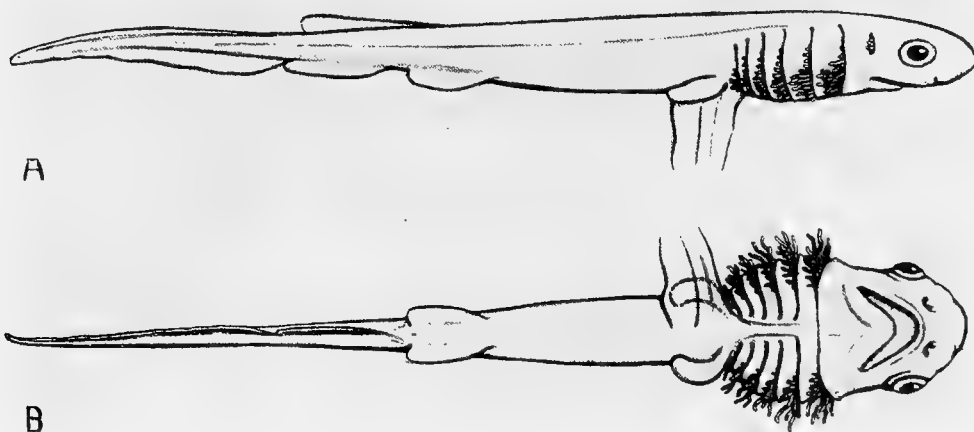
the 54-mm. in Figure 34, plate III. The head of the former looks decidedly older than that of the latter. The head in front of the mouth is shorter, and across the mouth region it is narrower. The nasal cavities are located well forward. The mouth of the 55-mm. fish looks less embryonic, older and better developed. The gill-arches are not so dilated and the filaments are, as noted above, entirely lacking. In both, the first gill-flap is continuous across the isthmus. The sensory-canal system on the under side of the head is well developed.

Here are two embryos differing in length by but one millimeter, but varying widely from each other. The morphological differences are principally in the head and mostly in the ventral head. In degree of development the mouth structures so differ that, on the basis of this one character with no others visible, one would separate these embryos as of two widely different stages. Whether this represents an actual difference in embryos of a shark whose variableness is greater than in any other known to me, or is due to a difference in artists cannot be said. Were the two embryos at hand, the matter might possibly be settled.

GARMAN'S EMBRYO OF 64 MILLIMETERS

When Dr. Thomas Barbour, now Director of the Museum of Comparative Zoology, Cambridge, Mass., returned in 1906 from a visit to Japan, he brought with him this embryo. It was figured but not described by Samuel Garman in 1913 (Figs. 7 and 8, pl. 61). For its historical interest and for the sake of completeness, Garman's figures (lateral and ventral aspects) are reproduced herein as text-figures and are described.

Lateral Aspect.—Comparison must be made of the 64-mm. embryo (Text-figure 29A) with that of 55 mm. (Figure 36, plate III). Excepting in the head region, the two



Text-figure 29

Two views (lateral and ventral) of a 64-mm. embryo of *Chlamydoselachus*.

After Garman, 1913, Figs. 7 and 8, pl. 61.

drawings show embryos much alike. The head of Garman's fish is thinner and is smoothly rounded down to the upper jaw. Dean's specimen is thick in head and gill-region and the head rounds steeply to the upper jaw. The mouth of the 64-mm. embryo is in about the same stage of development as that of the 55-mm. fish. The spiracle of Garman's fishlet is not so high on the head as that of the other embryo but is elongate vertically and has more gill-filaments protruding. There is some slight difference in the shape of the gill-openings, but both little fish are well supplied with external filaments. Remarkably alike are the fins, paired and unpaired. Both tails have about the same droop.

In Ventral View.—Garman's full-length figure of his 64-mm. embryo in this aspect is shown in Text-figure 29B. For adequate comparison we must turn to Figure 37, plate III, Dean's 55-mm. specimen in ventral head aspect. Garman's embryo has the mouth not quite so well developed, and the nostrils are not placed so far forward. The first gill-cover in each fish is continuous across the isthmus. Garman's specimen (Text-figure 29B) has a great number of short filaments protruding from each slit. Dean's fish has none showing in the figure in ventral aspect (Figure 37, plate III) although they are portrayed in the lateral view (Figure 36 on the same plate). As Text-figure 29B shows, the 64-mm. embryo has the pelvic fins well developed. Note the cloaca between their hinder ends. Anal and caudal show in the drawing. The pectoral fins and the yolk stalks look much alike.

These drawings (Text-figures 29A and B), made on a much smaller scale than Dean's, show few details. The specimen, loaned by Dr. Barbour, is before me as I write, and I can testify that the little fish is accurately drawn. The inclusion of Garman's figures herein help make the transition between the 54-mm. embryo and that now to be described.

DEAN'S EMBRYO MEASURING 66 MILLIMETERS

Third in the series of drawings of embryos noted above as being done by a different hand and at a later time, is the embryo under consideration. In the original drawings this 66-mm. sharklet is enlarged to 256 mm. (i.e., is $\times c$ 3.9). Seeking a younger embryo with which to compare it, I have made only secondary comparisons with Garman's 64-mm. specimen as being too close and because his figures show too few details. I have also passed over Dean's 55-mm. embryo which has but one full-length figure. Direct comparison will be made with the close neighbor of the 55-mm. embryo, the more typical 54-mm. fishlet, which like the present specimen, is portrayed in all three aspects.

Dorsal View.—Comparison of this 66-mm. embryo with the 54-mm. specimen—the former in Figure 38, plate IV; the latter in Figure 32, plate III—shows that the 66-mm. fish is plainly older. The front curve of the head is flatter, the eyes are prominent, the constriction back of the eyes is greater, but the sensory-pore system is hardly so clear. The gill-covers are widely distended, and there is still a profusion of external gill-filaments—but these are shorter and those in the spiracle are fewer. The differentiation in the trunk region, faintly foreshadowed in the dorsum of the 54-mm. fish, is here far more clearly

marked. This is to be seen all the way from head to the dorsal fin. Pectoral and (especially) pelvic fins show development. The dorsal fin is now clearly seen in the drawing and the upper lobe of the caudal stands out on the thicker vertebral part of the tail.

Seen from the Side.—More marked are the differences in the lateral views of the two embryos—the older (66 mm.) shown in Figure 39, plate IV, and the younger (54 mm.) in Figure 33 on plate III. The head of the older specimen is smaller and is curiously rounded. The eye is larger, the nasal groove has moved forward. The mouth is closed and the lower jaw is plainly longer. The spiracle is placed in about the mid-lateral line whereas it is above it in the 54-mm. fish. The first gill-cover has a ragged or frilled edge and seems retracted—as it is in the 54-mm. fish and (particularly) in the 46-mm. specimen (Figure 29, plate III). The gill-filaments in general are smaller, fewer and not so far protruded. The “back-of-the-neck” hollow seen in Fig. 33 has here become a great “sway-back” depression, giving the idea of a definite *neck* between head and body. The body is more humped than that of the 54-mm. embryo. The paired fins show growth. Dorsal and anal are larger and better differentiated. The tail bends gracefully downward. The ventral lobe is here sharply separated from the well-developed anal fin, unlike the close approximation seen in the 54-mm. fish. This is the earliest embryo showing the tail fin in approximately the adult condition.

Dean's 66-mm. embryo contrasts strongly with Garman's 64-mm. specimen. It has the top of head high and rounded. In the neck region it has a long “sway-back”, the body is decidedly arched, and the tail behind the dorsal-anal vertical bends down strongly. The dorsal region of Garman's fish (Text-figure 29A) is nearly straight, having at most very flat curves. Even more difference is to be found in the shape of the gill-flaps. Those of Dean's fish are convex posteriorly, save the first which has a frilled edge standing nearly vertical. For the rest—mouths, spiracles, fins, and tail-tips are very like each other.

In Ventral Aspect.—Seen from below (Figure 40, plate IV), the 66-mm. fish shows considerable development compared with the 54-mm. specimen (Figure 34, plate III). The head in front of the mouth is greatly shortened and more blunt. This has brought nares and eyes closer to the front of the head. The long mouth begins plainly to foreshadow that of the adult. The inner surface of the upper jaw is serrate, probably due to the presence of rudimentary teeth which have not yet erupted. Both upper and lower jaws are narrower in the transverse and longer in the sagittal plane—more like the adult. The head, back of the angle of the jaws, shows a marked constriction. The sensory-canal system is clearly portrayed. The gill-covers are still pretty widely distended, but with their outer edges bent toward the rear. The gill-filaments still protrude but less than in the preceding stage. The confluent first gill-covers form a convex U over the isthmus. Pectoral fins show little difference from those of the 54-mm. fish, but the pelvics are much further developed. The cloaca has become a longitudinal slit and on either side of its hinder end the abdominal pores make their first appearance. As in the 54-mm. embryo, so here, in the mid-ventral line is the rudiment of the trophic folds. The anal fin and the ventral lobe of the caudal are fairly distinct.

When Figure 40, plate IV (the 66-mm. embryo) is compared with Text-figure 29B (Garman's 64-mm. specimen), it is plainly seen that the two embryos are very much like each other. The heads are alike broad and blunt. The distance from the center of the upper jaw to the tip of the snout in the 66-mm. specimen is shorter than in the other. The first gill-covers in each are confluent across the isthmus—with a blunt backward central point in Figure 40, plate IV, and a straight line across in Text-figure 29B. Both heads in this aspect show a profusion of external gill-filaments in each gill-opening. In the 66-mm. embryo, there is seen the beginning of the trophic folds reaching from yolk stalk to cloaca. Nothing of the sort is to be seen in the 64-mm. fish.

AN EMBRYO 103 MM. IN LENGTH

This embryo, the last of the new lot of four drawn in three aspects, is about one and one-half times the length of the 66-mm. fishlet, but in the original drawing it measures approximately the same—257 mm. (i.e., $\times 3.9$).

Seen from Above.—The merest glance shows that this 103-mm. fishlet (Figure 41, plate IV) has advanced much over the preceding stage (Figure 38, plate IV). The head is smaller, more compact, more finished looking. The latero-sensory canals are well developed. The spiracles are so reduced in size that the external openings are barely visible. The gill-covers are far less distended than in the 66-mm. fish, and the filaments are somewhat fewer but generally longer. The paired fins show marked growth and the dorsal is somewhat in evidence.

In Lateral Aspect.—Seen in side view (Figure 42, plate IV) and in contrast with the like aspect of the 66-mm. specimen, it is apparent that the larger embryo has gone forward markedly in development. It now begins to look like the adult. Note the pointed snout and the long mouth with the fold above, marking off the jaw cartilage. Eye and nasal opening are in their normal positions. All the gill-covers are for the first time distinctly frilled. The external gill-filaments are still persistent. The lateral-line and head-canal systems are continuous. The fins, paired and unpaired, are well developed. The tail is straight and the lower lobe of the caudal has a faint notch near the tip. The little shark begins to look snake-like—*anguineus*.

Seen from Below. —In this aspect the 103-mm. fish (Figure 43, plate IV) looks more developed than does the 66-mm. embryo (Figure 40, plate IV). The head is narrower and more pointed. The mouth is slightly narrower and the lower jaw considerably longer—it distinctly recalls that of the adult. The gill-covers (especially the first pair) are seen to be frilled. They are less distended than those on the heads previously studied. The external gill-filaments persist and protrude. Both the paired fins, the pectorals especially, show much development. The cloacal opening looks as though it might be functional, and the abdominal pores are prominent. On the mid-line of the ventral trunk is the trophic ridge and on either side the somites show distinctly.

AN EMBRYO OF 124 MILLIMETERS

Having finished the study of the later-portrayed series of embryos shown each in three full-length drawings, we will now proceed to a consideration of some figures of

older embryos drawn at an earlier date and recorded in Dean's notebook. Here the "List" reads for the next stage—"Embr. of mm. 123 entire. Ventral (head) dorsal head". I do not find such figures, but I do find a full-length lateral drawing and another of a dorsal head, both marked "124". These drawings I take to have been made from the specimen referred to—the difference of one mm. being insignificant. Whether or not the "ventral head" was drawn cannot be said. But on the plates as made up by Dean, I find occasional scars on the board where drawings have been removed. It is of course possible that the drawing of the "ventral head" of this stage has been removed and lost. The drawings of the 124-mm. embryo will now be studied in comparison with those of the 103-mm. specimen—the preceeding stage.

Head in Dorsal Aspect.—When comparison is made of the drawing (Figure 44, plate IV) of the "dorsal head" of the 124-mm. embryo, with that of the head of the 103-mm. fish (Figure 41, plate IV), it looks older, more finished. The head of the 124-mm. fish looks longer and narrower, and the eyes are less conspicuous. The spiracle is not visible, being probably too small to show in this low magnification ($\times 2+$, the same magnification as Figure 45, plate IV, the fish in lateral view). The gill-covers are somewhat distended but reveal no trace of gill-filaments. The lateral-line system shows on the trunk but is indistinct on the head. The pectorals are smaller. One wishes for the drawing of the "ventral head" to show the form of the mouth and the ventral parts of the gill-covers, especially the first.

Full-length Lateral View.—It was noted that the 103-mm. fish, portrayed in lateral view in Figure 42, plate IV, showed some decided resemblance to the adult form. How much more is this true of the 124-mm. specimen seen in Figure 45, plate IV. Here the whole fish is plainly a young *Chlamydoselachus*. Note the pointed snout, the forwardly-placed nasal aperture, the eye in about the vertical of the middle of the mouth, the long lower jaw reaching close to the end of the snout. The gill-covers (the first much the larger) decrease in length normally from 1st to 6th, and have their dorsal edges backwardly bent as in the adult. No gill-filaments can be seen. The spiracle is not shown in this drawing, even though the original measures 257 mm. in length—i.e., $\times 2+$. The pectoral fin is much larger than that of the 103-mm. specimen, but the pelvic is of about the same size. The dorsal and anal are somewhat smaller than these fins are in the younger fish. The back is nearly straight from head to dorsal fin. The body has elongated, not in the tail region but in the body proper, i.e., between pectoral and pelvic fins. The tail ends in a fine-pointed caudal fin which droops slightly downward. The soft parts of the caudal fin are smaller than those of the 103-mm. fish. The lateral line is well developed and shows an interesting curvature behind the vertical through the tips of caudal and anal.

AN EMBRYO OF 175 MM. AND ITS YOLK SAC

The "List" next calls for "Embr. of mm. 175, entire, dorsal aspect with yolk". This I find as portrayed in Figure 11, plate I. In the original drawing, the fish, measured carefully over the curves, is 205-mm. long and the yolk sac measures 92 x 90 mm. On the page of Dean's notebook opposite the "List" is a record of seven specimens taken "April

25". Among them is a specimen of 205 mm. This I judged to be the specimen drawn and I concluded that it was drawn in natural size since the embryo of Figure 11, plate I measures 205 mm. around the curves. Furthermore, it seemed that a yolk sac 92 x 90 mm. would not be too large for an embryo of this size. But the figure bears in Dean's writing the notation "175" and the last embryo of the seven taken "April 25" is listed as "175" mm. So it seems clear that, in the original drawing, the 175-mm. embryo and yolk sac are enlarged 1.2 times. There is no drawing of the 205-mm. embryo.

Seen from Above.—The only embryo with which to compare this 175-mm. specimen (Figure II, plate I) is that of 124 mm. and of it the drawing of the head only (Figure 44, plate IV). The head of the 175-mm. fish looks distinctly older even though the remnants of external gill-filaments show in the arches. In contrast, the snout of the little 175-mm. fish is blunter than that of the 124-mm. embryo, the eyes far less prominent, and the gill-covers far less spread out. The presence of gill-filaments even though small, is not unusual since they are found in far older specimens as will be seen later. The pectoral and pelvic fins have a decidedly "grown up" appearance. Dorsal and anal fins are well developed and the lower lobe of the caudal looks very much like that of an adult. The tip of the caudal is bent downward and is devoid of a notch. The lateral-line system is clearly marked, and the latero-sensory canals and ampullae on the head are well delineated. On the trunk region, the lateral-line grooves appear to be connected across the dorsum by transverse broken lines drawn in white. These are like those shown in the tail-region of the 55-mm. embryo (Figure 36, plate III). They are surely inter-somitic grooves, not portions of the lateral-line system. This portrayal (Figure 11, plate I) shows the vitelline circulation in an advanced stage of development. It will be considered shortly. Altogether this is the most artistic drawing thus far found.

AN EMBRYO 185 MM. IN LENGTH

Dean's "List" calls next for an embryo of 185 mm. to be drawn full-length in lateral aspect without yolk. This drawing is reproduced herein as Figure 46, plate IV. The original drawing measures 185 mm., hence is natural size—the first of the embryos so drawn. This little fish looks very like an adult even though it was attached to the yolk sac by a yolk cord measuring 11 mm. in diameter. To see how far this embryo has progressed, it must be compared with the 124-mm. specimen (Figure 45, plate IV), seen in the same aspect. (The 175-mm. embryo cannot be used in comparison, since it is portrayed in dorsal aspect, and is moreover not drawn straight). The snout of the 185-mm. fishlet is more pointed (dorso-ventrally compressed); nasal capsule and eye are in their normal positions. The long lower jaw brings the mouth almost to the terminal position. The gill-flaps are nearly as normal as those of the fine 124-mm. embryo, which lacks the remnants of gill-filaments present in the 185-mm. fish. The body is humped and on it is a well-developed lateral line with latero-sensory branches on the side of the head, and with marked bends under the dorsal fin. Above the lateral line, the artist has inserted broken lines as if they were branches of the lateral line. They are spaced to correspond with the grooves between the myotomes immediately ventral to the lateral

line. The paired fins have well-developed bases. The dorsal and anal fins look much like those in the adult fish and even more is the caudal like the tail fin of an adult *Chlamydoselachus*. The trophic folds, noticeable in the 103-mm. fish, are here plainly visible.

Head in Ventral Aspect.—The list calls only for "Embr. 185 mm. lateral aspect". It does not call for ventral view of the head, but such a drawing I find. This is reproduced as Figure 47, plate IV. The next youngest head in like aspect with which it can be compared is that of the 103-mm. embryo (Figure 43, plate IV). Here one sees that the profuse external gill-filaments of the 103-mm. head are reduced to mere remnants in the gill-slits of the 185-mm. fish. Furthermore, the mouth of the older fish looks more finished, more nearly adult. The first gill-flaps are continuous across the isthmus. These flaps show some evidence of being "frilled". In the 103-mm. embryo, the yolk stalk has been cut off close to the body. In the 185-mm. fish the basal part is shown attached to the body. This is very large and I judge that here it is really part of the sac that is seen, that we have here the attachment of body to yolk directly comparable to that seen in the 390-mm. shark portrayed in color (Figure 49, plate V).

A YOUNG FRILLED SHARK 240 MM. LONG

The next embryo on the "List" is one of this size to be drawn in full length, lateral aspect, without yolk. This little fish was drawn slightly smaller (3 mm.) than natural size. As Figure 48, plate IV. shows, it is even more like the adult than is the 185-mm. specimen (Figure 46, plate IV). The long mouth has nearly attained the terminal position, nostril and eye call for no remarks, the gill-flaps are frilled and show short filaments in the openings. There is a small spiracular opening precisely in its adult location. All the fins are better developed and even more closely resemble the adult organs than those of the preceding stage. The lateral line runs the full length of the body and shows only very slight variations under the dorsal fin in contrast with both the 185- and the 124-mm. young. The little fish is still attached to its yolk sac by a cord 7 mm. in diameter. The caudal, like that of the 185-mm. fish, is slightly bent upward.

A 390-MM. CHLAMYDOSELACHUS IN NATURAL COLORS

Next and last, Dean's "List" calls for four embryos to be drawn. These were "taken about May 1, 1905", and were "Bt. in Tokyo, June 20". They measured in millimeters 317, 331 (yolk sac, 111 x 100), 352 and 390 (yolk sac, 100 x 90), and probably all came from one mother. However, since they were presumably twins and since the youngest differed from the largest embryo by only 38, and the others by 59 and 73 mm. respectively, it was clearly unnecessary to go to the expense of having all four drawn. So Dean seems to have compromised by having the largest specimen drawn *in color*. This exquisite drawing is accurately reproduced in the original colors as Figure 49, plate V.

It may be of interest to attempt to reconstruct the history of the specimen and of the drawing. Since the four embryos were "taken about May 1, 1905" and "Bt. in Tokyo, June 20", they must have been in preservative about seven weeks before they came into Dean's possession. Now Dean states (1901) that he had the active cooperation and

effective help of Prof. Mitsukuri of the Imperial University of Tokyo to the end that all specimens of *Chlamydoselachus* taken in the Gulf of Tokyo should be reserved for him (Dean). Hence one may judge that the fish had been taken by the fishermen to the Department of Zoology in the University, there opened and the embryos secured for Dean.

The original drawing (Figure 49, plate V) measures 382 mm. between perpendiculars, and the yolk sac is 92 x 70 mm. If the fish was drawn alive or just dead, the discrepancy of 8 mm. between its length and that of the largest of the four embryos listed above (390 mm.) may be disregarded, as it may for the discrepancy in yolk measurements (92 x 70 in the figure vs. 100 x 70 mm. in the notes). These may be errors of the artist. But I have shown earlier in this paper that embryos brought up within the mother from a depth of 300 to 500 fathoms, from a region of great pressure and low temperature, to the University of Tokyo in May, could only have survived a few minutes. Here then is what I judge to have been done when this specimen came in. A quick sketch in color was made while embryo and yolk were fresh. Then to preserve it, the fish was put in formalin (which bleaches out color less than alcohol). Later, and as soon as possible, the completed drawing was made—the size from the specimen in preservative, the color from the hasty color sketch. The embryo in preservative for a month would easily have shrunk 8 mm. The shrinkage of 8 mm. in the length of the long axis of the yolk is entirely within the limits as I have observed it in the large yolks of other fishes. To strengthen this case it may be noted that among Dean's frilled-shark materials there is a water-color sketch of the reproductive organs of a just-opened female *Chlamydoselachus* evidently intended as the basis of a figure in natural color. Unfortunately this drawing was never made or has been lost. But we do have here this beautiful drawing showing this late embryo, the yolk sac, and on the side of the egg the yolk-sac circulation, all in their natural colors.

There is in the Museum collection—it stands before me as I write—what I believe to be the very specimen from which the drawing (Figure 49, plate V) was made. The shape of the head and mouth, the fold across the snout above the upper jaw, the form and position of the gill-slits, the upturned pectoral fin, the form and position of the other fins and the tail, the irregularities in the lateral line, the shape and position of the yolk sac—all are practically identical. This is surely the fish from which the drawing was made. The fish, after at least 33 years in formalin and alcohol, measures 370 mm. in total length and the yolk mass 78 x 60 mm. But those who have had to do with specimens in preservative know that this decrease in the size of the fish is not beyond limits. However, the yolk has undergone even greater shrinkage than the fish. The ordinary fish-egg yolk shrinks considerably in preservative, but there is in the egg yolk of *Chlamydoselachus* an additional factor in its shrinking. There is in these yolks an unusual amount of oil which is dissolved out by the alcohol. This alcohol, even to this day, has to be changed frequently. This dissolving of the oil aids materially in the diminution of the volume of yolk as it hardens.

The likeness of this 15.35-inch embryo to an adult is close both in the general morphology and in the details. The mouth, reaching far back of the eye, is almost terminal and evidently has a great gape. There is the groove marking off the cartilage of the upper

jaw. The nasal aperture of the embryo is not yet completely divided into two. The gill-covers have pocket-like folds where they join the body. The first plainly extends across the throat—i.e., the isthmus and throat are “cloaked”. Note that there are visible very short gill-filaments. The body is humped above and on the ventral edge is seen one side of the tropeic folds.¹ Plainly visible is the latero-sensory canal on the first gill-cover and the lower jaw, and the lateral line extending along the body and the tail to its very tip—with the previously noted irregularities under the dorsal fin.

In this drawing, the artist has again inserted short dotted lines (in white) extending dorsally from the lateral line. These are more widely spaced than the zigzag intersegmental grooves seen along the sides of the body. Examination of the original specimen and of one but slightly smaller discloses that the intersegmental grooves above the lateral line are occasionally visible. Nothing in this region in this fish could easily be mistaken for branches of the lateral line.

The fins are very like those of the adult, including the well-formed caudal fin with the notch at the tip of the lower lobe—faintly presaged in the 103-mm. fish, but here seen plainly for the first time in this drawing of a large frilled shark embryo. What more can be said in description of this striking figure? The reader must study it for himself.

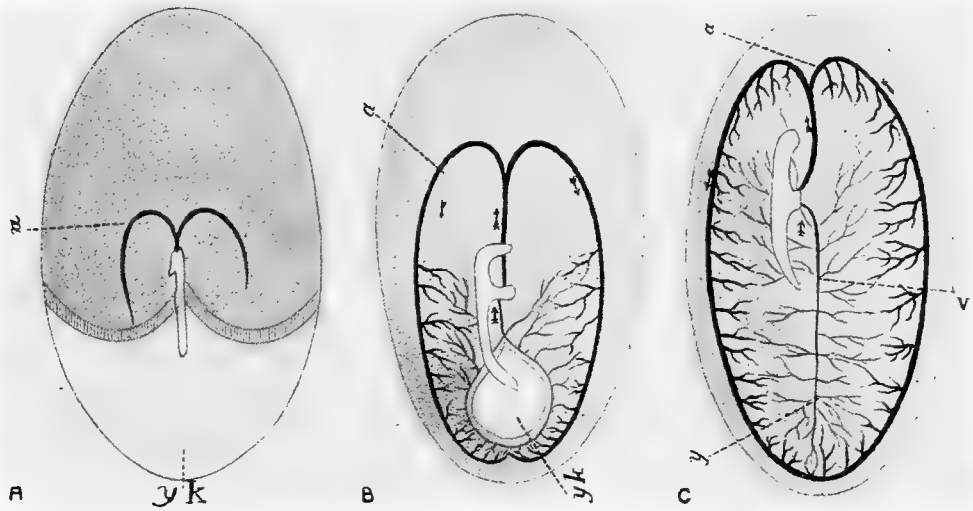
THE YOLK-SAC CIRCULATION

The vitelline blood vessels from small beginnings come finally to spread over all the large yolk sac of *Chlamydoselachus*. Their function is to bring food stuff to the developing embryo. These vessels have been briefly referred to earlier in this paper in describing certain embryos figured on their yolk sacs—the 39-mm. embryo (in color), the 43- and 50-mm. embryos and the 175-mm. fishlet (in gray), and lastly the 390-mm. shark (in color). The early stages of the development of this circulation are lacking in these drawings but the intermediate and later stages are shown. These portrayals are so informative as to call for special study.

Opportunities to study the yolk-sac circulation on the eggs of sharks occur very infrequently. In my investigations on live eggs and embryos of the sharks and rays elsewhere referred to, I was so occupied with other observations that those on the yolk-sac circulation were very incomplete. Dean's figures unfortunately do not show the early stages, so to make things clear, I refer the reader to Balfour's classical work (1885, pp. 465–466, pl. 9). In this he figures (diagrammatically) and describes the early circulation on the egg of *Pristiurus* essentially as it will presently be portrayed for *Chlamydoselachus*. Here is a synopsis of what he wrote.

As may be seen in Text-figure 30A, the blastoderm in this early stage covers about three-fifths of the yolk. The embryo is found in the bay of the blastoderm and from under its head extends forward the vitelline artery (*a*). This presently divides into two forks right and left and these are the beginnings of the arterial ring. In Text-figure 30B, it is

¹For data concerning this extraordinary structure, found in no other shark, the reader must turn to Gudger and Smith (1933, Article V of this Memorial Volume, pp. 283–284, Text-figure 12) by whom it is figured and comprehensively described.



Text-figure 30

Three diagrammatic figures showing the development of the vitelline circulation on the egg of *Pristiurus*. A is a beginning, C an intermediate, and D an advanced stage.

a, vitelline artery; v, vitelline vein, yk, yolk blastopore, y, (in C) marks the spot where the venous ring and yolk blastopore were closed by the growth of the blastoderm.

After Balfour, 1885, Figs. 1, 2, and 3, pl. 9.

seen that the blastoderm has grown over all the yolk save a central area (the so-called yolk blastopore, yk), forward of which the embryo is found. The two arms of the vitelline artery (a) are in the act of joining behind to form the arterial ring. These arms give off many small arteries on the inside of the hinder half of the ring. Surrounding the yolk blastopore, a venous ring has arisen in the edge of the blastoderm. From its anterior part, there has developed a main venous trunk which reaches to the yolk stalk. The venous ring receives many veinlets on its outer side.

In Text-figure 30c, the vitelline circulation has made much progress. The arterial ring is complete, has increased in size, and even in the anterior region gives off many small arteries. The yolk blastopore has disappeared, due to the complete enclosure of the yolk by the growing blastoderm. The letter y marks the point of closure of the blastopore. The venous ring has been replaced by the main venous trunk (v) which has grown not only longer but larger as it approaches the yolk stalk. With its many lateral branches, the vitelline venous system much resembles a tree. These veinlets receive blood from the arterioles, and the great venous trunk brings to the growing embryo much blood laden with food stuff.

With this brief explanation, let us now turn to Dean's drawing showing the earliest circulation on an egg of *Chlamydoselachus* found by him.

VITELLINE CIRCULATION IN THE 39-MM. EMBRYO

One of Dean's three drawings in color for the embryology of *Chlamydoselachus* portrays this embryo and yolk (Figure 50, plate V). In this the artist has shown the

proximal portions of both vitelline artery and vein. The artery extends out from under the head of the embryo as a single vessel until it forks narrowly into two branches before passing over the equator of the egg. The dendritic system of vessels under the tail of the embryo is venous and laden with food absorbed from the yolk mass. This circulation on the upper side of the egg carrying the 39-mm. embryo is essentially like that portrayed on a flat surface by Balfour (Text-figure 30). Unfortunately there is no drawing showing the relation of arterial and venous vessels on the opposite side of the egg of this 39-mm. *Chlamydoselachus*. For this we shall have presently to go to the drawings of the 43-mm. embryo and its yolk sac.

Arterial and Venous Trunks in the Yolk Cord.—Inspection of the yolk cord of the 39-mm. embryo (Figure 51, plate V) shows that the artist has not differentiated the trunks of artery and vein in the cord. They are not portrayed in the 43-mm. specimen (Figure 7, plate I). In the 50-mm. embryo the arterial and venous vessels are plainly shown in the yolk stalk (Figure 9, plate I), but (as in the 39-mm. specimen) they are not distinguished from each other. Probably they run side by side and are too small to be shown separately in these drawings made in this small but natural size. In the 175-mm. fishlet (Figure 11, plate I) the yolk cord cannot be seen due to the position of the wide head. Probably it is too short for the yolk-cord trunks to be seen, as is the case in the 390-mm. shark (Figure 49, plate V).

YOLK-SAC CIRCULATION OF THE 43-MM. SPECIMEN

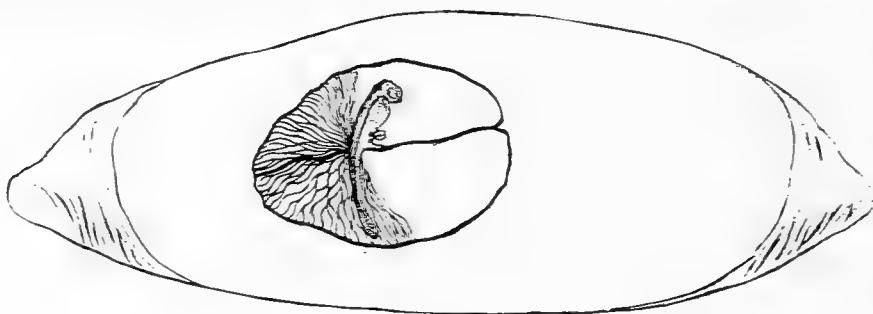
This is the only embryo and egg of *Chlamydoselachus* whose vitelline circulation has previously been described. This was done by Nishikawa (1898, p. 97) who had at least six eggs with young embryos (32–60 mm. long) but he seems not to have been aware of the studies of his predecessors—not even of Balfour's well-known work. Had he consulted this author, he surely would not have made such errors as fill his page and give point to Balfour's remark (1885, p. 465) "The observations recorded on the subject [the circulation of the yolk-sac in sharks] are, so far as I am acquainted with them, very imperfect, and in most cases the arteries and veins appear to have been transposed". What our Japanese author wrote illustrates this point.

The circulation in the yolk-sac could be clearly traced and is reproduced in Figs. 1 and 2 [my Text-figure 4, and Figures 7 and 8, plate I]. On leaving the umbilical cord [yolk cord] the artery and vein run in opposite directions. The former receives on its course a number of smaller veins from the two poles of the yolk-sac, and divides finally into three main branches. The artery runs for some distance without giving off any branch, and then divides into two main vessels, which, after running for a short distance parallel to each other, form at last, on the opposite side of the yolk-sac, an elongated, irregularly shaped arterial ring, from which numerous small vessels radiate toward the periphery. The arterial ring just mentioned is still wide apart in the embryo of 32 mm., but in one of 43 mm. its two halves almost touch each other [Figure 8, plate I], but in other respects there is no change in the circulation.

Nishikawa's description contains many errors. An attempt was made by the present writer to correct these by insertions in brackets, but when done the resulting paragraph was so conglomerate and confusing that it was discarded. It has seemed best to quote just what Nishikawa wrote, and then to describe in my own words the cir-

ulation as shown in Dean's drawings (Figures 7 and 8, plate I). The reader can then compare the two statements and detect the errors.

Circulation on Dorsal Surface of Yolk Sac.—As explained above, Dean had Nishikawa's figures redrawn for reproduction by lithography. It may be seen in the line cut (Text-figure 4) and in the copy (Figure 7, plate I) that the 43-mm. fish has considerable freedom of movement on its yolk sac, as is shown in the position of the artery under the tail of the reversed embryo. This artery is unlike that of the 39-mm. embryo (Figure 50, plate V) in that it gives off on the left side one small quickly bifurcating branch, but is like the former in that the main artery divides into two just where it passes over the equator of the yolk mass. The venous system on the embryonic side of this egg shows much growth and differentiation over that of the 39-mm. embryo portrayed in Figure 50, plate V. In the hinder and lower segment of this half of the yolk, the dendritic arrangement of the venous system shows about as in the 39-mm. embryo. But in the region just posterior to the yolk stalk, large veins on each side empty into the main trunk.



Text-figure 31

The egg of *Acanthias vulgaris* in its horny case. This is the earliest figure found portraying the embryo and its vitelline circulatory system. For explanation see caption to Text-figure 30.

After Leydig, 1852, Fig. 6, pl. III.

The oldest figure known to me portraying the circulatory system of a shark (*Acanthias vulgaris*=*Squalus acanthias*) is that by Leydig (1852, Fig. 67, pl. III) shown in my Text-figure 31. Here the vitelline artery branches at the edge of the blastoderm and forms the arterial ring (his "sinus terminalis"), which gives off many branches behind. These communicate with the developing venous system whose main trunk enters the yolk stalk from the rear. This figure portrays a circulation intermediate between that of Dean's 39- and 43-mm. embryos.

Circulation on Ventral Surface of Yolk.—The blood-vascular system on the ventral (lower) side of the egg carrying the 43-mm. embryo will now be considered. It is unfortunate that there is not at hand at least one figure showing in an earlier stage the development in *Chlamydoselachus* of the yolk-vascular system on this side of the egg. As shown in Figure 8, plate I, the bifurcating vitelline artery, just below the equator of the egg, has formed the arterial ring, which shows a number of striking irregularities. The

ring has contracted until now only about one-fifth the area of the yolk mass is not covered by the arterial system. The ring gives off a multitude of branches or small arteries on its outer side. These communicate by capillaries with the forming venous system as Figure 8 shows. As may be seen on the lower side in Figure 8, all the veins on this side of the ring are gathered to form the great vein entering the yolk stalk under the tail of the fishlet—if it were drawn in its normal position. The small veins formed on the upper side of the arterial ring (Figure 7) empty from both sides into the main vein just before it enters the yolk stalk.

VITELLINE CIRCULATION OF THE 50-MM. EMBRYO

Since this little fish is but 7 mm. longer than the 43-mm. specimen, its yolk-vascular system might be expected to be in about the same stage of development. However, on the dorsal surface (Figure 9, plate I), the artery, which is under the tail of the rotated embryo, shows six small branches before its main trunk passes over the equator of the egg to form the normal bifurcation. The venous system on the upper side of this yolk is far better developed than that of the younger embryo (Figure 7, plate I), the whole hinder surface of the egg being thickly covered with small veins.

In ventral aspect (Figure 10, plate I), it is seen that the arterial ring is in about the same stage of development as is that of the 43-mm. specimen (Figure 8, plate I). Notable is the fact that the irregularities of the two rings are almost identical. Here there is the same profusion of small arteries radiating outward from the ring, but not a single one on the inside.

So far as I can find, the earliest portrayal of the closing arterial ring on the ventral surface of an elasmobranch egg was made by Wyman (1867, Fig. 3, plate 1). On the yolk of a rapidly developing embryo of *Raia batis* in the selachian stage, the ring has nearly closed, and the yolk-sac circulatory system is in about the stage of that shown in Dean's Figures 9 and 10, plate I, for the 50-mm. *Chlamydoselachus*.

YOLK-SAC CIRCULATION OF THE 175-MM. FISH

Little can be seen of this on the dorsal side of the egg (Figure 11, plate I). Venous blood vessels seem to cover this side of the yolk pretty thoroughly. On the fish's right is a large vein which may be the principal one going into the yolk stalk. On the ventral surface (Figure 12, plate I), it is shown that the arterial ring is breaking up. Only parts of the original artery are seen and these for the first time give off branches on the *inside* of the ring as well as on the outside. The yolk-sac circulatory system of the 175-mm. embryo has plainly reached a high stage of development, and the growth of the little fish must go forward much more rapidly than ever with the incoming of larger amounts of food materials.

VITELLINE CIRCULATION OF THE 390-MM. SHARK

Compared with the circulatory system of the 175-mm. shark, this stage is noteworthy for the complete absence of the arterial ring. We see extending out under the head of the fish one long arterial trunk which breaks up into a multitude of branches. Hence it is

a reasonable conclusion that the disintegration of the ring, seen in process of going to pieces in Figure 10, plate I, has gone on to completion. Not enough of the venous system is shown to justify description.

Although, as stated above, I have never been so fortunate as to study the progressive development of the yolk-vascular system on an elasmobranch egg, I have done so on the large-yolked 20-mm. egg of the gaff-topsail catfish, *Felichthys felis*. Here was found the same artery coming out from under the head of the embryo, bifurcating to form the arterial ring. Then a venous system developed as in the sharks, with a main trunk coming in under the tail of the embryo. The closing of the arterial ring was very like that in elasmobranchs.

THE ADULT CHLAMYDOSELACHUS ANGUINEUS

At the head of Dean's "List of Figures" is this notation, "Adult—natural color" and on the line below "Adult—photo of head, lat. & ventral". The photographs—old, dark, and faded—I find. But, instead of a drawing of an adult in "natural color", I find drawings of two adults—a male and female shown in lateral aspect—and two drawings of the head, in dorsal and ventral aspects. The drawing of the head in lateral aspect was not needed since both adults were portrayed in this position. Presumably these specimens are shown in "natural color".

These figures are all reproduced on plate VI, which has been reserved for the adult stage. With the reproduction and description of these drawings, the life history of *Chlamydoselachus anguineus* as portrayed in Dean's drawings and recorded in his fragmentary notes will have been adequately figured and followed, and we will then have seen how correctly Samuel Garman named it the cloak-gilled snake-like shark.

AN ADULT FEMALE FRILLED SHARK

Such a *Chlamydoselachus* is portrayed in what is presumably natural color in Figure 52, plate VI. There is no record of its length and no indication as to the scale on which this figure is drawn. The original drawing measures 603 mm. to the broken-off tip, and with the tip completed—614 mm. (24.2 in.). A glance at the plate shows that the drawing of the female (614 mm.) is longer than that of the male (538 mm.) by 76 mm. (about 3 in.). This is to be expected. The female (shark or bony) fish is generally larger than the male. Gudger and Smith (1933, pp. 262–263, Tables IV and V) were able to record the lengths of 35 female specimens of *Chlamydoselachus* ranging from 610 to 1960 mm. (24 to 77.2 inches)—and averaging 1532 mm. (60.3 inches). They could find measurements for only 15 males. These ranged from 920 to 1650 mm. (36.25 to 65 inches) and averaged 1293 mm. (50.9 inches). However, one has to see the tables (Article V. of this volume, pp. 262–263) to have it made clear that the females uniformly run larger than the males. The largest male measured 1650, the next one but 1474 mm. There are 16 females ranging between these limits of the males, and there are 10 females ranging between 1670 and 1960 mm. The females average considerably larger than the males. This is

because the females must have body and blood to manufacture the huge ovarian eggs, and must have a larger body-space to carry during the long gestation period the 8 to 12 eggs and embryos such as are portrayed in Figure 49, plate V.

A mere glance at Figure 52, plate VI, shows a long and slender shark whose head and body from snout to pelvic fin are of approximately the same diameter throughout. This uniform size of body surely enables *Chlamydoselachus* to creep through the interstices of debris at the bottom of the sea that would stop any other shark and almost any large teleost other than an eel. Possibly this very slender body is connected with the feeding habits of the shark. However, this slender appearance must be considerably changed when the fish is gravid or when the ovaries contain nearly ripe eggs (Text-figure 7). This slenderness of the body will be emphasized by giving some ratios of total length to depth. Thus a male 1473 mm. long was in length 16.4 times the depth of the body. A non-gravid female 1910 mm. long gave a ratio of 11.5 to 1. A 920-mm. female gave a ratio of 12.3 to 1—a fair average between the other two. A female measuring 1860 mm. was judged from the figure to be gravid. Her ratio was 7.7 to 1. Lastly a figure of a full-bellied female, also presumably gravid, from measurements of the figure gave a ratio of 6.67 to 1.

Let us now go more into the details of the external form of our fish as seen in Figure 52, plate VI. The eye is round but the socket is somewhat distorted by the mouth being drawn gaping. The mouth is nearly terminal and the gape is very large in both vertical and horizontal measurements. The briar-like teeth are faintly indicated, but even plainer are the denticles on the lips and the plications in the skin at the angles of the jaws. The gill-covers are frilled, the frills being due to the points of the branchial rays which aid the covers in respiration. The gill-covers of the first pair are continuous across the isthmus. Where the covers are attached to the body are the curious curved surfaces noted in the embryos. Visible are the ends of the gill-filaments. Surely *Chlamydoselachus* is the "fringe-gilled" shark.

The back of this fish is nearly straight from the top of the head to the insertion of the dorsal fin. On head and cheek are some of the sensory canals and on the side of the body runs the lateral line, normal throughout—including the customary irregularity under the dorsal. The abdomen looks full and leads to the suspicion that this female is possibly gravid. Along the ventral surface of the abdomen are the curious tropeic folds probably functioning as bilge keels. These keels end between the pelvic fins and immediately in front of the cloacal aperture.

At the junction of trunk and tail and just in front of the caudal fin are the dorsal and anal fins set in a vertical line. Concerning this interesting concentration of the fins of *Chlamydoselachus*, Gudger and Smith (1933, p. 296) have this to say: "The close association of dorsal, anal and pelvic fins with the caudal gives the creature a fulcrum on which to straighten its body in striking forward to seize its prey. This was first suggested by Garman. In ordinary swimming, right and left strokes of the caudal will send the body forward with the sinuous motion common to all slender fishes."

AN ADULT MALE *CHLAMYDOSELACHUS*

An adult male frilled shark is accurately portrayed in Figure 53, plate VI. In the original drawing, this figure is 538 mm. (21.2 in.) in total length. From the fact that this drawing shows the mouth closed, one gets a clear idea of the great length of the jaws which reach to a point well behind the rear of the skull. For measurements of the jaws of four adult specimens of *Chlamydoselachus*, see Gudger and Smith (1933, p. 268). The extraordinary structure and functioning of the jaws of this shark have been admirably characterized by Goodey (1910, p. 550) as follows:

Perhaps the most important point in regard to the specialization of the skull of *Chlamydoselachus* is to be seen in the extreme length and mobility of the jaws. These are exceptionally long, extending from the anterior, almost terminal mouth to a point well behind the posterior limit of the cranium. This extension is remarkable; in fact, one quarter of the total length of the jaws is found in this region, and it is this feature, connected with the exceptional length of the hyomandibular, which gives the jaws their great mobility. Indeed, their disposition relative to the cranium is quite different from that found in any other Selachian whose skull I have been able to examine or to see a figure of. It resembles nothing among the Vertebrates so much, perhaps, as the general disposition of the jaws in certain of the Ophidia.

As seen in Figure 53, plate VI, in the front of the mouth are a few teeth, and above and slightly lateral is the vertical nostril with two divisions—the upper for ingress and the lower for egress of water. The gill-covers are normal, and it can be seen that the first pair flare widely and are continuous across the throat. Short external gill-filaments are seen in every slit as in the female on this plate. The lateral line runs straight back to the region of the dorsal fin where the usual (normal?) irregular bendings are found. The body cavity of the male is plainly not nearly so large as that of the female, nor is the trophic-fold region so well marked. On the other hand, the myomeres in the body of the male are distinct whereas none are shown on the trunk of the female.

The above are, however, but minor differences. The one particular thing, that at a glance differentiates this and all other male individuals from the females, is the presence of the myxopterygia or claspers. As shown in Figure 53, plate VI, these are grooved finger-like modifications of the hinder and inner parts of the pelvic fins. When the male inserts these into the cloaca of the female during copulation, he holds her fast for the passage of the spermatozoa. It is not necessary here to go further into the structure and function of these organs. These matters have been treated earlier in this article. This drawing is the best representation of the male *Chlamydoselachus* ever published.

There is another structure in which these particular drawings of the two sexes differ—i.e., in the end of the caudal fin. In the female the tail and tail fin—as properly restored—end in a fine point. And so do the caudal fins of most of the embryos studied. On the other hand the drawing of the tail fin of the adult male ends in a rounded point and there is a notch near the tip of the ventral lobe. Thus from these figures one might jump to the conclusion that the female fish have pointed caudals and the males notched ones. But this is not true. Gudger and Smith (1933, pp. 293–297) have gone rather fully into the question of the form of the tip of the tail in the frilled shark, reproducing every

published figure of an adult *Chlamydoselachus*, and recording its form in their own four specimens. But, unfortunately, they did not record the sex of each fish noted. This I have done for all the specimens figured by them. Of these, 2 males and 4 females have pointed tails, and one female has a tail that appears to be notched. Of the 6 adult specimens in the Museum collection (4 used in previous researches, and 2 found since), all—2 males and 4 females—have pointed tails, 3 straight and 3 drooping.

THE HEAD OF THE ADULT SHARK

The lateral aspect of the head of *Chlamydoselachus* in both sexes, and with mouth open and shut, is admirably portrayed in Figures 52 and 53, plate VI. What are needed to make the portrayals complete are drawings of the dorsal and ventral aspects. Dean's "List" for "Adult" calls for "photo of head lateral and ventral". These I find, but I also find two excellent drawings of the adult head seen from above and below. They will now be described. There are no notes for these as there are none for the photographs.

HEAD—DORSAL ASPECT

The head in dorsal view is shown in Figure 54, plate VI. From the angle of the jaws, the head narrows gradually to the rounded blunt snout—a marked contrast to the broad blunt snouts of the tiger and whale sharks and to the keen-pointed ones of the Isurid sharks. The eyes are set in shallow cavities. From the angle of the jaws, the head widens to its maximum over the hinder edge of the first gill-cover. In all the gill-slits, except the last, short external filaments are visible—as they are in the specimens represented in the full-length drawings. Whether or not this head is that of the male fish, portrayed in lateral view in Figure 53, plate VI, cannot be said, but it certainly is not that of the female fish of Figure 52 on the same plate. Her first gill-cover looks as if it had the edge bitten off. Also the space between the first and second arches is much wider than that between the second and third, etc. In Figure 54, the widths of the openings are very uniform save for the last ones at the bases of the pectoral fins. These fins are entirely normal. Running along the back on either side is the lateral line. Of the latero-sensory head canals, nothing can be seen save one curving gracefully in front of each first gill-cover. No spiracle is shown. The opening was probably so small that the artist did not find it. That this head seen in dorsal aspect is that of an adult *Chlamydoselachus* may be judged by comparing it with the head of the 175-mm. specimen portrayed in dorsal view (Figure 11, plate I).

HEAD—VENTRAL ASPECT

The ventral aspect of this same head (the figures have the same measurements) may be seen in Figure 55, plate VI. Above and on either side of the mouth, the nostrils show faintly. The almost terminal mouth, with some of the upper teeth showing, is very prominent. So great is the front-to-back gape, that the angle of the mouth is a little further than halfway back of the median point between tip of snout and hinder edge of the first gill-cover. The throat has the skin plicate to allow for expansion when large objects are swallowed. The gill-covers of the first arch are confluent across the isthmus or throat

—i.e. the shark is cloak-gilled (Greek, *Chlamys*, a cloak). Paired latero-sensory canals are found on each first gill-cover and extend far on the throat region toward the symphysis of lower jaw. The hindmost of these canals are continuations of the ones seen on the first pair of gill-covers in the dorsal aspect. The short gill-filaments are visible.

The stout pectoral fins with their strong bases look "finished". Beginning between them and extending backward are the tropeic folds or bilge keels with their deep median groove. One wishes that this excellent drawing portrayed the ventral surface clear back to the tip of the caudal fin.

As noted, Dean's "List" calls for "Adult, photo of head lat. & ventral". These I have found, old and faded. The specimen, from which these photographs were made, had been mutilated in both gill-regions—the parts of particular interest just here—and apparently had suffered partial maceration. Furthermore, the shrunken gill-flaps and the distorted gill-filaments indicate that they had undergone considerable drying. These photographs portray gill-region conditions unlike what are found in the eleven figures of heads and of whole fish reproduced by Gudger and Smith (1933). Such conditions were not found in a single one of the six specimens in the American Museum studied by Smith (1937), nor are they portrayed in any of Dean's four figures reproduced herein as plate VI. It is evident that the photographs do not portray a normal specimen as it appeared in life and that they possess no scientific value whatever. There are no notes to tell us by whom they were taken, why they were made, nor why they were included in Dean's records. They will not be reproduced in this article.

EXTERNAL GILL-FILAMENTS IN *CHLAMYDOSELACHUS*

Before concluding this study of the breeding habits and external embryonic development of *Chlamydoselachus*, the matter of its external gills must be taken up. These, as indicated above, are commonly found in the embryos but very rarely in adults. In the embryos they are in origin totally unlike the external gills found present in *Crossopterygii*, *Dipnoi*, and in *Amphibia*, and are considerably different in length and profusion from the external gills figured and described in the embryos of many species of elasmobranchs. *Chlamydoselachus* is the only shark known to me to possess in the adult stage, even occasionally, short external gill-filaments. This matter of external gill-filaments is so important that it must be considered carefully.

EXTERNAL GILL-FILAMENTS OF THE EMBRYOS

The embryos of all non-placental viviparous sharks and rays known to me have long external gills. The eggs of these elasmobranchs have thin diaphanous shells, through which uterine fluids readily penetrate. These fluids are milk-like secretions of the uterine mucosa and serve as food for the growing embryos, which absorb this food through their long filamentous gills. It has been indicated above that the relatively thick shells of *Chlamydoselachus* are burst by the growing embryo, are cast off into the uterus (Figure 11,

plate I), and are then or later thrown out into the sea. Two investigators (Hawkes, 1907; and Smith, 1937), have found highly vascularized areas in the wall of the right uterus. These observations suggest that these areas might have served to secrete food stuffs into the uterus. Then the long gestation period and the enormous size of the relatively late embryos still attached to large yolk sacs seem to indicate that these embryos grow not at the expense of the yolk alone. All these things lead to the inevitable question—"Do the external gills of the embryos of *Chlamydoselachus* serve to absorb food from a uterine secretion?" The facts and inferences as to such a possible source of food in *Chlamydoselachus* have been set forth above. It seems quite sure that in any case, these external gills of the non-extruded juvenile sharks serve as respiratory organs.

Chlamydoselachus has been ranked by the systematists as the lowest, most primitive living shark. Yet in its reproductive organs, as this paper shows, and in many other organs, as Smith has pointed out in his monograph on the anatomy (1937), it is very highly specialized. Its embryos have external gill-filaments, which never grow very long and which eventually shorten until they are almost or quite concealed from view by the gill-flaps. Now external gills, as they are ordinarily understood, are embryonic or ancestral organs which tend to become eliminated in the process of evolution. External gill-filaments are either evanescent structures of external origin, developed as outgrowths on the outermost edge of a visceral arch before the clefts have broken through, or they are precocious growths of normal gills which tend to shorten in the course of later development. Let us now study these filaments as they are shown in the drawings of the embryos of this archaic shark and see to which category they belong.

The first evidence of the presence of gill-filaments in the embryos of *Chlamydoselachus* is found in the 25-mm. stage as portrayed by Ziegler (1908, Fig. 2). Ziegler's figure (my Text-figure 27c) is poorly reproduced on soft paper, and the budding filaments show up indistinctly. However, in the figure these buds appear not on the outer edges of the gill-arches but on the hinder inner sides of arches 1-5, and on both sides of No. 6. Furthermore, it is clear that the gill-clefts have become perforated, and that the outside liquid penetrates into the pharynx through the slits.

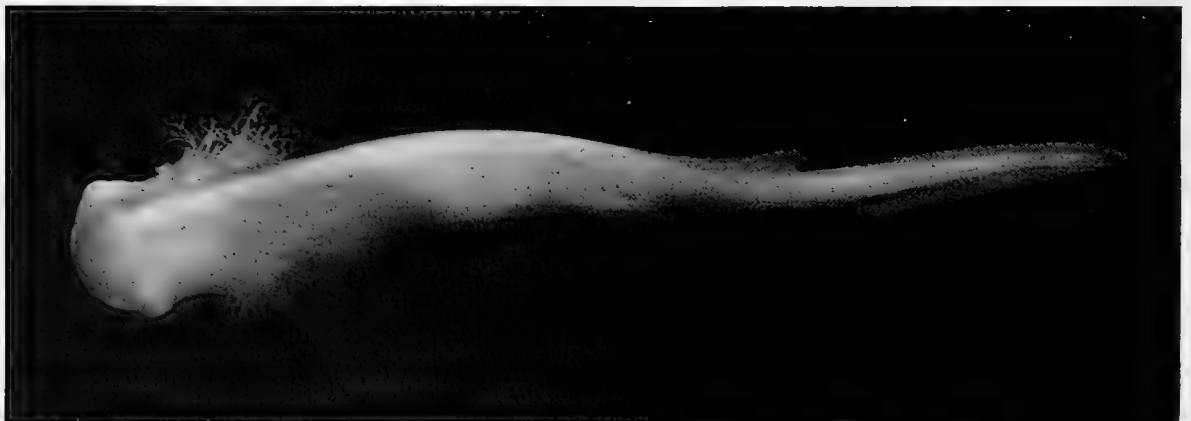
Brohmer's drawing (1909, Fig. 3) of his 25-mm. specimen (also poorly reproduced) shows the gill-filament buds on both sides of arch No. 2 (my Text-figure 27A). Probably they are present in a beginning stage on both sides of each arch. They are next seen (as far as data are at hand) in Nishikawa's 32-mm. embryo (Figures 19-21, plate II) where they appear on both sides of every arch—excepting of course the first. Passing over the 34-mm. specimen, we go to the 39-mm. embryo in which stage the filaments first begin to show externally, particularly in the first slit (Figure 25, plate II). These filaments are in about the same stage of development as those in Scammon's 18-mm. *Squalus* (1911, Fig. 27, pl. III). But in size and abundance they are far behind the filaments protruding from the gill-slits of Scammon's 20.6-mm. embryo of the dogfish.

External filaments are seen to be pretty well developed in Dean's "new series" of drawings of embryos 46, 54, 66, and 103 mm. in length. These can be best studied in the

ventral views reproduced in Plates III and IV. where they seem to be growing on both sides of each slit. That this is a fact, I have proved by microscopic examination of the head of an embryo about 45-mm. long found in the Dean material in the Museum. This specimen had been fixed in bichromate of potash and under the binocular microscope showed filaments on both the anterior and posterior sides of every arch save the hyoid—and some protruded even from the spiracle. These external filaments are somewhat better developed in the 103-mm. fish (Figures 41–43, plate IV) than in any younger embryos. But even here they are hardly so well-grown as those in Scammon's 20.6-mm. *Squalus* (his Fig. 28, tab. III).

Among the embryos loaned from Columbia University for this research, I could for a long time find no specimen with gill-filaments longer than those of the 46-mm. young (Figures 28–30, plate III) and of the 103-mm. fish (Figures 41–43, plate IV). However, one day in examining the egg with the split yolk (referred to previously) as having a capsule with the curious tendriform process seen in Figure 13, plate I, I removed the crumpled shell, and to my great surprise and pleasure found the little fish with long filaments now to be studied.

