XXI. *On the Osteology of* Polyodon folium.

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[Plates 55–57.]

This Ganoid appears to have been first described, under the name of *Squalus spatula*, by Maduit in the 'Journal de Physique' for 1774, pp. 384–386, plate 2, fig. 1. Subsequently, several zoologists described and figured the external appearance of *Polyodon* under the various synonyms of *Polyodon* (Lacépède), *Spatularia reticulata* (Shaw), and *Planirostra* (Lesueur). The systematic position of the genus appears to have changed as often as its name. Originally regarded as an Elasmobranch, and subsequently as a Teleostean, it was reserved for H. Müller, in 1846, to elucidate its real affinities and to indicate its marked distinctness from the other families of Ganoids by establishing the suborder Chondrostei for its reception.

The osteology and myology of *Polyodon* have received comparatively scanty attention. The following are the chief memoirs relating to its anatomical structure with which I am acquainted :—

I. 'Spatulariarum Anatomiam descripsit Tabulaque illustravit Albertus Wagner. Berolini, 1848.

II. The male and female urino-generative organs are described by Hyrtl. ('Geschlechts-u. Harnwerk bei den Ganoiden.' Denkschriften der K. Akad., Wien. Vol. iii.)

III. Owen gives a brief description of the structure of the skull in the 'Osteological Catalogue of the Museum of the Royal College of Surgeons, London.' Vol. i.

IV. Huxley also briefly describes the cranium in his 'Lectures on the Vertebrate Skull,' Lecture XI., p. 202, and in his 'Anatomy of Vertebrated Animals,' pp. 139–140.

V. Traquair ('The Ganoid Fishes of the British Carboniferous Formations,' Part I. —*Palæoniscidæ*) refers to the structure of the quadrato-pterygoid cartilage in *Polyodon*, and also supplies some interesting facts relating to the arrangement of the fin rays, and the disposition of the fulcra and rhomboidal scales; and also discusses the relationship of *Polyodon* to the Palæoniscidæ.

VI. BURT G. WILDER ("Notes on the North American Ganoids: *Amia, Lepidosteus, Acipenser*, and *Polyodon*." Proc. Am. Ass. for Advancement of Science, 1875 and 1876) has described the brain of this genus.

VII. GEGENBAUR has described and figured the shoulder-girdle and pectoral fin in his 'Untersuchungen zur vergleichenden Anatomie der Wirbelthiere.' Parts I. and II. 1864.

VIII. THACHER ("Ventral Fins of Ganoids," Trans. Connecticut Academy, vol. iv., 1877) describes and figures the structure of the ventral fins of *Polyodon*.

In so far as the above-mentioned memoirs refer to the structure of the cranium in *Polyodon*, I have ventured in this paper to supplement them by giving a more complete description of the skull accompanied by figures. I have also attempted to compare in detail the skull of *Polyodon* with the skulls of Teleostei, Elasmobranchs, Amphibia, and with that of its nearest living ally, the Sturgeon; and in addition, I have endeavoured, roughly and tentatively, to point out the bearing of the facts elucidated on the phylogenetic relationship of *Polyodon* to the Elasmobranchs on the one hand, and to the remaining Ganoids and to the Amphibia on the other.

The destination of my specimen, which belonged to the Museum of Comparative Anatomy of the University of Cambridge, prevented me from investigating its histological structure, and particularly the minute anatomy of the vertebral column.

Of the various papers and memoirs on the structure of the skull in the Ichthyopsida with which I am acquainted, I must acknowledge my especial indebtedness to Professor HUXLEY's articles on the "Amphibia" (Encyc. Britannica, vol. i.), and on *Ceratodus fosteri* (Proc. Zool. Soc., 1876); to Dr. TRAQUAIR's previously cited memoir on the Palæoniscidæ; and also to Professor W. K. PARKER, not only for the numerous memoirs with which he has enriched this department of anatomical science, but for many suggestions, and for the information which he has given me about results as yet unpublished.

My thanks are also due to my friend Mr. A. C. HADDON, Scholar of Christ's College, Cambridge, for the drawings from which the annexed plates were taken.

Membrane bones of the Cranium. (Plate 55, figs. 1, 2, 3, and Plate 56, fig. 4.)

The cranial membrane bones of *Polyodon* are thin, narrow, and much elongated, studded with small pointed Ganoid tubercles which radiate from the comparatively thick central portion of each splint towards the thinner and almost fibrous extremities. Their sutural margins are so closely interwoven that it is almost impossible to separate contiguous splints from one another, and in their regular and symmetrical arrangement they present a striking contrast to the dermal plates of the Sturgeon. A pair of mesially opposed splints (Plate 55, fig. 1, b^1) overlie the supraoccipital region, and extend backwards for a considerable distance dorsad of the coalesced anterior vetebræ, terminating behind in a pointed process. Though constricted in the centre, they expand at their extremities both in front and behind, and are connected on each side with short transverse processes from the inner edges of the lateral splints, c^1 and c^2. Anteriorly, they are suturally united to a second pair of splints of much the same character (b^2), which, however, are not in contact along the median line, but are separated by the interposition of the median azygous element, a^1. The lateral splints, c^1 and c^2, are applied along the lateral margins of the chondrocranium. The former is somewhat Y-shaped, with one arm much shorter than the other. The stem is produced backwards to the level of the pointed process formed by the bones b^1, to the expanded hinder ends of which the short arm of c^1 is attached, while the long arm passes forwards and unites with c^2. From the inferior surface of c^1 a vertical lamina of bone descends, and is applied by its oblique anterior margin along the whole length of a diagonal ridge that traverses the lateral aspect of the cranio-spinal cartilage and to the decurrent flap of cartilage in which the ridge terminates behind and above. Posteriorly, each vertical plate diverges outwards and becomes separated from the cartilage of the coalesced anterior vertebræ by a mass of muscle. The next lateral splint, c^2, continuously overlies the pterotic ridge and sphenotic process, roofs in the orbit, and extends forwards to the nasal capsule. A process from its inner margin unites it with the junction of the bones, b^1 and b^2. An elongated oval fontanelle, covered in by membrane in the fresh skull, is left on each side, between the splints b^1 internally, and c^1 and c^2 externally, and through its anterior part the cranial cartilage and the parietal foramina can be seen.

A much smaller median fontanelle also exists between the splint a^1 and the hinder extremities of the splints b^2, and a second pair of oblong lateral fontanelles are limited internally and externally by the bones b^2, c^2, and c^3. Looking into either of the last-mentioned vacuities, the cranial cartilage and the orbital cavity can be seen. Continuing forwards the series c^1 and c^2, there is a third splint, c^3, which extends from the roof of the nasal sac along the lateral margin of the base of the rostrum as far as the anterior ends of the median bone a^1 and the paired lateral splints b^2. We have, therefore, at the base of the rostrum three longitudinally arranged series of splints, viz.: a^1, b^1 and b^2, and c^1, c^2, and c^3, forming a medio-dorsal, an inner lateral, and an external lateral series; and from this point the bones of each series are serially repeated along the roof of the rostrum to its anterior end, but instead of being interrupted by fontanelles, the rostral roofing splints are firmly adherent to one another by their thin overlapping squamose margins. There are three successive median splints, a^2, a^3, and a^4, which are disposed along the medio-dorsal line of the rostrum. The series b is continued along the rostrum by the paired splints, b^3, b^4, and b^5. It will be noticed that the paired bones of this series are in contact along the median line, and alternate with the azygous elements of the series a. The bone c^3 is in like manner repeated by one or two long splints applied to the supero-lateral margin of the rostral cartilage; but as these are much overlapped by the rayed marginal ossicles d^1, they are not visible until the latter have been removed.

The marginal ossicles, d^1 d^1, partially overlap the preceding splints. Their rays unite with those of the star-shaped osseous spiculæ by which the flexible lateral edges of the rostrum are strengthened and supported.

Circum-orbital Bones.—The orbit is bounded behind, below, and in front by a series of four or five small elongated orbital bones. Of these, two are postorbital, and the others suborbital and preorbital elements. They very much resemble the corresponding bones in many Siluroids (Ex. *Silurus, Synodontis,* &c.). The last suborbital projects backwards beyond the postorbital series as in these genera. There are no supraorbital bones. The uppermost postorbital and the preorbital are loosely attached to the sphenotic process and to the inferior margin of the nasal opening respectively.

The difficulty of correlating these investing parostoses with those which exist in other Vertebrata has been referred to by Professor HUXLEY ('Vertebrate Skull,' p. 203), and is mainly due to the fact that ossification has continuously invaded the fibrous tracts, instead of originating in distinct and definite centres. Hence in *Polyodon* one continuous splint may cover regions of the subjacent chondrocranium, which in other Ganoids and in Teleostei are invested by several distinct splints.

This difficulty is further enhanced by the want of a perfectly satisfactory scheme for the systematic classification and definite nomenclature of such superficial splints. The only attempt in this direction with which I am acquainted is that suggested by Professor PARKER in his 'Morphology of the Skull' (pp. 343–346). From the consideration of the dermal armature in the Siluroid fish *Callichthys,* he regards its cranial splints as being the serial homologues of the supero-lateral and infero-lateral plates with which its body is invested.

Thus the two supraoccipital derm bones, the single parietal, the paired frontals, and the azygous ethmoid are the serial homologues, whether azygous or paired, of the upper three-fourths of the supero-lateral body plates; while the post-temporal, supratemporal, dermo-sphenotic, the circumorbital ossicles, the lachrymals and nasals correspond to the ventral fourths of those plates, which have been segmented off, and serve for the transmission of the cranial prolongation of the lateral line mucus canal. The subdivision of the infero-lateral body plates gives rise in the skull to the opercular bones, maxillæ, jugals, præmaxillæ, branchiostegal rays, and the external mandibular splints. This scheme seems to me to be susceptible of one or two slight modifications, which were suggested to me by a careful examination of the very generalised splints that invest the posterior cranial region of the Sturgeon and the rostrum of *Polyodon.* We may, I think, with advantage classify the body splints into four series—a median dorsal, a supero-lateral, a lateral, an infero-lateral, and a median ventral series, the lateral series being devoted to the transmission of the lateral slime canal, and each element perforated by a mucous pore. This arrangement is practically that which obtains in the post-cranial armature of the Siluroid genus *Loricaria.* The median dorsal series is represented in the trunk by the median row of scales or scutes, which in *Acipenser* and in other fishes is continued along the median line of the dorsum, and in the skull by the dermo-supraoccipital and dermo-ethmoid bones. This series is rarely continuous, but is repeatedly interrupted in the trunk by the development of the dorsal fins, and in the skull by the interpolation of certain elements of the supero-lateral series. The elements of the first series are usually azygous and mesial, as in *Acipenser, Amia,* and Siluroids, &c.; but both in the skull and in the trunk they may be broken up into distinct pieces, as, for example, in the former when there are paired dermo-supraoccipitals and paired dermo-ethmoids, as in *Polypterus, Lepidosteus* and many extinct Crossopterygian Ganoids, or paired dermo-supraoccipitals only, as in the extinct Labyrinthodonta.

The supero-lateral series is represented in the skull by the parietal and frontal bones. As is the case with the elements of the first series, the parietals and frontals may, in different crania, be either single and mesial, or paired and lateral in position.

When paired parietals and frontals co-exist with either paired dermo-ethmoids or paired dermo-supraoccipitals, the typical mesial position of the latter is obscured, and they appear to form elements of the series to which the former belong, and to be homologous with them.*

The lateral or slime-canal series of scales is represented in the cranium by the post-temporal, supra-temporal, dermo-sphenotic, and nasal bones lying above the orbit, and by the postorbital, suborbital, lachrymal, and preorbital elements situated below the orbit.

The membrane bones forming the infero-lateral series in the cranium are closely related to the mandibular and hyoid arches and to the palato-quadrate arcade, and in consequence are much more subdivided than are the elements of the supero-lateral series. They include, in a linear series, the supraclavicle, operculum, præoperculum, quadrato-jugal, jugal, maxilla, and præmaxilla, forming one group of homologues; the clavicle, suboperculum, and interoperculum form a second group; and the interclavicles, the branchiostegal rays, jugular plates, and mandibular splints constitute a third group of serial homologues. On arranging these elements in accordance with the transverse segmentation into visceral arches, we have the supraclavicle, clavicle, and interclavicle, in relation with the coraco-scapular arch; the operculum, suboperculum, branchiostegal rays and jugular plates in relation with the hyoid arch, and the preoperculum, interoperculum, angular, supra-angular, dentary, quadrato-jugal, jugal, and maxilla, associated with the mandibular arch and its pterygoid outgrowth. The medio-ventral series is not so distinct as either of the others; it is possibly represented in the skull by the azygous jugular plates, or more probably by the urohyal bones of Teleostei.

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* The bones which Mr. PARKER calls paired dermo-supraoccipitals in *Callichthys* seem to me to be really the first pair of supero-lateral plates, while his median parietal is really the dermo-supraoccipital. At all events the latter seems to correspond to the bone which in *Clarius* and other Siluroids is called by that name, and which is also perforated by a median foramen.

This slightly modified schema differs from the one suggested by Professor PARKER only in the recognition of a medio-dorsal and a medio-ventral series, and the consequent alteration in the elements which are to constitute homologous series. Thus I do not consider the dermo-supraoccipital, the parietals and frontals, and the dermo-ethmoid as serial homologues, but prefer to regard the first and the last as forming one series of homologues—the medio-dorsal, while the two other bones form a second series—the supero-lateral. As will be seen shortly, this arrangement is justified by the disposition of the elements of the cranial dermal armature in *Acipenser*.

We are now in a position to endeavour to ascertain how far the cranial parostoses of *Polyodon* may be expressed in terms of this schema.

HUXLEY* refers as follows to the posterior cranial splints and the fontanelles which they enclose: "In the dorsal region it presents an anterior and posterior pair of perichondrial ossifications, separated by oblong laminæ from lateral bony plates of the same character, but the homology of these with those in the roof of the Teleostean skull is not to my mind satisfactorily demonstrated." The "anterior and posterior pairs of ossifications" referred to are those marked b^1 and b^2, and the "lateral bony plates of the same character" are c^1 and c^2. According to OWEN† the two first-mentioned pairs of bones are the parietals and frontals respectively, and the two latter the mastoid and postfrontal elements.

At first sight it seemed not impossible that the splints b^1 were the homologues of the paired dermo-supraoccipitals of *Polypterus*, *Lepidosteus*, and the *Labyrinthodonta*, but as they evidently belong to the same supero-lateral series as the paired splints, b^2, which are separated by the medio-dorsal element a^1, I am inclined to agree with OWEN, and regard them as corresponding to the parietals of other vertebrata, mesially united owing to the suppression of the proper median bone—the dermo-supraoccipital. It will be noticed that the splints (b^3) forming the third pair of supero-lateral elements are also in contact along the median line of the skull, in front of the azygous element, a^1, just as the parietals are mesially opposed behind it, thus conforming to the alternating arrangement of the medio-dorsal and supero-lateral splints of the roof of the rostrum.

The next pair of supero-lateral splints (b^2) are clearly the equivalents of the frontals, while a^1, the median bone which separates them, is a dermo-ethmoid. Three serial homologues of the last-mentioned bone (a^2, a^3, a^4,) continue the median series to the end of the rostrum. In a similar manner the parietals and frontals are serially repeated by their paired homologues b^3, b^4, and b^5. The separation of the elements of the dermo-ethmoid series by the interpolation and mesial apposition of the paired supero-lateral splints has already been pointed out.

The bone c^1, the most posterior element of the lateral series, serves to attach the supraclavicle to the skull, and might, therefore, be regarded as a post-temporal splint, especially as there is no other bone which can possibly represent that element. Its

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* 'Lectures on the Vertebrate Skull,' p. 203.

† 'Osteological Catalogue of the Museum of the College of Surgeons,' vol. i. p. 83.

horizontal and descending plates would appear to correspond to the two processes for attachment to the postero-lateral angles of the skull into which the post-temporal bone is divided in *Amia, Lepidosteus,* and in the majority of Teleostei.

In the Sturgeon, however, Professor PARKER[*] has described a complete series of pectoral splints, consisting of an interclavicle, a clavicle, a supraclavicle, and a post-temporal, the latter being attached to the skull by the bone marked c^1 (fig. 1, p. 690), (supra-temporal, PARKER), which, in possessing horizontal and descending laminæ, is in every way comparable to the bone designated c^1 in *Polyodon* (Plate 55, fig. 1). That these two bones are homologues I have but little doubt, and if the bone called post-temporal in *Acipenser* is correctly so named, then we must regard both the former as being supra-temporal elements, the proper post-temporal being altogether suppressed in *Polyodon.*

Dr. TRAQUAIR,[†] in referring to the shoulder-girdle of *Polyodon,* calls the bone c^1 the squamosal, but as this term is now usually applied to the bone which in the higher Vertebrata results from the coalescence of the præoperculum with a supra-temporal element, it would seem better, if it represents any part of the compound squamosal, to regard c^1 as being a supra-temporal element only. I am, however, much inclined (for reasons to be mentioned in describing the shoulder-girdle) to regard the splint in question as being, in both Ganoids, the homologue of the post-temporal of Teleostei.

The splint c^2 overlies the pterotic ridge and the sphenotic process, forms a roof to the orbit, and extends forwards far enough to overlie the nasal capsules. I imagine that this splint represents the distinct supra-temporal, dermo-sphenotic, and, perhaps, the ecto-ethmoidal elements of *Acipenser.* The thickened sphenotic portion of this bone suggests that ossification first began in that region, but afterwards continuously invaded fibrous tracts in front and behind which in the Sturgeon are separately ossified from distinct centres.

The parostosis c^3 is apparently a nasal bone, but may possibly be a dermal ecto-ethmoid, and the splints which I have described as being applied to the supero-lateral margin of the cartilaginous rostrum, serially repeat these elements of the lateral line series.

The rayed marginal ossicles belong to the infero-lateral series, and the first of them is applied to the outer side of the nasal bone (c^3). It is hardly possible to correlate these ossicles with any that exist in other Fishes, but perhaps they may be regarded as corresponding to that part of the infero-lateral series which is generally represented in other Fishes by the premaxillæ. In *Acipenser* they are replaced by a series of bony plates which bound the infero-lateral margin of the rostrum.

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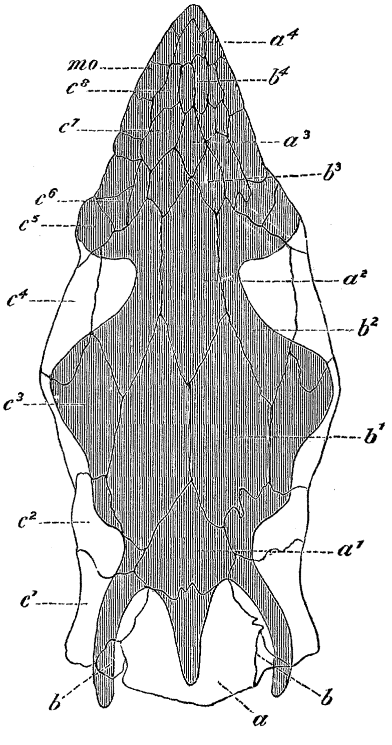
[*] "Monograph on the Structure and Development of the Shoulder-girdle and Sternum in the Vertebrata." Ray Society, 1878.

[†] "Ganoid Fishes of the British Carboniferous Formations, Part I.—Palæoniscidæ." Mem. Palæontographical Soc., 1877.

If the arrangement of the splints which invest the posterior cranial region of the Sturgeon throws light on the nature of those similarly located in *Polyodon*, it is also true that the disposition of the rostral splints in the latter Ganoid suggests the plan on which those of the former are arranged.

In no two specimens of *Acipenser* are the anterior cranial splints disposed in quite the same way, and the arrangement may even differ on opposite sides of the same skull. From an examination of several skulls, and especially of one now in the University Museum, and from which the annexed woodcut was taken, I think it may be demonstrated that the splints in both genera are arranged in accordance with a common plan.

Thus in the woodcut the splints marked a^1 to a^4 correspond to the medio-dorsal series in the typical scheme, and in *Polyodon*. The one marked a^1 is a dagger-shaped



bone, and evidently represents the dermo-supraoccipital. The next mesial splint (a^2) is a dermo-ethmoid, and in this specimen is separated from the preceding bone by the mesial apposition of b^1 b^1—two bones belonging to the supero-lateral series—though in most skulls the long blade of the dermo-supraoccipital completely separates them, and suturally unites with the hinder margin of the ethmoid.

