VIII.—*On the Calcification of the Vertebral Centra in Sharks and Rays.*

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CONTENTS.

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INTRODUCTION.

In this paper are recorded the results of an investigation undertaken at the instance of Dr. A. SMITH WOODWARD for the purpose of ascertaining to what extent the pattern presented by the calcified laminæ of the centrum is of value as an aid to the classification of Elasmobranch fishes, and to the identification of vertebræ found in the fossil state. The subject was dealt with exhaustively in 1879–1885 by HASSE, who, in his monograph 'Das natürliche System der Elasmobranchier,' claimed that the differences in the disposition of the calcified laminæ in the various genera and families of Elasmobranchs occur with such constancy and regularity that they may be accepted with confidence as an important factor in taxonomy. During the years, however, that have passed since the publication of this monograph the thesis has come to be looked upon with suspicion, and vertebrate morphologists at the present time do not, as a whole, regard HASSE's definitions of the Cyclospondyli, Tectospondyli, and Asterospondyli as consistently applicable to the genera and species included by him within those groups.

The material studied in the course of the investigation was to a large extent accumulated several years ago (see p. 313), and it was only the superior attraction of *Cephalodiscus* as a subject of research that prevented the work from being brought to an earlier conclusion. The examination of this accumulated material, and of that more recently acquired, was carried on in the HUXLEY Research Laboratory of the Imperial College of Science during the winter of 1917 and from May, 1919, to May, 1920, and I hereby acknowledge my great indebtedness to Prof. E. W. MACBRIDE and the administrative officers of the College for the facilities offered there for the prosecution of the work. I have further to thank Prof. MACBRIDE for frequent advice and for valuable suggestions made during the progress of the research. My thanks are also due, and are hereby tendered, to Dr. A. SMITH WOODWARD and Mr. C. TATE REGAN, of the British Museum (Natural History), for many helpful hints and suggestions. Acknowledgments and thanks for material kindly furnished by various donors are recorded on p. 313.

MATERIAL STUDIED.

Owing to an indefiniteness that prevails in the scope of the term Elasmobranchii, it may here be explained that the fishes studied in the course of the present investigation comprise the ordinary sharks, dog-fishes, monk-fish, skates, and rays, but do not include the Holocephali, nor the Cladodont, Acanthodian, and Pleuracanth fishes.

The fishes are those embraced within REGAN's Order 4, Euselachii (**29**, p. 722), and the classification of the fishes here adopted is the one propounded by him in the paper quoted. The convenient expression "Batoid fishes" (=Batoidei of GÜNTHER), as used in the following pages, is equivalent to the Hypotremata of REGAN ; it includes the Torpedinidæ, Rhinobatidæ, Raidiiæ, and Dasybatidæ, and excludes *Squatina* and

Pristiophorus, which two genera were associated by HASSE with the ray-like fishes. This is the sense in which REGAN uses the term Batoidei on p. 737, although in his classificatory table (p. 724) the Division Batoidei excludes the electric rays.

In the course of the investigations 151 fishes were examined, belonging to 44 genera and 68 species. Accepting REGAN'S classification of 1906 (**29**), they may be tabulated as follows:—

Division.	Family.	Specimens examined.	Genera.	Species.
Notidanoidei . .	Chlamydoselachidæ	0	0	0
	Hexanchidæ	2	1	1
Galeoidei	Odontaspididæ	3	2	3
	Lamnidæ	7	4	4
	Orectolobidæ	9	4	4
	Scyliorhinidæ	19	2	5
	Carchariidæ.	21	6	10
Squaloidei	Cochliodontidæ	0	0	0
	Hybodontidæ	0	0	0
	Cestraciontidæ	8	1	1
	Squalidæ—			
	Squalinæ	22	7	9
	Pristiophorinæ	4	2	4
	Squatinidæ	4	1	1
Narcobatoidei . . .	Torpedinidæ	12	3	4
Batoidei	Rhinobatidæ—			
	Pristinæ	5	1	3
	Rhinobatinæ.	7	3	5
	Raiidæ	17	1	5
	Dasybatidæ	11	6	9
Total	. . . .	151	44	68

The material used in the present investigation was brought together in a variety of ways. Much of it was accumulated during the years 1903–1907, when I was interested in the study of fishes owing to the fact that I was then assisting Sir E. RAY LANKESTER in rearranging the exhibited series of fishes in the British Museum (Natural History). Most of the sketches and notes made during those years were based upon specimens contained in the Museum collection. Further material was subsequently obtained by purchase in the markets of Grimsby, Folkestone, and other coast towns, and in Billingsgate Fish Market, London, and some was purchased from the Marine Biological Laboratory, at Plymouth. My acknowledgments are due to Mr. J. HORNELL for material from India during 1907–1910, to Prof. W. N. F. WOODLAND for specimens from Naples, and to Prof. W. A. HASWELL for some from Sydney.

More recently I have had the advantage of examining selected pieces of vertebral column excised from young and embryo fishes, owing to the kindness of Mr. C. TATE REGAN, Assistant Keeper in the Department of Zoology at the British Museum (Natural History). To him I offer my cordial thanks. For the use of other material in recent months I have to thank Prof. E. W. MacBride, of the Imperial College of Science, Prof. J. P. Hill, of University College, London, Prof. E. S. Goodrich, of Oxford, and Mr. R. H. Burne, of the Museum of the Royal College of Surgeons.

None of the material examined was specially fixed with a view to studying the histological detail. Pieces of the vertebral column of fresh specimens of some of the adult fishes might have been so fixed, but it was not considered necessary. Where there really was need for a study of fine histological structure, in the late embryos and young fish, special measures of fixation and preservation were not possible; these specimens proved to be so difficult to obtain that one was grateful to secure and examine whatever was available, regardless of its histological condition. The only exceptions were *Scyliorhinus canicula* and *Squalus acanthias*, which happen to be among the least interesting of the forms under consideration.

For checking the observations on the incipient activity of the perichondrium, referred to on p. 330, it is eminently desirable that specially prepared material should be examined when the opportunity offers. *Galeus canis*, of a length of 230 mm., would be suitable; also *Stegostoma tigrinum*, 210 mm. long, *Chiloscyllium plagiosum*, 120 mm. long, *Rhinobatus granulatus*, 233 mm. long and 82 mm. broad, *Trygonorhina fasciata*, 265 mm. long and 108 mm. broad, and post-cloacal vertebræ of a *Myliobatis*, measuring about 90 mm. in breadth.

The use of the generic and specific names as adopted by Regan (**29**) in conformity with accepted rules of priority in nomenclature necessitates the discarding of many names that have long been familiar to anatomists and embryologists. Lest such workers may not, in the alphabetical list of the genera and species of the fishes studied, recognise at once the fishes under the names that are in use at the British Museum (Natural History), I have given in brackets the more familiar names, or at all events the names which to me are more familiar, thus: *Scyliorhinus stellaris* [= *Scyllium catulus*]; *Somniosus microcephalus* [= *Læmargus borealis*].

Alphabetical List of Genera and Species of Fishes Examined.

Alopias vulpes.

Carcharias laticauda.
,, sp.
,, *walbeehmi.*
Carcharodon rondeletii.
Centrophorus calceus.
,, *squamosus.*
Cestracion philippi.
Cetorhinus maximus [= *Selache maxima*].
Chiloscyllium plagiosum.

Dasybatis [= *Trygon*] sp.
,, *thalassia.*

Echinorhinus spinosus.

Galeus canis.
Ginglymostoma cirratum.

Hemigaleus balfouri.
Heptanchus cinereus.
Hypnos subnigrum.

Lamnâ cornubica.

Mustelus vulgaris.
Myliobatis aquila.
,, *nieuhofi.*
,, sp.

Narcine brasiliensis.

Odontaspis americanus.
Orectolobus [= *Crossorhinus*] *barbatus.*
Oxynotus centrina [= *Centrina salviani*].

Pliotrema warreni.
Pristiophorus cirratus.
,, *japonicus.*
,, *nudipinnis.*
Pristis cuspidatus.
,, *pectinatus.*
,, *perrotteti.*
Pristiurus melanostomus.
Pteroplatea micrura.

Raia batis.
,, *clavata.*
,, *maculata.*
,, *marginata.*
,, *punctata.*
Rhinobatus granulatus.
,, *halavi.*
,, *undulatus.*
Rhinoptera javanica.
Rhynchobatus djeddensis.

Scapanorhynchus lewisi.
,, (*Mitsukurina*) *owstoni.*
Scyliorhinus analis [= *Scyllium anale*].
,, *canicula* [= *Scyllium canicula*].
,, *marmoratus* [= *Scyllium marmoratum*].
,, *stellaris* [= *Scyllium catulus*].
Scymnorhinus [= *Scymnus*] *lichia.*
Somniosus microcephalus [= *Læmargus borealis*].
,, *rostratus* [= *Læmargus rostratus*].
Sphyrna [= *Zygæna*] *blochii.*
,, ,, sp.
,, ,, *tudes.*
Spinax niger.
Squalus acanthias [= *Acanthias vulgaris*].
Squatina squatina [= *Rhina squatina*].
Stegostoma tigrinum.

Torpedo hebetans.
,, *narce* [= *ocellata*].
Triacis semifasciatus.
Trygonorhina fasciata.

Urogymnus asperrimus.
Urolophus (*Trygonoptera*) *testacea.*

Further particulars respecting the material studied are given at the beginning of each of the various sections of the chapter headed "Detailed Observations" (pp. 347–394).

METHODS OF INVESTIGATION.

The subject lends itself to investigation by four different methods :—a comparison of the structural features of the vertebræ in the adults of a large range of closely allied genera and a contrast between the vertebræ of genera that are more remotely related, a comparison of the vertebræ of the caudal, cloacal and trunk regions of the same individual fishes, a comparative study of the vertebral characters in embryos, young, and adults of certain selected species, and a tracing of the lines of evolution by a study of the vertebræ of extinct forms in conjunction with those of their nearest modern allies. The methods might be termed respectively the morphological, individual, developmental and palæontological methods. HASSE adopted mainly the first and last of the four, without, however, entirely neglecting the developmental method.

The last, or palæontological, has not been followed in the present inquiry, although the method is not without its value. It is of considerable interest, for instance, to note that in Jurassic forms of *Squatina* there are fewer calcified layers than in the existing species, and that in fossil Notidanids the centra are calcified to a greater extent than are those of *Heptanchus cinereus.* But the method exposes one to the risk of the fallacious process of arguing in a circle, for the taxonomic position of an extinct shark is to some extent decided by the features of the calcified parts of its vertebræ. *Palæospinax*, for instance, now regarded as allied to the Cestracionts, was when first discovered regarded as a Squalid because of the simplicity of its vertebræ. The identification of the fossil vertebræ, again, may possibly be at fault. It is extremely probable that the vertebra figured by HASSE as that of a *Crossorhinus* from the Gault of Cambridge (**15**, D, Plate 25, fig. 10) is not an Orectolobid at all; it is much more likely to be a Lamnid (*cf.* Plate 27, figs. 26 and 37).

The first method of inquiry mentioned above, that of the comparative study of the vertebræ of adult fishes, was largely followed by HASSE, and the bulkiness of his monograph is rather to be explained by this fact. In justice to him it may be pointed out that until the vertebræ of any particular fish are examined one cannot decide whether they are of interest or not; when the examination has been made, the author is performing a service to science by placing his observations on record, for even if the structures prove to have no very direct bearing on the elucidation of the problem, he spares his successors the labour of an independent examination of the vertebræ. Negative results, though disappointing from the author's point of view, are not without their value as an addition to knowledge.

The morphological method of inquiry, however, as it was pursued by HASSE, fails to carry conviction owing to his neglect of the second or individual method; he contrasted the trunk vertebræ, for instance, of one species with the caudal vertebræ of another without, in some cases, at all events, first ascertaining the extent of the differences that exist between the vertebræ of the trunk and caudal regions in these individual fishes. The method, also, is not of great service if adopted independently of the developmental method, and it is only in the Batoid fishes, where the membrana elastica externa disappears early, and the developmental method largely fails in consequence, that one is glad to fall back upon it as the main line of research.

Concerning the developmental method, but little need be said here, in view of the considerable detail in which the subject is treated in the chapter headed "Development of the Centra" (pp. 323–334). Suffice it to say that the study resolves itself largely into a delimiting of the sheath-cartilage by a diligent search for the remnants of the membrana elastica externa at as late a stage of development as possible. In some cases these remnants persist in the vertebræ of adult fishes (*Cestracion*, *Mustelus*), in others they disappear very early (*Torpedo*). The study of the mode of origin of certain constituent parts of the centrum by the generative activity of tracts of perichondrial connective tissue also comes within the scope of this part of the inquiry.

In some cases, it is to be noted, the results obtained by this method are rather at variance with those obtained by the "individual" method of research. In *Cetorhinus*, for instance, the hinder caudal vertebræ of the adult fish give a better indication of

Lamnid structure than do the trunk and anterior caudal vertebræ of the young fish (fig. 14, C, p. 361; fig. 13, A, p. 360; and **15**, D, Plate 32, fig. 3). Similarly, the hindermost caudal vertebræ of *Pristis* and *Rhynchobatus* exhibit a calcified four-rayed star, which is more Batoid in character than the gradually thickening "investing layer" around the double cone which is seen in trunk and anterior caudal vertebræ of late embryos (fig. 31, E, p. 385; fig. 28, A, p. 382).

The "individual" method has much to recommend it, and it is quite possible to conceive that the study of the whole vertebral column in a few appropriately chosen fishes may be more productive of results of morphological value than the study of isolated vertebræ taken one from each of a much greater number of species, particularly if these single vertebræ are not taken from corresponding regions of the body, so as to render the comparison just. One of the results of the present inquiry has been to show that in a range of closely allied forms the vertebræ of the caudal region differ less than do those of the trunk, and they are more elementary in structure; witness, for instance, the series of *Raia,* shown in fig. 33, p. 388. A series of *Torpedo*, *Rhinobatus*, or *Cestracion* would illustrate the same fact.

It is not a new thesis that the structure of the caudal vertebræ of sharks and rays is simpler than that of the vertebræ of the trunk region. KÖLLIKER, in 1864, wrote: "Die vorderen Wirbel von *Ginglymostoma* sind verwickelter gebaut als die des Schwanzes" (**20**, p. 53). And GADOW and ABBOTT write: "the tail of embryonic Elasmobranchs generally shows more primitive conditions or stages than the trunk," and "as the tail generally shows earlier stages than the trunk, a forward gradation can be made out in each embryo in passing from the tail towards the head" (**6**, pp. 181 and 178).

The general proposition, however, that the caudal vertebræ are in a less advanced stage of evolution than the trunk vertebræ is not universally accepted, for GRAHAM KERR, in his text-book of Embryology (London, 1919, p. 294) writes, that in sketching out the development of the vertebral column: "The assumption will be again made use of, as it was in dealing with the mesoderm segments, that the trunk region has in all probability departed least from the primitive conditions . . . Some writers will be found to assume that the caudal region is more nearly primitive." KERR'S conclusion is based upon the fact that the Vertebrate is essentially a cœlomate animal, and that the existence of a tail-region devoid of splanchnocœl is secondary. But while, as regards the general evolution of the vertebrate animal, few will deny that the anus was primarily posterior, and that the caudal appendage appeared as a later growth, the axial skeleton of the primitive vertebrate—as Prof. MACBRIDE has been good enough to point out—probably remained notochordal for a considerable time after the evolution of the tail, and any differences in the structure of the vertebræ of the caudal and trunk regions arose comparatively recently in a vertebral column that was, despite this late origin of the tail in comparison with the trunk, for a long time more or less uniform throughout.

At one period of the inquiry it seemed as though the hindermost caudal vertebræ, owing to their simplicity, might afford a clue to the significance of any substantial differences that might be observable in the trunk vertebræ of two species of fish. The hind caudal vertebræ of such two fishes being the same, one would only have to study the transition forwards in the two cases to arrive at the complete explanation of the differences. But, while some interesting results have been arrived at, the complete solution of the problem by the employment of this method fails, in consequence of the pattern in the hinder caudal vertebra becoming, in many cases, not simpler, but irregular and unreliable.

Among the few cases in which the irregularity is but little marked, one might mention *Raia*. As one passes backward in the caudal region, the longitudinal lamellæ, horizontal and vertical, become smaller and smaller and finally disappear, leaving only a double cone, long in proportion to its width, but not otherwise remarkable. Still further back, the double cone becomes a granular tube with its anterior and posterior ends enlarged.

Another interesting case is that of *Pristis*, previously alluded to. Almost all the vertebræ have a bulky, compact secondary calcification, of circular outline, but in the hindermost caudal vertebræ (fig. 31, E, p. 385) the circle gives place to horizontal and vertical rays, similar to those in less aberrant Batoids (*Raia*, fig. 32, E, F, p. 387; *Rhinobatus*, fig. 30, D, p. 383).

Yet another case worthy of mention is that of *Somniosus microcephalus* [= *Læmargus borealis*]. This shark is generally regarded as having no calcification in its vertebral column. But in the terminal vertebræ of the tail there are some five or six calcified, granular tubes with dilated ends, closely resembling the elongated double cones of *Raia* (*supra*), except in being larger. Applying the argument set out above, one concludes that the majority of the vertebræ of this shark, in having no calcification, are *more degenerate* than these few caudal vertebræ; and the conclusion is strengthened by the fact that in another species of the genus, *Somniosus rostratus*, the vertebræ are as typically Squaline as those of *Scymnorhinus*, there being well calcified double cones throughout the vertebral column.

This case naturally leads on to that of *Heptanchus*, in which the vertebræ of the middle part of the caudal fin have double cones and radiating secondary lamellæ, but as one passes forwards these gradually dwindle. The fact that the structure of the caudal vertebræ is more complex and more perfect than that of the trunk vertebræ does not tell against the argument; the conclusion to be drawn is that the trunk vertebræ are more advanced, along a line of degeneration, than the caudal (see p. 349). Pursuing the argument further, one would say that the vertebral column of *Hexanchus* is still more degenerate, for not only the trunk vertebræ, but the caudal vertebræ as well have no calcified structures.

It is argued elsewhere (pp. 328 and 362) that the comparative simplicity of the centra of *Scyliorhinus canicula* and *Scyliorhinus stellaris* is due to a reduction of intermedialia that are so well marked in *Scyliorhinus marmoratus*, and it is not beyond the bounds of possibility that the vertebral structure of the Squalinæ is of the same origin. The hindermost caudal vertebræ of *Scyliorhinus canicula*, *Scyliorhinus stellaris*, *Squalus acanthias*, and *Scymnorhinus lichia* were therefore carefully studied, in order to ascertain if in them the intermedialia are better developed than in the more anterior parts of the vertebral column ; but the search proved abortive. Similarly, the hindermost vertebræ of *Squatina* show no departure from the type of structure characteristic of the genus ; the rings diminish in number as one passes backward, but the pattern in the hindermost centra is still that of concentric rings.

Technique.

Small vertebræ, those of embryos, young fish and small adults, were decalcified and cut into serial sections by the ordinary paraffin-embedding method. The best results were obtained by decalcifying with a 3 per cent. solution of nitric acid in 90 per cent. alcohol, used for a period of about three weeks, more or less, according to the degree of calcification of the vertebræ.

The most suitable thickness for the sections is 0·008 mm. Since a piece of vertebral column consisting of three or four vertebræ yields a very long ribbon, those sections alone were mounted which pass through the middle of the length of the centrum ; the ribbon was searched, with the aid of a lens, for those sections in which the ring of the double cone is of minimum size.

For distinguishing calcified (now decalcified) parts from those composed of uncalcified cartilage the stain found to give the best results was EHRLICH'S hæmatoxylin fluid, saturated with Orange G, and diluted with twice its bulk of distilled water. In slides left in this solution for half an hour the calcified parts are stained deeply and the cartilaginous parts feebly.

For distinguishing the remains of the membrana elastica externa, upon which so much depends in an inquiry of this kind, the best results were secured by staining the sections for 10 minutes in a 0·5 per cent. solution of Congo Red in 90 per cent. alcohol, a method which is more expeditious than the former, since it is not necessary to pass the slide through the graded alcohols down to water, and then back again after staining.

As a general routine practice both of these methods were employed, portions of the same ribbon being stained, some with the former and some with the latter fluid. Bismarck Brown, a stain recommended by HASSE, was found to be less satisfactory than Congo Red. Eosin, Saffranin, Magenta, and Carmine stains were also tried, but discarded as being less efficient than those mentioned above.

For detecting the remains of the membrana elastica externa in difficult cases the best results are obtained by using a fairly high-power objective (4 mm.), and nearly closing the substage diaphragm. It is not always easy to distinguish between a small remnant of the membrana elastica externa and a flattened cartilage-cell, but as a rule the latter differs from the former in being surrounded by a clear space, owing to the shrinkage of the cell within the lacunar space in the matrix which it previously filled. There is no occasion to be discouraged by the fact that in some particular section the remnants of the membrane cannot be recognised; it not uncommonly happens, in *Scyliorhinus canicula*, for instance, that such remains are to be seen in one vertebra and not in that which immediately follows.

Large vertebræ, those more than 10 mm. in diameter, were cut with a very fine saw (dentist's ribbon-saw, with 25 teeth to the centimetre), and the thin slice was then ground under water upon a carborundum stone, and finished upon a razor-hone or water-of-Ayr stone. When thin enough to be transparent, the section was stained and mounted exactly like a section cut by the paraffin method. Sections of large dried vertebræ can be ground on glass-paper.

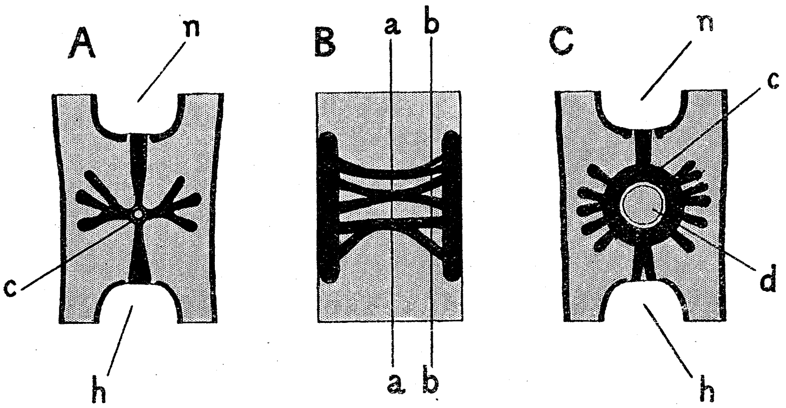

FIG. 1.—*Raia batis*, post-cloacal vertebra, × 2. Figures illustrating how the pattern of a transverse section taken near the end of a centrum differs from one taken through the middle of its length. The upper part of the neural arch and the lower part of the hæmal arch are not shown. A, transverse section of the vertebra cut midway between the anterior and posterior ends of the centrum, in the direction of the line *aa*. B, side view of the vertebra, after removal of the superficial calcification. The details of the arch-cartilages are not shown. C, transverse section of the vertebra taken near the end of the centrum, in the direction of the line *bb*; *c*, primary double-cone calcification; *d*, remains of the notochord; *h*, hæmal canal; *n*, neural canal.

In the case of large vertebræ a great deal can be learnt as to the disposition and relations of the various calcified parts by removing the uncalcified cartilage by means of a 5 per cent. solution of hot caustic soda. It is advisable not to carry the treatment too far, or the resulting structure will crumble; the aim is, not to dissolve the cartilage, but to soften it sufficiently to allow of its easy removal by steel instruments or a stiff brush.

For adequate comparison of one vertebra with another the most suitable sections are, as already pointed out, those cut through the part where the double cone is smallest; sections cut otherwise than through the middle of the length of the centrum are difficult to interpret, and except for the determining of special points of structure, are rather to be avoided. KÖLLIKER gives a figure of a *Galeus* vertebra cut towards the end of the centum (**19**, Plate 2, fig. 12, 3), and DANIEL gives two of *Cestracion* ('Journ. Morph.,' 26, 1915, Plate 6, figs. 19 and 22).

Transverse sections through the same vertebra present different patterns according to their relative distances from the middle, and in the case of vertebræ with radiating lamellæ the rays are usually found to be more numerous in the sections taken near the end of the centrum than in that through the middle of its length (*cf.* C and A in fig. 1, p. 320). This difference is due, as will be seen by reference to a side view of the centrum (fig. B; see also HASSE, **15**, D, Plate 30, fig. 29, *Carcharodon*), to a splitting of the lamellæ into two near the anterior and posterior ends. The increased size of the cone-section also makes a profound difference in the appearance.

TERMS EMPLOYED.

As a general rule in the following pages the vertebræ under consideration are described as selected from some particular region of the body, *e.g.*, branchial, mid-trunk, pre-cloacal, cloacal, post-cloacal, anterior caudal, mid-caudal, posterior caudal; but in many cases the region is indicated with more precision by reference to the fins, thus: "in front of the second dorsal fin," "above the anal fin," "halfway along the caudal fin."

The sheath-cartilage is that part of the definitive centrum which is developed from the chondrified sheath of the notochord (see p. 323). Its inner and outer limits respectively are marked by the membrana elastica interna and the membrana elastica externa. The sheath-cartilage differentiates early into three zones, the inner, middle and outer.

The term "double cone" has so long been in common use that its definition might be deemed scarcely necessary; but although in strict terminology the double cone is the calcified middle zone of the sheath-cartilage, the structure which on isolation from the vertebra is called the double cone possesses an "investing layer" (Belegschicht) formed from the calcification of the innermost part of the outer-zone cartilage. The dried double cones of *Scymnorhinus* and *Oxynotus*, as drawn in fig. 2, possess this

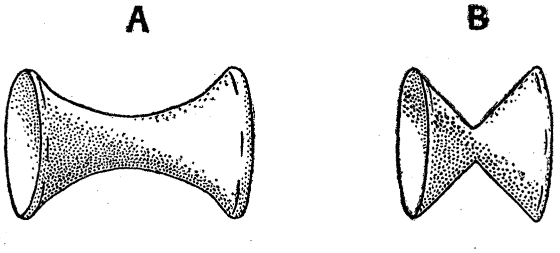

FIG. 2.—Double-cone calcification after removal of all cartilaginous parts. A, *Scymnorhinus lichia*, × 1·5. B, *Oxynotus centrina*, × 2.

investing layer; if the latter were scraped away, the double cone would be too fragile to handle. In descriptions of transverse sections, nevertheless, the term double cone is used in the strict sense—the part marked *c* in the text-figures is the calcified middle-zone cartilage, and the investing layer is separately marked *i l*.

The term arcualia is adopted from the paper by GADOW and ABBOTT (**6**) as meaning the arch-cartilages, *i.e.*, the cartilages of the neural and hæmal arches. The term intermedialia is a new one and refers to components of the centrum that are situated between the arcualia, either between the two basidorsal cartilages, or between the two basiventrals, or between a basidorsal and a basiventral cartilage. The intermedialia, as explained on p. 328, are products of the activity of the superficial perichondrium, and they make their appearance long after the arcualia are definitive structures.

Radiating lamellæ are longitudinally disposed calcified plates that lie in radial planes between the double cone and the surface of the centrum; seeing that in the majority of instances these are observed in transverse sections of the vertebræ, in which they appear as the rays of a star, the term "ray" is frequently employed instead of radiating lamella. Similarly, in the case of *Squatina*, the calcified lamellæ are really in the form of coaxial tubes, but by a pardonable licence in expression these are frequently spoken of as concentric circles or rings, since that is the appearance that they present in transverse sections.

The word diagonal is used as the equivalent of the German "schräg" in referring to those lamellæ which occupy an oblique position between horizontal and vertical lamellæ or wedges; it is used particularly in the case of the Carchariidæ.

Unless otherwise stated, the word "section" in this paper is used in the sense of a transverse section taken midway between the anterior and posterior ends of the centrum, *i.e.*, through the narrowest part of the double cone.

HISTORICAL REVIEW.

The monumental work on the calcification of the centra of the sharks and rays is the monograph by C. HASSE, entitled 'Das Natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule.' In most libraries the monograph is bound as a single volume of 392 pages and 48 plates, but the work was issued as a series of five parts, extending over a period of six years (1879–1885). HASSE had interested himself in the subject before 1879, and the results of his earlier work on fossil vertebræ (**14**) are included in the monograph.

Of the papers published prior to 1879 the most important are those of KÖLLIKER (**19** and **20**) and GOETTE (**13**); an abstract of the still earlier writings by RATHKE, JOH. MÜLLER, and LEYDIG is given by HASSE in his paper of 1892 (**16**).

Since 1885, the date of the issue of the final part of HASSE's monograph, but little in the way of original investigation has been done upon the vertebræ of sharks and rays, most writers who have had occasion to allude to the subject being content to make excerpts from HASSE's book. This, it may be observed in passing, is a good illustration of the paralysing effect that a bulky work has upon research in any particular branch of science. The publication of an imposing monograph creates an impression that the particular subject with which it deals is now disposed of; and unless it opens up controversial matters, the monograph chills the enthusiasm and checks the aspirations of those who might otherwise be tempted to write upon the subject. Small papers, on the other hand, have rather the effect of encouraging the production of others upon the same theme, investigators interested in the subject being induced thereby to add their quota to the sum total of existing knowledge.

Among the papers that have been produced since the issue of the final part of the monograph is one by HASSE himself (**16**), papers by KLAATSCH (**18**), a paper by GADOW and ABBOTT (**6**), and a contribution by SCHAUINSLAND, largely a compilation, but partly original, in HERTWIG'S handbook (**30**). While these deal with the development of the vertebræ of sharks and rays rather than with the value that may be attached to the pattern of the calcified areas as a means of classification, it is to be observed that development has an important bearing upon the question, and cannot be disregarded in any discussion of HASSE'S conclusions.

REGAN'S paper of 1906 (**29**), dealing with the classification of the Elasmobranchii, contains numerous references to the calcification of the centra in adult fishes. The criticism of HASSE'S scheme is in the main adverse, but the paper offers little that is constructive in its place; by recommending the retention of HASSE'S terms with new, restricted meanings (**29**, p. 737), the author makes a difficult subject rather more confused than before.

DEVELOPMENT OF THE CENTRA.

The notochord in the course of its development becomes invested by an envelope or sheath, produced by the chordal cells. This envelope in the case of Elasmobranch fishes undergoes differentiation into an external cuticular sheath, the membrana elastica externa, and an inner fibrous sheath, which is considerably thicker.*

On the differentiation of the sclerotomes from the myotomes the skeletogenous tissue applies itself to the sides of the notochordal sheath, but the right and left tracts of skeletogenous tissue are not continuous above and below the notochord. At a later period the arch-cartilages begin to differentiate in the upper and lower parts of the tracts, while the middle part of each tract becomes reduced, and thinned out into a layer of about two cells in thickness.

Skeletogenous cells now invade the fibrous sheath of the notochord through fenestrations in the membrana elastica externa,† particularly from the arch-bases, and

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* Good *résumés* of the opinions of various investigators regarding the structure and origin of the layers of the notochordal sheath are given by HASSE (**16**) and SCHAUINSLAND (**30**, p. 395).

† The origin of the cartilage of the notochordal sheath by immigration of skeletogenous cells was first observed by HASSE (**16**, 1892, figs. 10 and 11), although his interpretation of the process is different from that now generally accepted. The invasion through the membrana elastica externa was explained by KLAATSCH (**18**, II, 1893, p. 162, and Plate 7, fig. 8), and the observation has been confirmed by GADOW

produce a thickness of cartilage between the outer membrane (membrana elastica externa) and a structureless layer which is now recognisable as the membrana elastica interna.* The chondrified sheath is not for long continuous and uniform along the notochord, but soon differentiates into short tubes, or rings, of hyaline cartilage set end to end.† The rings thicken and lengthen, and develop into the vertebral bodies or centra, the chordal sheath in the intervening regions passing into a fibro-cartilaginous and ultimately into a fibrous condition, and persisting as the "intervertebral ligaments." In the middle of the length of each centrum thus delimited the notochord becomes constricted by the rapidly growing cartilage, but intervertebrally the notochord continues to increase in width, as well as in length. In this way there arises a series of typically biconcave or amphicœlous centra.

In *Hexanchus griseus*, *Heptanchus cinereus*, *Echinorhinus spinosus* and *Somniosus microcephalus* the intervertebral portions of the axial column are vastly longer than the vertebral portions, which latter are, except in the caudal regions of the second and fourth of these species, indicated merely by large fibrous septa set transversely to the notochord. In these four species the notochord is to a large extent liquefied in the adult. *Chlamydoselachus anguineus* in some respects resembles *Heptanchus*, but the differentiation of the notochordal sheath into structures that can be recognised as vertebral centra is, on the whole, less advanced (see p. 348).

The neural and hæmal arches of the vertebræ are developed independently of the centra,‡ except in so far as the immigration of cartilage-forming cells into the sheath proceeds to an exaggerated extent, if not entirely, at the arch-bases. The arch-

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and ABBOTT (**6**, 1895, p. 164), and SCHAUINSLAND (**30**, 1906, pp. 397 and 407). Whether the cells penetrate between the two layers of the sheath, or pass through the outer membrane and become lodged in the substance of the thickening inner layer, is a matter foreign to the scope of the present investigation; for a discussion of this point the reader is referred to SCHAUINSLAND'S summary (**30**, p. 397).

* This early invasion of the notochordal sheath renders the development of the centra of the Elasmobranch fishes profoundly different from that in other Vertebrates, and the fishes are consequently unsuited for drawing general deductions as to the morphology of the parts of vertebræ. An invasion of cartilage-forming cells into the chordal sheath occurs in Holocephali and Dipnoi, but not to the same extent as in the Elasmobranchii, and true centra are not formed. In other Vertebrates, the chordal sheath remains intact, except in so far as it is absorbed and replaced; and the "bodies" of the vertebræ are formed external to it. In Amphibia and Amniota the "bodies" appear to be formed almost entirely from the tissue of the neural and hæmal arches (GADOW, 'Phil. Trans.,' B, vol. 187, pp. 1–57, 1897), but in fishes with bony vertebræ (bony Ganoids and Teleosteans) there are independent contributions in the form of "bone-belts," deposits of bone in neutral fibrous tissue, adjacent to, but not derived from, the arch-bases (see p. 335 of the present paper).

† CARTIER, **2**, Plate 4, figs. 1–2; RABL **28**, Plate 6, figs. 9–11; KLAATSCH, **18**, II, p. 172, text-figs. 3–4; SCHAUINSLAND, **30**, p. 402, text-fig. 206.

‡ GADOW and ABBOTT (**6**, p. 218) write: "The formation of chordacentra being independent of the arcualia explains how and why the nnmber of 'centra' does not necessarily agree either with that of the arcualia or with that of the trunk-segments, *e.g.*, *Hexanchus*, and tail of most other Elasmobranchs." See also **6**, p. 194.

cartilages are morphologically external to the notochordal sheath, but owing to the fenestration, or to the total disappearance of the membrana elastica externa at the regions of apposition of the dorsal and ventral arches, the arch-cartilage becomes continuous with the cartilage of the sheath, and the limit between the two is no longer discernible.

The neural arches are complete, the principal components being basidorsal cartilages and interdorsal cartilages (intercalary plates); sometimes there are present small unpaired supradorsals and suprainterdorsals as well. Supradorsals are wanting in the Lamnidæ, and in some parts of the vertebral column the right and left basidorsals and the right and left interdorsals are confluent above the spinal cord. In the Orectolobidæ there is a tendency for the supradorsal cartilages to be small and disposed in a double series, right and left, not necessarily in pairs, however, for in some parts of the vertebral column the right and left elements alternate.