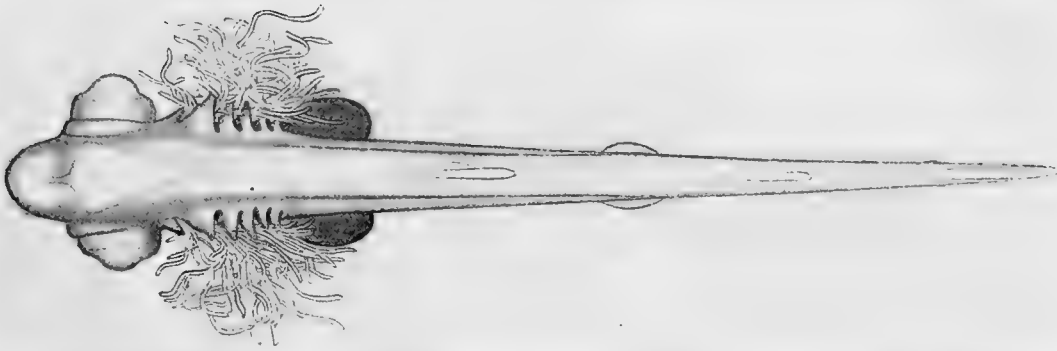
This specimen (71-mm. long), as seen in Text-figure 32, has longer and more profuse external gill-filaments than any young *Chlamydoselachus* figured by Dean. This will be noted at once when Text-figure 32 is contrasted with Figure 41, plate IV (the 103-mm. specimen). It is impossible to measure these filaments since they are more or less sinuous, and sometimes spirally coiled. Due to their being tangled, they sometimes appear to be branched, but under the binocular microscope this is seen to be an optical illusion due to their overlying each other. For comparison's sake, there is introduced here, as Text-figure 33, Scammon's figure of his 28-mm. *Squalus* in about the same stage of gill-filament development as the 71-mm. *Chlamydoselachus*. Possibly if the filaments of the little



Text-figure 32

A 71-mm. frilled shark with a profusion of external gill-filaments. These are the longest found in any specimen or drawing of this shark in this research.

Photograph by Charles H. Coles, A. M. N. H.



Text-figure 33

A drawing of a 28-mm. *Squalus acanthias* in about the same stage of external gill-filament development as is the young *Chlamydoselachus* shown in Text-figure 32.

After Scammon, 1911, Fig. 30a, Pl. III.

frilled shark could be straightened out they might be as long as those of the dogfish. The two little sharks are shown in the same size, though in life *Chlamydoselachus* is 2.5 times longer than *Squalus*. This shows how much faster and farther the dogfish had gone in development. For a frilled shark of approximately the same size as this *Squalus*, see Figure 23, plate II of a 34-mm. *Chlamydoselachus*.

In Dean's figures of older embryos measuring 124, 175, 185, 240, and 390 mm., and all drawn at an earlier date than those of 46, 54, 66, and 103 mm., the external filaments are very much reduced. They are hardly visible underneath the flaps. From all the data carefully marshalled above, I draw the conclusion that these so-called external gills of the larval frilled shark are nothing but precociously overgrown permanent gills, which later on shorten until but a bare remnant shows beyond the gill-opening, as may be seen in the largest (390-mm.) embryo portrayed by Dean (Figure 49, plate V).

From these facts, found in the drawings cited, it is clear that these protruding gill-filaments in the embryos of *Chlamydoselachus* are not true external filaments like those of the Crossopterygii, Dipnoi, and Amphibia. In the larvae of the dogfish and of the various rays dissected and studied by me, the external filaments are many, long, and plumose. By the time of hatching these have disappeared. Whatever may be the part of these external gills in the nutrition and respiration of the embryo, they are almost always absent in the adult.

EXTERNAL GILL-FILAMENTS IN THE ADULTS

No other adult shark or ray known to me has even the semblance of external gills, but some specimens of the adult *Chlamydoselachus* do have such a semblance. Allis (1923) has a drawing (reproduced by Gudger and Smith, 1933, in their Fig. 7, pl. II — Article V of this Memorial Volume) made from an adult head supplied to him by Dean, which shows such remnants of protruding filaments as are seen in Dean's figures on

Plate VI. Allis's figure in his article (1923) appears to be in natural size, and Dean's figure of a female fish in the original drawing measures 614 mm. (24.2 in.). This, it should be noted, is just about the size of a young specimen taken by the Prince of Monaco at Madeira, and pronounced by Collett (1890) to differ from adults only in the matter of size.

Elsewhere it has been stated that there are in the Museum collection six adult frilled sharks. What is the evidence from them as to protruding gill-filaments? Three of these sharks have been dissected by Smith (1937) who found that the gill-filaments did not show externally. Similar conditions were found in the three undissected specimens. None showed protruding filaments. We also have a head only, straight and well-preserved, but it shows no external filaments. As to the function of these slightly protruding gill-filaments, one can infer that they make the gills of such adults as possess them, somewhat more efficient in respiration.

From the data given, it is probable that some embryos of *Chlamydoselachus* (Figure 49, plate V) carry over into the adult stage remnants of their embryonic external gills. But it is evident that most adults lack such protruding gill-filaments. For figures in which they are absent, see Gudger and Smith's (1933) article on the natural history of *Chlamydoselachus*, wherein all known figures of the whole fish and of its head are reproduced. That external gills sometimes occur in the adult *Chlamydoselachus* is additional evidence of the unpredictable characteristics of this primitive shark. Perhaps I cannot do better than to quote Smith's summation (1937, p. 495)—“My outstanding impression of the frilled shark is that it presents a strange assemblage of characters ranging from very primitive to highly differentiated”.

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PLATE I
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE I
EGGS AND EGG CAPSULES OF *CHLAMYDOSELACHUS*

- Fig. 1. A ripe ovarian egg of the frilled shark. The original drawing measures 90 x 96 mm., and is presumably in natural size. See also Text-figure 12.
- Fig. 2. An asymmetrical oblong egg of the frilled shark. The asymmetry of this egg probably originated during the process of shell formation.
- Fig. 3. A symmetrical oblong egg of *Chlamydoselachus* surrounded by its transparent keratinoid capsule.
- Fig. 4. A round egg of the frilled shark—C of Dean's list.
- Fig. 5. Another encapsuled round egg—numbered B by Dean.
- Fig. 6. A third round egg—numbered A by Dean.
- Fig. 7. An ellipsoidal encapsuled egg having a 43-mm. embryo attached by a yolk stalk.
This figure is a copy of Nishikawa's drawing portrayed in natural size in Text-figure 4.
- Fig. 8. The vitelline blood vessels on the under side of the egg portrayed in Figure 7.
After Nishikawa, 1896, Fig. 2, pl. IV.
- Fig. 9. An ellipsoidal encapsuled egg with an older embryo (50 mm.) and a slightly more advanced vitelline circulation than that seen in Figure 7.
- Fig. 10. Underside of the egg shown in Figure 9. The yolk-sac circulation is slightly more advanced than that portrayed in Figure 8.
- Fig. 11. A 175-mm. embryo of *Chlamydoselachus* attached to its yolk sac and without its capsule.
- Fig. 12. Under side of egg portrayed in Figure 11. This shows a late stage of the vitelline blood vessels.
- Fig. 13. A tendriform process from the capsule of an asymmetrical oblong egg in the collections of Columbia University. This process is similar to that seen in Figure 2.
- Fig. 14. A much-branched tendriform process. Note its close similarity to those shown in Figures 13 and 2.

Each figure on this plate save number 13 is half the size of the original, and hence is presumably one half natural size.

Figure 13 is the only figure on these six plates not drawn by or for Dr. Bashford Dean.

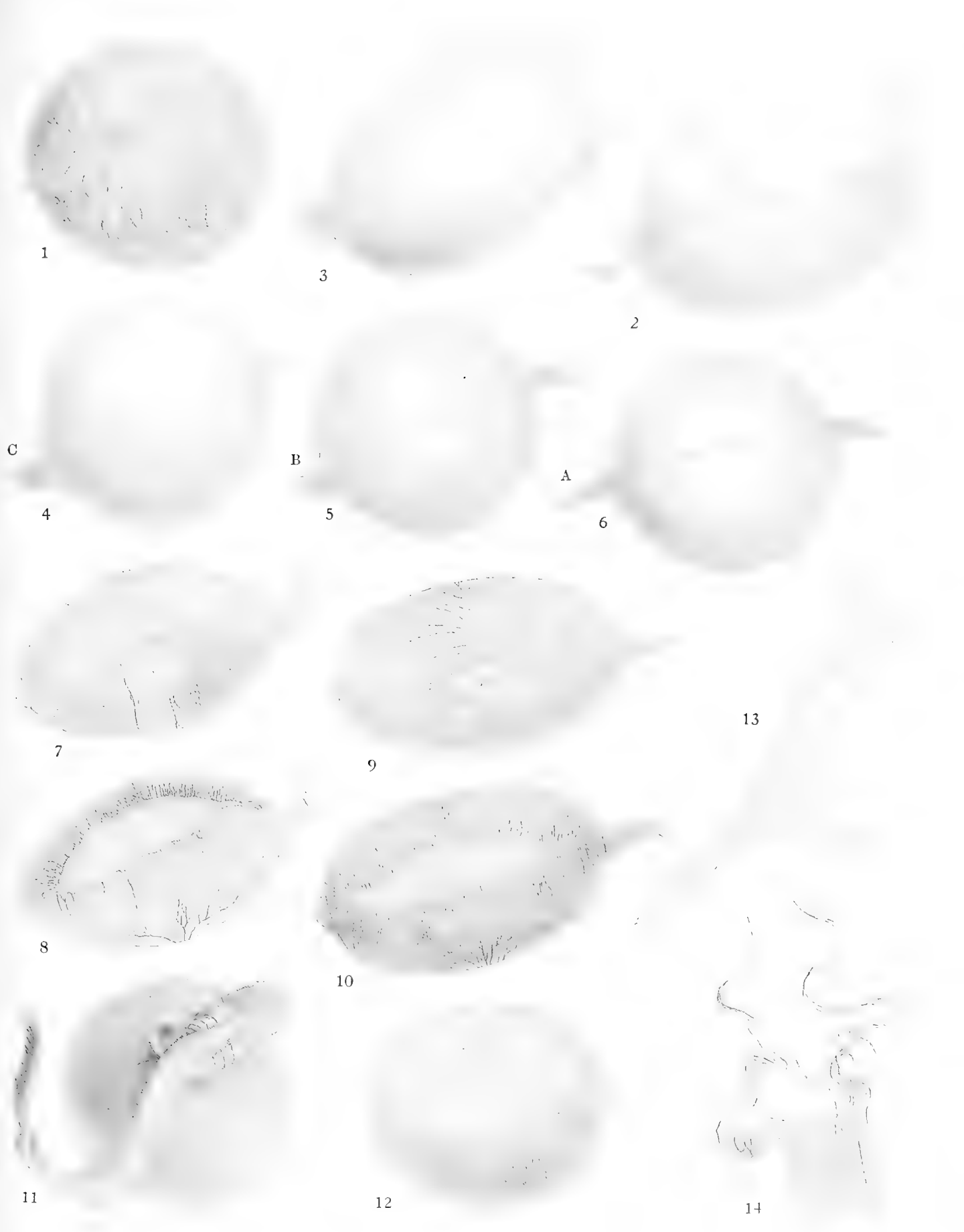
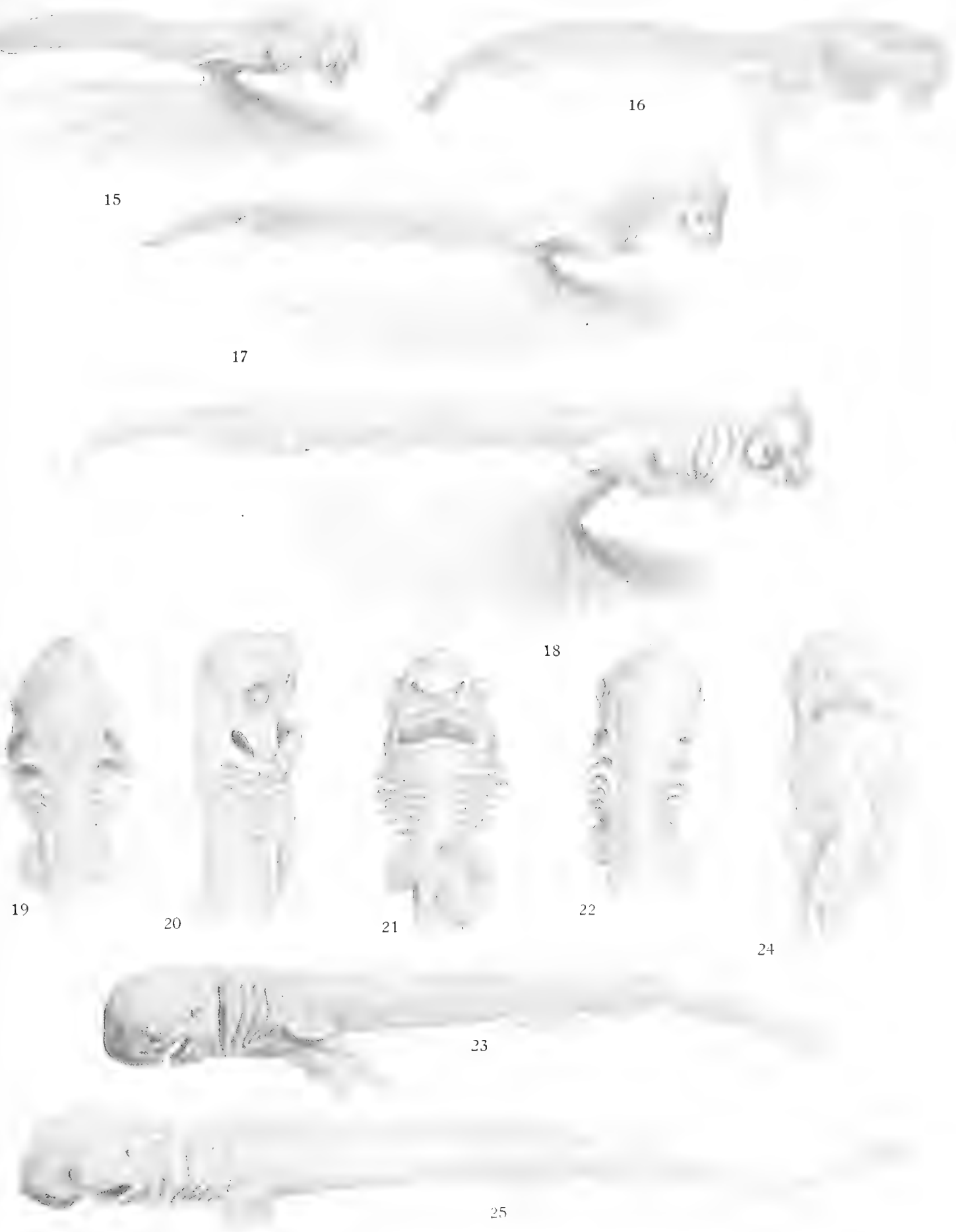


PLATE II
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE II
THE EARLIEST EMBRYOS OF *CHLAMYDOSELACHUS* OBTAINED
BY BASHFORD DEAN

- Fig. 15. The earliest embryo (11.5 mm.) of *Chlamydoselachus* figured by Dean. Original drawing = 121 mm. Note the attachment of the embryo to the yolk sac by a short yolk cord.
- Fig. 16. The 11.5-mm. embryo stained, cleared, and drawn considerably enlarged—to 161 mm.
- Fig. 17. A larger embryo (15.5 mm.) shown in lateral aspect. The original drawing measures 177 mm.
- Fig. 18. The largest (20 mm.) of Dean's very small embryos of the frilled shark. The original drawing measures 222 mm.
- Fig. 19. Dorsal view, head only, of Nishikawa's 32-mm. embryo, considerably enlarged.
- Fig. 20. Lateral aspect, the head only, of Nishikawa's 32-mm. embryo.
- Fig. 21. Head only of Nishikawa's 32-mm. embryo seen from below.
- Fig. 22. Dorsal aspect of head only of Dean's 34-mm. *Chlamydoselachus*.
- Fig. 23. Lateral view—full-length—of the 34-mm. embryo.
- Fig. 24. Ventral aspect of the head only of Dean's 34-mm. specimen.
- Fig. 25. Dean's 39-mm. embryo portrayed in full-length lateral aspect.

All the figures on this plate are reduced by one-third—i.e., are reproduced two-thirds the sizes of the original drawings.



BASHFORD DEAN DEL.

A. HOEN & Co. LITH.

EMBRYOLOGY OF CHLAMYDOSELACHUS

PLATE III
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE III
FRILLED SHARK EMBRYOS OF INTERMEDIATE SIZE:
39, 46, 48, 54, 55 MM.

- Fig. 26. An embryo of 39-mm. portrayed in full-length dorsal aspect.
- Fig. 27. Ventral view—full-length—of the 39-mm. specimen.
- Fig. 28. Full-length portrayal in dorsal aspect of a 46-mm. embryo.
- Fig. 29. Lateral full-length view of the 46-mm. embryo.
- Fig. 30. The 46-mm. embryo seen from below.
- Fig. 31. "Head only stained" of a 48-mm. embryo—ventral aspect.
- Fig. 32. A 54-mm. embryo shown in full-length dorsal view.
- Fig. 33. A full-length lateral view of the 54-mm. fishlet.
- Fig. 34. The tadpole-shaped 54-mm. embryo portrayed from below.
- Fig. 35. Dorsal aspect—head only—of a 55-mm. embryo.
- Fig. 36. Lateral full-length view of a 55-mm. specimen.
- Fig. 37. Head only of a 55-mm. embryo seen from below.

All figures on this plate have been reduced by one-third their original length.

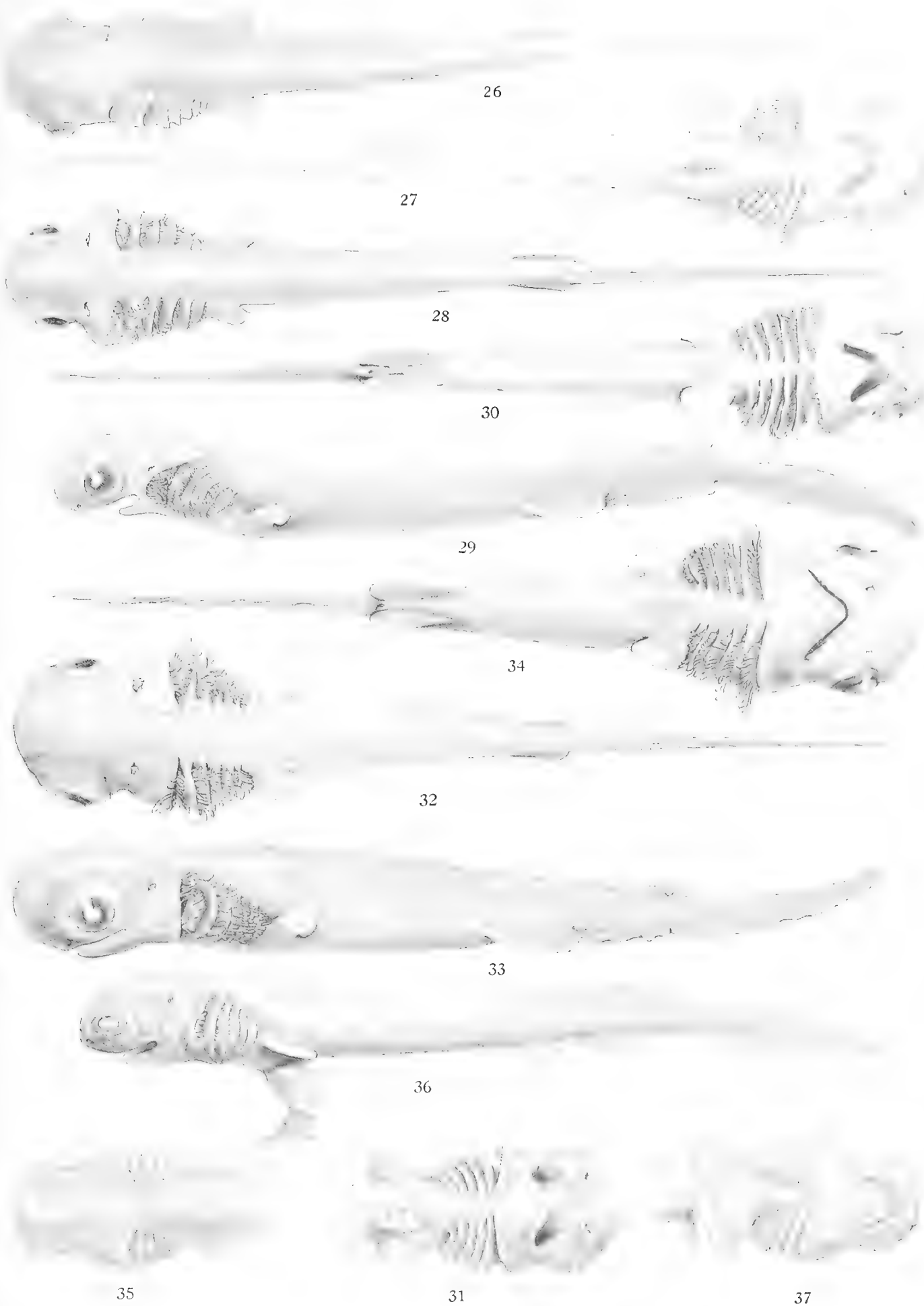
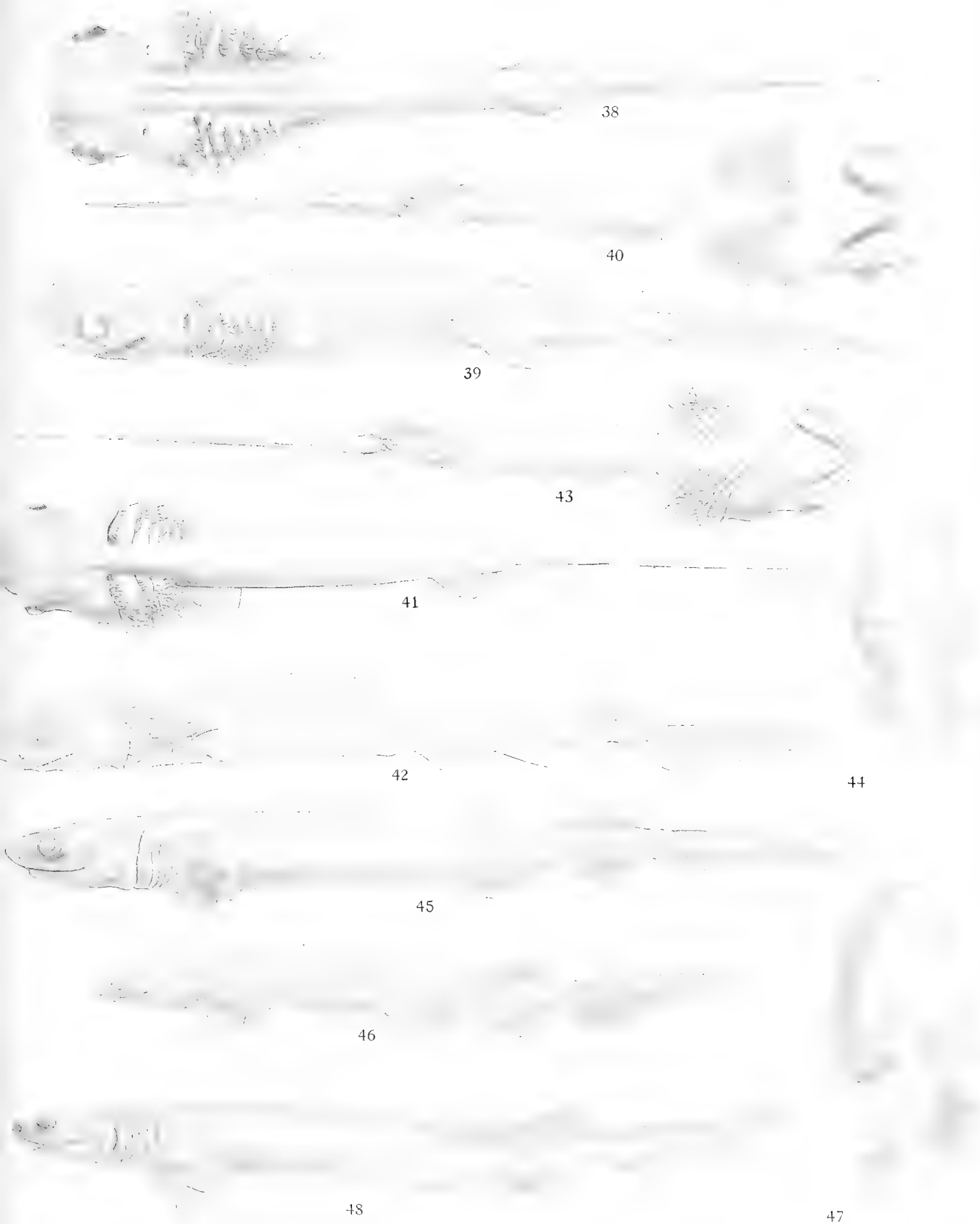


PLATE IV
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE IV
LARGER EMBRYOS OF *CHLAMYDOSELACHUS*:
66, 103, 124, 185, 240 MM.

- Fig. 38. Dorsal view—full-length—of a 66-mm. embryonic *Chlamydoselachus*.
- Fig. 39. A 66-mm. embryo of the frilled shark seen from the left side.
- Fig. 40. Ventral aspect of the 66-mm. specimen.
- Fig. 41. A specimen 103 mm. long viewed from above.
- Fig. 42. A 103-mm. embryonic frilled shark seen from the side.
- Fig. 43. A young 103-mm. *Chlamydoselachus* in ventral aspect.
- Fig. 44. Head of a 124-mm. embryo seen from above.
- Fig. 45. A 124-mm. *Chlamydoselachus* portrayed in lateral aspect.
- Fig. 46. Lateral view of an embryo 185 mm. long.
- Fig. 47. Head only of the 185-mm. embryo—ventral aspect.
- Fig. 48. An embryo measuring 240 mm. seen in lateral view.

All the figures on plate IV. are reproduced two-thirds the size of the original drawings.



BASHFORD DEAN DEL.

A. HOEN & CO. LITH.

EMBRYOLOGY OF CHLAMYDOSELACHUS



PLATE V
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE V

A 390-MM. FRILLED SHARK, A 39-MM. EMBRYO, AND A WIND EGG:
ALL PORTRAYED IN NATURAL COLORS

- Fig. 49. Dean's largest (390-mm.) embryo of *Chlamydoselachus* portrayed in lateral view in its natural colors.
- Fig. 50. A 39-mm. embryo, its yolk mass, and its yolk-vascular system shown in natural colors.
- Fig. 51. A wind egg of *Chlamydoselachus* shown in its natural colors.
- Figure 49 on this plate is reduced from 15.35 in. to 11 in. Figures 50 and 51 are reproduced in the size of the original drawings.





PLATE VI
EXTERNAL DEVELOPMENT OF *CHLAMYDOSELACHUS*

PLATE VI
MALE AND FEMALE SPECIMENS OF *CHLAMYDOSELACHUS*
AND TWO HEADS FROM ADULT FISH, ALL SHOWN IN
THEIR NATURAL COLORS

- Fig. 52. Lateral view of a female *Chlamydoselachus*.
Fig. 53. Lateral view of a male frilled shark.
Fig. 54. Dorsal view of the head of an adult frilled shark.
Fig. 55. Ventral view of the head of an adult *Chlamydoselachus*.

Figures 52 and 53, in the original drawings, measure 614 mm. (28.4 in.) and 538 mm. (21.2 in.) respectively. As reproduced on this plate, the fishes measure 505 mm. (19.9 in.) and 443 mm. (17.4 in.) each. Figures 54 and 55 are reproduced in the size of the original drawings.



THE
BASHFORD DEAN MEMORIAL VOLUME
ARCHAIC FISHES

Edited By
EUGENE WILLIS GUDGER

ARTICLE VIII

THE HETERODONTID SHARKS:
THEIR NATURAL HISTORY, AND THE EXTERNAL
DEVELOPMENT OF *HETERODONTUS JAPONICUS*
BASED ON NOTES AND DRAWINGS
BY BASHFORD DEAN

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ARTICLE VIII

THE HETERODONTID SHARKS: THEIR NATURAL HISTORY,
AND THE EXTERNAL DEVELOPMENT OF *HETERODONTUS*
(*CESTRACION*) *JAPONICUS* BASED ON NOTES
AND DRAWINGS BY BASHFORD DEAN

By BERTRAM G. SMITH

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THE HETERODONTID SHARKS: THEIR NATURAL HISTORY,
AND THE EXTERNAL DEVELOPMENT OF *HETERODONTUS*
(*CESTRACION*) *JAPONICUS* BASED ON NOTES
AND DRAWINGS BY BASHFORD DEAN

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INTRODUCTION

Sharks of the family Heterodontidae (Cestraciontidae) have an especially well-defined pedigree. The genus *Heterodontus* (*Cestracion*), which includes the only species living at the present time, dates at least from the Upper Jurassic; the family Cestraciontidae, as defined by Zittel (1932), from the Lower Jurassic. The closely related family Hybodontidae, represented only by fossils, dates from the Devonian or Lower Carboniferous to the Cretaceous. Therefore the geologic histories of the two families overlap; but the Hybodonts were approaching extinction when the Heterodonts came into being. Since there appears to be genetic continuity between the two families, one might readily conclude that the recorded lineage of sharks of the genus *Heterodontus* is more ancient than that of any other living vertebrate. In this circumstance we find the key to Dean's interest in the embryology of *Heterodontus*.

At the time when Dean began collecting the eggs and embryos of the Japanese Bullhead Shark, *Heterodontus japonicus*, all that was known concerning the embryonic development of any species of *Heterodontus* was contained in Haswell's brief account (1898) of the blastula and gastrula of *H. philipi*. This deficiency was the more notable in view of the fact that the family Heterodontidae has no other genus, besides *Heterodontus*, represented by living species. But *Heterodontus* was not, from Dean's point of view, merely another kind of shark to be studied in order to fill a gap in our knowledge of comparative embryology. It is well known that Dean, like many other biologists of his generation, was interested in the study of animals chiefly from the viewpoint of organic evolution. Thus it is not surprising to find in his notebook the following carefully worded statement:

The embryology of the Cestracionts [Heterodonts] is expected to prove of value not merely in comparison with other sharks, but in estimating the general significance of development in "recapitulating" ancestral characters. For granting that these sharks represent a peculiarly primitive branch of the descent-tree of Selachians, we would reasonably expect to find in their embryonic stages certain simpler, more archaic characters than in the corresponding stages of the commoner groups of sharks. Furthermore, and this is the importance of such a study, if we do find that *Cestracion* [*Heterodontus*] presents definitely more primitive embryonic characters than sharks of a more modern type, we can certainly maintain

that recapitulation is not to be given the scant courtesy with which it has come to be treated by a modern school of embryologists. In a word, the present theme may be found to provide a new (and critical) means of testing the value of the biogenetic law.

These hopes and expectations led to the publication, in 1901, of Dean's article entitled "Reminiscence of Holoblastic Cleavage in the Egg of the Shark, *Heterodontus* (*Cestracion*) *japonicus* Macleay." This contribution is reviewed, in considerable detail, later in the present paper. Our knowledge of the embryology of *Heterodontus* is still incomplete, so that the possibilities suggested by Dean have never been fully explored.

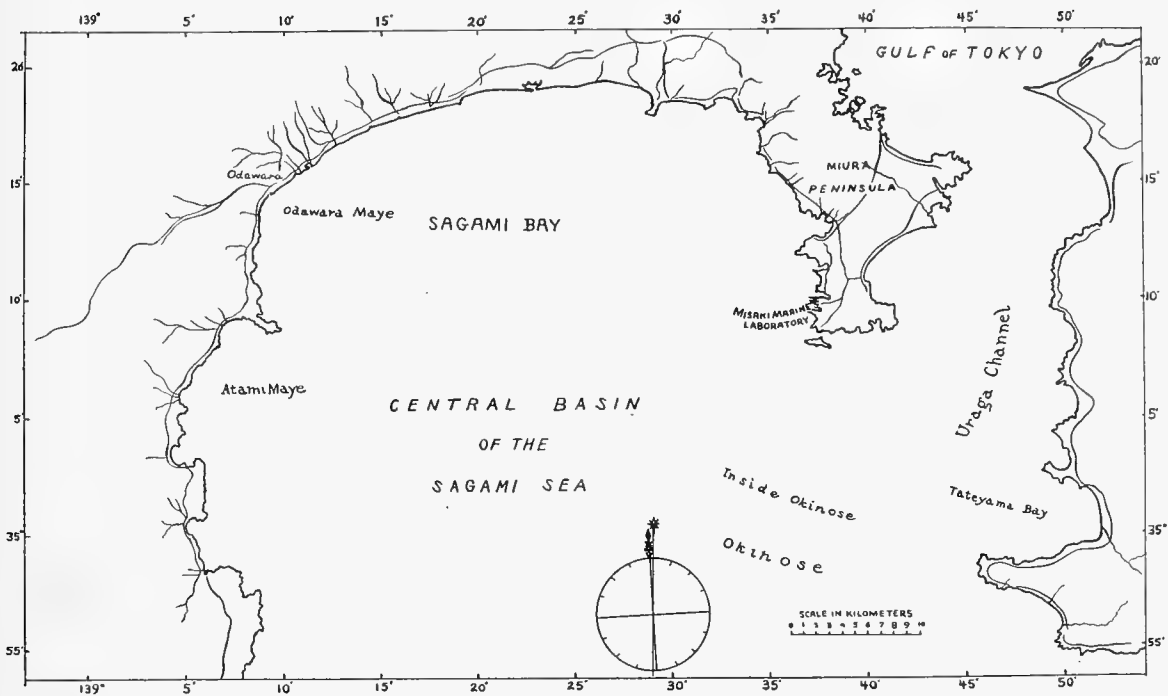
To Dr. E. W. Gudger, editor of the Dean Memorial Volume, I am indebted for many helpful suggestions throughout the preparation of this article, and especially for taking the major part in the difficult task of making up the plates.

MATERIAL AND RECORDS

For the proper evaluation of any scientific record, it is necessary that the reader should be informed concerning the identity, amount and source of the material, also the



Text-figure 1.
The Marine Zoological Station at Misaki, Japan.
From a photograph by Bashford Dean, 1904, p. 198.



Text-figure 2.

A map of the Sagami Sea, the Miura Peninsula, and part of the Gulf of Tokio, showing the position of the Misaki Laboratory in which Dr. Dean worked, and the waters from which his specimens of *Heterodontus* were taken.

From an old chart compiled by Professor I. Ijama.
After Gudger and Smith, 1933, Text-figure 3, page 251.

conditions under which the observations were made. In the present instance, this information is not so adequate as it would be if Dr. Dean had lived to finish his projected article on the embryology of *Heterodontus japonicus*; for his written records have come down to us in fragmentary and incomplete form.

THE SPECIMENS AND THEIR SOURCE

From Dean's notes, also from Mrs. Dean, we learn that eggs and embryos of *Heterodontus* were obtained in Japan in 1900, 1901 and 1905, while Dean was a guest of the Imperial University of Tokyo; also, collecting was carried on for him during his absences from Japan, in 1903, 1904 and 1906. The material was collected at the Marine Zoological Laboratory of the University (Text-figure 1) situated at Misaki on the Miura Peninsula which projects into the Sagami Sea between Sagami Bay and the Gulf of Tokyo (Text-figure 2). Collecting was done at various times throughout the year. The specimens represented numerous stages from early cleavage to young at the time of hatching, in all about 200 embryos. Of these, the majority were examined living, and notes and drawings were sometimes made before the embryos were preserved.

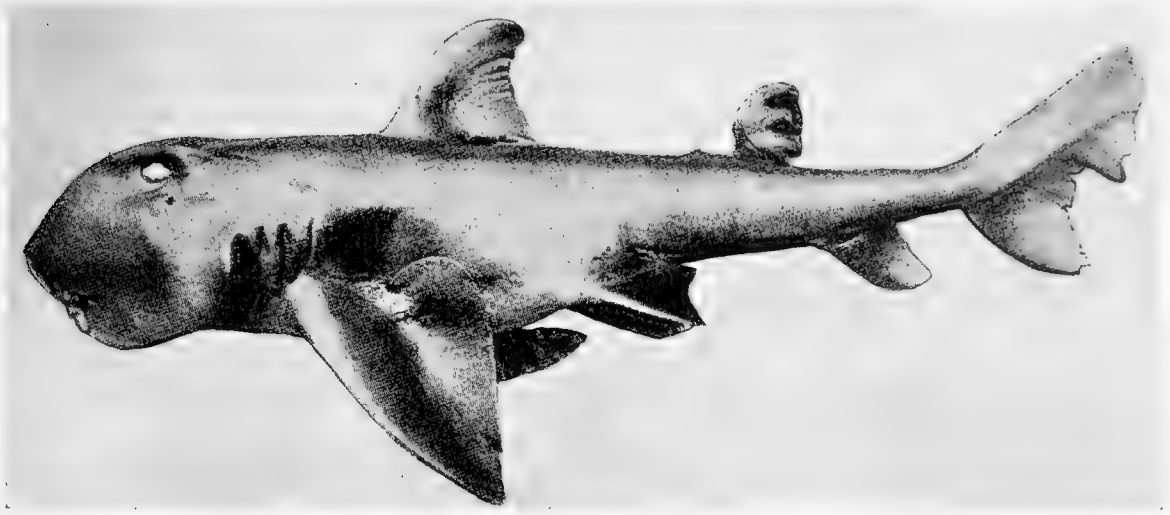
It is known that Dean, while in Japan, made extensive collections of biological material other than *Heterodontus*, and that he was also engaged in the collection of Japanese armor; but his keen interest in the embryology of *Heterodontus* is attested by the following statements included in a letter (Dean, 1901.2, p. 85) to the Columbia University Quarterly:

My first object in visiting Japan was to secure the eggs and embryos of the Port Jackson [sic] shark, a form which there is some reason to believe traces a direct descent from known sharks of Carboniferous times. Its embryos, therefore, might reasonably be looked upon to furnish evidence as to the relationships of the oldest sharks, and, therefore, as to the oldest backboned animals. At Misaki I soon found that this form was moderately common, and the native divers and fishermen finally brought me in a valuable series of its eggs.

In his article on the embryology of *Chlamydoselachus*, Gudger (1940) has noted that Dean collected embryos of *Heterodontus* and *Chlamydoselachus* in the same general locality (though in different habitats) and simultaneously. When we consider the results of the two undertakings, certain differences are very obvious: whereas for *Chlamydoselachus* there was a scarcity of early stages and a fairly complete series of older embryos, for *Heterodontus* nearly all stages are represented. To illustrate this, one need only compare the plates illustrating the present article with those of Gudger's article on the Embryology of *Chlamydoselachus*, No. VII in this Volume.

Of the approximately 200 embryos of *Heterodontus japonicus* collected by Dean, there are now, after more than 35 years, available for study only the following: (a) Six embryos in a crumpled condition, preserved in alcohol. Roughly measured, these range from 38 mm. to 90 mm. in length. In general, the condition of this material is as good as could be expected since it has been preserved for thirty-five or forty years. (b) A single embryo about 3.5 mm. long, stained, cleared and mounted *in toto* on a slide. (c) Twelve slides containing serial sections of seven different embryos in stages ranging from an early blastula to an embryo about 10 mm. long. Several series are imperfect or very incomplete, but the orientation is good and the stain (apparently borax carmine) has not faded appreciably. Nevertheless, the paucity of material is such that for the embryological portion of this article we must depend almost entirely on Dean's notes and drawings. Fortunately the drawings represent not only surface views, but quite a number of embryos that had been stained, cleared, and mounted whole.

It was at Misaki that Dean made the only photograph of a fresh-caught Japanese Bullhead Shark on record (my Text-figure 3, further described on page 693). This photograph is particularly valuable since there is but one juvenile and no adult specimen of *Heterodontus japonicus* in the American Museum at the present time. Fortunately, there are available two specimens of *H. quoyi*, one young and the other adult or nearly so; and two specimens of *H. francisci*, one nearly full-grown and the other undoubtedly adult. The external anatomy of all these specimens is briefly described in the section on "The Species of *Heterodontus*".



Text-figure 3.

Photograph of a fresh-caught Bullhead Shark (*Heterodontus*, probably *japonicus*) taken at Misaki, Japan.
The specimen is an adult female about 1043 mm. (41 inches) long.

After Dean, 1904, p. 203.

AUTHORSHIP OF THE DRAWINGS

Owing to the lapse of many years since the drawings of *Heterodontus* and *Chlamydoselachus* were made, the precise circumstances have become involved in some obscurity. When, where and by whom were the finished drawings made? It is known that Dean was an artist of no mean ability, and that he was skilled in the various techniques employed in illustrating his published works. He made pencil sketches with surprising speed and fidelity; he had an artist's ready perception of form and quick appraisal of light and shadow. His more finished drawings reveal an accuracy of outline and delicacy of shading that invariably arouse the admiration of the beholders. During his sojourn in Japan, he had learned to use the brush in making fine lines, often in color. It is known that he had made drawings similar to those of *Heterodontus*, and so it was natural that the idea should develop among some of his friends and associates that all the drawings of *Heterodontus* were the work of his own hands. But, considering the variety and the scope of Dean's activities, it seems physically impossible for him to have made all the drawings that illustrate his published works, and also the drawings that were left unpublished after his untimely death. It seems more likely that Dean often made sketches to illustrate the character of the drawings desired, and then left the execution of the finished drawings to artists whom he employed.

So far as *Chlamydoselachus* is concerned, the matter of the authorship of the drawings has been fully considered by Gudger (1940) who came to the conclusion that they were made by Japanese artists under Dean's direction. The same considerations hold for *Heterodontus*, with the following additional circumstances: The present writer remem-

bers that in 1911 Prof. Dean showed him the plate figures of the projected article on the embryology of *Heterodontus* and remarked that they were made by the best artist (or artists?) available. I do not recall whether he stated that the artists were Japanese, but it seems that some of the drawings bear intrinsic evidence of Japanese handiwork. A footnote to Dean's article (1901.1) on the "cleavage" of the egg of *Heterodontus* states that these drawings were made by Messrs. N. Yatsu and I. Kuwabara. In one of Dean's notebooks there is a table listing embryos of *Heterodontus japonicus* collected at Misaki, and recording occasional brief data concerning them. In this table there are many entries, in Dean's almost microscopic handwriting, reading "Yatsu drawn." Whether these drawings were preliminary sketches or figures intended for publication is not evident from these records; but on the original of Figure 40, plate VI, there was found, apparently in Dean's handwriting, the word "Yatsu".

After diligent inquiry it appears certain that some, at least, of the plate figures used to illustrate the present article were made by Yatsu, and that part of his work was done in this country. One can readily appreciate the advantages of having the drawings of preserved material made by one who had seen, and possibly sketched in color, the material in the living condition. That all the drawings were not made by the same person seems obvious. Whatever their origin, all who have seen them agree that most of them are remarkably well done.

WRITTEN RECORDS LEFT BY BASHFORD DEAN

Dean's notes concerning *Heterodontus* comprise three documents: First, a notebook containing a list of embryos collected (see also page 654), a very few miscellaneous notes, and a large number of rough sketches of embryos. Some of these sketches are in color, and are presumably made from living embryos as a preliminary to more finished portraits of preserved material. Most of these drawings are on pieces of stiff cardboard adhering to the pages of the notebook. Second, there is a notebook from which a considerable number of pages have been cut out and are missing. Of the remaining pages, all are blank except six, and these contain notes relating to the literature of paleontology and comparative anatomy, with special reference to the phylogenetic relationships of *Heterodontus*. Finally, there is a brief and very incomplete typed manuscript entitled: "Cestraciont Sharks and their Development." The "Table of Contents" attached to this manuscript reveals that a very comprehensive article, paleontologic, phylogenetic, embryologic and ecologic, was planned. Of this we find, in Dean's manuscript, only an introduction, brief sections dealing with the habits of the fish, methods of collecting its eggs, rate of embryonic development, the egg and its capsule; and a final longer section on "Segmentation" or cleavage. Of the 32 pages of this manuscript, 9 are devoted to cleavage. The text here is almost identical with portions of Dean's article entitled "Reminiscence of Holoblastic Cleavage in the Egg of the Shark, *Heterodontus (Cestracion) japonicus* Macleay," published in 1901. There is intrinsic evidence that the manuscript under consideration was written at a considerably later date, for in it reference is made to Goodrich's

volume on "Cyclostomes and Fishes" published in 1909. Therefore it appears that the portion of Dean's manuscript dealing with the phylogenetic aspects of cleavage is intended as a repetition, with revision, of the contents of his article published in 1901.

Considering these written records in their totality, none of the miscellaneous notes and only certain portions of the manuscript are in a condition suitable for publication without revision. These portions will be quoted verbatim. The manuscript was originally typed, but much of it is so complicated by changes and additions (in script) that both its style and its organization are impaired. It seems best to treat these portions as notes, to be rewritten and incorporated in the present article. Notwithstanding its limitations, Dean's manuscript does give us much interesting information not recorded elsewhere.

In concluding the introductory portion of his manuscript, Dean made the following acknowledgments:

Before beginning his descriptive paper, the writer wishes to acknowledge numerous courtesies which were extended him during various stages of his work. Especially to his colleagues in Japan, Dean Mitsukuri and Professor Ijima his sincere thanks are due for arrangements made at Misaki which resulted in the success of his collecting. He acknowledges also his indebtedness to the assistant at the station, Mr. T. Tsuchida, whose never-failing patience and diplomacy stood in good stead with the fisherpeople. Finally, he is indebted to Dr. Naohide Yatsu, whose help, at all seasons and in all ways both in Misaki and in New York, greatly lightened the burden of the work.

CLASSIFICATION AND SYNONYMY

Regan (1908) grouped the species of living Cestraciontidae (Heterodontidae) into two genera, *Gyropleurodus* and *Cestracion*. Nearly all later authors recognize only one genus (variously designated *Heterodontus*, *Cestracion* or *Centracion*) of the living Heterodontidae. The species included in this genus are collectively equivalent to those of Regan's two genera. The common name Bullhead Sharks has been used by Jordan and Evermann (1896), by Bridge (1904), and by many later authors, for the members of the family Heterodontidae.

HETERODONTUS AND *HETERODONTIDAE*

In the present article I have adopted the generic name *Heterodontus* for the six species of Bullhead Sharks represented by specimens living at the present time. Of these, the best-known is the Port Jackson Shark, *H. phillipi* (Text-figure 4). For the genus a synonym, *Cestracion*, is so firmly imbedded in the literature that it cannot be ignored. Nevertheless, there are fairly convincing reasons why the name *Heterodontus* should prevail. For my information regarding this matter I am indebted chiefly to Duméril (1865, pp. 423-426); Macley and Macleay, (1879, pp. 303 and 309) and Garman (1913, pp. 4, 155, and 180).



Text-figure 4.

A full-grown female Port Jackson Shark, *Heterodontus phillipi*, photographed from life. The four posterior gill-slits, which were indistinct in the original, have been strengthened.

After Saville-Kent, 1897, p. 194.

SYNONYMY

The term *Heterodontus* has priority over *Cestracion*, having been used by Blainville in 1816. The word means literally "different teeth", thus describing one of the most striking characteristics of the genus (Text-figure 10, page 670). The word *Cestracion* was first used by Klein, in 1742 and again in 1776, as a name for the Hammerhead Sharks, and has since been used by Duméril to designate the group of sharks termed, by Cuvier, *Zygaena*. In 1817 Cuvier, without assigning any reason, gave the generic name *Cestracion* to the Port Jackson Shark, the only living species of Bullhead Shark known at that time. Presumably he did not know that Blainville, a year previously, had already given to that species the generic name *Heterodontus*. Concerning the precise meaning of the name *Cestracion* (from the Greek) there seems to be room for doubt. The matter is discussed by MacLay and Macleay (1879) and by Garman (1913).

The generic name *Centracion* was given to one of the Bullhead Sharks by Gray (1831) in the first number of his "Zoological Miscellany" (p. 5). There he described a new species named by him *Centracion zebra*. Gray did not explain his choice of the word *Centracion*, and possibly the spelling was a mistake, for he wrote *Cestracion* instead of his own term *Centracion* when, in 1851, he adopted the name *Heterodontus* for the genus.

Garman (1913) followed Klein and also Duméril in adopting *Cestracion* as the generic name for the Hammerhead Sharks. In his choice of the name *Centracion* for the Bullhead Sharks, Garman was not so fortunate. He objected to the name *Heterodontus* for the reason that the word *Heterodon*, identical in derivation, had been applied by Latreille (1802) to a group of reptiles. To the present writer this objection does not seem so serious as the possibility that *Centracion* might be mistaken for *Cestracion* when these

names are used for different genera of sharks. I have not found the name *Centracion* used by any writers other than Gray and Garman.

For the reasons stated, I prefer the generic name *Heterodontus* Blainville for those species of Bullhead Sharks that are represented by specimens living at the present time. Since many authors, mainly paleontologists, have used the name *Cestracion* for the same genus, it is necessary to recognize this term in reviewing their publications. For convenient reference, I have compiled the following synonymy:

HETERODONTUS (Blainville)

Port Jackson Shark (in genus *Squalus*). Phillip, 1789, Voyage to Botany Bay, pp. 283–284, pl. *Heterodontus*. Blainville, 1816, Bull. Soc. Philom. Paris, 3. ser. 3, p. 121 (not *Heterodon* Latreille, 1802).

Les Cestracions. Cuvier, 1817, Règné Animal, II, p. 129 (not *Cestracion* Klein, 1742 and 1776; nor Walbaum, 1792).

Centracion. Gray, 1831, Zool. Misc., I, p. 5.

Heterodontus, *Tropidodus*, and *Gyropleurodus*. Gill, 1863, Proc. Acad. Nat. Sci. Philadelphia, 14, p. 489.

Heterodontus. Duméril, 1865, Histoire Naturelle des Poissons, I, p. 424.

Heterodontus Bl. Maclay and Macleay, 1879, Plagiostomata of the Pacific. Proc. Linn. Soc. New South Wales, 3, p. 309.

Heterodontus Bl. Ogilby, 1890, Australian Palaeichthytes. Proc. Linn. Soc. New South Wales, 2. ser. 4, p. 184.

Cestracion Cuvier. Woodward, 1889, Catalogue Fossil Fishes British Museum. Part I, p. 331. Woodward, 1891, Hybodont and Cestraciont Sharks of the Cretaceous Period. Proc. Yorkshire Geol. and Polytech. Soc., 12, part 1, p. 67.

Heterodontus Bl. Jordan and Fowler, 1903, Proc. U. S. Nat. Mus., 26, p. 599.

Centracion. Garman, 1913, Plagiostomia. Mem. Mus. Comp. Zool., 36, p. 180.

Having adopted the name *Heterodontus* for the genus that includes the only living representatives of the Bullhead Sharks, I think it appropriate that the family name for these sharks should be Heterodontidae. This name or its equivalent in a different language has already been used, in the sense indicated, by several authors: e.g., Strüver, 1864; Duméril, 1865, p. 623; Maclay and Macleay, 1879, p. 307; McCoy, 1890; Ogilby, 1890, p. 184; Bridge, 1904 ("Cambridge Natural History", vol. VII, p. 444); Jordan and Clark, 1930, p. 10. Since Klein (1742), Duméril (1865), and Garman (1913) have assigned the generic name *Cestracion* to the Hammerhead Sharks, it seems advisable to reserve the name Cestraciontidae for the family that includes these sharks, as done by Garman (1913, p. 155). Nevertheless, it should be borne in mind that the name Cestraciontidae has been widely used, particularly by paleontologists, for the family that includes the genus *Heterodontus* (*Cestracion*). It is so used by Woodward, 1889 ("Catalogue Fossil Fishes British Museum," Part I); Regan (1906 and 1908); and Zittel (1911, 1923 and 1932). These are authors who retain the name *Cestracion* for the genus of Bullhead Sharks under consideration. Goodrich (1909) uses the name Cestraciontidae for the family though he seems to prefer *Heterodontus* for the genus.

COMMON NAMES—BULLHEAD SHARKS

In view of the existing confusion in the use of scientific names for the genus and family under consideration, the need for an undisputed common name is obvious. A few authors (Waite, 1896; Dean, 1901.2 and 1904; and Whitley, 1938 and 1940) have used the term Port Jackson Shark in a generic sense; but to the present writer this practice seems very objectionable. For more than a century, the name Port Jackson Shark had been used for one species only—the one first found at Port Jackson—save in a few instances where the identification of species was incorrect.

Waite (1898 and 1899) has referred to *Heterodontus galeatus*, in which the supraorbital ridges are very tall, as the "Crested Shark", and Whitley (1938 and 1940) has called it the "Crested Port Jackson Shark". The name Crested Shark would be appropriate for the entire genus, but it has not been so used. Whether it would apply to the entire family Heterodontidae (Cestraciontidae) as at present constituted (following the most recent classification, that of Zittel, 1932) is problematical.

BULLHEAD SHARKS.—There is no satisfactory common name that has been used exclusively to designate all species of the genus *Heterodontus*, but the term Bullhead Sharks (from the form of the head and snout) has been used by Jordan and Evermann (1896) and by Bridge (1904) for the family Heterodontidae. Since all the surviving species of this family belong to one genus, *Heterodontus*, the name Bullhead Sharks will serve the needs of those who are mainly interested in recent forms. The same consideration applies even though many genera (e.g., *Hybodus*) included by Bridge in the family Heterodontidae, are now assigned to a separate family, the Hybodontidae. The fact that the common name Bullhead Shark seemingly applies to two (closely related) families of sharks, one entirely extinct, need trouble no one—least of all the paleontologists, who are not much interested in common names.

The name Bullhead Shark is appropriate for all six species of *Heterodontus*. Freminville's drawing (1840) of *H. quoyi*, which shows a small head, is inaccurate. A better drawing of the same specimen, by Valenciennes (1846), is reproduced as my Text-figure 16, page 676. For related fossil forms, the evidence is naturally incomplete; but an example with nearly perfect skeleton may be found in *Hybodus hauffianus* E. Fraas (Text-figures 27 and 28, page 695). The profile of the head and anterior part of the body bears a marked resemblance to *Heterodontus* as represented by my specimens of *H. quoyi* and *H. francisci*, described in a later section of this article. These specimens (two of each species) are not only "bullheaded" but more or less humpbacked, like the fossil *Hybodus*, in the region dorsal to the bases of the pectoral fins. This feature is not represented in some drawings of *Heterodontus*; but it is shown in Garman's outline drawing of an adult *H. phillipi* (1888, Fig. 1, pl. 18); in Macleay and Macleay's drawings of a very young specimen of *H. phillipi* (my Text-figure 8, page 668) and of a young female *H. japonicus* (my Text-figure 23, page 691); in Jordan's portrayal (1905, Fig. 315) of an adult *H. francisci*; also in Kumada and Hiyama's figure (1937) of an adult *Gyropleurodus peruanus* (*Heterodontus quoyi*). Dean's photograph of a fresh-caught Japanese Bullhead Shark (my

Text-figure 3) shows no more than a faint suggestion of this humpbacked appearance. The hump is only slightly developed in the adult *Heterodontus phillipi* photographed (from life) by Saville-Kent (my Text-figure 4). In one of my specimens of *H. francisci*, the hump is so low as to be scarcely noticeable. On the basis of all the available data, one can scarcely say that the hump is typical for the genus *Heterodontus*. It occurs in at least four species, but is decidedly variable. In those individuals in which the hump is well developed, the head and "shoulders" have a profile mildly suggestive of a buffalo bull. This resemblance may be partly responsible for the name "Bullhead Shark."

FAMILY AND GENERIC CHARACTERS

In this section we are concerned with the distinctive characters common to those representatives of the family Heterodontidae that have survived to the present time. Since all recent species belong to one genus, *Heterodontus*, the distinction between family and generic characters is, for our purpose, of little importance. In the family Heterodontidae, Bridge (1904) includes at least five other genera that are known only as fossils; nevertheless, his brief description constitutes an excellent introduction to the study of living Heterodontids. Some points in the following quotation (from Bridge, 1904, p. 444) are illustrated by references, in square brackets, to figures in the present article.

Family Heterodontidae (Bullhead Sharks)

Head large and high, with a blunt snout projecting but little in front of the small and almost terminal mouth, and with prominent supraorbital crests [Text-figures 3, 4 and 5]. Trunk thickset and almost trihedral, covered with fine shagreen. Nostrils ventral but nearly terminal, with oronasal grooves [Text-figures 25 and 40, pages 692 and 711]. Spiracles small, beneath the eyes [Text-figures 3 and 4]. Two dorsal fins, each with a spine in front, the first opposite the interval between the pectorals and the pelvics, the second in front of the anal. Vertebral centra asterospondylic when fully developed. Palatoquadrate cartilages with an extensive articulation with the sides of the preorbital regions of the cranium [Text-figure 33, page 700], the normal suspensoria of a hyostylic skull (hyomandibular cartilages) taking little share in their support. Dentition similar in both jaws [Text-figures 11 and 14c, pages 671 and 673]. Teeth at the symphysis numerous, small and conical, furnished with three to five cusps in the young; those behind broad and padlike, arranged in oblique rows, the teeth forming the two middle rows being much larger than those in the front or behind. Living species, oviparous. Egg cases large with an external spiral lamina [Text-figure 37, page 706; and Figures 76 to 78, plate VII].

Continuing, Bridge notes that all the living representatives of this family are inhabitants of the Pacific Ocean, and that they feed principally on molluscs, the shells of which are crushed by their massive grinding teeth. According to Bridge, the different species vary in size (length) from two to five feet.

Some additional characters of the family Heterodontidae (Cestraciontidae) are listed by Goodrich (1909) as follows: The base of the pectoral fin grows forward below the last three branchial slits (my Text-figure 6, page 666). The pectoral girdle is very powerful (see also Daniel, 1915, Fig. 6, pl. III). According to Goodrich the suspension of the

jaws of *Heterodontus* is hyostylic, but with a very extensive articulation of the palatoquadrate with the cranium, so that the hyomandibular scarcely acts as a real support (my Text-figure 33, page 700). The suspension of the jaws is further discussed on pages 699 to 701 of the present article.

Garman's definition (1913) of the family Heterodontidae (his Centraciontidae) attempts to separate family characters from generic ones; but since he excludes fossils, the description really applies to only one genus, *Heterodontus*. Garman writes:

The living species of this family are small sharks which have short bodies and heads, blunt snouts, small spiracles below the hinder part of the eye, a narrow mouth near the end of the snout, with about four lobes in each half of the upper lip, both cuspidate teeth and grinders, five gill-openings of which several are above the pectorals, eyes without nictitating membranes or folds, nostrils connected with the mouth by naso-oral grooves, without cirri, two dorsals each preceded by a strong rigid spine, an anal behind the second dorsal, a short deep caudal, small carinate scales, a preorbital articulation between upper jaw and skull, and asterospondylous vertebrae.