The splints a^2 to a^4 continue this series to the end of the rostrum, and, as in *Polyodon*, are more or less completely separated from one another by the interpolation of the paired elements of the next series. The scute marked a is the first of the medio-dorsal plates of the trunk. In the supero-lateral series, the paired osseous plates marked b^1 and b^2 are the parietals and frontals; and, as in *Polyodon*, the former are in contact mesially, though partially separated behind by the dermo-supraoccipital, which, as a distinct bone, does not exist in the latter Fish.

The bones b^3 and b^4 repeat the parietals and frontals along the sides of the snout.

The splint c^1 (post-temporal), the first splint of the third, or infero-lateral series, resembles the corresponding bone in *Polyodon* in developing an extensive descending osseous lamina which is applied by its anterior margin to the cartilage that forms the lateral walls of the cranio-spinal canal. The splints c^2–c^5, which are represented by a single bone (c^2) in *Polyodon*, correspond to the supra-temporal, dermo-sphenotic, supra-orbital, and ecto-ethmoid elements of the Teleostean skull. c^6 is a nasal bone, and c^7 and c^8 continue this series forwards along the rostrum.

Postorbital, suborbital, and præorbital bones surround the orbit, and the inferior margin of the rostrum is fringed by a series of five or six plate-like marginal ossicles (*m.o.*) precisely as in *Polyodon*.

Thus it will be seen that, notwithstanding the superficial differences between the cranial splints of the two genera, due to the tendency in *Polyodon* of the osseous centres to continuously invade fibrous tracts usually ossified separately, and to the irregular asymmetrical disposition and proneness to segmentation of the splints in *Acipenser*, their fundamental arrangement is much the same in both Ganoids.

The foregoing considerations seem to me to suggest an explanation of the dermal armature of *Ceratodus*, which is somewhat different from that proposed by Professor HUXLEY.* Comparing the skull of that Fish with those of *Acipenser* and *Polyodon*, it will be seen that the anterior and posterior median bones (A^1 and A^2) in the former are the equivalents of two elements in the medio-dorsal series of the latter, viz., the dermo-supraoccipital and dermo-ethmoid, while the anterior and posterior inner lateral bones (C^1 and D^2) correspond to the parietals and frontals.†

The bones marked E and D are elements of the lateral series, and probably correspond to the bones called supra-temporal in the Sturgeon, or, if coalescent, they would be the equivalent of the greater part of the bone c^2 in *Polyodon*.

But as Dr. GÜNTHER remarks the fact that all the cranial derm bones in *Ceratodus*, with the exception of the median ethmoid, lie external to the temporal muscles, throws considerable doubt on the results of any attempt to identify these bones with those which in other Vertebrata lie beneath the muscles and directly upon the cartilage of the cranial roof. The former are evidently ossifications of a more superficial fibrous tract than that in which the latter are usually formed.

If the two splints which invest the rostrum of the Pike's cranium, and are marked 2–2

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* "Contributions to Morphology. Ichthyopsida, No. 1.—On *Ceratodus fosteri*, with Observations on the Classification of Fishes." Proc. Zool. Soc., 1876.

† It will be noticed that in *Ceratodus*, as is commonly the case in *Acipenser*, the dermo-ethmoid and dermo-supraoccipital bones are suturally united.

in HUXLEY'S figure,* are not paired dermo-ethmoids, corresponding to the paired endosteally formed centres which in that Teleostean represent the median ethmoid of other Fishes, it would appear that they must correspond to the paired ossifications marked b^3 in both *Polyodon* and *Acipenser*, the serial homologues of the parietals and frontals. The bones marked 1 in the same figure apparently belong to the lateral series, and would probably represent the nasals of other Fishes.

It may also be mentioned that the generalised medio-dorsal and supero-lateral cranial plates which invest the rostra of such Teleostean Fishes as *Ostracion, Loricaria,* &c., exhibit the same alternating arrangement which has been pointed out in *Polyodon* and *Acipenser.*

The parasphenoid (Plate 55, figs. 2 and 3; Plate 56, fig. 4) is of great length, extending from a point just in front of the nasal capsules to a considerable distance beneath the coalesced anterior vertebræ. The postcranial part of the bone expands and bifurcates in order to allow the efferent branchial vessels to reach the anterior part of the dorsal aorta, and the two slightly divergent arms receive between them the anterior part of the massive notochord and the commencement of the hæmal canal. The cranial part of the bone is slightly convex below and concave above where it is applied to the cartilage of the basis cranii. After slightly expanding between the nasal sacs the parasphenoid contracts in the orbital region, and again expanding beneath the auditory capsules, sends off on each side a short triangular basi-temporal wing (*b.tp.*) which passes upwards and outwards between the foramina for the exit of the palatine and spiracular divisions of the seventh nerve, closely applied to the cartilage that forms the thin outer wall of the short Facial canal which traverses the outer wall of the periotic capsule between those foramina, and terminates above in a point just in front of the lower end of the groove for the head of the hyomandibular. At the base of this process the parasphenoid gives off a second and smaller process, which is directed outward and backwards as in *Amia,* and to the angle between the two the pharyngo-branchial of the first branchial arch is attached. (Plate 55, fig. 3, *b.tp.*)

Just in front of its bifurcation the lower surface of the parasphenoid is marked by two osseous knobs, and the lateral margins of its anterior moiety are slightly overlapped by the adjacent cartilage. In front of the parasphenoid, and anterior to the internasal area, there is a pair of splints (fig. 2, *vo.*) which appear to represent the vomers; and wedged in between their anterior ends there is a second mesial splint (p^2) extending backwards nearly to the anterior end of the parasphenoid. If the paired splints are correctly to be regarded as vomers, then this azygous splint would appear to be the homologue of the anterior parasphenoid described by PARKER† as existing in *Rana pipiens.*

In front of the mesial splint (p^2) there is a third median splint (p^3) continuing the

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* 'The Anatomy of Vertebrated Animals,' p. 154, fig. 46.

† "Structure and Development of the Skull of the Common Frog," Phil. Trans., Vol. 161, p. 193, 1871.

series to the end of the rostrum, and, as is the case with the medio-dorsal elements, they are separated from one another by the interposition and mutual apposition of the two pairs of splints (v^2, v^3) which serially repeat the vomers along the ventral surface of the rostrum. Hence, just as the elements of the medio-dorsal and supero-lateral series—the supraoccipital and dermo-ethmoid, the parietals and frontals—are serially repeated along the dorsal surface of the rostrum, so there is a similar serial repetition of the parasphenoid and vomers along the ventral surface.

There is also on each side a ventral series of rayed marginal ossicles (*m.o.*) which overlap the vomerine series. The rays of these ossicles are connected with those of the star-shaped spicules that support the ventral layer of the flexible coriaceous margin of the rostrum. In the interspace between the cartilage of the rostrum and the upper and lower layers of its flexible margin I noticed two large nerves running forwards to the extremity of the rostrum; these nerves are probably the rostral branches of the first and second divisions of the Trigeminus.

The Chondrocranium. (Plates 56 and 57, figs. 5, 6, and 7.)

When stripped of its investing parostoses the cranium presents the appearance represented in Plate 56, fig. 5.

Its most striking feature is the enormously elongated prenasal rostrum. The skull with its rostral prolongation is about one-third of the entire length of the axial skeleton, the rostrum alone being one-fourth of the length of body, and at least twice as long as the rest of the chondrocranium.

About eight or nine of the anterior vertebræ have so completely coalesced with each other and with the skull, that the only indications of the primitive segmentation into distinct vertebræ is the serial arrangement of the obliquely disposed pairs of foramina for the exit of the anterior and posterior roots of the spinal nerves, the anterior root leaving the spinal column below and a little in front of the posterior root.

The posterior limit of the cranium seems to be approximately indicated by a prominent ridge-like elevation of the lateral walls of the cartilaginous mass formed by the coalescence of the occipital region with the adjacent vertebræ. This ridge (Plate 57, fig. 7, *a*), which is mainly an outgrowth from the cartilage of the two anterior vertebræ, first becomes evident beneath the Vagus foramen, and then passes obliquely upwards and backwards between the foramina for the exit of the anterior and posterior roots of the first spinal nerve to terminate behind the postero-external angle of the skull in a free, decurrent, wing-like process (fig. 7). The vertical lamina of the post-temporal bone is applied to the outer side of this process, and its anterior margin just overlaps the oblique ridge (fig. 3). In front of the ridge the occipital region is slightly constricted, and behind it the bulging notochord and paired foramina for the spinal nerves become visible. When the chondrocranium is viewed from above (fig. 5) the ear capsules are seen to form conspicuous lateral outgrowths terminating anteriorly in projections which reach nearly to the antorbital region. The slightly contracted orbital region is limited in front by the almost pedunculated nasal capsules.

Behind the auditory region the cranial roof becomes constricted into a band-like area, which is formed partly by the coalesced apices of the anterior neural arches, and partly* by the roof of the occipital region. The divergent processes ($\phi\phi$) are the posterior ends of the decurrent flaps of cartilage previously mentioned.

The floor of the occipito-periotic region, where it rests on the parasphenoid, is very narrow, but the external walls diverge outwards as they pass upwards to join the margins of the flat and comparatively broad upper surface of this part of the skull; hence a transverse section is almost triangular in shape. The width of the cranium in this part is mainly due to the massive periotic sacs, and the growth of cartilage round the semicircular canals is thick enough to prevent them affording any external indications of their position. The upper and external margin of each otic capsule is produced outwards into a prominent pterotic ridge, and forwards into a stout sphenotic process, which arches outwards, downwards, and forwards, and also forms a roof to the hinder part of the orbit. Posteriorly the pterotic ridges terminate in the rounded blunt projections which form the postero-external angles of the otic capsules.

The outer face of each capsule is traversed by a deep vertical groove with a prominent anterior lip, which extends from the pterotic ridge to a point just above the facial foramen, and serves for the articulation of the hyomandibular. This groove, limited in point by its projecting anterior border, is seen in fig. 5 (*hy.g.*), as an emargination of the pterotic ridge behind the sphenotic process. The mesial portion of the cranial roof forms an elongated band-like area, flattened, like the pterotic ridges, by the impress of the overlying membrane bones—the parietals and frontals; but on each side of it, in the roof of the otic capsule, there is an *f*-shaped groove (*f.g.*), the anterior end of which diverges outwards into the sphenotic prominence, while its hinder end terminates on the postero-lateral margin of the pterotic ridge. The groove is visible externally through the oblong fontanelle, which on each side is left between the post-temporal, dermo-sphenotic, and parietal splints (fig. 1). In the posterior part of each groove there is an infundibuliform opening (*p.f.*), which is the outer termination of a short but wide canal leading into the cranial cavity; and in the anterior part there is a much smaller foramen, which communicates by a short narrow canal with a slit-like aperture (figs. 3 and 4, *x.*) on the infero-lateral surface of the otic cartilage, between the metapterygoid ligament and the articular groove for the reception of the head of the hyomandibular. These foramina will be referred to subsequently. In front of the wing-like sphenotic prominences the chondrocranium is constricted to form the orbits. A slight backward outgrowth from the upper margin of the ethmo-trabecular region, together with the produced orbital margins of the sphenotic process and pterotic ridge, furnish a partial roof to the orbit. Previous to the removal of the dermo-sphenotic bone (c^2), which extends continuously over each

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* As represented in Plate 56, fig. 5, this band-like area is one-sixteenth of an inch too wide.

of these processes, this roof was a complete one. A partial floor is formed for each orbit by a rough irregular outgrowth of cartilage (*o.f.*, figs. 3 and 4) from the inferior edge of its inner wall. There is no supraorbital ridge, the junction of the inner wall of the orbit with the cranial roof being gently rounded off. The aliethmoidal, aliseptal, and subnasal outgrowths have combined to form a cup-shaped nasal capsule, supported on a short, thick neck. The thick posterior wall of each capsule is slightly produced backwards over the orbit beneath the dermo-postfrontal bone, and the lower lip of the cup, besides being somewhat more prominent than the upper, is slightly emarginate. This emargination of the subnasal outgrowth corresponds in position to the laterally placed posterior narial aperture (fig. 3, *p.n.*); the anterior nares, though situated in front of the former, are also lateral in position (*a.n.*). I could detect nothing suggestive of the existence of either a free or a coalesced antorbital or palatine process. The only possible representative of that element is the slightly produced inferior and external angle of the posterior wall of the nasal sac. The long and depressed cartilaginous prenasal rostrum is small relatively to its size when invested with its splints. The upper surface is gently convex from side to side, but its floor and sides are straight. It diminishes very gradually in height, but rapidly in width, towards its slightly expanded and flattened anterior termination. As in *Acipenser*, the rostral axis is slightly tilted upwards, so as to make a widely open angle above with the cranial axis. The spatulate appearance of its anterior end, as seen in Plate 55, figs. 1 and 2, is not due to the configuration of the axial cartilage, but to the disposition of the investing membrane bones. The lateral margins of the extreme anterior end of the rostrum are slightly flattened out, as in *Raia* and *Rhinchobatus*, and, as in these genera, are suggestive of the presence of a pair of upper labial cartilages. The roof of the rostrum is complete, with the exception of a small median fontanelle (figs. 5 and 6, *a.m.f.*) situated just in front of the nasal sacs, and evidently corresponding to the much larger anterior median fontanelle of the Skate and *Rhinchobatus*. In general appearance the rostrum of *Polyodon* is very like that of the last-named Elasmobranch, as will be seen on referring to the excellent figures of the latter given by GEGENBAUR in his 'Untersuchungen zur vergleichenden Anatomie der Wirbelthiere' (plate iii., fig. 1; plate vi., fig. 3, and plate ix., fig. 2). The rostrum of *Rhinchobatus*, however, differs from that of *Polyodon* in the presence of labial cartilages coalesced with its anterior end, in the larger size of its median fontanelle, and in the absence of a lamina perpendicularis separating the cavity of the rostrum from the cranial cavity. But, as previously suggested, it is not improbable that the winglike expansions of the anterior end of rostrum in the Ganoid may point to the presence of upper labial cartilages which have coalesced with it.

HUXLEY,* in describing the chondrocranium of the Sturgeon, refers to the coalescence of the anterior vertebræ with each other and with the skull. He says: "At this point there is in the cranio-spinal cartilage of both the Sturgeon and Spatularia a

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* 'Lectures on Vertebrate Skull,' pp. 204, 205.

great dilatation of the neural canal, which is closed above only by a membranous fontanelle." This description, in so far as it refers to *Polyodon,* is not quite accurate. There is, it is true, a large posterior median fontanelle in the Sturgeon which extends forwards for a short distance in front of the Vagus foramen, and is therefore, in part at all events, a cranial fontanelle. But in *Polyodon* I could find nothing at all comparable to this large and conspicuous fontanelle of *Acipenser.* The neurapophyses of the anterior vertebræ coalesce over the spinal cord and anteriorly blend with the cartilage of the occipital roof, and the continuity of the roof of the spinal canal seems to be uninterrupted.

We may now consider the foramina which I have already referred to as existing in the *f*-shaped groove in the roof of the periotic capsula. Each infundibuliform orifice is situated on the outer side of the common canal by which the anterior and posterior vertical semicircular canals open into the membranous vestibule, and the short but relatively wide passage into which the orifice leads passes downwards and inwards beneath the arch of the posterior canal, and opens into the cranial cavity just behind the recess in which the vestibular sac is lodged (Plates 56 and 57, figs. 5, 6, and 7, *p.f.*) These foramina at first appeared to correspond to the paired posterior fontanelles which are seen in the roof of the Frog's chondrocranium when the overlying parieto-frontal bones have been removed, or to similar vacuities existing in the roof of the Salmon's skull, which in the latter are spaces left on each side of a recurrent growth of cartilage derived from the ethmoidal region. But these fenestræ have nothing to do with the otic capsule; they are always mesially placed with regard to it, and their passages of communication with the cranial cavity do not pass beneath the arch of the posterior vertical canal, or in any way perforate the periotic cartilage.

Another alternative is to regard these infundibuliform orifices and their canals as being due, like the parietal foramina of the Elasmobranchs, to the persistence of the canals by which the primitive auditory involutions of the embryo *Polyodon* communicated with the exterior. But this view may be met by the objection that in the Selachii the parietal foramina and their canals do not pass beneath the arch of the posterior vertical canal, but are situated altogether to the mesial side of the vestibule and its canals. Moreover, in the Shark these foramina do not communicate with the cranial cavity but with the central cavity of the periotic cartilage in which the membranous vestibule is lodged. In mitigation of the force of the first objection, it may be urged that in the young *Polyodon* the cœcal outgrowth from the vestibule, which eventually becomes the posterior vertical semicircular canal, may have grown round the primitive involution from the exterior instead of having its growth limited to the outer side of that ingrowth, as appears to have been the case in the young Shark. In opposition to the second objection it may be said that if the inner wall of the periotic capsule be atrophied, as it is in all Teleostei and Ganoids, then the parietal foramina will necessarily communicate with the cranial cavity, as do the infundibuliform orifices in *Polyodon.*

Both in the young Tadpole and in the very early stages of the developmental history of the Salmon, the chondrification of the roof of the periotic capsule is incomplete in the region of the primitive involution; and it seems conceivable that in *Polyodon* this primitive fenestration has been retained in the adult, while the atrophy of the inner or cranial wall of the capsule has caused it to communicate with the interior of the cranium.

Though the last view of the nature of these fenestræ seems to me to be the more probable one, yet it is possible that neither is correct, and that they may be of secondary origin—the result of local absorption of the cartilage of the otic capsule.

But if my view be correct, then the existence of these parietal foramina in *Polyodon* is an important anatomical feature in which that Fish differs from all other Ganoids and Teleostei, and approaches the Plagiostome Elasmobranchii. Mr. PARKER informs me that he has discovered similar perforations of the otic cartilage beneath the posterior canal in the Urodele Amphibian, *Siren lacertina*, to which he attaches a like significance. This fact is an important addition to the list of anatomical characters common to the Ganoids, Elasmobranchs and Amphibia.

I may add that in *Acipenser* there is a depression in the roof of the otic cartilage external to the posterior vertical semicircular canal, and at the bottom of it there is a fat-infiltrated canal which penetrates for a short distance into the substance of the cartilage, but does not communicate with the cranial cavity. The enormous growth of the cranial cartilage, which has effectually masked other embryonic features in the cranial structure of the Sturgeon, has probably obliterated the primitive communication of these canals with the cranial cavity.

The oblique lateral ridges and decurrent wing-like processes described in *Polyodon* are also represented in the Sturgeon. Behind the auditory organs, "and separated from them by a deep lateral fossa, are two wing-like processes, which are directed outwards and obliquely backwards, and proceed not from the walls of the cranium proper but from those of the spinal column, where it joins the skull."* This ridge, however, runs from above downwards and backwards, the foramina for anterior roots lying above the ridge, and those for posterior roots below it.

The second and smaller foramen (figs. 3 and 4, *x.*) in the anterior part of the *f*-shaped groove lies at the bottom of a deep basin-shaped depression in the roof of the otic cartilage, and communicates through a short canal with an elongated slit-like opening (*x.*) on the infero-lateral face of the periotic capsule, between the articular groove for the hyomandibular, and the attachment of the metapterygoid ligament. In the fresh specimen it was seen that the slit-like inferior opening was situated in the inner wall of the spiracular passage, and that the mucous membrane of the pharynx was continued through it into the canal, but the upper part of the latter and the depression into which it opened above, as well as the *f*-shaped groove, were filled with connective tissue infiltrated with fat. It may, in fact, be said that the first visceral

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* HUXLEY, *loc. cit.*

cleft splits into two canals, a large canal opening at the spiracle, and a smaller one which perforates the otic cartilage and opens on the superior surface of the skull. The canal is quite external to the semicircular canals and vestibule, though it approaches nearest to the horizontal canal. The meaning of this spiracular diverticulum, at first sight, was not very clear. I was inclined to regard it as having some connexion with the remarkable fenestration of the infero-lateral face of the periotic capsule which occurs in the very early stages of the embryo Salmon, and which PARKER* has called the "primordial fenestra ovalis," from its analogy to the fenestra ovalis of the abranchiate Vertebrata.