The hæmal arches are complete in the tail, and are constituted by the basiventral cartilages; interventral cartilages (intercalaries) are sometimes present, but with less regularity than the dorsal intercalaries. In the vertebræ that are situated anteriorly to the cloaca the hæmal arch is incomplete, and the basiventral cartilages are commonly termed "transverse processes"; they are continued at their outer extremities into the ribs.*

According to GADOW and ABBOTT (**6**, p. 171, No. 2; p. 173, No. 7; p. 189; and text-figure on p. 188) the intercalary cartilages arise by a severance of processes from sclerotomes whose major portions become the basalia. A dorsal pyramid of skeletogenous cells spreads downward at the side of the notochord, and its lower end becomes an interventral cartilage, while the more bulky upper portion develops into the basidorsal cartilage; similarly the interdorsal and basiventral cartilages are the upper and lower products of a tract of formative cells which, originating as a ventrolateral cluster, has spread upward at the side of the notochord.

The basidorsal cartilages are, with certain notable exceptions (Hexanchidæ, and the region of transition from the monospondylous trunk vertebræ to the diplospondylous caudal vertebræ in most Elasmobranchs), commonly set over the middle of the length of the centrum, whereas the interdorsals are set over the intervertebral ligaments. The ventral root of each spinal nerve issues behind the basidorsal or passes through it, and the dorsal root passes out either behind or through the interdorsal or intercalary plate.

The centra and the arches of the vertebræ are fairly rigid; movements of the vertebral column as a whole are permitted solely by the flexibility of the intervertebral ligaments and the tracts of white fibrous tissue that occur between the several plates of cartilage that constitute the neural and hæmal arches. There are

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* The vexed question whether the ribs in Elasmobranch fishes correspond with the ribs of the higher Vertebrates is discussed by SCHAUINSLAND, **30**, pp. 423–427.

no zygapophysial articulations of the neural arches such as occur in Teleostean fishes and bony Ganoids.

The cartilaginous layer of the notochordal sheath is early differentiated into three zones, the inner, middle and other zones of GOETTE, HASSE and others. The middle zone, composed of fibro-cartilage, soon undergoes calcification (except in the few species mentioned in a previous paragraph), and becomes the well-known "double cone" or dice-box of the vertebræ of sharks and rays (fig. 2, p. 321). The inner zone is usually composed of hyaline cartilage, and in the adult occurs principally in the region where the double-cone is narrowest (fig. 7, B, p. 352); it here constricts the notochord, sometimes to obliteration. Towards the anterior and posterior ends of the centrum it passes over into fibro-cartilage and fibrous tissue.

In some cases, where the obliteration of the notochord in the middle of the centrum is complete, or nearly complete, in the adult, a fibrous septum of considerable extent separates the persistent remnants of notochordal substance, as in *Hexanchus* and *Echinorhinus* (fig. 23, p. 373). In other cases the notochord is divided by a calcareous partition of small extent (*Scyliorhinus stellaris*, fig. 16, B, p. 363; *Cestracion philippi* and *Raia marginata*, fig. 4, p. 340). In less aberrant cases (Squalinæ) there is a persistent thin layer of cartilage (inner zone) immediately internal to the double-cone calcification, at the part where it is narrowest, and within this is a tract of persistent notochordal jelly, which shows a tendency to be tougher than usual, and to develop fibres longitudinally disposed. Between these extreme cases are various intermediate forms, in which the inner zone is present in the form of an incomplete septum, either of hyaline cartilage or of fibrous tissue, showing a concentric arrangement of the fibres; and running antero-posteriorly through the middle of this is a fine thread of notochordal substance, not jelly-like, but of a fibrous character, commonly termed the "funicle." In the hindermost caudal vertebræ of many forms (*Scyliorhinus stellaris*, *Raia marginata*), there is a long thin plug of hyaline cartilage, sometimes, but not always, perforated by a funicle.

The outer zone, composed at first of hyaline cartilage, grows in thickness, and in some forms (*Cestracion*, *Squatina*, *Pristiurus*, *Squalus*) constitutes a large proportion of the substance of the centrum. It may in the adult undergo partial calcification, by the development of an investing layer ("Belegschicht" of HASSE), immediately external to the double cone, and in intimate contact with it (fig. 22, p. 372). Or there may be developed in the outer-zone cartilage a number of calcareous lamellæ, longitudinally disposed. These lamellæ may radiate outward from the primary double cone, so that a transverse section of the centrum exhibits a star-like pattern (*Cestracion*, fig. 4, A, p. 340); or the calcified lamellæ may be in the form of concentric, longitudinally set tubes, so that a transverse section exhibits a series of concentric rings (*Squatina*, fig. 25, p. 377). Such calcified lamellæ as these are usually termed secondary lamellæ, since they are developed later than the primary double cone.

The calcification, both primary and secondary, consists of a deposition of lime-salts in the intercellular matrix of the cartilage ; it is not a redeposition of calcified tissue following upon an absorption of the original calcified matrix, such as one understands to be the distinguishing feature of true bone. The cells of the original cartilage persist as the cells of the ultimate calcified tissue, and are not immigrant cells like the cells of typical cartilage-bone.*

The double cone maintains its independence from the secondary calcification, and its outer limit can usually be distinguished by structural features even in cases where there is a uniform investing deposit of outer-zone calcification immediately external to it (fig. 22, p. 372).

The external surface of the centrum is rarely (*e.g.*, *Echinorhinus*) free from calcification. In the Squalinæ the superficial calcification usually takes the form of a thin layer, that differs from the layers found on the inner and outer surfaces of the arches in being a continuous crust, instead of a mosaic of tesseræ; but in cases where there is evidence of the neural arch having united with the hæmal arch external to the notochordal sheath, the layer of tesseræ may be continuous from arch to arch (*e.g.*, *Narcine*, HASSE, **15**, C, Plate 23, fig. 20). In other cases there may be calcified deposits so thick as to present the form of four calcified wedges, one dorsal, one ventral, and two lateral, with their bases external and their edges directed towards the vertebral axis (*e.g.*, *Mustelus*, fig. 8, A, p. 354).

These wedges are produced, as was first shown by KÖLLIKER in 1860 (**19**), by the activity of the superficial perichondrium that occurs external to the membrana elastica externa of the sheath in four tracts, namely, between the paired components of the neural arch, between those of the hæmal arch, and between the basidorsal and basiventral on each side of the notochordal sheath.

While these "Knochenzapfen" (KÖLLIKER, **19**), "Verbindungsstücke der Bögen" (GOETTE, **13**), or "Periostale Keile" (HASSE, **15**) are a characteristic feature of the Carcharidæ, they are also present, though in a less completely calcified form, in Lamnidæ, Odontaspididæ, Orectolobidæ, and Scyliorhinidæ. Whether fully or incompletely calcified, the structures in question are centrifugal in their mode of growth, the inner parts being the oldest and the outermost layers the most recently added.

The wedges of perichondrial origin do not find a place in the series of terms introduced by GADOW and ABBOTT in 1895 for "the cartilaginous pieces which form one Skleromere or Vertebra" (**6**, p. 170). The arch-cartilages (arcualia) of their terminology include the basalia (basidorsalia and basiventralia) and interbasalia (interdorsalia and interventralia), together with supradorsalia, etc. It is only the

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* Among those authors who consider that "bone" occurs in sharks and rays may be mentioned STARK ('Trans. Roy. Soc., Edinburgh,' xv, 1844, pp. 646 and 654), and GOETTE (**13**); opposed to this view are KÖLLIKER (**20**), GEGENBAUR (**9**), HASSE (**15**, B) and others. A discussion of the question took place in the pages of 'Nature' in 1898 (vol. 58, pp. 26 and 200).

basalia that are of interest in the present connection, for the others do not form part of the definitive centrum.

The four tracts of skeletogenous tissue and their ultimate products, situated above, below, and at the sides of the chordal sheath, between the four basalia as seen in a transverse section, are tracts of more importance than is conveyed by the term "Verbindungsstücke" of GOETTE and SCHAUINSLAND; they are in many cases determinate constituents of the centrum, not mere joining-up pieces. For the designation of these I propose the term *intermedialia*, a term to be employed not only for the sharply differentiated calcified wedges of the Carchariidæ, and their equivalents in the Lamnidæ, etc., but also to be applied in other cases, such as *Squalus* (fig. 22, B, *p*, p. 372), in which the precise limits of the tracts of perichondrial origin are in the adult difficult to distinguish, although a study of the embryonic vertebræ shows that they are in reality developed separately from the basalia. That the intermedial tracts in the British species of *Scyliorhinus* (*Scyliorhinus canicula* and *Scyliorhinus stellaris*) are reduced "periostale Keile," such as occur in the Carchariidæ and Lamnidæ, is clear from a comparison of the British with the more southern species, *Scyliorhinus marmoratus* and *Scyliorhinus maculatus* (*cf.* fig. 16, p. 363, and fig. 15; and see HASSE, **15**, D, Plate 34, figs. 19, 21, and Plate 33, figs. 2, 5).

It is to be noted that REGAN, one of the more recent critics of HASSE'S "system," while not regarding the great calcified wedges of the Carchariidæ as originating from arch-tissue, does not discuss the question of their perichondrial origin. He writes (**29**, p. 736, footnote): "This extension of the neural and hæmal plates round the chordal sheath appears to be often inversely proportional to the secondary calcification of the centra. In nearly all the Galeoidei the calcifications extend throughout the centrum, and the neural and hæmal arches do not extend downwards or upwards, but in *Pristiurus*, where the secondary calcification has disappeared, they meet round the centra." It may here be observed that the series *Scyliorhinus marmoratus*, *Scyliorhinus canicula*, *Pristiurus melanostomus* (fig. 15, B, p. 363; fig. 16, A and C) points to the bulk of the cartilage of the centrum in the last of the three being of sheath origin, and not due to union of the basidorsal and basiventral cartilages, for in the second of the three species the vestiges of the great wedges are recognisable, and they develop late and at a much greater distance from the axis of the centrum than in the first. The clue is given by the section of *Scyliorhinus marmoratus* through the caudal fin (fig. 15, C); if the lateral calcifications were as little developed as the upper vertical, and flatter, the appearance would be much the same as in a caudal centrum of *Scyliorhinus canicula*, but there is no question in *Scyliorhinus marmoratus* of a union of basidorsal and basiventral cartilages *internal* to the lateral calcification, for the membrana elastica externa is contiguous with the intermediale. It is true that in *Scyliorhinus canicula* and *Pristiurus melanostomus* there is, between the membrana elastica externa and the calcified intermediale, a narrow tract of cartilage whose origin it is difficult to trace, but it is evident it is not to this, but to the great mass of cartilage marked *o z* in fig. 16, A and C, that REGAN is referring when he speaks of the "meeting of the neural and hæmal arches."

It is possible that had KÖLLIKER seen the vertebræ of *Scyliorhinus marmoratus* or *maculatus*, he might not have written "Knorpelrinde der Bogen vollständig" for *Scyllium* (probably *canicula* or *stellare*), seeing that for the Carchariidæ and Lamnidæ he wrote "Knorpelige Bogen nicht verschmolzen." In both of his papers (**19**, pp. 210 and 231, and **20**, p. 74) he regards the four thick calcifications of *Scyliorhinus* as "Periostablagerungen" *on the outside* of the fused arches.

Returning to the characteristics of the more typical intermedialia, it is to be noted that whereas the basalia, so soon as they can be distinguished in ontogeny, are composed of embryonic hyaline cartilage, and after the embryonic stages grow by a kind of uniform expansion, the intermedialia develop late, and are produced by skeletogenous connective tissue, which generates cartilage on its inner face, and continues to generate layer after layer. The corresponding "intermedialia" of *Amia* and *Esox* calcify directly, without any intermediate condition of cartilage; they arise that is to say, as membrane-bone (SCHAUINSLAND, **30**, p. 444, fig. 243; p. 469, fig. 263). In *Ceratodus* and *Acipenser* the intermedial tracts remain in the form of indifferent, non-skeletogenous tissue (**30**, p. 483, fig. 274A; p. 432, fig. 228).

It is unfortunately necessary to be arbitrary in instituting a terminology for morphological entities that are differentiated out of the same original substance. The practice has been adopted by previous writers in their distinction of the arch-bases of Elasmobranch fishes from the sheath-cartilage, although the latter is produced from the former by a process of invasion of cartilage-forming cells through gaps in the membrana elastica externa. What is meant in their writings is that the term arch-bases (basalia) shall designate tracts of arch-cartilage external to the membrana elastica externa, while sheath-cartilage is cartilage situated internal to the membrane, or, where in adults the membrane is no longer distinguishable, cartilage which has been derived from that cartilaginous layer which in the embryo was situated internal to the membrana elastica externa.

Similarly with regard to the intermedialia; a distinction between basale and intermediale visible in the embryo may be lost in the adult, but it is convenient, nevertheless, to retain the distinction in adults, if only to dispel the idea of an arch-fusion external to the notochordal sheath. Arch-fusion certainly does occur in some Elasmobranchs, but it is in other cases possible to conceive that the basidorsal cartilage may in the adult be separated from the basiventral cartilage by an intermedial uncalcified cartilage which has originated *in situ*, and has not arisen by a creeping or spreading of the basal cartilages towards one another.

Although for the sake of brevity of expression it is stated above that the growth of the intermediale is due to the perichondrium, it is only in the initial stage that the perichondrial connective tissue itself is active. After that stage there exists, immediately internal to the part that persists as the perichondrium, a zone of small-celled, growing cartilage which is responsible for the expansion of the intermediale in a radial direction. This genetic zone or layer is three, four or five cells in thickness; the innermost cells gradually enlarge, and become more separated by cartilage-matrix, and thus add to the bulk of existing cartilage; the outer cells continue to multiply. Parts of the intermedialia that are destined to be calcified may undergo calcification almost immediately, so that in such cases the calcified lamina or wedge reaches nearly to the surface, being separated from the perichondrium proper by the thin growing zone only.

The precise mode of origin of the genetic layer of the intermediale from the perichondrium is in a few cases liable to misinterpretation, in consequence of the fact that the differentiation begins at the edges of the basalia, and does not commence simultaneously over the whole area. In a young *Galeus canis*, 230 mm. in length, the section of a vertebra between the pelvic and second dorsal fins (fig. 7, C, p. 352) shows the upper, lower and lateral parts of the membrana elastica externa still external, and covered by perichondrial connective tissue only. The basidorsal and basiventral cartilages thin out almost to nothing over the upper and lower parts of the lateral tracts, and it might be argued that in the later stages of development these cartilages spread towards one another, between the membrana elastica externa and the connective tissue, and ultimately meet. But careful examination of the slightly different stages that can be seen in the vertebræ of the fish in question—the development, for instance, reaches slightly different stages in consecutive vertebræ, and even on the two sides of the same vertebra—shows that it is the "cellular activity" that spreads, not the "cellular tissue." The cells that will, by subsequent division, produce the substance of the intermediale are differentiated from the connective tissue at the edges of the basalia, and are not immigrants from the basalia themselves. At the same time that these external changes are taking place the activity of the cartilage immediately internal to the membrana elastica externa is increased, and the inner and outer tissues soon become continuous.

In the vertebræ of a late embryo of *Mustelus*, of a length of 286 mm. (fig. 7, A, p. 352), exhibiting a slightly later phase of development than is shown in fig. C by the *Galeus* embryo, the sharp delimitation of the edges of the developing intermedialia may be to some extent taken as evidence of their independence from the basal cartilages. A later stage still would be that illustrated by the section of a young *Carcharias* vertebra (fig. D), and this leads on to the condition seen in the adult *Mustelus* (fig. 8, A, p. 354).

The developmental history of the intermediale of the Carchariidæ as set out above would no doubt have been more convincing if the successive stages had been worked out in embryos, young and adults of one and the same species, but such a series was not accessible. The facts as here elucidated are, however, in my opinion, such as will stand the test should a large series of *Mustelus*, *Galeus*, *Carcharias* or *Sphyrna* at some later time become available for investigation.

Another series illustrating the development of the intermedial components of the centrum is that shown in fig. 17, p. 365. *Chiloscyllium* was obtained in three stages of development, namely, an embryo of a length of 120 mm., one of a length of 240 mm., and an adult. The series of sections of caudal vertebræ is interesting as showing how each intermediale begins its development as a double structure (p' and p'' in fig. E). Each component enlarges, particularly in a radial direction (p' and p'' in fig. F), and the sheath-cartilage grows out horizontally between them and pushes the membrana elastica externa before it. After the stage of development figured at F, the perichondrium between p' and p'' becomes active and produces a large mass of cartilage, which does not undergo calcification (fig. D, p). The sheath-cartilage now presents the appearance of bulging out into the intermediale between the two radiating calcified lamellæ. In the trunk vertebræ the bulging is much more pronounced, and the middle part of the perichondrium of the upper median intermediale, as also that of the lower median, fails to become active as a cartilage-producer, and the membrana elastica externa reaches the surface of the centrum (figs. A and B).

Whereas in *Chiloscyllium* the sheath-cartilage continues to grow for a time in the vertical and lateral directions, and projects into the intermedialia, it is to be noted that in the Carchariidæ the sheath-cartilage grows out in the diagonal planes, and projects into the arch-bases. A study of the Carchariid material available goes to show that the diagonal calcified lamellæ are centrifugally-growing calcifications of the sheath-cartilage (fig. 8, p. 354), and although in late stages of development the most peripheral parts of the membrana elastica externa, at the extremities of the outgrowths of sheath-cartilage, are no longer to be recognised, it may be concluded, on the whole, that the diagonal calcified lamellæ belong to the sheath-cartilage. Nevertheless, one is not justified in making too arbitrary statements about the matter, for when calcification begins in cartilage of a certain origin, and has proceeded for a time in that cartilage, it may be continued later into cartilage of a different origin. Instances of this kind were observed in the vertebræ of one specimen of *Mustelus.* As shown in the upper right-hand diagonal tract of fig. 8, A, p. 354, the calcification of the diagonal ray, begun in the sheath-cartilage, has continued into the basidorsal cartilage. It is as though, in the course of the radial growth of the calcified lamella, the membrana elastica externa became caught or entangled in the calcifying tract, instead of being pushed outward beyond the area that is undergoing calcification. This aspect of the case seems to be justified from the convex appearance of the membrana elastica externa on the two sides of the calcified lamina; the sheath-cartilage here tends to bulge outward, but the middle part of the membrana elastica externa is fixed in the calcified lamina, and cannot follow the rest of the membrane as it is pushed radially outward.

In the Batoid fishes, the interpretation of the calcified structures in the centrum is rendered difficult, in consequence of some of the radiating lamellæ (*e.g.*, the vertical and horizontal rays in the caudal vertebræ) being of double origin. The inner parts, nearest the double cone, are derived from the outer zone of the sheath-cartilage, whereas the more peripheral parts are of perichondrial origin (*Rhinobatus* and *Dasybatis*, fig. 30, p. 383; and fig. 35, p. 391). Owing to the early disappearance of the membrana elastica externa in these Batoids, it is not possible to indicate any sharp delimitation between the two component parts. Although the lateral rays reach the surface in the middle portion of the tail, they do not reach the surface in the trunk region, where the basiventral cartilages are set so high up the side of the notochordal sheath as to unite with the basidorsals (fig. 32, A, p. 387); neither do they reach the surface in the vertebræ from the hinder part of the tail (fig. 30, D and E, p. 383). In some cases the internal and external components are distinct, and are separated by a tract of cartilage (fig. 32, D and E, p. 387); but, owing to the absence of any relics of the membrana elastica externa, it is not possible to say with any degree of conviction that the inner portion is developed solely in the sheath-cartilage, and that the outer part is solely of perichondrial origin.

By a happy chance, embryos of *Rhinobatus*, *Trygonorhina*, and *Myliobatis* were obtained at that stage of vertebral development when the secondary calcification, uniformly enlarging within the outer-zone cartilage, has just arrived so near the surface of the centrum that the perichondrium is coming into play as an active layer. In the caudal vertebræ there are four such perichondrial tracts (fig. 28, C, p. 382), and the conclusion to be drawn is that subsequent growth of the vertical and horizontal lamellæ is due to the perichondrial reinforcements, whereas the diagonal rays (fig. 30, B, p. 383; and fig. 28, C, *d*, p. 382), being independent of perichondrial activity, rather resemble the diagonal rays of the Carchariidæ. They are probably confined to the outer-zone cartilage, but there is no evidence to prove that they do not grow into the basal parts of the arch-cartilages. The membrana elastica externa being no longer recognisable, the limits of the sheath-cartilage cannot be definitely determined.

In *Torpedo* the external component seems to be wanting (fig. 26, B, p. 379), since the calcified rays do not quite reach the surface. There can be no doubt that the basal parts of the radiating lamellæ are of sheath-origin, for the upper and lower parts of the membrana elastica externa are still recognisable at a time when the secondary calcification around the double cone has already taken on a radiating appearance (fig. 27, p. 380). But the fact that the calcified rays of the adult do not actually reach the surface cannot be taken as proof that their outermost parts are not of perichondrial origin, for several instances are known in which there is delay in the process of calcification of perichondrially produced cartilage. While the cartilage that occurs between the outer edge of the calcified ray and the surface of the centrum in the adult *Torpedo* is a small-celled growing cartilage, there is not the same evidence as there is in the horizontal and vertical rays of caudal vertebræ of *Rhinobatus* and *Trygonorhina* that this tract is of perichondrial origin. In *Narcine*, another genus of the Torpedinidæ, the evidence of sections from a young specimen, 220 mm. long and 105 mm. broad, is in favour of the perichondrial origin of the outer parts of some of the rays, there being well-marked fibres in the cartilage, extending from the superficial connective tissue for a certain distance inward into the calcified rays.

In *Pristis* and *Rhynchobatus* there is a well-marked growing zone of small-celled, delicate cartilage, situated immediately external to the dense and uniform secondary calcification characteristic of these fishes (fig. 31, B, *g*, p. 385). In an embryo of *Pristis pectinatus*, of a total length of 265 mm., and in an embryo of *Rhynchobatus djeddensis*, of a length of 102 mm. (fig. 28, A, p. 382), the remains of the membrana elastica externa are still visible, and these are situated external to the growing zone. When the membrane disappears, as it does soon after the stage of development indicated, the growing zone continues its activity, and adds to the calcified mass already existing. There is thus proof that the growing zone is at first within the sheath-cartilage, and there is nothing to show that the later contributions to the calcified mass are of different origin from the former.

In *Cestracion* and *Squatina* also there may be recognised a growing zone, which in transverse sections presents itself as a ring of small-celled cartilage, situated a short distance external to the calcified rays of the former and the last-formed calcified ring of the latter. In *Cestracion* (fig. 21, A, p. 370), the remains of the membrana elastica externa, visible in the adult, are situated a short distance external to the growing zone, which is thus seen to belong to the chordal sheath. In *Squatina* the membrane is still visible in a ripe embryo (fig. 13, B, p. 360), and its position external to the growing zone at a time when there are four calcified rings present suggests that the later calcified rings of the adult (fig. 25, p. 377), like the early rings of the embryo, are all of sheath-origin.

There seems to be no special region of growth of the cartilage of the centrum in the Squalinæ, nor in such members of the Scyliorhinidæ as *Scyliorhinus stellaris* and *Pristiurus melanostomus.* The evidence in these species points to a uniform expansion of the cartilage. In the Carchariidæ, the positions taken up by the remnants of the membrana elastica externa go to show, as is pointed out above, that there is an out-pushing of the cartilage along the diagonal lines, in marked contrast with the failure of the sheath-cartilage to extend along the vertical and horizontal radii, where growth is provided for by the superficial perichondrium (fig. 8, p. 354), but, in some other Galeoidei, the out-pushing of the sheath-cartilage is, at all events for a time, towards the perichondrial tracts, and not along the diagonal lines (fig. 17, B, p. 365).

The arch-cartilages as a rule grow in thickness by a general expansion, as is evident from the even spacing of the cartilage cells in such of the middle parts as are uncalcified, and from the fact that the calcified tesseræ of the arches, both internal and external, develop in a nearly superficial position, and retain this relative position throughout life. Even in those cases in which the edge of the layer of tesseræ is no longer superficial (*e.g.*, *Galeus;* hindermost caudal vertebræ of *Alopias*, fig. 10, p. 357), the result has been brought about by an overgrowth of the outer parts of the wedges of perichondrial origin, and not by superficial additions to the arch-bases themselves.

CHORDA-CENTRA AND ARCO-CENTRA.

Although GADOW and ABBOTT (6) distinguish the centra of Elasmobranch fishes as chorda-centra, developed from the cartilage of the invaded notochordal sheath, whereas those of Amphibia and Amniota are arco-centra, developed from the component parts of the neural and hæmal arches, it is to be noted that it is only in some Elasmobranchs (*e.g.*, *Cestracion*, *Squatina*, *Pristiurus*) that the substance of the "body" or centrum is to any great extent derived from sheath-cartilage. In a large proportion of cases there are substantial contributions from the arches (*e.g.*, diagonal tracts of cartilage in Lamnidæ, etc., lateral parts of the centra of trunk vertebræ of Batoid fishes), and from intermedial tracts of superficial perichondrium between the arch-bases (*e.g.*, vertical and horizontal wedges of Carchariidæ and Lamnidæ).

As an addition to the literature of the "Neugliederung" of the vertebral column, the paper by GADOW and ABBOTT is of considerable value, since these authors show that the phenomenon is not a secondary one, due to the tracts of skeletogenous tissue that arise from the protovertebræ splitting and recombining to form the new segments, but is primary, and arises from the building up of the vertebræ by the association of skeletogenous cells formed from the posterior part of one body-segment with those from the anterior part of the next (6, pp. 187–189); but, where one may be disposed to differ from the authors, is in their disregard of the generative capacity of the middle portions of the dorso-ventrally extended pyramids of the sclerotomes.

Their views are summarised in the following paragraph (6, p. 189): "Each ventral pyramid"—*i.e.*, ventral portion of the sclerotome—"extends with its apex above the chorda, and founds there (separated from the ventral mass by the subsequent rapid growth of the chorda and its sheath) a cluster of cells, which remains henceforth behind the basal mass of the dorsal pyramid; this latter, through its downgrowing apex, founds a colony of cells, but below the chorda and in front of the basal ventral mass. Thus are produced the basalia and interbasalia. Each colony of cells retains its potentiality of developing into a separate independent piece of cartilage."

The cell-clusters that become the basidorsal and interdorsal cartilages are stated to undergo separation from those that develop into the interventral and basiventral cartilages by the rapid growth of the chorda and its sheath. This appears to be in accordance with the facts, for transverse sections through embryos of the appropriate stage of development show, at the sides of the notochord, a thin layer of not more than two or three cells; but, when the authors proceed to affirm that the dorsal and ventral parts are "connected only by the indifferent connective tissue of the membrana reuniens, but not by cartilage-forming cells," a protest may be lodged, for, while at this particular epoch of development the connective tissue is "indifferent," it really does in many cases possess the capacity for forming cartilage. The capacity is not evinced until the arch-cartilages are well differentiated.

It is unfortunate that GADOW and ABBOTT confined their studies to early stages of development, before the intermedial tracts become active as skeleton-producers, and that they limited their observations, on Elasmobranch fishes, to *Acanthias vulgaris*, *Centrophorus granulosus*, and *Scyllium catulus*,* for these are not well suited for a study of the products of the intermedial tracts. Had they included in their series some fairly late embryos of *Lamna*, *Alopias*, *Carcharias*, *Sphyrna*, or *Scyliorhinus marmoratus*, their decisions might have been different.

The centra of the Teleostean fishes and the bony Ganoids are, according to GADOW and ABBOTT, arco-centra, the bulk of the substance of the definitive centrum in these fishes being developed from the neural and hæmal arches; but if, as is claimed in the present paper, the great wedges of the Carchariid sharks are "intermedialia," *i.e.*, distinct entities developed from skeletogenous connective tissue occurring in four tracts between the edges of the arch-bases (p. 328), the same mode of origin must be accorded to the bulk of the bony substance of the centrum in the Teleosteans and Ganoids. GADOW and ABBOTT, indeed, admit that in the Trout very little arch-cartilage grows round the chordal sheath, and that "most of the material necessary for the formation of the centrum is indifferent membrana reuniens, and ossifies directly" (**6**, p. 216; apparently after SCHEEL, 'Morph. Jahrb.,' xx, 1, 1893).

Again, as regards the origin of the "bone-belts" of *Amia*, GADOW and ABBOTT are not altogether consistent, for, while on p. 207 they state that the spaces in which the bone-belts arise "are filled with indifferent connective tissue and ossify early"—a statement which is fully in accord with the later observations of SCHAUINSLAND (**30**)—yet on p. 208 they say that the centrum is "a compound structure, produced entirely by the arcualia."

On p. 202 they write: "Outside this elastica (externa) follows a thick zone of loose connective tissue which forms a layer of bone on its inner surface, and in this zone of connective tissue cartilage cells, from the basal portions of the arcualia, grow round the chordal sheath preparatory to the formation of the central discs." This spreading of cartilage-cells from the arch-bases is not convincingly shown in their text-figures of the sections studied (p. 204), and is not confirmed by SCHAUINSLAND, who, reviewing the work of SCHMIDT (1892), HAY (1895), and GOETTE (1897), and submitting original observations of his own, regards the bony masses of the centrum as not being preformed in cartilage (**30**, pp. 437–449). It is true that, in

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* These are the names as given by GADOW and ABBOTT; the first and third are in the present paper termed *Squalus acanthias* and *Scyliorhinus stellaris*.

the foremost two or three vertebræ, immediately behind the skull, the hæmal arches are set high, and nearly touch the neural arches (fig. 238, p. 440), and they are partly divided into a rib-carrying transverse process and a more ventrally placed mass of cartilage, which in the vertebræ of the middle part of the trunk is segregated as the cartilaginous core of the aortic support (fig. 239, *h*, p. 440); also, at the extreme posterior end of the tail there is a continuous cartilaginous sheath (p. 439); but, as regards the vertebræ of *Amia* generally, SCHAUINSLAND writes: "Auch darin stimmt *Amia* mit den Stören überein, dass die unteren und oberen Bögen durch einen weiten Zwischenraum getrennt und nicht durch Knorpel, sondern allein durch Bindegewebe miteinander verbunden sind" (p. 439; fig. 235, p. 436; see also fig. 243, p. 444, of a later stage, after ossification has begun).

In addition to "bone-belts," GADOW and ABBOTT recognise "cartilage-belts," which, although interpreted by them as arising from pyramids or clusters of skeletogenous cells growing out from the arcualia, may with equal propriety be regarded as autogenous structures, since, in an explanatory footnote on p. 203, they write: "In our 56-mm. *Amia*, the arcualia consist already of hyaline cartilage, with a definite boundary line against the pyramidal or crescent-shaped cell masses. In reality, both the arcualia and these masses are the offspring of the same matrix, namely, of the dorsal and ventral ends of the sklerotomes. Probably the arcualia turn first into cartilage, while the centrum-forming masses grow out later, and still later turn into cartilage, repeating the course of phylogenesis."

Even in the extinct Amioids, there is nothing to preclude the view that certain component parts of the "bodies" of the vertebræ are developed independently of the arcualia. In *Eurycormus* the hæmal arches are attached to the hypocentra, and in the caudal region the neural arches also are attached to the hypocentra, although in the trunk they merely alternate with the pleurocentra, owing to the fact that the hypocentra do not extend sufficiently upward to meet the neural arches. But there is nothing to suggest that the hypocentra and pleurocentra are developed as *outgrowths* from arch-tissue.

In *Osteorhachis* the neural arches alternate with the pleurocentra, and are separate from them. While it is possible, even probable, that there are a pair of interdorsal elements entering into the composition of each pleurocentrum, these elements do not necessarily constitute more than a small portion of it. The fact that the pleurocentrum is not in two parts, right and left, shows that it is not in a primitive condition. If it is composed of interdorsalia only, one would expect to find it a paired structure; if it consists of two interdorsals and a semicircular structure developed from a half-ring of skeletogenous tissue independently of them, the primitive condition would exhibit the triple origin; if, on the other hand, it consists of the half-ring only, then the argument as to its origin from arch-cartilage falls through. As regards the hypocentrum, although the projections that carry the ribs are almost without a doubt basiventral elements, it does not follow that the hypocentrum is solely a product of the basiventrals. There is always the possibility that both the hypocentra and the pleurocentra are preformed, in part at least, as "bone-belts" from tracts of the general skeletogenous tissue surrounding the notochordal sheath, tracts that are in themselves as independent in origin as the formative tracts destined to grow into the arcualia. The condition found in *Caturus,* in which there is evidence of the paired origin of the hypocentrum, should throw some light on the subject.

On the whole, therefore, the rigid distinction drawn by GADOW and ABBOTT (**6**, p. 190) between chorda-centra and arco-centra in fishes breaks down, for on closer examination it appears that there is not a great difference between *Lamna* and *Alopias,* on the one hand, and *Amia* and *Esox* on the other. In both series the arch-cartilages dip in almost to the middle, in both series the major portion of the remainder of the centrum is formed, not from arch-tissue, nor from chordal sheath, but from superficial skeletogenous tissue between the arch-bases. It is true that in *Lamna* and *Alopias* some part of the centrum is formed out of the chondrified notochordal sheath, whereas in *Amia* and *Esox* the chordal sheath can be disregarded as a component of the adult centrum, but the differences between the two kinds of centra are by no means so pronounced as GADOW and ABBOTT have claimed.

GENERAL ACCOUNT, A CRITICISM OF HASSE'S "SYSTEM."

Introduction.

HASSE'S views regarding the calcification of the centra of the vertebræ of Elasmobranch fishes are expressed in brief in the sentence: "Es können sich entweder um den einfachen, centralen Doppelkegel (Cyclospondylie) in der Aussenzone concentrische Verkalkungsschichten ablagern (Tectospondylie), oder es entwickeln sich in der Umgebung desselben, in der Aussenzone Kalkstrahlen (Asterospondylie)" (**15**, A, p. 29). Except in this solitary instance, HASSE does not apply the three terms to vertebræ, but to groups of fishes, such as "Plagiostomi tectospondyli" (see first footnote on p. 339 of the present paper), but it has become the common practice for writers to speak of cyclospondylous, tectospondylous, and asterospondylous vertebræ.

The three diagrammatic figures that HASSE gives to illustrate cyclospondyly, tectospondyly, and asterospondyly appear repeatedly in text-books and similar works,* and they are here reproduced once more, for purposes of criticism (fig. 3, p. 338).

Opinions differ as to the value of HASSE'S distinctions, but the general impression seems to be gaining ground that, although the differences in the patterns of the

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* *E.g.*, BRIDGE, T. W., 'Cambridge Natural History,' vol. 7, London, 1904, p. 198, fig. 113; SEDGWICK, A., 'Text-Book of Zoology,' vol. 2, London, 1905, p. 125, fig. 69; GOODRICH, E. S., E. Ray Lankester's 'Treatise on Zoology,' Part IX, fasc. 1, London, 1909, p. 137, fig. 95; KERR, J. G., 'Encyclopædia Britannica,' ed. xi, vol. 24, 1911, Article "Selachians," p. 594; ZITTEL, K., 'Grundzüge der Paläontologie,' Abth. ii, "Vertebrata," Aufl. iii, 1918, p. 45.

calcification of the centra as seen in transverse section are very striking and may prove to be of some taxonomic value, HASSE did not succeed in expressing and co-ordinating the facts in a scheme that adequately meets the requirements of the case. (See Views of Later Authors, p. 344.)

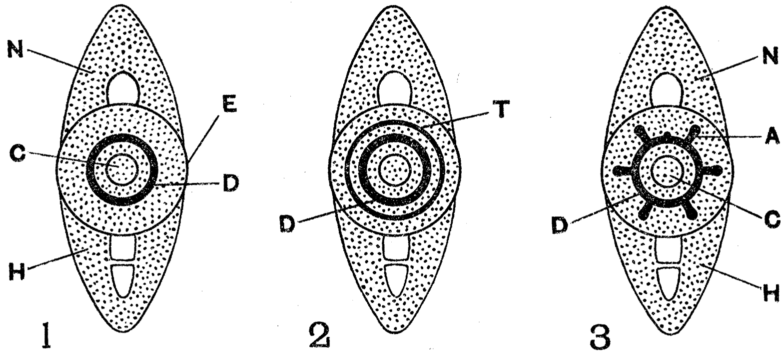

FIG. 3.—HASSE'S diagrams of cyclospondylous (1), tectospondylous (2), and asterospondylous (3) vertebræ, representing transverse sections of anterior caudal vertebræ of the three types, cut midway between the anterior and posterior ends of the centrum.