In the phrase "eyes without nictitating membranes or folds", it is not quite clear what Garman means by the word "folds". If he means a fold of ordinary skin, then my adult specimen of *H. quoyi* is an exception, for it possesses a fold of skin capable of overlapping the eye somewhat like an upper eyelid.

The genus *Heterodontus*, which Garman calls *Centracion*, is characterized by him (1913) as follows:

Head short, snout blunt, crown narrowed, between strong orbital ridges. Eyes small, lateral. Nostrils with two thick valves reaching the mouth and curving toward the grooves. No narial cirri. Mouth narrow, with thick labial folds on both jaws. Teeth alike in upper and lower jaws, cuspidate in the anterior series, elongate longitudinally ridged grinders posteriorly. Pectorals large, dorsals moderate, anal small, caudal short.

The present writer has not been able to examine specimens of all species of *Heterodontus*, but the evidence at hand indicates that unusual breadth of the head and anterior part of the body, and decided flatness of the ventral surfaces of both head and body, are typical for adult specimens of this genus. A slightly humpbacked appearance, observed in my specimens of *H. quoyi* and *H. francisci*, is possibly a generic or even a family character. The supraorbital ridge leans outward, overhanging the eye. The anterior teeth are quincuspid in the very young; and acutely tricuspid in older specimens, with the median cusp increasingly predominant. In the adult they are often simple, becoming blunt when old. The lips, nasal apertures and naso-oral grooves of a single specimen of *Heterodontus*, probably *francisci*, have been described in detail by Allis (1919, pp. 158-164 and Figs. 6 and 7, pl. I.

A vestigial sixth branchial arch was found by Hawkes (1905) in two species of *Heterodontus*—*phillipi* and *francisci*. The other species were not available for examination. Hawkes states that the presence of a rudimentary sixth branchial arch in *Heterodontus* is in harmony with the view that the Heterodontidae are in some respects inter-

mediate between the Notidanidae and Chlamydoselachidae on the one hand, and the remaining Selachii on the other. In *Heterodontus francisci* as figured by Daniel (1915) the vertebral column is better developed, and the notochord is more constricted than in *Heptanchus* and *Chlamydoselachus*. Presumably these structures are much alike in all species of *Heterodontus*.

THE SPECIES OF HETERODONTUS

In Volume VIII of his "Catalogue of the Fishes in the British Museum", under the heading Cestraciontidae, Günther (1870) lists and briefly describes four species of *Cestracion* (*Heterodontus*): *phillipi*, *quoyi*, *francisci*, and *galeatus*. Another species known at that time, *Heterodontus* (*Cestracion*) *zebra* Gray, was lumped (by Günther) with *phillipi*. Thus it appears that, of the species now recognized, all but one (*japonicus*) were known at this early date (1870), though *zebra* was not uniformly recognized as a distinct species. As we shall see later, even *japonicus* was then represented in museum collections, and drawings of this species had been published before it was identified as a species distinct from *phillipi*.

Garman (1913, pp. 180-181) gives a key to the species of *Heterodontus*, which he calls *Centracion*, based mainly on the position and shape of the anal fin, the position of the first dorsal with respect to the pectorals, and the color pattern of the entire body. This is followed by a synonymy and a comprehensive list of the distinctive external characters for each species. Garman's classification agrees, in the main, with that of Macley and Macleay (1879, 1884 and 1886) but differs from that of Regan (1908).

GARMAN'S KEY TO THE SPECIES OF CENTRACION (*HETERODONTUS*)

- Base of anal about two-thirds of its length distant from the caudal.
 - Origin of first dorsal above the hind portion of the pectoral base, hind margin concave.
 - Bands transverse and broad to absent. *galeatus* [page 686]
- Base of anal nearly one length distant from the caudal.
 - Origin of the first dorsal above the forward part of pectoral base, hind margin concave.
 - Spots black, small, scattered. *francisci* [page 681]
- Base of anal two-thirds of its length distant from the caudal.
 - Origin of first dorsal behind the end of the pectoral base, hind margin convex.
 - Spots black, moderate, more or less grouped in twos and fours. *quoyi* [page 676]
- Base of anal fin two or more times its length from that of the caudal.
 - Origin of first dorsal above the middle of the base of the pectoral, hind margin deeply concave.
 - Bands transverse, narrow. *zebra* [page 675]
- Base of anal little less than twice its length from that of the caudal.
 - Origin of first dorsal above mid-pectoral base; fin somewhat concave on hind margin.
 - Bands both transverse and longitudinal. *phillipi* [page 664]
- Base of anal about one and one-fourth times its length from that of the caudal.
 - Origin of first dorsal above the end of the pectoral base, hind margin concave ([some-times] convex in second dorsal).
 - Bands transverse, broad. *japonicus* [page 688]

According to Garman there are six species of *Heterodontus* (*Centracion*) living at the present time, and these are found only in the Pacific Ocean. But it is not certain that sharks of the genus *Heterodontus* originated in the Pacific, since fossil Heterodonts have been found in Bavaria and in England (see p. 698).

Two species are confined to the eastern Pacific Ocean: *Heterodontus francisci* off the coast of California and the western coast of Mexico; and *H. quoyi* around the Galapagos Islands (it has also been taken at the Lobos de Fuero Island, nearer the coast of Peru). In the western Pacific, *H. phillipi*, the Port Jackson shark, is found off the coasts of eastern and southern Australia, and off New Zealand; and *H. galeatus* occurs off New South Wales and Queensland. The two other species are *H. zebra*, ranging from China (rarely from Japan) to the East Indies; and *H. japonicus* from the coasts of the Japanese islands south of Hokkaido. Thus two species occur in Japanese waters: *H. zebra* has been taken in the Sagami Sea, but the species usually found there is *H. japonicus*, the Japanese Bullhead Shark.

It is not necessary here to go into details concerning the surface anatomy of the adults of these species, but a brief account of their distinctive characters will be helpful. The species are here discussed in the order of their recorded discovery—meaning not merely the capture and description of a specimen but its correct identification. In the section devoted to each species, jaws and teeth are described last.

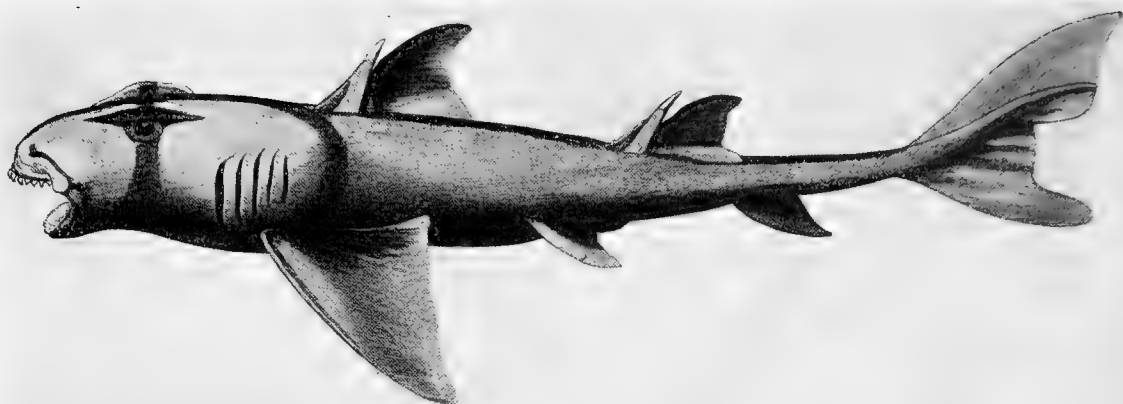
HETERODONTUS PHILLIPI BLAINVILLE

This, the Port Jackson Shark, is the best-known species, and for half a century it was the only species recognized. According to Whitley (1940) it occurs in the following Australian waters: South Queensland, New South Wales, Victoria, South Australia, Great Australian Bight to Southwestern Australia; commonest in the south. Found in littoral waters to depth of 94 fathoms.

The specific name, *phillipi*, has been spelled in different ways, but the species was named for Governor Phillip. His name is thus spelled on the title page of the book describing his voyage to New South Wales, with observations on the fauna and flora of that region. This book (Phillip, 1789) contains the first authentic description and drawings of the Port Jackson Shark—so named by Phillip because his specimen was captured at Port Jackson (Sydney Harbor), Australia. It was called *Le Squalé Phillip* by Lacépède (1798); *Heterodontus phillipi* by Blainville (1816); and *Centracion phillipi* by Cuvier (1817). An extensive synonymy is given by Garman (1913) under the title *Centracion phillipi*.

According to MacLay and Macleay (1879) this shark was called *Tabbigaw* by the Sydney aborigines. McCoy (1890) wrote that because of the form of the head and muzzle it was called the *Bulldog Shark* by Victorians. Saville-Kent (1897) states that *Oyster-crusher*, *Pigfish*, and *Bulldog Shark* are names by which the Port Jackson Shark was known locally to Australian fishermen.

Mainly because of its historical importance, the somewhat conventionalized (but otherwise correct) drawing of the Port Jackson shark in the volume describing Phillip's



Text-figure 5.

A Port Jackson Shark, *Heterodontus phillipi* Blainville. This female specimen, 610 mm. (24 inches) long, was captured at Port Jackson (Sydney Harbor), Australia.

After Phillip, 1789, pl. facing p. 283.

voyage is reproduced here (in Text-figure 5). For nearly a century this drawing remained the best portrait of *Heterodontus phillipi*. Under the heading "Port Jackson Shark", Phillip described the "new species" (in one sentence!) as follows:

The length of the specimen from which the drawing was taken is two feet; and it is about five inches and an half over at the broadest part, from thence tapering to the tail: the skin is rough, and the colour, in general, brown, palest on the under parts: over the eyes on each side is a prominence, or long ridge, of about three inches, under the middle of which the eyes are placed: the teeth are very numerous, there being at least ten or eleven rows; the forward teeth are small and sharp, but as they are placed more backward, they become more blunt and larger, and several rows are quite flat at top, forming a kind of bony palate, somewhat like that of the Wolf-fish; differing, however, in shape, being more inclined to square than round, which they are in that fish: the under jaw is furnished much in the same manner as the upper: the breathing holes are five in number, as is usual in the genus: on the back are two fins, and before each stands a strong spine, much as in the Prickly Hound, or Dog Fish: it has also two pectoral, and two ventral [pelvic] fins: but besides these, there is likewise an anal fin, placed at a middle distance between the last and the tail: the tail itself, is as it were divided, the upper part much longer than the under.

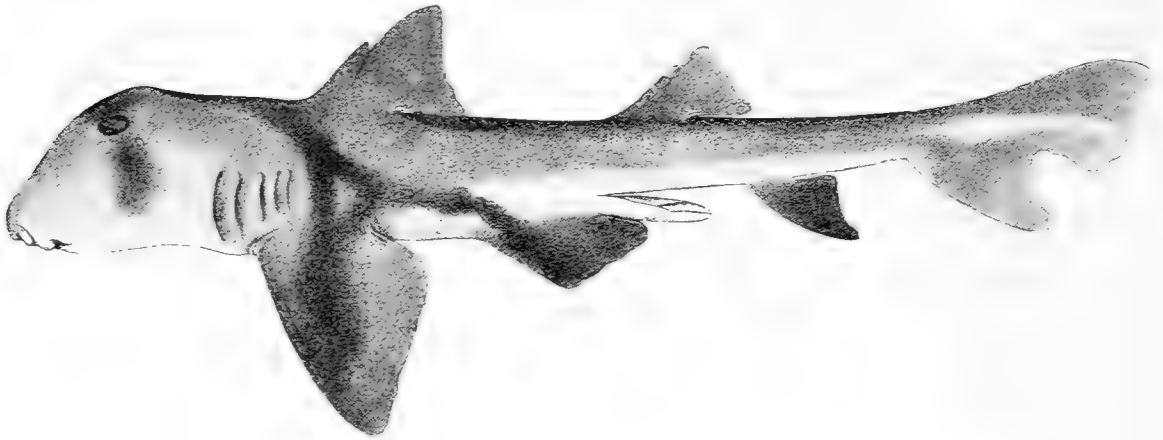
One may add that, in the words of Garman (1913), the spiracle is small, below the orbit and immediately behind a vertical from its posterior edge. The distribution of the lateral-line system of *Heterodontus phillipi* was earlier (1888) figured and described by Garman. For characters diagnostic of the species, see Garman's key. The photograph by Saville-Kent (my Text-figure 4) probably gives a better conception of the general appearance of this shark than any drawings reproduced herein.

Lesson's colored figure (1826) of a male *Heterodontus* (*Cestracion*) *phillipi* has been

criticised by Maclay and Macleay (1879), who alleged that it is so unlike the fish it is intended to represent as to suggest a doubt of its being the same species. In 1884 Maclay and Macleay stated definitely that this figure, which they call "a very bad one", does not represent the Port Jackson Shark. In Lesson's figure the color pattern of the body is unlike that of any other drawing of *Heterodontus phillipi* known to me, and the shape of the ventral lobe of the caudal fin is unlike that shown in all other drawings of specimens belonging to the genus *Heterodontus*. It is not necessary to reproduce this figure, since it was evidently drawn from a dried and distorted specimen.

Müller and Henle's full-length colored portrait (1841, pl. 31) labelled *Cestracion phillipi* is reproduced, under its proper name, as my Text-figure 21, page 690. In 1879 Macleay expressed a doubt as to the identity of the species represented by this figure, and in particular stated that the form of the six-cusped tooth pictured by Müller and Henle (but omitted from my Text-figure 21) had never, they believed, been seen in any adult specimen of the Port Jackson Shark. Further, in 1884, Maclay and Macleay stated that Müller and Henle's figure is most likely of the Japanese species, the number of vertical bands being identical, and that the tooth portrayed in the same plate is certainly not of either species. At the present time one can scarcely doubt that Müller and Henle's figure of the entire fish is a fairly accurate representation of the Japanese Bullhead Shark, *Heterodontus japonicus*. The same may be said of Brevoort's drawing (1856) of a specimen collected by the Perry Expedition to Japan. This specimen was labelled *Cestracion phillipi*; it is reproduced, under its proper name, as Text-figure 22, page 690.

Strüver (1864) has contributed what appears to be an accurate drawing of a badly posed specimen of *Heterodontus phillipi*. Perhaps this fish had been hardened in a laterally



Text-figure 6.

A full-grown male specimen of the Port Jackson Shark, *Heterodontus phillipi*, 795 mm. (31.4 inches) long. The external opening of the spiracle (retouched to make it more clearly visible) is shown behind, and a little below, the eye.

After Maclay and Macleay, 1879, Fig. 8, pl. 23. Right and left are here reversed.



Text-figure 7.

Dorsal view of the 795-mm. male specimen of *Heterodontus phillipi* shown, in lateral view, in Text-figure 6. The external openings of the spiracles are shown in the dark band crossing the head.

After Maclay and Macleay, 1879, Fig. 3, pl. 22.

flexed condition. The color pattern is not shown. The external spiracular opening is unusually large. It does not seem necessary to reproduce this figure.

In the order of historical sequence, the next authentic drawings of *Heterodontus phillipi* that have come to my attention are those of Maclay and Macleay (1879). Text-figure 6 is a copy of their drawing of an adult male specimen in lateral view. This is probably the best drawing of an adult male Port Jackson shark ever published. One should notice particularly the large head and the color pattern of the head and body. The authors state that the skin is roughly shagreened, and that the color in the fresh specimen is reddish-brown above and yellow with a pinkish tinge beneath. The color pattern (made up of brownish-black stripes) becomes indistinct within a few hours after death and in this drawing of a preserved specimen the color pattern is represented as seen in perfectly fresh specimens. In addition, the authors portray a dorsal view of the same adult specimen (my Text-figure 7). One is impressed by the breadth of the head including the branchial region. The color pattern of the dorsal surface is decidedly more complex than that of the lateral surface. The authors state that the average size of adult specimens of the Port Jackson Shark of both sexes is a little over three feet and that they seldom, if ever, attain a length of four feet. The external reproductive organs of an adult male are represented by Maclay and Macleay (1879) in their Figs. 24 and 25, pl. 24. Each myoxpterygium is armed with a sharp spine.

Of particular interest are Maclay and Macleay's figures (1879) showing lateral and dorsal views (my Text-figures 8 and 9) of a very young specimen only 225 mm. (8.8 inches) long. The authors state that this specimen was probably hatched only a day or two previ-



Text-figure 8.

Lateral view of a very young (recently hatched) female specimen of the Port Jackson Shark, *Heterodontus phillipi*, about 225 mm. (8.8 inches) long, drawn while fresh.

After Maclay and Macleay, 1879, Fig. 5, pl. 23. Right and left are here reversed.

ously; but to me it seems likely that it was about two weeks old. The entire color pattern is more distinct and somewhat more complex in this young specimen than in the adults. Concerning this specimen Maclay and Macleay wrote: "The very remarkable marking, the rounded form of the head and the proportionally large tail are peculiar to this stage". From the dorsal view of this specimen, we see that the head is not so broad, proportionally, as in the adult.

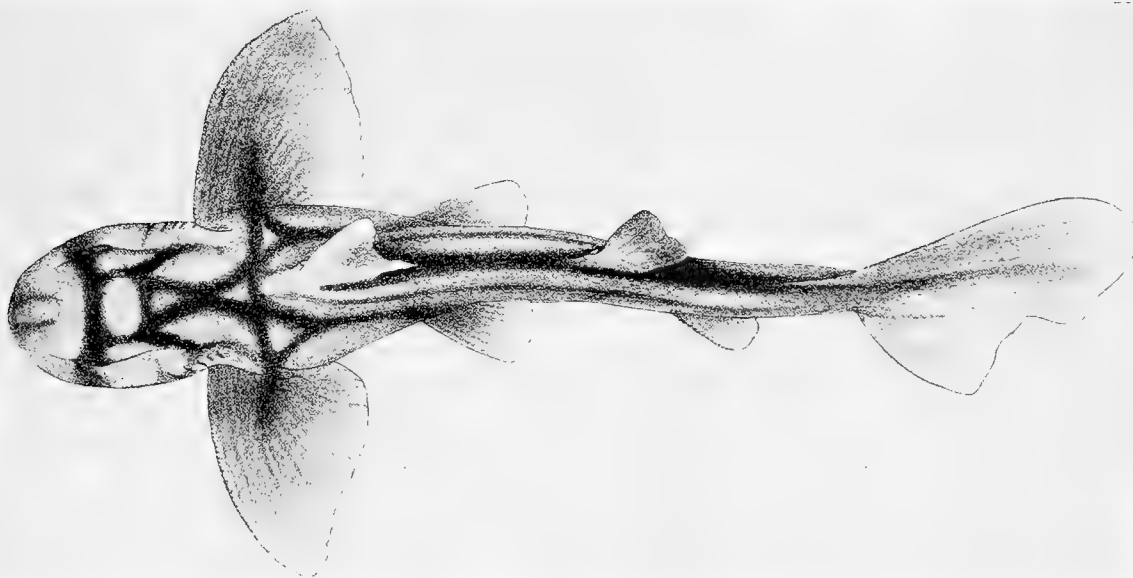
McCoy (1890) contributed two figures, in color, representing side views of male and female specimens of *Heterodontus phillipi*. The delicacy of the outlines of these drawings makes them unsuitable for reproduction here. In these figures the color pattern is not well shown, but McCoy's detailed description of the distribution of the dark-brown stripes corresponds closely with the pattern shown in Maclay's drawings (lateral and dorsal views). According to McCoy the dark-brown bands are most distinct in the young, nearly obsolete in the old, and invisible in stuffed, dried, or spirit specimens.

The photograph of the Port Jackson Shark by Saville-Kent (1897) is reproduced as my Text-figure 4, page 658. The specimen was alive when photographed. The original figure measures six and one-half inches long and is said to be one-tenth natural size. This would make the shark over five feet long. If the reduction is accurately stated, this is the largest Port Jackson Shark on record; but experience shows that one cannot always depend on records of this kind.

Waite (1898) collected specimens of the Port Jackson Shark, *Heterodontus phillipi*, from 14 different stations, and records that none of the specimens was longer than two feet. The majority were but little over 18 inches. He states that this shark is not known to grow longer than four and one-half feet, and that it is harmless.

Whitley's excellent representation (1940, Fig. 52) of a female *Heterodontus phillipi*, said to be after Waite, bears a remarkable resemblance to Saville-Kent's photograph reproduced as my Text-figure 4. The four posterior gill-slits and the color pattern of the sides of the body are more distinct in Whitley's figure. In addition, Whitley (1940, Fig. 53) has published an excellent original drawing of a female *Heterodontus phillipi*. Concerning the coloration, he writes: "Color grayish to light brownish. A dark blotch on snout. A blackish interorbital bar as broad as eye, continued and expanded below eye. A series of blackish stripes on body rather like harness."

Glands associated with the dorsal fin spines of certain sharks have been studied by Evans (1924). In *Squalus*, this author found a large groove along the base of each dorsal spine, on the side facing the fin. The groove is filled with a follicular gland, which was studied microscopically. Evans cites evidence that the secretion discharged by this gland has venomous properties. He states further that the dorsal fin spines of *Cestracion* (*Heterodontus*) *phillipi* are similar to those of *Squalus*, but with a shallower groove. This groove likewise contains a follicular gland, but the nature of the secretion was not studied in *Heterodontus*. The author makes comparisons of the dorsal fin spines of *Squalus* and *Cestracion* (*Heterodontus*) with those of some fossil *Cestracionts*, and of *Hybodus*. The presence of a large groove along the bases of the dorsal fin spines of these fossil forms suggests that, in life, glands were present at the bases of these spines also.

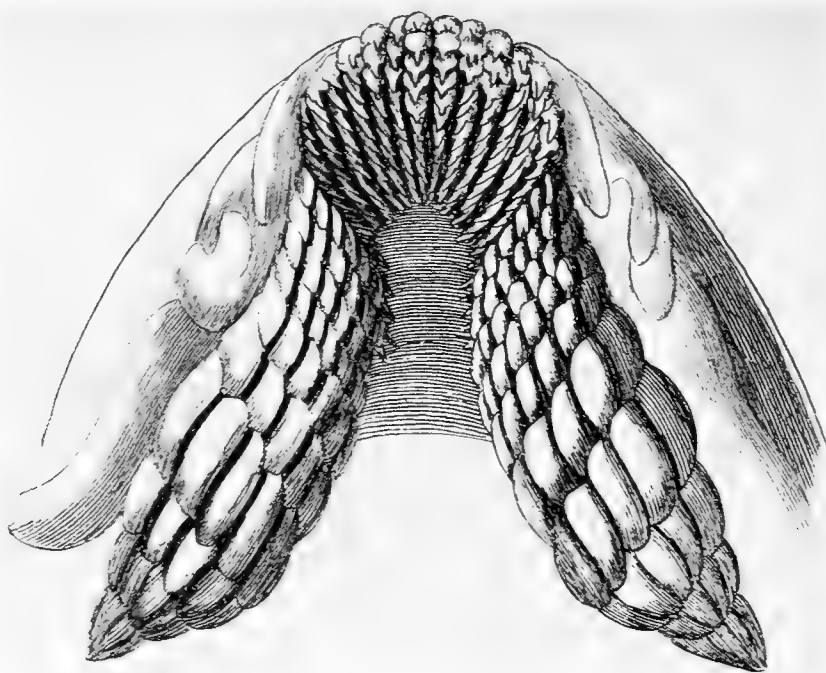


Text-figure 9.

Dorsal view of the very young female Port Jackson Shark, *Heterodontus phillipi*, about 225 mm. (8.8 inches) long, shown in lateral view in Text-figure 8. The drawing was made while the specimen was fresh.

After Macleay and Macleay, 1879, Fig. 1, pl. 22.

JAWS AND TEETH.—Goodrich (1909) contributes an outline drawing of an incomplete skull of *Heterodontus phillipi*, here reproduced as Text-figure 33, page 700. This drawing is introduced primarily to show the mode of suspension of the jaws; but when we compare this figure, showing these jaws in lateral aspect, with other figures (Text-figures 10, 11 and 14) showing them in dorsal and ventral aspects, we are impressed by their massive pincer-like character—somewhat like the jaws of *Heptanchus* outlined by



Text-figure 10.

Teeth of the Port Jackson Shark, *Heterodontus phillipi*. Whether the figure represents an upper or lower jaw is not stated, but apparently it is a lower jaw.

After Phillip, 1789, pl. facing p. 283.

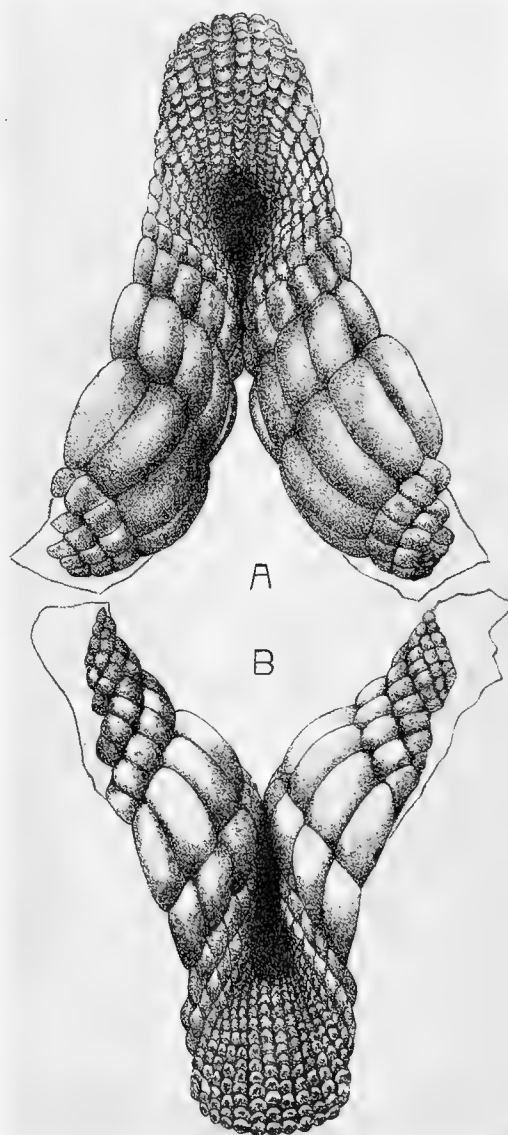
Goodrich, 1909, Fig. 59A. One can readily imagine how powerful these jaws are when equipped with the grinding teeth—set well back toward the angle of the jaws—and with the musculature necessary for crushing the shells of molluscs that form the principal food of this species of *Heterodontus*. Garman also (1913, Atlas, Fig. 4, pl. 47) has figured the jaws of *Heterodontus phillipi* in lateral view, but in form so different from Goodrich's portrayal that one might think the two drawings were made from different species.

Phillip's drawing (1789) of the teeth of the Port Jackson Shark is reproduced here as Text-figure 10. The author does not state whether this is an upper or a lower jaw, but upon comparison with the figures of Strüver (1864), Macleay and Macleay (my Text-figure 11) and McCoy (my Text-figure 14) it appears to be a lower jaw. In this specimen

(Text-figure 10) there are 33 rows of teeth. The anterior teeth (13 series or transverse rows) are distinctly tuberculate, but, due to the overlapping of the teeth in each row, their form is not completely shown except in the most anterior members of each series. Each anterior tooth possesses one large central cusp, and there may occasionally be seen in the drawing a rudimentary lateral cusp on one or both sides of the central cusp. The posterior teeth (ten rows on each side) are large, smoothly rounded, and in their natural arrangement combine to form an exposed surface resembling that of a stone-block pavement. Thus the anterior teeth are adapted for holding the prey, the posterior ones for crushing and grinding it.

Strüver (1864) made drawings of the teeth of both upper and lower jaws of *Heterodontus phillipi*. With respect to the dentition, upper and lower jaws are much alike, save that the lower is slightly shorter and more obtuse in front, which makes some difference in the arrangement of the teeth. In this respect the lower jaw resembles the jaw figured by Phillip (1789); but in Strüver's figures both jaws show a more gradual transition between anterior (cusped) teeth and posterior (grinding) teeth, so that the line of demarcation between the two kinds of teeth is not sharply defined. However, one might assign 15 transverse rows to the anterior region in the upper jaw, and 13 rows to this region in the lower jaw. The total number of teeth in the upper jaw is 33, in the lower jaw 31. In Strüver's figures the anterior teeth are pointed but without obvious secondary cusps; each posterior tooth has an indistinct longitudinal ridge.

Miklouho-Maclay (in Maclay and Macleay, 1879) figured the teeth of upper and lower jaws in both adult and young specimens of *H. phillipi*. The dentition of an adult, as shown in his figures (my Text-figure 11) resembles that represented in Strüver's drawings (1864). As in Strüver's figure, the lower jaw is shorter than the upper, and is more obtuse in front.

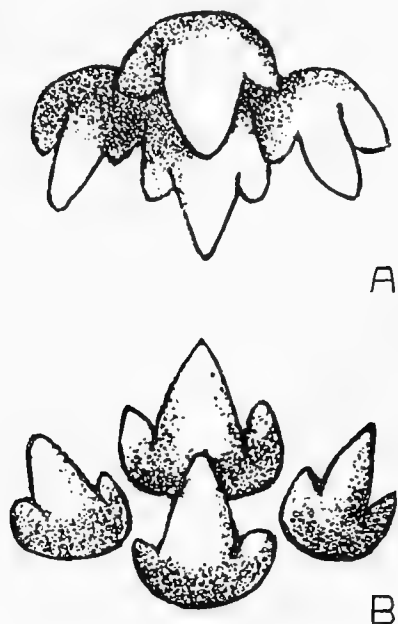


Text-figure 11.

Teeth of an adult *Heterodontus phillipi*:
A, upper jaw; B, lower jaw.

After Maclay and Macleay, 1879, Figs. 16 and 17, pl. 24.

The transition between anterior (cusped) teeth and posterior (grinding) teeth is so gradual that any division into two types must be somewhat arbitrary. However, of the 33 rows of teeth on the upper jaw one might assign 19 rows to the anterior region, leaving 14 (seven on each side) in the posterior region. In the lower jaw there are 32 rows of teeth of which 14 rows may be assigned to the anterior region, leaving 18 (nine on each side) for the posterior region. Thus there seem to be more rows



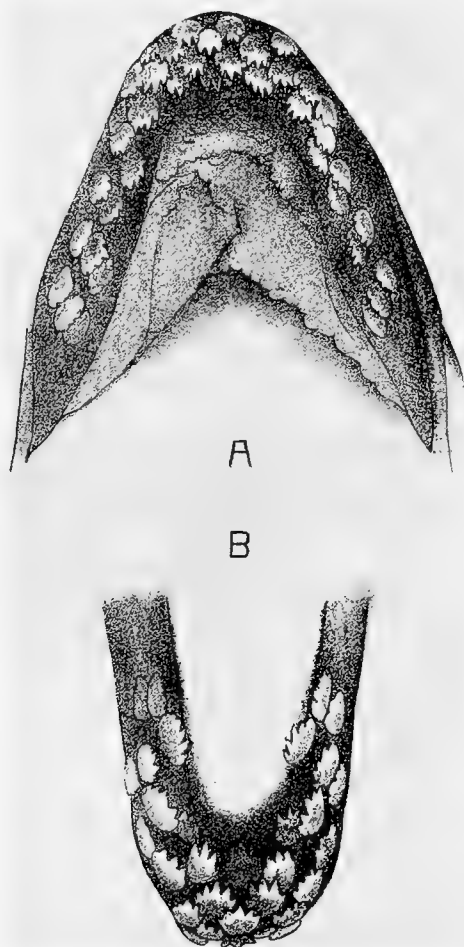
Text-figure 12.

Anterior teeth of a young *Heterodontus phillipi* about 761 mm. (22.1 inches) long: A, from the upper; B, from the lower jaw.

After Maclay and Macleay, 1879, Figs. 18A and 18B, p. 24.

of anterior (cusped) teeth on the upper jaw than on the lower (as in Strüver's figure). In another specimen Maclay counted 34 rows of teeth on the upper jaw and 31 on the lower. The largest number of rows of teeth noted by Maclay was 36 on an upper jaw; the largest number on a lower jaw is not stated, but we infer that it was less.

In Maclay's figures, as in Strüver's, the anterior teeth of the adult have only one cusp each; but in Maclay's figure these are more blunt as if worn by use. Maclay states that



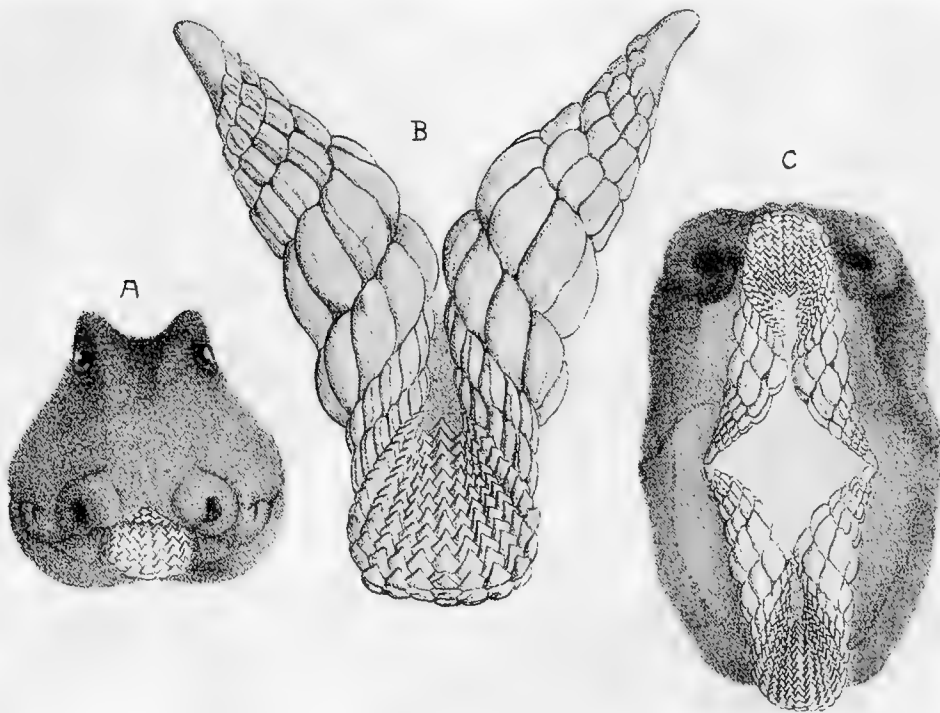
Text-figure 13.

Dentition of a very young (recently hatched) female *Heterodontus phillipi* about 225 mm. (8.8 inches) long: A, upper jaw; B, lower jaw.

After Maclay and Macleay, 1879, Figs. 14 and 15, pl. 24.

the anterior teeth (my Text-figure 12) of a not fully developed *Heterodontus phillipi* 761 mm. (22.1 inches) long are distinctly tricuspidate, the central cusp predominating, while those of the adult become almost pavement-like, with an inconspicuous cusp. He further states that on the posterior teeth of a young specimen 418 mm. (16.4 inches) long, a longitudinal ridge is much more pronounced than in older specimens.

Maclay (Maclay and Macleay, 1879) portrayed also the dentition of both upper and lower jaws in their very young specimen of *Heterodontus phillipi* only 225 mm. (8.8 inches) long. Comparatively few teeth are exposed (my Text-figure 13) and these are nearly all cuspidate. About 40 teeth are visible on the upper jaw and about 32 on the lower jaw, roughly arranged in transverse rows of two or three teeth each, giving about 17 rows on the upper jaw and 13 on the lower jaw. Most of these teeth have three to five cusps, and seldom a predominating central cusp. The cusps are best developed in the most anterior teeth and are less conspicuous posteriorly. They are absent in one or two teeth of the last row on each side. Maclay states that some other teeth came into view after the mucous membrane had been dissected off. He calls attention to "the very great similarity" between the dental armature of the young *Heterodontus* and that of (adult?) Notidanids.



Text-figure 14.

Head and teeth of the Port Jackson Shark, *Heterodontus phillipi*, in three aspects: A, anterior view of the head, mouth closed, showing exposure of teeth above and below. B, teeth of lower jaw in natural size. C, mouth widely opened, to show the similarity of dentition above and below.

After McCoy, 1890, pl. 113.

McCoy's descriptions and drawings (1890) of the teeth of *H. phillipi* (my Text-figure 14) are excellent. "Teeth alike in both jaws, the median front rows very small, acutely tricuspid when young, simple and with obtusely triangular cusp in middle age, blunt and hexagonal when old; more posterior teeth large, oblong, longer than broad, flattened, arranged in oblique, spiral rows on each side of the jaw, the anterior and posterior ones smaller than those in the middle." His figure of the lower jaw (my Text-figure 14B) reveals a distinct longitudinal ridge on each of the posterior grinding teeth—a feature mentioned but not figured by Maclay (1879). The lower jaw shows a distinct line of demarcation between anterior cusped teeth and posterior grinding teeth—as in the figure by Phillip (Text-figure 10) but not to the same degree. In this jaw there are only eleven transverse rows of anterior cusped teeth. These, with eight rows, on each side, of posterior grinding teeth, make a total of 27 rows in this lower jaw. Text-figures 14A and 14C show, respectively, the appearance of the mouth when it is closed and when it is open. The lower jaw in Text-figure 14C is identical with that in Text-figure 14B. The upper jaw, shown in Text-figure 14C, likewise has 27 rows of teeth. Of these, 12 or 13 rows are anterior or cuspidate teeth. The transition between cuspidate and grinding teeth is not so abrupt as it is in the lower jaw.

Garman (1913, Figs. 4 to 6, pl. 47) portrays the teeth of a male *Heterodontus phillipi* about 864 mm. (34 inches) long. The transition between anterior (cuspidate) and posterior (grinding) teeth is not so abrupt, in this specimen, as in some others. The dividing lines here chosen are somewhat arbitrary. The upper jaw has 13 transverse rows of anterior (cuspidate) teeth and 10 rows (5 on each side) of posterior (grinding) teeth, making a total of 23 rows. The lower jaw has 11 rows of anterior (cuspidate) teeth and 8 rows (4 on each side) of posterior (grinding) teeth, making a total of only 19 rows. Garman's figures of the posterior grinding teeth or "molars" show on each tooth a distinct longitudinal ridge or "keel", and on each side of this, many fine transverse ridges. Garman states that the ridges on the molars of younger specimens become less conspicuous with age and use, and that the harder the food in a particular locality the fainter the ridges appear.

To summarize the recorded data on the dentition of the adult or nearly adult *Heterodontus phillipi*, one may state that all the descriptions and drawings emphasize the decided differences between anterior and posterior teeth—differences that suggested the generic name, *Heterodontus*. When we compare the dentition of upper and lower jaws, we find that Bridge's statement "dentition similar on both jaws" is true of all specimens that have been described. One may be more definite and explain that the dentition (meaning the kind, number and arrangement of the teeth) is alike on upper and lower jaws, with certain slight reservations. First, as McCoy states, there are usually "a few more rows in upper than [in] lower jaw". Using the meager data available we find that the average number of transverse rows on the upper jaw (6 cases, average 31.0 rows) is slightly greater than on the lower jaw (6 cases, average 28.8 rows). In only one instance (McCoy's drawing) is the number of rows of teeth the same on both jaws. The largest number of teeth recorded

for an upper jaw is 36; for a lower jaw, 33. Second, I have noted that, in the figures of various authors, there is a slight difference in the shape of the opposed surfaces of upper and lower jaws: in the lower jaw this surface is a trifle shorter. This may account for the difference in the number of rows of teeth. Third, in every case recorded the upper jaw has more rows of anterior (cuspidate) teeth than the lower jaw.

HETERODONTUS ZEBRA GRAY

This species ranges from the coasts of China and (rarely) Japan, to the East Indies. It was first described in 1831 by Gray, who named it *Centracion zebra*. In 1851 he adopted the name *Heterodontus* for the genus.

The earliest drawings of this species that I have been able to find are those of Maclay and Macleay (1886). These were made from a preserved specimen, a young female about 518 mm. (20.4 inches) long, captured at Swatow in the South China Sea.



Text-figure 15.

A male specimen of *Heterodontus zebra* Gray, about 1220 mm. (48 inches) long.

From a drawing in color by Ito, 1931, Fig. 6, pl. V.

The color pattern is more adequately shown in my Text-figure 15, from a folio volume entitled "Illustrations of Japanese Aquatic Plants and Animals", published by the Japanese Fisheries Society in 1931. This represents an adult male about 1220 mm. (48 inches) long. The Japanese common name is said to be "Simanekozame".

The most conspicuous peculiarity of this species is the presence of numerous narrow transverse dark-brown stripes (Text-figure 15) which suggested the specific name, *zebra*. Except in a few places, these dark-brown stripes alternate with lighter-brown narrower ones. Garman (1913) states that in a 19-inch female specimen studied by him, the body and head are more slender, the head more pointed and the fins longer, than in other species of the genus. Maclay and Macleay's drawing of a dorsal view of their specimen shows head and body very narrow as compared with other species. In this drawing the head is rotated slightly, so the width cannot be measured for comparison with the total length. Maclay and Macleay's figures show prominent supraorbital ridges in both lateral and

anterior views but these are lacking in the Japanese drawing reproduced as my Text-figure 15. Maclay and Macleay state that the dorsal fins are very falcate. This feature is perhaps exaggerated in their drawing, which was made from a preserved specimen; it is more moderate and more life-like in the Japanese drawing. In the latter figure the anterior margin of the pectoral fin is opposite the fourth gill-slit, while in Maclay and Macleay's figure it is opposite the second.

THE TEETH.—According to Maclay and Macleay (1886), the anterior teeth of their young female specimen of *H. zebra* (518 mm. long) were five-cusped. Garman (1913) states that the anterior teeth are quincuspid in the young, tricuspid in the adult.

HETERODONTUS QUOYI FREMINVILLE

Examples of this species (Text-figure 16) have been taken off the western coast of South America, specifically at the Galapagos and Lobos de Afuera Islands—the latter



Text-figure 16.

Heterodontus quoyi Freminville: a male specimen about 475 mm. (18.7 inches) long, taken at the Galapagos Islands. The original figure, in color, is labelled *Cestracion pantherinus*.

After Valenciennes, 1846, Atlas (Poissons), Fig. 2, pl. 10.

close to the coast of Peru. In addition, a Heterodontid shark taken at the Lobos de Tierra Island, Peru, belongs to this species. This specimen was described and figured by Evermann and Radcliffe (1917) who named it *Gyropleurodus peruanus*. Of this fish they write: "The species appears to be most closely related to the poorly described *G. quoyi*, but differs in coloration, in insertion of anal, and relative size of pectoral". After a careful study of the matter, Beebe and Tee-Van (1941) conclude that all the Heterodontid sharks thus far taken off the western coast of South America belong to the species *peruanus* (*quoyi*) as redescribed by Valenciennes and later authors. They state that the alleged differences between *quoyi* and *peruanus* do not exist, although there is some individual variation in the color patterns. With this conclusion the present writer is thoroughly in accord. The native name of *H. quoyi* is "Gato" (Nichols and Murphy, 1922).

There remains some doubt concerning the identity of a Heterodontid shark taken off the western coast of Mexico, or perhaps of Central America, which was described and figured by Kumada and Hiyama (1937). They named it *Gyropleurodus peruanus*. Their drawing portrays a shark in most respects like *H. quoyi*, but the color pattern is intermediate between *H. quoyi* and *H. francisci*. Since the color pattern of the former is somewhat variable, the drawing was probably made from a specimen of *H. quoyi*; but there is no other record of the occurrence of this species so far north.

Heterodontus quoyi was first figured and described by Freminville (1840); and later by Valenciennes (1846 and 1855). Their figures are based on the same specimen, a male taken at the Galapagos Islands; but these differ so much that they might be considered as representing two different species. Valenciennes called this specimen *Cestracion pantherinus*, though it had been previously named *Cestracion quoyi* by Freminville. The brief accounts by Duméril (1865), Günther (1870), Maclay and Macleay (1879) are based on either Freminville's or Valenciennes' description and figure; they contain nothing new. Maclay and Macleay's figure (1879) is a copy of Freminville's. Until Garman (1913) described at least one new specimen (a female taken at the Galapagos Islands), Freminville's male specimen of *H. quoyi* remained the only example of the species. In his very inadequate description, some comparisons with *Heterodontus phillipi* are irrelevant since they involve the acceptance of erroneous features in Lesson's (1826) drawing of the Port Jackson Shark. Freminville's figure of *H. quoyi* does not inspire confidence, and I have therefore reproduced Valenciennes' life-like portrait of the same specimen (my Text-figure 16) as the basis of this account.

The length of Freminville's specimen is variously recorded as a little more than a foot and a half, by Freminville; 475 mm. (18.7 inches) by Valenciennes; 460 mm. (18.1 inches) by Duméril; and two feet (evidently a blunder) by Maclay and Macleay. Garman's female specimen measured 18 inches long. Garman states that its body is rather stout as compared with a specimen of *H. zebra* of equal length. Some passages in Garman's characterization imply that he had more than one specimen, but he does not give the lengths of any others.

The most noteworthy feature of Freminville's drawing of *H. quoyi* is the small size of the head. The author states that the head is smaller and a little more elongate than that of *Cestracion phillipi*. As portrayed by Freminville, the head is very small and pointed. In Valenciennes' drawing (my Text-figure 16) the head is proportionally much larger. Garman does not say that the head of his specimen (or specimens?) is small. He does write that the snout is blunt, the cheeks swollen, the eye and spiracle small. Freminville states that the supraorbital ridge is comparatively weak ("moins forte") but Garman records that it is strong, somewhat overhanging the orbit, not ending abruptly as in *H. francisci*. In Valenciennes' figure (my Text-figure 16) the posterior extremity of the supraorbital ridge ends rather abruptly, as in Kumada and Hiyama's figure of *H. francisci* (my Text-figure 18, page 682). Some specimens of *H. quoyi* examined by me show variations in the form of the supraorbital ridge, as described later.

Authors agree that in *H. quoyi* the origin of the first dorsal is well behind the root of the pectoral. Garman states that the dorsal fins are of moderate size, with convex hind margins; the base of the anal fin is two-thirds its length distant from the caudal; and the anterior gill-opening is more than twice as "wide" as the hindmost. Freminville states that the skin is entirely shagreened, is colored a ruddy-brown and is everywhere strewn with dark-brown spots, generally round. Concerning the coloration of *H. quoyi* Garman (1913) writes:

Back rusty-brown, yellow below, with scattered spots of black, from mere specks to spots as large as the orbit or larger, over the entire body and fins. Commonly the spots show a tendency toward grouping in twos and fours; in [some] cases they are more confluent. On some [specimens] there are five or six rather indefinite transverse bands of darker separated by spaces of equal width; a band crosses the nape, another lies in front and a third behind the first dorsal, one in front and one behind the second dorsal and one in front of the caudal. A darker area extends from each orbit across the cheek.

It remains to record some observations on two specimens of *H. quoyi*, from the collections of the American Museum of Natural History, which I have been permitted to examine. The larger specimen is a female about 527 mm. (20.75 inches) long, measured after 20 years' immersion in alcohol. It is probably adult or nearly adult. This specimen was collected on January 5, 1920, by Dr. R. C. Murphy, on the Lobos de Afuera Island (off the coast of Peru) where it was washed ashore in a dying condition. The other specimen is a male only 372 mm. (14.6 inches) long, and evidently very young. It was taken on June 9, 1925, by Dr. R. C. Murphy at Albemarle Island of the Galapagos group, from the stomach of a Tiger Shark (*Galeocerdo*). It seems in good condition after 15 years' preservation in alcohol. Concerning these specimens it is necessary to consider here only a few external characters, particularly those relating to the form of the body. Certain details, including additional measurements, are left for a later section of the present article entitled "Comparisons of *H. quoyi* and *H. francisci*".

In the absence of published drawings of either dorsal or ventral views of *H. quoyi* one is immediately impressed, upon examining these specimens, by the breadth of the head and by the flatness of the ventral surfaces of both head and body. The outline of the entire body, viewed from above, is quite tadpole-like. In the adult female the head is much broader, proportionally, than in the young male. The head height of the young male is greater, proportionally, than the head height of the adult female. In both specimens the body height is greatest immediately in front of the first dorsal fin, where it exceeds the height of the head sufficiently to give the fish a humpbacked appearance. In its middle third, the supraorbital ridge is low and broad. In both specimens, this portion is merely a fold of the skin not supported by the endoskeleton. In both specimens, the external spiracular openings are small, measuring from 2 to 3 mm. in their larger diameters. The first gill-slit is about twice the length of the fifth. The origin of the first dorsal is well behind the posterior end of the pectoral base. The base of the anal fin is about three-fourths its length from the caudal.

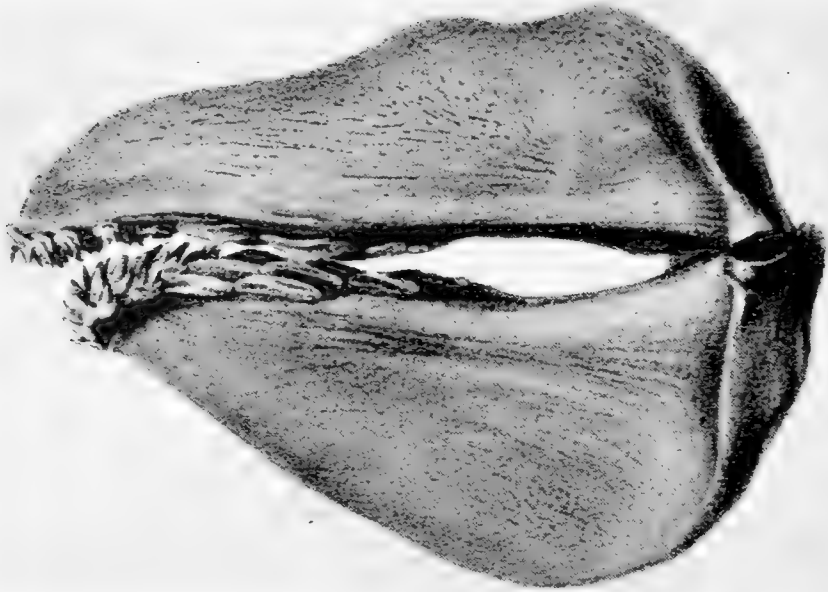
In my 527-mm. female specimen of *H. quoyi*, the entire supraorbital ridge is low, but it is lowest in its middle third where it is a mere fold of skin, not supported by the endoskeleton. This fold overlaps the eyeball like an upper eyelid. Its function is doubtless protection of the eye while the fish is forcing its way under rocks or into crevices. When pressed upon, this fold of the skin reduces the palpebral fissure to a narrow slit. Though in all species of *Heterodontus* the supraorbital ridge leans outward, thereby overhanging the eye, *H. quoyi* is probably the only species in which any part of it actually overlaps the eyeball. In my adult female specimen of *H. quoyi* the supraorbital ridge does not end abruptly, as it does in *H. francisci*.

In the same adult female specimen of *H. quoyi*, the "cheeks" appear swollen, and the gill-covers, especially the first, bulge outward as if inflated by pressure from within. It seems hardly likely that this condition could be produced by unequal shrinkage, since it does not occur in other specimens preserved in the same way. As viewed from above, the head is broad behind and somewhat pointed in front, like the head of a venomous snake. The ventral surface of the head is decidedly flat, and lies in the same plane as the ventral surface of the body. The nasal apertures open ventrad. As viewed from the side, the dorsal surface of the head slopes forward to a fairly sharp rostrum directly in front of the nostrils. The dorsal fins are small. The hind margin of the first dorsal is slightly convex, that of the second dorsal is almost straight. The dorsal spines are decidedly small but are much worn; they project less than a centimeter beyond the skin. The pectoral fins are broad and when extended (as far as possible in their rigid condition) the distance from tip to tip is about 250 mm., equal to nearly half the body length. The scales on the ventral surface of the body are smooth; those on the dorsal surface are tuberculate and are much larger than the scales on the ventral surface.

The form of my young specimen of *H. quoyi* (a male 372 mm. long) differs considerably from that of the adult specimen (a female). Both head and body are more slender, especially in width. The ventral surface of the head is not so flat as in the adult. The supraorbital ridges are taller proportionally; they are especially well developed at their posterior ends, where they terminate abruptly. Though the middle portion of each supraorbital ridge is depressed, it overhangs the eye much less than in the adult. The dorsal fins are proportionally larger, and the spines longer and sharper, than in the adult. The posterior edges of both dorsals are so frayed that the original shapes of their margins cannot be determined. It seems unlikely that any of the differences noted are due to sex. Some characters, like the abrupt termination of the supraorbital ridges, may be individual variations, but most of the differences are probably correlated with differences in age.

In my two specimens of *H. quoyi*, the entire body, including the fins, is ornamented with many dark-brown (nearly black) spots of various sizes. Of these, few are larger than the orbit. These spots are occasionally grouped in twos, threes and fours. On the dorsal surface there is a fairly regular bilateral arrangement of spots or groups of spots, though in the large female the spots on that surface are more or less obscured by a dark-brown ground color. On the ventral and ventrolateral surfaces the distribution is

random, and the spots are distinct because the ground color is a light-brown. In the small male specimen of *H. quoyi* the ground color is paler than in the adult female, so that the spots are everywhere clearly visible. I do not find in either specimen the "five or six rather indefinite transverse bands" mentioned by Garman (1913). The spots on the dorsal surface are distributed at fairly regular intervals in such fashion that when indistinct they might suggest broad transverse stripes; but such stripes would be more numerous than those described by Garman.



Text-figure 17.

Jaws and teeth of *Heterodontus quoyi*, in lateral view. The original is labelled *Centracion quoyi*.

After Garman, 1913, Atlas, Fig. 1, pl. 47.

JAWS AND TEETH.—In Garman's figure (1913) showing the jaws of *H. quoyi* in lateral view (my Text-figure 17) the upper jaw projects anteriorly beyond the lower jaw, as in his figure of the jaws of *H. phillipi* drawn from the same aspect. Both jaws appear very strong.

Some samples of both anterior and posterior teeth of *H. quoyi* are described and sketched by Freminville; but Garman (1913, Atlas, Figs. 1 to 3, pl. 47) portrays the entire dentition of both jaws. Authors agree that the anterior teeth are sharp and tricuspid, with the middle cusp prominent. Garman records that the "molar" teeth are elongate, narrow, each with a longitudinal ridge or keel. In Garman's drawings the upper jaw has 11 transverse rows of anterior (cuspidate) teeth and 8 rows (4 on each side) of posterior (grinding) teeth, making 19 rows in all. The lower jaw has 9 rows of anterior (cuspidate) teeth and 6 rows (3 on each side) of posterior (grinding) teeth, making 15 rows in all. In

general, the dentition resembles that of a half-grown specimen of *H. phillipi*. The anterior teeth of my adult female *H. quoyi* are tricuspid with the middle cusp prominent; but the anterior teeth of my young male specimen are quincuspid.

HETERODONTUS FRANCISCI GIRARD

This species has been taken off the coast of California and the western coast of Mexico—especially in the Gulf of California. It was first described by Girard (1856). The external form of the body has been figured by Macleay and Macleay (1879); Jordan and Evermann (1900, Fig. 9, pl. III); Jordan (1905, vol. 1, Fig. 315); Daniel (1934, Fig. 17); Kumada and Hiyama (1937, pls. 44 and 45). The best figures are probably those of Kumada. His figures of a 540-mm. female are reproduced as Text-figures 18 and 19.

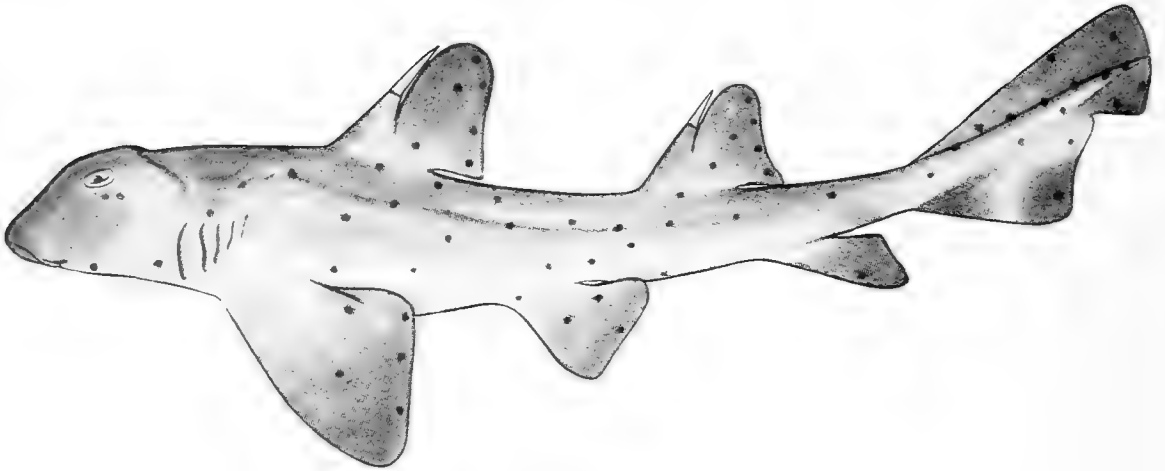
Girard's description of *Heterodontus francisci* (which he calls *Cestracion francisci*) is limited to a single paragraph, which I quote in full:

The largest of these specimens now before us, and measuring nearly two feet, bears a very strong resemblance to *C. phillipi*, though of a somewhat more bulky appearance. The bony ridge, above the eye, is much more developed, and the fins are larger also. The posterior margin of the caudal is bilobed instead of being rounded: an emargination corresponding to the top [sic] of the vertebral column. The anal is placed farther back; its tip projecting beyond the anterior margin of the inferior lobe of the caudal. The posterior extremity of the ventrals [pelvics] extends beyond the anterior margin of the second dorsal. Color, above yellowish-gray, darker in the young; beneath light yellow. Small roundish-black spots are spread all over the body and fins.