But further consideration suggested to me that the diverticulum in question might be nothing more than a result of the rapid growth of the cartilage of the ear-sacs round the upper part of the first visceral cleft, so as to constrict it off from the rest of the cleft which remains as the spiracular canal.

On examining a fresh Sturgeon's skull, I found a diverticulum of the spiracular passage precisely similar to, but relatively smaller than that described in *Polyodon*, and, as in the latter, opening into a basin-shaped depression in the roof of the otic capsule. The inferior orifice was just in front of the hyomandibular, and behind the mandibular gill; the upper part of the canal was filled with fat.

Periotic Bones (Plates 55 and 57, figs. 3 and 7).—At first it seemed evident that the membrane bones previously described were the only ossifications developed in connexion with the chondrocranium of *Polyodon*, but after a careful examination I detected a small circular ectosteal scale, marked with concentric lines of growth overlying the posterior part of the horizontal semicircular canal. This scale must be a rudimentary representative of the pterotic (*pt.o.*). Behind the latter and immediately in front of the Vagus foramen, there was a second small ectosteal scale, oval in shape and slightly larger than the first. From its relation to the ampulla of the posterior vertical semicircular canal, this ectosteal patch must represent an opisthotic element (*op.o.*).† These appear to be the only representatives of the otic bones of other Fishes. A careful investigation of the epiotic, prootic, and sphenotic regions, as well as of the rest of the external surface of the chondrocranium, failed to reveal the existence of any other ectosteal or of endosteal centres.

Cranial Foramina.—Certain foramina opening on the roof of the cranium have already been noticed, but there still remain those which perforate its lateral walls and serve for the transmission of the cranial nerves and vessels. A small foramen perforates the side walls of the broad posterior part of the rostrum, at about the same distance in front of the olfactory sacs as the anterior median fenestra (figs. 3 and 6, Z). In the absence of a supra-orbital ridge there is no antorbital foramen for the Ramus ophthalmicus superficialis which would appear to pass dorsad of the neck of each nasal

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* "Structure and Development of the Skull in the Salmon," Phil. Trans., 1872, p. 118.

† The relations of the otic bones to the horizontal and posterior vertical semicircular canals is well shown in Plate 57, fig. 7.

sac. On the anterior and posterior walls of each sac there is a small foramen, which I imagine may be the equivalents of the orbital and prenasal openings of the orbito-nasal canal of Elasmobranchs. The optic foramen (II) is situated at about the middle of the inner wall of the orbit; above it there is a small aperture (*m.o.*) for the motores oculi, and behind it are two relatively large foramina for the branches of the fifth nerve.

The Facial nerve (fig. 6, *Fa.*) on leaving the cranial cavity passes obliquely backwards and outwards through the cartilage of the otic capsule, and instead of opening directly on its external surface, communicates with a short antero-posterior canal, the outer wall of which is formed by an oblique bar of cartilage strengthened externally by the basi-temporal wing of the parasphenoid. The comparatively large anterior and posterior apertures of this canal are marked VII and VII′ in fig. 3. This obliquely disposed cartilaginous bar resembles a similar process (Knorpelspange), described by GEGENBAUR as holding a similar relation to the Facial foramen in *Rhinchobatus, Trygon*, and *Pristis*. In these Elasmobranchs the anterior opening of the canal is for the exit of the Ramus palatinus, while the posterior one transmits the common stem of the pre-spiracular and post-spiracular branches of the Facial nerve; and it seems probable that the canal in *Polyodon*, so similar in all other respects, subserves a like function. Whether the foramen marked *s* in fig. 6 is for the pre-spiracular nerve, or, as is more probable, simply transmits a vessel, I am unable to say. Immediately over the pointed apex of each basi-temporal ala the slit-like inferior termination (*x.*) of the canal, whose upper extremity opens into the anterior part of the *f*-shaped groove, can be seen.

Behind the posterior opening of the Facial canal is the small aperture for the exit of the Glossopharyngeal nerve, and still more posteriorly, and a little above it, is the large oval foramen for the Vagus. The anterior and posterior roots of the spinal nerves pass out of the spinal canal through a series of pairs of obliquely-disposed foramina, the one for the anterior root being inferior to, and slightly in advance of that for the posterior root. A supra-orbital foramen passes upwards through the posterior wall of the orbit, and opens into the adjacent part of the *f*-shaped groove.

Fig. 6 represents a vertical and longitudinal section of the cranium and rostrum. "The notochord, extremely large in the spinal column, rapidly diminishes in size as it enters the skull, and becoming a mere thread, terminates behind the pituitary fossa." The hæmal canal (*h.c.*) extends forwards between the diverging arms of the hinder part of the parasphenoid, and terminates where the former meet the body of the bone; and the canal (B) which is included between the upper halves of the neurapophyses, lying dorsad of the spinal canal and quite distinct from it, opens anteriorly on the hinder part of the cranial roof. The cranial cavity is high, but much compressed laterally. It extends forwards between the orbits, and is terminated anteriorly by a lamina perpendicularis, on either side of which the Olfactory nerves diverge to the nasal capsules. The spinal canal is enormously dilated in front, and with that part of the cranial cavity which lies behind the foramina for the Vagi, forms the comparatively high but compressed portion of the cranio-spinal canal. In front of these foramina the cavity gradually diminishes in height and width towards its rounded anterior termination against the lamina perpendicularis. As in other Ganoids and in all Teleostei, the inner wall of the periotic capsule is incomplete, the recess in which the membranous vestibular sac is lodged communicating widely with the cranial cavity. The letters *a.sc.*, *p.sc.*, and *h.sc.*, mark the openings of the semicircular canals into the vestibular recess. In the middle of the outer wall of this recess there is a small fenestra (*a*) which opens into the Facial canal behind the point where the seventh nerve enters the latter. The condition of my specimen would not admit of a successful dissection of the cranial nerves, hence I am unable to say definitely what vessels and nerves were transmitted by the closely aggregated foramina which perforate the side walls of the anterior part of the cranium.

The numerals VII (fig. 6) indicate the cranial end of the passage by which the Facial nerve reaches the Facial canal; V is the internally single aperture for the exit of the Trigeminus, and in front of it the small and shallow pituitary fossa is seen to be completely floored by cartilage. The small foramen (*Ca.*) on the anterior margin of the fossa may serve for the transmission of the carotid artery, while the small apertures indicated by the letters *m.o.* and *tr.* probably transmit the motores oculi, and the trochlearis. The external opening of the last-mentioned nerve is just in front of that for the fifth nerve;* II is the optic foramen. All these passages pass very obliquely outwards and forwards through the cranial walls. The Olfactory nerve breaks up into a number of small filaments, each of which reaches the olfactory mucous membrane through a separate opening in the inner wall of the nasal capsule, thus giving rise to a true cribriform plate. So far as I am aware, in all other branchiate Ichthyopsida this nerve passes bodily through a single large foramen to reach the interior of the nasal sac. The cavity of the rostrum is quite distinct from the cranial cavity, and terminates at some little distance behind its anterior end, which is much depressed and solid. It communicates with the exterior by the single median fenestra in its roof (*a.m.f.*), and by two lateral foramina (*z.*). It seems to me that this singular rostral cavity may be compared to the large "meso-ethmoidal fat cavity," which Mr. PARKER† has described as existing in the adult Salmon, in front of the coalesced orbito-sphenoids and lamina perpendicularis. Both occupy similar morphological areas, and each has a superior median foramen situated beneath the azygous dermo-ethmoid splint. If this comparison be correct, and the meso-ethmoidal fat cavity of *Salmo* is truly homologous with the rostral cavity of *Polyodon* and the Elasmobranchs, then its origin, as the result of a secondary fenestration of the internasal cartilage, is another example of a not unfrequent phenomenon in developmental history—the appearance of particular structure as a secondary feature, though normally and in the lower types it may be a primary one.

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* The aperture *v* seems to transmit a vessel.

† PARKER, "On the Structure and Development of the Skull in the Salmon." Phil. Trans., 1872, p. 108.

From what has been said, it is apparent that in all essential features the chondrocranium of *Acipenser* resembles that of *Polyodon.* The massive growth of the cranial cartilage in the former has masked many features which are very evident in the latter. To this cause are due the obliteration of the fore part of the cranial cavity, which, consequently, appears to terminate behind the orbits where the brain also ends, though in reality it is continued as a very narrow canal, upwards and forwards, nearly as far as the internasal region, and the conversion of the rostrum into an almost solid mass of cartilage, traversed by anastomosing fat cavities. To the same cause is due also the obliteration of the passage by which it is probable the parietal depression primitively communicated with the cranial cavity. The growth of the cartilage round the margins of the parasphenoid, over the junction of the latter with the vomers, and round the tracks of the rostral divisions of the fifth nerve, which in consequence run in deep grooves bounded by high ridges, are other examples of the same tendency. The nasal sacs are shallow cups hewn out of the rostral cartilage instead of being appended to it by short peduncles, as in *Polyodon.*

The large vacuity which interrupts the continuity of the roof of the cranio-spinal cartilage, and which is situated mainly behind the vagus foramen, is absent in *Polyodon,* except, perhaps, in so far as the anterior termination of the supra-spinal canal may be its representative in the latter genus. In the Sturgeon the wing-like processes of the cranio-spinal cartilage run backwards and downwards from the postero-lateral angles of the cranium, which is the contrary direction to that taken by the lateral ridges in *Polyodon.* In both genera the unusual lengthening of the post-auditory and pre-orbital regions of the chondrocranium as compared with the size of the brain, causes the Olfactory, the Pneumogastric, and the most anterior spinal nerves to run respectively forwards and backwards within the cranial cavity for a considerable distance before issuing through their respective foramina. A Facial canal, similar to but much longer and wider than that of *Polyodon,* exists also in *Acipenser.*

The Visceral Arches. (Plate 57, figs. 8 and 9.)

The two first visceral arches exhibit an interesting compromise between the peculiarities of the Elasmobranch and Teleostean types, for while the mandibular arch conforms mainly to the former type, the hyoid arch as distinctly follows the latter.

As is the case with the hyostylic Selachians, the quadrate and the pterygoid process together form a continuous bar of cartilage—the so-called "palato-quadrate bar" (fig. 8, *pg.,* Q.). This bar has no connexion with cranium, either directly or by ligament, but is suspended by its posterior extremity from the distal end of the symplectic, to which it is firmly attached by two slender ligaments. These ligaments pass from the rounded posterior margin of the quadrate cartilage backwards parallel to the anterior margin of the symplectic, and are attached, one to the proximal end of that cartilage, and the other to the contiguous extremity of the hyomandibular;

they evidently correspond to the symplectic ligament of the Shark. The palato-pterygoid cartilage is a laterally compressed bar, deep behind and concave externally, with a gently rounded and elevated postero-superior border and a transversely extended articular convexity for the proximal end of the mandible. Anteriorly, in the orbital region, the bar becomes constricted, with its upper margin gently concave and its plane a little twisted, so that its outer surface looks upwards and outwards, and its inner downwards and inwards; and, before curving inwards to join the corresponding bar of the opposite side, it becomes somewhat expanded, and at the same time tilted upwards. From the quadrate portion of the bar, a broad leaf-like outgrowth of cartilage (*or.p.*) passes forwards on the outer side of, and parallel to, the "palato-quadrate" arcade, and in close relation externally with the inner surface of the hinder part of the maxillary splint. To this curious outgrowth I shall have occasion to refer presently. The levator mandibularis muscle lies along the grooved outer surface of the palato-quadrate cartilage between it and the maxilla externally, and passing backwards from its anterior attachment curves sharply downwards behind, between the quadrate and its leaf-like process and passes to its connexion with the lower jaw.* Closely applied to nearly the whole length of the palato-quadrate lamina there is a thin splint-like maxilla. This bone (*mx.*) has an unusual backward extension, reaching, in fact, as far as the condylar end of the quadrate cartilage; its posterior third is closely adherent to the outer surface of the leaf-like process, and its middle third is separated from the main pterygoid bar by the levator mandibularis muscle, while its diminished and almost pointed anterior third clips the lower edge of the ectosteal scale (*m.pg.*) and the adjacent cartilage.

Thus the maxilla in its extension backwards to the outer side of the lower end of the quadrate corresponds to the entire infra-temporal arcade (maxilla, jugal, and quadrato-jugal) of other Vertebrata. Two other ossifications have a more intimate relation to the "palato-quadrate bar." Of these, one is composed of two thin round scale-like exostoses applied to the inner and outer sides of the expanded anterior end of the bar; each scale is marked with concentric lines of growth and separated from the other by intervening cartilage (fig. 8, *m.pg.*). The other bone is a long splint attached along the whole length of the inner side of the palato-quadrate cartilage from the inner side of the quadrate forwards to near the symphysial union of the two bars. Broad behind, the bone thins away in front, and its slightly sinuous anterior portion clips the upper edges of the two ectosteal scales. The splint is clearly a parosteal pterygoid, comparable to the bone so named in the Axolotl and other Urodele Amphibia.

Dr. TRAQUAIR† (plate vii., fig. 2) gives an inner view of the palato-quadrate cartilage, showing the pterygoid; but neither in this figure nor in fig. 1 does he represent the two ectosteal scales, or the leaf-like outgrowth from the quadrate.

The proximal end of the Meckelian cartilage (*Mk.c.*) is slightly bent upwards on its

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* *Vide* plate vii., fig. 2, in Dr. TRAQUAIR'S memoir, *loc. cit.*

† *Loc. cit.*

distal moiety, so that a short ascending process is produced which carries a transverse groove for the reception of the co-adapted articular end of the quadrate; its angular margin is gently rounded. Towards the ligamentous symphysis the axial core thins away, and finally terminates in a stout, cylindrical, mento-Meckelian bone.

A long dentary splint (*d.*) is applied along the whole length of the outer side of the cartilage; by the bending inwards of its upper and lower edges a groove is formed in which the axial cartilage and the mento-Meckelian ossicle lie. The splenial is a thin splint applied to the inner side of the proximal portion of the cartilage and reaches nearly to the articular end. There is no os articulare, nor any distinct angular, supra-angular, or coronary bones. Dr. TRAQUAIR* supplies a view of the mandible with its investing splints (plate vii., fig. 2).

Though the mandibular arch has no cartilaginous or osseous metapterygoid, yet the latter is not without a representative. The spiracular opening leads by a short tube directly into the pharynx, and in front of it, in the place of the spiracular cartilage, a strong ligament passes from the smaller of the two parasphenoidal alæ obliquely downwards and backwards beneath the spiracle to be attached to the anterior margin of the upper third of the hyomandibular.

Along the spiracular margin of this ligament the pharyngeal mucous membrane is produced into a number of short branchial filaments with attached bases and free extremities. I could not detect any cartilaginous rays in these filaments nor any cartilage in the ligament.

The gill filaments constitute a spiracular or mandibular gill, homologous with the structures so named in the Selachii; and the ligament is as clearly the representative of the metapterygoid ligament of that group from which, however, the former differs in being attached to the hyomandibular instead of to the quadrate cartilage. But it may be pointed out that in the Shark some at least of the fibres of the metapterygoid ligament are attached to the hyomandibular.

In *Acipenser,* in consequence of the increased transverse width of the skull, a long spiracular canal connects the external opening with the pharynx, and along the anterior margin of the slit-like pharyngeal opening of this canal the mucous membrane is produced into a series of branchial filaments precisely as in *Polyodon,* though there is nothing in the Sturgeon comparable to a metapterygoid ligament—a fact which supports Mr. PARKER's conclusion, that this element is represented by the triangular cartilage which, with its fellow, forms the posterior part of the roof of the protrusible proboscis.

I am not aware that the presence of spiracular gills has previously been noticed in any adult Vertebrata except the Elasmobranchii. Neither *Amia, Polypterus,* nor *Lepidosteus* possesses any traces of such structures. Hence, so far as this point is concerned, *Acipenser* and *Polyodon* resemble each other and the Elasmobranchii, and differ from the remainder of the Ganoidei and from all the Teleostei.

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* *Loc. cit.*

To determine the homologies of the two ectosteal patches (*m.pg.*) previously described as developed in connexion with the palato-pterygoid bar, is a task which is not very easy, and in order to do so it is necessary to form a true conception of the nature of the "palato-pterygoid" bar as it exists in different Vertebrata. This bar has been generally regarded as a forward outgrowth from the mandibular arch, which is eventually ossified from several distinct centres and so gives rise to the palatine, mesopterygoid, and pterygoid bones, the first mentioned being an ossification in the most anterior moiety of the bar. If this view be correct our task is an easy one, and we may at once regard the bone *m.pg.* as being the equivalent of the palatine bone of other Fishes.

But Professor PARKER has suggested another view as to the nature of this bar in the Vertebrata generally. In his opinion it is formed by the coalescence of a retral growth from the ethmoidal region (palatine process) with a forward outgrowth from the mandibular arch (pterygoid process). In accordance with this view the palatine bone is an ossification in the retral process, and is a preoral structure, while the mesopterygoid and pterygoid are developed in relation with the cartilaginous pterygoid process, and are therefore postoral elements. If, therefore, the upper jaw in *Polyodon* is formed by the union of the pterygoid processes only, then the ectosteal patches represent a mesopterygoid element. The evidence in favour of this theory as to the nature of the palato-pterygoid bar is very strong, and may be briefly set forth.

In the common Toad, in the adult skull, the primitive distinctness of the palatine and pterygoid processes is well seen. The cartilaginous pterygoid process forms less than half of the curvature of the subocular bar, the anterior part of which is formed by the retral palatine process. From the inner side of this process a transverse piece of cartilage, the ethmo-palatine, is given off, and is connected by fibrous tissue with the prefrontal region (ethmo-trabecular outgrowth). In front of the ethmo-palatine the palatine process is produced into a prepalatine spur, and behind it into a postpalatine process which is in ligamentous connexion with the anterior end of the pterygoid process.* In the Frog the segmentation of the palatine and pterygoid outgrowths has not been observed, neither has the primitive formation of this bar by the coalescence of retral and forward outgrowths been observed in any embryo Anura. This important desideratum is however supplied by the developmental history of the embryo Axolotl. In young embryos of 1¼, 2¼, and 3½ inches long, the stages A, B, and C of PARKER, the formation of these processes has been observed ('Morphology of the Skull,' PARKER and BETTANY, pp. 109–112). In stage A there is not the slightest trace of a pterygoid process in connexion with the suspensorial cartilage, but in the antorbital region a small transversely disposed rod of cartilage has appeared which is attached by ligament to the trabecular cartilage just above the broad tooth-bearing part of the palatine splint. This transverse rod is the homologue of the palatine process of the Toad. In stage B a pterygoid process has appeared growing forwards

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* PARKER, Phil. Trans., 1876, Plate 54, fig. 3.

from the anterior margin of the suspensorium; it is quite distinct from the palatine process, and in front of it there is a small free postpalatine segment which has been segmented off from the ethmo-palatine moiety in front of it. By stage C the postpalatine process has coalesced behind with the pterygoid bar, and in front is united by fibrous tissue to the remainder of the palatine outgrowth, almost precisely as in the Toad.

This want of synchronism in the first appearance of the two outgrowths in the Axolotl is evidence sufficiently strong to effectually preclude the idea that the palatine cartilage is a segment cut off from the pterygoid bar and united to the antorbital region of the trabecula.

Having established the anatomical distinctness of the two structures in question both in the adult skull and in the embryo Axolotl, and, in addition, in the latter a sequence in the developmental origin of the two parts, we may notice briefly the condition of these parts in the Teleostei and in Elasmobranchs.

In the Siluroidei there is a continuous bony outgrowth extending from the quadrate forwards to the prefrontal region. In no specimen of this family which I have had the opportunity of examining have I been able to detect any segmentation in this osseous bar, which either ends freely in front, or is attached by fibrous tissue to the vomer or to the prefrontal. A shaft-like cartilage-tipped bone is attached anteriorly to the prefrontal, and behind overlaps the outer or inner side of the previously mentioned osseous bar.

The latter clearly corresponds to the pterygoid process of the Amphibia, while the shaft-like bone is in every way comparable to the retral palatine process of the Axolotl and the Toad. In some Siluroids there is a facet on the middle of the inner face of the palatine bone by which it is applied to the prefrontal bone; this facet represents the ethmo-palatine process of the Toad, and the shaft-like bone thus exhibits prepalatine and postpalatine regions.