A, radiating lamellæ characteristic of asterospondylous vertebræ; C, remains of the notochord; D, primary double-cone calcification of the middle-zone cartilage; E, membrana elastica externa, the outer limit of the notochordal sheath; H, hæmal arch; N, neural arch; T, one of the concentric lamellæ characteristic of tectospondylous vertebræ. The cartilage next internal to the ring D is inner-zone cartilage, that between the rings D and E is outer-zone cartilage. Copied from HASSE (**15**, A, pp. 41, 44, 48).

The groups of fishes as delimited by HASSE are, with certain exceptions, natural groups, which is to be accounted for by the fact that his ultimate classification was not based upon the characters of the vertebræ solely; he wisely took also into consideration the characters of the placoid scales and teeth, the basal cartilages of the pectoral fin, and the presence or absence of an anal fin, and in difficult cases, where the features of the centra did not provide the confirmatory evidence that he needed, he was inclined to disregard, or at all events to belittle, the value of such evidence, with the result that his definitions regarding the patterns of the vertebral centra fail to be strictly applicable throughout the groups in question.

Cyclospondyly.

HASSE'S Plagiostomi cyclospondyli comprise the sharks and dog-fishes that are included within the first division of the family Squalidæ as delimited by REGAN (**29**, p. 723), namely, *Centroscyllium*, *Echinorhinus*, *Oxynotus* [*Centrina*], *Etmopterus* [*Spinax*], *Squalus* [*Acanthias*], *Scymnodon*, *Centroscymnus*, *Centrophorus*, *Scymnorhinus* [*Scymnus*], *Somniosus* [*Læmargus*], *Isistius*, and *Euprotomicrus*. According to HASSE'S briefer definitions (*e.g.*, **15**, A, pp. 42–44), and his diagrammatic figure (fig. 3, 1, above of the present paper), the calcification, excluding any superficial layers that may be present, consist of the double cone only, but in his more detailed accounts (*e.g.*, **15**, B, p. 86) he notes the presence, in most of the Cyclospondyli that he examined, of a calcareous deposit in the innermost part of the outer-zone cartilage, closely applied, as a Belegschicht, to the double-cone calcification (see fig. 22, p. 372 of the present paper).

Tectospondyly.

In his introductory remarks upon the Plagiostomi tectospondyli* HASSE states that the uniform characteristic feature of all is a strengthening of the vertebral body by the deposition in the outer-zone cartilage of calcified layers concentrically arranged about the central double cone.† These layers he regards as a further development of the simple deposit (Belegschicht) that occurs directly external to the double cone in most of the Plagiostomi cyclospondyli. The vertebra of *Pristiophorus*, with a single hollow calcified cylinder outside the double cone, is, according to his view, the most primitive found in modern Plagiostomi tectospondyli (**15**, A, p, 46, and **15**, C, p. 97), and his text-fig. 5 (**15**, A, p. 44, reproduced here as fig. 3, 2, p. 338) is based upon it. He regards the genus *Pristiophorus* as a connecting link between the Cyclospondyli, on the one hand, and the bulk of the Tectospondyli on the other.

Squatina conforms well with his definition, there being several concentric calcified layers in the outer zone, separated from one another by uncalcified cartilage (fig. 25, p. 377 ; and HASSE, **15**, A, p. 47, and **15**, C, p. 129).

The first-formed calcification in the outer-zone cartilage is only exceptionally (*Pristiophorus*, *Squatina*) separate from the double cone ;‡ in the true Batoid fishes

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* The Plagiostomi tectospondyli of HASSE comprise the Batoid fishes (Hypotremata of REGAN, **29**), *plus* the Pristiophorinæ and Squatinidæ ; the Plagiostomi cyclospondyli include the Squalidæ of REGAN *minus* the Pristiophorinæ; the Plagiostomi asterospondyli include the Galeoidei of REGAN, together with the first three families of his Squaloidei, viz., the Cochliodontidæ, Hybodontidæ and Cestraciontidæ. In the first part of his monograph, HASSE (**15**, A) proposed the group-names Elasmobranchii polyspondyli and Plagiostomi diplospondyli for the Chimeroid fishes and the Notidanid sharks respectively, but he discarded the names in his later work (**15**, B) and called the groups Die Holocephalen and Die Notidaniden. The names, however, reappear in his Stammtafel II of 1885 (**15**, E).

† "Das gemeinsame Merkmal Aller besteht darin, dass sich concentrisch um den centralen Doppelkegel, also auch ringförmig um die Chorda Verkalkungsschichten ablagern, welche, der Aussenzone angehörig, den Wirbelkörper solide machen" (**15**, C, p. 97). In his preliminary account of the development of the vertebral centrum, before he has yet introduced the terms tectospondyli and asterospondyli, he writes :— "Entweder lagern sich um letzteren" (*i.e.*, the double cone) "concentrische Lagen verkalkten Knorpels (siehe Holzschnitt V), die sich in grösserer oder geringerer Ausdehnung bis an die Peripherie erstrecken können . . . . oder es gehen von dem centralen Doppelkegel Kalkstrahlen aus (siehe Holzschnitt VI)" (**15**, A, p. 25). Comparing the Tectospondyli and Asterospondyli with the Cyclospondyli, he writes :— "Die Plagiostomi tecto- und asterospondyli eine Weiterentwicklung insofern zeigen, als sich bei den ersteren um oder unmittelbar an dem centralen Doppelkegel, in der Mittelzone des Wirkelkörpers Kalkablagerungen in concentrischen Lagen geltend machen, während bei letzteren von dem centralen Doppelkegel in radiärer Richtung gesonderte Kalkstrahlen ausgehen" (**15**, A, p. 40).

‡ In the middle of its length, that is to say; for the layer is confluent with the double cone at its anterior and posterior edges.

(= Hypotremata of REGAN) it is a Belegschicht, a calcified layer closely applied to the outer surface of the double cone (**15**, A, p. 46),* similar to that found in the Plagiostomi cyclospondyli. The later calcification in the Plagiostomi tectospondyli may be in the form of layers so uniform and dense as to produce a solid, compact mass nearly reaching to the surface of the centrum (*Pristis*, *Rhynchobatus*, etc., HASSE, **15**, C, Plate 16, figs. 56 and 52; Plate 19, fig. 3; Plate 20, fig 3; see also fig. 31, p. 385, of the present paper), or it may result in the production of radiating laminæ that present a star-like pattern in a transverse section of the centrum (*Raia*, fig. 4, B).

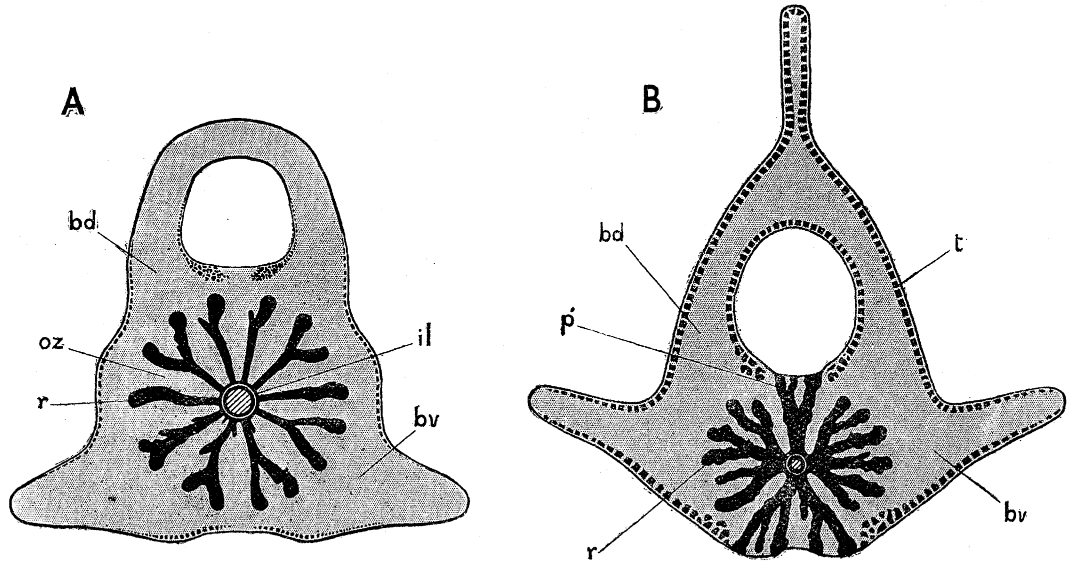

FIG. 4.—A, *Cestracion philippi*, × 2·4; B, *Raia marginata*, × 1·8. Transverse sections of trunk vertebræ cut midway between the anterior and posterior ends of the centrum. In the terms of HASSE (**15**) *Cestracion* exhibits asterospondyly, and *Raia* tectospondyly, but it will be noticed that the "star" is as well marked in the latter as in the former. (For explanation of the lettering, see p. 404.)

How HASSE came to include in his Plagiostomi tectospondyli, which, he states, are characterised by concentric calcified layers in their centra, Batoid fishes with strongly marked radiating laminæ, such as *Narcine brasiliensis* and *Trygonorhina fasciata* (**15**, C, Plate 23, fig. 21; Plate 15, fig. 49), as also *Raia marginata*, *Rhinobatus granulatus*, and *Torpedo narce* (fig. 4, B, above; fig. 30, A, p. 383; fig. 26, p. 379, of the present paper), is at first sight not clear, but it would seem that he derives such star-like forms of centra from the compact, *Pristis*-like condition by a failure in the calcification of certain radially disposed tracts of the outer-zone cartilage, for he explains the eight-rayed star or rosette of *Rhinobatus horkeli* (**15**, C, p. 114; Plate 15, fig. 27) as originating, by a process of incomplete calcification, from a compactly

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* It might at first seem from the wording of the passage at the top of p. 46 that he regarded the Belegschicht as belonging to the middle zone, but a study of the context shows that he really considered it as the inner part of the outer zone.

calcified centrum such as that of *Rhinobatus thouini* (**15**, C, p. 110 ; Plate 14, fig. 14) ; and *Rhinobatus cemikulus* and *Trygonorhina fasciata* (**15**, C, Plate 15, figs. 41 and 49), are but further derivatives along the same lines of modification. On the other hand, it is to be observed that he derives the complex pattern seen in *Narcine brasiliensis* and *Torpedo marmorata* as due to the branching of the four rays, vertical and horizontal, of the simple cross found in *Astrape dipterygia* (**15**, A, p. 48 ; **15**, C, pp. 178, 175, 173 ; Plate 23, figs. 21, 11, 3).

It would seem, further, that HASSE changed his views during the interval that supervened between the publication of his Allgemeiner Theil in 1879 and the appearance of the second Lieferung of his Besonderer Theil in 1882 ; in the former he remarks (**15**, A, p. 47) that in the Trygon family the four oblique rays of the eight-rayed star seen in a transverse section of the centrum are calcifications of the arch-bases, and the vertical and horizontal rays are developed from external perichondrium ; but, in his contribution of 1882, he affixes the mark *a′* to one of the oblique rays of *Urolophus aurantiacus* and to one of the lateral rays of *Tæniura lymna* (**15**, C, Plate 19, figs. 9 and 16), the mark *a′* standing for "Aussenlage der Aussenzone." It is only fair to add that, on p. 146, he expresses himself as somewhat in doubt about the matter, owing to there being no traces of the membrana elastica externa recognisable, and to the fact that he was unable to investigate the matter developmentally ; he notes that the vertical and lateral rays reach the perichondrium, and are reinforced by it, and he remarks that KÖLLIKER was of opinion that they were "periostale Keile," *i.e.*, situated external to the sheath-cartilage.

As regards the concentric character of the deposit in those Plagiostomi tectospondyli that show stellate patterns, it is true that, in his figures of *Trygonorhina fasciata*, *Narcine brasiliensis*, and *Torpedo* sp. (**15**, C, Plate 15, fig. 49 ; Plate 23, figs. 21 and 14), he shows lines of the successive deposits, such that, if these are continued from ray to ray across the intervening tracts of cartilage, they yield a series of concentric circles, but, on the other hand, similar zones of growth are shown in his figures of the radiating laminæ that occur in a number of forms that he includes in the Plagiostomi asterospondyli, *e.g.*, *Cestracion philippi*, *Crossorhinus barbatus*, and *Ginglymostoma rüppeli* (**15**, D, Plate 24, fig. 8 ; Plate 25, fig. 6 ; Plate 26, fig. 21).

Asterospondyly.

HASSE states that the vertebræ of his Plagiostomi asterospondyli* are distinguished by the following characters. The innermost deposit of calcareous matter in the outer zone of the cartilage of the notochordal sheath is closely applied to the surface of the double cone ; from it there project four oblique radiating calcified laminæ directed towards the arch-bases, and there may be other radiating laminæ,

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* The scope of HASSE'S Plagiostomi asterospondyli is given in the first footnote on p. 339.

commonly four in number. These last are horizontal and vertical in position, and are developed from the external perichondrium of the vertebral body.*

The description does not apply with any precision to the vertebræ of *Cestracion*, the first member that he includes in the group, for, in that genus, while the calcified rays are commonly (but not invariably) eight in number, they are not arranged according to the terms of his definition; instead of four of the rays being directed towards the middle of the arch-bases and the other four being disposed in horizontal and vertical positions, as, for instance, in *Mustelus* (fig. 8, A, p. 354), the eight rays are directed towards the *edges* of the four arch-bases (fig. 21, A, p. 370), and all of the rays are situated in the notochordal sheath, none being developed from the external perichondrium.

A similar relation might be supposed to obtain in early stages of development of *Ginglymostoma*, judging from his figure (**15**, D, Plate 26, fig. 19), in which the rays would seem to differ from those of *Cestracion* (**15**, D, Plate 24, fig. 7) solely in that the two ventrally directed rays are not separated from one another; but the figure is fallacious in that the membrana elastica externa is represented as pursuing a more or less circular course, as at *e* in fig. 18, A, p. 366, whereas careful study of embryonic material shows that it follows a sinuous course, as at *e e*. The inner parts of the lamellæ are at an early period continuous with the investing layer, and belong to the outer-zone region, but in the adult the bulk of the substance of the calcified lamellæ is of perichondrial origin, and the pattern of the transverse section comes to resemble that of *Stegostoma* (*cf.* **15**, D, *Ginglymostoma rüppeli*, Plate 26, fig. 21, and *Stegostoma fasciatum*, Plate 25, fig. 3). In *Chiloscyllium plagiosum* the eight rays begin to develop at the edges of the four arch-bases (fig. 17, E, p. 365), but they are *external* to the membrana elastica externa, and thus conform even less with his description of asterospondyly than do the rays of *Cestracion* and young *Ginglymostoma*.

In such forms as *Mustelus, Carcharias,* and *Sphyrna* the four diagonal rays, directed towards the middle parts of the arch-bases, are developed in the outer zone of the sheath-cartilage, and are thus comparable with the rays of *Cestracion*.

It would appear from a paragraph that occurs early in his monograph (**15**, A, p. 29, last paragraph) that HASSE originally intended his term asterospondyly to have reference mainly to the calcified rays that are developed within the outer-zone cartilage, *i.e.*, internal to the membrana elastica externa. It is only at the end of the paragraph that he alludes to the externally developed perichondrial calcifications, so that an inconsistency is introduced when he includes in his Plagiostomi asterospondyli such forms as the Lamidæ, for these, while they have the perichondrially produced wedges well developed, with numerous thin calcified lamellæ (fig. 9, *p′*,

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* "Die Wirbelkörper haben . . . sich erstrecken" (**15**, A, p. 49); "Die ringförmige Verkalkung . . . Schwanzwirbelsäule darbietet" (**15**, D, pp. 183–184). (See also **15**, A, p. 29, last paragraph.)

p. 356), have the four oblique rays, directed towards the middle parts of the arch-cartilages, developed very feebly or not at all.

As showing yet further how unsatisfactory are HASSE'S generalisations, it may be pointed out that in his remarks upon the Group Scyllia (**15**, A, p. 53) he says that the typical vertebræ of the group, exemplified by those of *Scyllium maculatum* and *marmoratum* (fig. 15, p. 363 of the present paper), exhibit eight rays developed in the outer-zone cartilage, namely, four diagonal rays directed towards the arch-bases, and four others, vertical and horizontal, which occur sometimes as single wedges, sometimes (as in *Scyliorhinus maculatus*) in the form of pairs of divaricated rays. His description of the origin of the eight rays, however, applies with equal precision to the vertebræ of *Dasybatis thalassia* and *Rhinobatus granulatus* (fig. 35, A, p. 391, and fig. 30, A, p. 383), in which there are four diagonal rays, connected at their inner ends with the double cone, directed towards the middle parts of the arch-cartilages, and not reaching the surface externally, and four other rays, vertical and horizontal, which are augmented at their outer extremities by perichondrial contributions. Yet the "Scyllia" are among HASSE'S Asterospondyli, whereas the genera *Dasybatis* and *Rhinobatus* are Tectospondyli.

The basis of HASSE'S third diagram, representing asterospondyly, is uncertain. He refers to the figure when describing the vertebræ of *Heptanchus* (**15**, A, p. 36), and it is to be noted that the figure shows six radiating lamellæ (fig. 3, 3, p. 338), which is the number commonly present in that genus. But *Heptanchus* is not one of HASSE'S Plagiostomi asterospondyli; it belongs to his group Plagiostomi diplospondyli. The only other Elasmobranch whose vertebra the figure at all resembles is *Cestracion*, but *Cestracion*, he says, has eight rays (**15**, A, p. 51). Elsewhere (**15**, D, p. 184) he remarks, nevertheless, that *Cestracion* is the most ancient of the living Plagiostomi asterospondyli, and presents evidence of affinity with *Heptanchus* in the characters of the calcified rays of the centrum, although the rays are more numerous.

The majority of the fishes that HASSE includes among the Plagiostomi asterospondyli have calcified lamellæ or wedges that are developed to a large extent, if not entirely, by the superficial perichondrium of the centrum; these structures are not introduced into the figure, and it fails to be representative in consequence of the omission. The whole of the calcified structures that he shows in the figure are situated within the limits of the membrana elastica externa, *i.e.*, they are in the substance of the chondrified notochordal sheath.

HASSE'S second diagram (fig. 3, 2, p. 338), representing tectospondyly, is based upon the vertebræ of *Pristiophorus* (*vide supra*). It shows a single calcified tube, external to the double cone and united therewith at its anterior and posterior ends only. That HASSE should have chosen the vertebra of *Pristiophorus* as his most typical example of tectospondyly, to be contrasted with vertebræ having radiating lamellæ, proves to be most unfortunate in view of REGAN'S discovery of radiating lamellæ in the Pristiophorid, *Pliotrema warreni*. See fig. 24, B, p. 375.

Views of Later Authors.

SMITH WOODWARD, referring to HASSE's employment of the characters of the vertebral centra of the Tectospondyli and Asterospondyli as a basis of classification, states that the features are to such an extent distinctive that he ventures to adopt the taxonomic arrangement (**32**, p. xxvi). He agrees with HASSE in regarding the Squatinidæ and Pristiophoridæ as surviving members of the ancestral stock that produced the Rays. But the absence of the anal fin in the Spinacidæ and the low position of the gill-clefts in some forms, such as *Acanthias*, lead him to regard the family as more related to the ancestral stock of the Rays than to that of the Sharks that possess vertebræ showing a star-like pattern in transverse section (*ibid.*, p. xxv).

SMITH WOODWARD does not admit cyclospondyly as a valid basis for a taxonomic group of fishes; there are, he says, known cyclospondylic members of each of the groups Tectospondyli and Asterospondyli (*ibid.*, p. xxvii). While in the opinion of SMITH WOODWARD the Squalinæ are derived from the base of the Tectospondylic series, *Palæospinax* is a Cestraciont, an early representative of the Asterospondyli; it has an anal fin, yet the vertebræ exhibit a simple double cone without radiating laminæ (*ibid.*, p. xxvii). "The *degree* of development of the vertebral centra," he states, "is of small importance." *Hybodus*, for instance, is an undoubted Cestraciont, yet there are no calcified structures in the centra of the vertebræ. "The acceleration of vertebral development," he adds, "and the retardation of the same, are singular features apparently having little correspondence with the specialization or otherwise of characters still more likely to change."

SMITH WOODWARD's classification is one in which HASSE's terms Tectospondyli and Asterospondyli are employed to designate sub-orders of the order Selachii, but with altered significance; the Tectospondyli embrace not only the Rays and the families Squatinidæ and Pristiophoridæ, but the family Spinacidæ (= Squalinæ) as well; and the Asterospondyli are enlarged in scope by the inclusion of the Notidanidæ (*ibid.*, pp. xxxiv–xlv).

GILL employs the group-names Cyclospondyli, Tectospondyli and Asterospondyli, but not strictly in HASSE's sense; his Cyclospondyli are HASSE's Diplospondyli, *i.e.*, the Notidanidæ or Hexanchidæ ('Bull. U.S. Nat. Mus.,' No. 16, 1883, p. 967); his Tectospondyli include the sharks without anal fin (HASSE's Cyclospondyli), and his Asterospondyli exclude the Cestraciontidæ (which are separated off as the Prosarthri), and include the Pristiophoridæ and Squatinidæ, which were part of HASSE's Tectospondyli. The rest of HASSE's Tectospondyli—the Batoid fishes—GILL terms the Hypotremi ('Mem. Nat. Acad. Sci.,' vi, mem. 6, Washington, 1893, pp. 129–130).

GREGORY adopts a compromise; in his sub-orders Cyclospondyli and Tectospondyli he includes the same fishes as HASSE did, but his order Asterospondyli differs from HASSE's Asterospondyli in that it excludes the Cestraciontidæ ('Ann. N.Y. Acad. Sci.,' vol. xvii, No. 3, part 2, September, 1907, p. 446).

Regan in 1906 (**29**, pp. 733–4), after referring to the predominance of the concentric laminæ in the Tectospondyli and of the radiating laminæ in the Asterospondyli, observes that "these terms have no practical application; both groups include types in which the secondary calcification of the vertebral centra has no laminar structure (*e.g.*, *Rhynchobatus*, *Oxyrhina*),* and others in which it is deposited as a series of concentric laminæ (*Squatina*, *Cetorhinus*); also in both are forms in which the calcification presents a radiating pattern in cross section (*e.g.*, *Narcine*, *Orectolobus*)." He proposes new definitions for Hasse's terms. "Asterospondylic centra," he writes (**29**, p. 737), "may be defined as those in which the secondary calcification leaves four principal uncalcified areas radiating from the central double cone to the bases of the neural and hæmal arches, and are characteristic of the sub-order Galeoidei, although in the Scyliorhinidæ a series of modifications set in which culminate in a complete reversion to the cyclospondylic type in the genera *Pristiurus* and *Pseudotriacis*. Tectospondylic centra are those with well-developed secondary calcifications not arranged on the asterospondylic plan. Hasse has applied this term to the various types of centra found in the Batoidei, and in *Squatina* and *Pristiophorus*, and it is impossible to give any definition which will include these and exclude *Cestracion*. Probably also the so-called asterospondylic centra of some Hybodonts would have to be included."

The new delimitation thus proposed is unfortunate in that the first of the new definitions renders Hasse's diagrammatic figure of asterospondyly (fig. 3, 3, p. 338), no longer applicable to "asterospondylic" vertebræ; and the definition is so worded that some of the caudal vertebræ of Batoids (*e.g.*, *Torpedo*, fig. 26, B, p. 379), would have to be regarded as asterospondylic. The difficulties in the way of consistent new definitions of Hasse's terms are almost insurmountable, and it would tax one's ingenuity to the utmost to draft short descriptions that would differentiate the vertebræ of *Mustelus* and *Dasybatis* (fig. 8, A, p. 354, and fig. 35, A, p. 391), as asterospondylic and tectospondylic respectively. A certain amount of confusion is bound to result from the retention of the terms with new meanings, and it is far preferable to discard them altogether (see p. 346).

Schauinsland, in his admirable summary of the views of Kölliker, Goette, and Hasse, states that the secondary calcifications in the vertebral centra have "eine weitgehende systematische Würdigung" (**30**, p. 405).

Goodrich† writes: "That these characters of the centrum are of considerable taxonomic value there can be no doubt, but the distinction between the various types does not seem to be as clear and sharp as was supposed."

Graham Kerr in 1911 writes‡: "The arrangement of the calcified tracts shows differences which are of taxonomic importance."

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* *Vide infra*, p. 358.

† 'Treatise on Zoology,' E. Ray Lankester, Part IX, fasc. 1, London, 1909, p. 135.

‡ 'Encyclopædia Britannica,' Ed. XI, vol. 24, Article "Selachians," p. 594.

Terms Asterospondylous and Tectospondylous better Discarded.

For the reasons given in the previous section, it is deemed advisable to discontinue the use of the terms asterospondylous and tectospondylous; the term cyclospondylous is less open to objection than these, but there is no great advantage to be gained in retaining it if the other terms of the series are no longer employed. The attempt to introduce a new series of descriptive terms, more accurate and more consistent in their application than those which it is proposed to discard, has not met with any great measure of success, for while some vertebræ offer characters that can be satisfactorily expressed by single descriptive words, there are others that do not lend themselves readily to the process; they fail to fit into a general scheme, because they do not present characters that can be regarded as specially distinctive.

As belonging to the first kind, those with features that can be pointed to as distinctive are *Cestracion*, *Squatina*, and *Squalus*. The centra of *Cestracion* might, for instance, be described as *actinospondylous*—they have calcified lamellæ that radiate outward from the primary double cone; the rays occur solely in the outer-zone cartilage, they are approximately equidistant, and their disposition is not influenced in any way by the arch-cartilages (fig. 4, A, p. 340). Those caudal vertebræ of *Heptanchus* that show a star-like pattern fall into the same category (fig. 5, A, p. 348).

The centra of *Squatina* exhibit a series of thin calcified lamellæ, which are set in a concentric manner around the primary double cone (fig. 25, p. 377). They occur in the outer-zone cartilage, and they are not affected by the arch-cartilages, in these respects differing from those of a young *Cetorhinus* (fig. 13, A, p. 360). The concentric lamellæ increase in number as the vertebra grows, the outermost lamella being the latest; they thus come to resemble the "rings" of annual growth in the section of the wood of a tree-trunk, and the vertebræ might accordingly be termed *xylospondylous*. An eminent Greek scholar was good enough to suggest *prasospondylous*, to suggest the coats of a leek, but the resemblance fails in that in the leek and onion the outer coats are the oldest, not the most recently formed.

In *Squalus*, *Spinax*, and *Oxynotus* the double cone is covered on its external surface with an investing layer of secondary calcification, developed from the inner part of the outer zone cartilage (fig. 22, p. 372). This calcified body, when exposed by scraping away the uncalcified cartilage from it, is seen to have a smooth surface, free from radial lamellæ; the term *litospondylous* applied to such a vertebra would be more appropriate than cyclospondylous, for the latter, largely from error—for HASSE distinctly refers to a Belegschicht—has come in course of time to signify that the central calcified structure consists of the double cone solely. Or, alternatively, the term *haplospondylous* might be used, signifying that the calcified parts are of single construction.

The absence of the double cone and of secondary calcifications from the vertebral column of *Hexanchus*, *Echinorhinus* (fig. 23, p. 373), and *Somniosus microcephalus* may, for the reasons given elsewhere, be regarded as a condition of degeneration, and not a primitive one. Having lost their calcifications, the vertebræ might be termed *lipospondylous*.

If a descriptive term were desired for the compact secondary calcification exhibited by the centra of *Rhynchobatus* and *Pristis* (fig. 31, p. 385), *sympektospondylous* might be suggested; but there is nothing to be gained by the introduction of the term, for the condition is so nearly approached by the vertebræ of some species of *Rhinobatus*, other species of which genus exhibit a characteristic eight-rayed star. Compare, for instance, the series *Rhinobatus thouini*, *horkeli*, and *cemiculus*, given by HASSE (**15**, C, Plate 14, fig. 14; Plate 15, figs. 27 and 41).

In the Carcharidæ there are diagonal calcified lamellæ (*Sphyrna*, fig. 8, B, p. 354) for which the prefix *chiasto-* might be appropriate. And in some genera, such as *Galeus* and *Mustelus*, the calcified intermedialia present the form of a massive cross with vertical and horizontal arms (fig. 8, A), suggesting the use of the prefix *stauro-*. But it would be difficult so to define a single word describing the structure of the vertebræ of a Carchariid shark that it would exclude the vertebræ of Batoids like *Trygonorhina* (HASSE, **15**, C, Plate 15, fig. 49).

The Batoids, indeed, would seem to defy all attempts to get them to fall naturally into any scheme such as that which HASSE set himself to propound. The differences observable in some cases between the vertebræ of the caudal and trunk regions are not merely differences in pattern, but differences in origin, as witness the horizontal rays, which in the trunk region do not reach the surface, and are not reinforced by perichondrially produced increments as are the horizontal rays in the caudal region (*Rhinobatus*, fig. 29, A, p. 382, and fig. 30, A).

The suggestions, therefore, that are set forth in the preceding paragraphs are made, not with a view to the adoption of the terms, but rather to show that a comprehensive and consistent terminology is not possible; it is here definitely recommended that the employment of the terms cyclo-, astero-, and tectospondylous should be discontinued, but the terms mentioned in the paragraphs above are equally to be rejected.

DETAILED OBSERVATIONS.

The letterpress of the various sections of the paper included under this heading has been made as brief as possible. The numerous text-figures drawn in illustration of the facts observed are treated rather diagrammatically, and they convey to the reader the author's views far more readily than a copious descriptive text. They are therefore left to a large extent to speak for themselves.

Chlamydoselachidæ.

No specimens of *Chlamydoselachus* were examined in the course of the investigation. This was not because material could not be procured, but because the account given by GOODEY* in 1910, taken in conjunction with the earlier description by GARMAN,† goes to show that the vertebræ are of little interest in the present connection. According to GARMAN (pp. 12–13), the notochord is unconstricted for the greater part of its length, although in the anterior region there are vertebral constrictions, with calcifications resembling those of *Centrophorus.* Behind this region the limits of the vertebræ can only be made out from the neural and other plates. GOODEY (pp. 553–561) finds double-cone calcifications in the caudal vertebræ as well as in those of the branchial region. It is probable that the examination of a large number of specimens would show that there is a good deal of individual variation within the species, and that the condition of the vertebral column is degenerate, not primitive.

Hexanchidæ.

The material available for study consisted of the vertebral column of a half-grown specimen of *Heptanchus cinereus,* about a metre in length, and the branchial region of the vertebral column of another specimen, of about the same size.

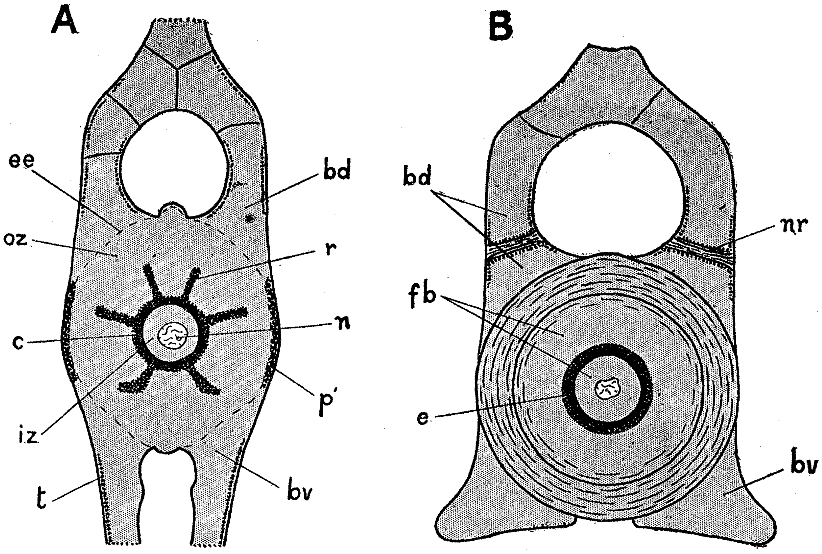

FIG. 5.—*Heptanchus cinereus,* half-grown fish, 1 metre long. A, vertebra from region of caudal fin, at a point two-thirds of the length of the caudal fin from its posterior end, × 5. B, mid-trunk vertebra, × 3·5.

e, calcified ring representing the last remnant of the double cone, *cf. e* in fig. 6; *fb,* fibro-cartilaginous septum, a modification of the outer-zone and inner-zone cartilage. (For explanation of other lettering, see p. 404.)

In *Hexanchus* there are no double cones or other calcified parts of the centra (KÖLLIKER, **20**, p. 51; HASSE, **15**, B, p. 43), and the positions of the "centra" can only be recognised by the presence of large transverse septa of fibro-cartilage occurring at intervals within the tubular sheath that surrounds the notochord. The

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* GOODEY, T., 'Proc. Zool. Soc.,' 1910, pp. 540–571.

† GARMAN, S., 'Bull. Mus. Comp. Zool.,' Harvard Coll., xii, 1, Camb., Mass., 1885–6.

same applies to *Heptanchus*, except that, in the caudal region, some of the vertebræ have double cones and radiating calcified lamellæ. The conditions found in these two genera point to the vertebral column being in a degenerate, and not in a primitive, condition, and indicate that the vertebræ of *Hexanchus* are more degenerate than those of *Heptanchus*. It is to be noted that in *Notidanus eximius*, of the Jurassic, the centra are more calcified than in the modern *Heptanchus* (HASSE, **15**, B, p. 52).

Accepting the general conclusion that the caudal vertebræ of a shark exhibit a less specialised condition than those of the trunk region (p. 317), the presence of double cones and radiating lamellæ in some of the hinder caudal vertebræ of *Heptanchus* implies that the absence of such calcifications from the trunk region is due to degeneration.

The structure of the double cone and radiating lamellæ of the caudal vertebræ of *Heptanchus* has been described by KÖLLIKER (**19**, Plate 2, figs. 2 and 3) and HASSE (**15**, A, p. 36, and **15**, B, p. 49, and Plates 6 and 7), and both of these authors have noted that, as one passes forward in the caudal region, the double cones shorten, and become merely rings of calcified cartilage. The specimen studied in the course of the present investigation seems to be remarkable, in that the rings, usually confined to the caudal region, extend through the whole of the trunk as well. Vertebræ from the branchial region of another fish of about the same size failed to show them.

The transition from the double cone to the ring is explained in fig. 6 (p. 350). The double cones of *Heptanchus* are present in their most complete form in that part of the caudal fin which is two-thirds of the length of the fin from its posterior end (fig. 6, 1, and fig. 5, A). The outer-zone cartilage (fig. 6, 1, *a*) is hyaline in character, and contains six radiating calcified lamellæ,* connected at their inner edges with the double cone, and not reaching the surface of the centrum (fig. 5, A, *r*). The remnants of the membrana elastica externa are readily recognisable (*e e*), and they go to show that the sheath-cartilage is of considerable bulk, and that the radiating lamellæ are calcifications of that cartilage.

At the root of the caudal fin the double cones are much shorter than in the region above specified, and the intervertebral ligaments are longer (fig. 6, 2). This antero-posterior compression of the double cone becomes more pronounced as one passes farther forward, until the calcified structure comes to consist of a two-layered circular plate (fig. 6, 3, *d*). Still farther forward, in the cloacal region, the more peripheral parts of the calcified structure disappear, and the inner part remains as a calcified ring, embedded in a transverse septum (fig. 5, B, *e*; fig. 6, 4, *e*). In the vertebræ of the tail there is an investing layer, a thin calcified deposit in outer-zone

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* The rays are not necessarily regular; they may be of unequal lengths, and may vary in number; KÖLLIKER mentions eight, and HASSE figures vertebræ with six and four respectively (**15**, B, Plate 6, figs. 11, 12).

cartilage, immediately external to the double cone; it is shown in fig. 5, but not in fig. 6, which is more diagrammatic.