Girard's comparison of the caudal fin of *H. francisci* with that of *H. phillipi* is based on Lesson's erroneous figure. The emargination corresponds to the tip, not the "top", of the vertebral column.

Some other points in which this species differs from *H. phillipi* are mentioned by Macleay and Macleay (1879) whose account differs in some respects from Girard's. Their drawings were made from an adult male *H. francisci*, 708 mm. (27.9 inches) long, from the Bay of Monterey, California. Dorsal and lateral views of the entire fish are shown, but without spots—perhaps the specimen had been long in alcohol. In the lateral view the pectoral and pelvic fins are not well displayed. As compared with *H. phillipi*, the head is proportionally broader and less high; its profile is less steep and more convex; the supraorbital ridges are less prominent, continuing almost to the snout and terminating abruptly behind the eyes. The spiracle is larger and farther from the eye. The first gill-opening is scarcely twice the length of the fifth. The dorsal spines are very strong and are more than half the length of the dorsal fins. The dorsal fins themselves are more broadly rounded at the apex and slightly emarginate behind.

Garman (1913) states that the color of *H. francisci* is grayish or olivaceous-brown with small scattered spots of black over body and fins. On large specimens the spots are sometimes absent or nearly so. The body is yellowish beneath. In the figures by Jordan (1905) and by Daniel (1934) a few small roundish-black spots of fairly uniform size are scattered over the entire body including the fins, and the supraorbital ridges differ from



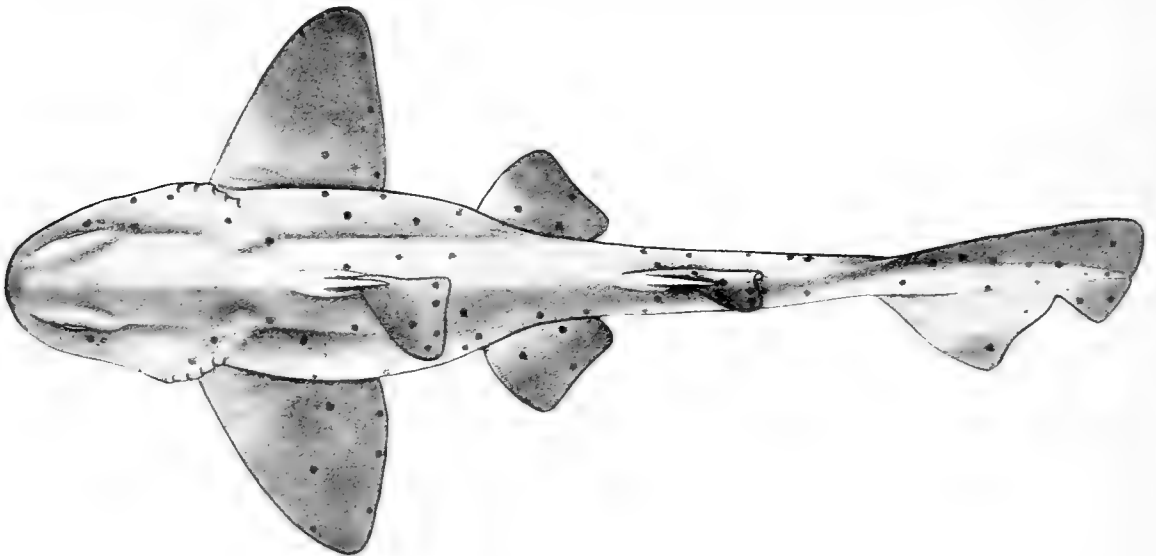
Text-figure 18.

Lateral view of a 540-mm. (21-inch) female specimen of *Heterodontus francisci* Girard.

After Kumada and Hyama, 1937, pl. 44.

those described by Maclay and Macleay (1879) and by Garman (1913) in not ending so abruptly behind the eyes.

The principal external characters of an adult or nearly adult female *H. francisci* are well illustrated in my Text-figures 18 and 19, after Kumada and Hiyama (1937). These authors state that this shark, which is abundant in their collection, scarcely exceeds two feet in length. The body is brown, the belly much fainter. Small round black spots are



Text-figure 19.

Dorsal view of the 540-mm. (21-inch) female specimen of *Heterodontus francisci* Girard, shown in lateral view in Text-figure 18.

After Kumada and Hyama, 1937, pl. 44.

scattered all over the body and fins. The authors list this species under the generic name *Gyroleurodus*.

To Kumada and Hiyama (1937) we are also indebted for figures representing dorsal and lateral views of a young female *H. francisci* about 240 mm. (9.84 inches) long. In this specimen, the supraorbital ridges are low in the middle third, as in the two specimens, respectively young and adult, of *H. quoyi* examined by me. The color pattern of the young specimen of *H. francisci* figured by Kumada differs from that of adults of this species. The spots are larger and more complex; on the dorsal surface they are arranged according to a definite pattern. The spots are more numerous on the dorsal surface than on the lateral and ventral surfaces; on the fins, excepting the caudal, they are either indistinct or absent. Each spot consists of a very dark central portion surrounded by a moderately dark zone. On the dorsal surface of head and body, the very dark spots are grouped in about ten transverse rows, each imbedded in a moderately dark stripe. On the body these stripes, each with its enclosed darker spots, are crescentic in outline, the concave margin facing forward; but on the head there are, anteriorly, two straight transverse stripes and, posteriorly, one crescentic stripe with its concave margin facing caudad. Collectively, these transverse stripes form a pattern which is bilaterally symmetrical with respect to the dorsal mid-line of the body.

The skeleton of *H. francisci* has been described by Daniel (1914 and 1915). From his figures it appears that the vertebral column is better developed and the notochord is more constricted in *Heterodontus* than in *Heptanchus* (Daniel, 1934) and *Chlamydoselachus* (Goodey, 1910, reviewed by Smith, 1937).

My material for the study of *H. francisci* consists of two female specimens (one is an adult) collected by Dr. C. H. Townsend of the Albatross Expedition of the American Museum of Natural History on April 10, 1911, at Angel de la Guardia Island, Gulf of California. The larger specimen is about 705 mm. (27.75 inches) long, and the smaller one 565 mm. (22.25 inches). Some additional measurements, for comparison with *H. quoyi*, are given on page 684.

The two specimens of *H. francisci* are much alike. In both, the head including the gill-region is broad, but in the larger fish it is broader in proportion to the total length. In the smaller and presumably younger specimen, the height of the head, in proportion to its width, is greater. The larger shark has a decided hump between the head and the first dorsal fin, but a similar hump on the smaller fish is less conspicuous. In both specimens, the supraorbital ridges are rather tall. They are supported throughout their length by the endoskeleton, and they terminate rather abruptly at their posterior ends. The length of the first gill-slit is about double that of the fifth, as in *H. quoyi*. The spiracular openings are comparatively large: in the larger specimen their longer diameter is from 4 mm. to 5 mm., in the smaller fish 3 mm. to 4 mm. Dorsal fins and dorsal spines are larger than in *H. quoyi*. In both specimens, the origin of the first dorsal is directly above the posterior margin of the pectoral base (as in Garman's *H. japonicus*). The hind margins of both dorsals are concave. The base of the anal fin is slightly more than its

length distant from the caudal. The scales on the dorsal surface of the body are not particularly large. A few dark spots are visible: these are small, widely scattered, and most of them were found only after a careful scrutiny.

JAWS AND TEETH.—In his "Atlas" (1913) Garman figures teeth and jaws of very young, medium-sized and adult specimens of *H. francisci*. In his figure showing the jaws in lateral view, they bear a close resemblance to those of *H. quoyi* (my Text-figure 17). In Daniel's figure of the skull of *H. francisci* 1915, Fig. 6, pl. III, the form of the jaws as seen in lateral view is somewhat intermediate between the two quite different forms portrayed by Goodrich (my Text-figure 33) and Garman (1913; Fig. 4, pl. 47) for *H. phillipi*. One infers that these differences are individual and not specific.

Macley and Macleay 1879 state that the front teeth of *H. francisci* are strongly tricuspid, those at the sides are longitudinally ridged. Garman (1913) writes that the anterior teeth have five cusps, the middle one the longest; with age the outer cusps become less apparent and the middle cusps much stronger. His drawings show the posterior teeth longitudinally ridged in all stages. In my two large female specimens the anterior teeth are tricuspid.

COMPARISON OF *HETERODONTUS QUOYI* AND *FRANCISCI*

In my descriptions of the specimens of *H. quoyi* and *H. francisci* belonging to the American Museum of Natural History, some statements were made concerning the form of the body. It seems desirable to bring together the data upon which these statements were based, in order that certain features in the two species may be accurately compared. Incidentally, a few comparisons will be made with other species.

The measurements upon which the present discussion is based are given in Table I. In this connection one should bear in mind that the female specimen of *H. quoyi* is presum-

TABLE I
SOME MEASUREMENTS IN MILLIMETERS OF FOUR SPECIMENS OF *HETERODONTUS*

Species	<i>H. quoyi</i>		<i>H. francisci</i>	
	Female	Male	Female	Female
Total length (from tip of snout to tip of tail fin)	527	372	705	565
Greatest width of head at first gillcovers	118	60	138	97
Greatest height of head at posterior end supraorbital ridge	64	41	86	67
Greatest height of body in transverse plane passing through fifth gillcovers	80	48	110	75
Length of first gillslit	30	15	34	28
Length of fifth gillslit	14	8	17	14
Longitudinal distance between bases of pectoral and first dorsal fins	25	12	0	0
Length of base of anal fin	28	18	42	32
Distance between base of anal fin and ventral lobe of caudal	34	23	43	33

ably adult or nearly adult, while the male of the same species is decidedly young. The larger specimen of *H. francisci* is known to be adult.

I may say at once that the two species are readily separable. In certain features of

their external anatomy they differ so much that they are distinguishable at a glance; but I suspect that even a gifted artist could not portray all their subtle and almost intangible differences of contour.

In both species the head is broader than the body (excluding the paired fins). The region of greatest breadth lies between the first gill-covers. In the large female specimen of *H. quoyi*, the greatest breadth equals 22.3 per cent of the total length; in the decidedly small and immature male specimen of the same species, only 16.1 per cent. In the larger female specimen of *H. francisci*, the greatest breadth equals 19.5 per cent of the total length; in the smaller female of the same species, only 17.1 per cent. It is apparent that in both species the breadth of the head, in proportion to total length, is greater in the older specimen; but when allowance is made for age (ignoring sex as a possible factor) *H. quoyi* is definitely broader than *H. francisci*. For further information we must have recourse to published drawings, which are not so satisfactory as specimens since we have no assurance that they were made from accurate measurements. There are no drawings of either dorsal or ventral views of *H. quoyi*. In Maclay and Macleay's dorsal view (1879) of their 708-mm. specimen of *H. francisci*, the greatest breadth (which is in the region of the first gill-covers) equals 17.5 per cent of the total length—a proportion somewhat smaller than that obtained for my larger specimen of *H. francisci*, which has almost exactly the same length.

It may be of interest to extend this comparison to other species, but there we must depend entirely on drawings which may not be made to scale. Maclay and Macleay's dorsal view of a full-grown specimen of *H. phillipi* (my Text-figure 7, page 667) has a head that appears broad as compared with most sharks, but is decidedly narrower than the heads of my adult specimens of *H. quoyi* and *H. francisci*. Maclay and Macleay's very young specimen of *H. phillipi* (my Text-figure 9, page 669) has a head that is much narrower than that of their adult of the same species. In a young female specimen of *H. zebra* described and figured by Maclay and Macleay (1886) the width of the head cannot be measured because in the dorsal view the head is turned slightly to one side; but it appears very narrow, and the entire body is narrow as compared with other species of *Heterodontus*. In a drawing by Maclay and Macleay representing a dorsal view of a young female specimen of *H. japonicus* about 406 mm. long (my Text-figure 24, page 691), the width of the head equals 15.7 per cent of the total length. This is slightly narrower than the head of my young male specimen of *H. quoyi*, and of course much narrower than the heads of adult specimens of *H. quoyi* and *H. francisci*.

In my adult female specimen of *H. quoyi*, the height of the head (including the supraorbital ridge) equals 54.2 per cent of its breadth, while in my young male of the same species the proportion is 68.3 per cent. In my larger female specimen of *H. francisci* the height of the head equals 62.3 per cent of its breadth; in the slightly smaller female of the same species the corresponding percentage is 69.0. We do not know if sex is a factor in determining the size or bodily proportions in these species, so this possibility must be ignored. With this reservation, the data indicate that in the adults of both

species the head is dorsoventrally depressed, but more so in *H. quoyi* than in *H. francisci*. In both species, during growth the head becomes broader and less tall proportionally, but only the ventral surface becomes actually flat. Because of differences in the shape of the head, its bulk in the two species cannot be compared by ordinary measurements.

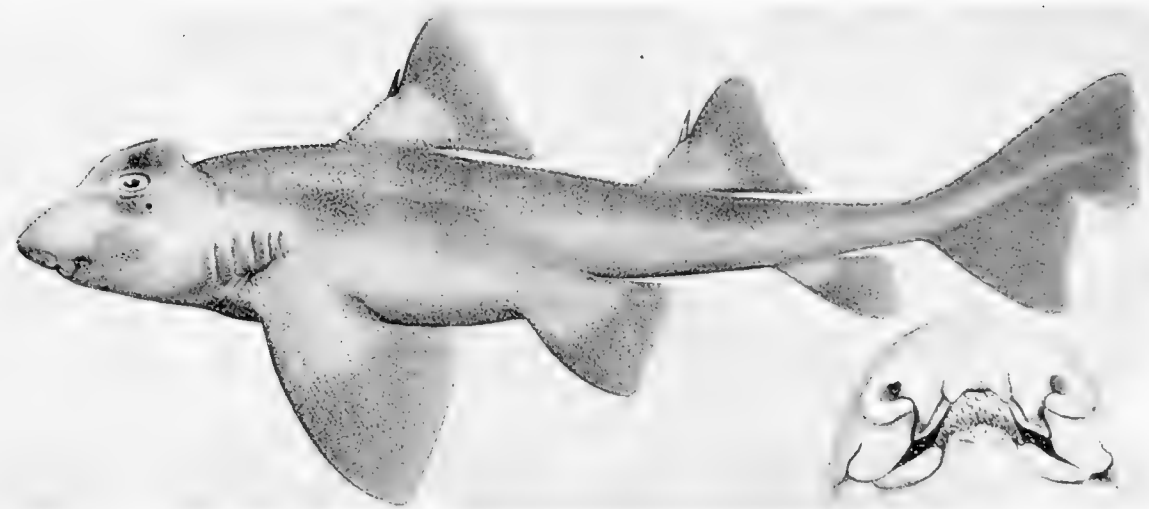
From the total evidence it appears that most species of *Heterodontus*, in adaptation to a bottom-dwelling mode of life, have differentiated moderately in the direction of a broadening of the head and anterior part of the body, accompanied by a lessening of the head height and a flattening of the ventral surface of both head and body. These features emerge in the course of development after hatching, and are not found in the very young—a circumstance which leads us to infer that the more or less remote ancestors of this group were not bottom-dwelling forms. From the meager information available, it is possible that *H. zebra* has evolved in a different direction, tending to become eel-like in form. This, also, is an adaptation to life on the ocean bottom.

Another feature common to my specimens of both *H. quoyi* and *H. francisci* is the slightly humpbacked appearance. This has already been mentioned as a possible generic or family character. The hump is not due to an arched condition of the body. In each of my specimens the greatest height of the dorsal surface, excluding the dorsal fins, occurs in the region above the fifth gill-slit, which is also above the base of the pectoral fin. In the pectoral region the ventral body wall is firm and the height of the body may be measured accurately. The height of the hump may be computed by subtracting the head height from the body height. Comparison of the height of the hump, in proportion to body height in different specimens, may be made on a percentage basis. In my large female specimen of *H. quoyi* the height of the hump equals 20 per cent of the body height; in the small male specimen of the same species, 14.5 per cent. In the larger female specimen of *H. francisci* the excess of body height over head height equals 21.8 per cent of the body height; in the slightly smaller female, 10.6 per cent. It is noteworthy that in *H. francisci* the smaller of two large female specimens has a hump only half the height of the other. Judging from the drawings that have been published, this variability occurs also in *H. phillipi* and *H. japonicus*.

HETERODONTUS GALEATUS GUNTHER

The range of *H. galeatus*, so far as known, is limited to the waters of Queensland and New South Wales. Whitley (1940) writes that in the northern part of New South Wales this species (which he calls *Molochophrys galeatus*) tends to replace *H. phillipi*.

H. galeatus was first described, from a single specimen, by Günther (1870). The first drawings of the entire fish are those of MacLay and Macleay (1879); they comprise lateral, dorsal and frontal views. These drawings were made from a stuffed female specimen (length not given) in the Australian Museum. A much better portrayal of a lateral view, published by Whitley (1940), is here reproduced as Text-figure 20. Whitley records that the length of sharks of this species is about five feet. Presumably this refers to adult specimens.



Text-figure 20.

A female specimen of *Heterodontus galeatus* Günther captured off Sandon Bluff, New South Wales, Australia. The inset figure shows the mouth opening, the nares, oro-nasal grooves, labial folds and some of the front teeth.

After Whitley, 1940, Fig. 56, p. 73.

The most outstanding peculiarity of this species is the unusual height of the supra-orbital ridges. These ridges approach each other anteriorly, and diverge posteriorly; they end abruptly a short distance behind the eye. Garman (1913) says that they end abruptly in young specimens, less so in old. As shown in a frontal view by Macleay and Macleay (1879) the ridges lean outward (laterad) at an angle of about 45 degrees from the median plane. Waite (1898 and 1899) and Whitley (1940) refer to this shark as the "crested species". The name Crested Shark seems appropriate, though it might with some justice be applied to any species of *Heterodontus*. The name "Crested Port Jackson Shark", used by Whitley, seems inadmissible.

Garman (1913) states that the form of *H. galeatus* is similar to that of *H. francisci*, but the head is short and angular. The anterior gill-opening is more than twice as "wide" (presumably meaning high or long) as the hindmost. The origin of the first dorsal fin is above the hinder part of the pectoral base; the hind margin of the first dorsal is concave. The base of the anal fin is about two-thirds of its length distant from the lower lobe of the caudal.

The color pattern is not well shown in Macleay and Macleay's lateral view (1879), but is quite distinct in their dorsal view of the same specimen. Six broad transverse dark stripes are said to be visible, but in the drawing the most posterior stripe is very faint. Garman (1913) states that the general color is brown, with a transverse stripe of darker across the orbits, widening upon the cheek; another band in front and one behind the ventrals (pelvics); one through the second dorsal and one in front of the anal, less definite than the anterior—making five instead of six as enumerated by Macleay and Macleay. The

color pattern is not very distinct in Whitley's figure (1940) reproduced as my Text-figure 20. Whitley states that the color is light-brownish, with the interorbital region and the back in front of (the first?) dorsal fin blackish; a broad blackish bar below the eye; back with some dark transverse bars, one at base of each dorsal fin most prominent, but not joining to depict a "harness". This shark sometimes becomes stained a reddish color on teeth or skin apparently through eating the purple sea urchins of Australian harbors.

At the time when Maclay and Macleay's description was written (1879), only two specimens of *H. galeatus* were known: the stuffed specimen in the Australian Museum, and Dr. Günther's specimen in the British Museum. Maclay and Macleay wrote that it was not at all improbable that the fish might not, after all, be of such very rare occurrence. "The general resemblance to *H. phillipi* is considerable, and fishermen are generally far from being acute observers of fish which are not of a marketable character." Ogilby (1890) wrote that, at Port Jackson, the species was almost as common as *H. phillipi*. He stated that he had also received specimens from Port Stephens, New South Wales. Waite (1898) made extensive collections of marine fishes in the waters adjoining New South Wales, including specimens of *H. phillipi* from 14 different stations. Concerning *H. galeatus* he wrote: "Although a careful lookout was kept for the crested species, *Heterodontus galeatus*, it was never taken and notwithstanding this fact, all the egg cases I saw southward in the shop windows of Wollongong and Kiama were of the latter species [*galeatus*], those of our commoner form (*phillipi*) being either rare or quite unknown".

TEETH.—Waite (1899) published a photograph of the teeth of both upper and lower jaws of *H. galeatus* (which he called *Gyropleurodus galeatus*) and stated that the teeth portrayed by Maclay and Macleay (1879, Figs. 30 and 31, pl. 25) and attributed to *H. galeatus*, were not of that species. The differences in the figures of the posterior teeth are very marked. In Waite's figure the posterior or grinding teeth are much smaller, more nearly uniform in size and more numerous. In Maclay and Macleay's figure they do not differ materially from those portrayed, by various authors, for other species, except that they are more elongate. In one respect the figures of the posterior teeth by Waite and by Maclay agree: the longitudinal ridge is distinct, perhaps stronger than in any other species. My general impression is that the teeth of *H. galeatus* figured by Waite are more primitive (in that the posterior or grinding teeth do not differ so much from the anterior or cuspidate teeth) than the teeth of any other species of *Heterodontus*.

HETERODONTUS JAPONICUS MACLEAY

For many years, specimens of *Heterodontus* collected in Japanese waters were classified as *Cestracion* (*Heterodontus*) *phillipi*, the Port Jackson Shark. Thus the specimens figured and described under this name by Müller and Henle (1841) and by Brevoort (1856) were collected in Japan. Also Siebold (1850, in his "Fauna Japonica") stated that a shark, which he called *Cestracion phillipi*, was very common during spring and summer along the southwestern coast of Japan, especially in the Bay of Nagasaki. He wrote that it attains a length of three feet and that it was much sought after for food by the Japanese. There

is now no doubt that the species of *Heterodontus* ordinarily taken in Japanese waters is not *H. phillipi* but a different species, named by Macleay (in Macleay and Macleay, 1879) *Heterodontus japonicus*. A related species, *H. zebra*, has been taken but rarely in Japanese waters, and there is no authentic record of *H. phillipi* ever having been taken off Japan. Thus the English common name, Japanese Bullhead Shark, seems appropriate for *Heterodontus japonicus*.

As stated early in this article, Dean collected eggs and embryos of *H. japonicus* in the Sagami Sea, at the entrance to the Gulf of Tokyo. In his notes Dean states that this shark is not uncommon along the coasts of the Japanese islands south of Hokkaido. In certain regions it is known to be abundant, as along the shores of the Inland Sea and in the Sagami Sea.

The Japanese Bullhead Shark has received several local names. Siebold (1850) stated that the local name was *Sasiwari*. Brevoort (1856) explains that this name is doubtless derived from *Sas-ir*, to stick in, and *war*, to cleave—in allusion to the spines in front of the dorsal fins. Jordan, Tanaka and Snyder (1913, p. 8) record the following colloquial names: *Nekozamé* (Tokyo market; Misaki; Sagami); *Sazaewari* (Prov. Shima; Osaka; Prov. Tosa); *Sazaiwari* (Nagasaki). It is called “Nekozame” in the volume entitled “Illustrations of Japanese Aquatic. . . Animals” (1913) elsewhere referred to. Dr. Dean calls it *Nekozamé*. A synonymy of scientific names follows:

HETERODONTUS JAPONICUS Macleay

- Cestracion phillipi*. Müller and Henle, 1841, Plagiostomen, p. 76, pl. 31.
Cestracion phillipi. Siebold, 1850, Fauna Japonica: Pisces, p. 304.
Heterodontus zebra (not Gray). Bleeker, 1854, Verh. Bat. Gen., 26, 127.
Cestracion phillipi. Brevoort, 1856, Perry Expedition, vol. II, Fig. 2, pl. 12.
Cestracion phillipi var. *japonicus*. Duméril, 1865, Elasm., p. 426.
Cestracion phillipi. Günther, 1870, Cat. Fishes Brit. Mus., vol. VIII, p. 415.
Heterodontus japonicus Mcl. Macleay and Macleay, 1884, Proc. Linn. Soc. New South Wales, 8, p. 428, pl. XX.
Heterodontus japonicus Mcl. Steindachner, 1896, Ann. K.K. Naturhist. Hofmus., Wien, 11, p. 224.
Heterodontus japonicus. Jordan and Fowler, 1903, Proc. U.S. Nat. Mus., 26, p. 599.
Cestracion japonicus (Duméril). Regan, 1908, Ann. Mag. Nat. Hist., 8. ser. 1, p. 496.
Cestracion japonicus. Garman, 1913, Plagiostomia. Mem. Mus. Comp. Zool., 36, p. 184.
Heterodontus japonicus Duméril. Jordan, Tanaka and Snyder, 1913, Journ. Coll. Sci., Imp. Univ. Tokyo, 33, Art. 1, p. 8.

The Japanese Bullhead Shark, *Heterodontus japonicus*, was first figured and described by Müller and Henle (1841). Their specimen and figure were labelled “*Cestracion phillipi*”. At the time when their monograph was published, only three species of *Heterodontus* (*Cestracion*) were known: *H. phillipi*, *H. zebra* and *H. quoyi*. No evidence other than the figure itself (my Text-figure 21) is necessary to prove that the specimen drawn was not one of these. Müller and Henle listed nine specimens of *H. phillipi* stored in various museums, and stated that they were collected in “Neuholland” (now



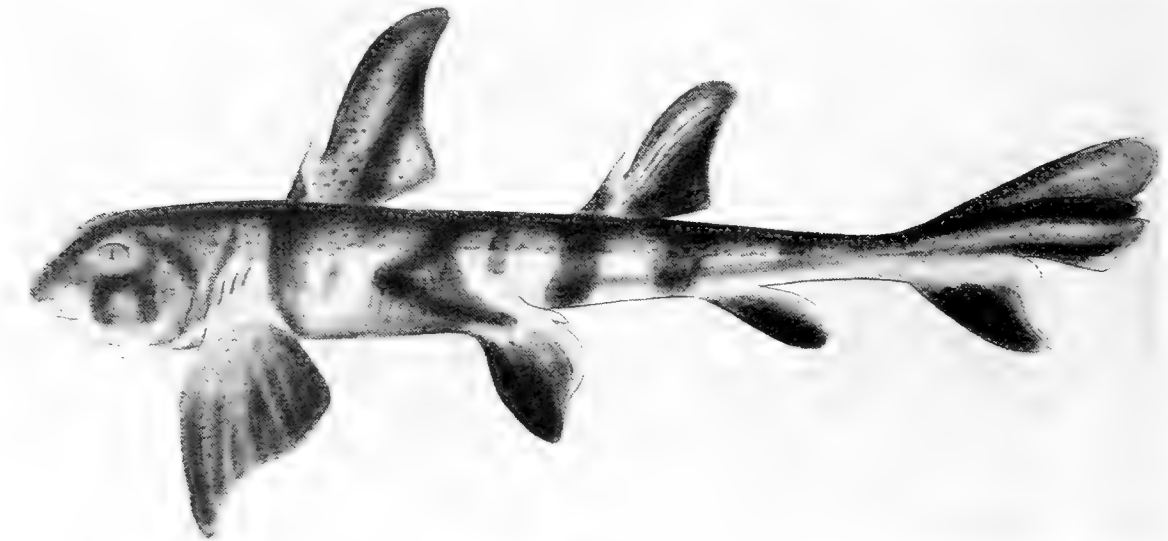
Text-figure 21.

A male Japanese Bullhead Shark, *Heterodontus japonicus* Macleay, length not recorded. The original figure is in color and is labelled *Cestracion phillipi*.

After Müller and Henle, 1841, pl. 31. Right and left are here reversed.

Australia) and in Japan. But *Heterodontus phillipi* does not occur in Japanese waters. Moreover, Siebold (1850, p. 304) noted that the Müller and Henle figure was drawn by Bürger from a fresh specimen collected in Japan.

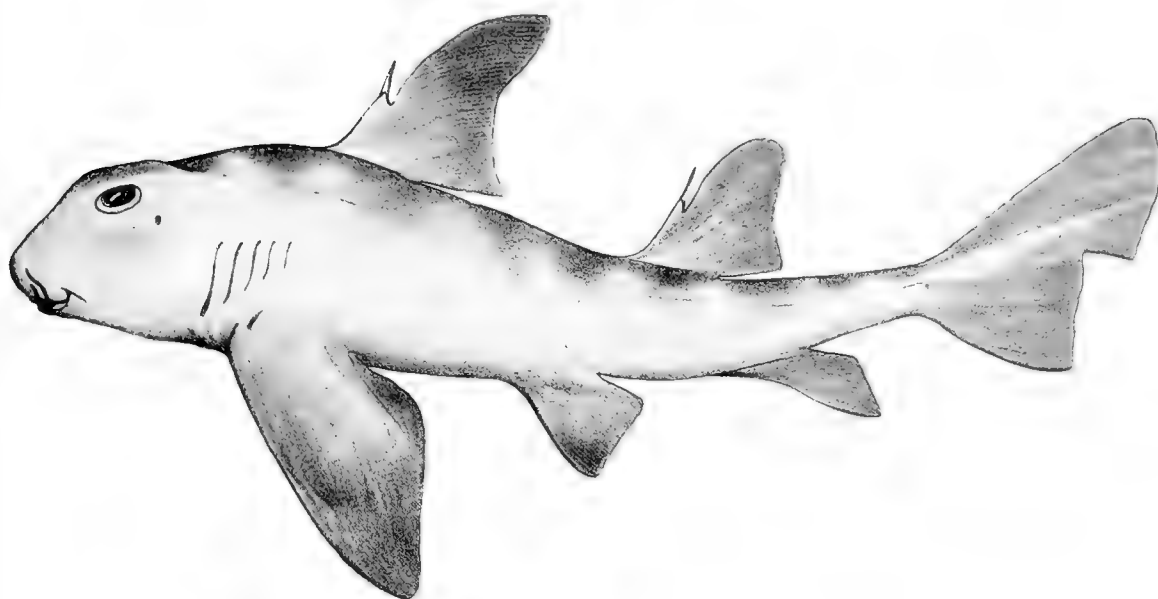
A specimen of *H. japonicus* described and figured by Brevoort (1856) was labelled "*Cestracion phillipi*". This specimen (my Text-figure 22) was collected at Simoda



Text-figure 22.

A very young (recently hatched) male Japanese Bullhead Shark, *Heterodontus japonicus*, collected by the Perry Expedition to Japan. The original figure, from a recently procured specimen only 216 mm. (8.5 inches) long, is in color and is labelled *Cestracion phillipi*.

After Brevoort, 1856, pl. XII.

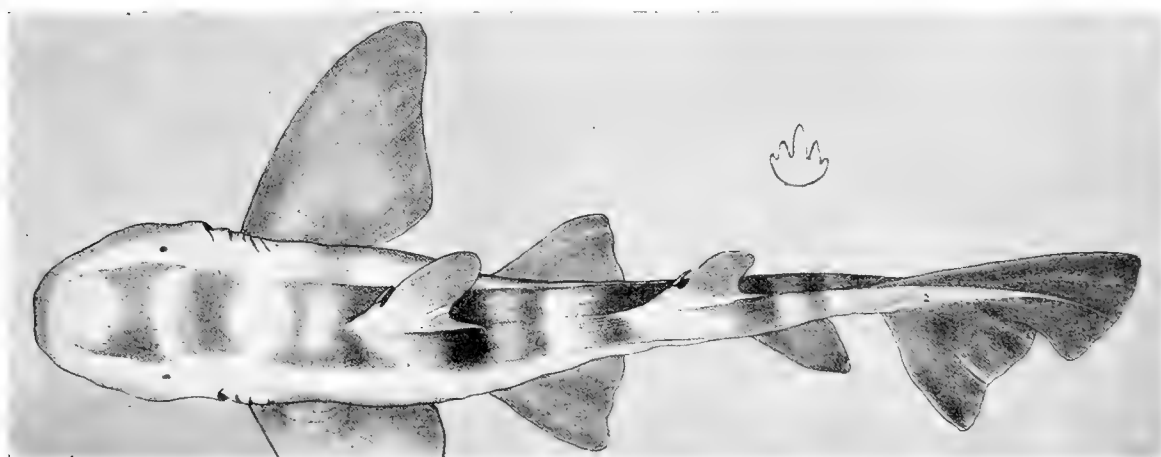


Text-figure 23.

A young female Japanese Bullhead Shark, *Heterodontus japonicus*. This specimen, collected in Japanese waters, was about 406 mm. (16 inches) long, and was drawn after preservation in alcohol.

After Maclay and Macleay, 1884, Fig. 1, pl. 20. Right and left are here reversed.

(Shimoda, at the entrance to the Sagami Sea?) by the Perry Expedition to Japan. Brevoort states that all the drawings of fishes were made from recently procured specimens; but that no professional zoologists accompanied the expedition, hence in making the drawings no close attention was paid to specific characters. From the small size of Brevoort's



Text-figure 24.

Dorsal view of the 406-mm. (16-inch) preserved female specimen of *Heterodontus japonicus* shown in lateral view in Text-figure 23. The inset figure is an outline of a front tooth.

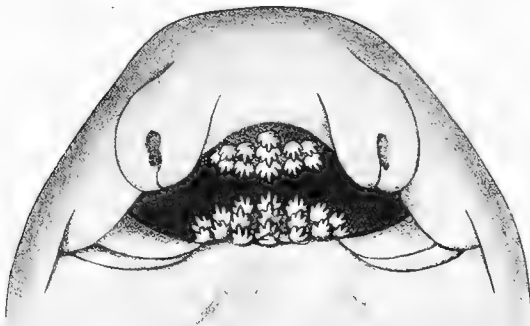
After Maclay and Macleay, 1884, Figs. 2 and 5, pl. 20.

specimen (only 216 mm. or 8.5 inches long) one infers that it must have been recently hatched. Brevoort's description of the color and color pattern follows:

Its general color is of a pale sepia-like brown, darker on back and fins, with a pinkish tinge on lower parts of the body. Irregular bands and large blotches of several shades of the same brown are distributed from the pectorals to the caudal, grouped in five principal bands, with smaller ones near the back between the first three large ones. The first of these last is just back of the pectorals, the second back of the first dorsal and in front of the ventrals, spreading laterally near the abdomen. The snout and cheeks are shaded also with darker-brown cloudings. Small pale-brown dots, besides the above, cover the back of the head and body and about one-half of the pectorals, dorsals and caudal. Ventrals, anal, and lower lobe of dorsal of a more uniform brown.

The first specimen to be described, figured and labelled *Heterodontus japonicus* is that of Maclay and Macleay (1884). This specimen is a 406-mm. (16-inch) female obtained from Japan; it is evidently not full-grown. The authors state that the "coloration and markings" of their specimen are not by any means distinct, the fish having been long in spirits; but the remains of numerous dark-brown bands across the back present a very different style of marking from those of the other known species of the genus. Maclay and Macleay's drawing of the entire fish in lateral view (my Text-figure 23) shows the transverse dark bands with essentially the same distribution as in Müller and Henle's figure, save that the band immediately in front of the first gill-slit is lacking. In their drawing of the same specimen in dorsal view (my Text-figure 24) the transverse bands are more prominent.

Maclay and Macleay's further description of their 406-mm. (16-inch) female specimen of *Heterodontus japonicus* is here given very nearly in the words of the authors, but with some rearrangement and clarification. They state that the snout is very bluntly rounded (my Text-figures 23 and 24). The mouth (Text-figure 25) differs from that of *H. phillipi* in having the inner nasal fold less long, the fold of the upper lip rounder and shorter, and the inferior margin of the fold of the lower lip covered with soft skin having only a very few scutellae (placoid scales). The spiracle (Text-figures 23 and 24) is distinct, and larger than in *H. phillipi*. It is placed a little below and behind the eye. The lateral line is straight and continuous from the supraorbital ridges. The first dorsal fin is high and



Text-figure 25.

Anterior part of the head of *Heterodontus japonicus* seen from the ventral side, showing the mouth opening, nares and oro-nasal grooves, the labial folds and some exposed anterior teeth. From the young female specimen about 406 mm. (16 inches) long, shown in

Text-figure 23 and 24.

After Maclay and Macleay, 1884, Fig. 3, pl. 20.

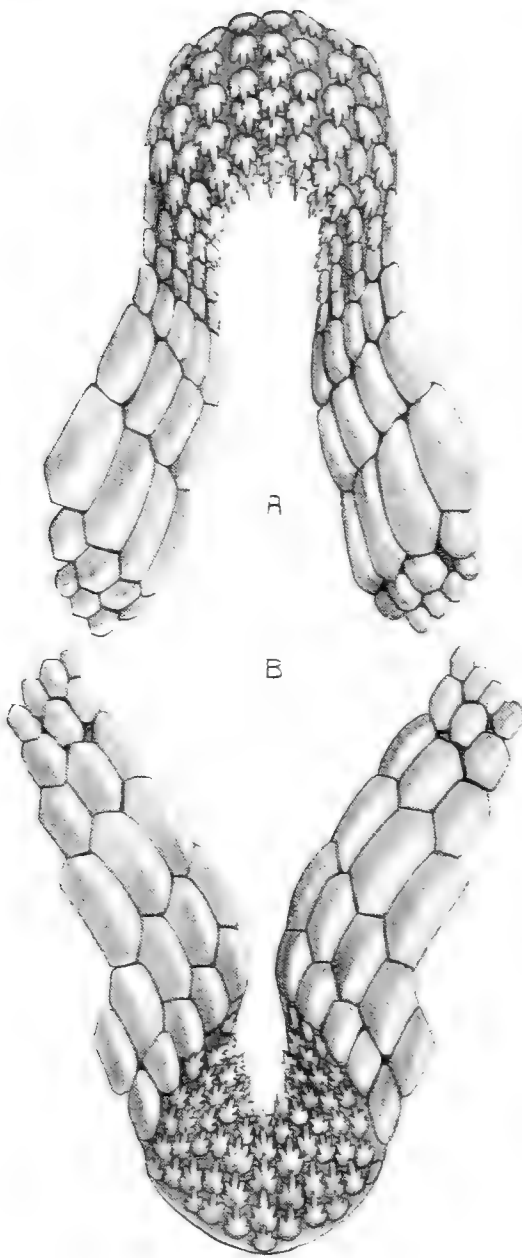
falciform; the height is exactly twice the length of the portion of the base attached to the back. The spine is small and acute (as compared with that of *H. phillipi*), being only half the length of the fin. The second dorsal is shaped like the first, but is less in height, and its base of attachment to the back is about the same. The distance between the two dorsals is equal to that between the second dorsal and the commencement of the caudal fin, and to that between the first dorsal and the eye. The pectorals are large and triangular, and about equal in length to the caudal. The ventrals (pelvics) are situated in a line intermediate between the two dorsals. The anal commences distinctly behind the second dorsal, and does not nearly reach the caudal. The lower lobe of the caudal is very deeply and less than rectangularly notched. The authors do not mention the hump on the anterior part of the body, which is quite prominent in their figure representing a lateral view (my Text-figure 23).

To Bashford Dean we are indebted for the only photograph of a fresh-caught adult Japanese Bullhead Shark on record. This was published (Dean, 1904) in the Popular Science Monthly in an article entitled "A Visit to the Japanese Zoological Station at Misaki" and is reproduced herein as Text-figure 3, page 655. The original legend reads "A Freshly Caught Port Jackson Shark", but since Dean states in the accompanying text that a Port Jackson Shark is abundant at Misaki, it is evident that he was using the name in a generic, not a specific sense—for *Heterodontus phillipi* does not occur at Misaki. Thus the species is almost certainly *H. japonicus*, though *H. zebra*, a more slender form, does occur somewhat rarely in the vicinity of Misaki. The photograph does not show the color pattern, which would make identification easy. In Dean's photograph, one must make some allowance for the trick of the camera in enlarging objects in the foreground: the pectoral fin is probably a little too large. Since the mouth is partly open, the lower jaw has sagged and the cranium is slightly upraised.

Among Dean's records there is a faded photograph showing a dorsal view of an adult or nearly adult *Heterodontus*, presumably *japonicus*. The supraorbital ridges are well shown. They are strongly upraised, though narrow, and approach each other at their anterior ends, diverging posteriorly. At their posterior ends they terminate rather abruptly, though not so abruptly as in *H. galeatus* (Text-figure 20 and in Macleay and Macleay's lateral view). The breadth of the head, measured between the first pair of gill-covers, equals 19 per cent of the total length. The pectoral fins are extended, and the distance from tip to tip equals 56 per cent of the total length.

A young female specimen of *Heterodontus japonicus* in the collections of the American Museum of Natural History measures about 280 mm. (eleven inches) in length "over all". It is described on page 757 and portrayed in Text-figure 65, of the present article.

There remains to be considered a figure of the Japanese Bullhead Shark contained in a folio volume entitled "Illustrations of Japanese Aquatic Plants and Animals", published by the Japanese Fisheries Society in 1931. An adult specimen of *Heterodontus japonicus* is there portrayed in color. Upon comparing this figure with those of other authors (including the photograph by Bashford Dean reproduced in my Text-figure 3) one gets



Text-figure 26.

Dentition of *Heterodontus japonicus*: A, upper jaw; B, lower jaw. Drawn from the young female specimen, 406 mm. (16 inches) long, shown in Text-figures 23 to 25.

After Macley and Macleay. 1884.
Figs. 4A and 4B, pl. 20.

an impression that it is inaccurate in several respects. The eye is too large and too near the top of the head; the supraorbital ridge is omitted or represented as part of a circular ridge extending entirely around the eye. The notch in the ventral lobe of the caudal fin is curved instead of angular. The dark brown transverse stripes are more regular and less numerous than in any other drawing of this species. For these reasons this figure is not reproduced here. The legend states that the species is not good for food—contrary to the statement in Siebold's "Fauna Japonica". "*De gustibus non est disputandum*".

TEETH.—In Macley and Macleay's young (16-inch) female specimen of the Japanese Bull-head Shark, there are 23 transverse rows of teeth in both upper and lower jaws (my Text-figure 26). The anterior (cuspidate) teeth are typically five-cusped. In the upper jaw, the number of teeth in the central row is eight (one is not visible in Text-figure 26). In the lower jaw, the transition between anterior (cuspidate) and posterior (grinding) teeth is very abrupt; in the upper jaw it is more gradual. In making comparisons with the teeth of other *Heterodontid* sharks, it should be borne in mind that Macley and Macleay's description is based on a single specimen, and that this specimen was a decidedly young one.

The development of the teeth of *Heterodontus japonicus* is further described in the final section of this article, which contains also a concise summary of the main course of development of the teeth of the entire genus.

AFFINITIES TO FOSSIL FORMS

In the introduction to this article I have pointed out that the genus *Heterodontus* includes some fossil forms, so that the paradoxical term "living fossils" might pardonably be



Text-figure 27.

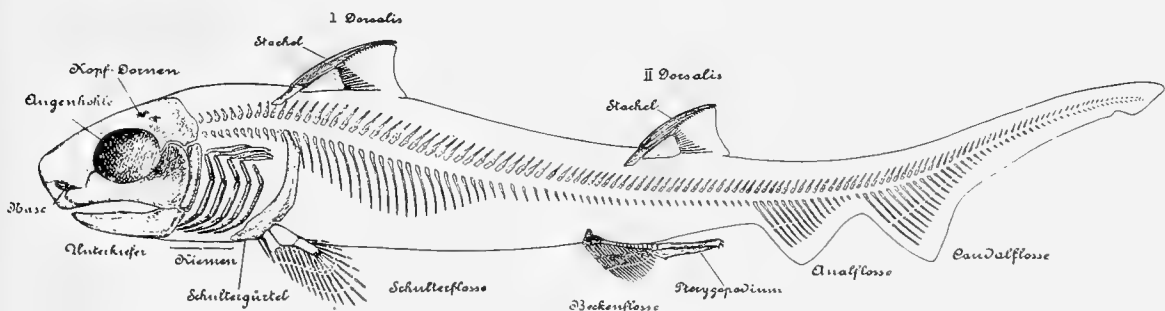
Hybodus hauffianus E. Fraas: skeleton, with skin (shagreen) outlining the entire body which is about 2240 mm. (88 inches) long. Upper Lias; Holzmaden, Württemberg.

After Koken, 1907, Taf. I.

applied to present-day representatives of the group. Of greater importance is the close relationship between the Heterodontidae and the Hybodontidae, which will now be discussed. Since paleontologists almost uniformly use the term *Cestracion* instead of *Heterodontus*, and *Cestraciontidae* in place of *Heterodontidae*, it is advisable, in reviewing their work, to adopt their language without a tiresome repetition of synonyms.

In his "Catalogue of the Fossil Fishes in the British Museum", Woodward (1889) defined the *Cestraciontidae* very broadly as follows: "Dorsal fins each armed with a spine, the first opposite to the space between the pectoral and pelvic fins. Teeth mostly obtuse, never fused into continuous plates; several series simultaneously in function". He further states that "No distinctive characteristics of value having yet been discovered, the so-called *Orodontidae* and *Hybodontidae* are included in this family".

This classification, or something like it, seems to have been adopted by Goodrich (1909) since he includes *Orodus* and *Hybodus* (the latter portrayed in my Text-figures 27 and 28) in the family *Cestraciontidae*. Regan (1906) had already separated the *Cestraciontidae* from the *Hybodontidae*. Most of the characters that Regan lists for the two families are identical, but he states that in the *Cestraciontidae* the pterygoquadrate



Text-figure 28.

Reconstruction of the skeleton and outline of the body of *Hybodus hauffianus* E. Fraas, based on a specimen about 1220 mm. (48 inches) long. Upper Lias of Holzmaden, Württemberg.

After Jaekel, 1906, Fig. 2.

(palatoquadrate) has a preorbital articulation with the cranium, while in the Hybodontidae the attachment is postorbital. Nine genera, including *Paleospinax* and *Synechodus*, were assigned to the Hybodontidae, leaving one genus, *Cestracion*, for the Cestraciontidae.

In the second German edition of his "Grundzüge der Paläontologie", Zittel (1911) listed in his family Cestraciontidae seven genera including *Cestracion*. Eight other genera, including *Hybodus* and *Orodus*, made up his family Hybodontidae. The most recent (fourth) German edition of Zittel (1923) departs only slightly from this classification. In the separation of the two families, Woodward appears to have taken part. In the second English edition of Zittel, revised by Woodward in 1932, the family Cestraciontidae includes only three genera (*Cestracion*, *Paleospinax*, and *Synechodus*) while the family Hybodontidae comprises thirteen genera including *Hybodus* and *Orodus*. Woodward's definitions of the two families deserve careful attention:

DISTINCTIVE CHARACTERS OF THE HYBODONTIDAE AND THE CESTRACIONTIDAE
According to Woodward in Zittel (1932).

HYBODONTIDAE	CESTRACIONTIDAE
Teeth numerous, mostly obtuse, never fused into continuous plates; several series simultaneously in function. Notochord persistent. Some ribs long and slender; neural arches also long and slender. Each of the two dorsal fins armed with a spine, which is as deep as the fin; the spine ornamented on the sides and bearing one or two rows of posterior denticles. Anal fin without spine. Tail heterocercal. Paired hooked head spines often present. Devonian or Lower Carboniferous to Cretaceous.	Teeth as in Hybodontidae. Vertebral centra cyclospondylic or asterospondylic. Ribs and neural arches very short and broad. Each of the two dorsal fins armed with a spine which is less deep than the fin; the spine is almost or completely unornamented, and without posterior denticles. Anal fin without spine. Tail heterocercal. No head spines. Lower Jurassic to Recent.

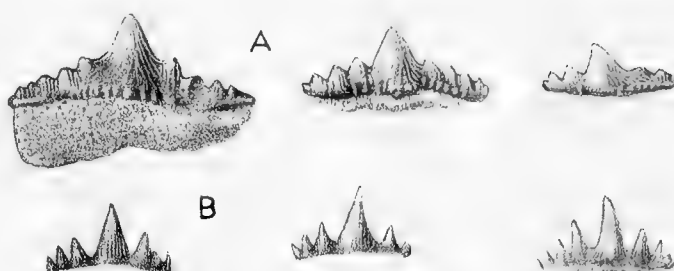
Several of the characters listed above are much alike in the two families. The degree of this likeness, and its significance, need some evaluation; but first let us note some possible additions to the list of resemblances. Certain peculiarities in the form of the head and anterior part of the body of some Cestracionts, leading to the common name "Bull-head Sharks", find a counterpart in fossil forms like *Hybodus* (Text-figures 27 and 28). This matter has been discussed on pages 660 and 686. A considerable degree of flatness of the ventral surfaces of both head and body may also be common to the two families. Woodward (1921) states that in their general appearance the Hybodonts resemble the Cestracionts. The pectoral girdles of both *Heterodontus* (Daniel, 1915, Fig. 8, pl. IV) and *Hybodus* (my Text-figures 27 and 28) are very strong.

Some of the characters common to the two families are included in the definitions presumably for comparison with other families in the same suborder, or to show inclusion

Text-figure 29.

Teeth of *Hybodus*, outer aspect, natural size: A, three associated teeth of *Hybodus delabechei* Charlesworth; B, three associated anterior teeth of *Hybodus reticulatus* Agassiz.

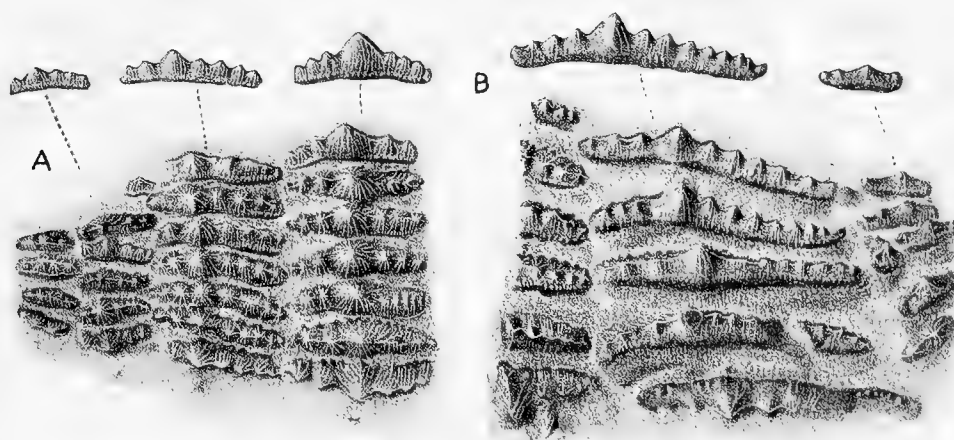
After Woodward, 1889, Part 1, pl. X.



in some larger group; but we are here concerned mainly with the interrelations of the two families. From this point of view, the descriptions of the teeth by Woodward are inadequate when isolated from the special accounts of the teeth of the various genera. There is considerable variation in the teeth of different genera in both families, and the differences are of the same kind.

In *Hybodus* the teeth (Text-figures 29 and 30) are all cuspidate. In the anterior teeth the cusps are more or less acute, with the central cusp predominant and the other cusps somewhat irregular in size and number. In the posterior teeth there is a tendency toward differentiation into grinders; for these teeth are larger than the anterior teeth and their cusps are almost or quite obtuse. But in some other genera of the family Hybodontidae, low rounded crushing teeth, slightly ridged and with only a few vestigial cusps, occur (e.g., as in *Orodus*, figured by Eastman, 1903; and *Acrodus*, beautifully illustrated by Woodward, 1889).

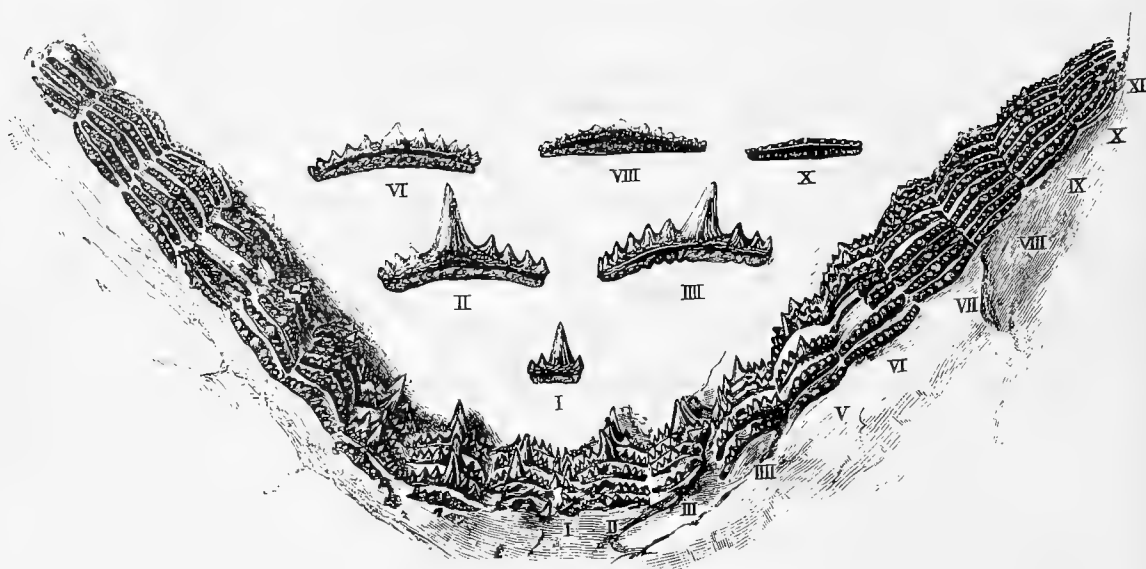
Similar differences occur in the three genera of the Cestraciontidae. The teeth of *Synechodus* (Text-figure 31) are much like those of *Hybodus* (Text-figures 29 and 30)



Text-figure 30.

Posterior teeth of *Hybodus*, in natural sizes. A, *Hybodus delabechei* Charlesworth: four posterior series of teeth, coronal aspect; one tooth of each of three series is shown also in side view. B, *Hybodus raricostatus* Agassiz: two posterior series of teeth and portions of a third, coronal aspect; two teeth are shown also in side view.

After Woodward, 1889, part 1, pl. X.



Text-figure 31.

Dentition of *Synechodus dubrisiensis* Mackie, a member of the family Heterodontidae (Cestraciontidae) represented only by fossils. These teeth are twice natural size, with six separate teeth enlarged four times. Upper Cretaceous, Sussex.

After Woodward, 1889, Part 1, Text-fig. 12, p. 326.

except that the anterior teeth of *Synechodus* are larger than the posterior ones. The teeth of *Paleospinax* show progress in the direction taken by *Heterodontus*: the few anterior teeth are high-crowned and prehensile with only a single pair of lateral denticles, while the posterior teeth are low-crowned with two or three pairs of lateral denticles reduced to minute beads (Zittel, 1932). Finally in *Heterodontus*, the only genus represented by living specimens, the anterior teeth of the adult are typically tricuspid, the central cusp predominating; while the posterior teeth are large, and set in oblique rows, without cusps but with the grinding surface of each tooth traversed by a slender longitudinal ridge—unless this is worn away by use. Nearly complete skeletons of *Heterodontus* (*Cestracion*) have been found in the Lithographic Limestone (Upper Jurassic) of Bavaria and the Chalk of England. The teeth of these fossils, which include several extinct species, are said to differ little from those of recent examples of the genus save that the crowns of the grinding teeth are rugose in addition to having a longitudinal keel.

The spines of the dorsal fins are not limited to sharks of the families under consideration, but one of the most obvious differences between the two families is the ornamentation of the dorsal spines in the Hybodontidae and the almost entire lack of it in the Heterodontidae. The "ornamentation" consists of longitudinal ridges along the sides and sometimes the front of the spine, and the presence of tubercles on its rear surface. In two genera of fossil Heterodontidae, *Paleospinax* and *Synechodus*, the dorsal fin spines are almost uniformly smooth, and in *Heterodontus* they are entirely smooth.

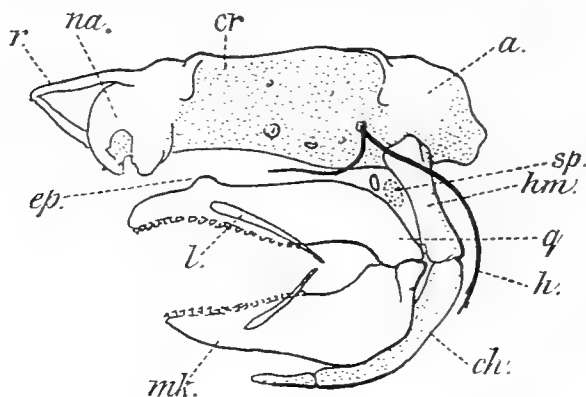
On the basis of the mode of suspension of the jaws, it appears impossible to make a clear-cut distinction between the families Hybodontidae and Cestraciontidae as constituted by Woodward (in Zittel, 1932). Some genera of the Hybodontidae (e.g., *Orodus*) are known only by their teeth, or by their teeth and dorsal spines. Where genera are represented by fairly complete skeletons (e.g., as in *Hybodus*), there is apparently some lack of uniformity in the method of jaw suspension. Nevertheless Woodward (1921) generalized as follows: "The Hybodonts. . . are especially interesting because, while their dentition and their general appearance resemble those of the existing Cestraciontidae, their skull is very different and more closely agrees with that of the Notidanidae". It is possible that the word skull, as used here, means cranium, as it seems to do in several places in Woodward's writings.

The terms autostylic, hyostylic and amphistylic were introduced by Huxley (1876) to designate three types of skull and of suspension of the first visceral arch—the mandibular arch, or the jaws. We are here concerned only with the second and third types as they occur in sharks. In both, the palatoquadrate cartilage (constituting the framework of the upper jaw) is quite distinct from the chondrocranium. The palatoquadrate is, at most, in contact with the cranium only by articular surfaces, and connected with it by ligaments. In front, the palatoquadrate is often loosely connected with the lateral ethmoid (preorbital) region of the skull by way of a palatobasal or ethmoid process (of the palatoquadrate), but this type of connection apparently has little or nothing to do with the classification under consideration. In most sharks, the dorsal element of the hyoid arch, called the hyomandibular cartilage, attains a large size, gains an attachment to the auditory capsule, and becomes the chief apparatus for suspending the palatoquadrate from the cranium. This type of suspension is called hyostylic, and is exemplified by the skull of *Scyllium* (Text-figure 32). In the hyostylic skull the upper jaw is held somewhat away from the cranium, and retains a considerable degree of mobility. In the amphistylic skull, according to Huxley, the palatoquadrate cartilage is wholly, or almost wholly, suspended by its own ligaments; the hyomandibular is small and contributes but little to its support. Some authors (e.g., Goodrich, 1909, p. 95) have interpreted, or modified, this definition to require that, in the typical amphistylic skull, the quadrate region of the upper jaw must have a postorbital articulation with the auditory capsule in addition to being connected with it by the hyomandibular: as in *Heptanchus* (Goodrich, 1909, Fig. 59A); a typical Acanthodian (Goodrich, 1909, Fig. 159); and in *Hybodus hauffianus* according to Jaekel (my Text-figure 28).