In the common Eel the primitive pterygoid cartilage is not wholly converted into bone, and a short slender piece of cartilage is left creeping along the inner side of the unsegmented osseous pterygoid. The palatine process is apparently absent in the adult. In the Conger Eel, however, the palatine process is a large unossified mass of cartilage applied to the outer side of the anterior end of the bony pterygoid process, and closely united by fibrous tissue to the persistently cartilaginous ethmo-trabecular region. The attached face of the palatine is slightly grooved, and between it and the ethmo-trabecular cartilage the rostral branch of the second division of the fifth nerve passes, precisely as is the case in the Skate.

From the Siluroid to the ordinary Osseous Fish the step is a short one, and if transitional links are needed they may be found in the *Cyprinoidei* and other generalised physostome Teleostei. In the Carp the ossified palatine process is attached by ligament only to the pterygoid process, and forms in conjunction with the latter a palato-pterygoid arcade. The regional distinctness of the palatine is well marked;

there is a prepalatine spur in front of the short ethmo-palatine connexion with the prefrontal and a postpalatine region behind which abuts against the mesopterygoid and pterygoid elements of the pterygoid outgrowth. It may be mentioned that the recorded facts of the development of the Teleostean skull show that the palatine is at first quite distinct both from the ethmo-trabecular and quadrate regions, as seen in Plates 1–3 of Mr. PARKER'S 'Memoir on the Structure and Development of the Salmon's Skull.'* Subsequently the palatine fuses behind either with the quadrate or with its pterygoid outgrowth.

In the Elasmobranchs the same structures are readily recognized. In some Selachii (*Notidanus*) and in some Batoidei (*Raja* and *Rhinchobatus*) there is a large recurrent cartilaginous process attached to the hinder wall of each nasal capsule, but in many Selachians, as in *Cestracion* and in *Mustelus*, there is no trace of any such free process. In *Raja* the thick proximal end of this process is perforated by a foramen for the transmission of the superior maxillary division of the fifth nerve, as is the case with the palatine process of the Conger Eel; and in *Rhinchobatus* it presents a division into regions strictly comparable to the prepalatine, ethmo-palatine, and postpalatine regions of the palatine process of the Teleostean and the Amphibian. In all Elasmobranchs a forward growth from the proximal half of the mandibular arch unites beneath the prefrontal region with its fellow of the opposite side to form the characteristic upper jaw of this group.

That this retral antorbital process of the Sharks and Rays is homologous with the palatine process of the Toad, the Axolotl, and the Siluroid, seems to me an incontestable fact, proved by its attachment to the prefrontal region, by its perforation in *Raja,* and by its regional subdivision in *Rhinchobatus.* But if this retral outgrowth be a true palatine element, then the forward outgrowth from the manibular arch—the so-called palato-pterygoid bar—must correspond to the pterygoid process of the Toad and Axolotl, and cannot therefore contain any palatine element. Consequently the term "palato-quadrate arcade" is not rightly applicable to the confluent pterygoid and quadrate cartilages, and ought to be replaced by the term "pterygo-quadrate."

We are now in a better position to determine the nature of the upper jaw and its ossifications in *Polyodon.* It is evident that in so far as relates to the palatine and pterygoid processes, this Ganoid so closely resembles those Selachii in which the mesially-united pterygoids are unaccompanied by even the rudiments of recurrent palatine outgrowths, that we must conclude that its upper jaws are formed in precisely the same way, *i.e.*, by the union of the pterygoid bars. The two ectosteal patches without doubt, therefore, correspond to the mesopterygoid elements of other Vertebrata.

It is impossible to say whether the palatine process has entirely aborted, or whether it has contributed to form any part of the thickened and somewhat produced posterior wall of the nasal capsule.

An alternative, suggested by the slightly upturned anterior end of each half of the

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* Phil. Trans., 1872.

upper jaw, that the palatine elements may have coalesced behind with pterygoid outgrowths and then united with each other beneath the basis cranii, has nothing to recommend its acceptance. In view of the strong resemblance in the structure of their jaws between *Polyodon* and Selachians, nothing short of actual demonstration can render this alternative explanation in any way tenable.

*The Hyoid Arch.**

The hyomandibular (*h.m.*) is a long, relatively slender, well ossified shaft-like bone, with a vertically expanded proximal end, a much constricted central portion, and a vertically compressed distal extremity. Its axis is inclined backwards at an angle of less than 30° with the cranio-spinal cartilage. The cartilage-tipped cranial end of the bone fits into the vertical groove on the external face of the otic capsule dorsad of the horizontal semicircular canal, as in Teleostei, and not ventrad as in Elasmobranchs. The symplectic (*sym.*) is a stout triangular piece of cartilage attached by its broad apex to the anterior angle of the distal end of the hyomandibular, and by its base to the lower part of the rounded posterior margin of the quadrate to which it is firmly attached by the two symplectic ligaments, while its long axis is directed forward at an angle of about 90° with that of the hyomandibular. A line drawn through the proximal end of the latter and the distal end of the former will make an angle of at least 135° with the fore part of the skull. It is this extraordinary inclination of the hyomandibular and the quadrate that carries backwards the articular end of the mandible to a point opposite to the foramina for the passage of the fourth or fifth pairs of spinal nerves, thus giving a backward extension to the gape which is far greater than that of any other living Vertebrate animal, approaching, nearest in this respect, to the amphistylic Selachians and autostylic Anurous Amphibians, but receding from the other extreme as exhibited in the relatively short gapes and forwardly-inclined suspensoria of the Teleostei.

The remainder of the hyoid arch consists of a stout curved interhyal segment (*i.hy.*) attached to the posterior margin of the symplectic near its distal end, a long and comparatively slender epi-ceratohyal segment, and an unossified hypohyal element which connects the arch to the anterior end of the first basibranchial. The only ossification in the distal half of this arch is an hourglass-shaped ceratohyal (*c.hy.*). The hyoid arch of *Acipenser* is essentially the same as that just described. In the segmentation of the proximal half of the arch into hyomandibular and symplectic pieces, and in the presence of an interhyal, *Polyodon* resembles the Teleostei, but resembles the Selachii in the non-segmentation of the epihyal from the ceratohyal, and in the attachment of the ventral half of the arch almost to the distal end of the symplectic; in the possession of hypohyals and absence of a basihyal, *Polyodon* resembles the Skate, but in the attachment of the former to the first basibranchial element approaches such Urodele Amphibians as the Axolotl and Menobranchus.

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* See also plate vii., fig. 1, in Dr. TRAQUAIR'S memoir on the Palæoniscidæ, previously cited.

The membranous fold that grows backwards from the hyoid arch over the gill opening is strengthened and supported by two thin squamose plates. Of these, one is attached to the outer side of the cartilaginous epiphysis at the distal end of the hyomandibular, and the other to the outer side of the interhyal cartilage. The first, which represents the operculum of the Osseous Fish, is produced backwards into several diverging, transversely striated flexible bony rays. It has no articular attachment, but is simply applied to lower end of the hyomandibular and retained in its place by fibrous tissue. The second, though usually described as a branchiostegal ray, seems to me to correspond rather to the interoperculum of *Ceratodus*, and, like the operculum, breaks up into a number of thin flexible rays. These two branching parostoses attached to the ventral and dorsal halves of the hyoid arch very curiously similate the two groups of coalesced cartilaginous rays, which in Selachii are attached, one to the hyomandibular, and the other to the ceratohyal. Lying in a groove on the outer side of the hyomandibular, I found a small cartilaginous filament, which I imagine is a remnant of one of these rays. A flattened nodule occupies a similar position in the Sturgeon, and I have also detected in *Lepidosteus* a small ray attached to the synchondrosis between the hyomandibular and symplectic bones and applied to the inner side of the operculum. HUXLEY has described similar structures attached to the inner side of the operculum and interoperculum of *Ceratodus* and *Lepidosiren*. The coexistence of these cartilaginous rays, which are so characteristic of the Shark and Rays, with the simple or branched parostoses which eventually replace them in the Teleostei, is an interesting transitional feature in these Ganoids and Dipnoid.

Branchiostegal rays may be regarded as the parostoseal representatives of such of the free cartilaginous rays as are attached to the lower end of the ceratohyal of the Shark.

The opercular gill, which is well developed in the Sturgeon, is altogether absent in *Polyodon.*

The Branchial Arches. (Plate, 57, fig. 9.)

The five branchial arches are very curious structures. The lateral half of each complete arch consists of a dorsal and a ventral segment uniting with each other at a very acute angle. The dorsal segment, formed by the pharyngobranchial and epibranchial elements, is directed backwards, downwards, and outwards to its union with the ventral segment while the latter passes forwards and inwards to join the mesobranchial pieces.

The first three arches possess the typical number of elements, viz., pharyngobranchial, epibranchial, ceratobranchial, and hypobranchials; the fourth arch has lost its pharyngobranchial and hypobranchial branchials, and the fifth retains only its ceratobranchial element.

The first pharyngobranchial (*p.br*^{1}.) is a short thick piece of cartilage attached by its conical extremity to the margin of the parasphenoid in the angle between the smaller ala and the body of that splint. The epibranchial (*ep.b*^{1}.) forms nearly the whole of the dorsal segment of the arch, and is a thin laterally compressed lamina of cartilage with a nearly straight inner, and a curved outer margin, resembling a segment of a circle. Ossification has invaded the proximal part of the cartilage, and given rise to an hourglass-shaped osseous epibranchial, and from its upper and posterior angle a short pointed ray is given off, which is directed upwards and backwards. The ceratobranchial (*c.b*^{1}.), which forms the greater part of the ventral segment resembles the epibranchial in shape ; there is a small semicircular ossification marked with concentric striæ near its ventral end. The short, stout, and slightly curved hypobranchial is attached to the anterior end of first basibranchial, in close contact with the hypohyal.

The second and third branchial arches, which differ but little from the first, are attached by their pharyngobranchial elements to the hinder edge of the cranial end of the epibranchial belonging to the arch in front, and not directly to the skull. The second epibranchial (*ep.b*^{2}.) also possesses a small cartilaginous ray, similar to that attached to the first. These hypobranchials are also attached to the first basibranchial element.

The hypobranchial of the third arch has its ventral end laterally compressed and bifid, like the proximal end of a rib, and between the two processes and the basibranchial to which they are applied, one of the lateral trunks of the aorta passes on its way to the gill filaments of the arch it supplies. The fourth arch consists of epibranchials and ceratobranchials only, though the latter may also contain a hypobranchial element. They possess ossifications similar to those in the corresponding elements of the preceding arches. The epibranchial is attached dorsally to the proximal end of the epibranchial of the third arch, and ventrally to the second basibranchial. The distal end of the fourth ceratobranchial forks into two processes, the anterior of which is applied to the junction of the first with the second basibranchial, while the posterior one is applied wholly to the latter; and between the two forks another branchial artery passes.

The fifth pair of ceratobranchials are wholly cartilaginous, and lie in the floor of pharynx; above, they are attached by ligament to the antecedent ceratobranchials, and below to the posterior end of the third basibranchial. The three basibranchials are entirely cartilaginous. The first has attached to it the hypohyal, and the hypobranchials of the next three arches; the second completes the fourth arch, and the third is attached posteriorly to the fifth pair of ceratobranchials. The coalescence of the hypobranchial elements of the third and fourth arches with second basibranchial in *Dactylethra* and *Pipa* suggests that possibly the second and third basibranchials of *Polyodon* may be the mesially coalesced hypobranchials of the fourth and fifth arches. But the existence of three basibranchial in *Acipenser*, and the fact that hypobranchial and pharyngobranchial segments are the most variable of the branchial elements, as is shown by their absence in such Urodele Amphibians as *Siredon* and *Menobranchus*, and by their suppression in the hinder branchial arches of most Fishes, seems to negative this view. It seems much more probable that the fourth and fifth ceratobranchials each contain an unsegmented hypobranchial element.

Comparison of the branchial arches of *Polyodon* with those of *Acipenser* does not reveal any important differences. In the latter the arches are more massive and rounded. The same elements are ossified, but ossification has more largely invaded the cartilage, so that the resultant bones are shaft-like and massive.

There are three basibranchials as in *Polyodon*, but the second is rudimentary, being reduced to a small nodule of cartilage imbedded in the ligament by which the hypobranchials of the third arch are connected together. The third and fourth hypobranchials have their ventral ends split for the transmission of a branchial artery. The aorta, lying ventrad of the basibranchial pieces, gives off a large lateral trunk for the supply of the gills in relation with the third, fourth, and fifth arches, which passes outwards, downwards, and backwards, between the forks of the third hypobranchial, and after giving off a branch for the third arch, passes backwards between the forks of the fourth hypobranchial to the convex side of the fourth arch.

The cartilaginous ray, which in *Polyodon* is attached to the second epibranchial, is represented in *Acipenser* by a cartilage much larger that the pharyngo-branchial, and is applied to the lateral wall of the skull immediately over the course of the jugular vein. The next arch has no such ray. These free rays in the Chondrosteous Ganoids correspond to the autogenous processes which are given off from the pharyngobranchials and epibranchials of the second, third, and fourth arches of the Salmon.

The splitting of the distal ends of the third and fourth hypobranchials, though I am not aware that it occurs in any Teleostei, is the rule amongst Ganoids. In *Amia* and *Lepidosteous*, the same branchial elements are similarly bifurcated, and I believe that such is also the case in *Polypterus*.

Thus it will be seen that, though conforming mainly to the Teleostean type, the branchial arches of *Polyodon* and *Acipenser* in possessing free rays, in the forking of the hypobranchials, and in the non-coalescence of the dorsal elements of the posterior arches, differ from those of most Teleostei. The almost entirely cartilaginous nature of the arches, and the inclination to each other of the dorsal and ventral segments, are interesting embryonic and Chimæroid features.

The bifurcation of the proximal ends of certain of the branchial arches in *Polyodon* (and in many Teleostei also), is an interesting survival of a feature which is transitory in the hyoid arch of the Shark and Skate, though permanent in the mandibular arch of Amphibia. Each free ray may be compared to free " otic process."

As has been already mentioned, the branchial and hyoid arches of *Polyodon* differ but very little from those of the Sturgeon, but as regards the mandibular arch the differences between the two genera are more marked, though mainly dependent on the adaptation of the osseous and cartilaginous elements of the palato-quadrate arcade to form the remarkable proboscidiform mouth of the latter. The metapterygoid ligament is absent in the Sturgeon, and the broad triangular plate of cartilage, which takes its place as the proximal element of the mandibular arch, is apposed by its upper extremity to its fellow in the median line beneath the basis cranii, while its lower end is applied to the posterior margin of the quadrate. In full-grown Sturgeons there are two ectosteal mesopterygoid plates, thicker than those in *Polyodon,* and applied to the inner and outer sides of the anterior ends of the two palato-quadrate bars, which are also in contact beneath the basis cranii. A massive pterygoid flanks the inner side of the axial cartilage, and a maxilla and a jugal the outer side. But a much more important difference between the two Ganoids is the presence of a palatine bone in *Acipenser,* apparently due to the ossification of the antero-lateral edge of the palato-quadrate cartilage, and of a quadrate ossicle. In the Sturgeon there is no trace of the leaf-like process which grows forwards from the quadrate cartilage of *Polyodon.**

The existence of this leaf-like outgrowth is one of the most interesting anatomical features possessed by this Ganoid. Its superficial relation to the levator mandibularis muscle which passes downwards between it and the main body of the pterygoid process to its insertion of the mandible, and its evident origin as an outgrowth from the proximal half of the first postoral arch at once suggests a comparison with the "orbitar process" of the Anurous Amphibia. In the Tadpoles of all the Anura whose cranial development has been worked out, a flap of cartilage grows out from the upper edge of the much-inclined mandibular pier, arches over the levator mandibularis, and either terminates freely above, as in the Frog, or joins the prefrontal region of the trabecula, as in the Toad.†

At a later stage, when the rotation backwards of the mandibular pier has caused it to take up a position nearly at right angles to the axis of the skull, the orbitar process, now much reduced in relative size, instead of being directed upwards, is now directed forwards, and appears as a styliform outgrowth from the hinder edge of the quadrate cartilage. It is this particular stage which is depicted in Plate 58, figs. 2 and 3, of Mr. PARKER's memoir,‡ and, though transitory in *Dactylethra capensis,* yet appears to be permanently retained by *Polyodon.*§

In the permanent retention of this embryonic feature, *Polyodon* is almost unique amongst Ichthyopsida, the Lamprey being the only fish in which the "orbitar process" has retained its probable primitive function of acting as a suspensor to the much-inclined suspensorium of Vertebrata possessing a suctorial mouth. This correlation of a suctorial mouth with the existence of a well-marked "orbitar process," and with a backward rotation of the suspensorium during the course of their cranial development, which is so marked a feature in the embryo Anura, at once suggests the probability

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* *Vide* PARKER, "Development of the Face in the Sturgeon," 'Monthly Microscopical Journal,' 1873.

† PARKER, "On the Structure and Development of the Skull in Batrachia," Part II., Plate 55, fig. 3, Phil. Trans., 1876.

‡ *Loc. cit.*, Phil. Trans., 1876.

§ Mr. PARKER informs me that he has found a distinct orbitar process in a half-grown *Otilophus margaritifer* and even in an adult *Bufo ornatus.*

that the young *Polyodon* possessed a suctorial mouth and passed through larval stages in several respects very similar to those of the former.

The study of the cranial development of *Acipenser* and *Polyodon* will probably reveal new and important anatomical features which are common to the Ganoids and the Amphibia.

Shoulder Girdle.

Dr. TRAQUAIR, in his memoir "On the Palæoniscidæ" (plate vii., fig. 1), supplies a sketch of the membrane bones which invest the cartilaginous pectoral girdle.* As to the identity of the bones lettered *l.cl.* and *c.l.* there can be no doubt; they correspond to the clavicle and inter-clavicle of other Ganoids. The bone marked *p.cl.* is clearly the equivalent of the bone which in *Acipenser* is called supra-clavicle by PARKER; but I agree with Dr. TRAQUAIR in regarding it as a post-clavicle, the true supra-clavicle being the long and sabre-shaped bone marked *s.cl.* The supra-clavicle is attached to the postero-external angle of the bone c^1, the squamosal of TRAQUAIR, which evidently corresponds to the bone which in the Sturgeon PARKER calls the supra-temporal. But this splint (c^1) corresponds in every respect to the post-temporal bone of other Ganoids; its horizontal and descending lamina are analogous to the two processes into which the Piscine post-temporal ordinarily divides, and like the latter serve to attach the pectoral girdle to the postero-lateral angles of the skull.

The cartilaginous part of the pectoral arch, though far less massive and of more delicate proportions, is essentially the same as in the Sturgeon; but while the latter resembles the Skate in having a distinct supra-scapular segment, *Polyodon* agrees with the Selachii in having that element confluent with the scapular.

It may be remarked that in both of these genera the scapular arch is essentially the same as in Elasmobranchs, with the exception that the large and distinct præcoracoid of the former has no representative in the latter. An examination of any ordinary Shark—*Acanthia* or *Squatina* for example—will show that the scapula segment is divided by a scapular fenestra into a scapula proper and a pre-scapular element, and, further, that there is a coraco-scapular fenestra perforating the coracoid cartilage immediately ventrad of the glenoid facets and opening into the floor of the scapular fenestra precisely as in *Polyodon* and *Acipenser*. Such a coraco-scapular fenestra is found in nearly all the Selachii which I have had the opportunity of examining.

The epicoracoid process in *Polyodon* does not extend so far along the inner surface of the inter-clavicle as in *Acipenser*.

The coraco-scapular cartilage is much the same in *Amia*, though much reduced in size proportionally to the size of the overlying derm bones; and the same may be said of these structures in *Lepidosteus*, though in the latter, scapula and coracoid are largely ossified. In both genera there is the same longitudinal clearage of the cartilage into distinct morphological elements by coraco-scapular and scapular fenestræ, having the same relations to each other as in *Polyodon*.

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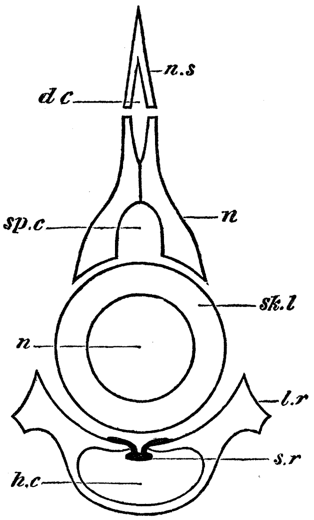
* For figures of coraco-scapular arch, *vide* GEGENBAUR, *op. cit.*, Part I., plate vi., figs. 3A, 3B, and 3C.