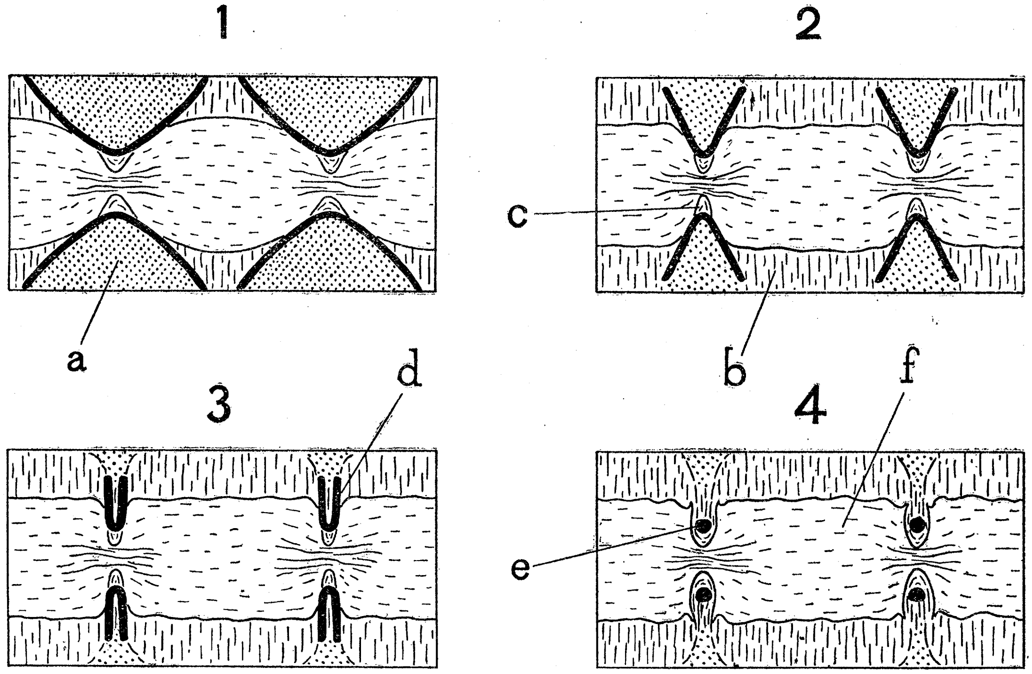

FIG. 6.—*Heptanchus cinereus.* Vertical sections through two consecutive centra, showing how the double cone, found in the vertebræ of the caudal fin, passes into the simple ring found in the more anterior vertebræ. To facilitate comparison the centra are represented as of the same size in the four regions selected. The upper edge of each figure marks the floor of the neural canal, the lower edge the roof of the hæmal canal.

1, vertebræ at the level of the hind end of the large anterior lobe of the caudal fin. 2, vertebræ at the root of the caudal fin. 3, vertebræ a short distance in front of the caudal fin. 4, vertebræ still farther forward, cloacal region.

a, hyaline cartilage (outer-zone cartilage); *b*, fibrous tissue, the greatly elongated intervertebral ligament; *c*, fibrous septum, a product of the inner-zone cartilage—it is traversed in the middle by the remains of the notochord; *d*, a two-layered circular plate, with fibro-cartilage between the two layers of the plate; it represents the double cone, antero-posteriorly compressed; *e*, calcified ring, the last remnant of the double cone (see also fig. 5, B, *e*); *f*, watery jelly, the remains of the notochord.

The arch-cartilages have calcified tesseræ, and the fact that these are better developed in the caudal than in the trunk region is a further argument in support of the view that the trunk vertebræ are in a degraded, and not in a primitive condition. At the sides of the caudal vertebræ, on a horizontal level with the middle of the centrum, are calcified tracts that lie just external to the membrana elastica externa (fig. 5, A, *p'*). These lateral tracts I regard as having been produced by the activity of the superficial perichondrium, and not by a fusion of neural and hæmal arch-cartilages; they are, in fact, intermedialia, but, instead of being bulky wedges as in the Carchariidæ, they are reduced to the form of thin plates. KÖLLIKER'S longitudinal section (**19**, Plate 2, fig. 2) is taken horizontally, and shows the plates, but fig. 6, 1, of the present paper represents a vertical section, and so the plates are not seen.

Carchariidæ.

In REGAN'S classification (**29**) the families of the Galeoidei follow in the order Odontaspididæ, Lamnidæ, Orectolobidæ, Scyliorhinidæ, Carchariidæ, but for reasons that will presently be apparent, it is advisable here to commence with the Carchariidæ, and to leave the Orectolobidæ till the last.

The material available for study consisted of:—

Carcharias laticauda, two young specimens in alcohol, 380 mm. long, and one young (? embryo), 277 mm. long, in the collection at the Roy. Coll. Science.

Carcharias walbeehmi, 810 mm. long, from Tuticorin, S. India, vertebral column in alcohol, presented by J. HORNELL, Esq.

Carcharias (*Scoliodon*) sp., adult, a few dried vertebræ, Brit. Mus. (Nat. Hist.).

Carcharias, sp. (? embryo), 133 mm. long, no locality, Brit. Mus. (Nat. Hist.).

Galeus canis, three adults, purchased from Marine Biol. Lab., Plymouth; also young (? new-born), 230 mm. long, no locality, Brit. Mus. (Nat. Hist.).

Triacis semifasciatus, young, 355 mm. long, no locality, Brit. Mus. (Nat. Hist.).

Mustelus vulgaris, five adults, and one late embryo, 286 mm. long, purchased from the Marine Biol. Lab., Plymouth.

Sphyrna tudes, young, 480 mm. long, and *Sphyrna blochii*, two, young, 510 and 430 mm. long, S. India, vertebral columns in alcohol, presented by J. HORNELL, Esq.

Hemigaleus balfouri, 760 mm. long, S. India, vertebral column in alcohol, presented by J. HORNELL, Esq.

The early development of the vertebræ of *Mustelus* has been already described in detail by GOETTE, HASSE, KLAATSCH and GÖPPERT, but most of the embryos studied by them are too young to be of great interest in the present connection. KLAATSCH in 1893 (**18**, II) described the vertebral structures in embryos measuring 30, 40, 45 and 55 mm. long, and in the first two he demonstrated the immigration of cartilage-forming cells from the arch-bases into the notochordal sheath. The embryos described by HASSE in 1882 (**15**, D, p. 281) measured 18 and 40 mm. in length, and those described by him in 1892 (**16**) from 12 to 40 mm.; GÖPPERT'S embryos measured 23, 48 and 70 mm. (**11**, Plate 14). The embryos studied by GOETTE (**13**) were larger (100 and 220 mm.), and more nearly approached the ripe embryo examined in the present inquiry (286 mm.). Among other young Carchariids that have been studied may be mentioned *Galeocerdo tigrinus* (HASSE, **15**, D, p. 259 and Plate 36, fig. 15), *Loxodon macrorhinus* (197·5 mm., HASSE, **15**, E, p. 23 and fig. 3), *Carcharias lamia* (200 mm., GOETTE, **13**, Plate 31, fig. 41); and during the present inquiry there were examined *Carcharias laticauda* (277 mm.) and *Galeus canis* (230 mm.).

The figure of *Galeus* shown at C in fig. 7, p. 352, agrees in general structure with that of *Mustelus* shown in HASSE's Plate 40, fig. 7 (**15**, D), although the diagonal rays are longer. The course of the membrana elastica externa is almost identical in the two cases; its outline is roughly octagonal, and it is superficial in four places, and marks off the arch-bases where it is not superficial. The young *Galeus* described by HASSE (**15**, D, p. 264 and Plate 38, fig. 3) is considerably older, and in its degree of development agrees nearly with the *Mustelus* here figured as fig. 7, A. The illustration given by HASSE is not clear; but taking the figure in conjunction with the text, it would seem that the author regarded the membrana elastica externa as stretching straight across the arch-bases, whereas there is incontestible evidence in *Mustelus* that, while the membrane keeps external to the diagonal calcified lamellæ (fig. 7, A, *d*), it occupies an internal position with regard to the perichondrial calcifications (*p'*). It follows the course rather of the line that HASSE marks *g* (Grenzzone), although not precisely.

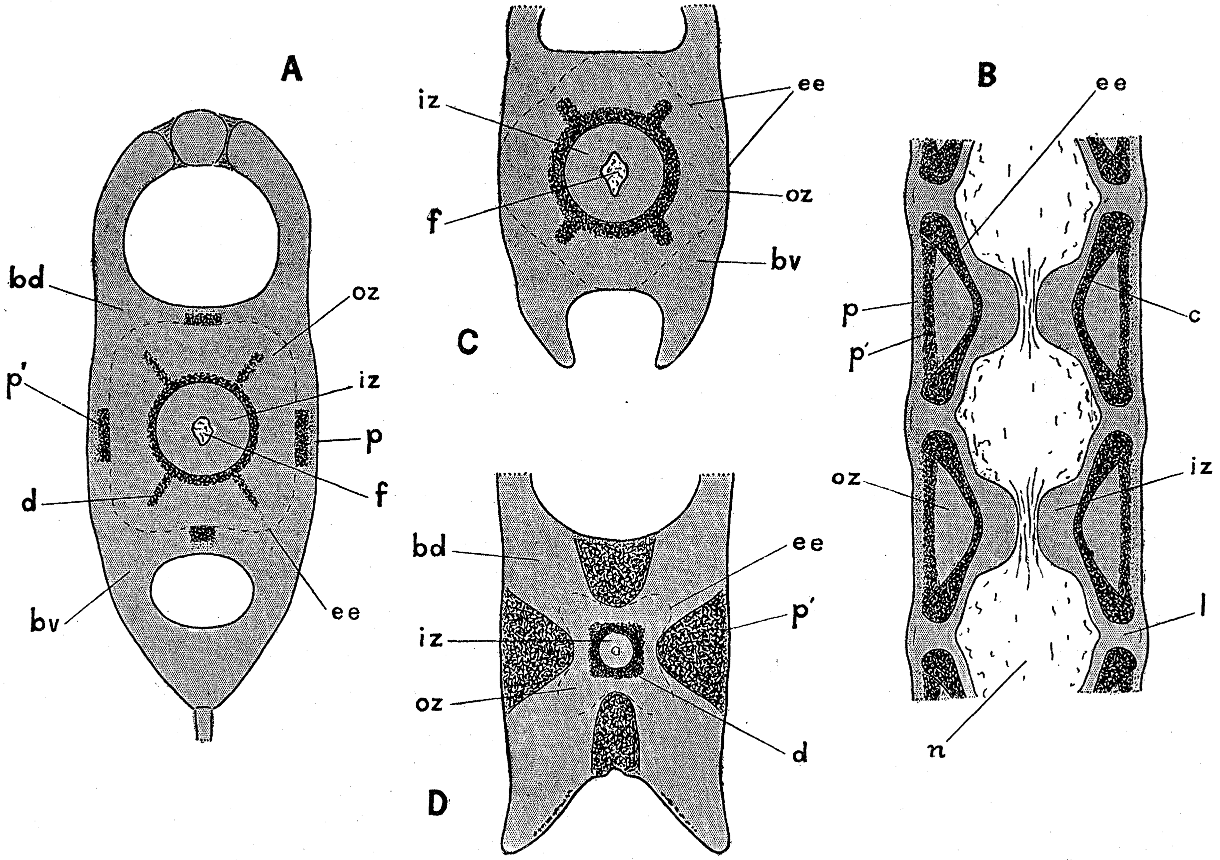

FIG. 7.—A, *Mustelus vulgaris*, late embryo, 286 mm. long, caudal vertebra from region of second dorsal fin, × 20. B, horizontal section of vertebræ from the same region, × 20. C, *Galeus canis*, young, 230 mm. long, vertebra from region between pelvic and second dorsal fins, × 18. D, *Carcharias laticauda*, young, 277 mm. long, mid-trunk vertebra, × 18. (For explanation of the lettering, see p. 404.)

It may here be remarked parenthetically that in the opinion of the present writer the Grenzzonen of HASSE have no morphological value; their limits are defined by differences in the texture of the cartilage due in some cases to an unimportant transition from hyaline to fibro-cartilage, and in some cases to unequal shrinkage of the cartilage in the process of embedding and section cutting. The unequal shrinkage results from the rigidity of the calcified parts being greater than that of the uncalcified parts of the centrum, even after the process of decalcification; and it is significant that in some instances a Grenzzone that is distinguishable in sections prepared by the paraffin-embedding method, is not seen in hand-cut slices. The matrix of the cartilage in the regions where the strains and stresses are greatest is altered in some way that results in its staining differently from the parts of the cartilage that are less affected. In a few cases a Grenzzone is a "growing zone," a tract of small-celled, actively dividing cartilage, sometimes rendered more conspicuous by the inclusion within it of blood-vessels that penetrate from the superficial connective tissue.

The intermedialia of the late embryo of *Mustelus* (fig. 7, A) are very distinct from the arch-cartilages, their cells being smaller and more crowded; the inner part (*p'*) is calcified, but not the more superficial part (*p*). The longitudinal section (B) shows the antero-posterior extent of the membrana elastica externa (*e e*), and illustrates how the inner-zone cartilage (*i z*) thins out abruptly towards the ends of the centrum. The double-cone calcification is seen to be thicker at the ends than at the middle, and the intermediale is confluent with the double cone at its anterior and posterior ends.

The section of the vertebra of *Carcharias laticauda*, shown in fig. 7, D, is interesting as showing the relatively late development of the diagonal calcified lamellæ, for in *Mustelus* (fig. A) the diagonals are well calcified at the time when the intermedialia begin to develop, and in *Galeus* (fig. C) they are present even before the perichondrial tracts of the intermedialia have begun to be active, the membrana elastica externa in those four regions being still superficial in position. Notwithstanding the late development of the diagonal calcified lamellæ in *Carcharias laticauda*, the diagonal out-pushings of the outer-zone cartilage are as well marked as if the lamellæ were already there.

HASSE's figure of a young *Galeocerdo* (**15**, D, Plate 36, fig. 15) is peculiar in showing the diagonal lamellæ unconnected with the double cone; the absence of the upper intermediale, also, strikes one as strange.

As will be seen, by comparing the young and adult conditions of the vertebra of *Mustelus* (fig. 7, A, and fig. 8, A), the intermedialia broaden with age. In the adult they have the form of wedges (Periostale Keile of HASSE), each with the thin edge directed towards the axis of the centrum, and the base still in contact with the superficial connective tissue. In old specimens the growth of the base, superficially or tangentially, is greatly in excess of the radial growth of the wedge, and the "side" of the wedge, that face which abuts upon the basidorsal or basiventral cartilage, is curved instead of being flat. In old specimens of *Galeus*, this proceeds to such an excessive degree that the base of the wedge comes to lie external to some of the tesseræ.

As regards the growth of the intermedialia in the radial direction, it is important to bear in mind that the growth is centrifugal, the latest increments being those that are most external and superficial. A casual glance at the sections might perhaps suggest that the intermedialia push their way inward, and in this way produce the curvature of the membrana elastica externa in the horizontal and vertical planes ; and it is not quite clear that SCHAUINSLAND did not intend to convey such a meaning when he wrote* that they " dringen erst nachträglich in sie [the membrana] hinein." As an actual fact, the distance between the inner portions of the two lateral intermedialia is slightly greater in the adult than in the late embryo examined.

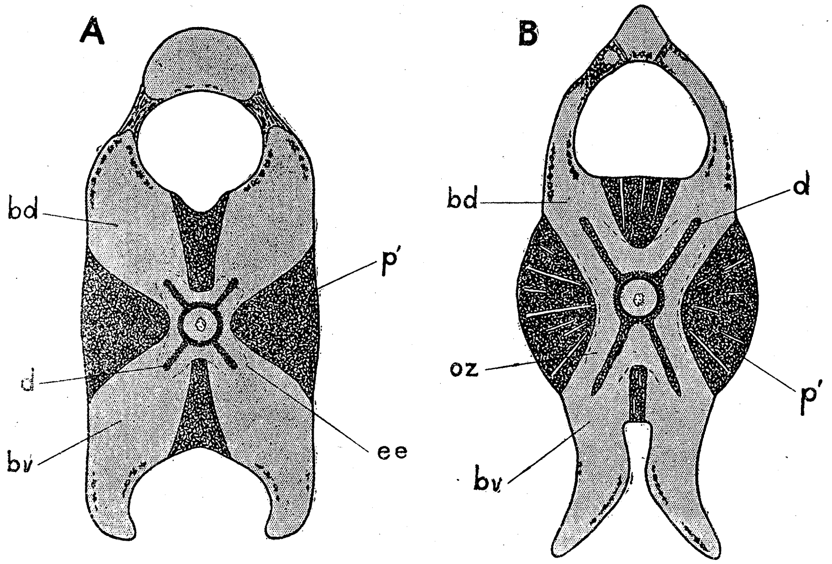

FIG. 8.—A, *Mustelus vulgaris*, adult, post-cloacal vertebra, × 5. B, *Sphyrna blochii*, young, 510 mm. long, pre-cloacal vertebra, × 7. (For explanation of the lettering, see p. 404.)

Another rather dubious remark of SCHAUINSLAND'S is that the diagonal calcified lamellæ " entstehen von der Mittelzone aus " (**30**, p. 405). This might mean that they belong morphologically to the double cone, and have their origin, like the double cone, in middle-zone cartilage, or it might mean that they are calcifications of the outer-zone cartilage which, beginning their development against the double cone, grow centrifugally away from it. The latter is the correct view ; they are solely outer-zone structures.

In *Mustelus*, the remnants of the membrana elastica externa can be distinguished

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* SCHAUINSLAND, **30**, p. 405 ; possibly after GOETTE, who says (**13**, p. 491) that the intermediale "drückt dabei die Aussenzone entsprechend ein, worauf seine Verkalkung sich in den Knorpel der letzteren fortsetzt, bis sie dem knöchernen Doppelkegel nahe kommt oder ihn theilweise erreicht. Auf diese Weise entstehen die schon erwähnten senkrechten und horizontalen Knochenleisten bei *Mustelus* und *Carcharias*."

in sections of vertebræ of the adult fish (fig. 8, A, *e e*), although the portions actually at the extremity of the diagonal lamellæ are missing. In one vertebra, however, the outward rate of calcification of the diagonal lamella exceeded, as it were, the rate of outward bulging of the sheath-cartilage, and the end-portion of the membrane became caught or entangled in the lamella, as is shown in the right upper quadrant of fig. 8, A. All four quadrants of the vertebra in question showed the phenomenon; the next vertebra to it exhibited the usual relations; in order to avoid the necessity of a separate figure, the exceptional relations are here illustrated in one of the quadrants of a vertebra which was in point of fact normal throughout. The exceptional condition is of interest in showing the disregard exhibited by a growing calcification for the mode of origin of the cartilage in which it is proceeding; it is immaterial that the calcification, begun in outer-zone cartilage, should be confined to that cartilage; it may proceed unchecked into the arch-cartilage external to the limiting membrane. Another instance of such disregard of the origin of the cartilage is given in the case of *Pliotrema* (p. 375).

In the adults of *Carcharias* and *Sphyrna* the lateral intermedialia are very obtuse, the base of the wedge being large and the radial extent relatively small. The calcification is usually compact in the former genus, but in *Sphyrna* there are radial rod-shaped tracts of uncalcified cartilage in the intermedialia (fig. 8, B), with blood-vessels penetrating into them. Similar tracts of uncalcified cartilage are shown in HASSE's figure of a young *Prionodon melanopterus* (**15**, D, Plate 39, fig. 12).

It is in *Carcharias*, *Sphyrna*, and *Galeocerdo* that the diagonal calcified lamellæ attain their greatest radial extent; in some specimens of *Galeus* and *Mustelus* they are very feebly developed.

In the caudal region of *Galeus*, where diplospondyly prevails, the centra are alternately long and short; the patterns of the calcified parts of the long and short centra, as seen in transverse section, prove on examination to be the same.

Lamnidæ and Odontaspididæ.

The material of these families available for study consisted of:—

Lamna cornubica, adult, disarticulated skeleton in formalin, in the collection at the Royal Coll. Science; and dried vertebræ of a young specimen, about 900 mm. long, Brit. Mus. (Nat. Hist.).

Carcharodon rondeletii, a few vertebræ prepared by the glycerine jelly method, in the collection at the Royal Coll. Science, apparently from Prof. J. PARKER, Otago.

Cetorhinus maximus, dried vertebræ of adult, Shanklin, Isle of Wight, Brit. Mus. (Nat. Hist.); and transverse section of trunk vertebra of a young specimen, Brit. Mus. (Nat. Hist.); also another slice, possibly from the same fish, in the Museum of the Roy. Coll. Surgeons.

Alopias vulpes, two dried tails, no history, Brit. Mus. (Nat. Hist.).

Odontaspis americanus, young, about 900 mm. long, in alcohol, Rio Grande do Sol, Brit. Mus. (Nat. Hist.).

Scapanorhynchus (*Mitsukurina*) *owstoni*, adult, vertebræ in formalin, Japan, Brit. Mus. (Nat. Hist.).

Scapanorhynchus lewisi, two vertebræ from the Upper Cretaceous of Sahel Alma, Mount Lebanon, Geol. Dept., Brit. Mus. (Nat. Hist.).

In the families Lamnidæ and Odontaspididæ the vertebral centra differ from those of the preceding family in the diagonal lamellæ being greatly reduced or absent, and in the intermedialia being less completely calcified. The diagonal lamellæ are commonly regarded as absent, but in *Lamna* they can be recognised if searched for (fig. 9, B), and in *Cetorhinus* (fig. 14, A, p. 361) there are calcified structures which may have the same value, although they are rather too irregular to enable one to be certain; but it is extremely doubtful whether the isolated calcifications marked *i* in the diagonally placed cartilages of *Cetorhinus* are parts of the diagonal lamellæ. These "islands" are probably calcifications in the arch-cartilages themselves, and not in sheath-cartilage bulging into the arch-cartilages.

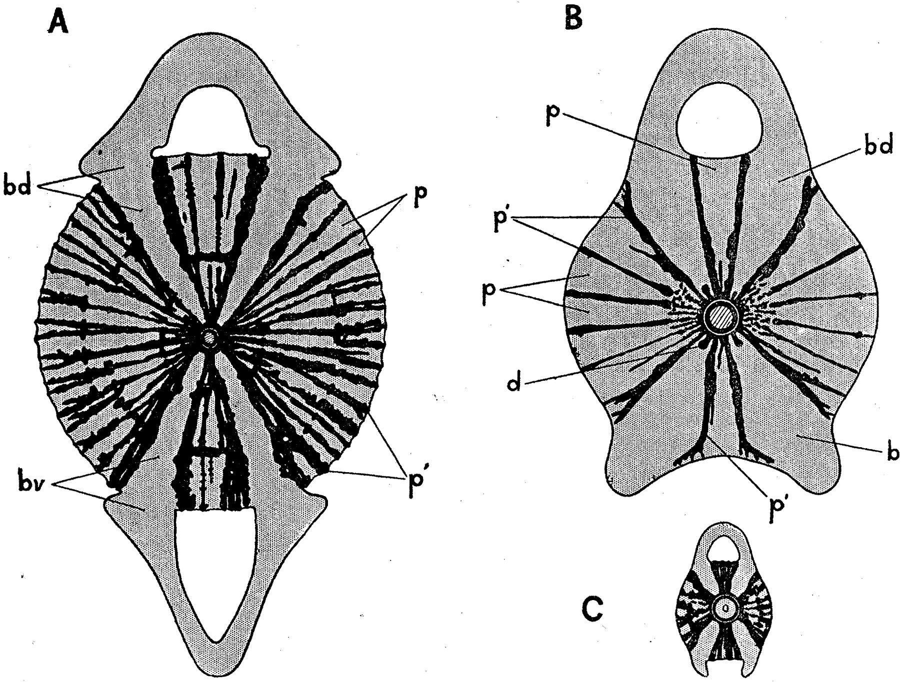

FIG. 9.—A, *Carcharodon rondeletii*, vertebra from anterior caudal region, × 0·75. B, *Lamna cornubica*, vertebra from cloacal region, nat. size. C, *Lamna cornubica*, half-grown, 920 mm. long, vertebra from cloacal region, nat. size. (For explanation of the lettering, see p. 404.)

The sharks of these families would seem to have a minimum of sheath-cartilage in the composition of their vertebræ. Remnants of the membrana elastica externa were found in *Odontaspis* alone of the fishes examined; although the young *Lamna* whose vertebra is represented in fig. 9, C, is a fish of about the same size, the search for the membrane proved unsuccessful. In *Odontaspis* the remains of the membrane occur at the innermost end of each of the diagonal cartilages, and the line probably continues round in a circle passing through the inner ends of the four intermedialia, which are continuous with the investing layer of the double cone. Hasse's figure of an embryo *Lamna* (**15**, D, Plate 28, fig. 5) shows that the investing layer develops early. The figure is not clear, but it would seem that the eight structures that project outward from the double cone are calcified parts of the already developing intermedialia, the middle part of each of which is uncalcified, as, for instance, in an adult *Scapanorhynchus* (fig. 11, B, p. 358). Hasse does not show the membrana elastica externa, although it would be almost certainly recognisable in such a vertebra as he figures.

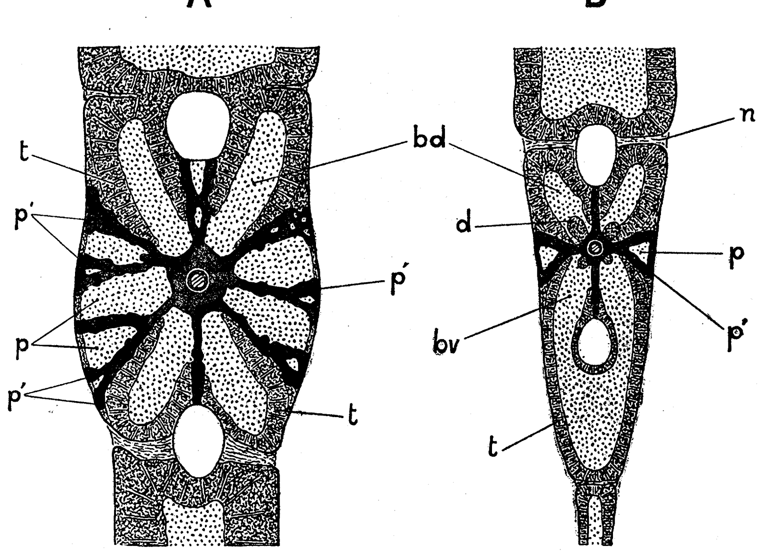

Fig. 10.—*Alopias vulpes*, × 3, posterior caudal vertebræ. A, taken at 250 mm., and B, at 120 mm. from the tip of the caudal fin. (For explanation of the lettering, see p. 404.)

The present investigation tends to confirm the observation of Kölliker (**20**, p. 75) that whereas in the Carchariidæ the inner ends of the intermedialia are regularly separate from the double cone in a section of the centrum taken midway between its anterior and posterior ends, in the families now under consideration the intermedialia are in adult fishes, and sometimes in young, confluent with the investing layer that surrounds the double cone. Each intermediale is, except in young *Cetorhinus* (fig. 13, A, p. 360), calcified on the two wedge-faces, *i.e.*, those faces which are in contact with arch-cartilage (fig. 11, A, *p'* and *p''*), and whereas the remainder may persist as uncalcified cartilage (fig. 11, *p*), it more usually has three or more radiating lamellæ within it (fig. 9, A and B). The intermedialia of *Cetorhinus* are exceptional in that in the young (fig. 13, A) the calcified lamellæ are all concentric, but the wedge-faces calcify later, and radiating lamellæ are developed external to the earlier concentric ones (fig. 14, A).

The figures of adult *Lamna* vertebræ given by KÖLLIKER (**20**, Plate 13, fig. 3), HASSE (**15**, D, Plate 28, fig. 6), and GOODRICH* agree with that here given (fig. 9, B) in all essential features. The internal parts tend to become more irregular as age advances, and there may be a certain amount of absorption of the early deposits; the total number of calcified lamellæ in the lateral intermedialia varies from four to seven, and the uncalcified parts are fairly bulky.

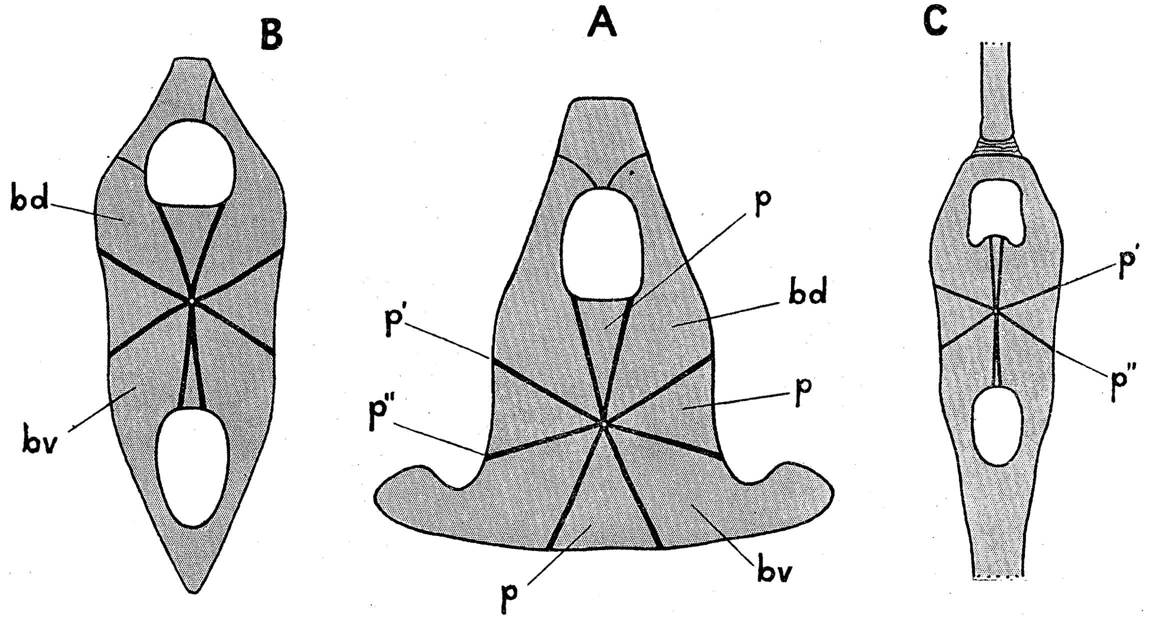

FIG. 11.—*Scapanorhynchus* (*Mitsukurina*) *owstoni*, nat. size. A, mid-trunk vertebra. B, anterior caudal vertebra. C, from middle of the length of the caudal fin. (For explanation of the lettering, see p. 404.)

In *Carcharodon* the radiating lamellæ of the intermedialia are much more numerous than in *Lamna* (*cf.* fig. 9, A and B), and there is a suggestion of a concentric arrangement, which is more or less apparent throughout the two families, and is not confined to *Cetorhinus* (KÖLLIKER, **20**, p. 72). Vertebræ of *Carcharodon* have been previously figured by KÖLLIKER (**20**, Plate 14, fig. 9), HASSE (**15**, D, Plate 30, fig. 30), and PARKER.† Those figured by PARKER are from his specimen A, a fish 10 feet long; that now figured is apparently from his specimen C, a fish 19 feet long.

The vertebræ of *Oxyrhina*, according to REGAN (**29**, p. 734), have no laminar structure, and exhibit a compact calcification like that of *Rhynchobatus*, but this is not in accord with the observations of KÖLLIKER (**20**, Plate 13, fig. 5) and HASSE (**15**, D, Plate 31, fig. 41), who in their figures represent distinct radial lamellæ.

While in the majority of the sharks now under consideration there are no superficial calcifications in the arch cartilages, it is to be noted that in the hindermost caudal vertebræ of *Alopias* the tesseræ are strongly developed (fig. 10, p. 357). Two tails of *Alopias vulpes* were available for study. The vertebræ at the root of the

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* 'Treatise on Zoology,' E. Ray Lankester, Part IX, fasc. 1, London, 1909, p. 136, fig. 94, B.

† 'Proc. Zool. Soc.,' 1887, Plate 6, figs. 13 and 14.

great caudal fin show no remarkable features; the radiating lamellæ in the lateral intermedialia are less numerous than those of *Carcharodon*, although more numerous than those of *Lamna*. HASSE'S figure of *Alopias* (**15**, D, Plate 29, fig. 17) shows the lamellæ thicker and fewer than those in the specimens now under consideration; his fish was a small one.

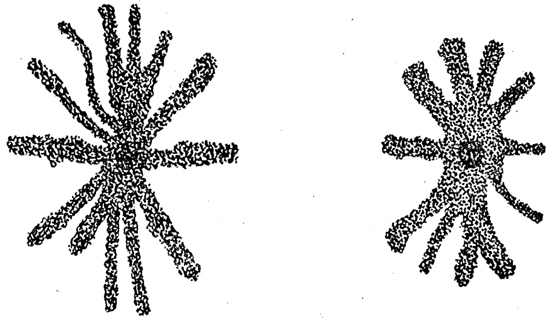

FIG. 12.—*Scapanorhynchus lewisi*, from the Upper Cretaceous of Mount Lebanon. Radiating lamellæ of two post-cloacal vertebræ, × 8.

In the part of the tail, however, about 250 mm. from the posterior extremity, the lamellæ of each lateral intermediale become reduced to a total of three or four (fig. 10, A), and in the region behind this the reduction is still greater. In fig. 10, B, are seen calcified nodules occupying the positions of the diagonal lamellæ, but these are not found in the more anterior vertebræ. What is of particular interest in these vertebræ is the manner in which the layers of tesseræ spread along the wedge-faces of the intermedialia, or, expressing it more correctly, the manner in which the outer parts of the intermedialia have expanded and spread over the tesseræ as the vertebræ grew in size; another instance of this is mentioned in the previous section in the case of *Galeus*. At a distance of 50 mm. from the posterior extremity of the excised vertebral column there are no secondary calcifications, only a typical double cone; and at 30 mm. from the extremity each centrum has two small, widely separated cones, with a rodlike granular or uncalcified part between (*cf. Raia*, pp. 318, 387).

In *Scapanorhynchus* it is only the wedge-faces of the intermedialia that calcify (fig. 11, p' and p''); the middle part of each (p), in formalin-preserved material, consists of a whitish-grey fibro-cartilage of cloudy appearance, in marked contrast with the pale blue hyaline cartilage of the arch-bases. The middle part of the double is very small, and the inner parts of the radiating calcified lamellæ are continuous with it. At the broad ends of the double cone the eight lamellæ are buttressed by partial lamellæ, which if more complete might extend so far as to appear in transverse sections through the middle of the length of the centrum, and thus cause such sections to resemble those of the more familiar sharks belonging to the family.

In REGAN'S classification (**29**) *Mitsukurina* is not recognised as generically distinct from the earlier extinct *Scapanorhynchus*, but it is to be noted that sections through the centra of *Scapanorhynchus lewisi* show radiating lamellæ more than eight in number (fig. 12). My thanks are due to Dr. A. SMITH WOODWARD for having the two vertebræ cut in order that they might be compared with those of *Scapanorhynchus owstoni*. They are two consecutive vertebræ of the same fish. The dorsal part is uppermost in each figure.