It will suffice here to attempt a comparison between the skulls of *Heterodontus* and *Hybodus*, with special reference to the manner in which the jaws are attached to the cranium. The skull of *Heterodontus* (Text-figure 33) is usually classed as hyostylic, though it does not conform closely to this type. One should examine also the more elaborate figures of the skull of *Heterodontus phillipi* by Huxley (1876, Fig. 8) and that of *H. francisci* by Daniel (1915, Fig. 6, pl. IV). In both figures the cranium is more closely molded on the palatoquadrate cartilages (upper jaws) than is represented in Goodrich's

figure (my Text-figure 33). According to Huxley, the hyomandibular is of moderate size; it articulates with a process on the underside of the auditory capsule and supports the posterior end of the palatoquadrate, with which it is connected by a strong ligamentous capsule. The huge palatoquadrate is connected with the cranium in the preorbital region by a broad joint (ethmoidal articulation) and in the orbital region by fibrous tissue. The postorbital region of the cranium of *Heterodontus* appears short, and the preorbital region long, as compared with most sharks. The cranium as a whole is much longer than the jaws, which appear as if thrust forward. Anteriorly the upper jaw extends almost or quite as far as the snout, but posteriorly it does not reach the auditory capsule. Thus the lower end of the hyomandibular cartilage is pulled forward.

In sharks of the genus *Hybodus*, according to Woodward (1916), the pterygoquadrate (palatoquadrate) is not articulated with the preorbital region of the cranium (as it is in *Heterodontus*). In *Hybodus hauffianus*, according to Jaekel (1906), the suspension of the jaws is amphistylic (my Text-figure 28, page 695). The skull of *Hybodus dubrisiensis*, as described by Woodward (1886) is even more typically amphistylic, resembling that of *Heptanchus*. Woodward's figure shows the palatoquadrate with a small but definite facet in position for a postorbital articulation with the cranium; the hyomandibular is slender, but evidently gives some support to the jaws. But in *Hybodus basanus*, as described by Woodward (1916), there is no articulation between the palatoquadrate



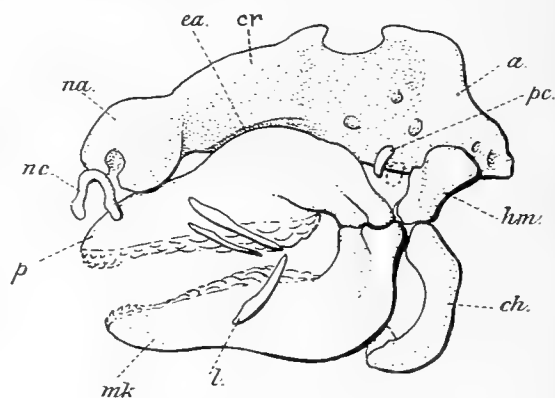
Text-figure 32.

Incomplete skulls of *Scyllium* and *Heterodontus*, illustrating methods of suspension of the jaws.

Text-figure 32. The skull of *Scyllium*, illustrating the hyostylic method of suspension of the jaws.

a., auditory capsule; ch., ceratohyal cartilage; cr., cranium; ep., ethmoid process; h., hyomandibular branch of facial nerve; hm., hyomandibular cartilage; l., labial cartilage; mk., Meckel's cartilage; na., nasal capsule; q., quadrate region of the palatoquadrate cartilage; r., rostral process; sp., spiracle.

After Goodrich, 1909, Fig. 59c.



Text-figure 33.

Text-figure 33. Cranium, jaws and hyoid arch of the Port Jackson shark, *Heterodontus phillipi*.

a., auditory capsule; ch., ceratohyal; ea., ethmoid articulation; hm., hyomandibular; l., labial cartilage; mk., Meckel's cartilage; na., nasal capsule; nc., nasal cartilage; q., quadrate region of the palatoquadrate; pc., prepiracular cartilage. A dotted ring behind the prepiracular cartilage indicates the position of the spiracle.

After Goodrich, 1909, Fig. 58A.

and the cranium. In the skull of *Hybodus basanus* (my Text-figure 34), the cranium is rather short, with a relatively large orbit and with short postorbital and rostral regions. The jaws, which are relatively large and massive, are longer than the cranium, so that the hyomandibular suspensorium extends backward, while the upper jaw extends forward as far as the end of the snout. The rami of the mandible, though deep and massive behind, rapidly taper forward and meet in a comparatively feeble symphysis which does not extend so far forward as the front of the

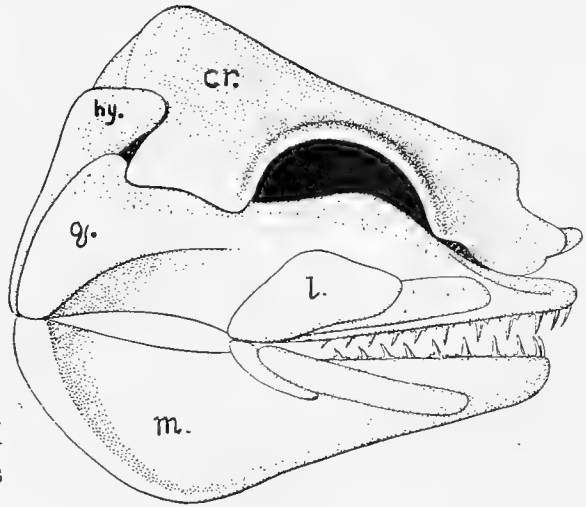
Text-figure 34.

Restoration of the skull of *Hybodus basanus* Egerton, a little less than one-half natural size.

The deeply shaded portion is the orbit.

cr., cranium; hy., hyomandibular; l., one of the labial cartilages; m., lower jaw or mandible; q., quadrate region of the palatoquadrate. The lettering does not appear on the original.

After Woodward, 1916, Fig. 3b.



upper jaw. The palatoquadrate is weak and depressed at its anterior end, but deepens rapidly backward. According to Woodward, it can scarcely have articulated with the postorbital prominence of the cranium.

According to Huxley (1876) the skull of *Heterodontus* is the link that connects the primitive amphistylic skull with the ordinary selachian skull, which is hyostylic. Likewise, Goodrich (1909) wrote: "... it is well established that *Hybodus* and *Synechodus* had typical amphistylic skulls, with the palatoquadrate and hyomandibular as in the Notidanidae and other primitive Elasmobranchs." This view accords with Woodward's observation (1886) that the skull of *Hybodus dubrisiensis* is typically amphistylic, and with Jaekel's interpretation of the skull of *Hybodus hauffianus* (my Text-figure 28); but it does not harmonize with Woodward's later statement (1916) that the pterygoquadrate (palatoquadrate) of *Hybodus basanus* "can scarcely have articulated with the postorbital prominence of the cranium". It seems remarkable that species of the same genus should differ in a manner so important; but if the skull of *Hybodus basanus* really does lack a post-orbital articulation with the cranium, then it is hyostylic and therefore more like the skull of *Heterodontus*. By the same token, if such divergences can exist within a single genus of Hybodonts, how trivial become the differences between the skulls of any species of the Mesozoic *Hybodus* and the present-day *Heterodontus*! In view of the well-known difficulties attending the restoration of the fossil vertebrate remains to life-like attitudes, one suspects that there is a flaw in the data somewhere; but, considering the long lapse of time, the evolution of the skull of *Heterodontus* from that of any Hybodont does not seem impossible.

It is apparent that paleontologists have experienced considerable difficulty in disentangling the Cestraciontidae from the Hybodontidae. The two families have, at least once, been lumped together, and authors have seldom agreed on the criteria by means of which they should be divided. Wherever the line has been drawn, the distinction seems more or less arbitrary: the differences between the families seem no more impressive than the differences between genera within at least one of the families. These facts cannot be wholly explained on the ground of difficulty in reading the paleontological record; for nearly complete skeletons belonging to several different genera have been obtained. The only adequate explanation is that there exists a close genetic relationship between the families. With respect to families other than the Hybodontidae, the Heterodontidae occupy a relatively isolated position. Woodward (1921) states that the Hybodonts are a generalized group from which several later families appear to have risen. They were the dominant sharks of the Jurassic and Early Cretaceous Periods. To the present writer it seems not only possible but highly probable that the Mesozoic *Hybodus*, or some Hybodont closely related to it, is the direct ancestor of *Heterodontus*. After this glimpse into the past, we return to the study of living Heterodontid sharks.

SEXUAL DIMORPHISM AND THE REPRODUCTIVE ORGANS

Concerning the Port Jackson Shark, *Heterodontus phillipi*, Macleay and Macleay (1879) state that the two sexes scarcely differ in size and marking. With the aid of special drawings, they describe the intromittent organs (myxopterygia or "claspers") of the male *H. phillipi*. More recently, the claspers of three species of *Heterodontus* (*phillipi*, *japonicus* and *galeatus*) have been described and figured by Leigh-Sharpe (1922 and 1926). Some marked specific differences in this organ are noted.

According to Dean's notes, *Heterodontus japonicus* shows marked sexual dimorphism. The female is larger than the male, heavier in body and somewhat different in proportions. Dean states that the female, when full-grown, measures about 1200 mm. (47 inches) in total length; the male, about 1000 mm. (39 inches). There is little difference in color, though Dean at one time believed that the males could invariably be distinguished, in the well of a fishing boat, by a darker and richer tone.

Since I have no adult female specimen of *H. japonicus* available for dissection, it is a satisfaction to be able to record the results of my examination of the reproductive organs of the larger female specimen of *H. francisci* belonging to the American Museum of Natural History. This shark is 705 mm. (27.7 inches) long, and is fully adult. The oviducts of both sides of the body are well developed, with especially large, thick-walled shell glands. Evidently both oviducts are functional. As in the adults of most sharks, the two oviducts have a common abdominal aperture. In decided contrast to the oviducts, the ovaries of the two sides of the body are very unequally developed.

On the right side, the large ovary contains eggs in various stages of development. Of these, the two largest measure about 35 mm. in diameter, the next largest one about

30 mm. The smaller ovocytes remaining in the ovary are all 12 mm. or less in diameter. It is not known whether *H. francisci*, like *H. japonicus*, matures and deposits its eggs in pairs; but it is possible that this may be the case, for the ovary under consideration had been injured in making a large incision in the body wall to admit the preserving fluid. From this opening, part of the ovary protruded, and one large mutilated follicle contained only a few fragments of an egg. The mesentery supporting the ovary extends posteriorly almost to the rectal gland. Throughout much of its extent it is thickened by what appears to be a posterior sterile portion of the ovary. This is probably the "epigonal organ" of certain sharks, which extends from the ovary along the dorsal body wall posteriorly to where it joins the mesentery of the rectal gland (Daniel, 1922, p. 316). On the left side of the body the ovary is rudimentary—so slender and smooth that it could scarcely be recognized as an ovary except by position and relations. The epigonal organ is much larger—quite as large as the one on the right side. The right and left epigonal organs differ in shape: the one on the right is broader and thicker anteriorly, tapering posteriorly; the reverse is true of the one on the left. Ovary and epigonal organ of the left side (like those on the right) are continuous structures, supported by a single continuous mesentery.

Among Dean's records I find a drawing of a dissection showing the reproductive organs of an adult female *Heterodontus japonicus*. This drawing (my Text-figure 35) is not labelled, nor is it described in Dean's notes, and in the absence of the dissection some features are obscure. In the mid-line near the top of the figure, one readily notes the common abdominal opening of the oviducts. On the extreme right side of the figure (left side of the fish) the oviduct with its three divisions—oviduct proper, shell gland and uterine portion—are easily identified. Halfway between the oviduct and the mid-line of the body there is an elongated object of which the anterior portion is a rudimentary ovary, the posterior larger portion the epigonal organ. This rudimentary ovary is not so slender as the corresponding ovary of *H. francisci* described in the preceding paragraph. The rectal gland is visible in the mid-line near the lower end of the abdominal cavity. On the left side of the figure (right side of the fish) the oviduct, excepting the posterior end of its uterine portion, is obscured by other organs. Apparently the intestine, which together with the stomach occupies a large part of the left side of the figure, has been transected at its posterior end to aid in turning it aside. The relations of the mesenteries on this side of the fish are obscure. It is probable that the epigonal organ of the right side of the fish is concealed by the stomach and intestines. It is unfortunate that these organs were not removed. The right ovary is conspicuous in the upper left part of the figure, and this organ deserves special consideration.

The right ovary shown in Text-figure 35 contains a number of large eggs, of which two are larger than the others. In one fish, Dean observed two ovarian eggs which were almost ripe, showing large "stigmata" (orange spots or germinal discs?). The other eggs of the same ovary were smaller. Nothing is written concerning the condition of the eggs, if any, in the other ovary. It is not known whether the fish whose ovarian eggs are



Text-figure 35.

Dissection showing the reproductive organs of an adult female *Heterodontus japonicus*.

Note that the right ovary contains two eggs much larger than the others.

From a drawing left by Bashford Dean. The paper on which this drawing was made is much darkened by age, hence the drawing is not so clear as it must have been originally.

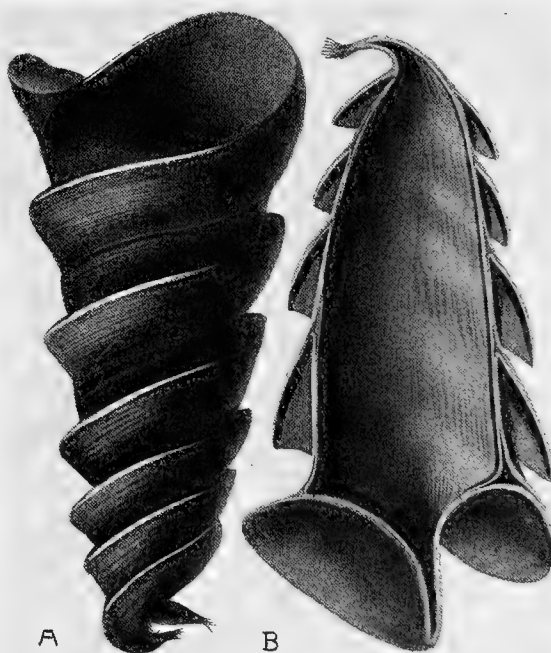
thus described is the one represented in Text-figure 35. Dean states that though several gravid sharks yielded each but a single encapsuled egg, in each case the condition of the "opposite" ovary indicated that another egg had already been laid. These observations support the data recorded in the section on "Egg-laying Habits", and indicate that two eggs are laid at about the same time. We also infer that occasionally both ovaries are functional at the same time. From Text-figure 35 it appears that the "uteri" of both sides are well developed.

THE EGG CAPSULE: ITS STRUCTURE AND FUNCTIONS

The earliest published drawings of the egg capsule of *Heterodontus phillipi* are those of Duméril (1865), reproduced as my Text-figures 36A and 36B. These drawings have been extensively copied, but Waite (1896) states that they are not very good, being doubtless drawn from dry and distorted specimens. The frayed condition at the apices of the two spiral appendages is an artifact. McCoy (1890) contributed a drawing that differs from Duméril's in that the apices of the two spiral appendages are blunt and are not frayed. McCoy states that these "eggs" (capsules) are conical in shape, about six inches long, and surrounded with two broad keels extending spirally and obliquely round the egg from one end to the other, like six turns of a broad screw; the substance is of a tough, dark-brown, horny appearance.

A suggestion as to the advantage of the peculiar form of the Heterodontid egg is offered by Allen (1892) as follows:

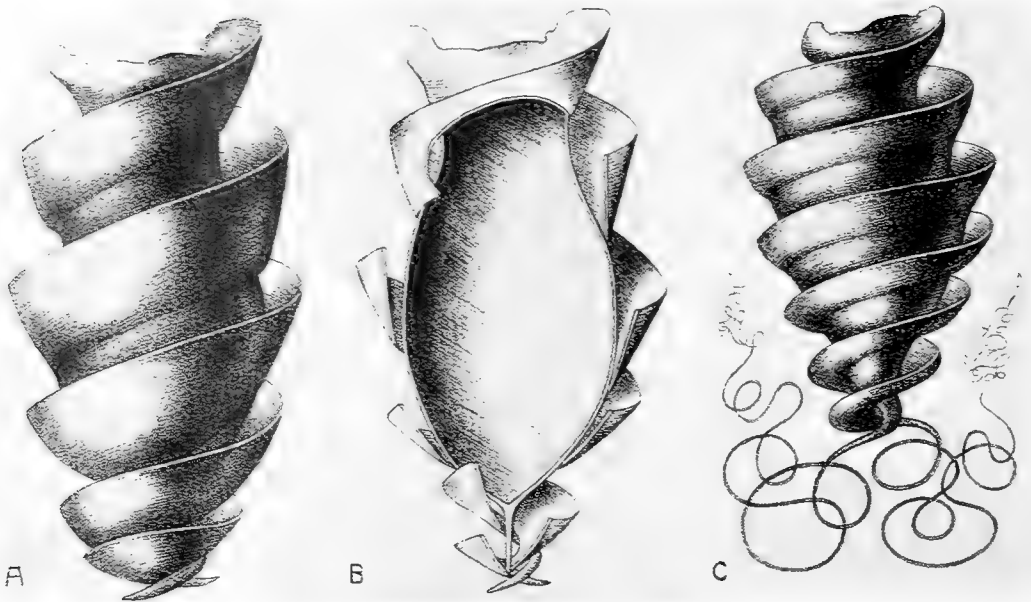
That well-known frequenter of Australian harbours, the Port Jackson Shark, lays a pear-shaped egg, with a sort of spiral staircase of leathery ridges winding around it outside, Chinese pagoda-wise, so that even if you bite it (I speak in the person of a predaceous fish) it eludes your teeth, and goes dodging off screw-fashion into the water beyond. There's no getting at this evasive body anywhere; when you think you have it, it wriggles away sideways and refuses to give any hold for jaws or palate. In fact, a more slippery or guileful egg was never yet devised by nature's unconscious ingenuity.



Text-figure 36.

Egg case of the Port Jackson shark, *Heterodontus phillipi*: A, entire specimen; B, egg case with interior exposed. According to Duméril the egg case is about 130 mm. (5.1 inches) long.

After Duméril, 1865, Atlas, Figs. 2 and 3, pl. 8.



Text-figure 37.

Egg capsules of *Heterodontus phillipi* and *H. galeatus*: A, egg case of *H. phillipi*; B, egg case of *H. phillipi* with interior exposed; C, egg capsule of *H. galeatus*. The author states that the egg case of *H. phillipi* is about six inches (152 mm.) long; that of *H. galeatus* 4.5 inches (114 mm.) long—presumably without the tendrils.

After Waite, 1896, pl. 12.

The only adequate account of the egg capsules of *Heterodontus phillipi* is that of Waite (1896), who also described the egg capsules of *H. galeatus*. His drawings of the egg capsules of both species are reproduced as my Text-figure 37. Because of their unique value, Waite's descriptions are here quoted in full.

The egg cases of both species [*phillipi* and *galeatus*] have the following points in common: All parts are composed of a flexible horn-like substance of brown color. The body consists of a chamber, shaped like a pear; the coronal portion is compressed into a cervix through which the young shark eventually escapes. From each side of the cervix, and integrally connected with it, arises a ribbon exactly resembling a strip of kelp. These ribbons are attached basally, their free edges turned towards the cervix and deflected considerably from the body. They pass round alternately and obliquely, and form the thread of a righthanded double screw, together making five or six turns to the base [smaller end of the capsule]. These ribbons originate [with] about half the width they quickly attain, and continue their course of even breadth, again narrowing on approaching the base. The interior, as shown by a section [Text-figure 37B] is wide and capacious; the fissure does not proceed to the base as generally portrayed, but terminates some distance short of it; the inside is marked with oblique striae corresponding to the direction of the spirals, and resembling the lines inside a vessel turned upon a potter's wheel.

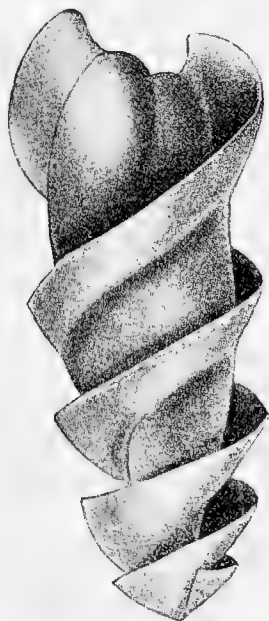
The principal differences between the egg cases of the two species may be recounted thus: *Cestracion* [*Heterodontus*] *phillipi* [Text-figures 37A and 37B]: Of larger size; about

six inches in length. The spirals are very broad and, in part, hide the body when viewed laterally; at the base they narrow quickly and terminate bluntly, and are not produced into tendrils. Beach-worn examples generally have the terminations more or less frayed.

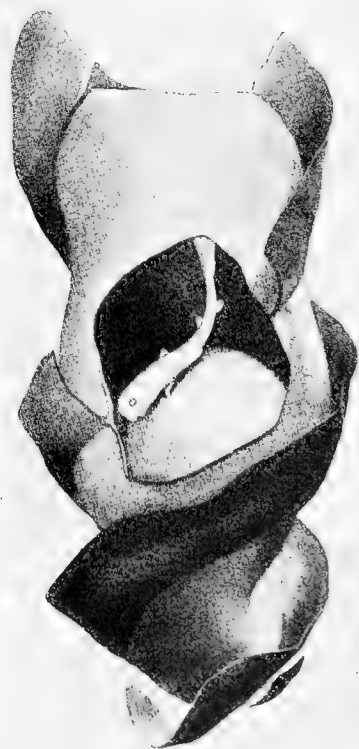
Cestracion [*Heterodontus*] *galeatus* [Text-figure 37c]: Of smaller size; about four inches and a half in length. The spirals are not very broad, and in no part hide the body completely; basally they become narrow and are produced into long flattened tendrils. In the most perfect specimen examined, each tendril is 90 inches in length, and tapers to the slenderest thread, becoming tangled and knotted like a skein of silk. They are, however, very tough, and may be unravelled without fear of breaking. One of the tendrils terminates in a thickened tag (shown in the figure) which, although doubtless an individual peculiarity, indicates that the tendrils are entire.

Further, Waite calls attention to the fact that the appendages, with which the egg capsules of sharks are furnished, serve to moor them in some suitable situation, otherwise they would be likely to be knocked about to the detriment of the contained embryo, or might even be washed ashore where their destruction would be certain. The spiral appendages of *Heterodontus phillipi* are no exception to the rule; the elastic flanges permit the egg to be forced further into a fissure, whence extraction is resisted by the free edges of the ribbon catching against the rocks. Although, in a lesser degree, the egg case of *H. galeatus* possesses these spirals, they do not appear to have the same use; for attachment is here effected by the entanglement of the tendrils among seaweed.

The egg capsule of *H. francisci* is figured by Daniel (1934, also in earlier editions). His figure is reproduced here as my Text-figure 38. This capsule lacks tendrils and bears a general resemblance to the egg capsule of *H. phillipi*; but it is more slender.



Text-figure 38.
Egg capsule of *Heterodontus francisci*.
After Daniel, 1922, Fig. 254, p. 318.



Text-figure 39.
An egg case of *Heterodontus japonicus* with an opening cut to show the young embryo within. The cleft in the upper left-hand portion of the figure follows the line of the respiratory groove.
After Doflein, 1906, p. 209.

The spiral flanges are narrow at the broader end of the capsule, and widen as they approach the narrower end.

Barnhart (1932) states that the egg case of *H. francisci* is about 120 mm. (4.7 inches) long, and 50 mm. (2 inches) wide at its largest diameter, with two wide flaps running spirally from end to end (as in his Fig.1). The size varies, depending probably on the age of the parent. I have no definite information concerning the egg cases of *H. zebra* and *H. quoyi*.

Before entering upon a somewhat detailed account of the structure and functions of the egg capsule of *Heterodontus japonicus*, it seems desirable to examine some general features of this capsule as a basis for comparisons with the other species already considered. Egg capsules of *H. japonicus* are illustrated in Text-figures 39 and 59 (page 752), also in Figures 76 to 78, plate VII. These capsules appear to be stout-bodied, like those of *H. phillipi* and *H. galeatus*—not slender like those of *H. francisci*. The width of the spiral flanges is less than in *H. phillipi*, greater than in *H. galeatus*, and approximately the same as in *H. francisci*. In the capsules of *H. japonicus* the two spiral flanges make comparatively few turns about the body of the capsule: each flange encircles it from one and one-half to two times. In the capsules of the other species considered, there are nearly twice as many turns of the spiral flanges. In other words, in the capsule of *H. japonicus* the spirals formed by the flanges are unusually loose. Since in this species the flanges are only moderately wide, it follows that an unusually large amount of the surface of the body of the capsule is exposed.

The primary function of an egg capsule is of course protective, but provision must be made for the aeration of the embryo and for its eventual hatching. The gross structure of the egg capsule of *Heterodontus japonicus*, and its role in respiration and hatching, are described in Dean's notes on which the following account is based.

The capsule of *H. japonicus* (Figures 76 to 78, pl. VII,) varies considerably in size: in length from 120 to 180 mm. (4.7 to 7 inches), and in weight from 145 to 238 grams, including yolk and embryo. It is somewhat conical in shape, drawn to a point at one end ("lower", distal or "vegetal") but to a "chisel-like" edge at the other ("upper", proximal or "animal"). It is provided with two marginal bands which encircle the capsule spirally somewhat as the "thread" surrounds a screw. These bands arise at the sides of the upper or broad end of the capsule, and are homologous with the marginal bands which occur in the egg capsules of many sharks and chimaeroids. But instead of passing straight downward, they wind about the capsule two and a half times (according to Dean's notes) until they terminate with short processes at the lower end. Here the spiral bands are wider and are more nearly transverse. The freshly deposited capsule is dark bottle-green in color, as shown for the first time in Dean's drawings (Figures 76 to 78, pl. VII). Later the capsules become paler, brownish or sometimes ochreous. Altogether they resemble certain large cysted brown sea-weeds, but whether this resemblance is a protective one is not known.

While the embryo of *H. japonicus* is developing, the capsule undergoes steady deterioration, as in *Chimaera* (Dean, 1906) and in other elasmobranchs. The substance of the capsule becomes thinner, more "tense" and fragile. An arrangement is also developed which enables the young fish to carry on respiration. At either side of the upper or larger end of the capsule, near the line of junction of each marginal band, there is a deep infolding in the wall (as indicated by the arrow in Figure 76, plate VII). Later, by a process of weathering, this respiratory groove opens and widens as a slit (Text-figure 59, page 752). (A respiratory slit of this kind in the eggs of elasmobranchs appears first to have been mentioned, though hardly described, by Home, 1810, page 213). In addition, similar respiratory slits appear at the "lower" or more pointed end of the capsule.

The upper slits in the egg capsule of *H. japonicus* play an active role in the process of hatching, which is described by Dean as follows:

By a continuation of the process of weathering, the upper slit comes to open not only in its lower portion (i. e., in the direction of the contained egg) but in an extended line along the upper and median margin [of capsule]. By this process the entire chisel-like rim of the capsule finally weathers open, and its sides separate, leaving a slit between. This follows the absorption of the hard wedge of albumen which has from the beginning blocked up the large end of the capsule. Old capsules, it was observed, are "tense", and hatching occurs with a rapidity which reminds one of the dehiscence of certain seed pods. The sides of the terminal aperture open and shut in a twinkling, and one is given the impression that the young fish is shot out of the capsule. There is a writhing on the part of the imprisoned fish, and it emerges with a rapidity which quite disconcerts the observer if, as in my own experience, he happens to be holding the egg capsule in his hand. [For further details, see page 753].

Among the capsules which passed through Dean's hands, there were several which were newly deposited and perfect except that none contained an egg. Such empty capsules are called "wind eggs". Externally, these capsules were quite indistinguishable from the others, except by their lighter weight. Dean assumed that they resulted from unilateral ovulation, during which the oviduct of the side opposite to the gravid one was stimulated to produce a capsule.

HABITS OF *HETERODONTUS*

In this section, and in those that follow, we are concerned primarily with the Japanese species, *Heterodontus japonicus*; but reference will be made to other species wherever information is available.

HABITAT AND GENERAL HABITS

There is a curious lack of information concerning the depths at which adults of some species of *Heterodontus* have been taken, though depths at which the eggs of one of these species have been found are recorded in a later section of this article. Osburn and Nichols (1916) record the capture of a specimen of *Gyropleurodus* (*Heterodontus*) *francisci* 8 inches long, dredged from 13 fathoms of water, in Magdalena Bay, Lower California.

Regarding the same species, Barnhart (1932) writes that, while many of these sharks have been taken in shallow water, there are several instances of large numbers being taken at depths of over 500 feet by rock-cod fishermen. He further states that this species migrates from shallow to deep water and from deep to shallow water at certain times of the year. Whitley (1940) states that *Heterodontus phillipi* is found in littoral waters to a depth of 94 fathoms.

According to Dean's notes, *Heterodontus japonicus* (called Nekosamé by the natives at Misaki) occurs in moderately shallow water, roughly between 3 and 20 fathoms. It frequents places where the sea bottom is covered with rock fragments or sea-weeds.

Concerning the habits of *Heterodontus*, other than feeding and spawning habits, our information is very meager. Of *H. phillipi*, the Port Jackson Shark, Macleay and Macleay (1879) write that the adults are very tenacious of life, but no data are given to support this statement. For *H. japonicus* it is possible to quote directly from Dean's manuscript as follows:

Cestracion [*Heterodontus japonicus*] is deliberate in its movements: it swims slowly, and changes its direction readily. Its great pectoral fins are inactive; in fact for a form so well provided with large fins it seems to make surprisingly little use of them. Nor is it alert. Indeed, the divers took by hand the greater number of specimens which were brought to me, although it may well be that the fish, being about to deposit eggs, were less attentive to externals than under usual conditions. The divers report that "Nekosamé" stays close to the bottom and spends its time "nosing" among rock fragments and seaweeds. When disturbed it swims off near the bottom, and not over the heads of the divers as many fishes do.

FOOD AND FEEDING HABITS

Concerning the Port Jackson Shark, *Heterodontus phillipi*, Macleay and Macleay (1879) wrote that its stomach is generally well-filled with fragments of shells, but these are not so well comminuted as might be expected from the character of the teeth; and that the "bowels" are often well charged with cestode worms. McCoy (1890) states that this shark is common in Hobson Bay (Victoria), and that the stomach is filled with fragments of shells. Some interesting information regarding the feeding habits of the Port Jackson shark is furnished by Saville-Kent (1897, pp. 192-193), as follows:

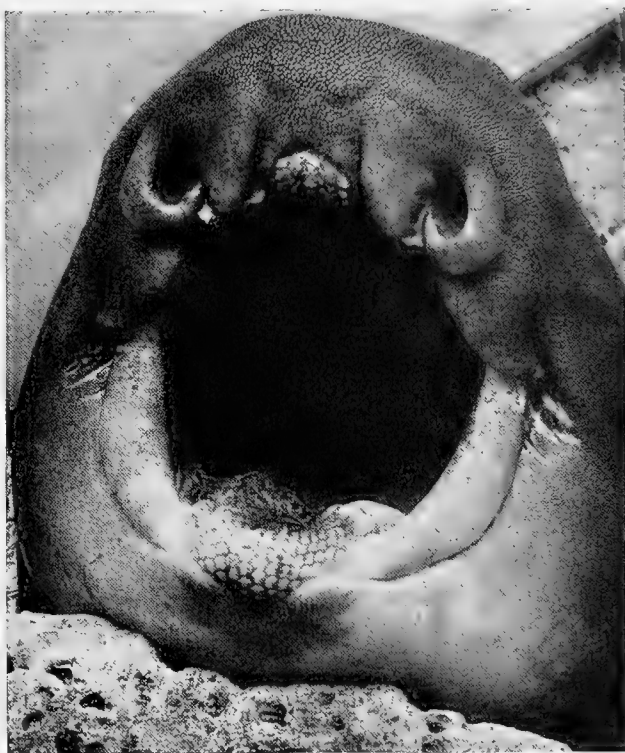
Oysters are the favorite food of this shark [*Heterodontus phillipi*], and in consequence of its predilection for this bivalve, it has proved a formidable enemy to oyster growers in both Tasmania and on the mainland seaboard. At Spring Bay, in the former island colony, the writer found it even necessary to fence round certain of the Government Oyster Reserves with closely matted brushwood in order to protect the oyster stock laid down, from this shark's depredations. In some localities, *Cestracion* [*Heterodontus*] feeds almost exclusively upon Sea Urchins or Echini, the sharp spines of which have apparently no other effect than the pleasant titillation of its palate. The proof of the extent to which this piquant food is favored by this shark is afforded by the fact that the entire pavement of teeth of captured specimens are not infrequently permanently stained a deep purple, through constant indulgence in a dietary of the commoner purple urchin.

Macley and Macleay (1879) state that Echini (Sea Urchins) form the chief food of *Heterodontus galeatus* and probably of all the genus. The strong dorsal spines and the prominent supraorbital ridges of these sharks enable them to force their way under rocks and stones in pursuit of their prey. A fine specimen of *H. galeatus* in the Macleay Museum had the dorsal spines worn down to half their proper length, evidently as a result of scraping against rocks, and its "viscera" were full of finely triturated Echinus tests.

My only information regarding the food and feeding habits of the Japanese Bullhead Shark is derived from Dean's manuscript, from which I quote the following:

It [*Heterodontus japonicus*] is a bottom feeder, and is known to have a varied diet: crustaceans, mollusks, fish and sea urchins. With its formidable dentition it crushes mollusks of considerable size, and its well-worn grinding teeth show that the crushing of shells is a frequent habit. At first sight the mouth appears extremely small, and one gets the impression from the narrow ends of the jaws which are exposed that the fish is a "nibbler", and cannot open its mouth widely. The photograph, however (Text-figure 40) shows how completely the shark may open its mouth; and the captive fish is apt to offer many demonstrations of this habit. The jaws in such cases will sometimes be snapped together noisily, indicating great muscular leverage. In the case figured, the fish was an old one and its mouth was by no means in good order.

On either side of the large teeth were tufts of sertularian hydroids; also there were half a dozen leeches in the neighborhood, some specimens measuring about $2\frac{1}{2}$ inches in length.



Text-figure 40.

View of the wide-open mouth of a new-caught *Heterodontus*, presumably *japonicus*. Note the large grinding teeth in the posterior part of the roof of the mouth.

From a photograph taken by Bashford Dean at Misaki, Japan.

BREEDING SEASON

Concerning the Port Jackson Shark, *Heterodontus phillipi*, Macley and Macleay (1879) state that, if the accounts of the fishermen are to be believed, it is very slow of reproduction—the females never having more than two eggs at a time and only one brood a year. McCoy (1890) states that *Cestracion* (*Heterodontus*) *phillipi* never lays more than two eggs at a time, and only once a year. He does not say how or where he obtained his information. In view of the results obtained by Dean through examination of

the ovaries of *H. japonicus*, the statement that the Port Jackson Shark spawns but once a year cannot be accepted without further evidence.

Waite (1896) writes that living eggs of Port Jackson Sharks (meaning both *H. phillipi* and *H. galeatus*) are most abundant in spring (August and September) but are found also throughout the summer. The empty egg cases may be found washed up on beaches at any time of the year, especially after stormy weather. At Jervis Bay, New South Wales, Haswell (1898) collected eggs of *H. phillipi* in blastula and gastrula stages during September (a spring month in the southern hemisphere). It appears that he found eggs in these stages in considerable numbers. He does not mention any later stages collected during September. Whitley (1940) states that he has observed developing embryos of *H. phillipi* in December, and young hatching in May.

Regarding the eggs of *H. francisci*, Barnhart (1932) states that material collected tends to show that several eggs are spawned during the year.

In the region of Misaki, according to Dean's notes, spawning of *Heterodontus japonicus* takes place throughout the entire year but the especial spawning season is evidently the month of March. The divers brought in the maximum number of eggs during April and May, and most of these were in stages which Dean estimated to be a month or six weeks old. Throughout June, eggs in early stages of development were brought in occasionally; throughout July, early stages were still more uncommon, perhaps one in twenty; and later in the season, early embryos were found but rarely. Supplementary evidence in regard to the breeding season was obtained by examining the ovaries. Judging from the condition of the ovarian eggs, Dean concluded that *H. japonicus* spawns a number of times during the "season", probably from six to twelve times, and that two eggs are matured at about the same time. During the spring months the eggs are evidently deposited at short intervals. This is deduced from the presence of almost ripe ovarian eggs in Japanese Bullhead Sharks from which encapsuled eggs were obtained. Further data bearing on the breeding season are given in the section on "Rate of Embryonic Development".

EGG-LAYING HABITS; THE NESTS

Waite (1896) wrote that the eggs of *Cestracion* (*Heterodontus*) *phillipi* were found in moderately shallow water, wedged in among rocks. Whether they were actually dropped into the crevices he did not know, but he thought it more probable that they were deposited on the sand at the bases of the rocks, into the fissures of which they were afterward swept by the tide. They were so jammed, larger end outward, that they could only be removed either by turning them around and withdrawing the small end first, or by actually unscrewing them; both forces being most unlikely to occur under natural conditions. When empty they are somewhat more pliable, which may account for the empty capsules being loosened and cast ashore. In a later publication (1899) Waite wrote that *H. phillipi* was common in Jervis Bay (New South Wales) which was for these fishes a favorite breeding resort. Here, empty egg cases could be found in large numbers washed

ashore or wedged in among rocks; here also, in 20 fathoms of water and under, living eggs might be freely obtained.

Haswell (1898) likewise collected capsules containing living eggs of *H. phillipi* in Jervis Bay, New South Wales. He states that he found many of these at low tide, sticking in the crevices of the rocks, firmly wedged in by means of the spiral flange which forms such a remarkable feature of the egg shell.

So little is known about the spawning habits of *H. galeatus* that the following account of their spawning grounds, quoted from Waite (1896), may be of interest:

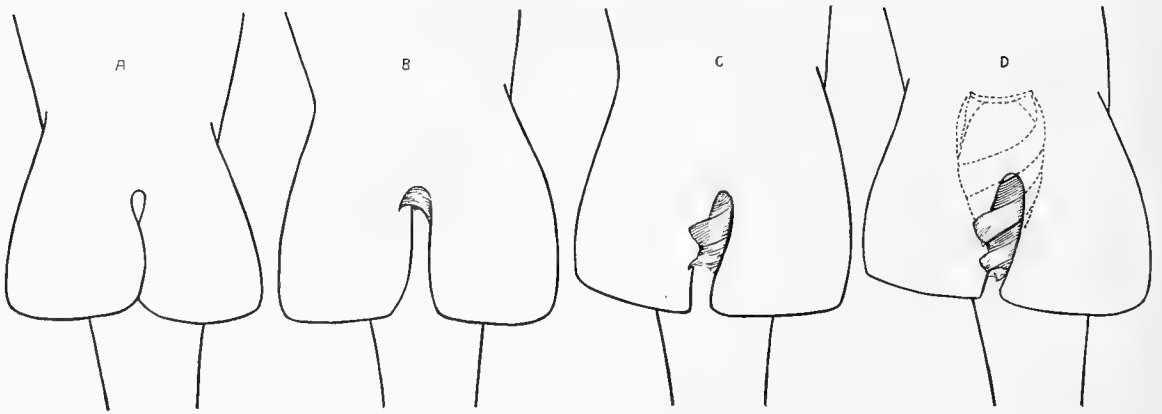
Although most rare upon the beaches, the eggs of *C. [Heterodontus] galeatus* prove to be not uncommon when searched for in their native habitat. Through the kindness of Messrs Darley and Grimshaw, I recently had the pleasure of searching for them 50 feet below the surface. Although not successful in obtaining specimens, I got an excellent idea of the general situation. In places, immense masses of brown seaweed grow to the height of two or three feet so densely that scores of eggs may be securely concealed among them, protected by their likeness to seaweed in color and texture. Mr. Cameron, the diver who kindly took me in charge, told me that he always finds the eggs in the weed, so attached by their long tendrils [Text-figure 37c] that it is scarcely possible to secure them whole, without cutting the seaweed. In deep water they are freer from the violent disturbances, tending to detach them, to which the eggs of the more common species (*H. phillipi*) are subject

Barnhart (1932) writes that eggs of *H. francisci* are frequently found wedged between or under rocks in the extreme low-tide zone.

In his notes Dean states that one can usually determine when a Heterodontid shark is gravid by noting the greater abdominal girth. Also, a digital examination can readily be made. In order to understand the process of egg laying in the Japanese Bullhead Shark, one should be familiar with the external form of the egg capsule which is described in a previous section of this article.

Heterodontus japonicus deposits two eggs at about the same time. In numerous instances encapsuled eggs were brought to the station (at Misaki) in pairs, and in the same stage of development. It was therefore assumed that they had been deposited in pairs. This assumption was verified on two occasions, when pairs of encapsuled eggs were taken directly from the fish. Evidence that two eggs mature at about the same time has been given in the section on the reproductive organs.

Data as to the mode of depositing the egg are scanty. The fish is apt to fold its pelvic fins around the cloacal region, and one must bend the fins aside in order to see if a capsule is protruding. In one instance, a shark brought to the station deposited an egg within a few hours (Text-figures 41A to 41D). When the fish was first examined (Text-figure 41A) no trace of a capsule could be seen between the pelvic fins. An hour or two later, the smaller end of the capsule protruded slightly (Text-figure 41B). Within an hour, a second turn of the capsule's lateral frill or spiral lamina could be seen (Text-figure 41C) and in less than an hour later there appeared Text-figure 41D the third turn of the frill. At this time the egg slipped out, and Dean noted that in the final rapid phase of



Text-figure 41.

Ventral view of the pelvic region of a female *Heterodontus japonicus* showing a series of stages (A to D) in the process of extrusion of the encapsuled egg. In A, the cloacal region is shown between the pelvic fins, but the extrusion of the egg has not commenced. In D, the dotted lines represent portions of the egg case still within the body of the mother.

From drawing left by Bashford Dean.

extrusion the capsule rotated about its long axis as though it had been unscrewed. Evidently this was not the only occasion when Dean saw an egg protruding from the cloacal aperture of one of these sharks, for on the margin of his drawing reproduced as my Text-figure 41D there was found a penciled note in Dean's handwriting: "Sometimes 4 ridges show".

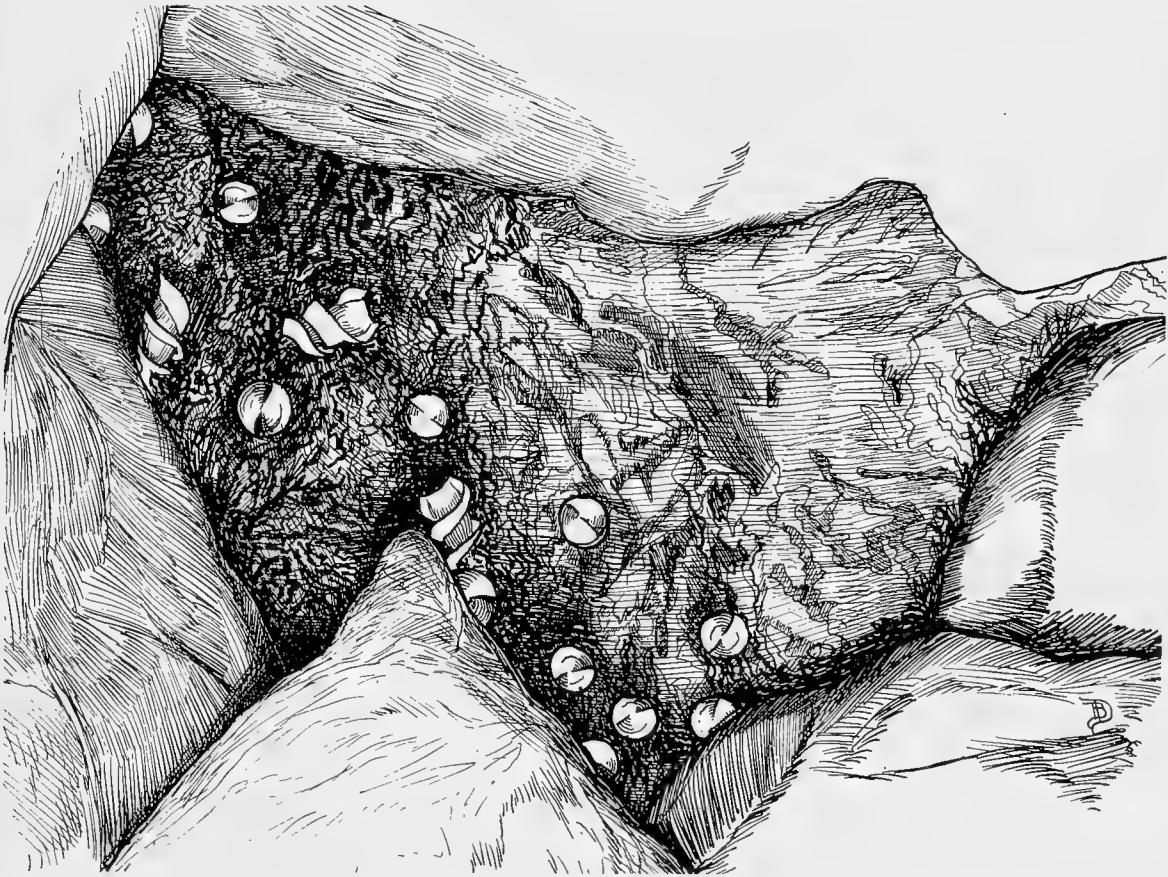
Dean thought that, in the case just described, the final extrusion of the capsule was hastened by unskillful handling of the fish. But he notes that there are several considerations indicating that the sudden extrusion of the capsule, which he observed, may have been like the normal process of deposition. The capsule at this stage is very slimy. The shark exercises a voluntary control over the sphincters of the oviducal apertures. It can tighten or loosen its hold on the capsule, and it may even envelop the entire cloacal region with the bases of the pelvic fins. The very suddenness of the process may have a distinct advantage to the fish, for by it the capsule, on account of its peculiar form, is caused to rotate—a motion which would obviously project it downward and backward in a straight line, making it less subject to deflection by water currents.

EGGS FOUND IN NESTS.—Of special interest is Dean's account of the occurrence of the eggs of *Heterodontus japonicus* in "nests" on the sea bottom:

It is well known by the fishermen that the eggs of "Nekosamé" are found among rock fragments. On sandy bottom and in weedy reaches they rarely occur. The professional divers (with suits) whom I employed to search for these eggs in the neighborhood of Misaki examined carefully various kinds of bottom in water from three to eight fathoms, but without success, for at that time we had not discovered where the eggs are usually located. For this discovery I was indebted to the fishermen who dive for *Haliotis*, and from them I learned that the eggs of *Cestracion* (*Heterodontus*) occur in "nests". An instance of their mode of occurrence may be cited.

A "nest" was discovered October 4, 1905, in the channel off the fishing town of Miura-Misaki behind the island Jogashima, at a depth of 28 feet. It contained 15 eggs in various stages of development. The bottom of the nest was of seaweed, its sides were formed by irregular rock masses, some of large size, and the nest was largely concealed by several flat stones which the divers removed only with difficulty. (It appeared fortunately that this particular spot was rich in *Haliotis* and was being inspected with great care). The eggs were shown to be arranged in a space about six feet long, the greater number of them lying together closely embedded in the seaweed, "four out of five" of them being wedged in, with the little end of the capsule downward. I visited the spot and it may be worth while to picture a restoration of this nest (Text-figure 42) as near as I could make it out without diving, relying upon the fisherman's reconstruction.

From the preceding account, it appears that there is similarity in the egg capsules and in the spawning habits of *Heterodontus phillipi* and *H. japonicus*. In both species, the capsules are surrounded by a pair of broad spiral valve-like appendages which end



Text-figure 42.

Reconstruction of a typical "nest" of *Heterodontus japonicus* found at the bottom of the Sagami Sea at a depth of 28 feet. The nest was surrounded by large rock fragments. Some encapsuled eggs may be seen entangled among sea weeds at the bottom of the nest, and other eggs are wedged into crevices in the rocks.

From a drawing by Bashford Dean, whose initials appear in the lower right-hand corner.

bluntly, without tendrils. These eggs are deposited on the sea bottom among large rock fragments, or surrounded by rocks. In such situations, some become entangled in seaweeds, others wedged into crevices between rocks. The egg capsules of *Heterodontus galeatus* are different, in that the spiral appendages are narrower and end in very long and slender tendrils which become thoroughly entangled among seaweeds. The only records available indicate that living eggs of these species have been taken at the following depths: *Heterodontus japonicus* at 28 feet; *H. phillipi* at 120 feet or less: and *H. galeatus* at a depth of 50 feet. There is no record of any direct observations of the process of egg laying by any species of Heterodont shark in its natural habitat.

METHOD OF COLLECTING EGGS AND EMBRYOS

The earliest developmental stages of the egg of *Heterodontus phillipi* figured by Haswell (1898) were already in late cleavage. These were eggs that had been deposited—as stated more explicitly in a later article by the same author (Haswell, 1916). In this later paper, Haswell described some eggs taken from oviducts (“uteri”). Of these, the two earliest stages were portrayed in a figure which is reproduced as my Text-figure 49A and 49B (page 731). The other eggs, taken from uteri some weeks later, showed more advanced stages of cleavage.

As previously stated, the eggs of *Heterodontus japonicus* were collected at all seasons of the year. According to Dean’s notes, the greatest numbers of encapsuled eggs were taken during the month of May. They were gathered in small numbers daily, the maximum catch being 21, a number as large as 8 or 10 being uncommon. The greatest number of eggs came from the fishing village of Nagai, between Misaki and Hayama.

The precise method used in collecting the eggs is not only interesting but is of technical importance. It is well described in Dean’s own words:

In collecting eggs of *Cestracion* [*Heterodontus*] divers are indispensable. But these are fortunately numerous in the neighborhood of Misaki, where they are constantly scrutinizing the shore rocks for edible mollusks, especially *Haliotis*. They have thus an excellent training, for if they can detect these protectively colored limpets, they can observe closely enough to collect shark eggs; moreover they are in the habit of examining fissures between the rocks, and they frequently displace stones of considerable size. In general their operations are usually carried on in water of from 12 to 30 feet, though they sometimes exploit a depth of 40 feet—all this without the use of special suits, the divers usually swimming to the bottom, remaining under several minutes (2 to 6). They operate usually in pairs, going about in sampans, each boat provided with a screen, and an *hibachi* (fire-pot) over which the fishers crouch during intervals of rest. A familiar sound near the zoological station at Misaki is the peculiar whistle of the diver as he expands his lungs before going down.

Dean states that the eggs are hardy, and are readily kept alive in floating cages. Thus the various embryonic stages may be selected from time to time. The stage of development may be determined with fair precision without the necessity of opening capsules at random, for the character of the capsule gives a clue to the period of incubation. The

capsules with a slimy coating are those recently deposited, and the degree of sliminess lessens perceptibly during the first days and weeks. The capsule then acquires a smooth but elastic surface; the spiral band is thick and rubber-like. In later stages the capsule becomes rougher in texture, thinner and more brittle; its upper and lower edges become frayed, and its lateral band is apt to be imperfect. On its surface various foreign growths appear: bryozoa and barnacles especially.

When capsules were opened and kept in aquaria, the young (still within the capsules) lived for some time. Early stages were kept alive for several days, especially if well-covered with albumen; later stages lived for weeks. Death in such cases results ultimately from invasion of bacteria and infusoria: these attack the yolk, causing it to soften in spots and finally to break down.

Several times, Dean obtained gravid females; but he never found eggs whose capsules were in an early stage of formation. The adult *Heterodontus japonicus* is not often taken. It rarely is caught in seines, probably because it occurs in regions where rocks are abundant and where a seine is not likely to be drawn. Even when netted, it is rarely retained, for it is not marketable (see also pages 688 and 694). Since it was found impracticable to secure a large supply of spawning fish, the stages of fertilization and beginning cleavage were not obtained. These stages doubtless occur during the descent of the egg and its enclosure in the capsule. The earliest embryonic stages studied by Dean were fairly early (but not the earliest) cleavage stages (Figures 7 and 8, plate I). These were eggs already in capsules which were practically completed, and were soon to be deposited. Dean states that the egg is in a blastula stage at the time of deposition.

Heterodontus japonicus, like *H. phillipi*, is oviparous and not ovoviviparous. In both species, the earliest stages of cleavage occur while the egg is still in the oviduct.

EMBRYONIC DEVELOPMENT OF *HETERODONTUS JAPONICUS*

As the title of this article indicates, we are here concerned primarily with the embryology of the Japanese Bullhead Shark, as set forth in Dean's notes and drawings; but the observations of other authors, working mainly with *H. phillipi* or with *H. japonicus*, will be noted for comparison. It will be evident that descriptions of the development of *H. phillipi* are confined to the early stages; while practically all that is known concerning the embryology of *Heterodontus japonicus* has been either discovered by Dean or made possible by his labors.

RATE OF EMBRYONIC DEVELOPMENT

Under "Breeding Seasons", I have already recorded observations to the effect that eggs of *H. phillipi* in blastula and gastrula stages are abundant in August and September (spring months in the southern hemisphere) and that hatching has been observed in May. In the absence of more adequate data, this indicates a probable duration of nine months for embryonic development. Whitley (1940) states that the period of incubation for *H. galeatus* is "at least five months".

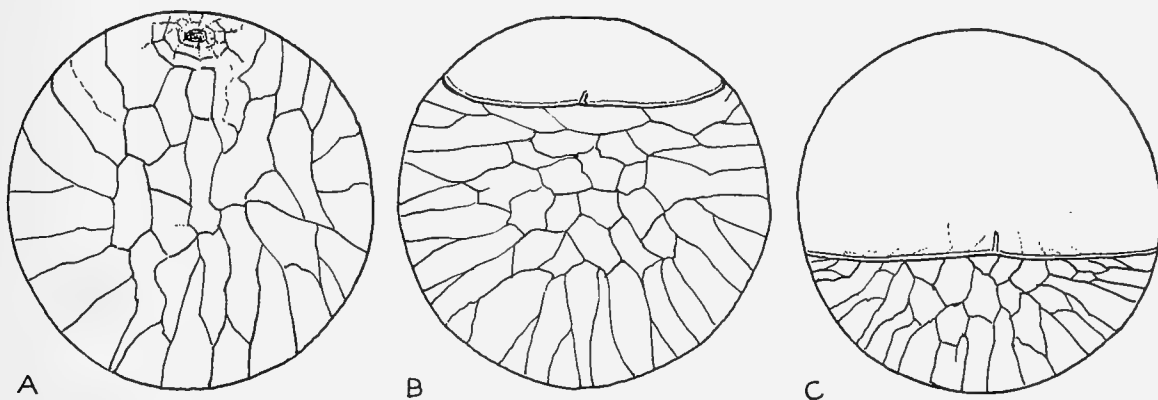
Barnhart (1932) notes that it takes eight to ten weeks for the young of *H. francisci* to hatch from the egg case, at which time the yolk is completely absorbed and the young shark is 14.5 inches long. Eggs have been hatched in the aquarium of the Scripps Institution at La Jolla, California, in June, September and December. Nothing is said about the temperature of the aquarium water in comparison with that of the ocean water at the depths where eggs are found.

In his brief manuscript containing a summary of his observations on the embryology of *Heterodontus japonicus*, Dean states that the term of development (before hatching) is reckoned at about one year, with the possibility that it may extend over a period of two years, at an average water temperature of about 65° F. He writes that, in his estimate of the rate of development, he was aided by the fact that eggs found in any one season are usually in about the same stage. This latter statement may need further qualification. Some generalities bearing on this subject are recorded under "Breeding Season" on page 712 of the present article. It is there stated that in the vicinity of Misaki spawning occurs throughout the year, though the special spawning season is evidently the month of March. From the original data contained in Dean's notebook, it appears more likely that spawning reaches its height during the month of April and continues at a rapidly reduced rate during the months of May and June, after which it is almost negligible. As might be expected, there is an increasing range of variation in the stages collected during each month after the first month of spring. Hatching has been observed in April, at which time the young shark is presumably at least a year old.

In Dean's manuscript there is an outline for a time scale in which it was intended to give the stage of development that predominates in each month, by reference to Balfour's stages in *Pristiurus* and other sharks. Unfortunately, the spaces left for the letters indicating the stages have not been filled in. There is also a series of diagrams or outline drawings representing developmental stages from the time of spawning to the time of hatching. All excepting the last two (which are outlines copied from Figures 82 and 84, plate VII) are reproduced as my Text-figures 43 to 45. Two of the original drawings are annotated with the names of months. Fortunately these are drawings representing stages for which data would otherwise be lacking. In the legends for Text-figures 43 to 45, I have specified the month or months in which each stage seems to predominate according to the information at hand, but we can be fairly certain only for the months of April, May and June.

Dean records that a total of approximately 200 embryos of *Heterodontus japonicus* were collected for him at Misaki. In his notebook there is a table giving individual records for 135 living embryos collected during April, May, June and July (up to July 6 only). This table is dated at the top, in Dean's handwriting, "Dec. 15, 1904". It is probable that it does not contain any entries subsequent to this date, for all the entries are in chronological order and there are no gaps in the series affording space for further entries. We know that Dean was in Japan (though not continuously at Misaki) from July to October in the year 1900; March to July in 1901; and June to October in 1905.