Vertebral Column, and the Skeleton of the Fins.

I do not propose to give a detailed description of the axial skeleton, as the destination of my specimen would not admit of the requisite dissection. The large unconstricted and unsegmented notochord is surrounded by a relatively thick skeletogenous layer which supports the neural and hæmal arches. The cartilaginous neural arches, though confluent near the cranium, are distinct in the central and posterior regions of the vertebral column. Above the spinal cord they coalesce, and dorsad of the true medullary canal a second or dorsal tube is formed between the slightly-divergent apices of the neuropophyses and the arms of the Y-shaped ossified neural spines, which terminates anteriorly on the upper surface of the cranio-spinal cartilage. A precisely similar canal is found in the Sturgeon and in *Ceratodus*, but not, so far as I am aware, in any Selachian or Teleostean. In the central and posterior regions of the column the neural spines become double, one being attached to each neuropophysis, as is not unfrequently the case in certain Teleostei. Interposed between the true neural arches there is a series of small, triangular, intercalated cartilages. In front of each intercalated piece there is a small foramen for the exit of the anterior root of a spinal nerve, the posterior root passing outwards just over the apex of each cartilage, as shown in Plate 55, fig. 3. The hæmal arches, which are not continuous with the neural arches, are attached along the ventral surface of the notochord; each arch is incomplete above, along the medio-ventral line of the notochord, but below it completely encloses the dorsal aorta, the walls of which are co-extensive with those of the cartilaginous hæmal canal. Each lateral half of each arch contributes to the formation of the continuous lateral ridge which alone repre-



n.s. Neural spine.
d.c. Dorsal canal.
sp.c. Spinal canal.
n. Notochord.
sk.l. Skeletogenous layer.
l.r. Lateral ridge.
h.c. Hæmal canal.
n. Nemopophysis.
s.r. Sub-notochordal rod.

sents the well-ossified ribs and transverse processes of the Sturgeon. Behind the anus the ridges converge slightly, and together with the well-ossified inferior caudal arches which are attached to them, form the canal in which the caudal vein is contained.

A transverse section of the vertebral column in the caudal region would disclose two canals—one immediately below the notochord, and containing the dorsal aorta; and a second ventrad of the first, containing, as previously mentioned, the caudal vein. In comparing such a section with the transverse section through the tail of an embryo *Scyllium*, given by BALFOUR ('Journal of Anatomy,' vol. xi.), it is evident that if chondrification were to affect the cells which lie between the aorta and the caudal vein, two precisely similar cartilage-bounded canals would be formed. Wedged in between the bases of each two adjacent hæmal arches, there is a small piece of cartilage exactly corresponding in position below the notochord to the intercalated cartilages above. These are interhæmal cartilages, analogous to similarly-situated structures described by GEGENBAUR[*] as existing in the Sturgeon.

But perhaps the most remarkable structure in connexion with the vertebral column is a stout, flattened, fibrous band which is attached to the narrow membranous interspace which exists between the broad pedate bases of the hæmal arches and projects downwards into the cavity of the aortic canal (fig. 2). Anteriorly, this fibrous band blends with the cartilage of the basis cranii, but posteriorly it may be traced nearly to the end of the tail.

As to the significance of this curious structure I can offer no suggestion, but it is not a little remarkable that it exactly corresponds in position and relations to the "sub-notochordal rod" which was first observed by GÖTTE in the embryo Frog, and subsequently and independently by BALFOUR and SEMPER in the developing *Scyllium*.

In the Shark the "sub-notochordal rod" appears to be formed from a ridge of cells which runs along the medio-dorsal line of the alimentary canal.[†] The cells at the extreme summit of this ridge become gradually constricted off to form a linear rod, the splitting off taking place from before backwards. The formation of this rod by segmentation from the summit of the hypoblast is an almost exact repetition of the process by which the notochord itself is derived from the same germinal layer. When the dorsal aorta is formed, the "sub-notochordal rod" becomes separated from the summit of the alimentary canal, and the aorta interposed between the two. At the period of its fullest development the rod extends anteriorly to a point in front of auditory capsules, but terminates a little behind the apex of the notochord; posteriorly, it extends nearly to the end of the tail. When at its maximum size the "sub-notochordal rod" lies immediately beneath the notochordal sheath and dorsad of the aorta; and it even projects into the cavity of the latter, which consequently appears in transverse section as reniform in outline, with the hilum directed upwards.

[*] Jenaische Zeit. 1867.

[†] BALFOUR, 'Journal of Anatomy and Physiology,' vol. xi.

If this rod, instead of completely disappearing as it does in the Frog and the Shark, were to increase in size and persist, it would occupy a position analogous in every way to that of the fibrous band in *Polyodon.*

It may be remarked that the "sub-notochordal rod" of these Vertebrata occupies a position in relation to the aorta which is not altogether without *analogy* to the position of the "endostyle" of the *Ascidians* in relation to the blood sinus which in these animals lies on the hæmal side of the branchial sac.[*]

Skeleton of the Fins.

The structure of the pectoral fins has been described and figured by GEGENBAUR.[†] The dorsal and anal fins are each supported by two series of well-ossified, shaft-like interspinous bones, each bone supporting at least two fin rays. There is also a third series of interspinous cartilages formed by a number of small cubical pieces of cartilage which occupy the interspaces between the distal ends of the bones of the second series. A similar peripheral fringe of small cartilages, and similarly arranged, is found in the pectoral fins, and also in the ventral portion of the caudal fin attached to the free ends of the inferior caudal arches. In the Selachii a similar peripheral fringe of small cartilages is to be found in the mesial, and in some cases in the paired fins also. None of the interspinous bones or cartilages exhibited any of that tendency to coalescence which is so marked in the mesial fins of the Selachii. On the other hand, the evident formation of the ventral fins by the coalescence of a series of originally distinct cartilaginous rays is clearly indicative of a more primitive condition of these structures than can be found in any other living Vertebrate animal.[‡]

SUMMARY AND CONCLUSION.

In the foregoing description of the skeletal structures of *Polyodon* I have compared the latter with *Acipenser,* in so far as the special features under discussion were concerned, in order to demonstrate the close relationship that exists between the two forms in almost every detail of their anatomy. It will now be necessary to compare the two genera as to the points in which they differ from one another, and also to compare them with the remaining recent Ganoidei on the one hand, and with the Elasmobranchii and Amphibia on the other. In order to do this, it will be advantageous briefly to recapitulate the more important anatomical facts with which such a comparison is concerned, and which have been given in detail in the earlier part of this paper.

In the following paragraphs are enumerated those features in the osteology of *Polyodon* and *Acipenser* which are of greatest importance in relation to more general conclusions.

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[*] *Vide* also Dr. HUGO EISIG'S paper on "Nebendarm d. Capitellidæ" in the 'Zoologischer Anzeiger,' No. 7, 1878.

[†] *Op. cit.* Plate 8.

[‡] THACHER, *loc. cit.*

I. The very generalised cranial splints arranged in a medio-dorsal, a supero-lateral, and a lateral series, investing the dorsal surface of the chondrocranium, and corresponding to the dermo-ethmoid, the parietal and frontals, the post-temporal, the dermo-sphenotic, and the nasal bones of other Ganoids and Teleostei; the serial repetition of these dermal elements along the dorsal surface of a massive and prolonged prenasal rostrum; the median parasphenoid and paired vomers, which in like manner are repeated by a series of homologues applied along the ventral surface of the rostrum; while the infero-lateral series of splints includes an operculum, an interoperculum, a maxilla, and a multi-segmented premaxilla, but no preoperculum, suboperculum, branchiostegal rays, or median or paired jugular plates.

II. The massive and persistent chondrocranium entirely devoid of any such endosteal ossifications as basioccipital, exoccipital, alisphenoid, orbitosphenoid, or prefrontal elements, all of which are represented in the crania of the remaining recent Ganoidei, if we regard *Ceratodus* and *Lepidosiren* as being members of a distinct primary group, the Dipnoi; while diminutive scale-like opisthotic and pterotic exostoses alone represent in *Polyodon* the well-ossified periotic bones of other Ganoids and Teleostei.

III. The union of the anterior ends of the persistently cartilaginous quadrato-pterygoid arcades of their hyostylic skulls in a medio-ventral symphysis beneath the olfactory capsules, as in the Selachii. Associated with each arcade, which is suspended from the hyomandibular by a pair of symplectic ligaments, there are ectosteal mesopterygoid plates, and a parosteal pterygoid bone; and in addition, in *Acipenser*, a well-ossified palatine element. The proximal segment of the mandibular arch is either represented by a metapterygoid cartilage (*Acipenser*), or by a strong metapterygoid ligament passing from the skull downwards and backwards beneath the spiracle to its insertion into the upper third of the hyomandibular (*Polyodon*).

IV. The enormous backward extension of the gape, due to the great posterior inclination of the hyomandibular and quadrate; and the production of the latter into a large and persistent "orbitar process," between which and the quadrato-pterygoid bar the levator mandibularis muscle lies, precisely as is the case with the Tadpoles of the Anurous Amphibia.

V. The presence of persistent spiracles, and of mandibular branchiæ attached to the posterior margin of the metapterygoid ligament (*Polyodon*).

VI. The perforation of the outer wall of the periotic capsule by an antero-posterior canal, as in the Elasmobranchs *Trygon*, *Pristis*, and *Rhinchobatus;* and the fenestration of the roof of the capsule by a canal passing beneath the arch of the posterior vertical semicircular canal to communicate with the cranial cavity, which may possibly represent the orifice of the primitive involution to form the internal ear.

VII. The persistent unossified Meckelian cartilages, flanked by dentary and splenial elements, and with ossified lower labial cartilages (mento-Meckelian bones) interposed between their symphysial ends.

VIII. The cartilaginous branchial arches, consisting of dorsal and ventral segments uniting at an acute angle, and possessing small epibranchial and ceratobranchial ossifications. The absence of a basihyal element, and the consequent union of the hypohyals with the anterior end of the first basibranchial piece.

IX. The massive, unsegmented, unconstricted, and persistent notochord, extending into the basis cranii as far as the pituitary fossa, and surrounded by a relatively thick skeletogenous layer, which in *Polyodon* supports dorsally the cartilaginous neural arches, and ventrally the hæmal arches that enclose the dorsal aorta, the latter being also produced on each side into the continuous ridge which alone represents the transverse processes and ribs of other Ichthyopsida. The appearance of inferior arches in the caudal region gives rise to the formation of a second ventral canal lying beneath that in which the aorta is contained, and enclosing the azygous cardinal vein. In *Acipenser* the axial notochord and its sheath support well-ossified neural arches, transverse processes, and ribs. In both genera a curious flattened, fibrous band traverses the medio-ventral line of the notochord, projecting into the dorsal aorta, and presenting interesting analogies in its position and relations to the "sub-notochordal rod" of the developing Frog and Shark. In both *Polyodon* and *Acipenser* the elements of the anterior part of the vertebral column are almost indistinguishably fused with each other and with the cranium into a continuous cranio-spinal mass.

X. The presence of rudimentary intercalated neural arches lying behind the foramina for the exit of the anterior roots of the spinal nerves, and below those for the passage of the posterior roots; and also of interhæmal cartilages having a similar relation to the true hæmal arches.

XI. Cartilaginous scapular arches that conform to the Selachian type, but which are accompanied by post-temporal, supraclavicular, postclavicular, clavicular, and interclavicular derm bones.

XII. In the structure of the pectoral, ventral, anal, and caudal fins, *Polyodon* and *Acipenser* to some extent resemble the Selachii, and notably in that their fins possess a marginal fringe of small cubical cartilages, in the segmentation of their interspinous bones and cartilages, and also in the fact that the latter are less numerous than the fin-rays which they support.

A. *Comparison of* Polyodon *with* Acipenser.

Though so closely related to *Polyodon,* and agreeing with that genus in most of the anatomical features to which attention has been directed in the preceding paragraphs, the Sturgeon differs from the former in several points, of which the most important are—the ossification of the retral palatine outgrowths as palatine bones; the representation of the proximal elements of the mandibular arches by large metapterygoid cartilages, which are so coadapted as to form the hinder part of the roof of the protrusible proboscidiform mouth, and not merely by metapterygoid ligaments as in

Polyodon; the possession of jugal and quadrate ossicles, and well-developed osseous transverse processes, neural arches, neural spines and ribs. The massive growth of the cranial cartilage in *Acipenser* has obliterated the parietal foramina and the cavity of the prenasal rostrum, diminished the antero-posterior extent of the cranial cavity, and caused the abortion of the cranial prolongation of the notochord. The posterior median fontanelle of *Acipenser* has no existence in *Polyodon,* and in the former the fibrous tracts ossify as distinct splints, and not continuously, as in the latter. To these more or less important differences we may add that in *Acipenser* there is a well-developed opercular gill, a siphonal stomach, and a simple non-cellular air-bladder; whereas in *Polyodon* there is no opercular gill, the stomach is cœcal, and the air-bladder cellular. With these, for the most part relatively unimportant exceptions, the agreement between the two genera, even in the minutiæ of their skeletal anatomy, is very striking. It will be noticed that, in so far as the Sturgeon recedes from the *Polyodon* type, it becomes more specialised, and approaches the higher Ganoids and the Teleostei.

B. *Comparison of* Polyodon *with the Elasmobranchii.*

Not the least interesting feature in the osteology of *Polyodon* is its possession of a remarkable combination of characters, usually regarded as specially distinctive of the Plagiostome Elasmobranchs. Of these, we may mention the unossified chondrocranium; the formation of the upper jaw by the union of the pterygo-quadrate bars in a median symphysis beneath the basis cranii; the attachment of the quadrate cartilage to the hyomandibular by means of symplectic ligaments; the abortion of the proximal segment of the mandibular arch and its representation by a metapterygoid ligament which bounds the spiracle in front, supports a mandibular gill, and is attached behind and below to the hyomandibular; the presence of a Facial canal; the rudimentary cartilaginous ray attached to the hyomandibular, as in *Acipenser,* which it is possible may represent the hyoid rays of the Selachii; and the parosteal operculum and interoperculum, resembling in their branched and subdivided condition the cartilaginous rays which they have replaced.

The presence of intercalated neural arches, the prolongation of a fleshy lobe into the upper division of the caudal fin, the abortive condition of the ribs, and the structure of the shoulder girdle and pectoral fins, are also evidences of a like affinity. Of the more numerous minor points to which the same significance must be attached, I may mention the absence of a basihyal as in the Rays, the non-segmentation of the epihyal from the ceratohyal, and the prolonged prenasal rostrum, with its probably coalesced first pair of labial cartilages. On the other hand the condition of the ventral fins and of the vertebral column is far more primitive than in the Selachii.

The lateral position of the anterior and posterior nares, the structure of the pectoral, ventral, anal, and dorsal fins, as well as the segmentation and disposition of the interspinous cartilages and their relation to the more numerous fin rays, are to some extent a transition towards the structure of the same parts in the typical Elasmobranchii. In nearly all of those characters *Polyodon* differs from all other living Ganoids, with the exception of *Acipenser* and its nearest living and fossil allies. The extent to which this close correspondence in structure between the chondrosteous Ganoids and the Elasmobranchii bears on the presumed phylogenetic relationship of the former to the latter will be referred to subsequently.

C. *Comparison of* Polyodon *with the Higher Ganoids and with the Teleostei.*

Comparison of *Polyodon* with the more specialised Ganoids and with the Teleostei shows that the former resembles the latter in possessing cranial and pectoral splints, rudimentary periotic ossifications, and in the partial ossification of its visceral arches; in the presence of opercular bones, in the division of the proximal half of the hyoid arch into hyomandibular and symplectic segments, and in presence of an interhyal element. I may also mention the absorption of the inner wall of the otic capsule, and the development of a lamina perpendicularis; the absence of labial or extra-branchial cartilages with the doubtful exception of such as may be confluent with the anterior end of the produced prenasal rostrum. The non-lobate character of the pectoral fins, and the lateral position of the anterior and posterior nares, as well as the fact that the interspinous bones, though thrice segmented, are not more numerous than the segments of the axial skeleton, as indicated by the neural arches, may also be regarded as instances of specialisation in the same direction.

Previous to discussing the relations of *Polyodon* to the Amphibia we may consider the bearing of the facts elucidated in preceding detailed comparison of the genus with the Elasmobranchii, and with the other Ganoids, on its systematic position. Several anatomists have attempted to give expression to the important structural differences between the two genera of *Polyodon* and *Acipenser* and the remaining recent and fossil Ganoids in various schemes of classification, and it will be advantageous to give a brief sketch of their views.

Agassiz,[*] in his newly constituted order of the Ganoidei, included *Acipenser* and *Polyodon* in the family Acipenserides.

Heinrich Müller,[†] in his classical paper on the anatomy of the recent Ganoids, classified them as follows:—

α. Holostei.—Osseous vertebral column.
  Family I. Lepidosteini . . . *Lepidosteus.*
  Family II. Polypterini . . . *Polypterus.*
β. Chondrostei.—Cartilaginous vertebral column and persistent notochord.
  Family III. Acipenserini . . . *Acipenser* (*Scaphirhynchus*).
  Family IV. Spatulariæ . . . *Polyodon* (Lacép.); *Planirostra* (Raf.).

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[*] Agassiz, Pois. Foss.

[†] 'Ueber den Bau und die Grenzen der Ganoiden.' Abhandl. Ak. Wiss. Berlin, 1864.

GIEBEL,* in his classification of fossil Fishes, retained H. MÜLLER's subdivisions of Holostei and Chondrostei, the genera *Polyodon* and *Acipenser* being relegated to the last-mentioned group.

VOGT,† in a system of classification of recent and extinct Ganoids, divided the order into the three suborders of (I.) Loricata, which contained the families Cephalaspida, Acipenserida, and Spatularida; (II.) Rhombifera, including Lepidosteidæ, Polypteridæ, and the extinct Ganoids with rhomboidal scales; (III.) Cyclifera, comprising the Amiadæ and the cycliferous fossil genera.

HUXLEY,‡ in his essay on 'The Systematic Arrangement of the Fishes of the Devonian Epoch,' and subsequently in his 'Anatomy of Vertebrate Animals,' arranged the recent and fossil members of this order in the following suborders:—

I. Amiadæ.
II. Lepidosteidæ.
III. Crossopterygidæ.
IV. Chondrosteidæ.
V. Cephalaspidæ.
VI. Placodermi.
VII. Acanthodidæ.

LÜTKEN,§ declining to separate the Ganoids from the Teleostei, regarded the former simply as a subdivision of the Physostomi, thus:—

Subclass I. Teleostei.
  Order I. Air-duct absent (*Physoclysti*).
  ,, II. Air-duct present (*Physostomi*).
    Suborder I. Containing MÜLLER's families of the physostome Teleostei, and, in addition, the *Amiidæ*, the *Leptolepidæ*, the *Megaluri*, and the *Caturi* of the Jurassic period.
    ,, II. *Ganoidei.*—Nearly all the recent and extinct Ganoids.
    ,, III. *Sturiones* (*Acipenser, Polyodon*).

It will be noticed that, in so far as *Polyodon* and *Acipenser* are concerned, LÜTKEN agrees with H. MÜLLER in regarding them as constituting a group equal in morphological value to that in which all the other Ganoids are contained.

CARUS‖ retains the Chondrostei as a distinct suborder for the reception of the two genera, while the suborder Phractosomata contains the Placodermi and the

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* 'Fauna der Vorwelt,' vol. I., pt. 3. Leipzig, 1848

† 'Zoologische Briefe,' vol. II. Frankfurt, 1852.

‡ Mem. Geol. Survey, sec. X.

§ *Vide* German translation in 'Palæontographica,' Band xxii., 1873. Mag. Nat. Hist. 1871.

‖ 'Handbuch der Zoologie' (CARUS und GERSTÆCKER).

Cephalaspidæ, the remaining recent and fossil Ganoids being distributed among seven other suborders.

OWEN* included *Cephalaspis, Pterichthys, Pteraspis, Coccosteus,* and the Sturionidæ (gen. *Acipenser, Chondrosteus, Polyodon*) in the suborder Placoganoidei; while the remaining Ganoids, both recent and extinct, are included in his second suborder of Lepidoganoidei.