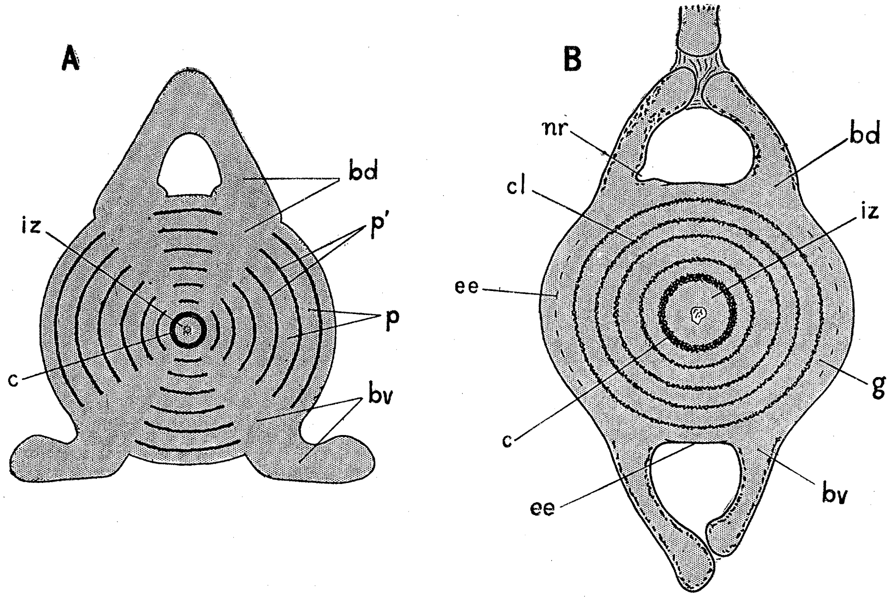

FIG. 13.—A, *Cetorhinus maximus*, young trunk vertebra, × 0·6. B, *Squatina squatina*, ripe embryo, 264 mm. long, caudal vertebra, from region of first dorsal fin, × 14. (For explanation of the lettering, see p. 404.)

It has already been pointed out that in young specimens of *Cetorhinus* the calcified lamellæ in the intermedialia are concentric. HASSE shows this in the caudal vertebræ (**15**, D, Plate 32, figs. 3 and 4); in fig. 13, A, above, it is demonstrated in a trunk vertebra. Allusion has also been made (p. 316) to the fact that for indicating taxonomic relationship the hind caudal vertebræ of the adult are in this genus more reliable than the trunk and anterior caudal vertebræ of the young; fig. 14, C, is recognisable as Lamnoid in character, but fig. 13, A, is peculiar. It will be noticed, further, how, in passing backward from the root of the caudal fin (fig. 14, A, B, C), the concentric laminæ dwindle and the radially disposed parts become relatively more important.

The wedge-faces, usually the first parts to undergo calcification, here calcify late. The concentric lamellæ of the young persist in the adult (fig. 14, A), and when isolated by removal of the cartilage by putrefactive maceration they are seen to be sieve-like (KÖLLIKER, **20**, Plate 14, fig. 10), each perforation in the lamella being connected with a short calcified tube, which in life transmits a blood-vessel. These radiating tubes occur in great numbers, and give a characteristic appearance to the transverse section of the vertebra.

At the inner ends of the arch-cartilages are imperfectly defined calcifications that may possibly be the equivalents of the diagonal rays of the Carchariidæ. In the middle of those parts of the arch-cartilages that are situated between the intermedialia there are calcified islands (figs. A and B, *i*) which vary considerably in size; in the vertebræ of the mid-trunk and branchial regions there are none in the basiventral cartilages; those in the basidorsals of the vertebræ of the branchial region are large and shaped like the letter T.

The vertebra shown as fig. 14, A, taken from the region just anterior to the caudal fin, is reproduced half the natural size. It is small, as the vertebræ of the basking shark go, for those of the precloacal region measure some 150 mm. across horizontally, while the maximum diameter of the open end of the double cone is 180 mm. The vertebræ of the branchial region are small, even smaller than that reproduced in fig. A.

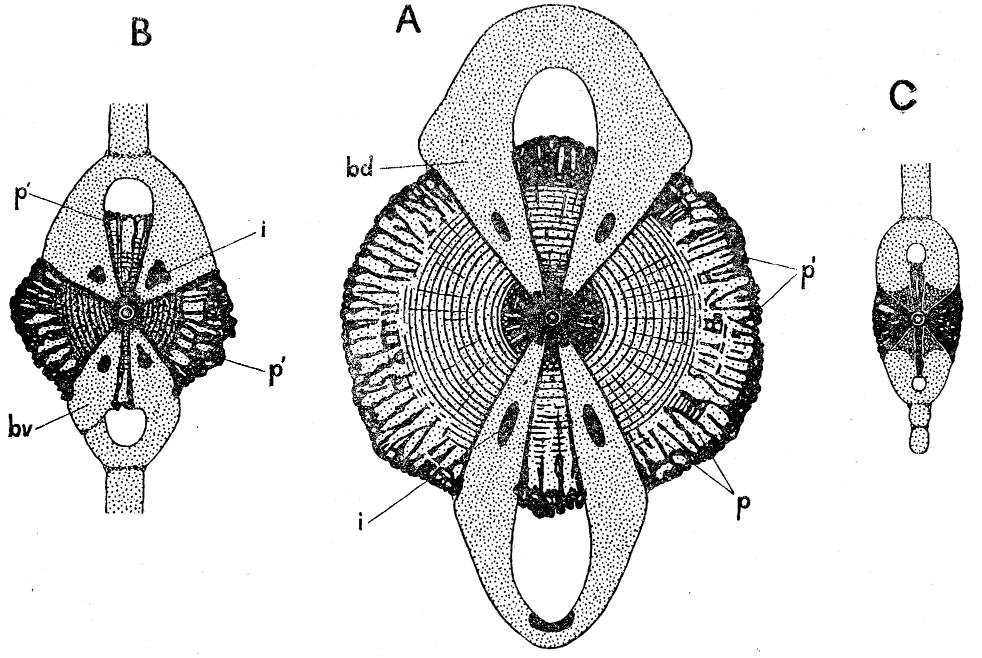

FIG. 14.—*Cetorhinus maximus*, × 0·5. A, caudal vertebra, from region just anterior to the caudal fin. B, vertebra about midway between those shown as figs. A and C. C, one of the hindermost vertebræ. (For explanation of the lettering, see p. 404.)

Judging from a plaster cast of a skeleton of *Cetorhinus* made at the Bergen Museum, and now exhibited at the Brit. Mus. (Nat. Hist.), caudal diplospondyly begins at the 35th vertebra. Counting each vertebral body in the caudal region as a centrum, without entering into the vexed question whether it is a centrum or a half-centrum, the vertebra drawn as fig. 14, A, would be the 52nd. Behind this there are another 54 centra.

In conclusion it may be pointed out, as an item of interest to the palæontologist, who frequently has to deal with isolated vertebral centra of Lamnid and Odontaspid sharks, that in the trunk region the ventral intermediale is wider than the dorsal, in the cloacal region they are about equal, and as one passes backward along the tail the ventral intermediale becomes narrower and narrower. For the application of this knowledge, however, it is first necessary to know which is the dorsal side of the centrum, and in an isolated centrum this is not easy to ascertain.

Scyliorhinidæ.

The material available consisted of:—

Scyliorhinus canicula, six adults, purchased from the Marine Biol. Lab., Plymouth. Embryos, 5, 7, 10 and 55 mm. long, in the collection at the Royal Coll. Science.

Scyliorhinus stellaris, three adults; and one half-grown, 610 mm. long; purchased from the Marine Biol. Lab., Plymouth.

Scyliorhinus marmoratus, no locality, Brit. Mus. (Nat. Hist.).

Scyliorhinus analis, two, Sydney, presented by Prof. W. A. HASWELL.

Pristiurus melanostomus, two, Brit. Mus. (Nat. Hist.).

To HASSE is due the discovery that the key to the interpretation of the vertebral structure of the common dog-fishes, *Scyliorhinus canicula* and *Scyliorhinus stellaris*, is to be found in such species as *maculatus* and *marmoratus* (**15**, D, pp. 242–253, and Plates 33–34). These latter species possess well-marked diagonal lamellæ, and intermedialia (periostale Strahlen und Keile). The diagonal lamellæ are as well developed as is the Carchariidæ (*cf.* fig. 15, A and B, p. 363, and fig. 8, p. 354), and bear the same relation to the sheath-cartilage; but the intermedialia are calcified only on the wedge-faces, as in *Scapanorhynchus* (fig. 11, p. 358), there remaining a wedge of unaltered cartilage in each.

As one approaches the end of the tail in *Scyliorhinus marmoratus* the outer-zone cartilage becomes relatively more abundant, and the intermedialia more reduced. In fig. 15, C, it will be noticed that the ventral intermediale has disappeared, the dorsal one is reduced to a minimum, and the laterals are flatter, and relatively smaller than in the anterior parts of the vertebral column.

In *Scyliorhinus stellaris* the intermedialia are more completely calcified than in *Scyliorhinus marmoratus*, and their edges grade off into the layer of tesseræ of the arch-cartilages. The trunk vertebra that is represented in fig. 16, B, was taken from an adult fish, and the limits of the outer-zone cartilage could not be distinguished; the position of the membrana elastica externa indicated in the figure was ascertained from a half-grown fish measuring 610 mm. in length. HASSE figures a caudal vertebra of a much younger fish, showing the membrana elastica externa still superficial in the four regions where the intermedialia will later be developed (**15**, D, Plate 34, fig. 17). A similar stage of development is seen in GOETTE's ripe embryo of *Scyliorhinus canicula* (**13**, Plate 29, fig. 18).

GOETTE, it is to be observed, dismisses the intermedialia of *Scyliorhinus* as mere "dünne Fortsetzungen" of the arch-cartilages, and "Verbindungsstücke der Wirbelbögen untereinander," and he is unable to agree with KÖLLIKER as to their perichondrial origin (**13**, p. 491); but he holds the same view with regard to the intermedial wedges of the Carchariidæ, in spite of the fact that his own figures (figs. 38 and 41) demonstrate the mode of origin that is claimed by KÖLLIKER.

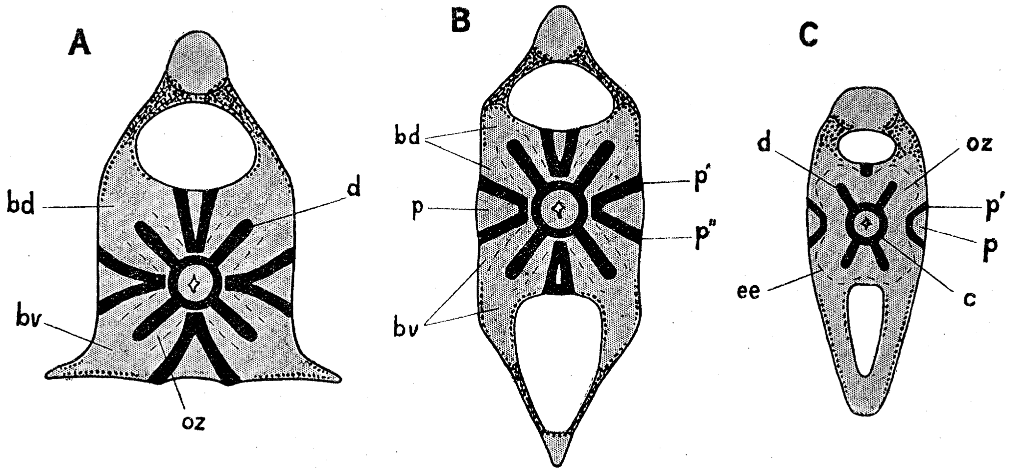

FIG. 15.—*Scyliorhinus marmoratus*, × 8. A, vertebra from region of pectoral girdle. B, from region just anterior to the anal fin. C, from middle of the length of the caudal fin. (For explanation of the lettering, see p. 404.)

In a full-grown specimen of *Scyliorhinus canicula*, the calcification is less abundant than in a full-grown *Scyliorhinus stellaris*, and the relations are such as are shown in fig. 16, A. It will be noticed that there is a well-marked investing layer (*i l*) around

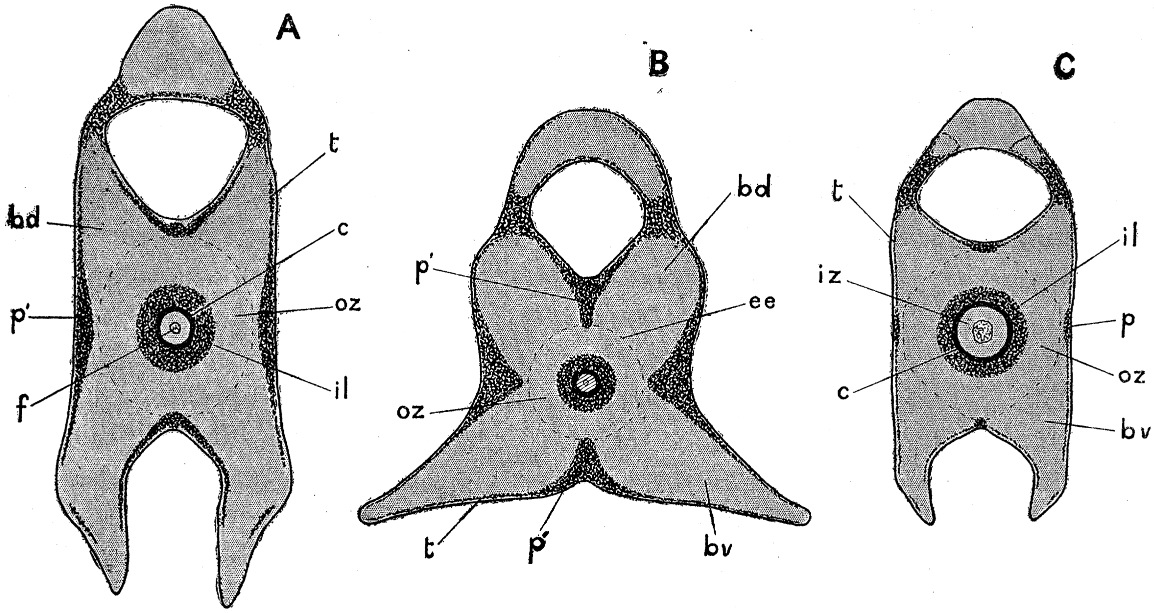

FIG. 16.—A, *Scyliorhinus canicula*, caudal vertebra, from region of first dorsal fin, × 8. B, *Scyliorhinus stellaris*, pre-cloacal vertebra, × 3·5. C, *Pristiurus melanostomus*, vertebra from region between first and second dorsal fins, × 9. (For explanation of the lettering, see p. 404.)

the double cone (*c*) in both species. The vertebræ of *Scyliorhinus analis* resemble those of *Scyliorhinus canicula*, not those of *Scyliorhinus marmoratus*.

In *Pristiurus melanostomus* (fig. 16, C) the degree of calcification of the intermedialia is at a minimum, and the general condition approaches that found in Squalines (*cf.* fig. 22, B). In his account of the skeleton of *Pseudotriacis microdon*, JACQUET describes only the external features of the vertebræ,* but REGAN has put it on record that in this fish the secondary calcification is feeble, as in *Pristiurus*.†

Orectolobidæ.

The material available consisted of—

Ginglymostoma cirratum, young, 325 mm. long, South Seas; and late embryo, 210 mm. long, South America, Brit. Mus. (Nat. Hist.).

Orectolobus barbatus, half-grown, 700 mm. long, in alcohol, Mus. Roy. Coll. Surg., London; and branchial region of a smaller specimen, about 460 mm. long, Brit. Mus. (Nat. Hist.).

Chiloscyllium plagiosum, adult, no locality; also young, 240 mm. long; also embryo, 120 mm. long, Brit. Mus. (Nat. Hist.).

Stegostoma tigrinum, half-grown, 660 mm. long, South India, vertebral column in alcohol, presented by J. HORNELL, Esq.; also embryo, 210 mm. long, N.W. Australia, Brit. Mus. (Nat. Hist.).

There is a fairly close agreement in the vertebral structure of *Chiloscyllium*, *Ginglymostoma*, and *Stegostoma*, whereas *Orectolobus* stands rather apart. Vertebræ of *Rhinodon* were not available for study; they do not seem ever to have been described. HASSE remarks on his inability to procure any for examination (**15**, E, p. 3).

A marked peculiarity is to be noted in the early development of the intermedialia of *Chiloscyllium*, *Ginglymostoma*, and *Stegostoma*. In an embryo of *Chiloscyllium*, for instance, in which the perichondrium is just beginning to become active, the membrana elastica externa occupies a superficial position in the customary four places, dorsal, ventral, and lateral; but, instead of the *whole* of each perichondrial tract becoming active as a cartilage-producer, the activity is for a considerable time restricted to its two longitudinal margins, the middle part only responding later. In fig. 17, E, the perichondrium of the right lateral tract has at p' and p'' produced a small amount of cartilage on its inner face, and this has already undergone calcification; between p' and p'', however, the perichondrium is as yet inert, and the membrana elastica externa is still external. It remains external for some time longer, during which the parts p' and p'' increase considerably (fig. F) by successive superficial increments, and the maintenance of its external position is to be attributed

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* JACQUET, M., 'Bull. Mus. Océan. Monaco,' No. 36, 1905, pp. 28, eight Plates.

† REGAN, C. T., **29**, p. 745; and 'Ann. Mag. Nat. Hist.,' ser. 8, i, 1908, p. 464.

to a radial extension of the outer-zone cartilage. The actual distance, as measured in the slides, between the part marked *e e* and the nearest part of the cone (*c*), is greater in F than in E, but the inner parts of *p′* and *p″* are in F at the same distance from the double cone as in E.

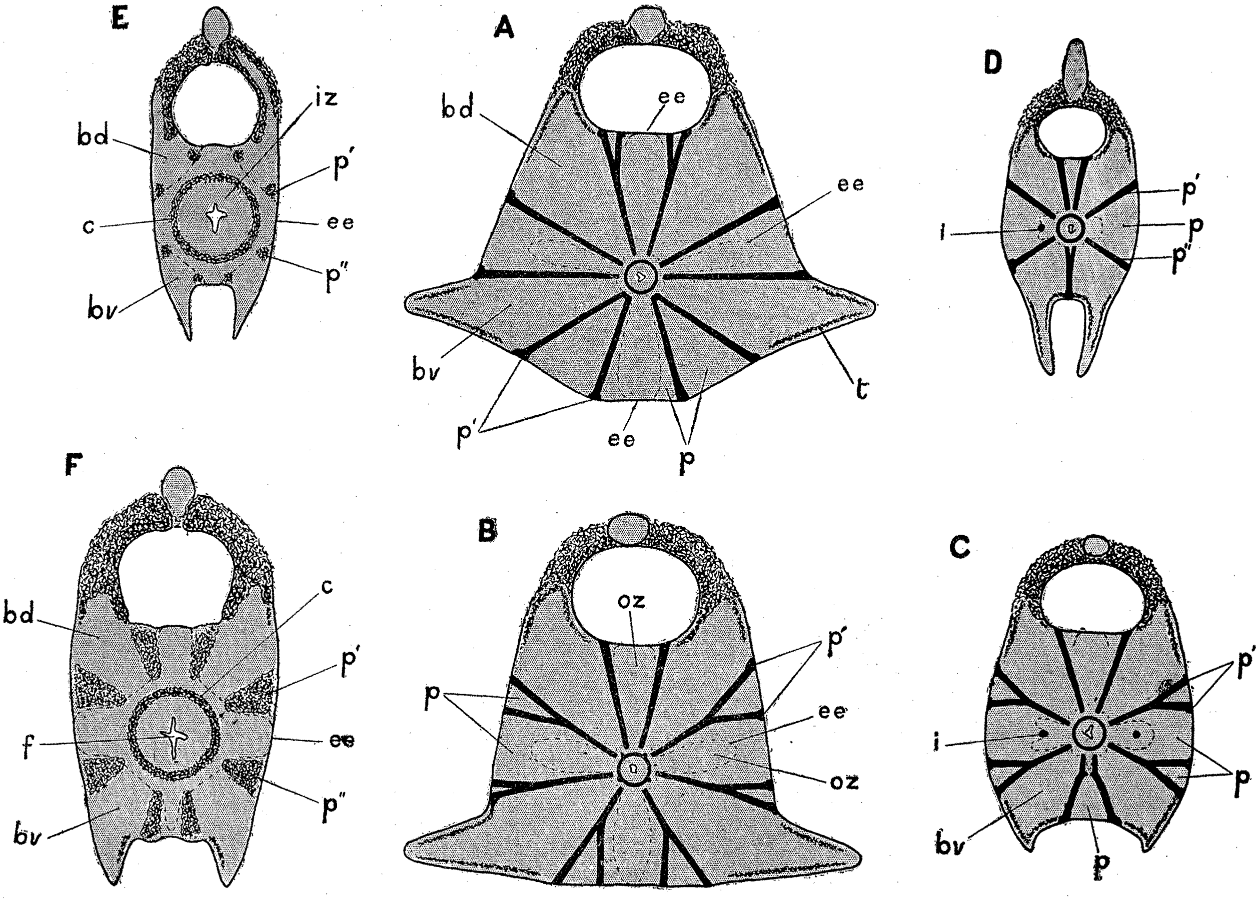

FIG. 17.—*Chiloscyllium plagiosum.* A, trunk vertebra of adult, from region of pectoral girdle, × 7. B, vertebra from region just anterior to base of pelvic fins, × 7. C, from region between first and second dorsal fins, × 7. D, from region of hind end of anal fin, × 7. E, vertebra from region just behind the first dorsal fin; embryo, 120 mm. long, × 17. F, vertebra from region just behind the first dorsal fin; embryo, 240 mm. long, × 17. (For explanation of the lettering, see p. 404.)

In fig. D, the magnification of which is less than that of figs. E and F, the parts *p′* and *p″* have grown into extensive radial lamellæ, but the outward spreading of the sheath-cartilage in the horizontal direction has ceased, and the membrana elastica externa is separated from the lateral surface of the centrum by a mass of uncalcified cartilage (*p*), produced by the part of the perichondrium which was at first inert. The same fate does not befall the outer-zone cartilage in the vertical direction; the upper tract continues to grow upward, and to maintain the membrana elastica externa in a superficial position, in all vertebræ (A–D); in the lower tract, however, the activity of growth of the sheath-cartilage diminishes as one passes backward along the vertebral column (B, C).

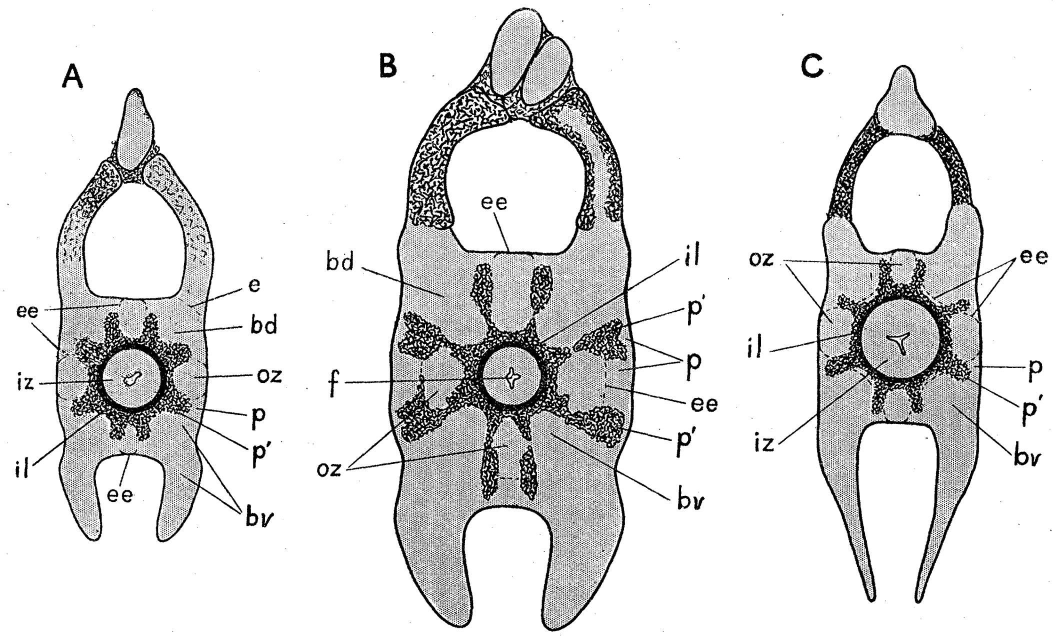

FIG. 18.—A, *Ginglymostoma cirratum*, late embryo, 210 mm. long; vertebra between first and second dorsal fins, × 13·5. B, *Ginglymostoma cirratum*, young, 325 mm. long; vertebra between first and second dorsal fins, × 13·5. C, *Stegostoma tigrinum*, embryo, 210 mm. long; vertebra between pelvic and second dorsal fins, × 13·5.

e, position of membrana elastica externa according to HASSE, **15**, D, Plate 26, fig. 19; *ee*, position as ascertained in the present investigation. (For explanation of other lettering, see p. 404.)

In vertebræ of the caudal region may be found calcified islands in the horizontal plane that contains the axis of the centrum; they may develop late, and lie within the outer-zone cartilage (fig. C, right side), or they may develop in such a manner as to check the outward bulging of the sheath-cartilage (figs. C and D, left side). Diagonal rays are not altogether wanting; traces of them are shown in fig. B.

The lateral calcified rays are simple in the anterior and posterior parts of the vertebral column, but forked in the middle parts (*cf.* A, D and B, C); the upper rays fork only in the branchial region (A); the lower rays are confluent in the hindermost vertebræ (D), simple in the anterior caudal (C), forked more anteriorly (B), and in the branchial region are V-shaped, rather than Y-shaped (A).

Ginglymostoma and *Stegostoma* differ from *Chiloscyllium* in the greater extent to which the investing layer is developed (*cf.* figs. 18 and 17); and, largely as a consequence of this, the innermost parts of the eight calcified lamellæ originate in sheath-cartilage (fig. 18, A and C). Further than this, the perichondrially produced cartilage undergoes calcification rather later, so that the outer ends of the calcified rays are relatively farther from the surface. The line of demarcation between the uncalcified perichondrial cartilage and the arch-cartilage is not so well marked as in *Chiloscyllium*, the texture of the two cartilages being almost the same, whereas in *Chiloscyllium* the perichondrially produced cartilage is a small-celled cartilage ; in fig. 18, A, the limit between the two cartilages follows roughly the indicating line that is drawn from the letter p' ; the cartilage immediately above the line is new cartilage of perichondrial origin (p), that below the line is the original, although still expanding, arch-cartilage (bv). The stage of development shown by the young *Ginglymostoma* in fig. 18, B, is relatively later than that of the young *Chiloscyllium* represented in fig. 17, F, for the lateral parts of the membrana elastica externa are no longer superficial.

In fig. 18, B, it will be noticed that there is a constriction between the proximal and distal parts of the rays, or even a separation of the parts, which is of interest in connection with KÖLLIKER's figure of *Ginglymostoma* (**20**, Plate 13, fig. 1, 1), in which the detachment is still more pronounced. Vertebræ of full-grown *Ginglystoma* were not available for study. According to HASSE's figure (**15**, D, Plate 26, fig. 21), the caudal vertebræ closely resemble those of *Stegostoma;* in the anterior trunk region the rays branch to a very great extent (*ibid.*, Plate 26, fig. 24).

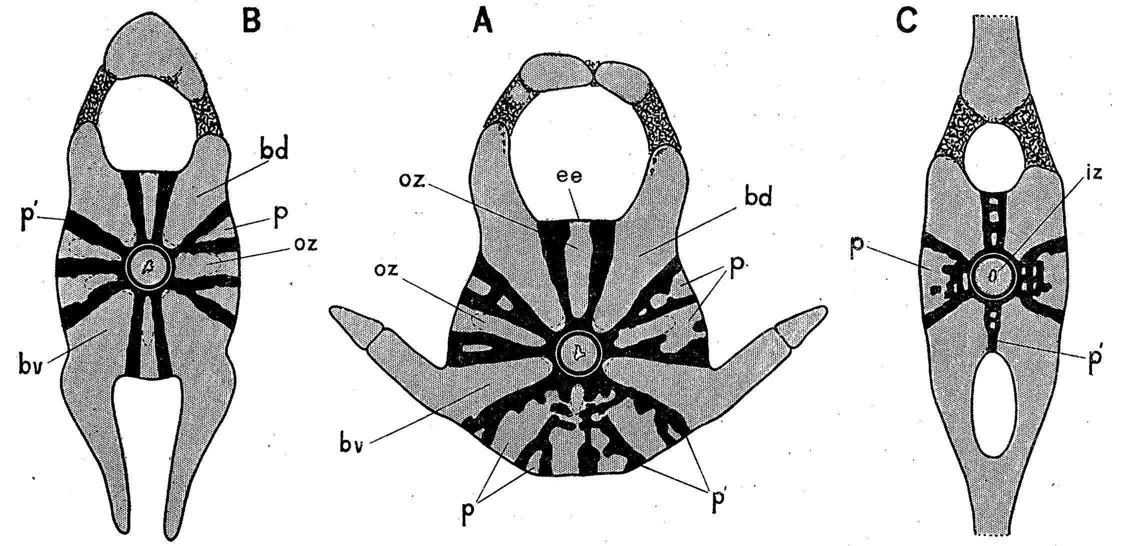

FIG. 19.—*Stegostoma tigrinum*, 660 mm. long, × 6. A, vertebra from region of pectoral girdle. B, vertebra from post-cloacal region ; for younger stage, see fig. 18, C. C, vertebra from region half-way along the caudal fin. (For explanation of the lettering, see p. 404.)

HASSE's interpretation of the parts of the vertebra (**15**, D, Plate 26, fig. 19) differs materially from that here given, for he represents the membrana elastica externa as following a more or less circular course, as shown at e in fig. 18, A, of this paper. Similarly, in *Stegostoma*, the particular tract of cartilage which, on the right side of fig. 19, B, of this paper is marked p, to signify cartilage of the intermediale, is marked by HASSE, on the left side of his fig. 3, Plate 25, with the letter a, to denote outer-zone cartilage. It is strange that HASSE, while regarding the calcified lamellæ of *Chiloscyllium* (**15**, D, Plate 40, figs. 4 and 5) as parts of the Periostale Keile, did not do so in *Stegostoma* and *Ginglymostoma* (*ibid.*, p. 197, para. 2; p. 202, para. 5).

Comparison of figs. 19 and 17 shows that in a well-grown, though not adult *Stegostoma* the rays, while more irregular, have the same general arrangement as in *Chiloscyllium.* Remnants of the membrana elastica externa can be seen in all except the hindermost vertebræ. The normal condition in the anterior caudal vertebræ is evidently one in which the lateral rays are two Y-shaped rays (**15**, D, Plate 25, fig. 3), but in the material examined it happened, curiously enough, that three successive vertebræ possessed three separate rays on one side (fig. 19, B), with outgrowths of outer-zone cartilage between them.

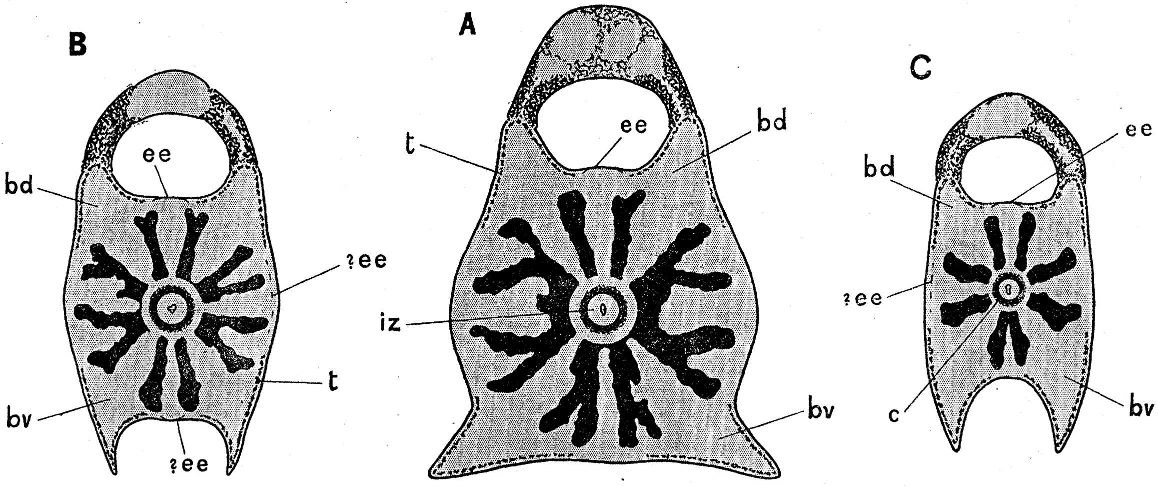

FIG. 20.—*Orectolobus barbatus*, 700 mm. long, × 4·6. A, pre-cloacal vertebra. B, vertebra from region in front of second dorsal fin. C, vertebra from region of anal fin. (For explanation of the lettering, see p. 404.)

The vertebræ of *Orectobolus*, although possessing the eight calcified rays, simple or forked, present considerable difficulties in the way of the interpretation of the parts, as compared with those of the three preceding genera. The larger of the two specimens available for study was only half-grown, being not more than 700 mm. long, but its vertebræ appear to be less developed, although slightly larger, than those figured by HASSE (**15**, D, Plate 25, figs. 4–6). In fig. 20, the calcified rays are seen not to touch the double cone, nor do they reach the surface, yet they are represented as extending from double cone to surface in HASSE's fig. 6. HUBRECHT gives a figure* just clear enough to be recognisable as an Orectolobid vertebra, and he states that the radiating calcified lamellæ are "allenthalben von der Elastica externa umschlossen," which is the same view as that of HASSE (**15**, D, p. 199). In my own sections the only unmistakable remnants of the membrana elastica externa are those in the floor of the neural canal, but there are

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* BRONN's 'Klassen und Ordnungen des Thierreichs,' Bd. VI, Abth. 1, Lief. 3, 1878, Plate 10, fig. 13.

doubtful remnants in the roof of the hæmal canal of the caudal vertebræ, and others at the side of the centrum (fig. 20, B and C, ? *e e*), which, if verified by recourse to more suitable material, would necessitate an admission that the calcified rays are not perichondrial in origin, and thus differ from those of *Chiloscyllium* and *Stegostoma*. It is difficult without further evidence to accept this position, but it is to be noted that in some parts, as at *t* in fig. B, there are tesseræ immediately external to one of the calcified rays, which could scarcely happen if the ray were growing outwardly by additions from the external perichondrium. Further research on this genus is clearly in demand.

In the sharks of the family Orectolobidæ the supradorsal cartilages in certain parts of the vertebral column tend to run in double series, but not with any regularity (fig. 18, B; fig. 19, A; fig. 20, A; and HASSE, **15**, D, Plate 25, fig. 6; Plate 40, fig. 4).

Cestraciontidæ.

The material available consisted of:—

Cestracion philippi, three adults and one young, 260 mm. long, Brit. Mus. (Nat. Hist.); and caudal regions of three fishes, large, medium, and small; also a ripe embryo, 180 mm. long, Sydney, presented by Prof. W. A. HASWELL.

The characteristic structure of the caudal vertebræ of *Cestracion* is that displayed in figs. 21, A and C. The calcified rays as seen in the section are eight in number,* but one or more of them may be forked; they are approximately symmetrical in disposition, and the upper and lower pair are directed towards the inner edges of the basidorsal and basiventral cartilages respectively, while the laterals are directed towards the outer edges of those cartilages. The inner ends of the rays are from the first in contact with the double cone, which has a very thin investing layer, and the outer ends are in some cases strangely enlarged. None of the rays reach the surface; they all terminate well within the sheath-cartilage, the outer limit of which is indicated by the remnants of the membrana elastica externa that are visible even in the adult.