During the season of 1900, the work was of a preliminary nature; considerable time was spent in exploring the sea bottom in search of favorable localities for collecting. Since the table in Dean's notebook contains no entries later than July 6, none of the entries could apply to specimens taken during the summer of 1900. Therefore it seems likely that all the entries in the table apply to one season only; the spring and summer of 1901. However this may be, we have no individual records for embryos collected earlier than April nor later than July 6 in any year, despite Dean's statement that collecting was carried out for him "at various intervals throughout the year". It is known to Dean's colleagues that collecting for him was carried on at various times during his absences from Japan. That some records are missing is obvious. I have found no records for individual embryos aside from those in Dean's table. The missing records include all stages over 35 mm. total length, excepting a few newly hatched.

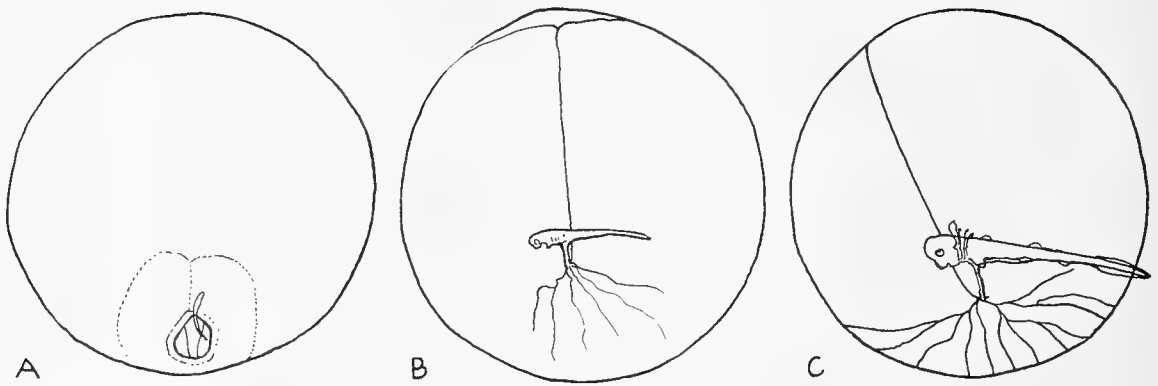


Text-figure 43.

Diagrams representing stages in the early development of *Heterodontus japonicus*. A, blastula stage shortly after deposition of the egg, which occurs chiefly in March and April. The egg is drawn as seen from above, with the upper pole, which Dean calls the animal pole, in the center. The germinal disc appears near the equator in the upper part of the figure. B and C, stages in gastrulation and early embryo-formation found most frequently in May.

From drawings left by Bashford Dean

Of the 135 embryos listed by Dean, 14 were taken in April, 59 in May, 20 in June, and 42 in July (first week only). This distribution does not quite accord with Dean's statement, recorded in his manuscript, that "The divers brought in the maximum number of eggs during April and May", unless some records for April are missing. From the original records it appears that most of the 14 eggs collected during April were in late cleavage, or blastula, stages (Text-figure 43A). This, according to Dean, implies that the eggs were newly spawned. A very few had reached an early gastrula stage, and (significantly) one was in the hatching stage. During May, a great majority of the 59 eggs collected were in gastrula stages (Text-figures 43B and 43C), but there was a sprinkling of eggs in both younger and older stages. A few yolk sacs bore embryos old enough to perform wriggling movements. In June, with only 20 embryos, the range of



Text-figure 44.

Outlines representing stages in the early development of *Heterodontus japonicus*. The stages shown in A and B are most abundant in collections made in June; the stage shown in C is probably representative of the month of July. In A, the extent of the area vasculosa is indicated by dotted lines; in B and C, the principal blood vessels are represented by solid lines.

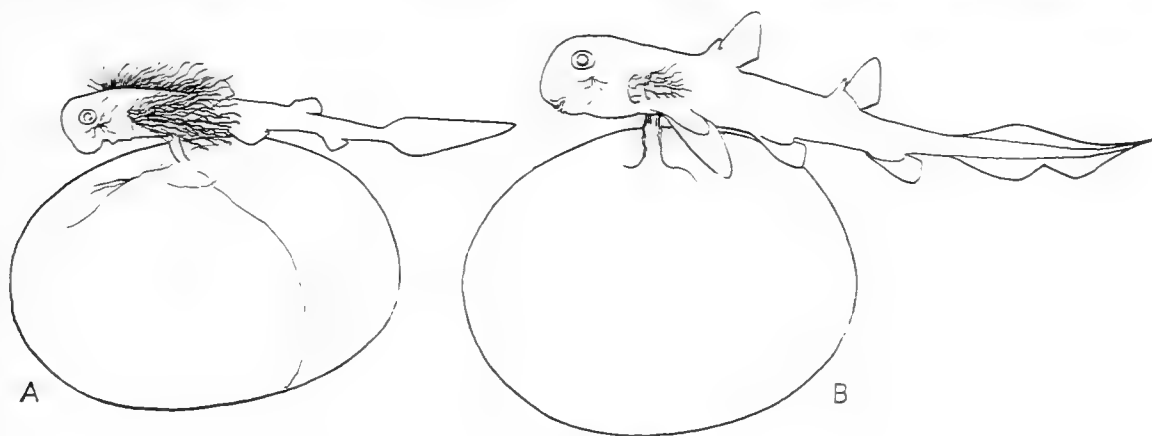
From drawings left by Bashford Dean.

variation was greater: there were embryos of all stages from late cleavage to one of 31 mm. total length. The average condition was somewhere between the stages shown in Text-figures 44A and 44B. It should be noted that by this time the average condition no longer represents accurately the rate of development of eggs spawned in April, on account of the lag occasioned by continued spawning. Of the 42 eggs taken in July, the majority were collected on July 3 and opened the same day; the others were taken on July 4 and opened on July 6. Here, there are surprising numbers of gastrulae and of slightly later stages, which can hardly be considered as representative of this month; but there are twelve embryos ranging from 15 to 35 mm. long. For July as a whole we have no adequate data indicating the average stage of development, but in view of what follows we assign Text-figure 44c to this month. The original drawing reproduced as Text-figure 45A bears the annotation "Aug-Sept". The next later stage, represented by Text-figure 45B, we assign to October because the following one, portrayed in Figure 82, plate VII, is marked, on the original, "Nov-Dec".

The newly hatched young, in dorsal view, is represented by Figure 83, plate VII. A slightly older specimen, in lateral view, is portrayed in Figure 84, plate VII. In his manuscript Dean states: "In capsules that have long been incubated, I have found in April the only stages where the young is about to escape from the capsule". He records also that "in a single instance the act of hatching was observed". This event took place early in April, and is described on pages 709 and 753 of the present article. It is important to note that this specimen had been collected only a few days previously. The young shark at hatching is said by Dean to measure about 7 inches (180 mm.) long. As indicated by the original notes, this measurement refers to the single specimen of *H. japonicus* observed in the act of hatching.

Dean states that at first sight his list of embryos of various sizes seems to yield reasonably complete evidence that the entire term is twelve months or thereabouts. On the other hand, he realizes that a weak spot in the evidence lies in the fact that the series of later stages is not complete. He is not sure that stages such as those assigned to August-September, October and November-December are the dominant ones for the months that have been suggested. Specimens in these stages are not at all common, and the range of size has become so varied that one cannot tell whether a stage such as the one represented in Text-figure 45B is really the sequent of the one portrayed in Text-figure 45A, or is much older (i.e., from an egg which was deposited, say, in September of the previous year). Development is probably much slower during the winter months. The age of the embryo represented in Figure 82, plate VII, which is hardly less than seven or eight months, might be 14 to 20 months. And at hatching the embryo, which can hardly be less than 12 months old, is possibly aged 20 to 24 months.

The only direct observations on the growth rate are not in favor of the view that the incubation period greatly exceeds one year. A late embryo in its opened capsule was placed in an aquarium on August 10. It measured 45 mm. in total length. On October 5, that is, within a little less than two months, it had attained a length of 110 millimeters. This growth is so extraordinarily rapid (for a shark) that if the same rate were continued, estimating roughly an increase in length of 30 mm. each month, the young fish would have hatched by December or January (the young at hatching measure about 180 mm.). This would make the entire period of incubation, assuming that the egg was spawned in April, from nine to ten months. But the experiment was probably not conducted under strictly natural conditions. The temperature of the aquarium must have been considerably higher than that of the sea bottom; and if the egg, after opening of the capsule, was left uncovered the embryo may have been better aerated than it would have been if the capsule



Text-figure 45.

Outlines representing stages in the development of *Heterodontus japonicus*. A, stage collected mainly during August and September; B, stage presumably most abundant during the month of October.

From drawings left by Bashford Dean.

had not been opened. Under these conditions development must have been almost abnormally rapid. As a somewhat parallel case, I note that embryos and larvae of the amphibian *Cryptobranchus allegheniensis*, kept during winter at moderate temperatures in a basement, developed much more rapidly than embryos and larvae of the same species left in their natural environment—in cavities under rocks in a stream often frozen over.

Much of the evidence here presented is complicated by the fact that egg laying may occur at any time of the year, though most often in spring. Moreover, it is obvious that much variation in the rate of development is to be expected because of differences in temperature, seasonal and otherwise. We have Dean's statement that eggs were collected, in one instance, at a depth of 28 feet, and that *Heterodontus japonicus* is known to inhabit depths varying from 3 to 20 fathoms (18 to 120 feet). At the maximum depth the water is presumably much colder than it is near the surface, or in a laboratory aquarium. Aeration of the eggs is another factor to be considered. An egg exposed to water currents, particularly an offshore current, is presumably better aerated than one shut off from such currents. Lacking adequate data, it would be rash to attempt to estimate the amount of variation in the rate of development due to environmental causes, but it must be considerable.

GENERAL MODE OF DEVELOPMENT

This subtitle is inserted mainly to afford an opportunity to introduce at this point Dean's evaluation of his results from the study of the embryology of *Heterodontus japonicus*, and his hopes for future accomplishments, in his own words taken from his brief and very incomplete manuscript:

Heterodontus, although separated from its nearest genera during long ages (at least since the earliest Mesozoic), exhibits a plan of development not differing greatly from that described among sharks of the present time. The egg is about the same relative size, its envelopes are similar, its early development follows the same course, its embryos have essentially the same forms as *Scyllium*, *Pristiurus* or *Squalus*. It must not, however, be concluded that its embryology is lacking in interest, for, as will be seen in the following pages, the differences which occur in Cestraciant development are in clear accord with its more ancient lineage, and we will find that these differences will give us an interesting light on the puzzling question of to what degree development may in time come to be modified. It will be seen, for example, that a Cestraciant still retains traces of an holoblastic cleavage, and that its blastoderm still grows around the egg before the embryo is of large size, features which stand clearly in the gap which has separated the plan of development of recent sharks from that which occurs in ganoids and lungfishes, a plan which, on many grounds, must also have existed in primitive sharks. But these considerations may best be examined in later pages of our work.

In a somewhat similar vein, Haswell (1898) had previously written concerning *Heterodontus phillipi*: “. . . the hope is not an unreasonably sanguine one that the embryonic development of a type so ancient might exhibit some important primitive features. With regard to the stages now described, however, any expectation of the kind cannot be said to have been fulfilled; and what impresses one most is the extraordinary persistence

of certain characters which are not known to have any vital significance." As an example, he cites the "orange spot" which forms such a striking feature of the egg of an elasmobranch in its early stages. This, in Haswell's opinion, has been handed down with little change from Paleozoic times. The evidence for this view is not given, but it probably rests on the fact that the "orange spot" appears in the eggs of genera that have been segregated in different families from a very early period.

It is not from surface features alone, nor from early stages alone, that one should look for developmental characters linking *Heterodontus* to the most primitive elasmobranchs. In studying the phylogenetic relationships of the various groups of vertebrates, the later stages of embryonic development often yield evidence more satisfactory than anything the early stages afford. In *Heterodontus*, the field of organogeny is largely unexplored. There are, to be sure, a few contributions that deal wholly or incidentally with the development of organ systems in *Heterodontus*: such as those of Osburn (1907) on the origin of paired limbs; Luther (1909) on the musculature innervated by the trigeminal nerve; and de Beer (1924.1,2 and.3) on the development of the head. Since it does not lie within the province of the present article to review the literature on organogeny, no attempt has been made to make this list complete.

THE EGG AND ITS MEMBRANES

The orientation of the early blastoderm of *Heterodontus phillipi* within the egg capsule has been described by Haswell (1898). He states that the blastoderm, which appears as a circular reddish-orange spot about 2 mm. in diameter, occupies a constant position in the egg: it is always situated much nearer the broader end of the egg shell. The extremity of the blastoderm destined to become posterior is always directed away from the broader end of the egg shell. This indicates that the egg is anchored by the albumen in such fashion that it is free to rotate only about an axis that corresponds to the long axis of the capsule. In the egg of *Pristiurus*, the germinal disc is always situated at the pole of the egg which is near the rounded end of the egg capsule (Leydig, 1852).

In Dean's article entitled "Reminiscence of Holoblastic Cleavage in *Heterodontus (Cestracion) japonicus*", published in 1901, there is some ambiguity in his use of the term "animal pole". This difficulty arises in part from our preconceptions, for certain features of the egg during early development are apparently unique. In his later manuscript Dean seldom uses the term "animal pole", thereby attaining greater clarity in his description of the egg, which follows:

The egg [of *Heterodontus japonicus*] measures from 40 to 50 mm. in diameter. It is pale greenish-yellow in color, but bright red in the germinal spot [Figure 79, plate VII]. It is of semifluid consistency, as in sharks generally, and can be removed unbroken from the capsule only with the greatest difficulty. It is enclosed in a glistening, somewhat firm vitelline membrane, and supported by viscid albumen, which in turn is attached to the stout capsule. The orientation of the egg is conditioned by gravity, the germinal area [equivalent to the "orange-yellow spot" of other Elasmobranchs] remaining near the upper pole. It probably does not take its position [precisely] at the upper pole although this was not decided, since as

soon as the capsule is opened, the tension maintained by the albumen is destroyed and the germinal area probably loses its normal position. In nearly every case it remained near the equator of the egg. The albumen is thick and glairy, transparent save at the extreme upper and lower regions [of the capsule?]. Here it becomes opaque and is attached firmly to the capsule. The albumen shows clearly its origin in tunics: one envelope is especially clear near the egg, forming a whitish membrane, reminding one of the inner layer of the albumen of an amphibian egg (e.g., *Necturus*). When this is ruptured the contour of the egg is disturbed. When the albumen is in part removed, as when the upper portion of the capsule is cut away with the attached albumen, so that the egg is better exposed, there is a relaxed pressure which results in a flattening of the exposed surface of the egg and, in cases, gives rise to the rupture of the vitelline membrane. In such cases the egg appears with a hernia-like expansion. Under usual conditions an egg may be shifted about within the capsule so that the germinal area can be seen.

As one sees from an inspection of Figures 1 to 6, plate I, there are furrows, traversing the region of the upper pole, which are apparently cleavage furrows. Their pattern suggests that this region may be a primary center of development; but it will soon be superseded by the germinal disc, which is already undergoing segmentation and will presently assume complete control. These subjects are fully discussed in the two following sections.

REMINISCENCE OF TOTAL CLEAVAGE

The portion of Dean's manuscript dealing with this topic is in a finished condition as compared with most other parts. It is evidently a revision of his article published in 1901. In the figures illustrating that article, the outline of the germinal disc, which is small and very faint in the original drawings, does not appear with sufficient clearness to attract the attention of the observer, especially since it is not labelled. In most of the drawings, as reproduced in 1901, the outline of the germinal disc cannot be seen at all, even with the aid of a strong reading glass. Therefore I have had some of these drawings reproduced by lithography (Figures 1 to 6, plate I), and have inserted here the corresponding portions of Dean's manuscript without change save for the rearrangement of some tabulated matter, the substitution of reference numerals to meet a revised arrangement and enumeration of the figures, and the insertion of some additional references to figures.

The peculiar interest in the development of *Heterodontus* is that it still bears witness to an earlier condition of holoblastic cleavage. There can be no doubt that the great size of the egg of recent selachians is a secondary embryological character, and that the early ancestors of sharks produced eggs which, like those of ganoids and lungfishes, were small, poor in yolk and fertilized externally. Indeed we already know that the Palaeozoic Cladoseiachians and Acanthodians were not provided with intromittent appendages, and that therefore small eggs and a more or less holoblastic cleavage probably then prevailed within the group of sharks. We have found furthermore [Dean, 1906] that a recent Chimaeroid, *Chimaera coliei*, undergoes in its early stages a curious process of fragmentation of the egg which can best be explained on the ground that it represents a form of holoblastic cleavage, specialized and retained for a new physiological function. On such evidence, accordingly, there was

strong reason, *a priori*, for prophesying that in so conservative a shark as *Cestracion* [*Heterodontus*] there might still—in spite of the great size of the egg—persist traces of the ancestral holoblastism. It was of peculiar interest, therefore, to find such a condition present.

The earlier stages [Figures 1 to 6, plate I; and Figure 79, plate VII] invariably showed a series of lines (furrows) traversing the surface of the eggs in a fashion which corresponds closely with the early superficial furrows appearing in the eggs of *Amia* [Dean, 1906] or, better still, *Lepidosteus* [Eycleshymer, 1899]—and in these [latter?] instances there is no question that the furrows represent cleavage.

Before, however, considering the question of the homology of these “cleavage” lines in the egg of *Cestracion* [*Heterodontus*] we may describe their conditions in various stages. In the ripe ovarian egg no traces of these lines occur. In an egg taken from the oviduct—the earliest stage in my material—the furrows in the yolk region are already present, almost as numerous as in later stages. But there is this very noteworthy difference, that in the neighborhood of the (red) germinal area there appear a number of unpigmented lines and circles [Figures 40 to 43, plate IV] occupying a wide zone between the red germinal area and the yellow yolk region—the most conspicuous of these being a white circle immediately surrounding the germ [Figures 7 and 8, plate I].

As development proceeds, this entire intermediate zone becomes less and less conspicuous: it is later noted in the early stages of gastrulation. I believe that this zone represents a region in which the interblastomeral spaces of the segmented germ pass over into the furrow spaces on the surface of the yolk region. For this was clearly seen in the earliest stage which I was able to collect (capsule taken from the oviduct); especially clear were the lines when one carefully removes the living germ (e.g. in a spoon-shaped spatula) and examines it (in salt solution) by transmitted light. Such a preparation will be seen in [Figure 7, plate I] from a camera drawing. It shows a stage of late cleavage (? 7–10 cleavage) [more likely sixth to seventh cleavage] with the blastomeres containing the red pigment situated in an irregular central area, and with the surrounding unpigmented band traversed radially by shallow furrows. The latter spread out peripherally and could not be traced further since the soft yolk around the margins had escaped in the preparation. In another and older specimen, from a capsule which was partly protruding from the oviduct, the condition of the marginal zone could be seen more satisfactorily [Figure 8, plate I]. In this, the preparation was partly hardened (sublimate-acetic) before it was examined by transmitted light. There could then be seen not only the central pigmented blastomeres but in the circle surrounding them a series of blastomeres, somewhat larger in outline and separated from one another by wider spaces. Beyond these, and in the region of the yolk, were a number of faintly outlined blastomeres, whose intervening spaces suddenly dilated into the beginnings of the great furrows which traverse widely on the surface of the egg. It may be remarked that stages of or near this period give but the faintest indication of blastomeres in the “transitional zone” if examined as opaque objects, whether in living or in hardened material [Figure 9, plate I]; and it is clear that the indication of these blastomeres is marked out not by actual separation of the cells, but by shallow superficial grooves and by a thinning away of the cytoplasm in planes in which (perhaps in earlier stages of ontogeny) cell boundaries probably existed. By this process the yolk had become drawn into the central portion of each potential blastomere, leaving the intervening parts transparent—conspicuous when examined by transmitted light.

Examining now a series of early stages (all drawn from living specimens) we may convince ourselves as to the character and disposition of these larger furrows. In Figures [1 and 2, plate I] are shown two blastulae as they appeared in the open capsule, viewed from above. The germinal area [indicated by a tiny circle] lies nearly or quite at the margin of the

drawing. I note that when the albumen is removed close to the egg (so that the surface may be better examined) the germinal area passes out of sight below the equator of the egg. Indeed it is quite probable that the germinal area has its normal position nearer the upper pole before the tension of the albumen is relaxed by the rupture of the wall of the capsule. In these stages the earliest [Figure 1, plate I] has the fewest furrows. All show the furrows clustered in the upper part of the egg, and extending thence more or less radially toward the periphery. In side view [Figures 3 to 5, plate I] (the egg having been rotated into this position by means of hooked needles thrust into the albumen) the furrows are seen to pass down the sides of the egg in nearly parallel series precisely as they do in *Lepidosteus*, *Amia* or *Necturus*: some of the furrows extend lower than their fellows, and all round out, flattening at the ends. [Figure 6, plate I, shows a somewhat oblique view of the lower hemisphere, with the furrows converging toward the vegetal pole]. The similarity of such a stage to the blastula of a ganoid is made the more striking by the range of color in the Cestraciont egg. The animal pole is of a pale-straw tone, the lower hemisphere is greenish-yellow and the intermediate (equatorial) zone has usually an orange or brownish cast. [In his notebook Dean states that the equatorial zone has a greenish color. For the upper hemisphere, the colors are shown in Figure 79, plate VII].

Another regard in which the furrows indicate their homology with cleavage lines is their behavior with respect to the downgrowing blastoderm [a product of the germinal disc]. This begins at the side of the segmented "animal pole" of the egg, extends across it and encloses the egg in such a way that the [yolk] blastopore closes at nearly the opposite point on the equator of the egg to the one where the germ was situated, in this regard suggesting the conditions of *Lepidosteus* or *Amia*. In this connection it is to be noted that when the [yolk] blastopore in *Cestracion* [*Heterodontus*] is closing one may see through it a few long furrows which belong to that portion of the egg (near the equator) where the lines become nearly parallel (Figures 52 to 56, plate V).

It is none the less an extraordinary thing to maintain that a shark's egg, especially one as large as [that of] *Heterodontus*, possesses a form of holoblastic cleavage. Accordingly it would not be amiss to consider the objections which might be urged against such a thesis. Let us tabulate the objections as follows, and set against them the facts favorable to the view that a rudimentary holoblastism is present.

Concerning the Homology of the Furrows of the Egg of *Heterodontus* to Cleavage Furrows of a Holoblastic Egg:

They may be surface wrinkles only.—In this event we might expect them to occur in the mature egg, to be more or less inconstant, and to be subject to change by artificial means. They are, however, absent in the egg about the time of fertilization. They are constant in all early stages examined (about a hundred specimens). They are not altered in shape and position by artificial means, such as pressure or tension; nor do they become obliterated (according to observations on an opened egg which was kept alive for thirty hours). They can be distinguished after the egg has broken, and it can then be seen that the furrows are not superficial merely, but that they pass deep into the yolk, by actual measurement at least 1.5 mm. in the upper part of the egg. Moreover the furrows do not occur at hazard. One always finds a central series of segments in the upper part of the egg, and in the lower part a peripheral series, with furrows nearly parallel; occasionally, moreover, as in the egg of *Lepidosteus* or *Amia*, several of the marginal furrows may be traced into the region of the vegetal pole and may even traverse it [Figure 6, plate I]. These numerous, close and constant correspondences can hardly, therefore, be without homological significance.

These furrows are known to occur in no other Selachian.—Compare, however, the segmentation stages of *Chimaera* [Dean, 1906], and take into account the paleontological history of Heterodont sharks. In a word it is precisely since they do occur in *Heterodontus* that these furrows may well be homologous with cleavage lines.

The furrows have not been traced back into the earliest segmentation stages.—A gap in the evidence, truly, but by no means a fatal one. In earliest stages examined a continuity has been shown between the inter-blastomeral spaces in the germ and the circum-germinal furrows.

The furrows may have no relation to the nuclei.—We note however, that the furrows do not occur in the egg about the time of fertilization: i.e. prior to segmentation. It has been demonstrated that nuclei are abundant in the region beyond the germinal area, to a distance of about 10 degrees on all sides. We have some reason to infer that they extend further peripherally since the neighboring circum-germinal yolk is similar in character to that in the region where they occur. Unhappily, however, owing to technical difficulties, the outer region of the yolk has not been sectioned. But it does not follow that, because nuclei in this region have not been demonstrated, the furrows in question cannot be concerned with cleavage. For such an objection would apply equally well to the case of such eggs as those of *Necturus* where nuclei have not been demonstrated in the vegetal region, yet where one does not question the homology of the furrows with cleavage lines.

The furrows may be due to the action of merocytes, which are known in Pristiurus and Torpedo to form blastomere-like structures.—Even in this event the furrows must be classified broadly, I think, as within the category of cleavage lines, and hence as an expression of a holoblastic condition. For if an egg subdivides, when deprived of its nucleus and later provided with a sperm nucleus, does not this division come under the general head of cleavage? There is, however, no evidence that furrows of so distinct a type have ever been produced in a meroblastic egg by merocytes. There is on the contrary evidence for assuming that merocytic division in *Cestracion* [*Heterodontus*] would be less evident than in more modern types of sharks. For all will agree that polyspermy, in vertebrates at least, is a secondary character and less apt, therefore, to have been prominent in the oldest sharks, like *Cestracion*. Indeed, we already know, thanks to Rückert's studies (1899) that the migration of merocytes into the yolk is less marked in *Pristiurus* (an older form) than in *Torpedo* (a later and derived form).

We conclude, accordingly, that the weight of the evidence is unquestionably in favor of regarding the furrows in the early *Cestracion* egg as the homologues of cleavage lines.

Among Dean's records I find several photographs of eggs exhibiting the alleged "holoblastic" cleavage furrows. These photographs are in part identical with those published in Dean's article (1901) on cleavage. Some of the photographs show the furrows quite as clearly as they are portrayed in Dean's drawings. But it is not likely that these drawings were made from photographs. Inserted in Dean's notebook there are many carefully executed drawings of these "cleavage" stages, annotated in Dean's handwriting. Some correspond to the drawings already published; but few, if any, correspond to the photographs.

In some of the drawings found in Dean's notebook the region of the upper pole of the egg, which Dean sometimes calls the animal pole, has the appearance of a well-defined large blastoderm or region of micromeres, from which nearly parallel furrows radiate like meridians down over the equatorial region (as in Figures 1 to 6, plate I). Thus the egg has

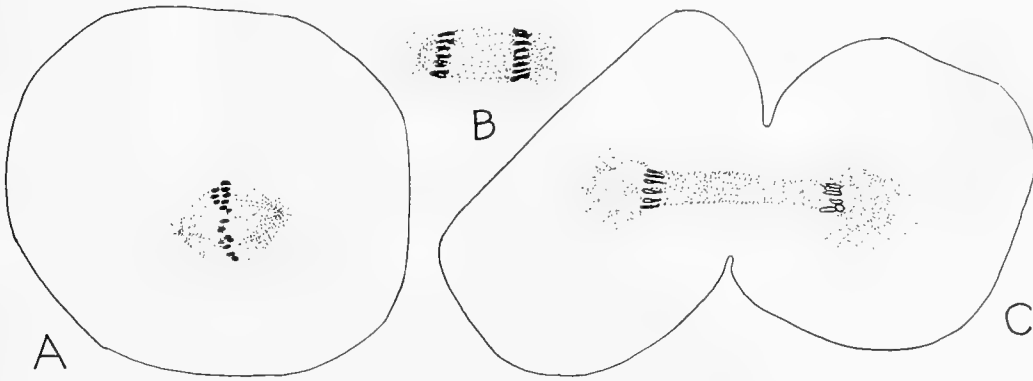
the appearance of an egg of *Lepidosteus* (Eycleshymer, 1899), or of the amphibian *Cryptobranchus* (Smith, 1912), in an advanced stage of cleavage. In nearly every drawing of the egg of *Heterodontus japonicus* in the stages under consideration there is indicated, in addition to the "cleavage" pattern just described, a very small circular germinal disc similar to that of other Elasmobranchs. The germinal disc is usually situated a few degrees above the equator. From Dean's note and manuscript it appears that this conventional germinal disc (described as reddish in *H. japonicus*, reddish-yellow, orange-yellow or simply orange in other Elasmobranchs) is already cut up into blastomeres (Figures 7 and 8, plate I). In a preliminary sketch, found in Dean's notebook, of the egg represented in Figure 5, plate I, the small circular area is labelled "b'd'm" (blastoderm).

The most puzzling thing about the cleavage of the egg of *Heterodontus* as described by Dean is that there are apparently two distinct centers of blastomere formation. If there are really two, the relationship between them is not clear. On this topic Dean (1901.1, p. 4) comments as follows: "There is evidence that the present position of the germ disc is a secondary one, for in eggs just deposited, (1) it is nearer the animal pole than in later stages; (2) there is a kind of track, whitish in color, extending from the direction of the upper pole of the egg, suggesting therefore that the disc has shifted its position, leaving a wake behind". Dean (1901.1, p. 7) writes further: "*Cestracion* (*Heterodontus*) also indicates that the change in the position of the germ disc occurred before holoblastic cleavage was given up, and we have with it a suggestion that it was from some new or modified physiological cause that a distinction came to arise between the germ disc and the region of the upper pole." Certain it is that the tiny germinal disc soon takes the lead in the formation of the embryo.

DISCOIDAL CLEAVAGE AND THE BLASTULA

Figure 79, plate VII, in color, shows the general appearance of the egg at the beginning of the stages about to be described. In this egg, the furrows traversing the general surface assume a pattern that is not the most fortunate to illustrate Dean's thesis that they are cleavage furrows, but the drawing is the best one available to portray the colors as described in Dean's notes. In his notebook Dean has written, concerning this early stage, that the uppermost portion of the egg is "light" (yellow) and the equatorial region is "greenish" (yellow). The region below the equatorial zone is designated simply "yolk". In the drawing, the germinal disc appears pink (Dean calls it "reddish"), and it is surrounded by a white zone—repeatedly mentioned by Dean in his notes.

Attention must now be focussed on the progress of segmentation within the germinal disc. The very early stages of cleavage in the germinal disc of *Heterodontus japonicus* have not been described. These stages must occur while the egg is still in the oviduct, before or during the formation of the capsule. The earliest stages obtained by Dean are those illustrated in Figures 7 and 8, plate I. These eggs were taken from the body of the fish; they were enclosed in capsules that were practically complete, and were soon to be deposited. A later stage is portrayed in Figure 9, plate I. In this drawing the blasto-



Text-figure 46.

Some stages of mitosis in the blastomeres of *Heterodontus japonicus*: A, metaphase or middle phase of mitosis; B, anaphase; C, early telophase. In C, the chromosomes have begun their transformation within chromosomal vesicles.

From drawings left by Bashford Dean.

derm is surrounded by a very shallow circular groove. The type of cleavage is, of course, discoidal. It is sufficient to add that the cleavage patterns of these blastoderms are not essentially unlike those of other Elasmobranchs: e. g., *Scyllium* as portrayed by Rückert, 1899, Figs. 10 and 11, pl. LII.

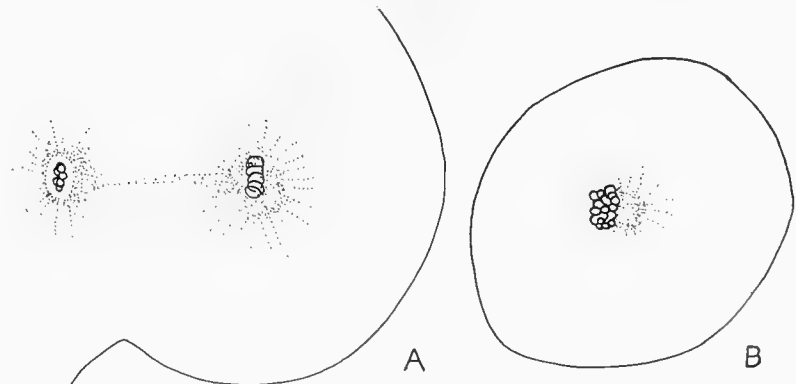
There is a noticeable gap between the figures thus far discussed and the one illustrating the earliest gastrula stage. This gap is partly bridged by Dean's drawing showing the segmentation cavity of a blastoderm dissected off the yolk mass and viewed by transmitted light. Upon focussing with the low power of the microscope through the thin roof of the blastocoele, an optical section is obtained which shows that the cavity is crescent-shaped (Figure 10, plate I).

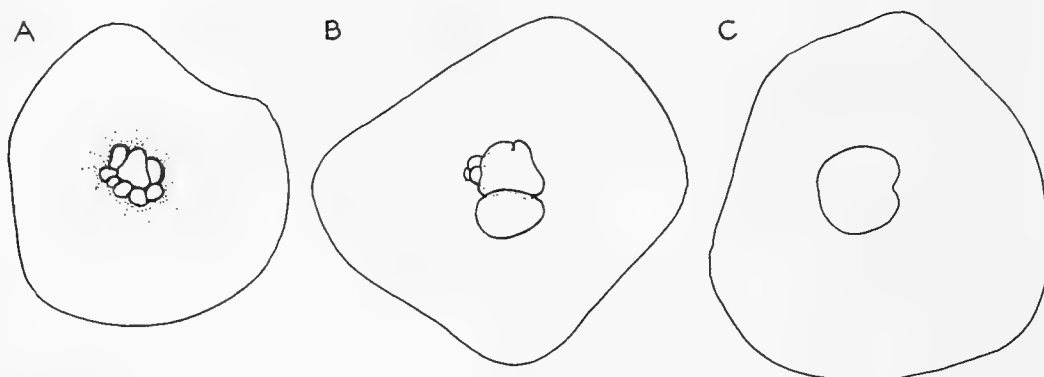
There are no other figures, suitable for reproduction, showing the cellular structure of the blastoderm in a later stage of cleavage; but the colored drawing reproduced as my Figure 80, plate VII, shows the general appearance of what is presumably a late blastula (compare Figure 44, plate IV). In Figure 80, plate VII, the blastoderm is probably confined to the elliptical reddish area; but when the corresponding figure on plate IV is

Text-figure 47.

Late stages of mitosis in the blastoderm of *Heterodontus japonicus*. In A, late telophase, the formation of chromosomal vesicles is nearly complete; in B, the chromosomal vesicles of a single daughter nucleus are represented.

From drawings left by Bashford Dean.





Text-figure 48.

Late stages in the reconstruction of a "resting" nucleus in the blastoderm of *Heterodontus japonicus*. In A, the daughter nucleus is composed of chromosomal vesicles—some fused into larger vesicles. In B, the process of fusion is almost complete, but maternal and paternal components are segregated in two distinct groups. In C, the duplex character of the nucleus is indicated only by a notch on one side.

From drawings left by Bashford Dean.

compared with those that immediately precede and follow it, one gets the impression that the pale-yellow zone also is a part of the blastoderm. On this view, it becomes easier to explain the round dark spot at the posterior (lower) end of Figure 80, plate VII: it may be derived from the crescentic area (dark when viewed by reflected light) which is the optical expression of the segmentation cavity. But one notes, in this figure, that the posterior and lateral margins of the reddish area are slightly upraised, which is fairly convincing evidence that this area alone constitutes the blastoderm. If we consider the blastoderm to be confined to the reddish area, then the dark spot may be simply an oil globule. Probably, the figure under consideration was drawn, under low magnification, as seen through a thick layer of albumen.

It does not lie within the scope of this article, as indicated by its title, to consider the internal development. Nevertheless, it seems desirable to bring together the scanty available data concerning the early stages. The few drawings made from microscopic sections, found among Dean's records, seem of sufficient historical interest to justify their inclusion here. These drawings (Text-figures 46 to 48) are concerned with mitosis during cleavage. The originals, probably drawn by Dean himself, lack explanations or labels save the words "*Cestracion* blastomeres" written below Text-figures 46A, 47B and 48B; also the words "*Cestracion*—budding of blastomeres" under Text-figure 47A. These explanations are in Dean's handwriting. The drawings are not dated, but the paper is yellow with age. In the light of our present knowledge, the transformation of chromosomes within chromosomal vesicles is clearly portrayed in Text-figures 46C and 47A. Chromosomal vesicles of a single daughter nucleus are shown in Text-figure 47B. Fusion, in varying degrees, of chromosomal vesicles derived from the same parent is shown in Text-

figure 48A and 48B. In the latter figures the nucleus appears double, and in Text-figure 48C it is notched. These are indications of the duplex character of the nucleus, which consists of both maternal and paternal components. Had the preceding stages of mitosis been favorably oriented, doubtless the duplex organization of the nucleus would have been revealed there also. At the time when Dean's drawings were presumably made, observations of this kind on the segmenting eggs of vertebrates were rare. For a fairly adequate bibliography of the literature on the individuality of the germ nuclei and the history of the chromosomal vesicles during cleavage, the reader is referred to the contributions of Richards (1917) and Smith (1929).

In an early section of this article, mention has been made of a few slides bearing serial sections of embryos of *Heterodontus* (presumably *japonicus*). These include sagittal sections of three blastoderms in early, advanced, and late blastula stages respectively. In the sections, which were cut in paraffin, the early blastula measures about 1.1 mm. long, the advanced blastula 1.3 mm., and the late blastula about 3 mm. In life these blastulae must have been appreciably larger, since such material shrinks during the process of preparing it for sectioning. In all essential respects the two earlier blastulae, as represented in sections, are like those of other Selachians: e.g., *Torpedo* and *Pristiurus* as portrayed by Rückert (1899, Figs. 51 and 53, pl. LVI). They closely resemble the corresponding stages of *Heterodontus phillipi*, discussed in the final paragraphs of this section. The late blastula is imperfect, so that comparisons are unprofitable.

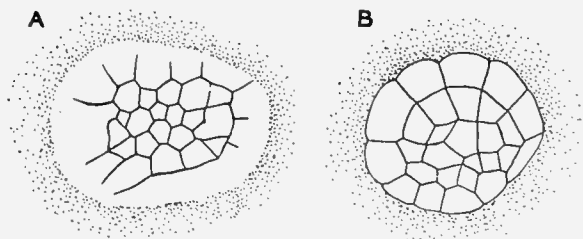
In a brief contribution, Haswell (1916) describes surface views of two very early stages of cleavage in the germinal discs of eggs taken from oviducts of *H. phillipi* (my Text-figure 49A and 49B). He states that in both eggs the cleavage lines are entirely confined to the area of the orange spot, and do not show any trace of a tendency to become extended beyond its limits. Two other eggs, taken from "uteri" some weeks later, showed more advanced stages of cleavage. Neither in these eggs, nor in those studied in 1898 (described in the next paragraph), did Haswell find any indications of furrows such as those of *H. japonicus* interpreted by Dean as a reminiscence of holoblastic cleavage.

Haswell (1898) studied the later stages of cleavage in *H. phillipi* from eggs that had been deposited in the sea. He states that during cleavage the blastoderm appears as a circular reddish-orange spot, around which is a narrow light-yellow band. When this orange spot has attained a diameter of about 2 mm. it assumes an oval shape, its longer axis corresponding with the future long axis of the body. At its posterior end appears

Text-figure 49.

Surface views of early cleavage in two blastoderms, A and B, of *Heterodontus phillipi*. The eggs were taken from the oviducts.

After Haswell, 1916, Fig. 1.

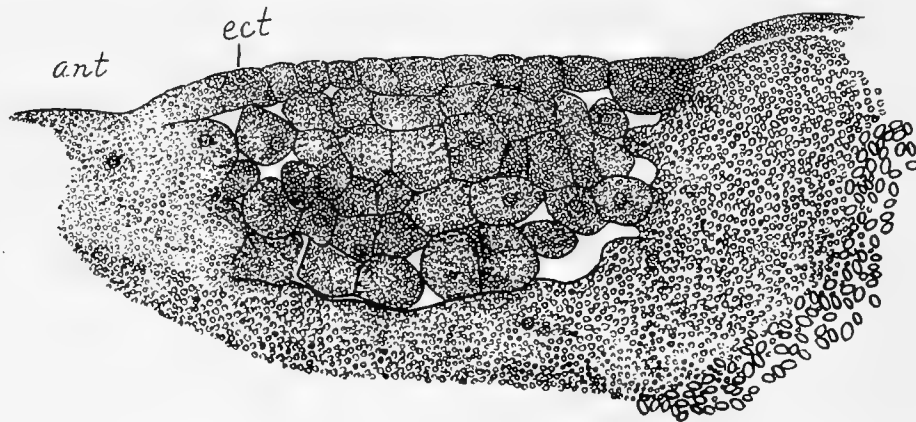


a crescentic dark area which has very much the appearance of a cleft passing through the blastoderm. The study of sections reveals that this dark area is really a cavity, the segmentation cavity, covered by a thin transparent roof. As the blastoderm extends, this dark area becomes less strongly marked and gradually disappears. (It has previously been noted that a similar crescentic "dark" area occurs also in *H. japonicus* at a corresponding stage, as evidenced by a sketch, without explanation, found among Dean's drawings. In this sketch, dark and light areas are reversed, since the object was drawn, under low magnification, by transmitted light). In the egg of *H. phillipi* the light-yellow border, previously mentioned, extends more rapidly than the blastoderm, and soon forms a broad zone around the latter. It is quite evident that Haswell does not consider the light-yellow zone to be a part of the blastoderm; it is apparently the superficial expression of the "parablast" (periblast).

The internal structure of some early stages in the development of *H. phillipi* is the chief topic of Haswell's article published in 1898. Beginning with a fairly early stage of cleavage, the development of the germinal disc through the blastula and gastrula stages is described and illustrated by figures drawn from sections. Two of these figures, representing early and late blastula stages, are reproduced here as my Text-figures 50 and 51. Their resemblance to Dean's sections of corresponding stages of *H. japonicus* has already been pointed out.

GASTRULATION AND EARLY EMBRYOGENY

In Elasmobranchs the changes that occur during gastrulation and early embryo formation are complex, and cannot be adequately described without recourse to serial sections. My only information concerning these stages in *Heterodontus japonicus* is obtained from Dean's drawings of both opaque and cleared total embryos, and from one

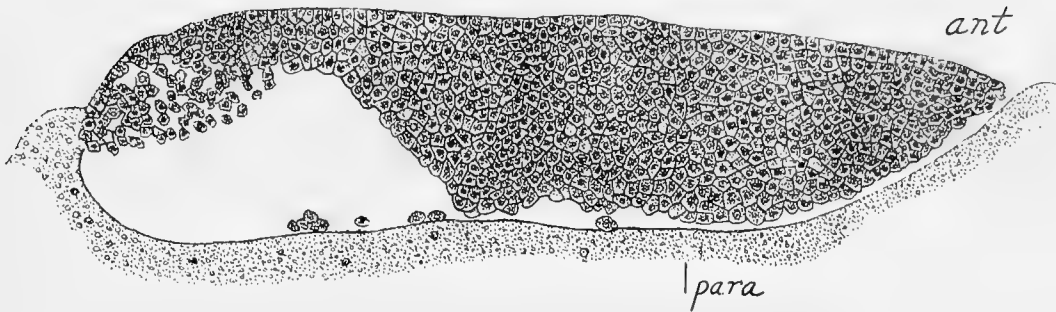


Text-figure 50.

Sagittal section of a blastoderm of *Heterodontus phillipi* in a stage showing the beginning of the segmentation cavity (at the posterior end, to the right of and below the segmented area in the figure).

ant, anterior; ect, ectoderm.

After Haswell, 1898, Fig. 1, pl. IV.



Text-figure 51.

Sagittal section of a blastoderm of *Heterodontus phillipi* in a stage in which the segmentation cavity is well established.

ant, anterior; para, parablast or periblast.

After Haswell, 1898, Fig. 4, pl. IV.

series of sagittal sections of a gastrula stage. It has therefore been necessary to interpret Dean's drawings in the light of what is known concerning the development of other species of Elasmobranchs. The most helpful contributions are those of the Zieglers (1892 and 1902); Haswell (1898); Rückert (1885 and 1899); and Scammon (1911).

Among Dean's drawings, the one reproduced as Figure 11, plate I, represents the earliest blastoderm that shows indications of gastrulation. This blastoderm is decidedly elongate—a transient phase in its development. Its margins, constituting the embryonic rim or germinal ring, are slightly upraised, particularly at the posterior (lower) end. At this end a small and rather indistinct pit indicates the site of beginning invagination; but the pit may be an artifact. The central portion of the blastoderm retains some of the reddish color characteristic of the germinal disc of an earlier stage. The pale-yellowish zone surrounding the blastoderm is broadest at its anterior (upper) end. It represents the marginal portion of the periblast. The original figure bears the notation "5 mm." in Dean's handwriting. This probably refers to the length of the blastoderm.

Figures 45 and 46, plate IV, show the rapid disappearance of color within the blastoderm except for a narrow line along its border. They show also the change from an elliptical outline to one that is approximately circular. Figure 12, plate I, represents a blastoderm a little older than that shown in Figure 11, plate I. It is only moderately elliptical, and the presence of an upraised portion at the posterior end constituting the so-called embryonic shield indicates that it is a gastrula. The median groove traversing the ectoderm of the embryonic shield is the neural groove. Figure 13, plate I, is slightly later and corresponds to Figure 47, plate IV, which shows the entire egg in color. Here, and in the following stage (Figure 48, plate IV), one notes the extension of the blastoderm over the surface of the yolk. That this extension is relatively rapid may be deduced from the slight increase in the size of the embryo proper between the stages represented by Figures 46 to 48, plate IV.

Figure 14, plate I, represents the first of a series of embryos of *H. japonicus* detached from the yolk mass, stained, cleared and mounted *in toto*. These embryos may have been

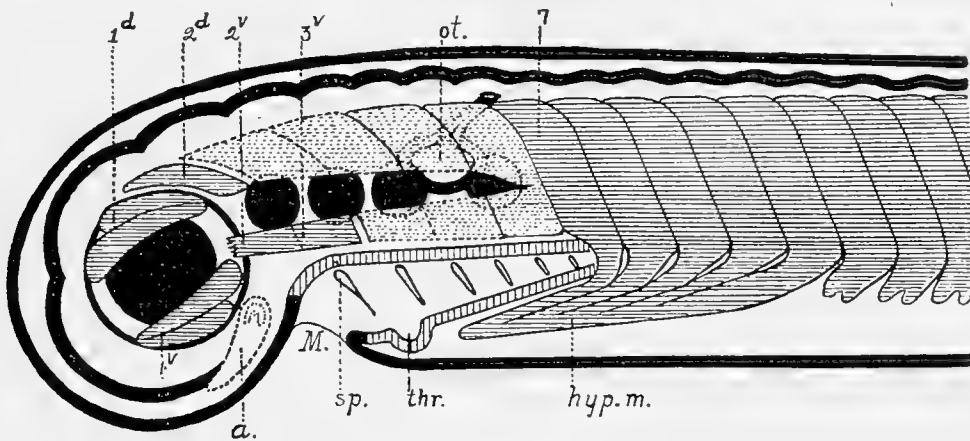
drawn directly, under low magnification, by transmitted light; but in the table in Dean's notebook many embryos are listed as photographed and also drawn. Most of the drawings must be interpreted as optical sections, so it is possible that they were drawn from photomicrographs. Such drawings show only what can be seen by focussing at a single level, and are sometimes difficult to interpret. It is unfortunate that, with very few exceptions, the embryos from which Dean's drawings were made cannot be found. As an aid to the study of the drawings, I have examined, under both monocular and binocular microscopes, a close series of Elasmobranch embryos, chiefly *Squalus acanthias*, stained and mounted by me nearly thirty years ago.

Figure 14, plate I, represents a stage intermediate between Figures 12 and 13. It lacks the high lights characteristic of a surface view. Posteriorly, it represents that portion of the thickened margin of the blastoderm adjoining the embryonic shield. Here, by a process of inturning accompanied by a limited amount of concrescence and a very considerable amount of overgrowth, the thin rim of the early blastoderm has formed a deeper layer, the entoderm, not shown in the drawing. In the angle between the superficial layer (ectoderm) and the entoderm a middle layer, the mesoderm, is being proliferated. The thickened margin of the blastoderm contains all three germ layers, hence it is sometimes called the germinal ring. At the posterior end of the figure a pair of dark zones, one on each side of the mid-line, probably contain axial mesoderm. Anteriorly, a dark zone having the form of an arch represents an optical section through upraised ectoderm at the edge of the germinal shield. The neural groove is out of focus and is not shown.

Figure 15, plate I, represents a stage slightly later than Figure 13. It shows a well-defined notochord, with its characteristic irregular transverse striations, extending along the mid-line of the lower two-thirds of the figure. On each side of the notochord we see the axial mesoderm, very thin and not ready to be cut into somites. Lateral to this, on each side, a broad dark zone represents the inner limb of the neural folds. The outer limb of the neural folds forms the margin of all the anterior two-thirds of the figure. The beginning of the fore-gut may be present in this stage, but if so, it is not clearly shown. The figure is possibly a ventral view.

Figure 16, plate I, is the earliest drawing showing mesoblastic somites. Of these, four pairs are complete. In the head region the neural folds appear asymmetric. On the left side, both outer and inner limbs of the neural folds are well shown, but on the right side the inner limb is incomplete. Evidently the drawing represents an optical section, and the apparent asymmetry of the neural folds is due to a slight rotation of the embryo on its long axis. The continuation of this rotation will soon bring the embryo to lie on its left side. Parenthetically, it may be remarked that the embryo of *Torpedo*, as figured by Ziegler (1892 and 1902), tends to lie on its right side; but in my whole mounts of *Squalus*, the embryo lies on its left side as in *Heterodontus japonicus*. In the stage under consideration the beginning of the fore-gut, extending forward beneath the brain as a pocket-like portion of the entoderm, is presumably present; but it occurs at a lower level than the structures shown in the drawing.

In Figure 16, plate I, there are some incomplete intersegmental grooves marking off three or four (probably four) pairs of incomplete somites in front of those that are complete. The anterior portion of the notochord is slightly obscured by the inner limb of the left neural fold; but it appears to extend forward farther than the first intersegmental groove, which is quite distinct. It is difficult to identify accurately all the limits of the primary brain vesicles in this drawing; but it seems fairly obvious that the first intersegmental groove marks the posterior end of the midbrain. In none of the following drawings do we find the somites extending so far forward, though the series often ends anteriorly with one or two incomplete somites. The region of incomplete somites in



Text-figure. 52.

Diagram showing the relation between head somites and body somites in a larval *Squalus acanthias*. The somites that degenerate in ontogeny are indicated by broken lines.

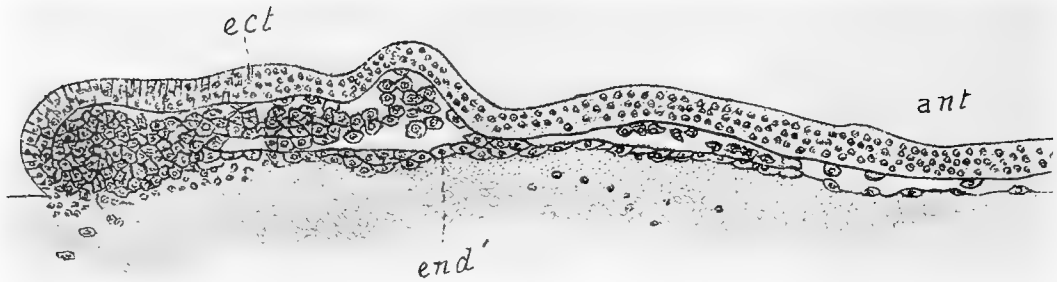
1d, dorsal moiety of the first myotome; 1v, ventral moiety of the first myotome; 2d, 2v, dorsal and ventral moieties of the second myotome; 3v, ventral moiety of the third myotome; 7, seventh myotome; a., anterior cavities; hyp.m., hypoglossal musculature; M., mouth; ot., otic capsule; sp., spiracle; thr., thyroid.

After Neal, 1918, Fig. 10.

Figure 16, plate 1, probably coincides with the four somites that, in *Squalus*, degenerate during ontogeny. These have been figured by Neal (1918) in a diagram reproduced herein as Text-figure 52. The occurrence, in sharks, of four anterior somites that subsequently disappear is doubtless of evolutionary significance, indicating a metameric origin of the posterior part of the cranium. These somites serve also to connect the anterior head somites with the body somites and thereby establish their serial relationship.

Before proceeding further with the account of the external development of the Japanese Bullhead Shark, it seems advisable to consider what is known concerning the internal changes during gastrulation in *Heterodontus*.

The internal structure of some embryos of *H. phillipi* in early gastrula stages has been studied in serial sections by Haswell (1898). Three of his figures are reproduced as my Text-figures 53 to 55. Before considering these stages directly, it is necessary to describe some preparations for gastrulation made by the advanced blastula.



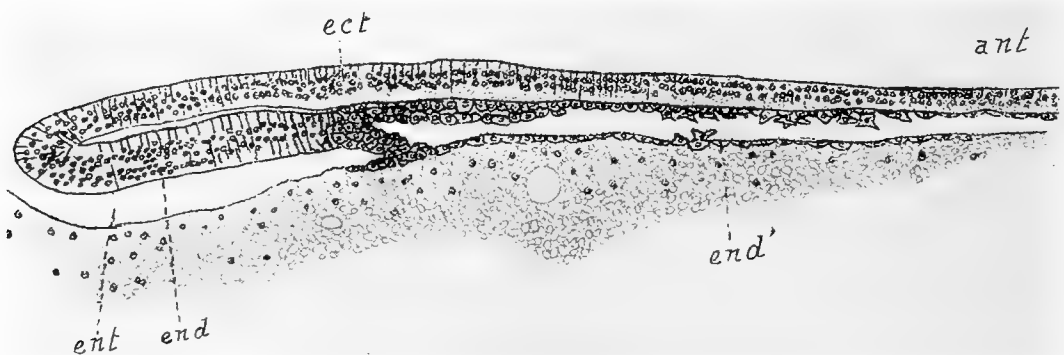
Text-figure 53.

Sagittal section of a blastoderm of *Heterodontus phillipi* in a stage in which gastrulation has just begun.

ant, anterior; ect, ectoderm; end', parablast or periblast entoderm.

After Haswell, 1898, Fig. 6, pl. V.

The blastula represented in my Text-figure 51 (after Haswell) is not ready for gastrulation. Before gastrulation begins, the blastoderm increases somewhat in diameter, and the segmentation cavity (or blastocoele) extends throughout almost its entire length. The floor of this cavity consists of a layer of yolk with unusually fine granules, unsegmented but containing nuclei. Haswell (1898) refers to this layer as the "parablast", but it is evidently the "periblast" or "yolk syncytium" of other authors (e.g., Ziegler, 1902). As shown in Haswell's figure of a very late blastula, the roof of the blastocoele becomes very thin except in its anterior third. At the posterior end of the segmentation cavity there is a collection of cells of irregular shape. Most of these cells have evidently come from the roof of the blastula; but Haswell states that some of them are evidently being formed from the parablast of the floor of the cavity, and that this accumulation of cells constitutes the starting point in the formation of the parablast entoderm (end') in Text-figures 53 and 54). In the embryo represented in Text-figure 53, the formation of parablast entoderm is particularly active at the posterior end.



Text-figure 54.

Sagittal section of a blastoderm of *Heterodontus phillipi* in an early gastrula stage.

ant, anterior; ect, ectoderm; end, entoderm; end', parablast (periblast) entoderm; ent, archenteric cavity.

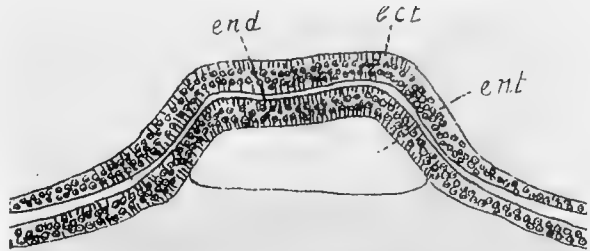
After Haswell, 1898, Fig. 7, pl. V.

Text-figure 55.

Transverse section through the posterior portion of a blastoderm of *Heterodontus phillipi* in a stage somewhat later than the preceding, but before the differentiation of the notochord.

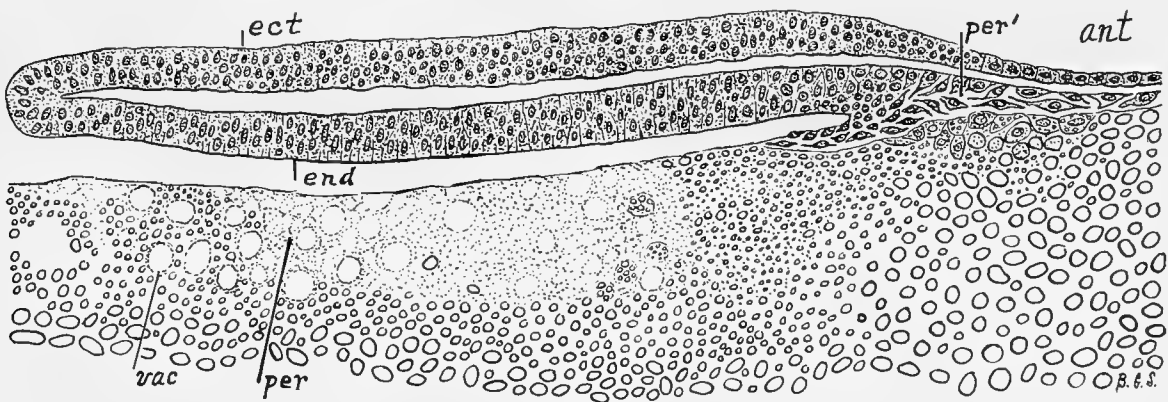
ect, ectoderm; end, entoderm; ent, archenteric cavity.

After Haswell, 1898, Fig. 8, pl. V.



In *Heterodontus phillipi*, as in other Elasmobranchs, gastrulation takes place mainly by a process of involution. According to Haswell (1898) the first phase of gastrulation consists of an arching upward of the posterior portion of the blastoderm, so that where it passes into the parablast it becomes, for a short distance, vertical. It soon inclines forward (as illustrated in my Text-figure 53), forming the embryonic rim which extends along the entire posterior margin of the blastoderm. At the same time the accumulation of cells at the posterior end increases at the expense of the segmentation cavity. In the stage represented by Text-figure 53 the segmentation cavity has become extremely shallow, and its roof has acquired a compact epithelial character.