Dr. GÜNTHER,† in his catalogue of living Fishes, retains H. MÜLLER'S subdivisions of Holostei and Chondrostei, and uses them in the sense originally suggested by their author, the latter group including the families of the Acipenseridæ (*Acipenser* and *Scaphirhynchus*), and *Polyodon.* Dr. GÜNTHER further removes *Polyodon* from the Acipenseridæ and elevates it to the rank of a distinct family, under the name of Polyodontidæ.

It will be seen from the foregoing brief account of the various schemes for the classification of the extinct and living Ganoids which have been proposed, that in the majority of cases the systematic importance of the Chondrosteous Ganoids is regarded as being equivalent only to that of each of the other families of Ganoids. But I submit that the facts elucidated in the earlier part of this paper, and briefly summarised above, afford abundant evidence in favour of adhering to H. MÜLLER'S two primary divisions of Ganoidei (Chondrostei and Holostei), or to LÜTKEN'S two groups of 'Ganoidei proper' and 'Sturiones.'

Though there can be but little doubt as to the primary group of Fishes to which the Chondrostei should be relegated, yet the remarkable combination of characters generally regarded as more or less distinctive of the Teleostei, the Elasmobranchs, and the Amphibia possessed by *Polyodon* and, though to a less extent, by *Acipenser* also, even if they do not justify the elevation of these genera to a primary subdivision of the class, at all events render it necessary that these facts, which so clearly demonstrate their distinctness from all other Ganoids, should receive adequate expression in any natural system of classification.

Omitting for a moment any reference to the Amphibian tendencies of *Polyodon,* it seems probable that the true position of *Polyodon* is that of an annectent group, between the Elasmobranchs on the one hand, and the divergent stems of the Teleostei and Ganoidei on the other. The existence of such transitional families as the Chondrosteidæ and the Palæoniscidæ, by which the Acipenseroid and Polyodontoid types are related to the more typical Ganoids, renders doubtful the necessity of establishing a primary group for the reception of those types. While, therefore, the Chondrostei may be retained with the remaining Ganoids in the same order, yet it seems necessary that the distinction between the two groups should be definitely expressed. We may, I think, retain the two subdivisions first instituted by H. MÜLLER, though it seems advisable to remodel the definitions on which they were based. As before stated, the

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* Palæontology. 1861.

† 'British Museum Catalogue of Fishes,' vol. viii.

most distinctive feature about *Acipenser* and *Polyodon* is the remarkably Selachian character of their mandibular arches, and it is to those structures that we must look for definitions of the subsidiary groups. In both genera the pterygoid outgrowth from the proximal segment of each mandibular arch is united with its fellow in a median symphysis, as in the Selachii; in all the remaining recent Ganoids these outgrowths are connected through the intervention of a palatine bone with the prefrontal region of the skull.

We may therefore classify Ganoids into two main groups as follows :—

Ganoidei,

α. *Selachoidei.*—Pterygoid processes united in a median symphysis. Persistent and unsegmented notochord. Persistent spiracles and mandibular branchiæ.

Genera—*Polyodon, Acipenser, Scaphirhynchus,* and *Chondrosteus.*

β. *Teleosteoidei.*—Pterygoid processes not united with each other, but connected directly, or indirectly through the intervention of a palatine bone, with the prefrontal region of the cranium. Vertebral column generally ossified into distinct vertebræ; notochord aborted; no mandibular branchiæ.

Genera—*Amia, Polypterus, Calamoichthys,* and *Lepidosteus.*

In deciding upon the claims of the fossil Ganoids to be included in one or the other of these two groups, we are compelled to rely altogether on the structure of the upper jaw. Tested in this way, we must refer the Crossopterygidæ, Lepidosteidæ, Palæoniscidæ, and Platysomidæ to the group of Teleosteoid Ganoids. The Acanthodidæ probably belong to the Selachoid group.

The distinctness of the Selachoid and Teleosteoid groups is materially lessened when an attempt is made to include the fossil genera of Ganoids in either of them. *Acipenser* and *Chondrosteus* in the former group, and the Palæoniscidæ and the Platysomidæ in the latter, partially bridge over the gap which exists between the two when only the recent forms are considered.

Dr. TRAQUAIR,* in his valuable paper "On the Ganoids of the Carboniferous Formations," refers the families Palæoniscidæ and Platysomidæ to the suborder Acipenseroidei, which also includes *Acipenser, Chondrosteus,* and *Polyodon.*

The principal characters by which this suborder is defined and distinguished from the other suborders of Crossopterygii, Amioidei, and Lepidosteoidei, as given by Dr. TRAQUAIR, are as follows ;—

"Suborder II. *Acipenseroidei.*—Tail completely heterocercal; notochord persistent; paired fins non-lobate, infra-claviculars present, rays of dorsal and anal fins exceeding in number their supporting interspinous bones; præoperculum when present tending to extend forwards over the cheek; branchiostegal rays in most, but large jugulars in

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* *Op. cit.*

none. Skin in many furnished with osseous scutes, or with rhomboidal scales, in some naked, save on the prolongation of the body along the upper lobe of the caudal fin."

Though Dr. TRAQUAIR may have adduced sufficient evidence to justify the separation of Palæoniscidæ and Platysomidæ from the Lepidosteoid forms with which they have so long been associated, nevertheless I venture to think that he has not been so successful in his efforts to establish the claims of those two families to be included in the same group with the Acipenseroid forms. Most of the characters on which he relies for justifying the union of the Palæoniscidæ with the Selachoid Ganoids, are certain generalised structures which are common to widely diverse groups of Fishes, and the force which these facts possess as evidences of affinity is very considerably lessened by considerations based upon more specialised structures. For example, paired interclavicles are common not only to the special groups under discussion, but also to the recent and extinct Crossopterygidæ; segmentation of the interspinous bones or cartilages is characteristic of nearly all Ganoids, of Ceratodus, and of Elasmobranchs; while the fin-rays are more numerous than the bones or cartilages which support them in such diverse forms as certain Crossopterygii, Ceratodus, and Lepidosiren, and the same may be said of the corneous fibres which represent those structures in the Holocephali and Elasmobranchii. Similar remarks might be made on the persistence of the notochord, the absence of ossified ribs, and the condition of the caudal fin. On the other hand, the more specialised structures of the Palæoniscidæ point strongly to the conclusion that they are more closely related to the Teleosteoid than to the Selachoid Ganoids. The dermal armature of Palæoniscidæ is essentially the same as that of the Crossopterygii and the Amiidæ, and the latter groups further agree with the former in possessing a complete series of opercular bones. The hyomandibular of *Palæoniscus* is strikingly like that of *Polypterus*, and the former also resembles the latter in the character of the preoperculum which extends forwards over the cheek towards the orbit, as well as in the possession of a transverse chain of supra-temporal ossicles behind the posterior margin of the cranial buckler.

And in addition, the Palæoniscidæ possess well-ossified, quadrate, metapterygoid, and articular elements; and there is also evidence that the chondrocranium was not altogether devoid of ossific centres. Most of the characters which appear to support the view that the Palæoniscidæ are closely related to *Polyodon* and *Acipenser* seem to be only evidence of generalisation or the persistence of ancestral features common alike to these forms and to many other Ganoids, and not of any special affinity between any of the groups which may happen to possess them. But far outweighing the evidence in favour of such affinity is that furnished by an examination of the structure of the upper jaw in *Palæoniscus* and its allies. Dr. TRAQUAIR has shown that in that genus the upper jaws somewhat resemble the same parts in *Polyodon*, and notably in possessing long parosteal pterygoid bones, between which and the backwardly-produced maxilla the levator mandibularis muscle must have passed precisely as was described in the earlier part of this paper as existing in *Polyodon*. Nevertheless, in Palæoniscus it would appear that the pterygoids were attached to the prefrontal region, as is the case in all the Telesteoid Ganoids, but differed in this respect from the disposition of those parts in *Polyodon* and its allies. While, therefore, it may be admitted that the Palæoniscidæ and the Platysomidæ are to some extent annectent forms between the two main subdivisions of the Ganoids, yet at present the balance of evidence is against their being included with the Selachoid forms, and in favour of their classification with the Teleosteoidei, though whether they should provisionally be classed with the Lepidosteoid forms, or form the nucleus of a new group is not, as yet, quite clear.

A careful comparison of the dermal armature of the Placodermi and the Cephalaspidæ with that of *Polyodon* and *Acipenser*, failed to suggest the existence of any near relationship between these widely different forms, or to throw any light on the nature of the cranial buckler in the two Palæzoic families.

D. *Comparison of* Polyodon *with the Amphibia.*

A comparison of the skull of *Polyodon* with the skulls of the Anura and Urodela leads to interesting though somewhat perplexing results, which are not without significance in relation to the phylogeny of the three most important groups of Ichthyopsida. The majority of living Ganoidei, both in their osteology and myology, exhibit many indications of affinity to the Amphibia, and *Polyodon* is no exception to this rule. There are several interesting points of agreement with the Urodela. The fenestration of the roof of the periotic capsule in *Polyodon* is comparable in position and in its relations to the arch of the posterior vertical semicircular canal to a similar vacuity, which in *Siren lacertina* represents the primitive involution to form the internal ear; and it is noteworthy that in this point both forms agree with each other and differ from the Plagiostomi where the parietal foramina are situated to the inner or mesial side of the vestibular sac and its canals. *Polyodon,* in common with all other Ganoids, agrees with the majority of Urodèla in the absence of a basihyal and the attachment of the hypohyals to the first mesobranchial segment. With the Anura, *Polyodon* agrees in the ossification of its lower labial cartilages as mento-Meckelian bones. But perhaps the most remarkable feature in which *Polyodon* resembles the Anurous Amphibia is the possession of a forwardly directed "orbitar process" associated with a suspensorium so much inclined backwards that the angle of the gape is extended even beyond the posterior limits of the skull. The Marsipobranchii are the only other adult Ichthyopsida in which this singular process has as yet been discovered. So far as I am aware no such structure, or even a rudiment of it, has yet been detected in any of the Elasmobranchii, the Teleostei, or in any of the Urodela, either in the adult or in the embryo. The precise significance of the structure in question is not very clear, but one suggestion may be made. The condition of the "orbitar process" as an apparently functionless rudiment in *Polyodon* does not throw any light on its primary origin or function; but its existence and relations in the adult Lamprey, as well as its transitory condition in the developing Frog, suggest that originally it may have acted as a kind of anterior suspensor to the much inclined mandibular pier of such primitive Vertebrata as happened to possess a suctorial mouth, prior to the adaptation of the palato-pterygoid bar to that purpose. Hence the existence of an "orbitar process" in the permanently suctorial mouth of the Marsipobranchii, and as a rudiment in the temporarily suctorial mouth of the young Tadpole. These facts, coupled with the rotation of the quadrate cartilage, which from the direction and relations of the "orbitar process" we may infer to have taken place, are sufficient to render extremely probable the existence of a close parallelism between the developmental history of the cranium in the embryo *Polyodon* and such otherwise dissimilar forms of Anurous Amphibia as *Bufo ornatus, Dactylethra capensis, Rana temporaria,* and *Otilophus margaritifer,* though I am not aware that anything has yet been made known about the cranial embryology of the former.

The existence in this very generalised Ganoid of so remarkable a combination of Selachian and Amphibian characters at once suggests an inquiry into the probable ancestral relations to the progenitors of those two groups, and the first question for solution is, whether the Ganoids are more closely related phylogenetically to the Amphibia or to the Elasmobranchii? The embryology of the Ganoids is at present altogether unknown, and from this source, at all events, no clue can be obtained as to the phylogeny of the group; consequently we are dependent upon such conclusions as may be drawn from comparative anatomy. An analysis of the structural features common to any two of the three groups seems to me to lend very strong support to the view that the Ganoids and the Amphibia are of monophyletic origin.

The two groups agree with each other in—

I. The possession of morphological or functional lungs.

II. The rudimentary condition of the cerebellum.

III. The persistence of the embryonic connexion between the efferent renal ducts (Wolffian ducts) and the Mullerian ducts, due to the incomplete splitting of the primitive segmental duct.

IV. The development of parosteal and endosteal ossifications in relation with their originally cartilaginous crania.

V. The possession of a conus arteriosus with valves.

VI. The existence of functional external gills in the embryos.

In all of these points both the Urodela and the Anura agree with the Ganoids, while the anatomical facts to which reference is made in paragraphs III., V., and VI., are common alike to the Ganoids, the Amphibia, and the Elasmobranchs.

The Urodela and the Ganoids have also certain minor characters in common, which are not shared by the Anura, and these are—the possession of a dentigerous splenial, the fenestration of the roof of the otic capsule (*Polyodon* and *Siren lacertina*), the absence of a basihyal and the attachment of the hypohyals to the first basibranchial segment. On the other hand, nearly all Ganoids in possessing mento-Meckelian ossicles, and the Ganoid *Polyodon* in possessing an "orbitar process," agree with most adult or embryo Anura. In *Polypterus* among Ganoids, in all Anura, and in not a few Urodela, there is a tendency towards the development of a more or less extensive interorbital ossification comparable to the "os en ceinture" of the Frog. But perhaps the most important of all the characters by which the Ganoid-Amphibian stem is distinguished from the Elasmobranch stem is the presence of a cœcal diverticulum from the fore part of the alimentary canal, which in its varying degrees of development forms the functional lung of the Amphibian, or the swim-bladder of the Ganoid—a structure which, though partially respiratory, is mainly mechanical in function.

Finally may be mentioned the existence of such transitional forms as the Dipnoi, which in so many features are connecting links between the Amphibia and the more generalised Crossopterygian Ganoids. It may now, perhaps, be permissible to assume that the primitive ancestors of the Ganoids and Amphibians were differentiated from the Elasmobranch stock prior to the evolution of their two main groups of descendants.

The fundamental similarities between the main divisions of the Amphibia lead us to believe that they have been derived from some one ancestral form. That the divergence of the Anura and Urodela took place at a very early period is evident not only from the differences observable when their adult structures are compared, but also from the extreme dissimilarity of their larval forms. Even if we admit that differences which now exist between the larvæ are the result of adaptive modification in one or other of them subsequent to the evolution of the two types, there will still remain those existing between the adults which are scarcely less important.

As far as our deficient knowledge of the development of the cranium in the Urodela will admit of any attempt to make general statements, it would appear that the very characteristic metamorphosis of the mandibular arch of the young Tadpole which results in the attachment of the forwardly inclined mandibular pier to the prefrontal region by a vertically disposed palato-pterygoid bar, and in the development of an "orbitar" outgrowth from the quadrate, while the non-functional Meckelian cartilages are superseded in their use as jaws by the labial cartilages, never occurs in any of the caudate Amphibia. In the latter also there are no labial cartilages, and even when horny jaw sheaths are present, as in the adult *Siren*, they are not supported by labial cartilages, as in the Tadpoles of the Anura, but by the dentary and premaxillary bones. But the wide difference between the two types is most decisively shown when such Perennibranchiate forms as *Proteus* and *Menobranchus* are compared with any of the Anura.

In *Menobranchus** the suspensorium retains its primitive position at right angles to the cranial axis, and the palatine and rudimentary pterygoid processes are widely sundered; the trabeculæ retain their embryonic condition as simple nearly parallel

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* HUXLEY, Proc. Zool. Soc., 1874.

bars entirely devoid of any ossific centres, and, as is the case with no other Vertebrate animal, the parachordals are permanently distinct from one another, the notochord lying between them in a stratum of connective tissue. In *Proteus,* and also in *Menopoma,* the proximal segment of the hyoid arch persists as a large and distinct hyomandibular cartilage, and is especially large and attached by ligament to the periotic capsule in the former, so that the distal part of the arch is directly connected with the skull by its own proper proximal segment. In addition, there may be mentioned the absence of an opercular fold for the protection of the gills in all Perennibranchiata, with the exception of a rudiment in *Siredon;* the persistence of external gills combined with the non-development of internal branchiæ, the absence of eyelids, and the imperfect condition of the inter-auricular septum. Unless many of these features are due to the degradation of the more immediate predecessors of the recent Urodela, we must believe that the primitive common ancestor of the Urodela and the Anurous Amphibia was in many respects of a lower organization than any living Marsipobranch or Selachian. On the other hand, there are reasons for believing that the Perennibranchiate Urodela owe much of their simplicity of structure to the fact that they are the descendants of Caducibranchiate forms which have undergone a certain amount of retrograde metamorphosis. The comparative ease with which the former under the influence of suitable natural or artificial conditions become Caducibranchiate, as shown by the interesting experiments of Fräulein MARIE VON CHAUVIN,* suggests that the change is nothing more than the assumption of a more immediate ancestral habit of life. As to the relation of the Ganoidei to this ancestral form, or to either of its two groups of descendants, two suggestions may be made. The close analogy between the Polyodontidæ and the Anura in the nature of their cranial metamorphoses which I infer to exist from the existence and relations of the "orbitar process" in both groups, combined with the fundamental differences which exist both between the larval and the adult Anura and Urodela, is somewhat unexpected and inexplicable, on the view that the two latter are more closely related to one another than is either of them to any of the Ganoid *Polyodon.* On the other hand, is it possible that *Polyodon* may have been an offshoot from the first evolved Anura subsequently to the divergence from the Urodela, and that while the Ganoid has retained its piscine habit, the two other groups have been modified along parallel lines and adapted to an air-breathing life? But an affirmative answer to this question involves the inadmissible conclusion that the phylogenetic relationship of the Anura to the Polyodontidæ, and presumably therefore to all other Ganoids and to the Teleostei, is closer than that of the former to the Urodela. Such a conclusion is also negatived by many other considerations. The close correspondence which can be traced between the caudate and the non-caudate Amphibia in the arrangement of their generative and vascular systems, and in the structure of the vertebral column, pectoral and pelvic arches, and their limb-skeletons, is so marked that it can hardly be explained in any other way than by

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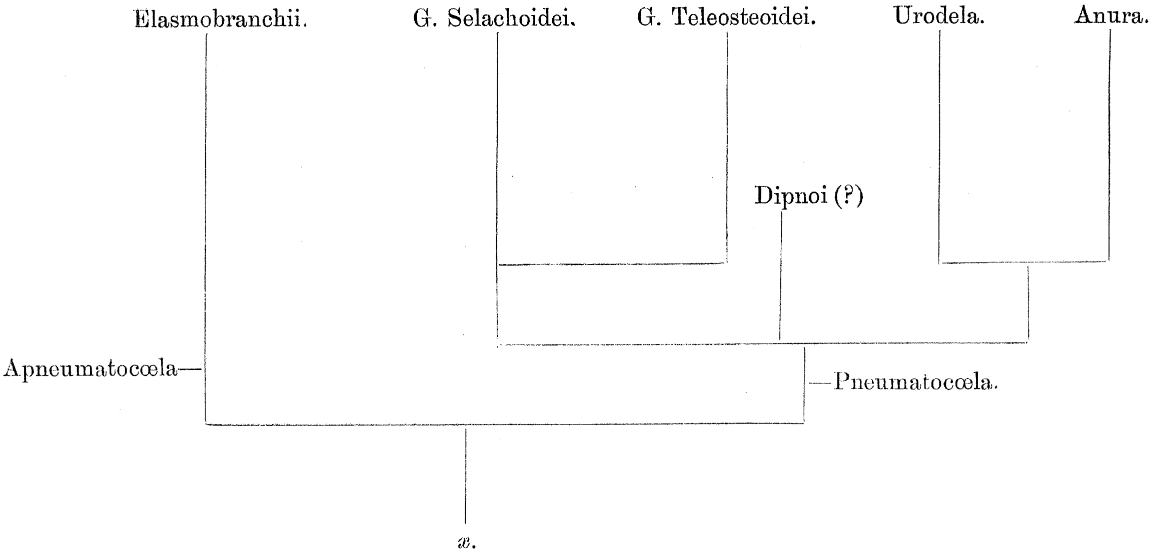
* Zeitschrift für Wissenschaftliche Zoologie. Bd. xxvii., 1876.

admitting their community of descent. We must therefore conclude that the important differences between the two types are probably due to their early separation from each other, and to the fact that the lowest Urodela have undergone much retrograde metamorphosis in their cranial structure, while adaptive changes have profoundly modified the adult and larval forms of both groups since they first came into existence. An alternative suggestion which may be made is to regard the Ganoid-Amphibian phylum as splitting into its two main constituent groups, the primeval Amphibia afterwards differentiating into Urodela and Anura, while the primitive root-stock of the Ganoids gave rise to the Teleosteoidei and to the Teleostei proper, the Selachoidei types persisting with relatively little modification as representatives of those early progenitors of their order.