The vertebra shown at fig. 21, C, is from the same region of the tail as that shown at A, but is taken from a younger fish; the membrana elastica externa is superficial above, below, and at the sides of the centrum. In older vertebræ (*e.g.*, A) it is superficial above, but not in the other three regions, and here difficulties arise in regard to the interpretation of the parts that are immediately external to the membrane. As is shown on the right side of fig. A, the calcifications (? p') may be separate from the tesseræ of the arch-cartilages (*t*), or they may be in continuous series with them, as shown below and on the left side, and there is nothing in the histological structure to enable one to decide whether there is in the parts in question a perichondrial activity, producing a feebly developed intermediale, or a

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* 'Bei Cestracion . . . sind regelrecht acht Strahlen vorhanden,' **15**, A, p. 51, para. 2.

fusion of arch-cartilages such as the continuity in the layer of tesseræ might suggest. In the trunk region there can scarcely be any doubt that the basidorsal and basiventral cartilages are continuous at the sides of the centrum (fig. 21, D), just as there is in the Batoid fishes (*cf.* A and B, fig. 4, p. 340). What adds to the difficulty in the way of interpretation is that in some of the more posterior caudal vertebræ (fig. 21, B), the calcification marked ?*p*′, or at least some part of it, is *internal* to the membrana elastica externa. In the hindermost vertebræ the calcified rays become fewer and more irregular (fig. B).

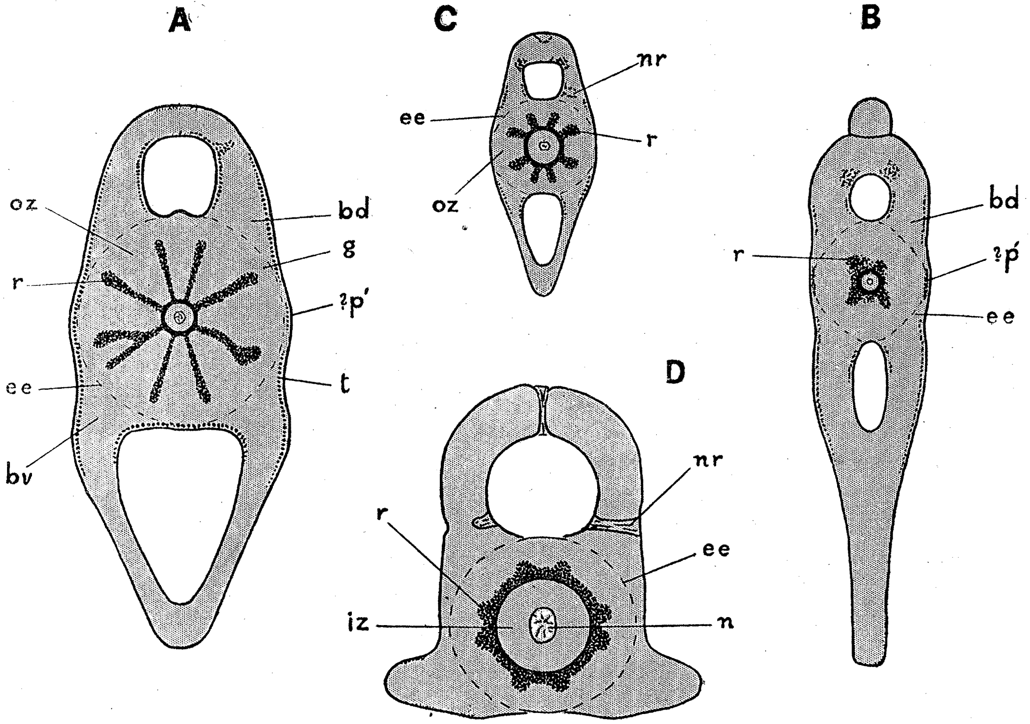

FIG. 21.—*Cestracion philippi.* A, caudal vertebra from region of second dorsal fin, × 3. B, a more posterior vertebra of the same fish, from region of hinder part of front lobe of caudal fin, × 3. C, vertebra from region of second dorsal fin of a half-grown fish, × 3. D, vertebra from branchial region of a ripe embryo, 180 mm. long, × 9. (For explanation of the lettering, see p. 404.)

In the trunk region of the vertebral column eight primary rays can be distinguished in early stages of development (fig. 21, D), but in adults the rays are more numerous, and they are so evenly spaced around the double cone that it is not possible to explain how the condition can have arisen by a process of forking and branching of the eight rays. In fig. 4, A, p. 340, for instance, while the upper and lower pairs can be identified, it is to be noted that there are three main lateral rays, instead of two, on each side.

HASSE does not give a really characteristic figure of the vertebra of *Cestracion,* but his interpretation of the calcified rays as belonging to the outer-zone cartilage is in agreement with that here given (**15**, D, Plate 24). The figures given by

Daniel ('Journ. Morph.,' xxvi, 1915, Plate 6, figs. 20 and 23) show that the vertebral structure of *Cestracion francisci* agrees with that of *Cestracion philippi;* there are eight radiating lamellæ in the caudal vertebra that he figures, and twelve in a vertebra from the branchial region.

Squalinæ.

The material available consisted of:—

Echinorhinus spinosus, vertebral column in formalin solution, Brit. Mus. (Nat. Hist.); also selected vertebræ in alcohol, in the collection at the Royal Coll. Science.

Oxynotus centrina, two, Brit. Mus. (Nat. Hist.).

Spinax niger, two, Brit. Mus. (Nat. Hist.).

Squalus acanthias, two adults, purchased, Grimsby; three adults, purchased, Folkestone; one adult, purchased, Plymouth; one embryo, 60 mm. long, and two late embryos, 210 mm. long, in the collection at the Royal Coll. Science.

Centrophorus calceus, vertebral column of adult in alcohol, presented by Prof. W. N. F. Woodland; one young, 250 mm. long, Brit. Mus. (Nat. Hist.).

Centrophorus squamosus, vertebral column in alcohol, Brit. Mus. (Nat. Hist.).

Scymnorhinus lichia, vertebral columns of two specimens, in formalin solution, Brit. Mus. (Nat. Hist.).

Somniosus microcephalus, vertebræ in alcohol, Brit. Mus. (Nat. Hist.).

Somniosus rostratus, skeleton in alcohol, Brit. Mus. (Nat. Hist.).

There is a striking uniformity in the essential features of the vertebræ of the Squaline fishes, not only as between different fishes, but also as between the caudal and trunk vertebræ of the same individual fishes. The double cone may be either long or comparatively short (fig. 2, p. 321), and it is fairly wide open in the middle; a moderately thick investing layer is present in most cases. Remnants of the membrana elastica externa are usually recognisable in the vertebræ of adult fishes (fig. 22, p. 372), and these serve to show that there is a large proportion of outer-zone cartilage entering into the composition of the definitive centrum.

The outer crust on the arches commonly takes the form of a continuous compact layer rather than a series of separable tesseræ. The crust is thick in the case of *Scymnorhinus*, particularly at the anterior and posterior ends of the centrum, where it is continuous with the investing layer of the double cone; in preparing the double cone of *Scymnorhinus* represented in fig. 2, A, the end portions of the crust were removed by means of a file.

In the trunk vertebræ of the Squalinæ the basiventral cartilages are set fairly high up, and there is an obvious fusion of the basidorsal and basiventral cartilages on each side of the centrum (fig. 22, A and C); the basiventral may in some cases be segmented into an upper part which bears the rib, and a lower part, termed the aortic support (*Somniosus*, Schauinsland, **30**, p. 411, fig. 213, C).

In caudal vertebræ there is a lateral tract which I regard as of perichondrial origin (fig. 22, B, *p*); though mainly cartilaginous, it may be partly calcified.* On the inner side of this, but external to the membrana elastica externa, is a calcified layer that is continuous above and below with the general external crust of the arch-cartilages; the origin of this part is doubtful. In the floor of the neural canal and in the roof of the hæmal canal there is a continuous curved calcified layer, but the middle parts of this lie on the inner side of the membrana elastica externa, and thus occur in the sheath-cartilage.

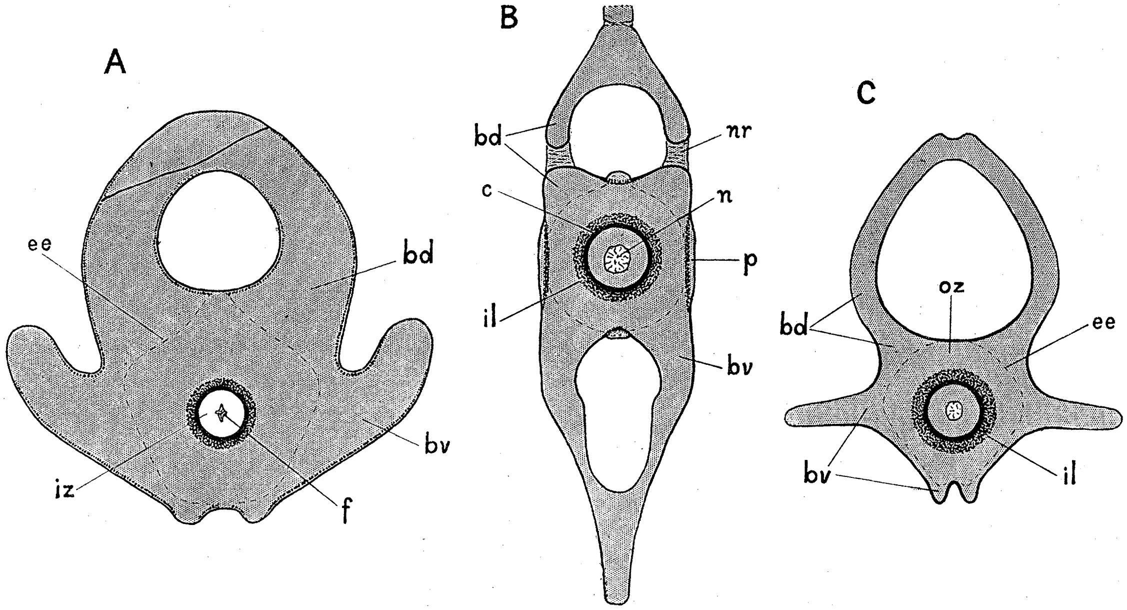

FIG. 22.—A, *Oxynotus centrina*, trunk vertebra, × 3. B, *Squalus acanthias*, caudal vertebra, × 4. C, *Spinax niger*, trunk vertebra, × 10. (For explanation of the lettering, see p. 404.) (The part marked *iz* in fig. A should have been shaded, as in B and C.)

Sections through the vertebræ of the ripe embryo of *Squalus acanthias* show an early differentiation of the sheath-cartilage into the three zones, with incipient calcification of the middle zone; the notochord is as yet scarcely constricted by the growing inner-zone cartilage; the membrana elastica externa is still external at the sides of the centrum, and above and below. No illustration is here given, since the features are exactly those shown in the figures of GOETTE (**13**, Plate 30, fig. 30) and HASSE (**15**, B, Plate 11, fig. 19). In the embryo of a length of 60 mm. the differentiation of the sheath into the three zones has not yet taken place.

Except in the terminal caudal vertebræ, there are in *Somniosus microcephalus* and *Echinorhinus spinosus* no calcified structures. As in the case of *Hexanchus,* the intervertebral ligaments are long, and the "centra" are represented by thick septa, perforated in the middle by the funicle (fig. 23). The vertebral column in these fishes

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* It is not shown in HASSE's figure, **15**, B, Plate 12, fig. 20.

is clearly degenerate, and it is of particular interest to recall the fact that in *Somniosus rostratus* the vertebræ are not reduced in number as they are in *Somniosus microcephalus*, and they are typically Squaline in character, the double cones being well developed, although the external crust of the arches is thin or wanting.* Seeing that HASSE's figures of *Echinorhinus* (**15**, B, Plate 9) are drawn of the natural size, it is clear that his specimen was not more than half-grown.

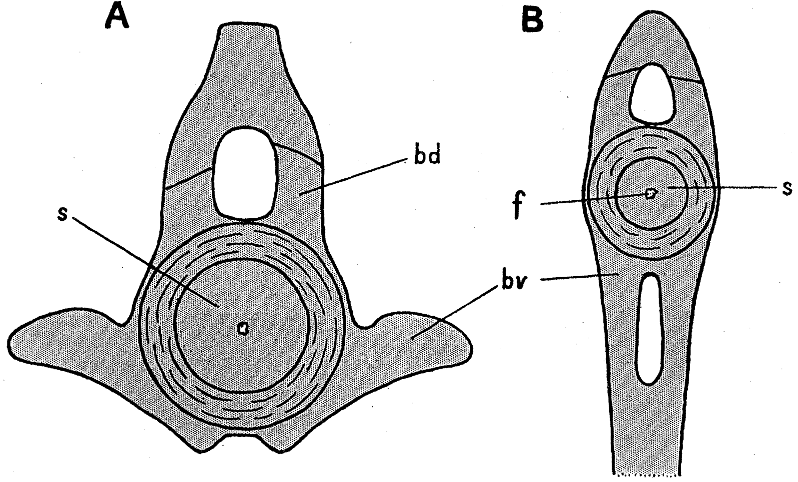

FIG. 23.—*Echinorhinus spinosus*, nat. size. No parts are calcified. A, mid-trunk vertebra. B, vertebra from region between second dorsal and caudal fins. (For explanation of the lettering, see p. 404.)

The terminal caudal vertebræ of *Echinorhinus* were not available for study; in those of *Somniosus microcephalus*, as mentioned on p. 318, there are reduced vertebral structures, namely, external patches of irregular granular calcification (HASSE, **15**, B, Plate 8, fig. 5; also HELBING,* p. 446 [112]) and internal granular calcified tubes or rods with dilated ends, representing degenerate double cones.

No specimen of *Centroscyllium* was available, but KÖLLIKER has remarked (**20**, p. 55) that the vertebræ resemble those of *Squalus* (*Acanthias*). It will be observed that KÖLLIKER regards the thin tract that lies external to the membrana elastica externa at the side of the centrum as due to a fusion of the arch-cartilages, such as occurs in the trunk region, and not as a new structure of perichondrial origin. One can see, he writes, " dass die Wirbelkörper eine zarte Belegung von den knorpeligen Bogen besitzen und dass die oberflächliche Verkalkung derselben diesem der Chordascheide fremden Knorpel angehört." HASSE's figures of *Centroscyllium* (**15**, B, Plate 10) show that the vertebræ present no special features.

HASSE records that the vertebræ of *Isistius* agree with those of *Somniosus rostratus* and *Scymnorhinus*, but approach the latter more than the former (**15**, E, p. 8). WOODLAND's figures of the vertebræ of *Centrophorus* call for no special comment

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* HELBING, 'Nova Acta Abh. kaiserl. Leop.-Carol. Akad.,' lxxxii, 4, Halle, 1904, pp. 438–448 (104–114) also HASSE, **15**, B, Plate 8, figs. 7–12.

('Proc. Zool. Soc.,' 1906 (1907), Plate 58, figs. 7 and 8); neither do HASSE's figures (**15**, B, Plate 11).

Whereas caudal diplospondyly prevails in Elasmobranchs generally, it has been held that *Scymnorhinus* is exceptional (**6**, p. 195). The specimen of *Scymnorhinus* examined in the course of this inquiry exhibits the same diplospondyly as the other members of the family; so also does the figure given by MAYER (**24**, Plate 18, fig. 9).

Pristiophorinæ.

The material available consisted of—

Pristiophorus cirratus, late embryo, total length 300 mm., of which the rostral saw measures 75 mm., New South Wales, Brit. Mus. (Nat. Hist.).

Pristiophorus japonicus, adult, Brit. Mus. (Nat. Hist.).

Pristiophorus nudipinnis, caudal vertebræ, Brit. Mus. (Nat. Hist.).

Pliotrema warreni, skeleton in alcohol, South Africa, Brit. Mus. (Nat. Hist.).

The general features of the vertebræ of *Pristiophorus* are displayed in fig. 24, A. Around the double cone, but separated from it by a broad tract of cartilage, is a calcified tube, that appears in section as a square with truncated corners. This tube is at its anterior and posterior ends confluent with the broad parts of the double cone; it is not to be regarded as a wide-standing investing layer, for a thin investing layer is present also, situated immediately external to the double cone. In HASSE's figure of the vertebra of the same species (*Pristiophorus japonicus*, **15**, C, Plate 13, fig. 5) the lateral parts of the main calcified "ring" are incomplete, but his figure of *Pristiophorus cirratus* (*ibid.*, fig. 4) agrees with fig. 24, A, of the present paper.

There are four small superficial calcifications of perichondrial origin (p') above, below, and at the sides of the centrum. Remnants of the membrana elastica externa are recognisable in the adult, and, in *Pristiophorus japonicus*, the course taken by the membrane, as seen in a transverse section, is one that passes through the inner part of an intermedial calcification, then across the corner of the main ring, and then through the inner part of the next intermediale. Thus it will be seen that the outer-zone cartilage bulges out horizontally and vertically, and that the calcified ring occurs partly in sheath-cartilage and partly in arch-cartilage. That too much importance should not be attached to this, however, is evident from the fact that, in caudal vertebræ of *Pristiophorus nudipinnis*,* the course of the membrane, while agreeing, in so far as its relations to the intermedial calcification are concerned, pursues a less sinuous line, and remains external to the main calcified ring. The ring is consequently, in this latter species, a structure that belongs solely to the sheath-cartilage.

In *Pliotrema warreni* (fig. 24, B) the main calcified ring is thin, and with a

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* Only posterior caudal vertebræ, from the base of the caudal fin, were available for study.

tendency to be discontinuous; from it there project eight strongly marked rays, that broaden externally, and fail to reach the surface. The upper and the lateral calcified intermedialia are wanting, and the lower one is small. The membrana elastica externa follows the same course as in *Pristiophorus japonicus* (fig. 24, A), the parts in the diagonal positions being internal to the calcified ring. It passes through the inner part of the lower intermedial calcification, and just reaches the surface of the centrum above, at the bottom of a slight depression between the two basidorsal cartilages. At the sides of the centrum the membrane is separated from the surface by a tract of cartilage, which, by analogy with *Pristiophorus*, would be taken to be intermedial cartilage, but, in the absence of embryological evidence, the point cannot be decided, for the texture of the cartilage affords no indication of its mode of origin. Similarly, in the case of the outer parts of the eight calcified rays, a difficulty arises; the membrana elastica externa passes obliquely through each ray, the main portion of the calcification lying external to it. On the assumption that the part marked ?*p* is cartilage of perichondrial origin, one would conclude that the major portion of the calcified ray is also of perichondrial origin, and the deduction is strengthened by the discontinuity between the tesseræ of the basidorsal and basiventral cartilages, but the general appearances strongly suggest that the rays are calcifications in the arch-cartilages themselves (fig. 24, B, ?*p*′, ?*bd*).

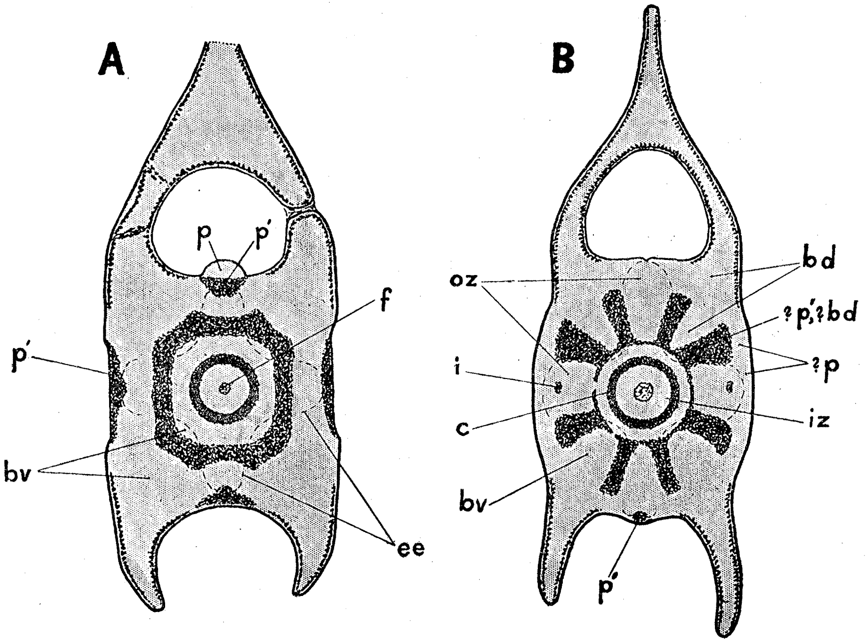

FIG. 24.—A, *Pristiophorus japonicus*, vertebra from region between pelvic and second dorsal fins, × 7. B, *Pliotrema warreni*, vertebra from region just behind first dorsal fin, × 7·5. (For explanation of the lettering, see p. 404.)

Returning to *Pristiophorus* (fig. 24, A), it will be noticed that the double projections from the main ring in the diagonal positions are the counterparts of the basal portions of the eight rays of *Pliotrema*, and there can be no question here as to the projections being parts that belong to the arch-cartilages. The detailed study of the development of the vertebræ of both *Pristiophorus* and *Pliotrema* is greatly to be desired. The only young specimen available was one of *Pristiophorus cirratus;* although the fish was fairly large, measuring 300 mm. in total length, there is in the vertebræ no calcification, except that of the double cone.

The description given by HASWELL* is not clear, for, although he writes that the vertebræ of *Pristiophorus* are "devoid of radiating lamellæ," he says that in transverse section they "exhibit, as in the case of *Selache*, two pairs of cartilaginous tracts, passing from near the centre to the supero-lateral and infero-lateral parts of the vertebræ."

Squatinidæ.

The material available consisted of:—

Squatina squatina, vertebral column of adult, in alcohol, Jersey, presented by J. HORNELL, Esq.; vertebral column of adult, Oxford Univ. Museum, lent by Prof. E. S. GOODRICH; ripe embryo, 264 mm. long, purchased from Marine Biol. Lab., Plymouth; a younger embryo, Naples, presented by Prof. W. N. F. WOODLAND.

The vertebræ of *Squatina* are peculiar, and unique in character, and there are no connecting links that would serve to associate them with the vertebræ of other Elasmobranchs. In the centrum there occur, external to the double cone, several coaxial, thin, calcified tubes, appearing as circles or ellipses in a median transverse section. The number of these is greater in the trunk region than in the caudal; in the vertebræ drawn in fig. 25 there are 27 and 23 rings in A and B respectively; the number, also, increases with age (*cf.* fig. 13, B, p. 360, and fig. 25, B).

Remains of the membrana elastica externa are not to be found in the adult, but in a ripe embryo they can be seen above, below, and at the sides of the centrum. In the first two situations the membrane is superficial (fig. 13, B), but at the sides of the centrum there lies externally to it a thin tract of cartilage.† There is no reason to believe that in either the caudal or the trunk vertebræ this tract is of perichondrial origin; the perichondrium does not present signs of exceptional activity, at all events in the two embryos examined, and it is significant that in the adult the layer of tesseræ is continuous from basiventral to basidorsal cartilage (fig. 25), pointing to the conclusion that the layer is composed of arch-cartilage. But in the floor of the neural canal of the adult the calcified layer is not composed of tesseræ; it is a smooth calcified crust, apparently perichondrial; below the centrum the tesseræ are discontinuous, and there are no superficial calcifications near the median plane; in other words, there is no evidence of fusion between the two basidorsal cartilages, nor between the two basiventrals.

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* 'Proc. Linn. Soc., N.S.W.,' ix, 1884, pp. 115 and 100.

† Similar relations are shown in the trunk vertebra of an embryo, 160 mm. long, figured by GOETTE (**13**, Plate 31, fig. 43).

SCHAUINSLAND (**30**, p. 413), following GOETTE (**13**), attributes the union of the basidorsal with the basiventral cartilage at the side of the centrum to the high position of the basiventral cartilage, resulting from the general flattening of the body, much the same as occurs in the Batoid fishes; but this does not explain the union of the two cartilages in the caudal region.

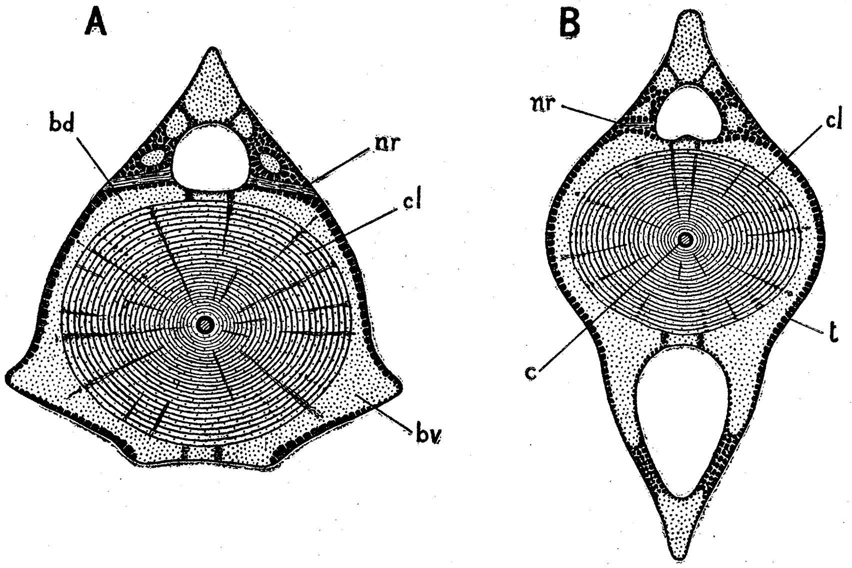

FIG. 25.—*Squatina squatina*, × 2. A, mid-trunk vertebra. B, anterior caudal vertebra. (For explanation of the lettering, see p. 404.)

The caudal vertebra shown in fig. 13, B, exhibits four calcified rings external to the double cone.* Outside the outermost ring, and internal to the remains of the membrana elastica externa, in the position marked *g*, is a growing zone, in the inner part of which the fifth ring will be developed, while the outer part will persist as the growing zone. The presumption is that this growing zone, now in the outer-zone cartilage, remains morphologically within the membrana elastica externa, even after the remnants of that membrane are no longer to be detected; that is to say, since in fig. 13, B, the four rings belong to the sheath-cartilage, the presumption is that all the 23 rings shown in fig. 25, B, are of sheath-origin. If this be admitted as a valid argument, then *Squatina* is one of the most chorda-centrous of the Elasmobranch fishes.

Militating against the acceptance of this view, though perhaps not seriously, is the fact that, in the centra of the embryo, portions of the membrana elastica externa may occasionally be found entangled and left behind in the older, more central parts of the outer-zone cartilage; the growing zone, that is to say, may in some places spread to the outer side of the membrane.

In the adult the radiating markings that are seen in a transverse section are

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* The trunk vertebræ of this fish have five rings, the vertebræ in the middle of the caudal fin only three.

partially calcified tubes containing blood-vessels that penetrate from without, somewhat similar to those seen passing through the concentric lamellæ of *Cetorhinus* (fig. 14, A, p. 361), although less numerous.

HASSE takes the view adopted above, that the calcified lamellæ of *Squatina* belong to outer-zone cartilage, and that there is a growing zone situated immediately internal to the membrana elastica externa (**15**, C, p. 129, and Plate 17, figs. 3 and 4, *a*). The earlier observations of JOH. MÜLLER (**26**) and KÖLLIKER (**20**) on the vertebræ of *Squatina* call for no special comment.

Torpedinidæ.

The material available consisted of :—

Torpedo narce, adult, also embryos and young, 82 mm. long, 50 mm. broad; 110 mm. long, 58 mm. broad; 165 mm. long, 93 mm. broad; 223 mm. long, 133 mm. broad; Mediterranean, Brit. Mus. (Nat. Hist.). Also vertebral column of adult, in alcohol, Naples, presented by Prof. W. N. F. WOODLAND.

Torpedo hebetans, vertebral column, dried, Brit. Mus. (Nat. Hist.). Also fresh adult, purchased in London.

Narcine brasiliensis, embryo, 53 mm. long, 20 mm. broad; and embryo, 104 mm. long, 58 mm. broad, Jamaica, Brit. Mus. (Nat. Hist.). Also young, 220 mm. long, 105 mm. broad, no locality, Brit. Mus. (Nat. Hist.).

Hypnos subnigrum, embryo, 65 mm. long, 42 mm. broad, Sydney, in the collection at the Royal Coll. Science.

The Batoid fishes, of which the Torpedinidæ are the first to be considered, require to be judged on their own merits, apart from the sharks, for, while their caudal vertebræ are largely comparable with those of sharks, the trunk vertebræ are greatly influenced by the extent to which the basiventral element has mounted up the side of the centrum and united with the basidorsal; this affects not only the mode of growth of the centrum, but particularly the pattern of the calcification. The interpretation of the vertebral structure of the Batoids is beset with difficulties, and the complete solution of the problem cannot be said to have been yet attained.

KLAATSCH has shown (**18**, II, pp. 168–170) that in *Torpedo* the immigration of cartilage-producing cells into the primary notochordal sheath occurs remarkably early (embryo, 26 mm. long), and the membrana elastica externa becomes reduced so soon that it cannot be relied upon as a distinctive delimiting layer. SCHAUINSLAND is of opinion (**30**, p. 418) that in the caudal as well as in the trunk region the basiventral is united with the basidorsal cartilage at the side of the centrum, and this at an early stage of development (embryo, 45 mm. long).

In an embryo of *Torpedo narce* measuring 82 mm. long and 50 mm. broad, the only parts of the membrana elastica externa to be recognised are those in the floor of the neural canal and the roof of the hæmal canal. The secondary calcification is in the form of an investing layer, about twice as thick as the cone which it surrounds; the outline of its section is not strictly circular, but already shows indications of the six outgrowths which become more pronounced later.

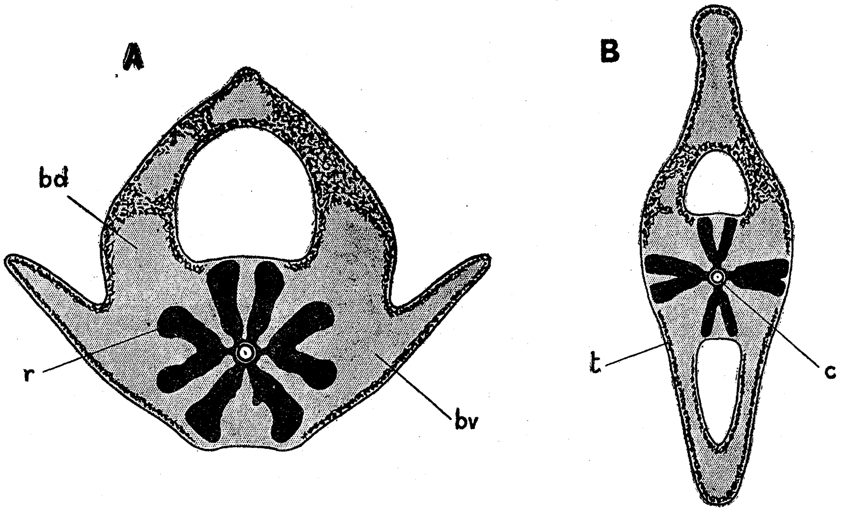

FIG. 26.—*Torpedo narce*, adult, × 7. A, mid-trunk vertebra. B, anterior caudal vertebra. (For explanation of the lettering, see p. 404.)

In the next stage available, an embryo measuring 110 mm. in length and 58 mm. in breadth, there are, in both trunk and caudal regions, six outgrowths of the secondary calcification, namely, two above, two below, and a massive one on each side (fig. 27, p. 380). [In GOETTE's figure of a young *Torpedo ocellata* (= *narce*), measuring 90 mm. in length, there are only four outgrowths, the upper and lower being single and broad (**13**, Plate 33, fig. 59), but he says (p. 489) that they branch later into a total of eight.] The parts of the membrana elastica externa seen in the earlier stage are still recognisable, and superficial in position (*e e*). In the two still later stages (165 × 93 mm., and 223 × 133 mm.) the six outgrowths are all radially longer, and they tend to enlarge at their outer ends, the lateral ones showing an indication of forking.

In the adult *Torpedo narce* (fig. 26) the lateral rays are well forked in the trunk vertebræ, less obviously so in the caudal. In the trunk vertebræ the outer ends of the rays are rounded and slightly enlarged. The upper and lower rays just fail to reach the surface; there are no tesseræ in these regions, and there are no evidences of perichondrial reinforcements such as occur in the three families that follow. In the caudal vertebræ also the rays fail to reach the surface; the tesseræ are discontinuous at the sides as well as above and below. The general impression conveyed by the sections, although there is no proof, is that the whole of the secondary calcification is of sheath-origin.

In the caudal vertebræ of *Torpedo hebetans* the transverse section exhibits four short, stout calcified rays directed vertically and horizontally; their outer ends are swollen and are set at some little distance from the surface of the centrum. In the trunk region the lateral rays tend to fork and become Y-shaped, but the vertical rays show little indication of division; they merely broaden out.

The figures of *Torpedo marmorata* given by Kölliker (**19**, Plate 3, fig. 5) and Hasse (**15**, C, Plate 23, fig. 11) agree with one another in that the lateral rays are Y-shaped, and the double upper and lower rays form a letter X; the upper and lower rays are drawn as just reaching the surface.

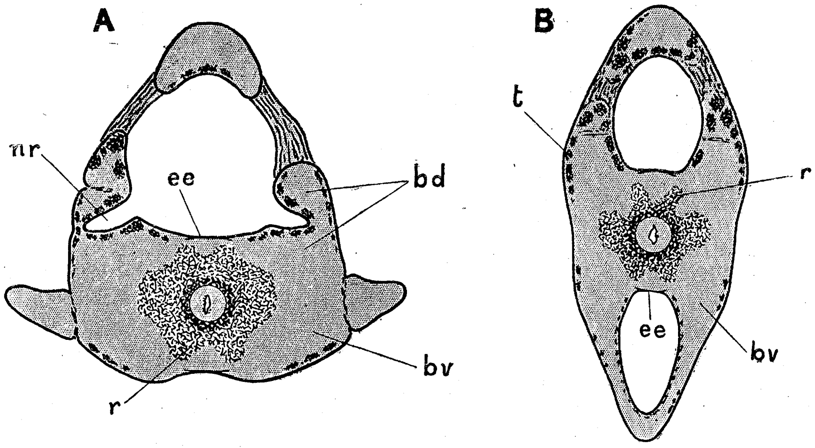

Fig. 27.—*Torpedo narce*, young, 110 mm. long, 58 mm. broad, × 18. A, mid-trunk vertebra. B, vertebra from region of first dorsal fin. (For explanation of the lettering, see p. 404.)

In *Narcine brasiliensis* there is some evidence, such as is not forthcoming in the case of *Torpedo*, that where the calcified secondary rays come near enough to the surface of the centrum they are reinforced by the perichondrium; this is shown in the third stage available (young, 220 mm. long, 105 mm. broad). In the first stage (53 × 20 mm.) the secondary calcification is merely an investing layer, with roughly circular outline; in the second stage (104 × 58 mm.) there are outgrowths somewhat similar to those shown in the figure of young *Torpedo* (fig. 27, B), except that they are less strongly developed.

If the fossil vertebra figured by Hasse (**15**, C, Plate 23, fig. 23) is correctly referred to *Narcine*, it shows that there is a very much greater complexity in this extinct species than in the modern forms.

Rhinobatidæ.

The material available consisted of—

Pristinæ.

Pristis cuspidatus, two, length from base of rostral saw to tip of tail about one metre, S. India, vertebral columns in alcohol, presented by J. Hornell, Esq.;

also late embryo, total length 350 mm., of which the saw measures 115 mm., Travancore, Brit. Mus. (Nat. Hist.).

Pristis pectinatus, embryo, total length 265 mm., of which the saw measures 85 mm., no locality, Brit. Mus. (Nat. Hist.).

Pristis perrotteti, dried vertebræ, Brit. Mus. (Nat. Hist.).

Rhinobatinæ.

Rhynchobatus djeddensis, young, 685 mm. long, Tuticorin, S. India, vertebral column in alcohol, presented by J. HORNELL, Esq.; also embryo, 102 mm. long, Kurrachee, Brit. Mus. (Nat. Hist.).

Rhinobatus halavi, dried vertebræ, Brit. Mus. (Nat. Hist.).

Rhinobatus granulatus, skeleton in alcohol, Oxford Univ. Museum, lent by Prof. E. S. GOODRICH; also young, 233 mm. long, 82 mm. broad, in the collection at the Royal Coll. Science.