The stage represented by Text-figure 54 possesses a definite entoderm, hence it is a well-established gastrula. To the present writer it seems that the cleft, separating the poorly-defined layer of cells marked *end'* from the irregular layer above, is mainly an artifact. Text-figure 55 is a transverse section through the archenteric cavity of a stage a little farther advanced than the one shown in Text-figure 54. It shows no new features, but is helpful in affording a different point of view. At first the floor of the archenteric cavity consists only of yolk; but soon the anterior portion of the archenteron will form an entodermal pocket, the fore-gut.



Text-figure 56.

Sagittal section, approximately median, of *Heterodontus* (presumably *japonicus*) in an advanced gastrula stage.

ant, anterior; ect, ectoderm; end, endoderm; per, periblast; per', periblast endoderm; vac, vacuole.

Drawn from a slide simply labelled *Cestracion*, in the collection left by Bashford Dean.

The gastrula of *Heterodontus* (presumably *japonicus*), represented by serial sagittal sections found among Dean's embryological preparations, is in a stage considerably later than Haswell's embryo shown in median sagittal section in my Text-figure 54. A median sagittal section of Dean's gastrula is represented in Text-figure 56. The section cuts through the entire length of the blastoderm, which measures 8 mm. (on the slide); but the embryo proper, shown in the figure, is only about one millimeter long. Both ectoderm and the definitive entoderm, as shown in the drawing, are decidedly thick; but at the anterior end of the embryo the ectoderm gradually decreases in thickness until in the extra-embryonic portion of the blastoderm it is a simple squamous epithelium. The periblast is represented by a pale zone of predominantly fine yolk granules interspersed with cytoplasm, underlying the archenteric cavity and extending a short distance anterior to it. Beneath the archenteric cavity it is much thicker (deeper) than it is anteriorly. This thick portion lacks nuclei, but contains a number of fairly large vacuoles. Underlying the anterior end of the definitive entoderm, and extending forward beneath the ectoderm, is a thin layer of irregularly shaped cells that constitute the periblast entoderm. They seem to grade into the definitive entoderm, and perhaps contribute to it; anteriorly, the layer becomes even thinner and in the extra-embryonic portion of the blastoderm it is represented (in sections) by a single row of sparsely distributed cells lying between the ectoderm and the yolk mass. Underlying the thick portion of the periblast entoderm, a little distance anterior to the archenteric cavity, there are a few periblast cells (not merely nuclei) imbedded in the yolk.

The advanced gastrula of *Torpedo* figured in median sagittal section by Ziegler (1892) is in about the same stage as the embryo of *Heterodontus japonicus* represented in my Text-figure 56. Ziegler's figure shows the section continuing throughout the entire length of the blastoderm. A striking difference is the much greater thickness (2 to 5 cells deep) and compactness of the periblast entoderm in the extra-embryonic portion of the blastoderm, as compared with Dean's gastrula in which this layer is only one cell thick and the cells are separated by fairly wide intercellular spaces.

THE YOLK BLASTOPORE

Before going further with a description of strictly embryonic development it seems advisable to give brief attention to the formation and closure of the yolk blastopore, which may be regarded as a delayed phase of gastrulation.

The yolk blastopore is simply that portion of the surface of the yolk mass which, subsequent to the beginning of gastrulation, is not yet covered by the blastoderm (Figures 46 to 59, plates IV and V). It is bounded by the rim of the blastoderm and is continuous with the floor of the archenteric cavity. The name blastopore seems more appropriate after the blastoderm has covered more than half the yolk mass, but the morphological relations are the same in earlier stages. One reason for regarding the yolk blastopore as related to gastrulation is that, in heavily yolk-laden eggs, circumcrescence (overgrowth of the yolk by the blastoderm) is an important factor in gastrulation—it assists in laying

down the definitive entoderm. In later stages, circumcrescence provides a protective and vascular covering for the yolk mass. These extra-embryonic structures will be eventually resorbed.

The yolk blastopore of *Heterodontus japonicus* is probably unique in that the surface of the yolk is traversed by furrows that appear to be cleavage furrows. These are clearly shown in Figures 46 to 56, plates IV and V. They are distinct in some of Dean's photographs, both published and unpublished (cf. page 727). In Figures 52 to 56, plate V, the appearance of the yolk blastopore is strikingly like that of the yolk plug of some amphibian eggs (e.g., *Cryptobranchus* as described by Smith, 1912, Figs. 115 and 138 to 140). In both cases the yolk is traversed by furrows, and the pattern is much the same. It is obvious that in nearly all the drawings of developing eggs of *H. japonicus*, in stages from the beginning of gastrulation until after the closure of the yolk blastopore (Figures 46 to 61, plates IV and V), some of the problematical cleavage furrows are visible even after they have been covered by the translucent blastoderm.

The closing phases of the yolk blastopore (Figures 57 to 61, plate V) are marked by variability in its outlines and by the presence of the vitelline vessels (considered in a later section). Figure 61, plate V, represents the final stage in the closure of the blastopore. The site of closure is not far behind the yolk stalk.

In a portion of his manuscript already quoted in my section on "General Mode of Development", Dean states that the blastoderm of *Heterodontus japonicus* "still grows around the egg before the embryo is of large size" and seems to regard this as a character of considerable phylogenetic importance. This view implies that in more modern sharks closure of the yolk blastopore is delayed. Some measurements of the size of the early embryo in relation to the size of the entire blastoderm have a bearing on the problem.

The advanced gastrula of *Heterodontus japonicus* represented in surface view in Figure 13, plate I, has a blastoderm about ten times as long as the embryo proper, which is about one millimeter long; while a gastrula of *Torpedo ocellatus* in about the same stage, drawn by Ziegler (1892, Text-fig. 3) in surface view, has a blastoderm only five times its length. A similar comparison may be made in median sagittal sections. Dean's gastrula represented in my Text-figure 56 has a blastoderm (extra-embryonic portion not shown in the drawing) about eight times as long as the embryo proper; while Ziegler's figure (1892, Fig. 15, Taf. III) of a gastrula of *Torpedo ocellatus* in approximately the same stage has a blastoderm (drawn entire) about three and one-half times the length of the embryo proper. These measurements indicate that the blastoderm of *Heterodontus japonicus* grows faster, or at least spreads out more rapidly, in proportion to the size of the embryo, than does the blastoderm of *Torpedo ocellatus*.

There remains the question concerning the comparative sizes or stages of development of embryos at the time when overgrowth of the yolk by the blastoderm is completed. The egg (yolk mass) of *H. japonicus* in the early stages of embryonic development measures from 40 to 50 mm. in diameter. The egg depicted in Figure 61, plate V, is in the stage in which the yolk blastopore has just closed. As compared with the other eggs in approxi-

mately the same stage, it has an unusually large yolk mass, probably about 50 mm. in diameter. The length of the embryo (when straightened) equals about one-fourth of the diameter of the yolk mass. One wishes for similar data concerning modern sharks, but a cursory search of the literature reveals nothing that is helpful in this connection.

LATER EMBRYONIC DEVELOPMENT

The account of the embryonic development of *Heterodontus japonicus* has been interrupted quite arbitrarily, following the stage with four pairs of mesoblastic somites, in order to consider the yolk blastopore before reaching a stage too far removed from its origin. The remaining stages of embryonic development, as represented in Dean's drawings, will now be considered in serial order.

Figure 17, plate I, represents a cleared embryo with 12 pairs of complete and one pair of posterior incomplete somites. The course of the right neural fold in this figure is not easy to follow, but it seems quite certain that the neural folds have almost met anteriorly as well as posteriorly. What appears to be a neural fold on the right side of the figure is the floor of the neural plate seen in optical section. According to this interpretation, the head region has rotated anticlockwise through almost 90 degrees. In the absence of rotation, it would be impossible to obtain a side view of the beginning cephalic flexure and the structures underlying the brain. The pocket situated ventrad and caudad to the brain is the fore-gut. The arch-like anterior intestinal portal, leading from the broad subgerminal cavity into the narrower fore-gut, is plainly visible. An embryo of *Squalus acanthias* possessing the same number of somites has the neural tube almost closed throughout its length.

Figure 18, plate I, represents a cleared embryo with 12 pairs of complete somites, one posterior and two anterior incomplete somites. The latter appear to be undergoing degeneration. The neural folds appear to be united in their middle thirds. Anteriorly, the folds appear less close together than in Figure 17, and the cephalic flexure is less pronounced; the amount of rotation in the head region is less. Evidently the brain is not quite so far along in its development, despite the fact that some other structures are slightly more advanced. The fore-gut and the anterior intestinal portal are well shown. A sheet of mesoderm is found dorsal, anterior and ventral to the fore-gut; its ventral portion is evidently mesenchymatous. The deep dent at the anterior end of the right neural fold is an artifact.

Figure 19, plate I, represents a cleared embryo with 14 pairs of complete somites and one pair of anterior incomplete somites. The neural tube is closed except for a short distance at each end. There is a pronounced cephalic flexure and a beginning cervical flexure. The fore-gut is enlarged dorso-ventrally. This drawing shows a decided undercutting and uplifting of both head and tail-bud.

Figure 20, plate II, represents a cleared embryo with 18 complete somites and one anterior incomplete somite. The right side only is shown, but presumably the left side has the same number. The cephalic and cervical flexures are slightly more pronounced

than in the preceding drawing. The brain shows differentiation into the primary vesicles (forebrain, midbrain, hindbrain) and there are indications of a secondary division of the hindbrain into myelencephalon and metencephalon. The bulge at the side of the forebrain represents an early stage in the formation of the optic vesicle.

I have found in Dean's collection of microscopic slides a total mount of an 18-somite embryo labelled "*Cestracion*." This appears to be the specimen from which Figure 20, plate II, was drawn. The embryo is slightly overstained, but corresponds to the drawing in every respect save that the small round black spot in the region of the neurenteric canal is lacking, and the triangular dark area (mesodermal?) at the anterior end of the fore-gut is not so sharply defined. In view of the scarcity of information concerning sizes of the embryos represented in the plates, it is interesting to note that this 18-somite embryo, measured on the slide, is 3.5 mm. (about one-eighth inch) long.

Figure 21, plate II, portrays in surface view an embryo of about 24 somites (one side only). This figure, and the one immediately following, appear to be drawn at a magnification lower than that employed for the cleared specimens that precede them. The body of this embryo leans to the left, while the head is turned slightly to the right. The tail bud projects for some distance beyond the posterior rim of the blastoderm, and the head is entirely free from the underlying structures. In this embryo both cephalic and cervical flexures have almost reached their maximum. The right optic vesicle and lens are faintly indicated. The pronounced bulging in the hyoid region and that dorsal to the midbrain are probably abnormal.

In Figure 22, plate II, a surface view, only 20 somites are readily visible; but in the caudal region four or five more are faintly indicated, making a total of about 25. In addition, there is an incomplete somite, probably degenerating, at the anterior end of the series. This embryo appears normal save for the presence of a large bulge of the ectoderm over the midbrain and a lesser bulge of the same kind dorsal to the anterior (incomplete) somite. For the first time in this series, we see something like a yolk stalk—in this stage very short and thick. The rudimentary eye is decidedly larger than in the preceding drawing, and there is more differentiation in the branchial region. Of the visceral arches the mandibular, hyoid and first branchial are recognizable; of the branchial grooves, the spiracular (Y-shaped) and first branchial. The forebrain bulges a little dorsally.

Figure 23, plate II, represents a cleared embryo with at least 26 somites. It seems to be drawn at a slightly higher magnification than the two preceding figures which are surface views. It can scarcely be said to possess a yolk stalk since it is attached to the yolk mass along almost the entire length of the body proper. Vitelline arteries and veins are faintly indicated on the extra-embryonic blastoderm near the embryo. The optic vesicle shows a distinct chorioid fissure. Dorsally, in the region of the hindbrain, there is a somewhat indistinct otic vesicle. The blister-like elevation of the ectoderm, dorsal to the midbrain and to the anterior part of the hindbrain, is probably abnormal. Some neuromeres occur in the myelencephalon, immediately behind the otic vesicle. Between the foregut and the diencephalon there is a straight bar of tissue which may represent the

anlage of the epithelial hypophysis. It extends from the oral ectoderm to a slight depression in the floor of the diencephalon—an evagination which may be the rudiment of the infundibulum.

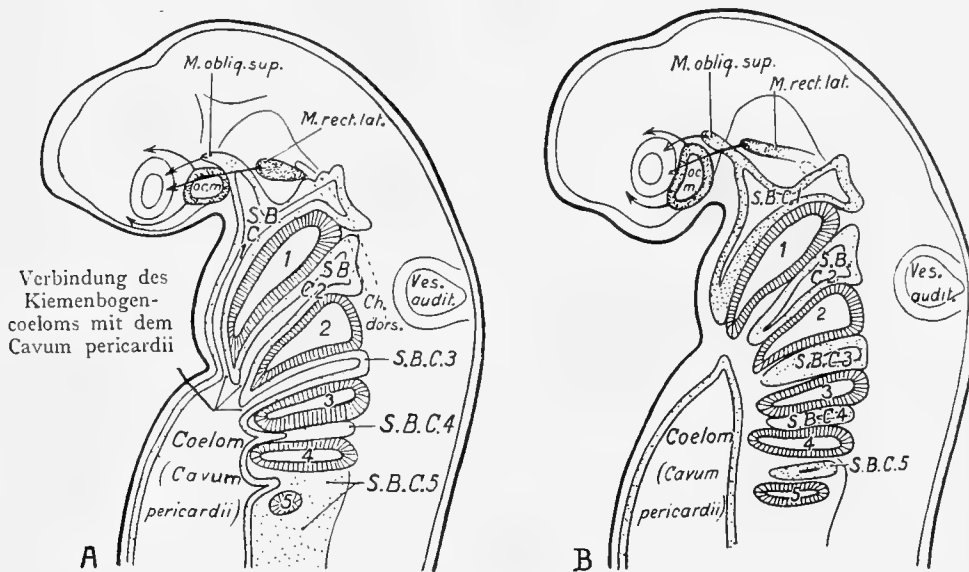
Figure 24, plate II, represents in surface view an embryo with at least 28 somites. Unlike the preceding embryos, this one was drawn from the left side and has been reproduced with right and left sides reversed to facilitate comparisons with other figures on the same plate. It is evidently drawn to the same scale as Figures 21 and 22 (same plate). There is some increase in length but little advance in external differentiation. However, spiracular and first branchial grooves begin to look like gill-clefts. This is the first drawing to show distinctly the region of the heart—just in front of the broad yolk stalk. There is a slight caudal flexure. The angular projection of the forebrain is probably abnormal.

Figure 25, plate II, a surface view, portrays an embryo with about 35 complete somites. Like the preceding figure, this one was drawn from the left side and has been reproduced with right and left reversed. Here, for the first time in this series, we find the sites of the spiracular cleft and the first and second gill-clefts sharply defined. It is not certain that the closing plates between branchial grooves and pharyngeal pouches are already perforated, but this seems a good place to begin referring to these fissures as clefts instead of grooves. The cervical flexure is pretty well straightened out, but in the cephalic flexure there is not much change. The dark spot dorsal to the first gill-cleft (not the spiracular cleft) indicates the site of the otic vesicle. The region of the heart is clearly indicated.

Figure 26, plate II, pictures a cleared embryo with about 37 complete somites and one or two incomplete somites at the anterior end of the series. This drawing appears to have been made at a higher magnification than the preceding figure. The principal divisions of the brain are fairly well shown, though not so clearly as in Figure 20 of the same plate. One notes, in the branchial region, the entoderm-lined spiracular cleft and gill-clefts alternating with mesodermal visceral arches. The greater size of the spiracular cleft is noteworthy, considering its small size in the adult. In its early stages it looks like a gill-cleft, and indeed it is homologous with the gill-clefts. The notochord is clearly visible throughout most of its length; it ends anteriorly just above the spiracular cleft. Almost at the tip of the tail bud, the neurenteric canal is sharply outlined. Though the hind-gut is rather vaguely defined, there is a distinct posterior intestinal portal. Auricular and ventricular divisions of the heart can be distinguished. The optic cup shows a very thin outer and a thick inner layer; these layers are united along the borders of the chorioid fissure. The otic vesicle, dorsal to the first gill-slit, is quite prominent.

In front of the dorsal part of the spiracular cleft and close to the brain (Figure 26, plate II) there is a thick-walled roughly circular sac which may be a "head cavity" or head somite. In Elasmobranchs and perhaps in vertebrates generally, the muscles that move the eyeball arise (Marshall, 1881; Van Wijhe, 1882; Scammon, 1911; Neal, 1918) from mesodermal segments (head somites) which are serially homologous with the somites

of the trunk (Text-figure 52, page 735). In Elasmobranchs the head somites, like the trunk somites of vertebrates generally, are at first hollow and their cavities communicate with the primitive coelomic cavity. In the head, this communication is by way of the pharyngeal or visceral arches (mandibular, hyoid and branchial arches), as shown for *Torpedo* in Text-figure 57A. These channels quickly close (Text-figure 57B) and the somites become solid structures.



Text-figure 57.

Diagrams showing the origin of eye muscles, and the extensions of the primitive coelomic cavity into the gill-arches, in selachian embryos. In A, the cavities of the pharyngeal arches are shown communicating with the pericardial portion of the coelomic cavity; in B, which is a later stage, the connections of these cavities have been lost.

1, 2, 3, 4, gill-clefts; S.B.C.1—5, pharyngeal arch extensions of the coelomic cavity; ch.dors., chorda dorsalis; oc.m., anlagen of the oculomotor muscles; M. obliq. sup. and M. rect.lat., anlagen of the superior oblique and lateral rectus muscles respectively; ves.audit., otic vesicle.

After Corning, 1925, Figs. 222 and 223; based on Frioriep's (1902) Figs. 4 and 5 (*Torpedo ocellatus*).

Figure 27, plate II, portrays a cleared embryo of about 41 complete somites. Like the preceding figure, it appears to have been drawn under unusually high magnification. This embryo exhibits a moderate caudal and a pronounced cervical flexure—the latter presumably unusual for this stage since it does not appear in the stages immediately following. The optic cup shows, more distinctly than heretofore, the outer as well as the inner layer. The otic vesicle is larger, and nearer the branchial region; it is dorsal to the first gill-cleft. The bulbus cordis and the ventral aorta are distinctly outlined and the latter has given rise to the first three aortic arches. The hind-gut is outlined faintly along its ventral border and at both anterior and posterior ends of its dorsal border. The neurenteric canal is well shown.

Figure 28, plate II, represents a surface view of an embryo with at least 50 complete somites. It is drawn at a magnification corresponding to Figures 24 and 25 on the same plate. In this embryo the caudal flexure attains an unusual degree of curvature—the posterior half of the embryo is hook-shaped. A cervical flexure is lacking, but the cephalic flexure is slightly greater than in any previous stage. There is a yolk stalk, not shown in the drawings that immediately precede this one, and just above the yolk stalk there appears to be a tubular mid-gut. Of interest are the thin roof of the medulla (not seen in any previous stage) represented by the heavily shaded portion of the hindbrain; the closure of the ventral portion of the spiracular cleft; and the large size of the first gill-cleft. The second gill-cleft is of moderate size, and the sites of the future third and fourth gill-clefts are occupied by pharyngeal grooves. If the circular pale spot on the forebrain indicates the position of the eye, then it is nearer the dorsal end of the mandibular arch than it has been in any preceding stage. In this surface view, one cannot be sure of the position of the otic vesicle, but it appears to be dorsal to the first gill-cleft.

Figure 29, plate II, portrays a surface view of an embryo with about 55 complete somites. The mid-gut is not so far advanced in its development as it is in the preceding figure. The lower two-thirds of the spiracular cleft is closed, and there is a distinct third gill-cleft. The mandibular arch is more prominent than it has been in previous stages. The myelencephalon (medulla oblongata) shows prominent neuromeres. The otic vesicle appears to be dorsal to the first branchial arch. In the last three stages studied, there has been a steady growth of the forebrain.

Figure 30, plate II, pictures the head and anterior part of the body of a cleared embryo drawn at a higher magnification than that employed for the surface views just considered. The number of somites is unknown, and it is not certain that this specimen is older than the one represented in the preceding figure. Evidently the artist had trouble in getting a clear view of some parts of this large embryo, for the drawing does not show as much detail as one would expect in a figure of this size. There is a slight cervical flexure and the usual pronounced cephalic flexure. The form of the brain has undergone some changes; in particular the telencephalon or secondary forebrain has increased in size. The spiracular cleft is not shown. The otic vesicle is still situated dorsal to the first gill-cleft, though in adult sharks its derivative, the membranous labyrinth, is more closely associated with the spiracular canal; e.g., as in *Chlamydoselachus* (Smith, 1937, pp. 423 to 430 and Text-figure 82.)

Figure 31, plate II, portrays a surface view of an embryo with about 74 somites—now represented by myomeres. This embryo is the first to show a fin bud—the pectoral. Rudiments of the first and second dorsal fins, and of a pelvic fin, are recognizable only by comparison with the figures that follow. The tail is bordered by a continuous fin fold out of which will emerge the anal and caudal fins. There seems to be a low fold connecting the rudiments of all the unpaired fins; but one cannot be sure, from the figure, whether pectoral and pelvic fin rudiments are connected by a fin fold. The yolk stalk is now attached to the pectoral region only, just behind the heart. The spiracu-

lar cleft is closed except for a small dorsal portion. For the first time, in this series, we see rudimentary gill-filaments projecting from gill-clefts—the first, second and third, in this embryo. Due to differential growth of associated parts, the eye is now situated very close to the dorsal end of the mandibular arch where a swelling indicates the anlage of the future maxillary process. The position of the otic vesicle is no longer indicated in surface views. There is a shallow olfactory pit. The hind-gut is fairly well defined.

Figure 32, plate II, portrays in surface view an embryo with about 85 myomeres. One notes that the yolk stalk is more slender, and that there are five gill-clefts. Gill-filaments project from all five gill-clefts, but there are none from the spiracular cleft. The rudiment of the maxillary process is more prominent than in the preceding stage.

Figure 33, plate III, represents a surface view of an embryo with at least 88 myomeres (those near the tip of the tail are indistinct). This embryo shows a decided advance over the preceding one. To be sure, no new structures have emerged save a single gill-filament protruding from the spiracular cleft; but all the embryonic structures mentioned in the preceding drawings are present in a more advanced stage of development. The myomeres show a higher degree of differentiation. The rudiments of the fins—pectoral, pelvic, first and second dorsals, anal, and caudal—are recognizable at a glance, though all the median fin rudiments appear to be connected by a fin fold. Both pectoral and pelvic fin rudiments are very broad at the base, but they are evidently not connected by a fin fold. One sees, more clearly than in the two preceding figures, the contour of the brain. The yolk stalk is more slender, as one would expect in this stage. There seems to be some injury to the cardiac region.

Figure 34, plate III, pictures in surface view an embryo somewhat older than the one shown in the preceding figure, but evidently drawn at a lower magnification. The myomeres are not visible. All the fin rudiments are now discrete: *i.e.*, not connected by a fin fold. Gill-filaments are more numerous, and some are decidedly larger. The spiracular gill-cleft reveals four or five short gill-filaments; this cleft is now somewhat farther from the first and nearer the eye. As compared with the preceding figure, there is a remarkable enlargement of a region of the brain comprising the mesencephalon (mid-brain) and metencephalon (anterior division of the hindbrain, containing the cerebellum). The olfactory pit is larger and deeper. The maxillary process of the mandibular arch is no longer clearly defined in surface views. It extends beneath the posterior rim of the optic cup.

An embryo in Dean's collection, slightly older than the one represented in Figure 34, plate III, is about 38 mm. (1.5 inches) long. Its external gill-filaments are slightly longer than those represented in this figure.

Figure 35, plate III, shows almost maximal development of the external gill-filaments. The spiracular cleft is closer to the eye and directly posterior to it. The mouth opening, bordered by rudimentary labial folds, is now recognizable. The pectoral fin is quite large, and the caudal fin is very long. The dorsal fins are taller, and narrower at their

bases, than in the preceding stages. Cartilaginous fin rays are indicated in both dorsal fins, also in the pelvic fin.

An embryo in the same stage of development as the one represented in Figure 35, plate III, was found in Dean's collection. It measures about 50 mm. (2 inches) in length. Its external gill-filaments are abundant and resemble those shown in the figure.

The embryo portrayed in Figure 36, plate III, is obviously older. This is shown by the marked development of the cartilaginous fin rays and by the increased size of the cranium. Due to the persistence of the cephalic flexure, the mouth opening still faces caudad as well as ventrad. The spiracular cleft, situated just behind the eye, is shown more distinctly than in the preceding figure. Indistinct myomeres, extending to the extreme tip of the tail fin, are indicated in the posterior half of the figure. This embryo is remarkable for the entire absence of external gill-filaments—a deficiency that is more striking when we observe that both the preceding and the following stages show a luxuriant development of these filaments. There is an indistinct lateral line.

Figure 81, plate VII, represents (in color) an embryo only slightly older than the one just described. This beautiful figure is noteworthy in several respects. First, it shows the extreme development of the external gill-filaments; second, a tuft of these comprising about 9 or 10 filaments protrudes from the spiracular cleft; third, the figure represents the oldest embryo in which the eye is known to possess a chorioid fissure; fourth, it shows a rudimentary supraorbital ridge; fifth, the pelvic fin appears to possess a rudimentary myxopterygium; and sixth, the figure shows the entire yolk sac.

Figure 37, plate III, is noteworthy for the size of the external gills, which are as long, and almost as abundant, as those in the embryo just considered. In some features, the embryo portrayed in this drawing is decidedly more advanced in its development. This is particularly true of the mouth region. The cephalic flexure has unbent to a degree that brings the mouth into nearly its adult position. This change is accompanied by increased depth of the branchial and pectoral regions, so that the profile of the ventral surface is straightened (cf. Figure 36, plate III). Only five gill-filaments protrude from the spiracular cleft. Structures in the branchial and pectoral regions are obscured by the gill-filaments. There is a supraorbital ridge, best developed at its posterior end. Some of the fins are larger than in the preceding stages. The lateral line is indistinct.

An embryo in Dean's collection appears to be identical with the one represented in Figure 37, plate III. It is about 70 mm. (2.75 inches) long. Another embryo, in Dean's collection, which appears slightly more advanced in its development, measures only about 60 mm. (2.36 inches) in length. Its external gill-filaments have reached their maximal development.

The embryo portrayed in Figure 38, plate III, shows important changes. The head, including the branchial region, has increased in depth so that in side view the embryo is shaped more like a tadpole. Through a sort of telescoping of the branchial and pectoral regions, the three posterior gill-clefts have come to lie dorsal to the base of the pectoral fin, as in the adult. The distance between the spiracular cleft and the first gill-cleft has

greatly increased. The fins, excepting the caudal, are larger than in the preceding figure, and all the fins show an advance in differentiation. The tips of the spines of the dorsal fins are now exposed, and the ventral lobe of the caudal fin exhibits the notch that is characteristic of adults of the genus *Heterodontus*. The lateral line, extending along the side of the body, is fairly distinct, and portions of the sensory canal system of the head are indicated by white lines in the drawing. The external gill-filaments are shorter, more delicate, and perhaps less numerous, than in the preceding stage. Seven or eight filaments project from the spiracular cleft. The demibranch on the anterior side of the first branchial cleft shows some of the shortened gill-filaments that persist in the adult. In this drawing, the supraorbital fold would scarcely be noticed if one were not familiar with its form in the adult fish.

One of Dean's embryos is about 72 mm. (2.8 inches) long. It is slightly less advanced in its general development than the one represented in Figure 38, plate III, but has external gills that resemble those shown in this figure. Another embryo in Dean's collection, apparently identical with the one depicted in Figure 38, plate III, is about 78 mm. (3 inches) long.

Figure 39, plate III, represents an embryo definitely older than the preceding. This is shown by the emergence of several new features. The body proper, and the bases of certain fins, are covered with dermal denticles. The color pattern of the embryo at the time of hatching is vaguely foreshadowed. The dorsal fins have acquired somewhat their form in the adult, though in adults of this species the posterior margin of the second dorsal is sometimes partly or wholly convex. The tips of the spines of the dorsal fins are barely visible. If one looks sharply he may see, just behind the gill-clefts and continuing caudad for some distance, a series of grooves parallel to the gill-clefts and spaced like them, but not so distinct. These grooves are better shown in Figure 84, plate VII, considered later. The supraorbital ridges are hardly noticeable and are perhaps not well developed in this embryo. The general form of the body, now approximately the same as in the adult, differs little from that represented in the preceding figure. The spiracular opening is not shown.

An embryo in Dean's collection, apparently identical with the one represented in Figure 39, plate III, is broken in two in the middle and is somewhat mutilated in this region. It cannot be accurately measured but is about 90 mm. (3.5 inches) long.

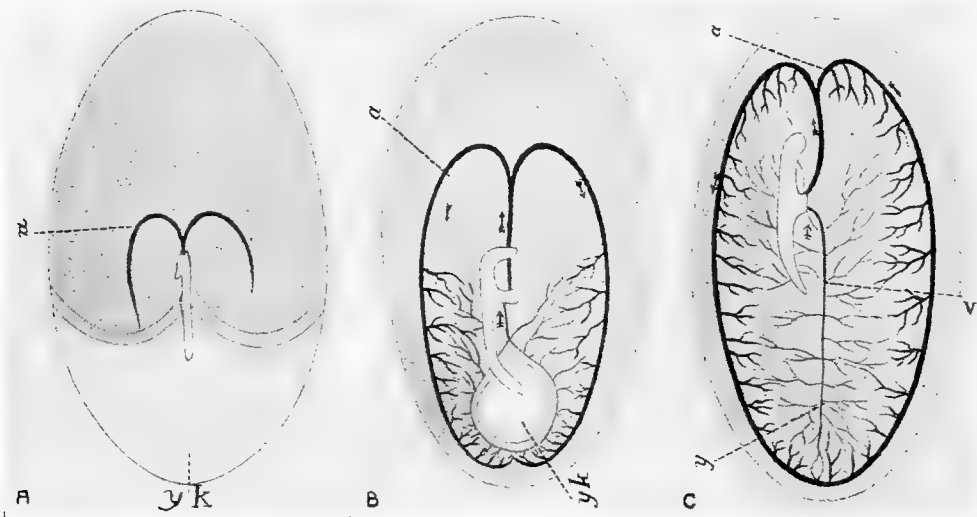
The embryo depicted (in color) in Figure 82, plate VII, is a little older than the one represented in Figure 39, plate III. The presence of a sizable yolk sac shows that it was taken long before hatching. In some respects, this embryo is unique and is probably either distorted, abnormal or inaccurately drawn. In particular, the nasal opening appears high up on the front of the head and not connected with the mouth by a naso-labial groove. Upon comparing this figure with later stages (Figures 83 and 84, plate VII), the size of the dermal denticles arranged in a V-shaped pattern posterior to the eye appears exaggerated. The dorsal portion of the pelvic fin forms a finger-shaped projection pointing dorsad. This may possibly be an upturned rudimentary myxopterygium. Aside from

these problematical features, the figure shows a moderate advance in pigmentation and a slight increase in the size of the pectoral and first dorsal fins. It is of interest principally because it is the most advanced embryo figured with a yolk sac.

The stage at hatching, portrayed in Figure 83, plate VII, is discussed in a later section of this article. The embryo represented in Figure 84, same plate, is two weeks older and therefore the consideration of this figure is likewise deferred.

THE VITELLINE CIRCULATION

Since the vitelline circulation in *Heterodontus japonicus* is essentially like that of other sharks, the diagrammatic figures by Balfour (1885) representing stages in the de-



Text-figure 58.

Diagrammatic figures showing the development of the vitelline circulation on the egg of *Pristiurus*: A, early; B, intermediate; and C, advanced stages.

a, vitelline artery; v, vitelline vein; yk, yolk blastopore. The letter y (in C) marks the spot where the venous ring and the yolk blastopore were closed by the growth of the blastoderm.

After Balfour, 1885, Figs. 1, 2, and 3, pl. 9.

velopment of the vitelline vessels of *Pristiurus* will serve as an introduction to the study of Dean's drawings. Three of Balfour's figures are reproduced as my Text-figure 58.

A single unpaired vitelline artery emerges from the yolk stalk and proceeds cephalad along the blastoderm under cover of the head of the embryo (Text-figure 58A). This arterial trunk divides to form two arcuate branches that turn toward the posterior margin of the blastoderm. In the stage represented in Text-figure 58B, the blastoderm has overgrown the entire surface of the yolk mass excepting a small nearly circular area (yk, the yolk blastopore) posterior to the yolk stalk. The two main arterial branches have almost surrounded the yolk blastopore, but are situated at some distance from it. Numerous small secondary branches grow toward the yolk blastopore, and some of these connect

with small veins emptying into a venous ring close to the margin of the blastoderm. The main trunk of the vitelline vein drains the venous ring and courses straight to the yolk stalk.

In the stage shown in Text-figure 58c, the yolk blastopore has been entirely overgrown by the blastoderm. The venous ring has disappeared, and the area formerly occupied by the yolk blastopore is now traversed by a continuation of the main trunk of the vitelline vein. This trunk now receives numerous small veins, usually joining it at right angles. The arterial ring, formed by the two main branches of the vitelline artery, gives off numerous secondary branches which subdivide repeatedly as they grow toward the venules. The arterioles interdigitate with the venules or connect with them presumably by means of capillaries. There are no branches extending in a centrifugal direction from the arterial ring. The main arterial trunk does not give off side branches. The later stages in the development of the vitelline vessels of *Pristiurus* need not be considered.

Dean's series of figures depicting stages in the development of the vitelline vessels of *Heterodontus japonicus* is the most extensive and detailed portrayal of these vessels in any Elasmobranch known to the writer. Even the smallest vessels appear to be drawn with great fidelity and accuracy, but owing to their profusion many of them, even in the original drawings, can be distinguished only by using a reading glass.

In Dean's series of drawings, the first to show vitelline vessels is Figure 56, plate V. In this figure two delicate arteries on each side, branches of a median unpaired vitelline artery, proceed laterad and then caudad. These arteries give off a few short secondary branches barely distinguishable in the drawing. The posterior artery on the right is in process of disappearance, having lost its connection with the main trunk. The thick red ring surrounding the yolk blastopore in this and in earlier stages is not a blood vessel; it is the remains of the pigment of the "orange spot", now confined to the extreme margins of the blastoderm.

In Figure 57, plate V, there are two branches of the vitelline arterial trunk on the left, but only one on the right; there are only faint indications of secondary branches. A great many very small venules (best seen with a reading glass) drain into the red zone surrounding the yolk blastopore. Presumably the red zone now contains a venous ring or at least a venous network.

The simple pattern of the arteries pictured in Text-figure 58A is attained, in *Heterodontus japonicus*, only after the early developmental irregularities have been smoothed out. In Figure 58, plate V, we see such an arterial pattern, but the veins have attained the stage shown in Text-figure 58B. In *H. japonicus* the venules that drain into the venous ring are very numerous, but they are so slender and set so closely together that individual venules can be made out only with the aid of a reading glass. In the stage represented in Figure 58, plate V, there is an irregular venous ring. This figure, and some of those that follow, are complicated by the presence of the problematical "holoblastic cleavage" pattern, described by Dean and illustrated by Figures 1 to 6, plate I, of this article. These "cleavage" furrows have been overgrown by the blastoderm, but in the living egg they

show through it. In the original, a spot in front of the embryo probably represents the optical effect of an oil globule in the yolk mass. It has been removed.

In Figure 59, plate V, the pattern of both arteries and veins is essentially the same as in the preceding figure, but the yolk blastopore is smaller and some of the venules seem to drain into an incomplete inner venous circle. This, perhaps, is an individual variation. The venules are longer than those delineated in the preceding figure. The vitelline vein, crossed by the tail of the embryo, may be seen leading forward to the yolk stalk which is attached to the pectoral region of the embryo.

Figure 60, plate V, shows right and left branches of the vitelline artery diverging more widely than in the preceding stages; their extremities extend to the margin of the figure. The yolk blastopore is reduced to a tiny circular area just behind the pelvic region of the curved embryo. A venous circle is lacking, and the venules converge toward irregular masses, colored red, closely surrounding the yolk blastopore. These masses may, in part, represent pigment, but it seems likely that they consist mainly of extravasated blood. Some of the venules begin at the extreme lower edge of the figure. The embryo lies partly on its right side, so that a blood vessel, presumably the vitelline vein, appears to the left of its ventral surface.

In Figure 61, plate V, the trunk and the two main branches of the vitelline artery are more prominent than in any of the preceding figures; but the branches extend to the opposite side of the egg, which is not represented by a drawing. The yolk blastopore has completely disappeared. The vitelline vein receives two parallel main branches close to the yolk stalk. The veins and venules have assumed a dendritic pattern. The round spot underneath the middle of the embryo is probably the optical effect of an oil globule in the yolk mass.

The egg represented in Figure 62, plate V, is anomalous. It bears two embryos (twins) each with its own vitelline artery and vein; but the two veins drain the same nexus, into which all the venules empty. The unpaired vitelline arterial trunk leading toward the top of the figure is longer than any shown in earlier stages. This artery ends in the usual two branches, but the other artery passes to the margin of the figure and cannot be traced further.

In Figure 63, plate V, the vitelline artery passes to the opposite side of the egg before branching. This figure, taken in connection with those that follow, indicates that the arterial circle forms entirely on the hemisphere of the egg farther away from the yolk stalk. The vitelline vein is still short and its manner of branching dendritic.

Figure 64, plate VI, represents a stage slightly later than the preceding, though the vitelline artery divides before reaching the upper part of the figure. Leading to the yolk stalk, there are two main vitelline veins; the more anterior branches of these veins are the strongest. This is an example of a tendency, by no means universal, for the vitelline veins to occur in two groups, right and left respectively. Figure 65, plate VI, is perhaps intended to represent the reverse side of the same egg, since the drawings of this plate retain their original paired arrangement; but a careful study shows that the two figures

are not entirely compatible, though they represent different aspects of two eggs in nearly the same stage. This is the first drawing to show the arterial circle, though it may occur in an earlier stage. The arterial circle gives off many branches that reach the margin of the figure, but none of these appear in Figure 64, plate VI, except possibly a few connecting with the vitelline vein. Figure 65 shows the vitelline artery giving off two side branches, but these are not present in Figure 64. Likewise the venules of the two figures do not correspond. The embryo, as shown by its orientation, is now free to rotate at least 90 degrees on the axis of the yolk stalk.

Figure 66 and 67, plate VI, are companion drawings. The arterial ring shown in Figure 67 is very narrow, and its branches are numerous. Some of the arterioles reach the surface shown in Figure 66; and conversely, some of the venules shown in profusion on this surface interdigitate and probably connect with the arterioles on the opposite side of the egg. There are two vitelline veins, coursing nearly parallel to each other, each with its own system of branches.

An extreme example of the tendency for the vitelline veins to occur in two groups, right and left, is found in the egg represented in Figure 78, plate VII. The arrangement here reminds one of the condition found in the corresponding stage of *Chlamydoselachus* (Gudger, 1940, pages 603 and 619; Figure 7, plate I; and Text-figure 4). All the smaller vitelline veins, in *Chlamydoselachus*, drain into a single median vein; but two groups of veins, right and left, are prominent.

Figures 68 and 69, plate VI, are companion figures representing different aspects of the same egg—in a stage slightly later than the preceding. There is no essential difference in the pattern of the vitelline vessels save that the arterial circle is nearly closed by the coalescence of segments that have become approximated. The two main branches, right and left, of the vitelline veins unite before reaching the yolk stalk.

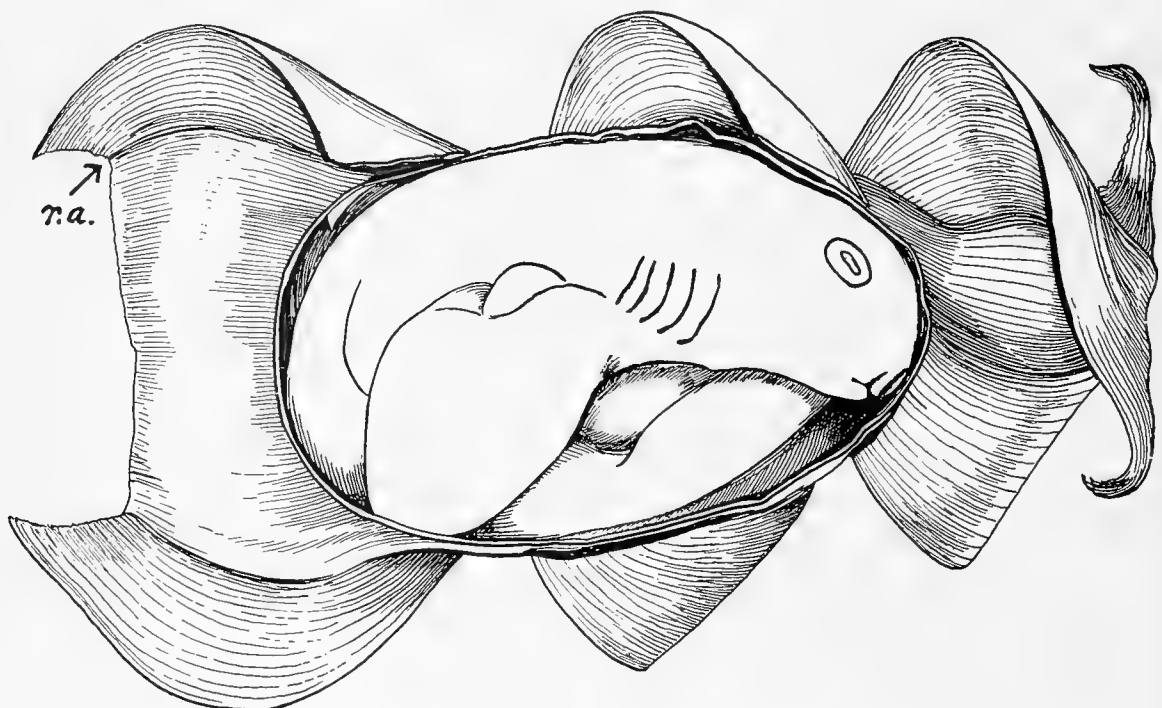
Figures 70 and 71 (companion figures on plate VI) are similar to the preceding with the exception that Figure 71 shows complete absence of the arterial circle. This has been replaced by an extension of the main trunk of the vitelline artery. The portion of the arterial trunk derived from the arterial circle branches profusely, while the stem portion, shown in Figure 70, lacks branches. This figure represents the latest stage in which the patterns of both arteries and veins retain a high degree of bilateral symmetry.

Figure 72, plate VI, shows little change from the preceding stage save that the veins and venules are more profuse. Its companion, Figure 73, plate VI, exhibits a decided lack of symmetry in both arteries and veins. Its most striking feature is that, on one side, a large number of venules reach almost to the main branches of the vitelline artery. The dark area around the head of the embryo in Figure 72 is probably the optical effect of an oil drop in the yolk mass.

Figure 74, plate VI, shows around its margin a profuse interdigitation and interconnection of arteries and veins. The same situation prevails in the upper portion of Figure 75, which shows the reverse side of the same egg. Here, as in the preceding stage, the vitelline artery has two main, though unequal, branches. The large circular dark area

around the base of the yolk stalk in Figure 74 probably represents the optical effect of an oil globule in the yolk mass.

The only remaining figure showing the vitelline vessels of *Heterodontus japonicus* is Figure 81, plate VII. This represents a much later stage. The large vessel on the right side of the figure is the vitelline artery; therefore the embryo must have reversed its original orientation on the yolk sac. A profuse system of vitelline veins is distributed to the left side of the figure (original right side of the yolk sac). Evidently there is a similar group on the opposite side, as in Figure 78, plate VII.



Text-figure 59.

An embryo of *Heterodontus japonicus* shortly before hatching, showing its coiled condition and its orientation within the capsule.

r. a., respiratory aperture.

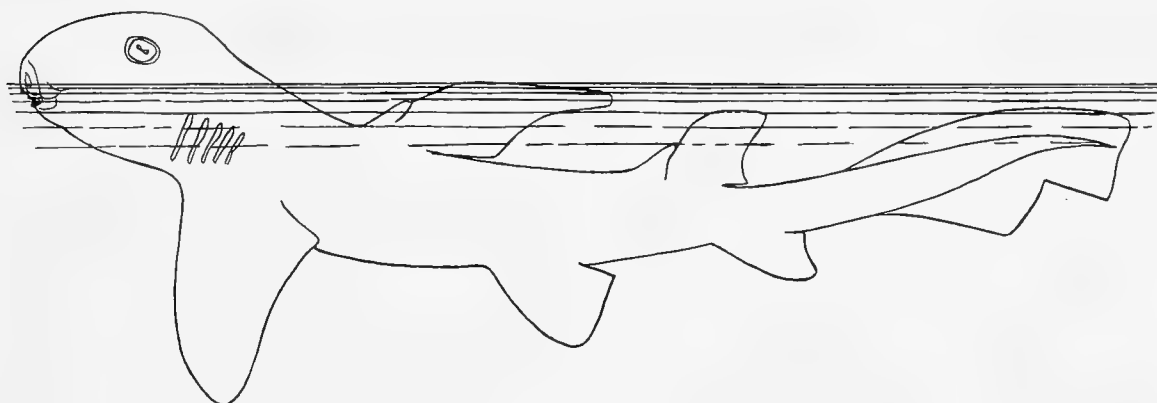
From a drawing left by Bashford Dean, but evidently not his handiwork. It has been necessary to correct the positions of the gill-clefts, eye, mouth, and nasal aperture.

HATCHING AND THE NEWLY HATCHED YOUNG

The part played by the egg capsule in the mechanics of hatching is described, for *Heterodontus japonicus*, on page 709. It has already been mentioned that, in his notebook, Dean records the length of a newly hatched Japanese Bullhead Shark as about 7 inches (180 mm.). This was the length of the fish observed in the act of escaping from the egg capsule. A newly hatched fish, in dorsal view, is portrayed in Figure 83, plate VII.

Since the young fish pictured in Figure 84, plate VII, is only two weeks older, it is best considered in this section. Dean's observations are here quoted from his typed manuscript.

A stage shortly before hatching is shown [Text-figure 59]. The young fish is coiled compactly, the fins wrapping around the body, the head being below [i.e., toward the small end of the capsule], the trunk bent into a loop and the tail continued so that it approaches the larger end of the capsule. The snout lies close to the breathing apertures of the smaller end of the capsule, and the gill-openings are not [very] distant from the right and left apertures of the capsule's larger end. These apertures at such a stage are large, the weathering of their margins having progressed to such a degree that a considerable current of water may be circulated through the capsule from the smaller to the larger end. The circulation is effected by the young fish, for in the partly opened capsule one may see with what strong muscular effort the fish is compressing and expanding its gill-pouches, drawing the water in through its mouth at the smaller end of the capsule and ejecting it in the opposite direction.



Text-figure 60.

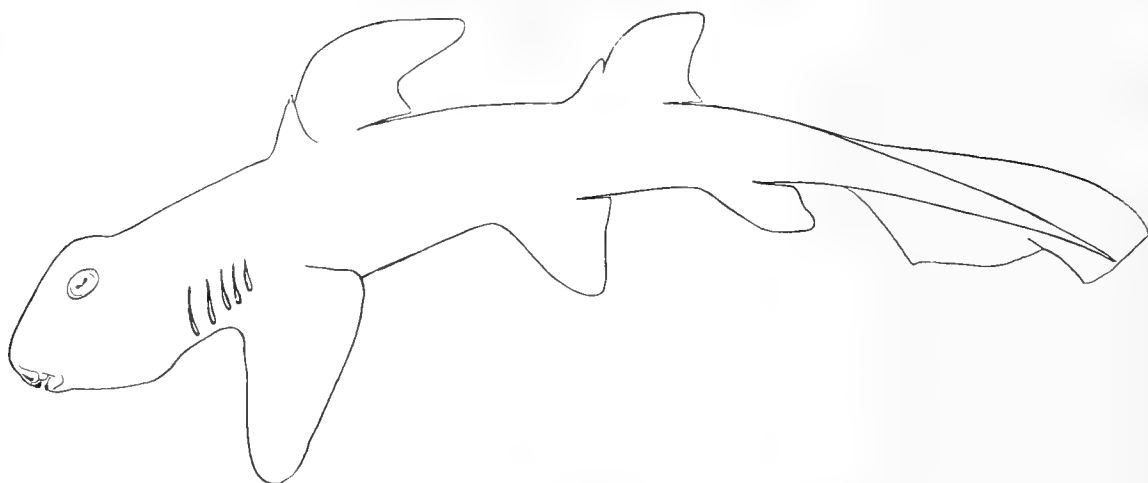
Outline drawing showing the attitude of a newly hatched *Heterodontus japonicus*, with its head upraised and partly out of water as if seeking to escape from the aquarium in which it was confined.

From a drawing left by Bashford Dean.

In a single instance the act of hatching was observed. An egg was brought in which was curiously light in weight, its walls papery and studded with barnacles: at first sight it seemed empty, but an examination showed that the larger end of the capsule had not opened. On April 4, it was placed in a laboratory aquarium: four days later, happening to take it in my hand, I felt it suddenly vibrate, as though it enclosed a young fish which had been alarmed by my touching it. This movement lasted a few seconds, then the fish suddenly appeared. The hatching took place so quickly and unexpectedly that its details were not followed. The valve opened and closed, and there was a young fish swimming about in the aquarium. It had emerged tail foremost, that was about all that was definitely noticed.¹

A student of animal behavior would have been interested in this newly hatched fish. For it showed the most finished instincts. It swam around the aquarium actively for about half a minute, breathing quickly and expanding its gills. It had from the beginning the move-

¹In Dean's original notes it is stated, in his own handwriting, that the young fish had emerged head foremost. Considering that in this stage the yolk mass had almost entirely disappeared, it appears probable that the fish would be able to reverse its orientation within the capsule, and thus either end might escape first from the capsule—presumably from its broad end.



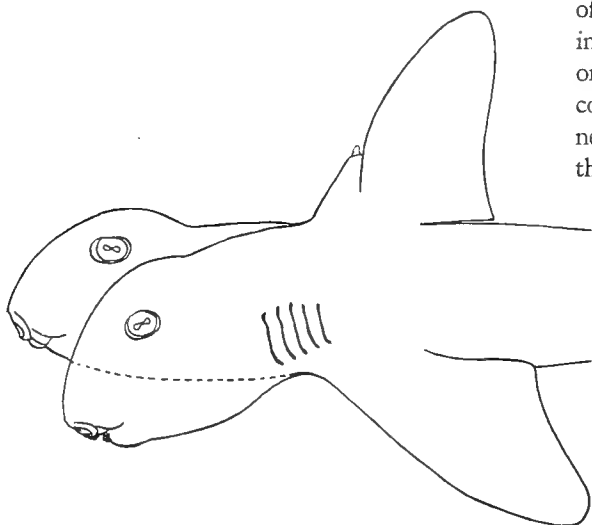
Text-figure 61.

Attitude of a newly hatched *Heterodontus japonicus*, with its back arched upward, exploring the corners of the aquarium.

From a drawing left by Bashford Dean. This drawing has been slightly modified to secure correct positions for the gill-clefts and the pectoral fin.

ments of the grown fish, it swam easily and quickly, it readily changed direction, and I soon found that it could swim around obstacles; and, if touched, it could draw itself backward, using its pectorals as supports. At first it was inclined to thrust its head out of water [Text-figure 60] as if anxious to escape, and in doing this it showed considerable flexibility in its neck, and it would even arch the back upward: at times it would explore the corners of the aquarium [Text-figure 61], the head and anterior part of the body flexing downward: occasionally it would bend the head, showing again the suppleness of the neck [Text-figure 62]. A period of rest was next observed, then a period of activity, these alternating with more or less regularity. A position of rest is shown [Text-figure 63] when the young fish raises its head, spreads out its pectorals and depresses its unpaired fins, the tail flattened against the bottom, the tip of the dorsals falling over on the (left) side. The latter habit may be explained in one

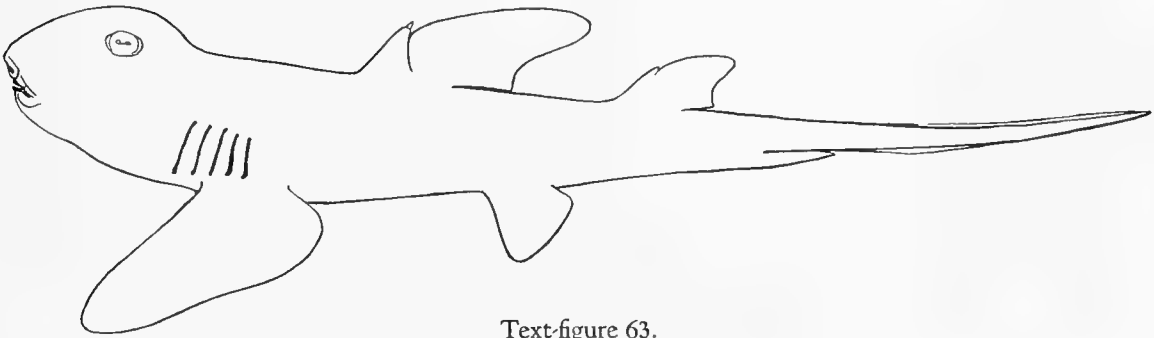
of two ways: either as a survival of its flattening of the fins during the period of incubation, or as a larval adaptation by which it becomes inconspicuous or less easily seized by a predatory neighbor. The young fish impressed one with the finished character of its movements: it



Text-figure 62.

Diagram showing two attitudes of the head of a newly hatched *Heterodontus japonicus*, illustrating the flexibility of the neck.

From a drawing left by Bashford Dean. The gill-clefts have been redrawn in a more nearly correct position.



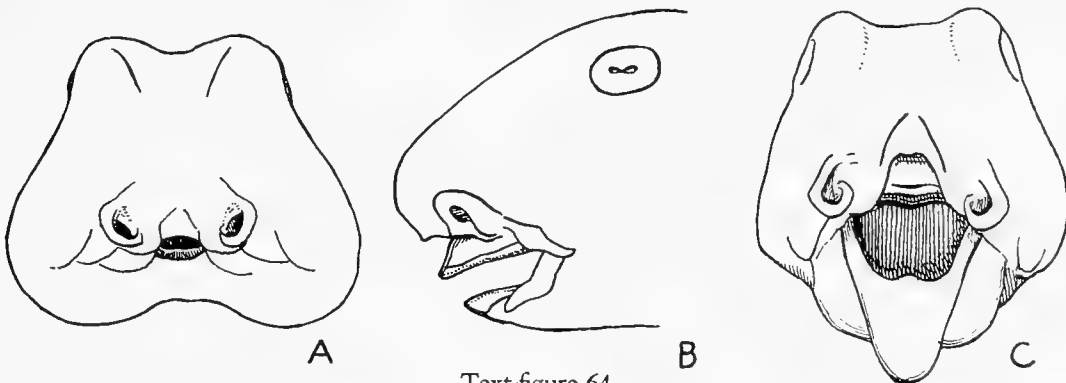
Text-figure 63.

A position sometimes assumed by a newly hatched *Heterodontus japonicus* when resting on the bottom of the aquarium.

From a drawing left by Bashford Dean. The gill-clefts have been redrawn in a more nearly correct position.

swam easily and well, it showed varied movements of its pectorals: it bit, retreated and advanced, it stood on the defensive, and it opened its mouth widely [Text-figures 64B and 64C] as though to inspire fear. During [ordinary] breathing [Text-figures 64A] it showed normally only the most anterior teeth.

The color of the fish at hatching is dark [Figure 83, plate VII] with a series of light bands: it is covered with a dense "bloom" of mucus. Two weeks later [Figure 84, plate VII] it has grown 25 mm.; it has changed color, shows a kind of opisthure¹, holds its fins more rigidly. The present figure indicates that down the sides of the body, in this as in [some] earlier stages, there is a row of (16-17) deep vertical creases immediately behind the gill-slits. They suggest a continuation of the line of the gills, with which obviously they have nothing to do. One reflects that it would be easy for an enthusiast to construct a phylogeny in which these deep creases fused with gut pouches and became of respiratory value. The spiracle is still of considerable size, and the dermal denticles are prominent. The latter condition is doubtless protective, guarding against injury from rubbing, and correlated with a long period of incubation in a capsule.



Text-figure 64.

Drawings showing the mouth of a newly hatched *Heterodontus japonicus* in three different poses:

A, during ordinary breathing; B, moderately and C, widely open.

From drawings left by Bashford Dean.

¹Opisthure: The posterior end of the caudal axis of certain fishes and embryos of fishes, which degenerates into a rudimentary organ, or becomes absorbed in the permanent caudal fin developed in front of it (Century Dictionary).

In his manuscript Dean states that, at the time of hatching, the yolk sac has been completely resorbed. A small scar (about 8 x 5 mm.) shows where it last appeared. In a footnote to this manuscript Dean quotes Goodrich's statement (1909, p. 132) that the yolk sac protrudes from the ventral surface of the embryo often after birth [hatching?]. Dean gravely doubts that this occurs in sharks under normal conditions. "I have witnessed birth [hatching] in the cases of *Cestracion* (*Heterodontus*), *Spinax*, *Raja*, *Pristiurus*,



Text-figure 65.

A young female specimen, 280 mm. (11 inches) long, of *Heterodontus japonicus* in the collection of the American Museum of Natural History. Probably it was obtained at Misaki by Bashford Dean. The color pattern has faded considerably, and is not well shown in the photograph. The mouth cavity has been opened by a lateral incision, here shown closed by several stitches.

Photograph, American Museum of Natural History.

and in no instance was there still an external yolk sac. Viviparous sharks will, however, under the stress of capture frequently give birth to young more or less immature". Very likely, in oviparous sharks, hatching may be slightly hastened by handling the egg capsules. In his original notes on *Heterodontus japonicus*, Dean writes concerning the fish observed in the act of hatching: "Yolk sac, so large [size indicated by a circle 3 mm. in diameter], yellow, apparent between pectorals". But Dean does not definitely state that this diminutive yolk sac protruded from the body of the fish. Perhaps it had been drawn into the body, and the yellow color was subsequently visible through the skin.