We may venture more clearly to express the foregoing conclusions as to the relations of *Polyodon* and the other Ganoids to the Amphibia and Elasmobranchii by the aid of the following diagram :—



As to the nature of the primitive ancestor (*x*.) from whence the divergent Elasmobranch, Ganoid, and Amphibian stems have been derived, we may infer that it possessed an amphistylic skull, perhaps not differing essentially from that of the recent *Notidanus;* a persistent notochord supporting dorsally a series of neural and intercalated arches, which were related to the anterior and posterior roots of the spinal nerves, as in the embryo Selachian and in the adult Marsipobranch, and also in relation ventrally with a similarly double series of hæmal arches enclosing the dorsal aorta ; that respiration was carried on by external gills, which were developed in connexion with the mandibular as well as from the other visceral arches, and were probably destitute of an opercular covering ; persistent segmental openings may have been present, and also an archipterygium composed of three proximal segments (propterygium, mesopterygium, and metapterygium), each supporting a series of radial cartilages, but entirely devoid both of morphological and functional lungs. Such an ancestral type may be supposed to have very early differentiated into the two groups of Apneumatocœla and Pneumatocœla, the former becoming the root-stock of the modern Elasmobranchii, which have retained not a few of the characteristics of their prototype, while the latter, by acquiring rudimentary and more or less functional lungs, became the primitive double-breathers from which have been derived the Ganoids and Amphibia. Of these primitive Pneumatocœla it is possible that the recent *Lepidosiren*, *Protopterus*, and *Ceratodus* are the nearest, though much modified, living allies. The Amphibia developed more complex lungs and a chiropterygium, and became adapted to a terrestrial life, while what remained of the Ganoid-Amphibian stem after the separation of the Amphibia, differentiated into the Teleosteoid Ganoids, the Teleostei proper, and into the progenitors of the Selachoid Ganoids, all of which acquired an ichthyopterygium, and in the more specialised forms the originally complex and more or less respiratory primitive lungs became much simplified in structure and mainly mechanical in function. If the view which I have here ventured to suggest be correct, then we may regard these forms as being the relatively little modified descendants of the common stock from which the other Ganoids and the Teleostei have been differentiated, and as bearing a relation to the latter comparable to that in which the Tragulina stand to all the other recent ruminating Artiodactyla. That the Selachoid Ganoids have departed less from the ancestral type (*x.*) than any of the other groups, with the exception of the Selachii, is evinced by the structure of their vertebral column, fins, and chondrocranium, by their retention of mandibular gills, and by several other less important features. Two facts in the cranial structure of *Polyodon* are not easy to explain, viz., the formation of the upper jaw, and the existence of the "orbitar process." The union of the pterygoid processes in a median symphysis may have been the primitive condition of the jaw in the ancestral form (*x.*) and in the primitive Pneumatocœla, but that while persistent in Elasmobranchs and in *Polyodon*, it has been superseded by a different arrangement, viz., the union of the pterygoid processes with retral palatine outgrowths, in all other Ganoids and in all Teleostei and Amphibia; or we may conceive that, whatever may have been the primitive condition of these structures, the development of similarly constituted jaws in the Shark and in *Polyodon* is simply due to a parallelism in adaptive modification, though this latter alternative is far less probable. Neither is it easy to account for the retention of the "orbitar process" by *Polyodon*. It may have been an adaptive modification, correlated with a suctorial mouth in the larval forms of those Ganoids that were first differentiated from the Ganoid-Amphibian stem, and independently developed; or, and this is more probable, it may have been possessed by certain primitive suctorial-mouthed Pneumatocœla, but has become obsolete in all their descendants except *Polyodon* and the embryos of the Anurous Amphibia.*

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* The probability that the primitive common ancestors of the Ganoids and Amphibians possessed suctorial mouths seems to me to be very great, and if this view be correct, the curious differences which

Thus it would seem that the Polyodontidæ constitute a remarkably central group of Fishes. They resemble the Elasmobranchs in retaining many of the features which were characteristic of their presumptive common ancestor; and they further resemble the Amphibia and the higher Ganoids in having undergone a certain amount of specialisation in the same direction, and that they are not altogether without indications of having undergone a certain amount of retrogression is evident from the localised distribution of their rhomboidal scales.

HAECKEL'S[*] pedigree of the "non-amnionate craniota" is somewhat different from that which I have ventured to suggest. He appears to regard the Amphibia, the Dipnoi, and the Halisauria as constituting one line of descent from a primitive pre-Selachian stem, while the Ganoids and the Teleostei are derivatives of the group of Plagiostome Elasmobranchs, the Chondrosteous Ganoids forming a transition type between the latter and the higher Ganoids. If this view be correct, we are required to believe that morphological or functional lungs have been developed quite independently on precisely the same plan, and with every grade of transition between their extreme modifications in two diverging groups of Ichthyopsida, modified for entirely different habits of life. The *à priori* improbability of such a course being adopted seems to me to be very great. The complex double swim-bladder of the Crossopterygian Ganoids is connected by a gradual transition in almost every anatomical detail with the simple, undivided air-bladder of the Physoclisti on the one hand, and through the double, cellular and functional lungs of the Dipnoi, with the more perfect and exclusively air-breathing structures of the Amphibia on the other. The best explanation of such facts seems to me to be the assumption that the two extremes of lung structure have been derived by progressive modification in opposite directions from some intermediate type of structure which, as I have suggested, may have been possessed by the primitive Pneumatocœla. Such evidence in favour of the monophyletic origin of the Pneumatocœla drawn from the consideration of a single organ, is, as I have tried to show, supported and strengthened by the existence of numerous other points of agreement, in both osteology and myology, between their two main groups of descendants. Moreover, if we accept HAECKEL'S views on the ancestral relations of the Dipnoi, it becomes exceedingly difficult to explain the existence of numerous points of agreement with the Crossopterygidæ which is so striking a feature in the anatomy of those Fishes. On the other hand, if the Dipnoi are looked upon as the much modified descendants of the primitive Pneumatocœla, there is much less difficulty in explaining their affinities to the early Ganoids in the structure of the vertebral column and fins, and their Amphibian tendencies, which are so clearly shown in the structure of their lungs, heart, nostrils, &c.

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exist in the cranial metamorphoses of the larval Urodela and Anura are to some extent explicable. The embryos of *Polyodon* and the Anura retain for a time this primitive suctorial mouth, but in the larval Urodela it has been replaced by a masticatory mouth, the suctorial stage being altogether suppressed.

[*] "Naturliche Schöpfungsgeschichte," 1873.

The remarkable correspondence in so many features between the Elasmobranchs and the Selachoid Ganoids is readily explicable on the view of their community of descent, and the retention of many ancestral structures in both groups; and any support which this agreement may lend to the view of the direct descent of the Ganoids from the Elasmobranchs is very much diminished in value by the existence of other facts, previously referred to, which strongly points to the monophyletic origin of the Amphibian and Ganoid stocks.

Description of the Plates.

The figures are nearly all of life-size, and the lettering is uniform throughout. The cartilage is tinted blue, the cartilage bones are coloured yellow, while the membrane bones remain white.

a^1. Dermo-ethmoid.
a^2, *a*^{3}, and *a*^{4}. Rostral splints belonging to the medio-dorsal series.
b^1. Parietals.
b^2. Frontals.
b^3, *b*^{4}, and *b*^{5}. Rostral splints belonging to the supero-lateral series.
b.br^1. First basibranchial element.
b.tp. Basitemporal ala.
c^1. Post-temporal.
c^2. Dermo-sphenotic.
c^3. Nasals or dermo-prefrontals.
c.br^1., *c.br*^{4}. Cerato-branchials.
c.h. Ceratohyal.
D. Dentary.
ep.br. Epibranchial.
h.m. Hyomandibular.
h.hy. Hypohyal.
h.br. Hypobranchial.
i.hy. Interhyal.
i.op. Interoperculum.
mg.o. Dorsal or ventral marginal ossicles of rostrum.
m.pg. Mesopterygoid.
mt.pg. Metapterygoid ligament.
mx. Maxilla.
Mk.c. Meckel's cartilage.
op. Opisthotic.

or.p. Orbitar process.
op. Operculum.
pg.p. Pterygoid process.
p.br. Pharyngo-branchial.
pt.r. Pterotic ridge.
p.f. Parietal foramen.
pt. Pterotic.
pa.s. Parasphenoid.
p^2, p^3. Rostral homologues of the parasphenoid.
Q. Quadrate cartilage.
sp.r. Sphenotic ridge.
sy.l. Symplectic ligaments.
Vo. Vomer.
V^2 and V^3. Rostral homologues of the vomers.

Nerves.

II. Optic.
m.o. Motores oculi.
tr. Trochlearis.
V, V″. Foramina for exit of branches of trigeminus.
VII′, VII′. Anterior and posterior openings of facial canal.
IX. Glossopharyngeal.
Vg. Vagus.

PLATE 55.

Fig. 1. Dorsal aspect of the skull. Reduced one-half.
Fig. 2. Ventral view. Reduced one-half.
  hy.g. Articular groove for head of hyomandibular.
  x. Prolongation of first visceral cleft.
  h.c. Hæmal canal.
Fig. 3. Side view of the cranium. Natural size.
  a.n. Anterior nares.
  p.n. Posterior narial opening.
  o.f. Orbital floor.
  i.h. Inter-hæmal cartilages.
  i.n. Inter-neural cartilages.
  a.r. Anterior root of spinal nerve.
  p.r. Posterior root.
  z. Foramen in side wall of rostrum.

PLATE 56.

Fig. 4. View of ventral surface of cranium. Life size.

Fig. 5. View of upper surface of chondrocranium when the insisting parostoses have been removed. Life size.

a.m.f. Anterior median fontanelle.
f.g. *f*-shaped groove.
hy.g. Groove for head of hyomandibular.
p.f. Parietal foramen.
γ. Superior opening of first visceral cleft.
ϕ. Upper and posterior extremity of the oblique ridge.

Fig. 6. Vertical and longitudinal section. Reduced one-half.

B. Canal lying above spinal canal.
ar′. and *pr′.* Anterior and posterior root of first spinal nerve.
p.sc., a.sc., h.sc. Foramina by which the anterior and posterior vertical and the horizontal semicircular canals leave the recess in which the membranous vestibular sac lies.
Ca. Carotid foramen.
Py. Pituitary fossa.
Fa. Foramen by which the facial nerve leaves the cranium.
h.c. Hæmal canal.
n.c. Notochord.

PLATE 57.

Fig. 7. Side view of the otic capsule, which has been dissected to show the semicircular canals and their relations to the parietal foramen, and pterotic and opisthotic bones. Natural size.

a. Oblique ridge, terminating above and behind in the decurrent flap of cartilage ϕ.

Fig. 8. Mandibular and hyoid arches, and opercular bones. Life size.

mt.pg.l. Metapterygoid ligament.

Fig. 9. Branchial arches.

r.r′. Rays attached to first and second epibranchials.

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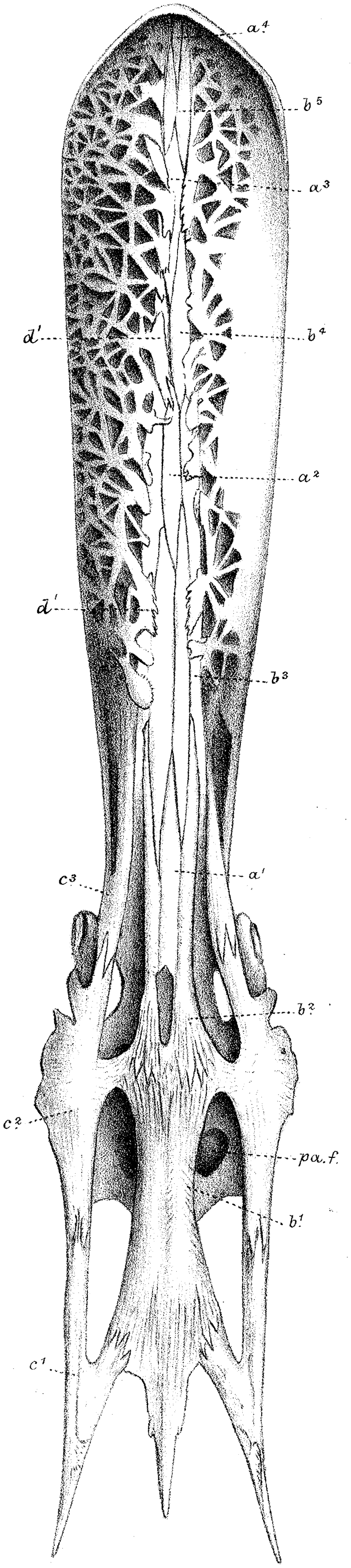

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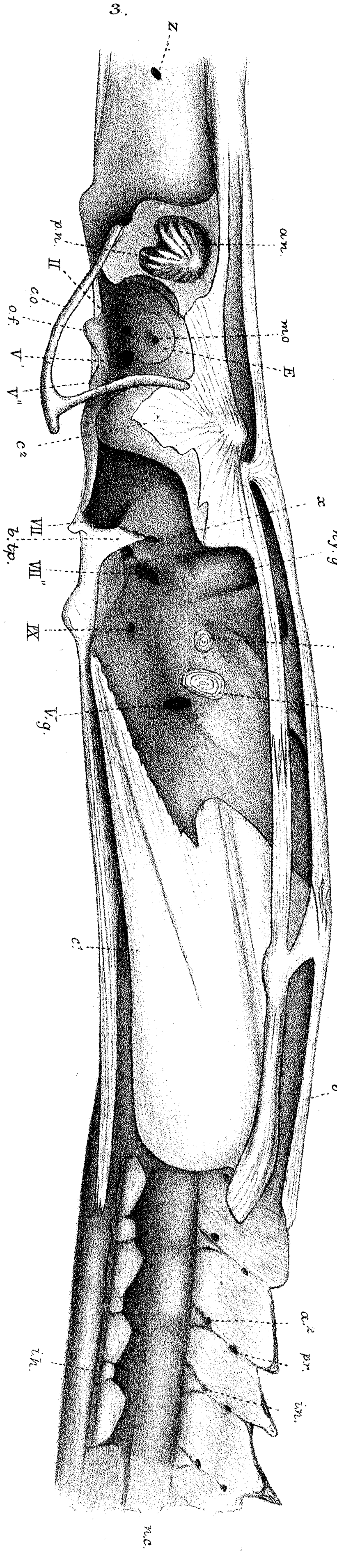

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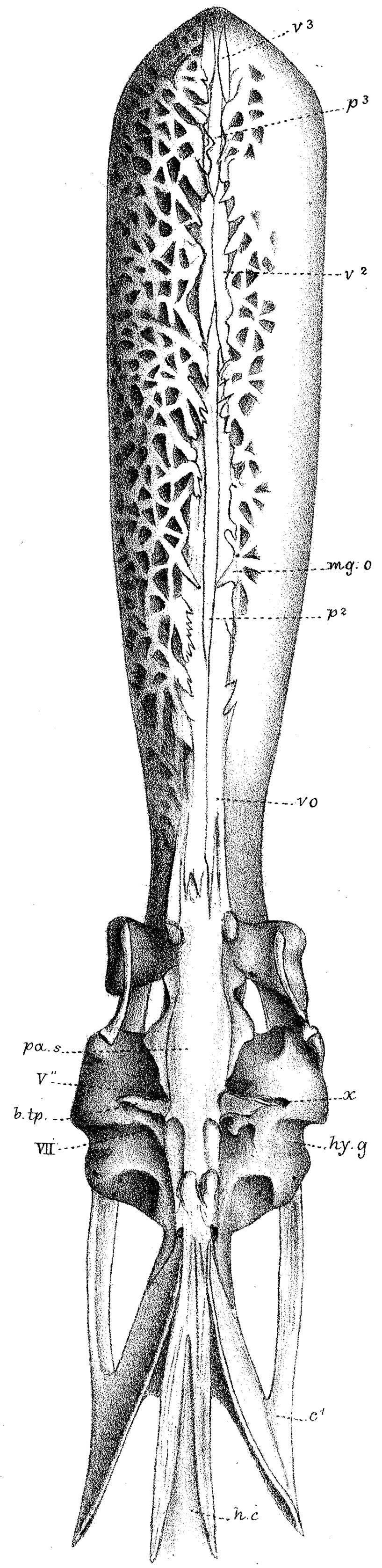

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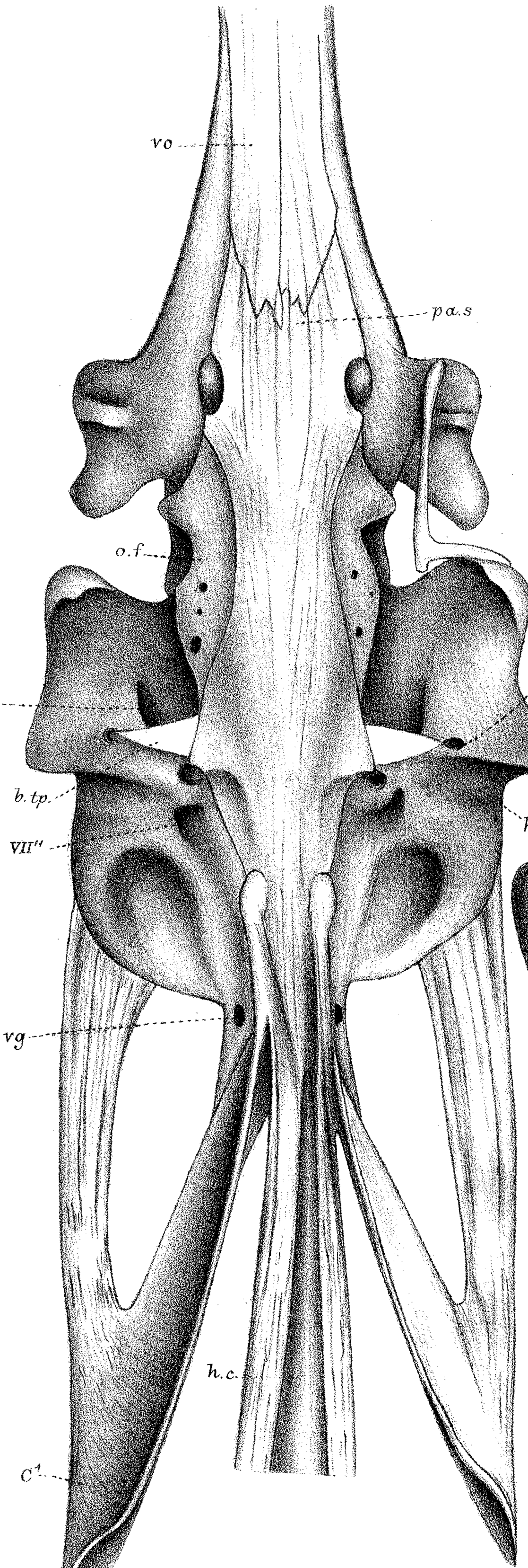