Rhinobatus undulatus, ripe embryo, 220 mm. long, Rio Grande do Sol, Brit. Mus. (Nat. Hist.).

Trygonorhina fasciata, young, 265 mm. long, 108 mm. broad, Sydney, in the collection at the Royal Coll. Science.

The caudal vertebræ of *Rhinobatus granulatus* (fig. 30, A, p. 383) or *Trygonorhina fasciata* (15, C, Plate 15, fig. 49) may be looked upon as the most generalised of the vertebræ of the Batoid fishes, and most characteristic of the sub-order. There are eight rays seen in the transverse section, four being diagonal, and not reaching the surface, while the other four, vertical and horizontal, reach the surface, and are reinforced by perichondrial increments. In a young *Rhinobatus,* measuring 233 mm. in length and 82 mm. in breadth, the secondary calcification, in the form of a gradually thickening investing layer around the double cone, has just reached the surface in four places (fig. 28, C, *p*), and in these places there is histological evidence to show that the perichondrium is beginning to be active. In earlier stages of development the growing zone is most probably circular in section, and situated immediately external to the calcified investing layer; but when this circular growing zone in the course of its enlargement approaches the surface of the centrum at the four parts indicated, the perichondrium immediately adjacent becomes rejuvenated, as it were, and in sections exhibits signs of activity, in marked contrast with the indifferent appearance of the general perichondrium that lies external to the parts where there are tesseræ.

In the trunk region of the same fish (fig. 28, B) much the same stage has been reached, but the lower tract of active perichondrium is very extensive, and the ventral tesseræ are more widely separated; and, owing to the union of the basiventral with the basidorsal cartilage, the growing zone does not reach the surface laterally. The lower edge of these sections is of particular interest, in that it shows a duplicity of genetic tissue which cannot but be very transient. Immediately ventral to the calcified mass is a thin growing zone of small cells, below this is a thin tract of cartilage-matrix with few cells, and below this again is an active genetic layer, which a careful scrutiny of the right and left ends shows to be continuous with

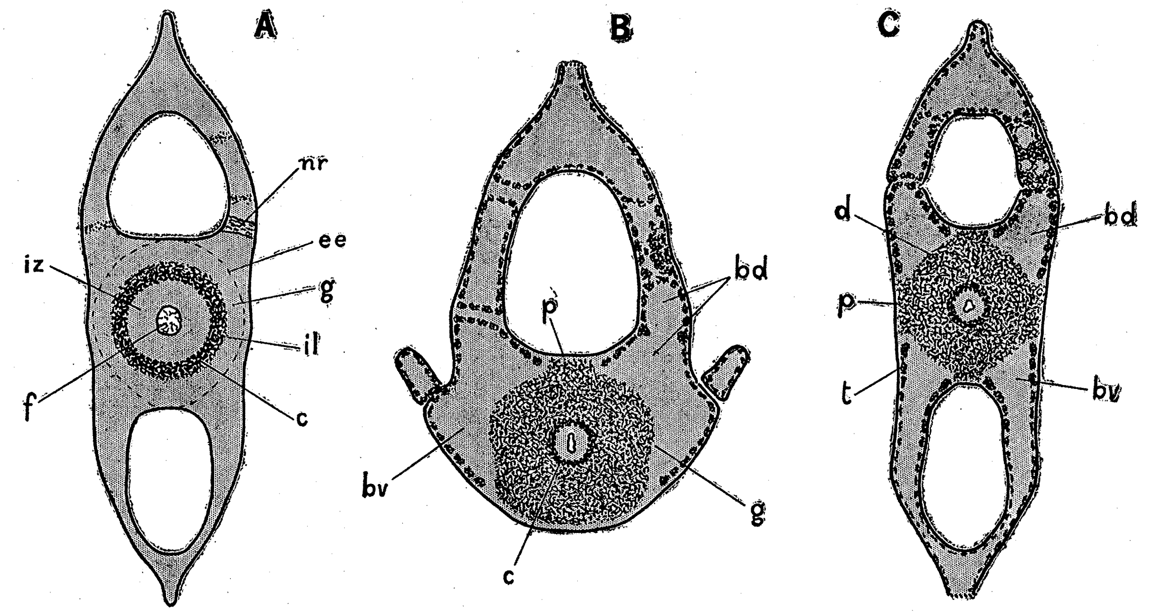

FIG. 28.—A, *Rhynchobatus djeddensis*, embryo, 102 mm. long; vertebra from region behind first dorsal fin, × 25. B, *Rhinobatus granulatus*, young, 233 mm. long, 82 mm. broad; mid-trunk vertebra, × 15. C, from region between pelvic and first dorsal fins, × 15. (For explanation of the lettering, see p. 404.)

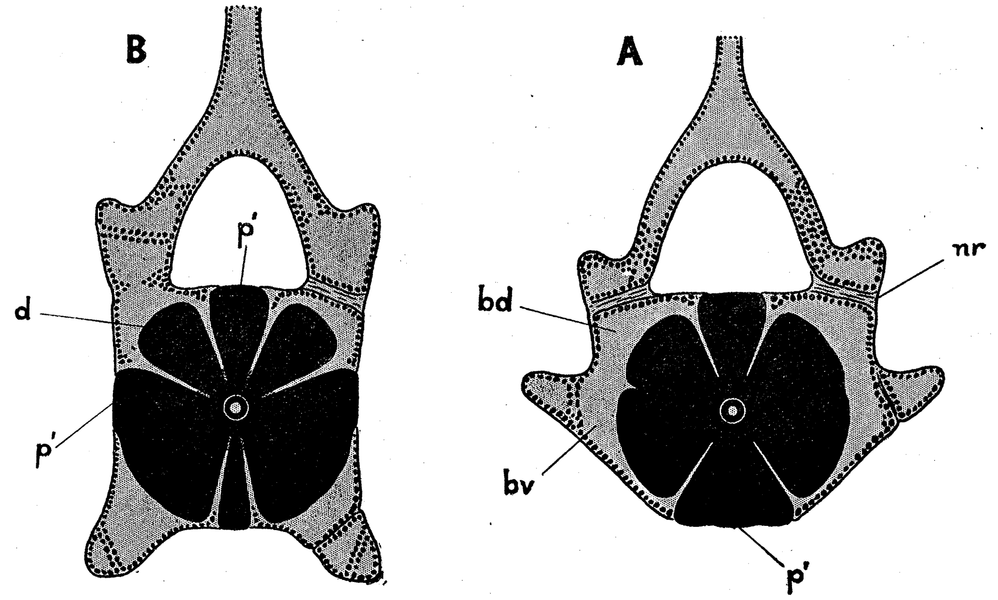

FIG. 29.—*Rhinobatus granulatus*, × 3. A, a mid-trunk vertebra, the second free vertebra behind the fused mass that is continuous with the back of the skull. B, vertebra from cloacal region. (For explanation of the lettering, see p. 404.)

the general perichondrium. The activity of the original growing zone is, as it were, infectious, and has been imparted to the connective tissue lying external to the cartilage.

What follows next can only be surmised, until slightly older stages are available for study, but seeing that the calcified rays in the areas in question maintain their connection with the surface in the adult (fig. 30, A; fig. 29, A), the most natural conclusion to be drawn is that the increments that are made subsequently to the stage of development shown in fig. 28 are due to perichondrial activity. The more external parts of the horizontal and vertical rays of fig. 30, A, may thus be regarded as intermedialia, comparable with those of *Mustelus* (fig. 8, A, *p'*, p. 354).

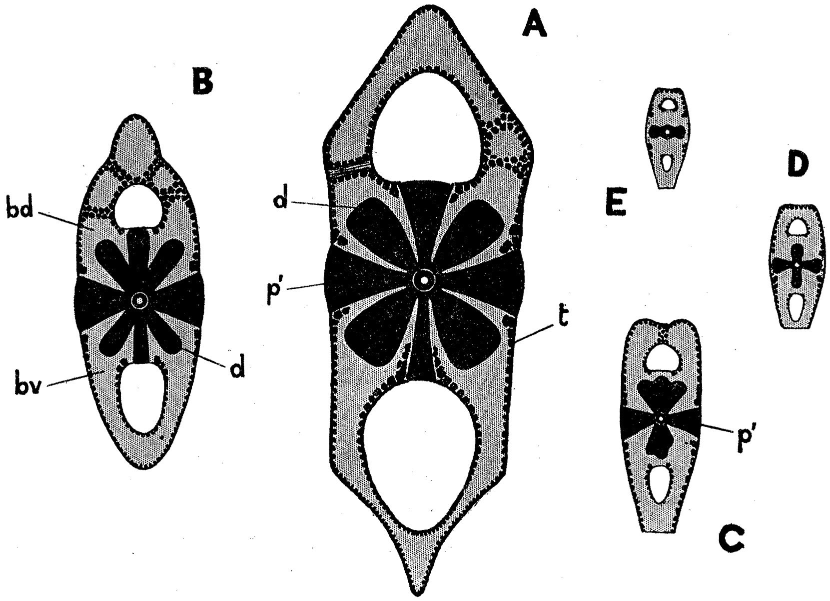

FIG. 30.—*Rhinobatus granulatus*, × 3. A, caudal vertebra, taken a short distance in front of the first dorsal fin. B, vertebra from the base of the caudal fin. C, from half-way between the base of the caudal fin and the extreme hind end of the vertebral column. D, from about half-way between C and the extreme hind end of the vertebral column. E, vertebra a short distance behind D. (For explanation of the lettering, see p. 404.)

In support of this view is the fact that when, as in the vertical rays of fig. 30, D, the rays fail to reach the surface, their ends are rounded, and the perichondrium in the floor of the neural canal and in the roof of the hæmal canal does not differ histologically from the general external perichondrium; these rays, that is to say, grow by virtue of the original growing zone. In further support of the view is the fact that in some Batoids there is evidence that the perichondrial tracts may become active without experiencing the stimulus due to the approaching primary growing zone. In some of the caudal vertebræ of *Raia*, for instance, the inner and outer parts of the horizontal rays are discontinuous (fig. 32, D, E, p. 387); the inner part has grown outward by increments from the primary growing zone, the superficial part is growing outward by virtue of a perichondrial meristem.

As regards the diagonal rays (fig. 30, A, *d*), there can be no doubt that they continue to grow from the original growing zone. The early disappearance of the membrana elastica externa renders it impossible to say whether there is, as in the Carchariidæ, a definite outward growth of sheath-cartilage, with the diagonal rays calcifying within it (fig. 8), or whether there is a spreading of the ray into the arch-cartilage; all that is certain is that the investing layer, from which they primarily arose, is a structure belonging to the outer-zone cartilage. The presence of tesseræ in fig. 30, A, in the interval between the lower vertical and lower diagonal rays rather suggests that the part of the cartilage that is immediately adjacent to the vertical ray is arch-cartilage.

In the anterior caudal region there are four distinct diagonal rays, but as one passes backward along the tail these tend to become confluent with the vertical rays (fig. 30, A, B, C). On the other hand, in the trunk region the diagonal rays tend to fuse with the horizontal rays; in fig. 29, B, the lower diagonal rays have lost their identity, and in fig. 29, A, the upper diagonals as well.

The young specimen of *Rhinobatus undulatus* and the young *Trygonorhina fasciata* present features almost identical with those exhibited by the young *Rhinobatus granulatus* (fig. 28, B and C). A figure of the caudal vertebra of an adult *Trygonorhina* is given by HASSE (**15**, C, Plate 15, fig. 49), showing a star with eight rather slender rays.

The figure of *Rhinobatus granulatus* given by KÖLLIKER (**20**, Plate 13, fig. 2), is that of a section through the fused vertebral mass that occurs behind the skull, and does not show any of the real characteristics of the vertebræ of the species. The species studied by HASSE, *Rhinobatus cemiculus* (**15**, C, Plate 15, fig. 41), *Rhinobatus horkeli* (Plate 15, fig. 27), *Rhinobatus thouini* (Plate 14, fig. 14), constitute a graded series, the first of which has an open eight-rayed star, like *Trygonorhina*, and the last a compact calcareous mass, like *Pristis*. The differences observable within the limits of the genus are very remarkable.

The vertebræ of adult specimens of *Pristis cuspidatus* (fig. 31) and *Rhynchobatus djeddensis* are similar in possessing a compact calcified mass, with a circular outline as seen in transverse section; in those cases in which the circular outline is not strictly adhered to there is a tendency for the mass to bulge out in the horizontal and vertical lines, as if to form horizontal and vertical rays. The layer of tesseræ is usually, though not invariably, incomplete in these parts, but in the vertebræ of the trunk region the lateral layers of tesseræ are almost always continuous. In the hindermost caudal vertebræ the pattern gives place to a simple cross of vertical and horizontal rays, which do not reach the surface (fig. 31, E); this occurs in *Rhynchobatus* as well as in *Pristis*.

The relation of the compact mass of *Pristis* to the more typical eight-rayed cross is explained by reference to *Rhinobatus*. In the trunk vertebræ of *Rhinobatus granulatus* there is a tendency for the rays to broaden out and coalesce, and, as is shown by fig. 29, A, where the horizontal and diagonal rays are amalgamated, it only needs the further coalescence of the lateral calcified masses with the vertical rays to produce the effect found in *Pristis*. The series of the three species of *Rhinobatus* studied by HASSE (*supra*) is another illustration of the same point.

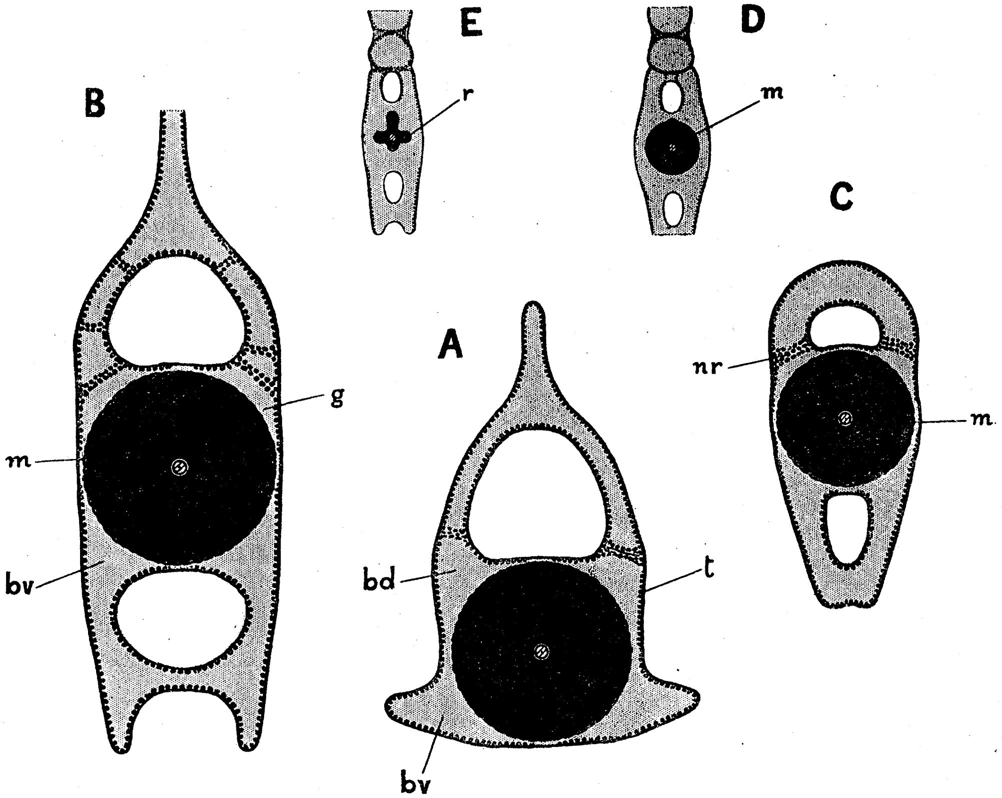

FIG. 31.—*Pristis cuspidatus*, half-grown fish, measuring about 1 metre from base of rostral saw to tip of tail. A, mid-trunk vertebra, × 3. B, vertebra from cloacal region, × 3. C, vertebra from root of caudal fin, × 3. D, vertebra from middle of caudal fin, × 4·5. E, vertebra near the posterior extremity of the vertebral column, × 4·5. (For explanation of the lettering, see p. 404.)

In the embryonic specimen of *Rhynchobatus djeddensis* (fig. 28, A), the membrana elastica externa is still visible; it is superficial above and below, but at the sides there is a thin tract of cartilage lying external to it. The double cone has only a thin investing layer, scarcely yet calcified, and between the latter and the membrana elastica externa is the zone of growth. Seeing that the growing zone is at present within the outer-zone cartilage, and that its activity persists continuously throughout life, there would appear to be some justification in regarding those later deposits of the calcified mass of the adult that are produced after the membrana elastica externa has disappeared as of sheath origin also.

The embryo of *Pristis pectinatus* examined exhibits a later stage, the investing layer being comparatively thick and well calcified; the membrana elastica externa is still visible, and lies external to the growing zone. In the late embryo of *Pristis cuspidatus* studied there are no signs of the membrana elastica externa, and the calcified mass has already acquired a close resemblance to that found in the adult.

Raiidæ.

The material available consisted of:—

Raia marginata, large, vertebræ in alcohol, Brit. Mus. (Nat. Hist.).

Raia clavata, adult, purchased in London; also dried vertebræ, Brit. Mus. (Nat. Hist.).

Raia batis, five, purchased in London; also embryo, 100 mm. long, 37 mm. broad.

Raia punctata, adult, purchased in London; also young, Naples, vertebral column in alcohol, presented by Prof. W. N. F. WOODLAND.

Raia maculata, two, half-grown, purchased in London; also four young, 275 mm. long, 185 mm. broad; 240 mm. × 165 mm.; 145 mm. × 100 mm.; 145 mm. × 92 mm., Plymouth, Brit. Mus. (Nat. Hist.).

In the vertebral centra of *Raia* the secondary calcification is less abundant than in those of *Rhinobatus granulatus*, described in detail in the previous section. All the radiating lamellæ are thinner; the vertical rays mostly reach the surface in all except the very hindermost vertebræ (fig. 32, F), and in conformity with the arguments already adduced, the more superficial portions of them may be regarded as of perichondrial origin. In the most anterior vertebræ (fig. A) the parsimony of calcification is apparent from the tendency of the vertical rays to fork. The lateral rays rarely reach the surface, and it not infrequently happens that such perichondrial deposits as may occur are separate from the lateral rays (figs. D, E). The matter is not so easy of solution as in *Rhinobatus*, however, for the lateral tesseræ are early continuous (fig. 34), and one must admit, in consequence, that there is some arch-component in the lateral calcified masses.

Diagonal rays as such cannot be distinguished; one must rather say that there are lateral parts which fork and branch irregularly. The irregularity is here illustrated not only by fig. 32, A–D, but by fig. 33. The upper row in fig. 33 represents the calcified star in four selected vertebræ of a large specimen of *Raia marginata*; and the series may be amplified by the addition of fig. 4, B, p. 340, which is drawn from an anterior trunk vertebra of the same fish. This last figure differs from the first of fig. 33 in having the upper vertical ray branched.

The lower four horizontal rows of fig. 33 illustrate the considerable variation that may be observed in different individuals of the same species; the figures are strictly comparable, since the vertebræ were selected from corresponding regions of the body in the four fishes. The specimen of *Raia punctata* examined had vertebræ agreeing with those shown in the third horizontal row.

In vertebræ of *Raia batis* from the region just behind the second dorsal fin there is no internal calcification except the double cone. Within the double cone is a long plug of inner-zone cartilage, which terminates abruptly in front and behind; the remains of the notochord in the intervertebral regions and in the broadest parts of the cones is watery rather than gelatinous. In vertebræ still more posterior the narrowest part of the double cone is granular and irregular, and in dried preparations from which the cartilage has been removed the two cones break apart. The last ten or twelve vertebræ of the tail have no calcification in the interior of the centrum.

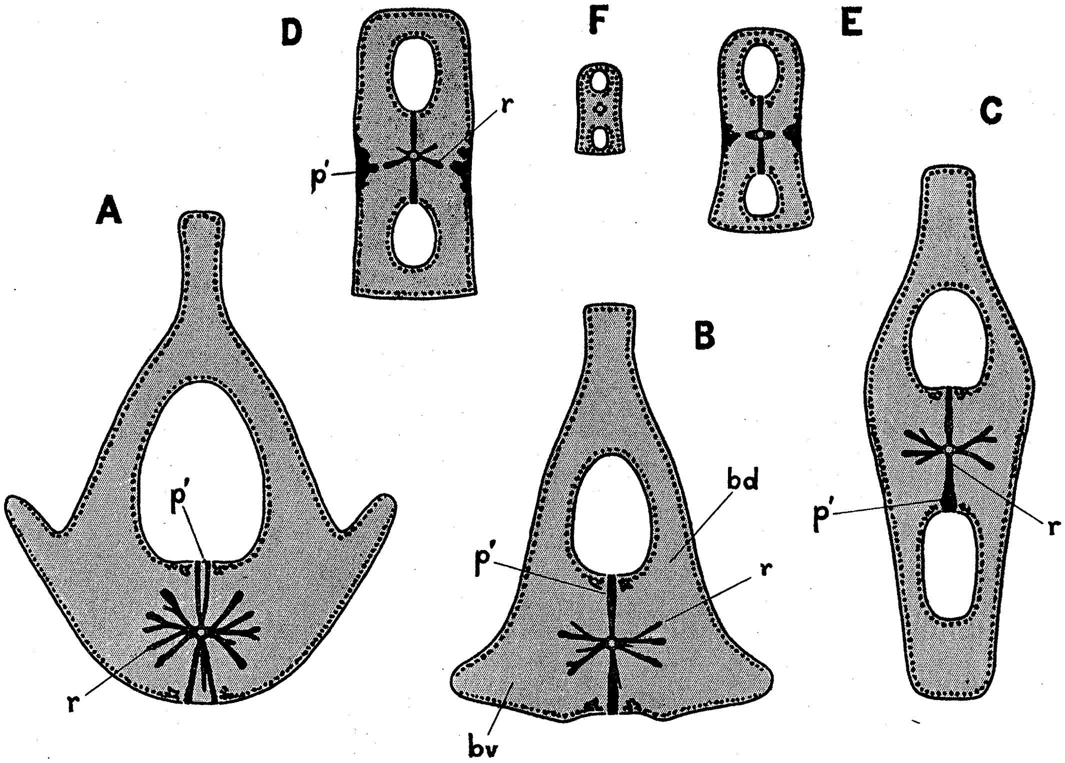

FIG. 32.—*Raia batis*, × 1·5. A, mid-trunk vertebra. B, vertebra from cloacal region. C, post-cloacal vertebra. D, vertebra from region midway between cloaca and first dorsal fin. E, vertebra from region of first dorsal fin. F, vertebra from region of second dorsal fin. (For explanation of the lettering, see p. 404.)

In the absence of any evidence to the contrary, it may be taken that the lateral rays that do not reach the surface—they do so occasionally in the caudal vertebræ—are structures belonging to the outer zone of the sheath; this is the view taken by HASSE (**15**, C, Plate 22, fig. 11, *a*′).

In a young *Raia maculata*, measuring 145 mm. in length and 100 mm. in breadth, the membrana elastica externa is still recognisable. Vertebræ from the region of the second dorsal fin show the membrane superficial in the floor of the neural canal and in the roof of the hæmal canal; there are no tesseræ in these positions. At the sides of the centrum the tesseræ are continuous, and a thin tract of cartilage occurs between them and the membrana elastica externa. There is thus evidence here, as already pointed out by previous writers, of a union of the basidorsal and basiventral cartilages; there is no evidence, however, of confluence of the right and left basidorsal cartilages, nor of the two basiventral cartilages. The double cone is surrounded by a very thin investing layer.

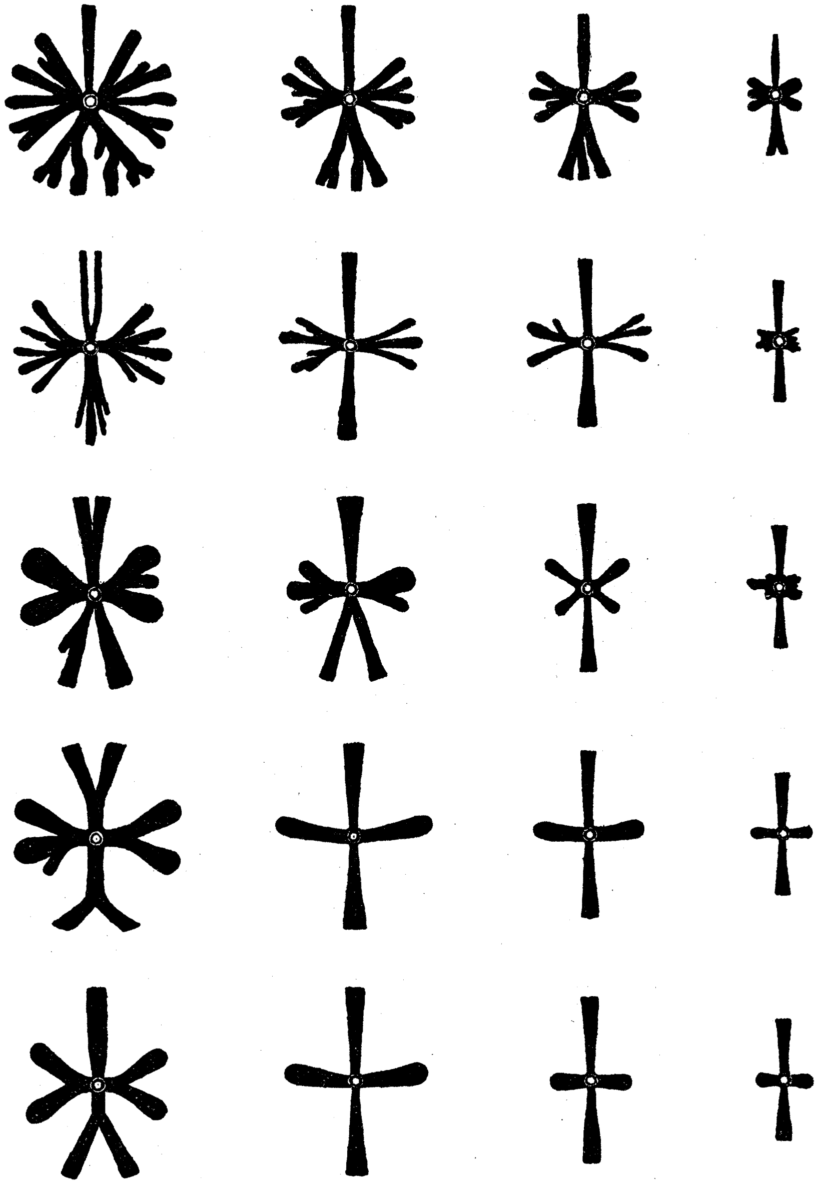

Fig. 33.—Patterns of the calcified rays of the centra of *Raia*, as seen in transverse sections. Upper horizontal row, *Raia marginata*; other rows, *Raia batis*. Left-hand vertical row, mid-trunk vertebræ; second row, vertebræ from cloacal region; third row, post-cloacal vertebræ; right-hand row, vertebræ from region midway between cloaca and first dorsal fin.

A vertebra from the region of the first dorsal fin (fig. 34, B) shows, between the lateral tesseræ and the membrana elastica externa, a wider tract of cartilage than in the vertebra mentioned above. The investing layer is not circular in outline, but exhibits signs of the early development of the upper and lower vertical rays, the lower rudiment being in some cases discontinuous from the general investing layer. Since the upper and lower parts of the membrana elastica externa are still visible and superficial, it is clear that these basal parts of the future vertical rays are derived from sheath-cartilage, and the remarks as to perichondrial increments apply only to the later developed, more distal portions.

A vertebra from the cloacal region (fig. 34, A) shows a thicker investing layer than the last, and there are no longer any signs of the membrana elastica externa in the dorsal and ventral positions; in each of these positions there is a small-celled growing zone, but the evidence is less clear than in *Rhinobatus* that the perichondrium is about to reinforce the original genetic tissue. This particular stage of development is not quite advanced enough to enable one to prove that similar conditions will prevail in *Raia*.

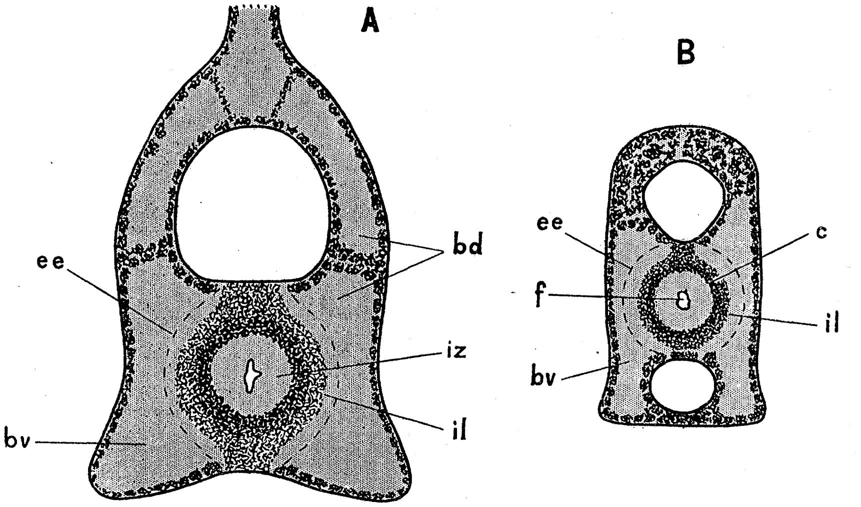

FIG. 34.—*Raia maculata*, young, 145 mm. long, 100 mm. broad, × 24. A, vertebra from cloacal region. B, from region of first dorsal fin. (For explanation of the lettering, see p. 404.)

In his description of the vertebral structure of a young *Raia clavata*, 120 mm. in length, GOETTE (**13**, p. 489, and Plate 32, fig. 54) refers to an independent origin of the rays; he shows four small calcified patches in diagonal positions, and isolated from the double cone. But it would seem that the section is taken, not through a trunk vertebra, but through the fused vertebral mass that occurs behind the skull. The caudal vertebra of an embryo, measuring 70 mm., also figured by GOETTE (Plate 32, fig. 47), does not differ materially from the vertebra described above from the region of the second dorsal fin of *Raia maculata*.

Dasybatidæ.

The material available consisted of:—

Pteroplatea micrura, two, vertebral columns in alcohol, Madras, presented by J. HORNELL, Esq.

Urolophus (*Trygonoptera*) *testacea*, late embryo, length to base of tail 75 mm., breadth 50 mm., Sydney, presented by Prof. J. P. HILL.

Dasybatis sp., embryo, length to base of tail 45 mm., breadth 50 mm., no locality, Brit. Mus. (Nat. Hist.).

Dasybatis thalassia, two, dried vertebræ, Brit. Mus. (Nat. Hist.).

Urogymnus asperrimus, dried vertebræ, Brit. Mus. (Nat. Hist.).

Myliobatis aquila, young, length to base of tail 185 mm., in the collection at the Royal Coll. Science.

Myliobatis nieuhofi, young, breadth 330 mm., Tuticorin, S. India, vertebral column in alcohol, presented by J. HORNELL, Esq.

Myliobatis sp., late embryo, length to base of tail 70 mm., breadth 90 mm., Japan, Brit. Mus. (Nat. Hist.).

Rhinoptera javanica, Tuticorin, S. India, vertebral column in alcohol, presented by J. HORNELL, Esq.

With the exception of *Pteroplatea*, the fishes of the family Dasybatidæ exhibit a general agreement in their vertebral structure. The characteristic type, as seen in caudal vertebræ of *Dasybatis* (fig. 35, A), is clearly the same as that of *Rhinobatus* (fig. 30, A, p. 383), and departures from this type are explicable without difficulty.

In *Dasybatis* itself the lateral rays in the caudal vertebræ may break up into two (fig. 35, B), or more, sometimes in a very irregular manner. The lateral rays may become exceptionally thick, without branching (*Rhinoptera*, fig. 36, C), or it may happen that the diagonal rays thicken, while the horizontal and vertical rays remain thin (*Urogymnus*, fig. 36, A).

There is a tendency, particularly in *Dasybatis* (fig. 35), for the outer parts of the vertical and horizontal rays to be flanked by tesseræ, indicating that those parts are situated *between* arch-components, which they prevent from coalescing. Such outer parts may be regarded as of perichondrial origin, although the more central parts of the same rays are clearly calcifications within sheath-cartilage. When, as in the caudal vertebræ of *Myliobatis* (fig. 37, B), the vertical and lateral rays do not reach the surface, a doubt is introduced, for while one might argue that the outer parts of the rays are here of sheath-origin, the possibility is not excluded (*infra*) that the tract of cartilage lying beyond the peripheral end of each may be uncalcified cartilage of perichondrial origin, and that the outer part of the calcified ray may have originated from the same genetic tissue.

In the specimen of *Myliobatis* examined by HASSE (15, C, p. 151, and Plate 20, fig. 3), the vertical rays are less distinct, and the outline of the calcified mass is more circular, rather resembling that of *Pristis* (fig. 31, C, p. 385). KÖLLIKER, on the other hand, writes that the young *Myliobatis* that he studied agrees with *Rhinobatus granulatus* in its vertebral structure (**20**, p. 55).

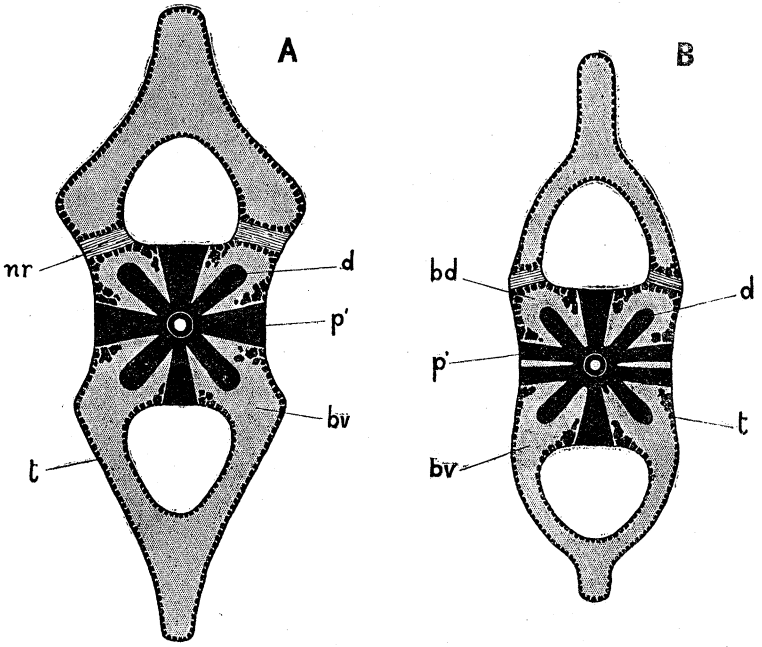

FIG. 35.—*Dasybatis thalassia.* Composite figures of several consecutive caudal vertebræ, from the region just in front of the tail-spines. A, from a large specimen, × 2. B, from a smaller fish, × 2. (For explanation of the lettering, see p. 404.)