Dean's figure of a young *H. japonicus* aged two weeks after hatching (Figure 84, plate VII) should be compared with Brevoort's figure representing another specimen in approximately the same stage (Text-figure 22, page 690). Dean's specimen was 205 mm. (8.2 inches) long, while Brevoort's measured 216 mm. (8.5 inches). Dean's fish was a female, Brevoort's a male. In the drawing Brevoort's specimen appears to be more slender, and the fins longer. The transverse furrows of the ventrolateral body wall are not so numerous and well-defined in Brevoort's figure as they are in Dean's. The color pattern in Brevoort's figure approaches more nearly that of the adult as portrayed in my Text-

figure 21. Some portions of the color pattern of Brevoort's specimen appear to be unique. It is possible that an adequate collection of this species would reveal considerable variation in the color pattern in all stages of its development.

A 280-MM. YOUNG *HETERODONTUS JAPONICUS*

This young female (Text-figure 65) belongs to the collections of the American Museum of Natural History and was probably procured in Japanese waters by Bashford Dean. It is one of the specimens used by Dean for the study of the developing teeth. An incision leading from the mouth nearly to the first gill-slit was made in order to expose the mouth cavity. This incision was closed by large stitches with fine white thread, but still shows as an irregular line in the photograph (Text-figure 65). Two lines, both nearly vertical but meeting at an acute angle, at the extreme anterior end of the snout, are mere artifacts—creases in the skin—and have nothing to do with the olfactory organ. The fifth gill-slit is smaller and less conspicuous than the others, both in the specimen itself and in the photograph. The spiracular opening is still large enough to be sharply defined. The parallel vertical grooves along the side of the body posterior to the gill-slits are less numerous, less regular and less conspicuous than they are in the specimen represented in Figure 84, plate VII, which is considerably younger. Some careful measurements of the specimen under consideration are given in Table II.

TABLE II
SOME MEASUREMENTS IN MILLIMETERS OF A 280-MM. FEMALE
HETERODONTUS JAPONICUS

Total length	280
Greatest width of head (at first gill-covers)	44
Greatest height of head (at posterior end supraorbital ridge)	35
Greatest height of body (in a transverse plane passing through fifth gill-covers)	42
Length of first gill-slit	17
Length of fifth gill-slit	8
Base of first dorsal overlaps base of pectoral	8
Length of base of anal fin	16
Distance between base of anal fin and ventral lobe of caudal	27
Distance from tip to tip of extended pectoral fins	160
Vertical distance from ventral surface to tip of extended first dorsal fin	100

Most important for the identification of the species is the fact that the color pattern of this 280-mm. fish is fairly well preserved (though it does not show well in the photograph). The color pattern agrees in most respects with the color pattern of the younger specimens portrayed in Figures 83 and 84, plate VII. If one ignored the color pattern and depended entirely on Garman's key (page 663 of the present article) one would be very likely to classify this specimen as *Heterodontus phillipi* instead of *H. japonicus*. But the differences in the color patterns of the two species are very great, especially in young

specimens (compare Text-figures 8 and 9, page 668, with Figures 83 and 84, plate VII). Garman's key, which depends mainly on the positions of certain of the fins, was perhaps not intended to apply to such young specimens. Changes in the spacing of the fins may be brought about by differential growth.

EXTERNAL AND INTERNAL GILL-FILAMENTS

To the list of embryos of *Heterodontus japonicus*, already described, that bear external gill-filaments, one must add those embryos represented by Figures 66, 68, 70, 72 and 74, plate VI. In the last-named figure the external gill-filaments are very profuse.

So far as one may judge from the series of embryos portrayed in Dean's drawings, marked individual variations in the degree of development of the external gill-filaments of *Heterodontus japonicus* are rare. To be sure, the embryo pictured in Figure 36, plate III, is entirely lacking in external filaments; whereas in another embryo of approximately the same general stage (Figure 81, plate VII) the external filaments attain their maximum development. But it is probable that the condition shown in Figure 36, plate III, is exceptional. If this embryo were left out, the remaining series (including those embryos, already noted, which are not represented by drawings) would show a fairly regular gradation in the development and regression of the external gill-filaments.

The latest member of this series of embryos showing external gills is the one represented in Figure 38, plate III. Therefore the external gill-filaments of *Heterodontus japonicus* are not known to persist to such an advanced stage of general development as they do in *Chlamydoselachus* (Gudger, 1940, pages 629-630 and plate VI). Of *Chlamydoselachus*, a female specimen 614 mm. long and a male specimen 538 mm. long are portrayed with short external gills. These specimens had attained the adult form, but were not full-grown and were probably not sexually mature. The reproductive organs of a 1398-mm. female *Chlamydoselachus* dissected by me (Smith, 1937, Text-figure 85) were decidedly immature, and in a female *Chlamydoselachus* 1550 mm. long (*ibid.*, Text-figure 86) they were just approaching maturity. In these specimens, as well as in the two sexually mature females dissected by me, the gill-filaments did not show externally with the gill-flaps closed.

The question arises, what is the relation of the external gill-filaments of the embryo to the permanent gill-filaments of the adult? Of *Chlamydoselachus*, Gudger (1940, p. 639) writes: "these so-called external gills of the frilled shark are nothing but precociously overgrown permanent gills, which later on shorten until but a bare remnant shows beyond the gill-opening." I have been able to examine gills of *Heterodontus* in critical stages of their development and to observe that the external gill-filaments are not fundamentally different from the rudiments of the permanent filaments, but are essentially the same structures lengthened distally. It is better to begin with the adult stage and to trace the history of the gill-filaments backward.

I have had no adult specimen of *H. japonicus*, but I have examined the gill-filaments in an adult *H. quoyi*. Here, the filaments are short and deep-set, so that the gill-flaps must be pried well apart before one can observe the filaments with a lens. The fundamental

plan of these gill-filaments is not unlike that described for *Chlamydoselachus* (Smith 1937). Each filament of *Heterodontus* is a narrow band attached by one edge to the gill-septum which it traverses in a radial direction. Thus the filaments lie approximately parallel to one another; they are very numerous and are set close together. The extreme distal end of each filament stands slightly away from the gill-septum; in other words, the distal ends are free from direct attachment to the septum. Each filament bears on both surfaces a series of close-set parallel ridges, the lamellae, which extend transversely to the long axis of the filament. In *Heterodontus* the close-set lamellae project slightly beyond the free edge of the filament, giving it a serrated appearance.

In the 280-mm. (11-inch) young female *Heterodontus japonicus* the gill-filaments are much the same as in the adult specimen of *H. quoyi*; but the filaments are longer and their distal extremities project farther from the gill-septum. Except for their serrated appearance, these finger-shaped extremities of the gill-filaments suggest the rudimentary filaments of the early embryo. The filaments of this specimen are easily exposed, since they cover a considerable extent of the gill-septum. They are not, however, visible when the gill-flap is closed.

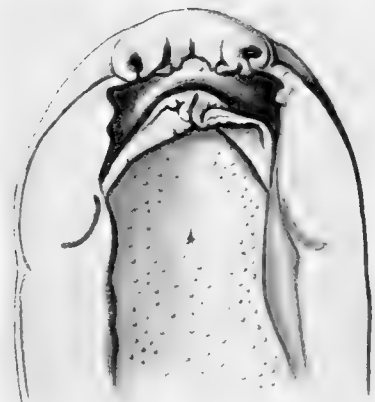
In the 78-mm. (three-inch) embryo of *H. japonicus* already mentioned, I found the rudiments of the internal gill-filaments (those that persist in the adult) in connection with external filaments (shown in Figure 38, plate III). The two kinds of gill-filaments are continuous structures. The rudimentary internal filaments are attached, throughout all but a small distal portion, to the gill-septum and are distinguished by the presence of rudimentary lamellae. The distal ends of these internal filaments are continuous with the rod-like external gill-filaments, which lack lamellae.

Bearing in mind this relationship between the external gill-filaments of the embryo and the internal gill-filaments of the adult, the occurrence of gill-filaments protruding from the spiracular cleft is conclusive evidence (if such evidence were needed) that the spiracular cleft in sharks was primitively a gill-cleft functioning in the usual manner. During early development the spiracular cleft is as large as the gill-clefts, with which it is serially homologous; but during later development its external orifice becomes very small, and the spiracular canal takes on special functions concerned with respiration. In some specimens of *Heterodontus* the spiracle is so small that it seems vestigial.

Text-figure 66

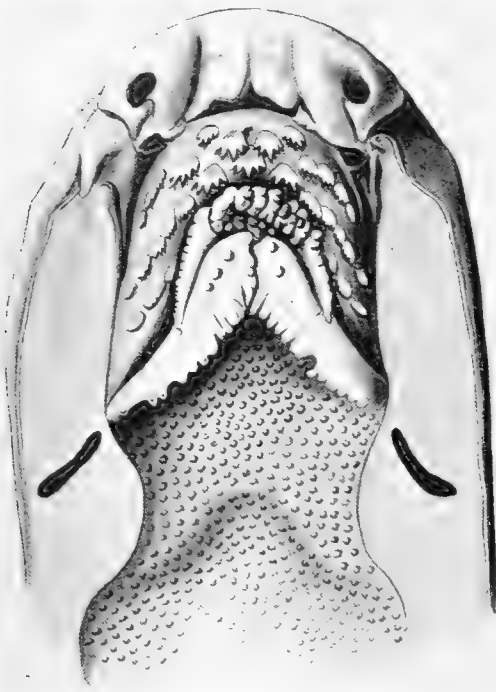
Roof of the mouth cavity of a 78-mm. (3-inch) embryo of *Heterodontus japonicus*. The dental ridge, formed by the upper jaw, is situated between the olfactory region anteriorly and the breathing valve posteriorly. The small pit, shown in the center of the figure, leads into Rathke's pouch.

From a drawing left by Bashford Dean.



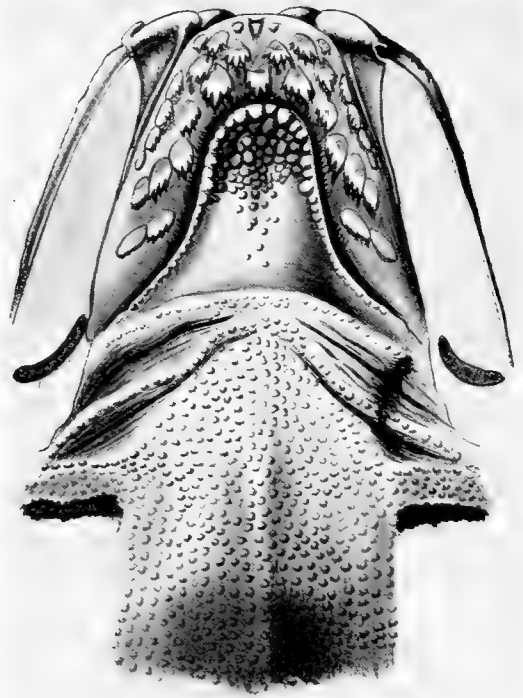
DEVELOPMENT OF THE TEETH

Among Dean's drawings of *Heterodontus japonicus* are four figures, which were found mounted in serial order, illustrating the development of the teeth. These are reproduced as my Text-figures 66 to 69. There are no records concerning the original drawings, neither accompanying the drawings nor in Dean's notebooks.



Text-figure 67.

Interior of the mouth and pharynx of a young (probably recently hatched) Japanese Bullhead Shark, *Heterodontus japonicus*.



Text-figure 68

Text-figure 67. Roof of the oro-pharyngeal cavity, revealing the teeth of the upper jaw, the breathing valve, and the pharyngeal denticles.

Text-figure 68. Floor of the oro-pharyngeal cavity, showing the teeth of the lower jaw, also both oral and pharyngeal denticles.

After drawings left by Bashford Dean.

The earliest stage, represented by Text-figure 66, represents the roof of the mouth cavity viewed from below. This drawing was made from the 78-mm. embryo, in Dean's collection, described and figured (Figure 38, plate III) in the present article. The lower jaw of this embryo has been cut away in order to expose the roof of the mouth. I have compared this dissection with Dean's drawing (Text-figure 66) and can state that the drawing corresponds, in every detail, with the structures revealed by the dissection. Teeth are not yet visible; but the arch-like dental ridge (formed by the lower surface of

the palatoquadrate cartilages covered with mucous membrane) is readily seen between the olfactory region anteriorly, and what appears to be a breathing valve¹ posteriorly. The small pit represented in the center of the figure presumably leads into Rathke's pouch.

Text-figure 67, like the preceding, represents an upper jaw. It is the first drawing, of this series, portraying teeth. Presumably, this drawing was made from a recently hatched specimen. (For similar teeth of a recently hatched *H. phillipi*, observe Text-figure 13, page 672). The anterior teeth represented in Text-figure 67 are larger than the posterior teeth (contrary to the condition in the adult) and each anterior tooth possesses five cusps. Posteriorly, the number of cusps grades from five to none. More distinctly than in Text-figure 66, the breathing valve appears divided into two main portions, anterior and posterior respectively. The central third of the anterior portion is subdivided into a large number of short lobules. The filamentous portions of the breathing valve bear an irregular fringe of lobules.

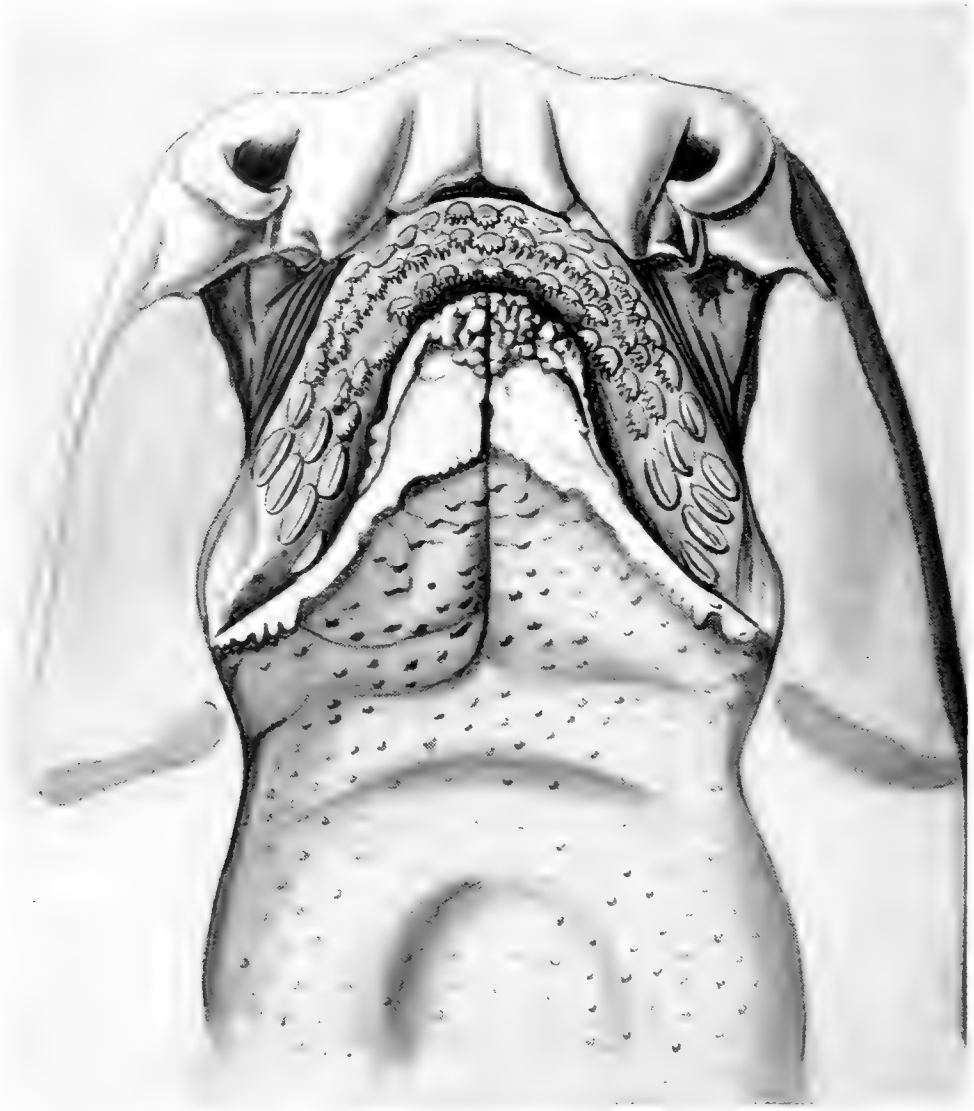
Text-figure 68 portrays what is apparently the same stage in a lower jaw. This drawing should be compared with Text-figure 13, showing the teeth of a recently hatched specimen of *H. phillipi*. There is no sharp division between anterior (cuspidate) and posterior (grinding) teeth, and the total number of transverse rows is less than in the adult. The anterior two-thirds of the teeth are typically five-cusped. The extreme posterior teeth are almost or quite lacking in cusps. In the intermediate region, the number of cusps is usually four. As in the upper jaw, the extreme posterior teeth, which lack cusps, are smaller than the largest anterior teeth. In the absence of any drawing showing the teeth in an earlier stage, it seems probable that most of the anterior teeth possess five cusps from the beginning—for it is known that Dean had a fairly close series of stages from which to select specimens for drawings. In the figure under consideration there is a row of unusually large oral denticles situated close to the inner margin of the jaw. Between these denticles and the teeth drawn in broad view, one may see the serrated edges of an inconspicuous inner row of teeth.

Text-figure 69 represents the roof of the mouth cavity of the 280-mm. female *Heterodontus japonicus* portrayed in Text-figure 65, page 756. Text-figure 69 depicts faithfully not only the form but the precise number and arrangement of the teeth in this specimen. There are three longitudinal rows, with an extra tooth at the extreme posterior end making a transverse row of four. The anterior teeth are still typically five-cusped. Two transverse rows of the most posterior teeth lack cusps, but each of these teeth bears a prominent longitudinal ridge. The posterior ridged teeth are much larger (especially longer) than the anterior teeth. The transition between anterior (cuspidate) and posterior (grinding) teeth is more abrupt than it is in earlier stages. The middle portion of the anterior division of the breathing valve consists of a compact group of long finger-like lobules—which may be seen more clearly in the specimen than in the drawing.

¹I have found this problematical breathing valve not only in the 78-mm. embryo of *Heterodontus japonicus*, but also in the 280-mm. specimen of the same species and in a young 368-mm. *H. quoyi*. I have had no opportunity to observe it in the living fish, hence cannot state positively what is its function; but its position and structure suggest strongly that it is a breathing valve.

In the present article, the structure of the adult teeth of *Heterodontus* has been described for every species except *japonicus*. Teeth of young specimens (after hatching) have been described for every species except *galeatus*. Teeth of an embryo of *Heterodontus* have not been described for any species.

Upon comparing the accounts, by various authors, of the teeth of the six species of *Heterodontus*, it seems to the writer that the specific differences are not very great and



Text-figure 69

Roof of the mouth of a 280-mm. (11-inch) young *Heterodontus japonicus*, showing teeth of the upper jaw.

From a drawing left by Bashford Dean.

that most of the observed differences are correlated with age and use. The most important points may be summarized as follows: The most anterior of the cuspidate teeth begin, as a rule, with five cusps, but some of the more posterior cuspidate teeth begin with only three or four cusps. The typically five-cusped condition of the anterior teeth persists until long after hatching. Before the adult (sexually mature) stage is reached, the number of cusps in these teeth is reduced to three, with the central cusp most prominent. Gradually the lateral cusps become inconspicuous or even absent. With age and use (the food consisting mainly of molluscs, crustaceans, and sea urchins) the central cusp may become worn down until the anterior teeth, collectively, appear almost pavement-like. (The word pavement, as used here, refers to the old-fashioned much-worn stone-block pavement). The posterior or grinding teeth never have prominent cusps, and some are entirely without cusps. The few rudimentary cusps that appear in the early stages soon give place to a longitudinal ridge, useful in grinding the food. In older specimens, this ridge may be entirely worn away, leaving the tooth with a smooth rounded surface. Thus the posterior teeth become more pavement-like than the anterior teeth; in the adult they are much larger and stronger. In their prime, the anterior teeth are well-fitted for prehension, the posterior teeth for crushing and grinding. All the descriptions and illustrations of both young and adult teeth emphasize the differences between anterior and posterior teeth—differences that suggested the generic name, *HETERODONTUS*.



Another view (see also Text-figure 1) of the Marine Zoological Station at Misaki where Dr. Dean studied the Japanese Bullhead Shark.

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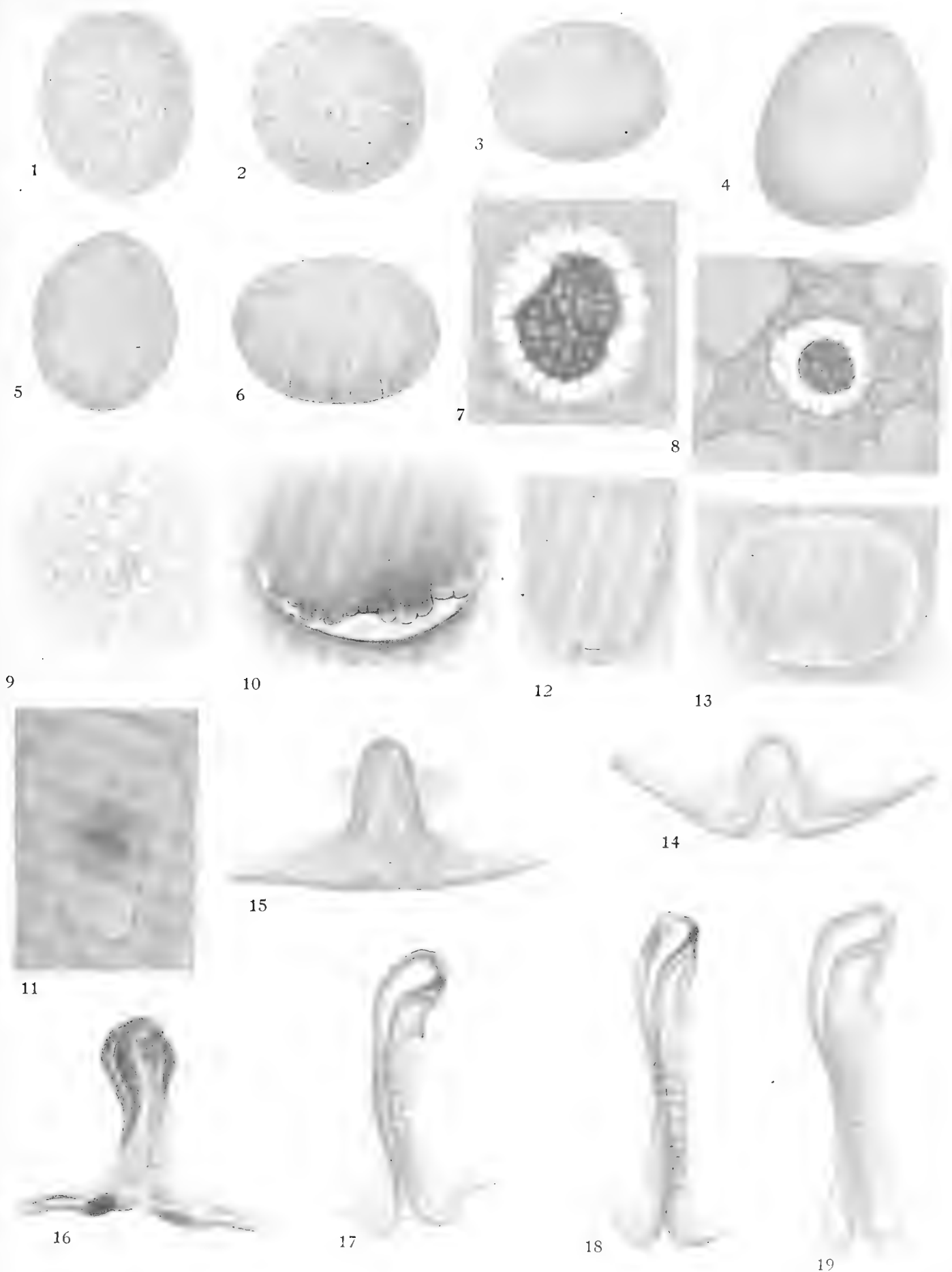
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PLATE I
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE I

EARLY DEVELOPMENT OF THE EGG OF *HETERODONTUS JAPONICUS*

- Fig. 1. Egg taken at time of deposition. Polar view of upper hemisphere. The germinal disc ("orange spot") is indicated by a tiny circle close to top of figure.
- Fig. 2. Upper hemisphere of an egg in a slightly later stage. The germinal disc is situated on the side of the egg away from the observer. It is indicated, as if seen through the egg, by a tiny dotted circle near the right hand margin of the figure.
- Fig. 3. Lateral view of an egg in a stage between Figures 1 and 2. The position of the germinal disc is not indicated.
- Fig. 4. Lateral view of an egg similar to the one shown in Figure 3. The germinal disc is indicated by a small dark spot on the right of the figure.
- Fig. 5. An egg shown in lateral, slightly oblique, view. The germinal disc is indicated, as if seen through the egg, by a dotted circle in the upper right quadrant of the figure.
- Fig. 6. An egg in a slightly later stage, oriented with ordinarily lower pole nearly uppermost. The germinal disc is situated on the side of the egg away from the observer. It is indicated by a tiny dotted circle in the upper left quadrant of the figure.
- . Figs. 1 to 6 have been published by Dean in the *Annotationes Zoologicae Japonensis*, 1901, vol. 4. They show furrows interpreted by Dean as a reminiscence of holoblastic cleavage. Eggs in these stages vary from 40 to 50 millimeters in diameter.
- Fig. 7. The earliest observed stage of cleavage in the germinal disc. This region, constituting the early blastoderm, was removed from the yolk mass. Viewed by transmitted light, it was drawn, under magnification, in natural colors.
- Fig. 8. A later stage in the segmentation of the germinal disc. The blastoderm, removed from the egg and viewed by transmitted light, was drawn under magnification in natural colors.
- Fig. 9. Slightly later stage of cleavage in a germinal disc viewed as an opaque object.
- Fig. 10. Blastoderm in an advanced cleavage stage, removed from the yolk and viewed by transmitted light. The crescentic light area in lower part of figure is the blastocoele seen by focussing downward through its roof.
- Fig. 11. Elongate blastoderm, perhaps ready for gastrulation, viewed as an opaque object and drawn in natural colors. This blastoderm is 5 mm. long. The pale area surrounding it is the marginal zone of the periblast.
- Fig. 12. Surface view of a blastoderm in an early stage of gastrulation. Note, at the posterior (lower) end, the neural groove bordered by upraised neural folds.
- Fig. 13. Surface view of a blastoderm, with rudimentary embryo, slightly later than the preceding.
- Fig. 14. Optical section through embryonic region in a stage intermediate between Figures 12 and 13. This figure, like the remaining ones of this plate, was drawn from a cleared preparation.
- Fig. 15. Optical section of an embryo slightly later than the one shown in Figure 13.
- Fig. 16. Optical section of an embryo with 4 pairs of complete mesoblastic somites.
- Fig. 17. Optical section of an embryo with 12 pairs of complete somites.
- Fig. 18. Optical section of an embryo with 14 or 15 pairs of somites.
- Fig. 19. Optical section of an embryo with 15 or 16 pairs of somites.



BASFORD DEAN, DIR.

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EMBRYOLOGY OF HETERODONTUS JAPONICUS

PLATE II
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE II
LATER EMBRYOS OF *HETERODONTUS JAPONICUS*

- Fig. 20. A cleared embryo with 18 complete somites. Measured on the slide, it is 3.5 mm. (about one-eighth inch) long.
- Fig. 21. Surface view of an embryo with about 24 somites.
Like some of the embryos represented in the surface views that follow, this one appears to have been drawn at a lower magnification than that used for cleared preparations.
- Fig. 22. Surface view of an embryo with about 25 somites.
- Fig. 23. A cleared embryo with at least 26 somites.
- Fig. 24. Surface view of an embryo with at least 28 somites.
This figure was drawn from the left side, but it has been reversed to facilitate comparison with other figures on this plate.
- Fig. 25. Surface view of an embryo with about 35 somites. This figure, like the preceding, was drawn from the left side but has been reversed.
- Fig. 26. A cleared embryo with about 37 complete somites.
- Fig. 27. An embryo with about 41 complete somites, drawn after being cleared.
- Fig. 28. Surface view of an embryo with at least 50 complete somites.
- Fig. 29. An embryo with about 55 complete somites, drawn in surface view.
- Fig. 30. Head and anterior part of the body of a cleared embryo. The number of somites is unknown.
- Fig. 31. Surface view of an embryo with about 74 somites, now represented by myomeres.
- Fig. 32. An embryo with about 85 myomeres, drawn in surface view.
Since all the figures of this plate are lateral views, the number of somites (in later stages represented by myomeres) is recorded for one side only.

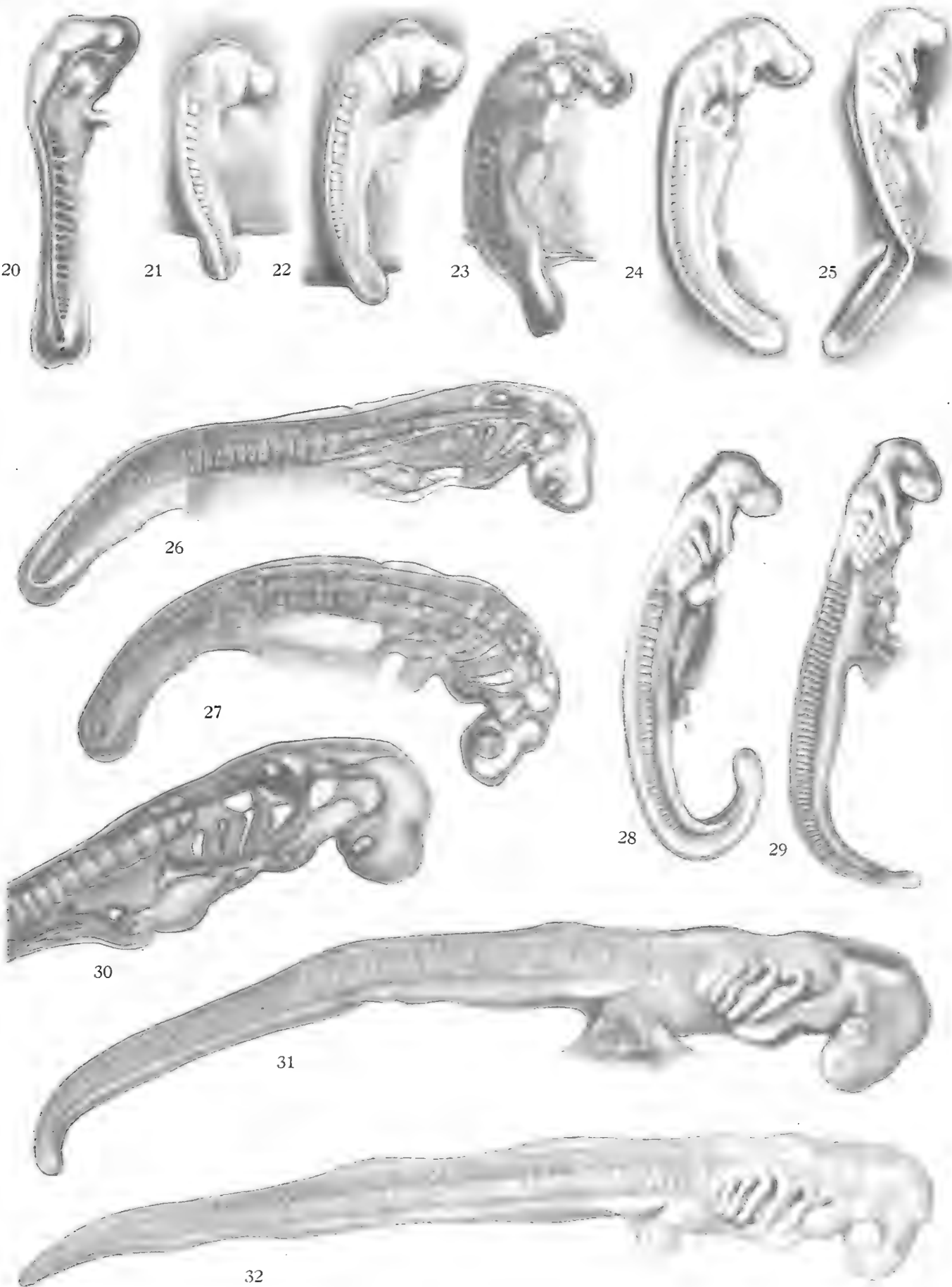


PLATE III
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE III
LATE EMBRYOS OF *HETERODONTUS JAPONICUS*

- Fig. 33. An embryo with at least 88 myomeres (those near the tip of the tail are indistinct).
- Fig. 34. An embryo somewhat later than the preceding. The myomeres are not visible externally.
Another embryo, in Dean's collection, slightly older than the one portrayed here, but younger than the one represented in the following figure, measures 38 mm. (about one and one-half inches) long.
- Fig. 35. An embryo later than the one shown in the preceding figure. Except at the tip of the tail, the myomeres are not visible externally.
Another embryo in the same stage of development, found in Dean's collection, measures about 50 mm. (two inches) long.
- Fig. 36. An embryo, with myomeres visible only in the posterior half of the figure. The absence of external gill-filaments in this stage is unusual.
- Fig. 37. An embryo with profuse external gills. It measures about 70 mm. (two and three-fourths inches) long.
- Fig. 38. This embryo is approximately 78 mm. (three inches) long. It has shorter and more delicate external gills.
- Fig. 39. Note the lack of external gills in this embryo, which is about 90 mm. (three and one-half inches) long.

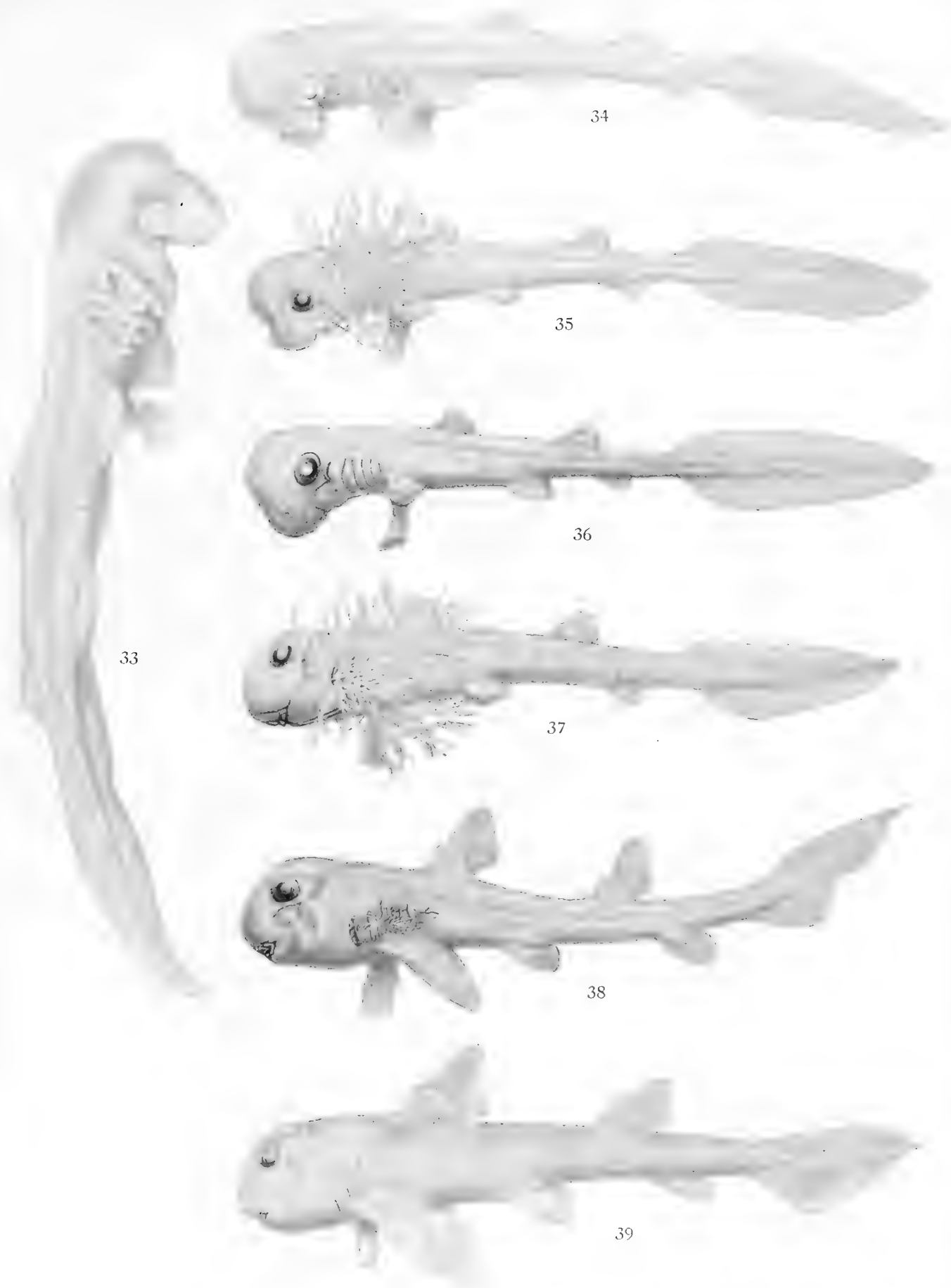


PLATE IV
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE IV
ENTIRE EGGS OF *HETERODONTUS JAPONICUS*
SHOWING THE RELATIONS OF THE EMBRYO AND
THE OVERGROWTH OF THE YOLK MASS BY THE BLASTODERM

- Figs. 40 to 42. Upper hemisphere of eggs taken shortly after deposition. The germinal disc or "orange spot" is presumably undergoing cleavage. In Figures 40 and 41, the disc is surrounded by concentric white zones; in Figure 42, by a single white zone (periblast?).
- Fig. 43. A slightly older egg in which the germinal disc is in a late blastula stage.
- Fig. 44. The germinal disc or blastoderm is now almost ready for gastrulation.
For larger and more accurate drawings of blastoderms in approximately the same stage, see Figure 11, plate I, and Figure 80, plate VII.
- Fig. 45. An egg slightly later than the preceding. The blastoderm is larger, and is circular in outline.
- Fig. 46. This blastoderm is much larger than the preceding one. Its posterior (lower) margin is upraised and is in a very early stage of gastrulation. See also Figure 12, plate I.
- Fig. 47. A still larger blastoderm showing at its posterior edge the upraised embryonic area. For details see Figures 13 and 14, plate I.
- Fig. 48. There is shown here a marked increase in the size of the blastoderm. The embryo shows a definite head region. An embryo in approximately the same stage is shown in detail in Figure 16, plate I.
- Figs. 49 to 51. These figures show the blastoderm spreading over a hemisphere of the egg while the embryo, situated at the slight notch in the posterior margin of the blastoderm, is still very small and cannot be accurately delineated on this scale. The three stages are probably equivalent to Figures 22, 24, and 25, plate II.

The drawings of this plate are in natural colors, save that the embryos represented in Figures 49 to 51, which in life are colorless and translucent, are portrayed in opaque white. All the drawings are reproduced about natural size. In all the figures, the yolk mass shows the furrows interpreted, by Dean, as a reminiscence of holoblastic cleavage.

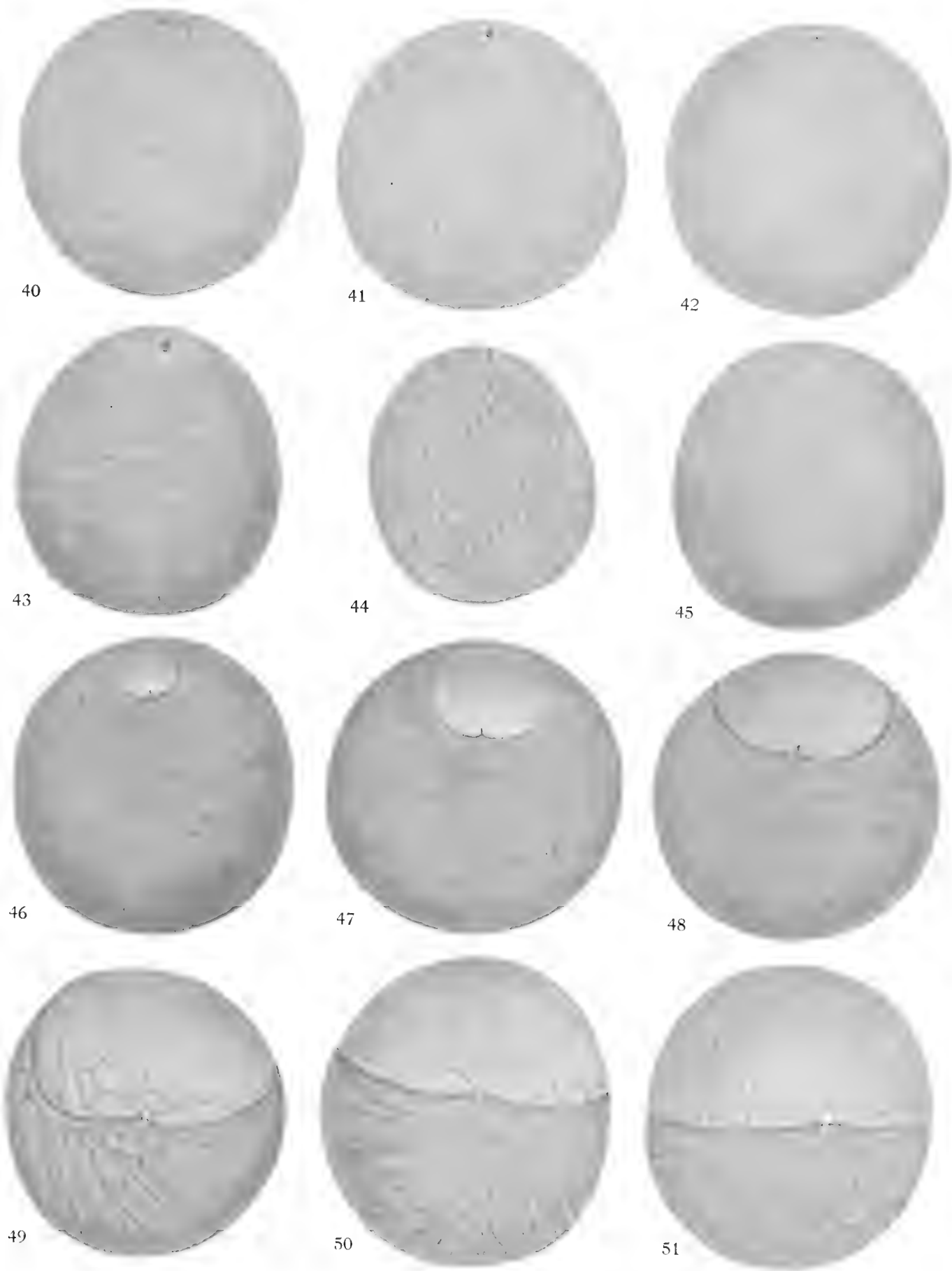


PLATE V
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE V
ENTIRE EGGS OF *HETERODONTUS JAPONICUS*
SHOWING CLOSURE OF YOLK BLASTOPORE
AND ORIGIN OF VITELLINE VESSELS

- Fig. 52. The blastoderm covers more than a hemisphere of the yolk mass. The stage of embryonic development is perhaps equivalent to that shown in Figure 26, plate II.
- Fig. 53. In this figure the yolk blastopore is appreciably smaller, though the embryo is no larger than the one represented in the preceding figure.
- Fig. 54. Here the embryo appears to be in a stage slightly younger than the one shown in Figure 53, though the yolk blastopore is smaller.
- Fig. 55. In this figure the embryo is in a stage approximately the same as the preceding.
- Fig. 56. This is the first stage showing vitelline vessels, here entirely arterial. The main arterial trunk is not visible. There are two pairs of secondary vitelline arteries, right and left. The embryo is larger than the one shown in the preceding figure.
- Fig. 57. This figure shows a decided increase in the size of the embryo and in the degree of closure of the blastopore. There are two vitelline arteries on the left, but only one on the right. A venous ring, surrounding the yolk blastopore, is in process of formation.
- Fig. 58. The main trunk of the vitelline artery is shown proceeding forward from the yolk stalk, and branching to form only one pair of arcuate arteries. A multitude of radially-directed vitelline venules drain into the venous ring.
- Fig. 59. The yolk blastopore is nearly closed. There is no change in the arterial pattern, but the venules are further developed. The embryo is in approximately the same stage as the one represented in Figure 29, plate II.
- Fig. 60. The venous ring has contracted almost to the point of disappearance. The arterial pattern is unchanged. The embryo is decidedly larger than the one shown in the preceding figure.
- Fig. 61. In this figure the vitelline vessels are especially well shown. Right and left vitelline veins extend to the margin of the figure. There are two main branches of the vitelline vein, extending from the plexiform group of venules to the yolk stalk.
- Fig. 62. An egg with two embryos (identical twins), perhaps with a single tail. Each embryo has its own vitelline artery and vein, but the veins drain the same nexus of venules.
- Fig. 63. The arterial vitelline trunk passes unbranched to the other side of the egg. There is a single vitelline vein draining a dendritic group of venules. The embryo still heads in the direction of the vitelline artery.

Figures 52 to 59 show stages in the closure of the yolk blastopore. In Figures 52 to 56 the problematical "cleavage" furrows of the yolk are conspicuous in the yolk blastopore. In Figures 53 and 54 some of these furrows show faintly, and in Figures 58 and 59 many of them show conspicuously through the translucent blastoderm.

Figures 56 to 63 show early stages in the development of the vitelline vessels. In some of these drawings, the pattern of the vessels is more or less obscured by the presence of "cleavage" furrows in the yolk, which show through the blastoderm.

All these drawings are in natural colors save that the embryos, which in life are colorless and translucent, are portrayed in opaque white. With the possible exception of Figures 58, 59 and 60, all the drawings are here reproduced about natural size.

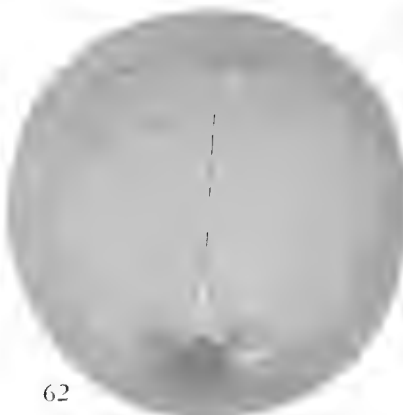
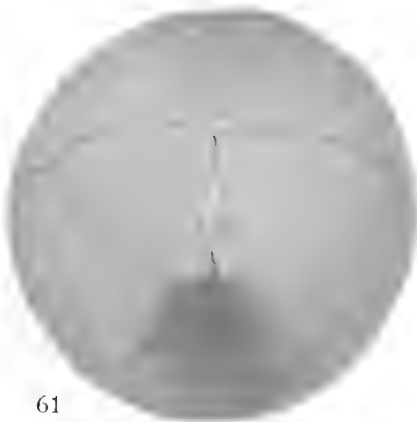
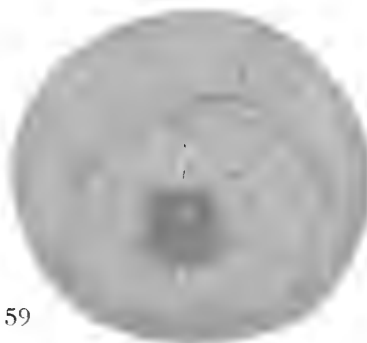


PLATE VI
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

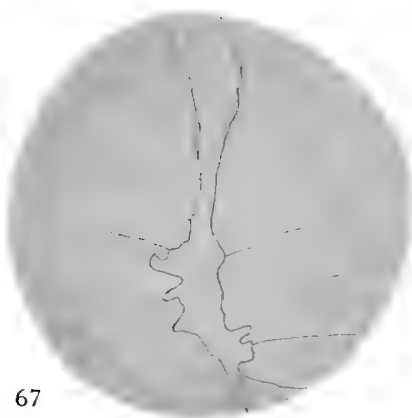
PLATE VI
FURTHER DEVELOPMENT OF THE VITELLINE VESSELS
IN *HETERODONTUS JAPONICUS*

- Fig. 64. In this figure the embryo, for the first time in this series, lies at right angles to the direction of the vitelline artery, showing that the embryo is able to rotate by twisting the yolk stalk. The vitelline artery branches before reaching the margin of the figure. There are two vitelline veins leading to the yolk stalk.
- Fig. 65. An egg in nearly the same stage as the preceding, showing the hemisphere opposite the one to which the embryo is attached. The two main branches of the vitelline artery have joined anteriorly to form the arterial circle.
- Fig. 66. A later stage in which the arterial pattern resembles that shown in Figure 64, while the branching of the vitelline veins is much more profuse and extensive.
- Fig. 67. Opposite hemisphere of the egg represented in the preceding figure, showing the convergence of right and left sides of the arterial circle, which is profusely branched.
- Fig. 68. Here the embryo has been tilted to expose the yolk stalk, which shows the main trunk of the vitelline veins. The vitelline artery does not branch before passing to the other hemisphere of the egg.
- Fig. 69. The opposite hemisphere of the egg portrayed in the preceding figure. The arterial circle is nearly obliterated by the coalescence of right and left sides.
- Fig. 70. The arterial and venous vitelline trunks are here seen pursuing parallel courses as they enter the yolk stalk. The larger branches of the vitelline vein occur in two groups, right and left.
- Fig. 71. The opposite hemisphere of the egg represented in the preceding figure. The right and left sides of the arterial circle have coalesced to form an extension of the main arterial trunk.
- Fig. 72. Both arterial and venous patterns are similar to those shown in Figure 70, but the branching of the veins is more profuse.
- Fig. 73. The opposite hemisphere of the egg depicted in the preceding figure, showing a symmetrical branching of the vitelline artery.
- Fig. 74. In this figure there is a fairly long vitelline vein having side branches. The embryo is in a stage slightly older than the one represented in Figure 35, plate III.
- Fig. 75. Opposite hemisphere of the egg portrayed in the preceding figure. The pattern of the arterial branching is nearly symmetrical, though quite unlike that shown in Figure 71.

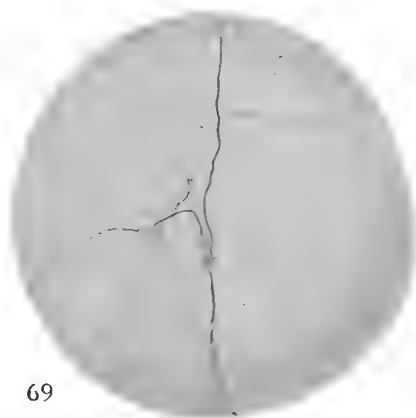
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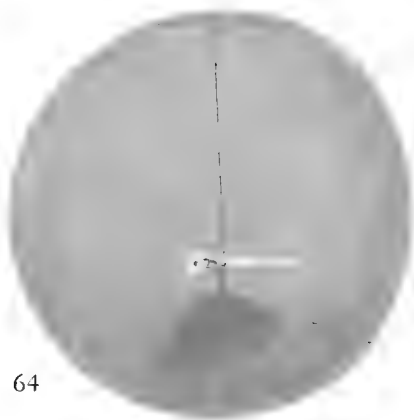
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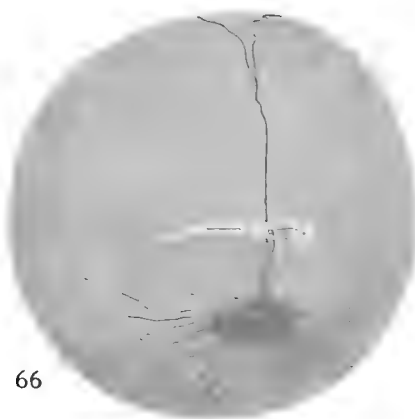
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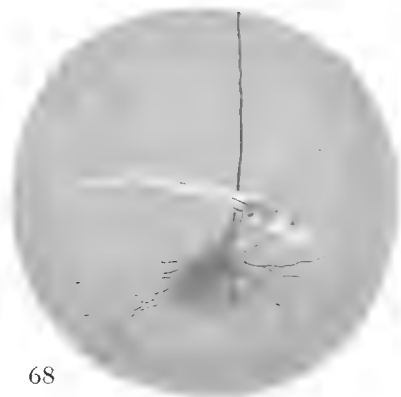
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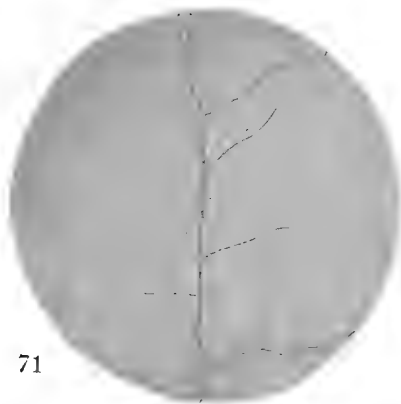
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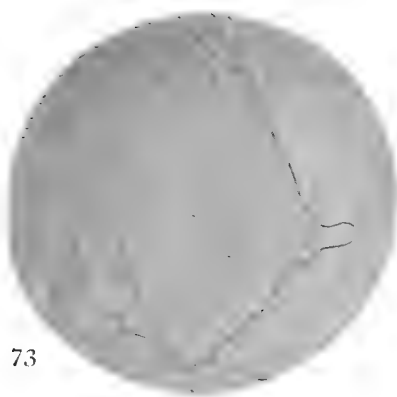
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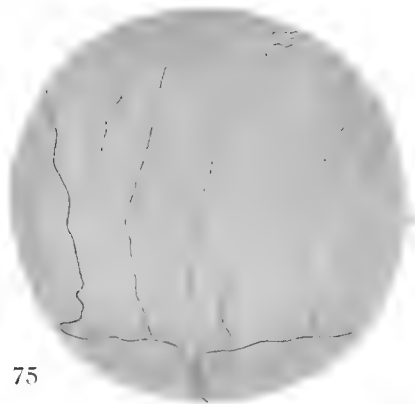
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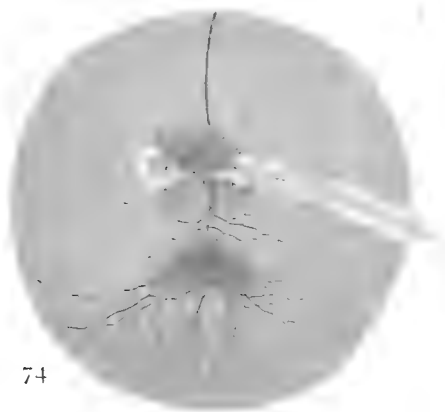
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PLATE VII
EMBRYOLOGY OF *HETERODONTUS JAPONICUS*

PLATE VII
EGG CAPSULES, EGGS, EMBRYOS
AND NEWLY HATCHED YOUNG OF *HETERODONTUS JAPONICUS*

- Fig. 76. An egg capsule in side view. The arrow points towards the respiratory groove, just beginning to deepen and lengthen into the respiratory cleft. The length of the capsule varies from 120 to 180 mm. (four to seven inches).
- Fig. 77. Oral, upper or proximal view (showing the larger end) of the capsule.
- Fig. 78. An egg case opened to show the yolk sac and embryo within.
- Fig. 79. Upper hemisphere of an egg at the time of deposition. This figure shows the tiny germinal disc (reddish, surrounded by a white zone) and some problematical furrows distributed over the greater part of the surface of the yolk.
Reproduced about four-fifths natural size.
- Fig. 80. A late blastula drawn as an opaque object seen through a layer of albumen. The blastoderm is limited to the reddish area, which is surrounded by a pale yellowish zone, the periblast.
- Fig. 81. Advanced embryo with yolk stalk and yolk sac. The figure is slightly larger than natural size. The external gill-filaments have reached their maximal development.
- Fig. 82. Later embryo with yolk stalk and yolk sac. In some respects (e.g., the position of the nasal apertures) this embryo is either distorted, abnormal or incorrectly drawn.
- Fig. 83. Dorsal view of a newly hatched *Heterodontus japonicus*. Its length is about 180 mm. (seven inches).
- Fig. 84. Lateral view of a young female *Heterodontus japonicus*, about two weeks after hatching. Its length is about 205 mm. (eight inches).

All the figures of this plate are in natural colors.



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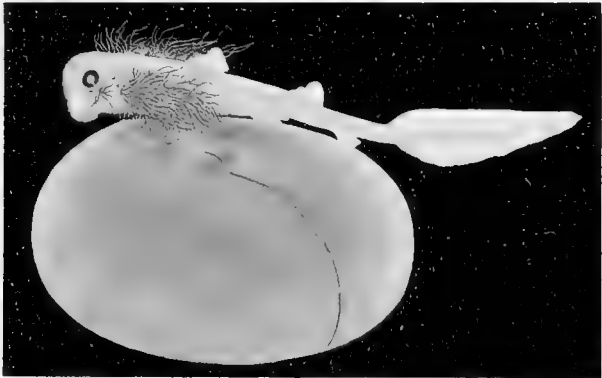
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EUGENE WILLIS GUDGER

ARTICLE VI

THE ANATOMY OF THE FRILLED SHARK
CHLAMYDOSELACHUS ANGUINEUS Garman

By BERTRAM G. SMITH

Professor of Anatomy
New York University College of Medicine
New York City



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THE BREEDING HABITS, REPRODUCTIVE ORGANS
AND EXTERNAL EMBRYONIC DEVELOPMENT
OF CHLAMYDOSELACHUS, BASED ON NOTES
AND DRAWINGS BY BASHFORD DEAN

By E. W. GUDGER
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BASED ON NOTES AND DRAWINGS
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