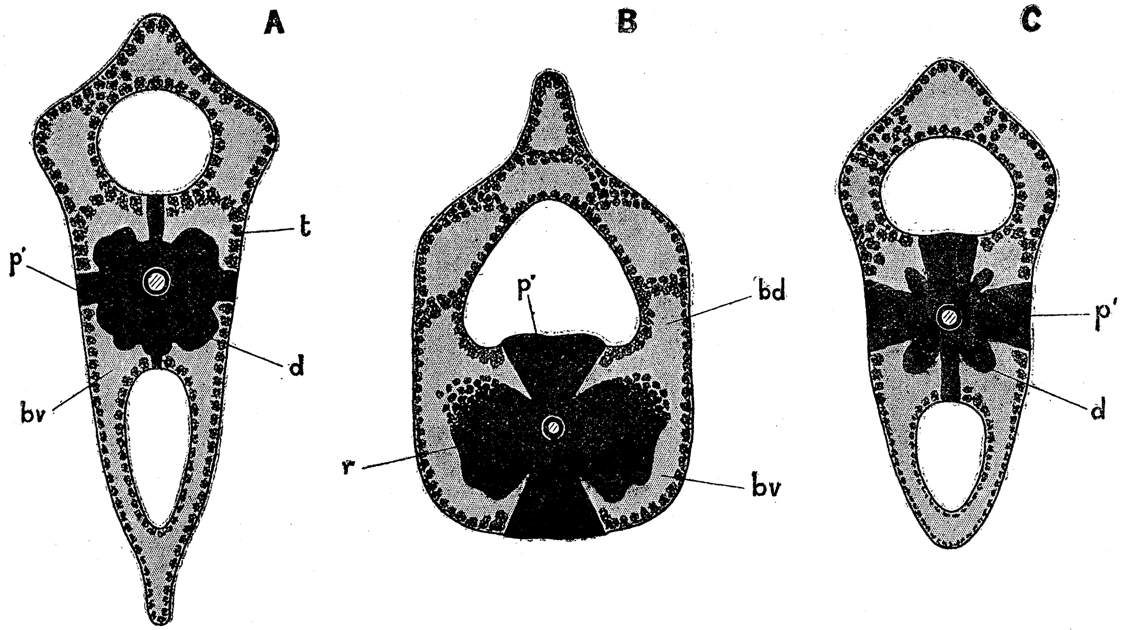

FIG. 36.—A, *Urogymnus asperrimus*, vertebra from base of tail, × 4·2. B, *Rhinoptera javanica*, pre-cloacal vertebra, × 4·2. C, from region immediately behind the dorsal fin, × 4·2. (For explanation of the lettering, see p. 404.)

Judging from HASSE's figures of caudal vertebræ of *Hypolophus*, *Urolophus* and *Tæniura* (**15**, C, Plate 19, figs. 3, 9, 16), it would seem that instances of excessive secondary calcification are not uncommon in the family.

In the trunk region of the Dasybatidæ there is the usual coalescence of the basidorsal with the basiventral cartilages, and in consequence thereof a failure of any of the lateral calcifications to reach the surface (*e.g.*, fig. 37, A). In *Rhinoptera* (fig. 36, B), and to a less extent in *Dasybatis*, the outer parts of the calcification may be granular rather than compact.

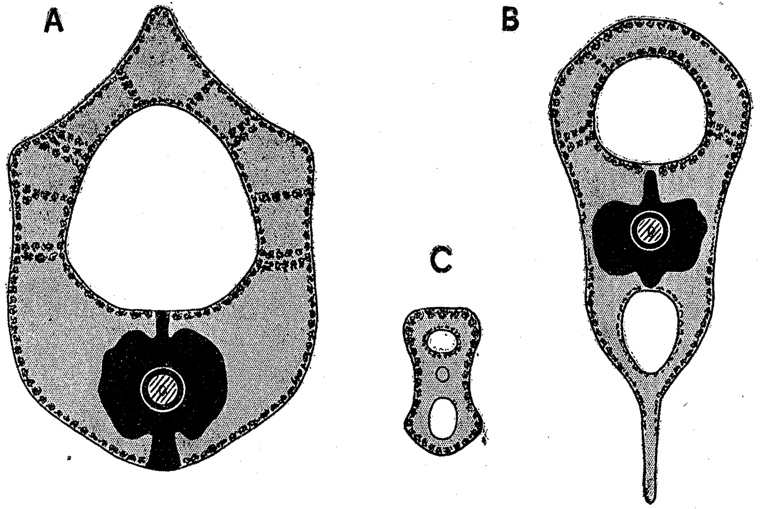

FIG. 37.—*Myliobatis nieuhofi*, 330 mm. broad, × 9. A, pre-cloacal vertebra. B, post-cloacal vertebra, from region of dorsal fin. C, from basal part of the tail-whip.

Although in the caudal vertebra of *Rhinoptera javanica* that is shown in fig. 36, C, the lateral rays reach the surface and break the series of tesseræ, a reduction in the length of the rays occurs in the anterior caudal vertebræ, and there is evidence that arch-fusion is not confined to the trunk region. HASSE's figure of the side view of caudal vertebræ of *Rhinoptera* (**15**, C, Plate 21, fig. 26), shows a continuous vertical band of tesseræ, which is not to be found in vertebræ slightly more posterior than those that he figures.

The vertebral centra of *Pteroplatea* are very specialised, mainly in the direction of degeneration. The membrana elastica externa can be recognised in the adult (fig. 38, *e e*), which is unusual in Batoids ; and within it are large, irregularly shaped, granular deposits, which in a transverse section are disposed more or less in a circle around a central cartilaginous core. The core itself may contain a few irregular granular calcifications of smaller size. Occasionally, as is shown on the right side of fig. B, the granular calcification may be confluent with the tesseræ.

In a longitudinal section through the anterior caudal vertebræ the calcified nodules are seen to be set lengthwise in series of four, and the terminal members of the series are confluent with transverse calcified plates, which are evidently the widely separated and greatly flattened cones of the centrum. The posterior plate of one centrum and the anterior plate of the next enclose between them some relics of the original notochordal substance. The granular nodules between the two flattened cones of the same centrum are comparable with the granular deposits found in the long terminal caudal vertebræ of *Raia* (p. 318).

Two specimens of *Pteroplatea micrura* were studied, and the vertebral structure of each was as described above. HASSE, however, in a transverse section of a trunk vertebra (**15**, C, Plate 19, fig. 11), figures a continuous calcareous deposit around a thin double cone. The former he regards as an outer-zone derivative (**15**, C, p. 141), which may be correct, but there is nothing in my own sections to prove it.

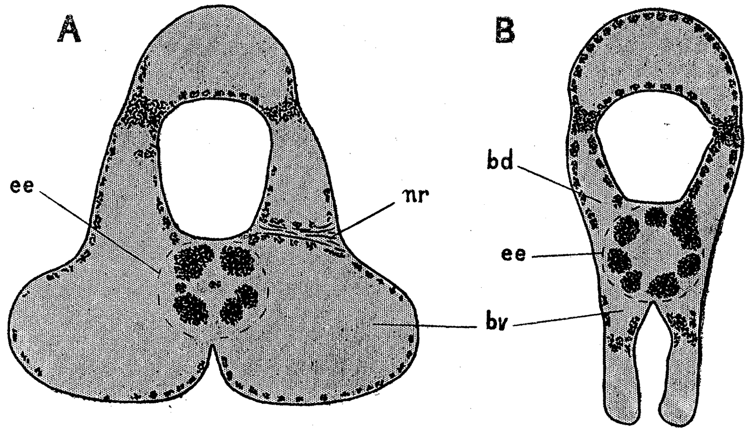

FIG. 38.—*Pteroplatea micrura*, × 12. A, pre-cloacal vertebra. B, vertebra from region of tail-spine. (For explanation of the lettering, see p. 404.)

Of the embryos studied, that of *Urolophus* (*Trygonoptera*) *testacea*, 50 mm. in breadth, proves to be too young to show any calcification. The *Dasybatis* embryo, measuring 50 mm. in breadth and 45 mm. from snout to base of tail shows, in both trunk and caudal vertebræ, a well-formed double cone, but no investing layer; the membrana elastica externa is to be observed above and below the centrum, and occupies a superficial position, but the other parts of the membrane are no longer to be detected.

The embryo of *Myliobatis*, 90 mm. broad, shows a developing investing layer, which in the trunk region nearly extends to the surface above and below; the membrana elastic externa is recognisable above, and is superficial. In the caudal vertebræ at the base of the tail-whip the membrane is superficial above and below the centrum; it can also be recognised at the sides, and is there seen to be separated from the actual surface by about two layers of cartilage-cells, which create the impression that they have originated from the perichondrium, and not by a "creeping" of the basidorsal and basiventral cartilages towards one another. There is also evidence in these sections that, until the arch-cartilages have reached the stage of development at which the tesseræ begin to calcify, parts of them are increased by perichondrial additions.

CONCLUSIONS AS TO THE TAXONOMIC VALUE OF THE CALCIFIED PARTS OF THE CENTRA.

As regards the value that may be attached to the patterns of the calcified structures in the centrum as an aid to taxonomy, it may be pointed out, as one of the results of the present investigation, that species and genera, which on other grounds are considered to be nearly related, conform with one another fairly well in the matter of the calcification of the vertebral centra. The Squalines, for instance, agree in the absence of radiating and concentric lamellæ, and exhibit at most an "investing layer" external to the primary double cone (fig. 22, p. 372). The absence of calcified structures in the centra of *Echinorhinus spinosus* (fig. 23, p. 373), and *Somniosus microcephalus* presents no difficulties, for the former is clearly a degraded representative of such a form as *Centroscyllium*, while the latter has within its own genus a species, *Somniosus rostratus*, possessing typical Squaline vertebræ.

The Chlamydoselachidæ and Notidanidæ may in like manner be regarded as having a degenerate vertebral column, which in its more perfect form would exhibit calcified lamellæ radiating in a bulky sheath-cartilage. The evidences of degradation are, as in *Echinorhinus* and *Somniosus*, the partial liquefaction of the notochordal substance, the elongation of the intervertebral portions of the column at the expense of the vertebral, and the tendency to the development of large plate-like transverse septa in the vertebral regions. Further evidence is forthcoming in the occurrence, in the hinder caudal vertebræ of *Heptanchus*, of calcified double cones with radiating secondary lamellæ, usually six in number (fig. 5, A, p. 348). These calcified parts disappear as one passes forwards, and the observations should be taken in conjunction with the general conclusion, arrived at from other sources, that caudal vertebræ in sharks exhibit a more primitive or more typical condition of structure than the trunk vertebræ (p. 317).

The only other forms that exhibit radiating calcified lamellæ that belong exclusively to the sheath-cartilage are the various species of *Cestracion* (fig. 21, p. 370).* This is not, however, to be taken as necessarily implying close affinity with *Heptanchus*; indeed, the fact that the characteristic number of rays in *Heptanchus* is six, while in *Cestracion* it is eight, tells rather against it. The fossil genera, such as *Palæospinax*, that are commonly regarded as allied to *Cestracion*, although their centra have no radiating calcified laminæ, may possibly be degenerate, but the more probable explanation is that they branched off from the parental stock prior to the evolution in the Cestracionts proper of the calcified lamellæ external to the double cone.

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* And possibly *Orectolobus* (see p. 396).

The members of the family Carchariidæ agree with one another in the possession of large, well calcified intermedialia, of perichondrial origin, not derived from the arch-cartilage nor from the sheath-cartilage; they also agree in the fact that the sheath-cartilage bulges out towards and into the arch-bases, and includes a diagonally placed calcified lamella in each outgrowth.

The Lamnidæ and Odontaspididæ agree among themselves, and differ from the Carchariidæ in the great reduction, or absence, of diagonal outgrowths of sheath-cartilage and their included calcified lamellæ, and they differ further from the Carchariidæ in the intermedialia not being compactly calcified, but consisting largely of cartilage. This cartilage of the intermediale is calcified on the faces that touch the arch-cartilages, and usually contains within it several radiating lamellæ (*Carcharodon*, fig. 9, A, p. 356), although these last are wanting in *Scapanorhynchus* (fig. 11, p. 358). *Cetorhinus* is exceptional in the lateness of the development of the radiating lamellæ of the intermedialia, all the early lamellæ being of the concentric type (fig. 13, A, p. 360). Even in the adult *Cetorhinus* (fig. 14, A, p. 361), and in some other forms, there is a tendency for the calcified parts of the intermedialia to exhibit a concentric arrangement. While in the Carchariidæ the calcified innermost parts of the intermedial wedges are separate from the investing layer, they are continuous with it in the Odontaspididæ and Lamnidæ (except young *Cetorhinus*).

These two families, the Lamnidæ and Odontaspididæ, are probably those in which, of all Elasmobranchii, the vertebræ are the least chordacentrous; the part of the centrum of the adult fish that is constructed out of the cartilage of the notochordal sheath is very small. There is nothing exceptional in the double cone and the inner-zone cartilage, but the outer-zone cartilage and its products are at a minimum of development.

The concentric lamellæ of *Squatina* are unique among Elasmobranchii, and the family Squatinidæ, so far as its vertebral structure is concerned, stands alone. The lamellæ are of sheath-origin, and are not to be confused with the early laminæ of *Cetorhinus*, which are developed in the intermedialia (fig. 13, p. 360).

As regards the Scyliorhinidæ, the typical vertebræ of the family are clearly those of such a species as *Scyliorhinus marmoratus* (fig. 15, p. 363), in which there is a very obvious approach to the Carchariidæ in the outward growth of the sheath-cartilage in the four diagonal positions, and the presence of a radiating calcified lamella in each outgrowth. The intermedialia are relatively large, and have the form of cartilaginous wedges, calcified on each surface that abuts upon arch-cartilage. The vertebræ of the British species, *Scyliorhinus canicula* and *Scyliorhinus stellaris*, depart from the type seen in *Scyliorhinus marmoratus* in the absence of the diagonal calcified lamellæ, and in the flattening out of the intermedialia, so that they extend only a short distance inward (fig. 16, A and B, p. 363); they are completely calcified, and at their edges they merge insensibly into the tesseræ of the arch-cartilages. In *Pseudotriacis* and *Pristiurus* the intermedialia are still further reduced, and the condition of the vertebral centrum comes to resemble that found in the Squalinæ (*cf.* fig. 16, C, p. 363, and fig. 22, B, p. 372), a coincidence which is of no taxonomic importance.

In the family Orectolobidæ, the genera *Chiloscyllium*, *Stegostoma*, and *Ginglymostoma* agree in having radiating calcified lamellæ of perichondrial origin, usually commencing in eight regions (fig. 18, A and C, p. 366, and fig. 17, E and F, p. 365), but liable to fork or branch subsequently (fig. 17, A and B; and HASSE, **15**, D, Plate 26, fig. 24). They may be connected with the double cone by an investing layer (fig. 18), or may be independent of the double cone (fig. 17). The cartilage of the outer zone of the notochordal sheath bulges out horizontally and vertically into the intermedialia.

In *Orectolobus* a different type prevails, at all events in young and half-grown specimens. There are primarily eight radiating lamellæ (fig. 20, C, p. 368), but, so far as is shown by the position of the remnants of the membrana elastica externa that are still recognisable, these rays would seem to be developed within the outer-zone cartilage, and not to be of perichondrial origin. Whether in full-grown specimens outward growth of the rays is continued by perichondrial activity, is at present doubtful; HASSE's figures (**15**, D, Plate 25, figs. 4–6) are drawn from vertebræ no larger than those of the 700 mm. specimen examined in the course of the present investigation, yet he represents the rays as reaching the surface, exactly as in *Stegostoma* and *Ginglymostoma* (*ibid.*, Plate 25, fig. 3, and Plate 26, fig. 21).

The vertebræ of *Rhinodon* do not seem to have been described; none were available for study in the present inquiry.

As regards family relationships, it is to be noted that while of the five families grouped by REGAN (**29**) in the Division Galeoidei the families Odontaspididæ, Lamnidæ, Scyliorhinidæ and Carchariidæ agree in the essential structural features of the vertebral centra, the family Orectolobidæ stands aloof.

There is nothing in the vertebral structure of the Pristiophorinæ to suggest that they are at all closely related to the Squaline sharks. Accepting the vertebral structure of *Pliotrema* as being more typical than that of *Pristiophorus* (*cf.* B and A, fig. 24, p. 375), there is to be noticed a resemblance to the Orectolobidæ in the manner in which the outer-zone cartilage bulges out horizontally and vertically. The eight calcified lamellæ bear some resemblance to those of a young *Chiloscyllium* (fig. 17, F, p. 365).

In the case of the Batoid fishes the characters of the vertebral centra do not appear to have any very direct bearing on the classification of the families within the limits of the sub-order. As a characteristic pattern for the Batoids one might select the eight-rayed star such as occurs in the anterior caudal vertebræ of *Rhinobatus* (fig. 30, A, p. 383). Of the eight rays, four are diagonal, and the others vertical and horizontal. The development of all of them commences in the outer-zone cartilage (fig. 28, C, p. 382), and the diagonal rays may continue to increase in the diagonally expanding sheath-cartilage, much the same as in Carchariidæ, or they may possibly extend into the arch-cartilage; the early disappearance of the membrana elastica externa precludes one from arriving at any definite conclusion on the point. The horizontal and vertical rays continue to grow by perichondrial increments, and the outer parts of these rays thus resemble the horizontal and vertical rays of *Mustelus* (fig. 8, A, p. 354).

The practice of founding a scheme of classification upon the characters of one organ or system of organs is to be condemned, and it has already been pointed out that HASSE was clearly too confident in hoping to classify the Elasmobranchii by the characters of the calcification of their vertebral centra, but the suggestion may here be offered to taxonomists of the future to look into the question of the relations between the Batoids and the Carchariid sharks. The inquiry might reveal other evidence of the possible origin of the Batoids from the base of the Carchariid stock.

In REGAN'S classification (**29**) the Batoids or Hypotremata are divided into four families, the Torpedinidæ, Rhinobatidæ, Raiidæ and Dasybatidæ. Accepting the eight-rayed star, of the type just described, as characteristic of the Rhinobatidæ, it is to be noted that it appears also in the Dasybatidæ (fig. 36, C, p. 391, and fig. 35, A, p. 391). In *Raia*, the sole representative of the Raiidæ examined, the vertical rays resemble those of the type just alluded to, while the horizontal rays, although similar, tend towards reduction (fig. 32, D and E, p. 387); the diagonal rays, if present at all, are irregular in their arrangement and growth.

Rhynchobatus and *Pristis* (fig. 31, p. 385) present a compact calcification of circular outline in transverse sections, but this is a condition which can be derived from the star in question by a process of broadening of all the rays until the intervening uncalcified parts disappear, a process the key to which is furnished by the vertebræ of the trunk region of *Rhinobatus* (fig. 29, p. 382). It is further to be noted that in the hindermost vertebræ of both *Rhynchobatus* and *Pristis* the outline is not circular, vertical and horizontal rays being recognisable (fig. 31, E); this condition recalls that found in the hinder caudal vertebræ of *Rhinobatus*, in which the diagonal rays are wanting, and only the vertical and horizontal rays are present (fig. 30, D, p. 383). There is no evidence in the vertebræ of *Rhynchobatus* and *Pristis* of any perichondrial contributions, and a study of young specimens of these genera points to the conclusion that the secondary calcification is wholly derived from the outer-zone cartilage (fig. 28, A, p. 382).

Included among the Dasybatidæ is a remarkable form, *Pteroplatea*, whose vertebræ are aberrant, in that they do not possess a recognisable double cone; the notochord has disappeared in the middle part of the centrum, and the calcification takes the form of a number of irregular nodules arranged in a circular manner just inside the membrana elastica externa (fig. 38, p. 393). This condition is evidently one of degeneration, and can have no value in taxonomy.

Although *Torpedo narce* exhibits an eight-rayed star, this does not exhibit the same features as the star of *Rhinobatus* mentioned above; there are no diagonal rays, but the vertical and horizontal rays are duplicated (fig. 26, p. 379). The rays may grow out independently from the investing layer into the outer-zone cartilage, or two may arise as a single outgrowth, and fork subsequently (fig. 27, p. 380). In *Torpedo hebetans* the tendency for the rays to fork is less than in *Torpedo narce;* in *Narcine brasiliensis* it is much greater (HASSE, **15**, C, Plate 23, fig. 21). It is somewhat doubtful, owing to the early disappearance of the membrana elastica externa, whether the later growth of the calcified lamellæ is due to perichondrial activity (see p. 332). The centra of *Torpedo* and *Narcine* are readily distinguished from those of other Batoid fishes, and the conditions are such as to support a division of the Batoids into the Torpendinidæ on the one hand, and the Rhinobatidæ, Raiidæ, and Dasybatidæ on the other, as is proposed in REGAN's classification.

SUMMARY.

In Elasmobranch fishes, the centrum—by which is understood that portion of the vertebra which is left after cutting away the projecting parts—is composed of two, sometimes three, kinds of cartilage, more or less calcified, namely: (1) sheath-cartilage; (2) arch-bases (the parts of the basidorsals and basiventrals nearest the notochord); and (3) intermedialia.

The sheath-cartilage, arising from skeletogenous cells that at an early stage migrate into the notochordal sheath through the membrana elastica externa from the basidorsal and basiventral cartilages, is early differentiated into inner, middle, and outer zones. The inner-zone cartilage is usually hyaline, and any calcification that may occur in it exhibits no regularity of texture; it is commonly traversed in the middle by the remains of the notochord, from which it is separated by the membrana elastica interna. The middle zone is composed of a close-celled cartilage with scanty intercellular matrix; the cells are fusiform, and their long axes are circumferentially disposed. The cartilage calcifies early, except in a few species, and the calcified structure constitutes the primary "double cone."

Calcification in the outer-zone cartilage occurs subsequently to that in the middle zone, and the calcified layers and lamellæ are consequently termed "secondary." Calcification of the innermost part of the outer-zone cartilage is of common occurrence, and produces an investment or "investing layer" (Belegschicht of HASSE) around the double cone, from which it may be distinguished by its rounder, more widely spaced cells, and its later origin. Further, whereas the calcification of the middle-zone cartilage proceeds simultaneously throughout the whole thickness of the middle zone, the calcification of the investing layer is progressive, the innermost part, in contact with the primary calcification, being the first-formed. The calcified lamellæ occurring in the outer-zone cartilage, whether radiating (*Cestracion*, fig. 4, A, p. 340) or concentric (*Squatina*, fig. 25, p. 377), are centrifugal in their mode of growth; in the case of radiating lamellæ the new increments are applied to the external edges; in the case of concentric lamellæ the most external lamella is the most recently calcified. The investing layer may increased to such an extent as to produce a solid calcified mass around the double cone (*Pristis*, fig. 31, p. 385).

The third kind of cartilage, occurring in wedge-shaped masses, which it is proposed to term the "intermedialia" (Periostale Keile of HASSE), is developed later than the arch-cartilage and the sheath-cartilage (see p. 327); it increases centrifugally, usually from a growing zone just internal to the perichondrium. The initial cells of this growing zone arise from the perichondrium itself, just external to the membrana elastica externa. The cartilage of the intermedialia may calcify partially, with radiating lamellæ (*Lamna*, fig. 9, p. 356) or concentric lamellæ (*Cetorhinus*, young, fig. 13, p. 360) alternating with tracts of uncalcified cartilage; or the calcification may be complete (*Mustelus*, fig. 8, A, p. 354); or the intermediale may be reduced to a thin external layer (*Pristiurus*, fig. 16, C, p. 363). The matter is discussed at length in pages 327–331.

The present paper records the results of a study of the secondary and perichondrial calcifications in young and adult fishes belonging to 68 species and 44 genera. The results go to show that HASSE, in his great work, 'Das Natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule' (**15**), overestimated the importance of the disposition of the calcified masses and laminæ in the centrum as a taxonomic feature, and that, although his main groups of the Elasmobranch fishes are generally admitted to be, with certain reservations, natural groups, his classification was to a large extent arrived at by ignoring the vertebral characters in the sense in which he had described them. The centra of some of his Tectospondyli exhibit in transverse section a "star" quite as perfect as those found in his Asterospondyli (fig. 4, p. 340); and in the latter group he associated such forms as *Cestracion* and *Lamna* (fig. 21, A, p. 370, and fig. 9, B, p. 356) in which the "stars" are of different origins.

HASSE's choice of the vertebra of *Pristiophorus* to illustrate tectospondyly in its most typical form (see p. 339) is singularly unfortunate in view of the discovery by REGAN that in a Pristiophorid from South Africa (*Pliotrema warreni*) the vertebræ have strongly marked radiating lamellæ (fig. 24, B, p. 375).

It is considered desirable to discard for general descriptive purposes the terms cyclospondylous, tectospondylous and asterospondylous. An attempt to introduce a new set of terms to describe the patterns of the lamellæ of the centra is not likely to succeed, because, while some types can with precision be designated by single words, others present great difficulties; and when in the same genus the patterns vary as much as they do in the several species of *Rhinobatus* (**15**, C, Plate 14, fig. 14;

Plate 15, figs. 27 and 41), it becomes clear that no great advantage is to be gained by the coining of new descriptive names for them. The matter is discussed at length on pp. 346–347.

It would appear that the calcified masses and lamellæ in the centra, developed in various positions in response to physiological demands for a strengthening of the cartilage for resisting stresses in certain directions, grow in definite directions, independently of the mode of origin of the cartilage in which the calcification is taking place. In *Stegostoma* (fig. 18, C, p. 366), for instance, the remnants of the membrana elastica externa show that while the inner part of each radiating lamella is developed in the sheath-cartilage, the outer part is developed in cartilage external to the sheath.

Similarly, in *Pristiophorus japonicus* and *Pristiophorus nudipinnis* there is a tubular calcification disposed lengthwise externally to the double cone, and free from it except at the two ends. A section through the middle of the centrum shows that this calcification is in the latter species a product of the sheath solely, whereas in the former (fig. 24, A, p. 375) there are, owing to the more sinuous course of the membrana elastica externa, four portions that occur in sheath-cartilage, while the other four are calcified parts of the arch-cartilages.

Again, in *Mustelus* it can be shown that, whereas the diagonal calcified lamellæ are usually in sheath-cartilage entirely, it sometimes happens that, owing to the failure of the sheath-cartilage to grow out sufficiently rapidly in the diagonal tracts, the calcification of the more distal parts of the lamellæ may occur in arch-cartilage (fig. 8, A, p. 354, right upper diagonal ray).

On the other hand, such disregard of the origin of the cartilage is not shown in the vertebræ of young *Cetorhinus* as compared with those of *Squatina* (fig. 13, p. 360), the concentric lamellæ of the former not being continued through the diagonal cartilages. The explanation of this is probably to be found in the fact that, while the intermedialia, in which the calcified lamellæ occur, are increasing by means of an external growing zone, the diagonal cartilages—basal parts of the basidorsals and basiventrals—are increasing by a general and uniform radial extension. In *Squatina* the growing zone, here of sheath-origin, is continuous all round.

It is clear from the difference in the origin of the concentric calcified lamellæ in the young *Squatina* and *Cetorhinus*, in the one case from sheath-cartilage, in the other from perichondrially produced cartilage external to the notochordal sheath—as also the difference in the origin of the radial calcified lamellæ in *Cestracion* and *Lamna* (fig. 4, A, p. 340, and fig. 9, B, p. 356), from sheath-cartilage and perichondrium respectively—that we are here dealing with cases of convergence, a homoplastic attainment of similar results in distantly related genera. It is equally clear from the resemblances, that there are certain mechanical advantages to be gained by the calcification being in the form of concentric tubes in the first pair of genera, and in the form of radiating longitudinal lamellæ in the second pair. The question that arises from a study of these forms is—what mechanical principles are involved that have resulted in the evolution of concentric lamellæ in the former, whereas in the latter the necessary strength is attained by the development of radiating lamellæ? There is here indicated a promising investigation for anyone interested in the relation between mechanical requirements and the methods by which they are satisfied. Are there any resemblances, for instance, in the mode of flexure of the vertebral column associated with the habits of the fishes in question; are there any differences in the mode of attachment of the muscles to the vertebræ in the young *Squatina* and *Cetorhinus*, on the one hand, and the adult *Cestracion* and *Lamna*, on the other; is there any reason that can be ascertained for the concentric arrangement of the layers being continued throughout life in *Squatina*, whereas in *Cetorhinus* the later calcifications (fig. 14, A, p. 361) are mostly of the radial type?

There is nothing in the vertebral structure of *Squatina* and *Pristiophorus* to justify HASSE's view—now largely discredited—that there is any close affinity between these genera and the Batoid fishes.

In some Batoids (*e.g.*, *Rhinobatus*, fig. 28, B, C, p. 382), the secondary calcification proceeds for a time by a gradual increase in the thickness of the investing layer until the surface is reached—in two places in the trunk vertebræ, in four in the caudal—and thereafter the increase in these two or four areas is by growing zones of perichondrial origin. The major parts of these lamellæ in the adult are thus external to the sheath, but their innermost parts are developed within the sheath-cartilage.

The Batoid fishes differ from the Sharks in the early disappearance of the membrana elastica externa; the part that longest remains recognisable is that between the two basidorsal cartilages. It is only in a few forms (*e.g.*, *Rhynchobatus*, fig. 28, A, p. 382) that any other relics of the membrane can be detected after the investing layer has begun to calcify. *Pteroplatea* is an exceptional form, showing remnants of the membrane in vertebræ of the adult (fig. 38, p. 393).

The results of the present investigation go to show that the distinction drawn by GADOW and ABBOTT (6) between chorda-centra and arco-centra is not so absolute as they claim. As regards chorda-centra, it is shown that in some Elasmobranch fishes (Lamnidæ) the part of the centrum of the adult that is developed from the notochordal sheath is small. On the other hand, in Amioid fishes, and possibly in some other forms with arco-centra not here considered, the centra appear to be derived in large part from skeletogenous tissue distinct from that of the arch-cartilages (p. 335).

In this paper the vertebræ of a number of species are figured for the first time, *e.g.*, those of *Scapanorhynchus owstoni* (fig. 11, p. 358), and *Pliotrema warreni* (fig. 24, B, p. 375); and figures are given of the vertebræ of species that have not been adequately dealt with in previous papers, *e.g.*, those of *Raia* (fig. 32, p. 387), *Cestracion* (fig. 4, A, p. 340, and fig. 21, p. 370), *Cetorhinus* (fig. 14, p. 361), *Rhinobatus* (figs. 29 and 30, pp. 382 and 383). The figures of the vertebræ of late embryos are new, or are more correct representations than those already published. Special reference may be made to the figures of *Chiloscyllium* (fig. 17, E and F, p. 365), *Stegostoma* (fig. 18, C, p. 366), and *Rhinobatus* (fig. 28, B and C, p. 382).

In the course of the investigation there has been adopted a method of research that has hitherto been rather neglected, namely, that of studying the range and method of change of the pattern of the calcified laminæ of the centrum throughout the whole length of the vertebral column of the same individual fish, *e.g.*, in *Chiloscyllium* (fig. 17, A–D, p. 365), *Raia* (fig. 32, p. 387), and *Rhinobatus* (figs. 29 and 30, pp. 382 and 383).

The vertebræ of the great basking shark, *Rhinodon typicus*, do not seem yet to have been examined; it would be of considerable interest to ascertain how nearly they resemble those of *Ginglymostoma*, with which genus *Rhinodon* is associated by REGAN (**29**, p. 745).

The vertebræ of *Orectolobus*, both of young and adult fishes, deserve further investigation if the material can be procured; also the vertebræ of late embryos of *Lamna* and *Alopias*.

EXPLANATION OF THE TEXT-FIGURES.

The text-figures illustrating this paper are all partly diagrammatic; in some cases they are composite figures, drawn from two or three consecutive vertebræ. In the illustrations of HASSE's monograph (**15**) it is not easy, owing to a lack of diagrammatic treatment, to tell at a glance which parts are calcified and which are not, and a comparison between the various figures is thereby rendered difficult; the difficulty, moreover, is increased by the calcified parts being drawn darker than the cartilaginous parts in some of the figures, and lighter in others (**15**, D, *cf.* figs. 5 and 7, Plate 24; figs. 7 and 8, Plate 28; figs. 17 and 18, Plate 29).

In the present paper the texture of the various parts of the vertebræ is suggested, rather than represented in actual detail. In the figures that were drawn from dried vertebræ of adult fishes, the calcified parts are shown in black (fig. 9, A, p. 356); but in the drawings of sections of decalcified vertebræ cut with the microtome the look or appearance of the calcified parts is better secured by representing them by "broken" black areas, with a "scribbled" effect (fig. 8, p. 354). Lines of growth of calcified lamellæ, sometimes recognisable in the sections of the vertebræ, are not introduced into the figures. The lines in question are always more or less concentric around the primary double cone, whether they occur in radiating lamellæ, as in *Cestracion* and *Torpedo*, or in a solid mass, as in *Pristis*; and they have no direct bearing on the main thesis of the present paper. All calcareous accretion of secondary origin is centrifugal, and there is thus no occasion to represent the lines or zones of growth in the figures.

The distinction between the primary cone calcification and the secondary calcification immediately around it, recognisable in the actual sections by a difference in texture or colour, is exaggerated in the figures, and in many cases a thin, white line is introduced to indicate the limit between the primary double cone and the investing layer. The white circle does not represent uncalcified cartilage; it is but a conventional means of drawing a distinction between the two kinds of calcification. If the septum in the middle of the double cone is calcified, it is diagonally shaded in the figures, in order to distinguish it from the double cone, with which it is really continuous at its edges (fig. 9, B, p. 356).

If on examination of a section of a dried vertebra with a lens the tesseræ appear as a continuous layer, they are shown by means of a thick black line, but if the individual tesseræ can be distinguished by the use of a lens, they are shown separately. Further, when the tesseræ are more granular in texture than usual, the granular effect is suggested by the tesseræ being drawn as "broken" or "scribbled" areas. Fibrous tissue is shown only in those cases in which its omission would be likely to create a wrong impression.

In the neural arches there frequently appear in the text-figures discontinuities of the cartilage, irregular, oblique, and sometimes present on one side of the figure only (fig. 11, B, p. 358). These represent the limits between the arch-components, the basidorsals and interdorsals, and the supradorsals (if such are present). They are introduced into the figures as they appear in the slices drawn, and no further interpretation of them is attempted. The motor roots of the spinal nerves commonly issue through the basidorsal cartilages in the sections selected, or else through a notch in the posterior border, and this affects the appearance of the figure by the introduction of a definite passage (fig. 29, A, p. 382), or, if the section includes only the margin of the foramen, a crowd of calcified tesseræ (fig. 34, A, p. 389). Since the present investigation concerns the centra almost exclusively, no special regard is paid to such points as these.

The broken line that indicates the position of the membrana elastica externa is, of course, greatly exaggerated. Except in the early stages of development, the remnants of this membrane have to be diligently searched for with a fairly high power of the microscope.

Explanation of the Lettering of the Text-figures.

A special lettering is employed in figs. 1, 3, and 6, and to these figures the abbreviations set out below do not apply.

bd, basidorsal cartilage, the principal component of the neural arch.

bv, basiventral cartilage, the principal component of the hæmal arch.

c, primary double cone, a calcification of the cartilage of the middle zone of the notochordal sheath.

cl, concentric calcified lamellæ in the outer-zone cartilage (*Squatina*, fig. 25, p. 377).

d, diagonal calcified lamella.

ee, membrana elastica externa, marking the outer limit of the cartilage of the notochordal sheath.

f, funiculus chordæ, the reduced notochordal remains in the middle of the length of the centrum.

g, growing zone.

i, island, or isolated nodule of calcified cartilage.

il, investing layer (Belegschicht of Hasse), a calcification of outer-zone cartilage immediately external to the double cone.

iz, inner-zone cartilage of the notochordal sheath.

l, intervertebral ligament.

m, solid calcified mass around the primary double cone (*Pristis*, fig. 31, B, p. 385).

n, remains of the notochord.

nr, passage for nerve-root.

oz, outer-zone cartilage of the notochordal sheath.

p, cartilaginous part of the intermediale, a structure of perichondrial origin, and not derived from sheath-cartilage, nor from arch-cartilage.

p', p'', calcified parts of the intermedialia.

r, radiating calcified lamellæ; they may be set independently upon the double cone (fig. 21, A, p. 370), or may radiate from a common base (fig. 4, B, p. 340).

s, septum, a transverse partition of fibrous, fibro-cartilaginous, or calcified tissue, usually traversed in the middle by the funicle.

t, tesseræ, granular calcifications just below the surface of the arch-cartilages; commonly in the form of a mosaic, but sometimes occurring as a continuous crust.

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