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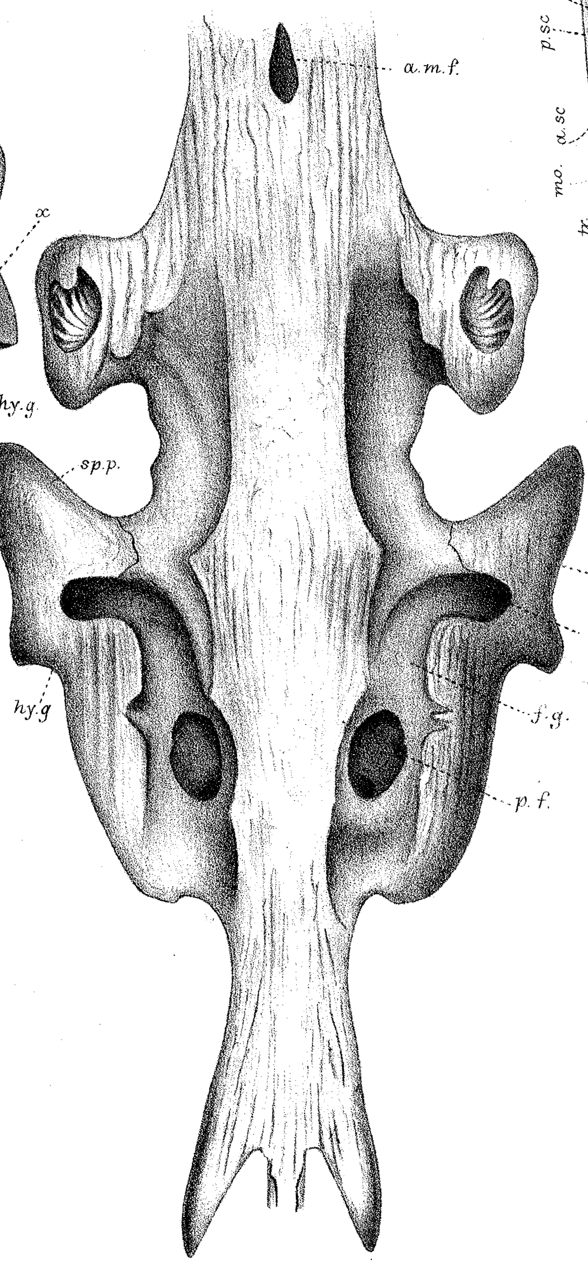

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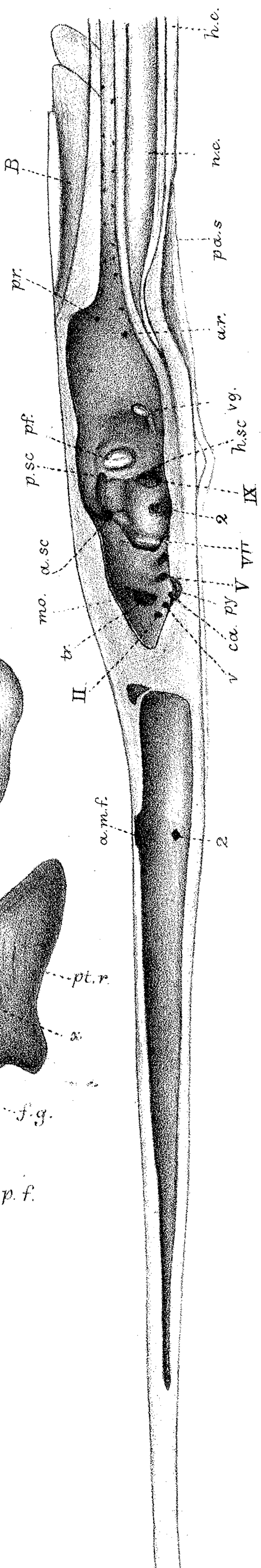

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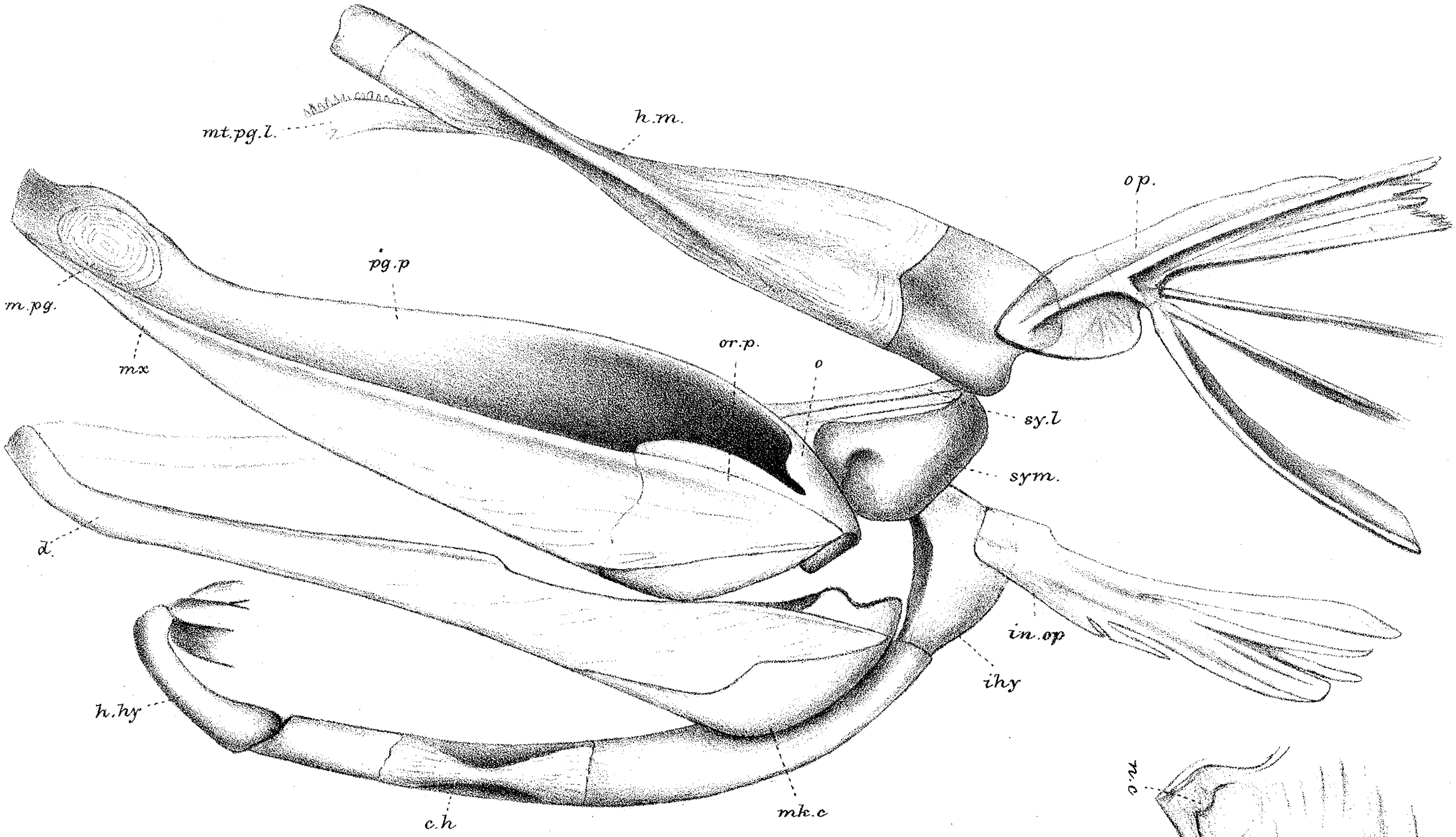
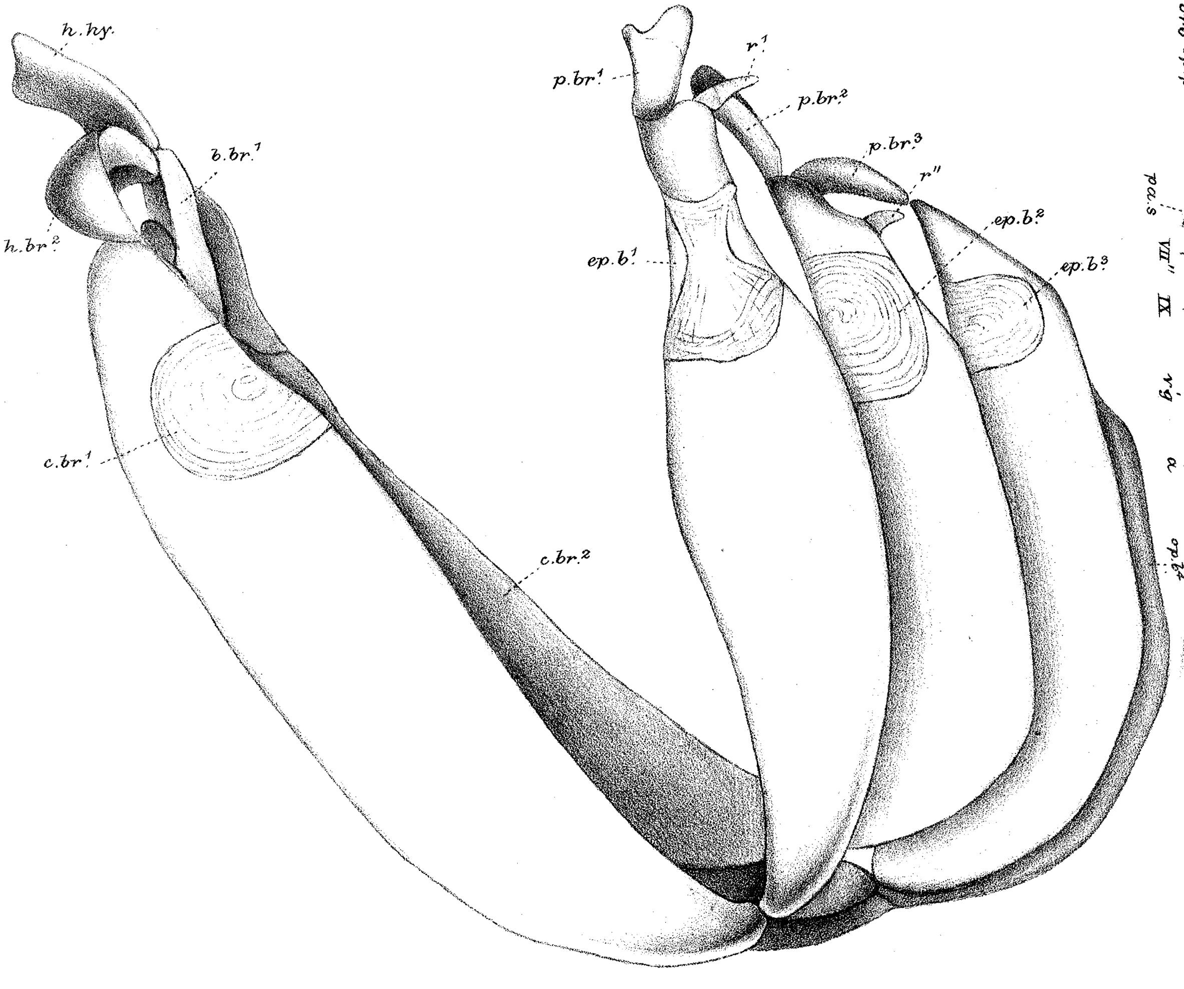
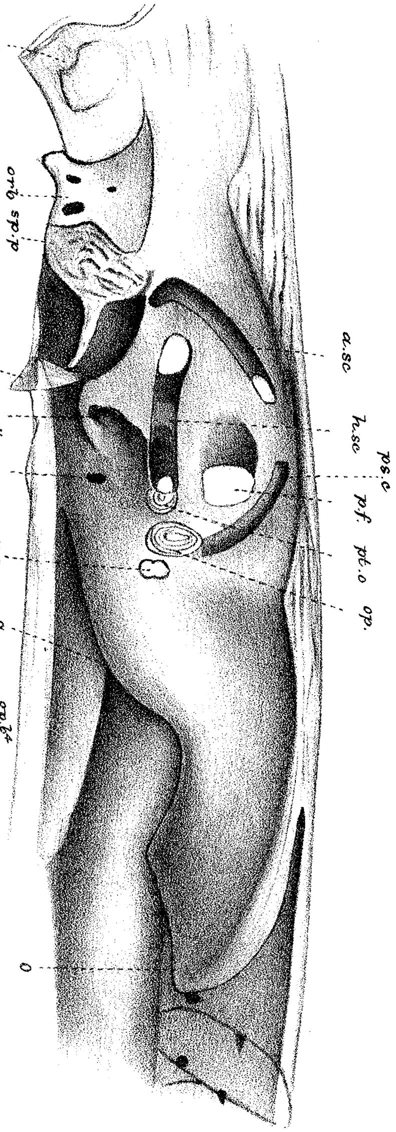
Bridge. Phil. Trans. 1878. Plate 57.







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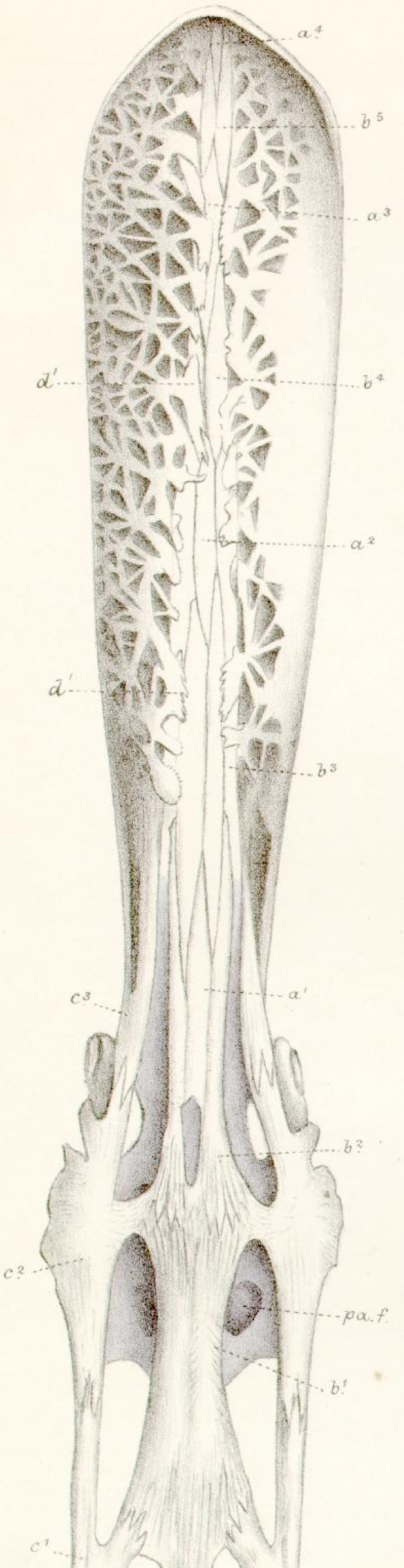

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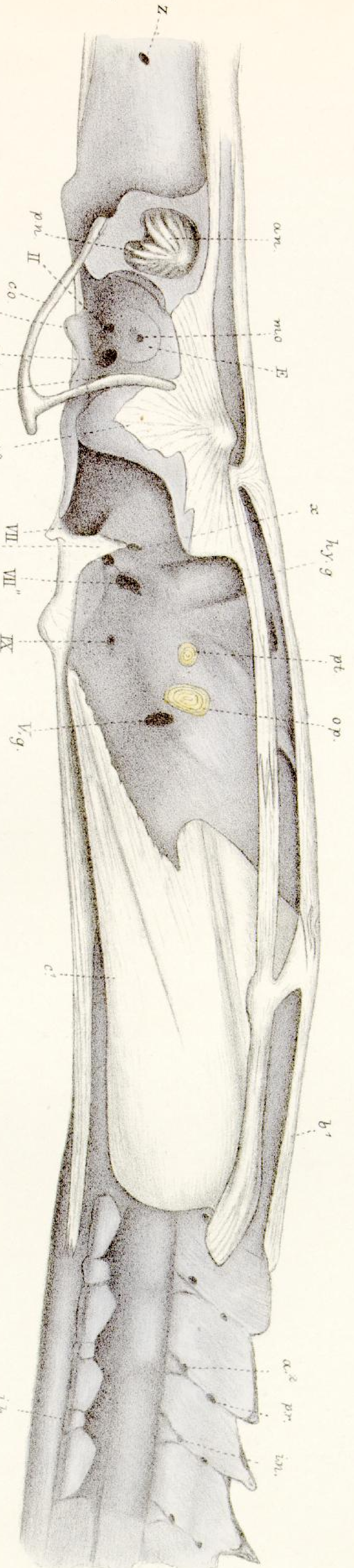

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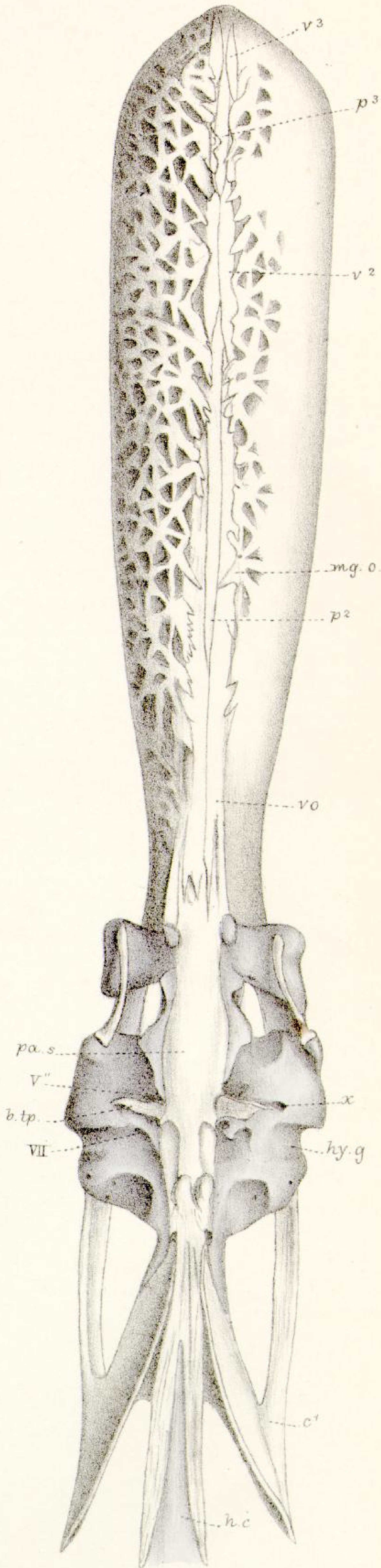

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p.r. Posterior root.
z. Foramen in side wall of rostrum.

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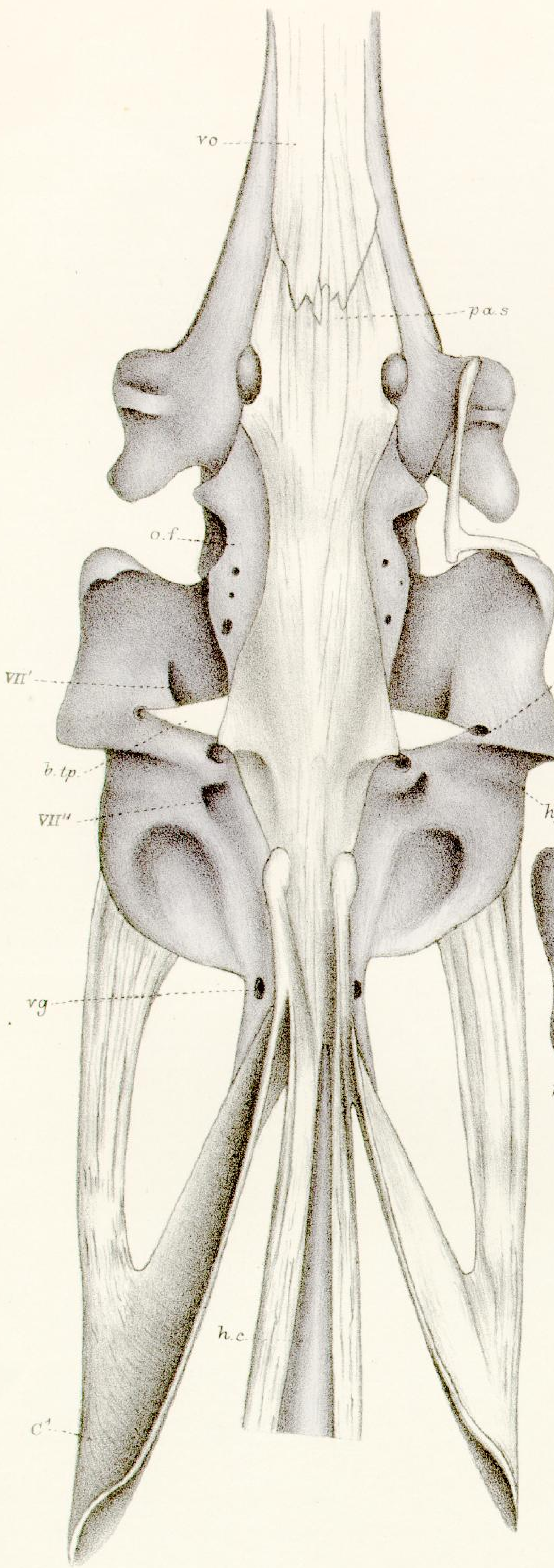

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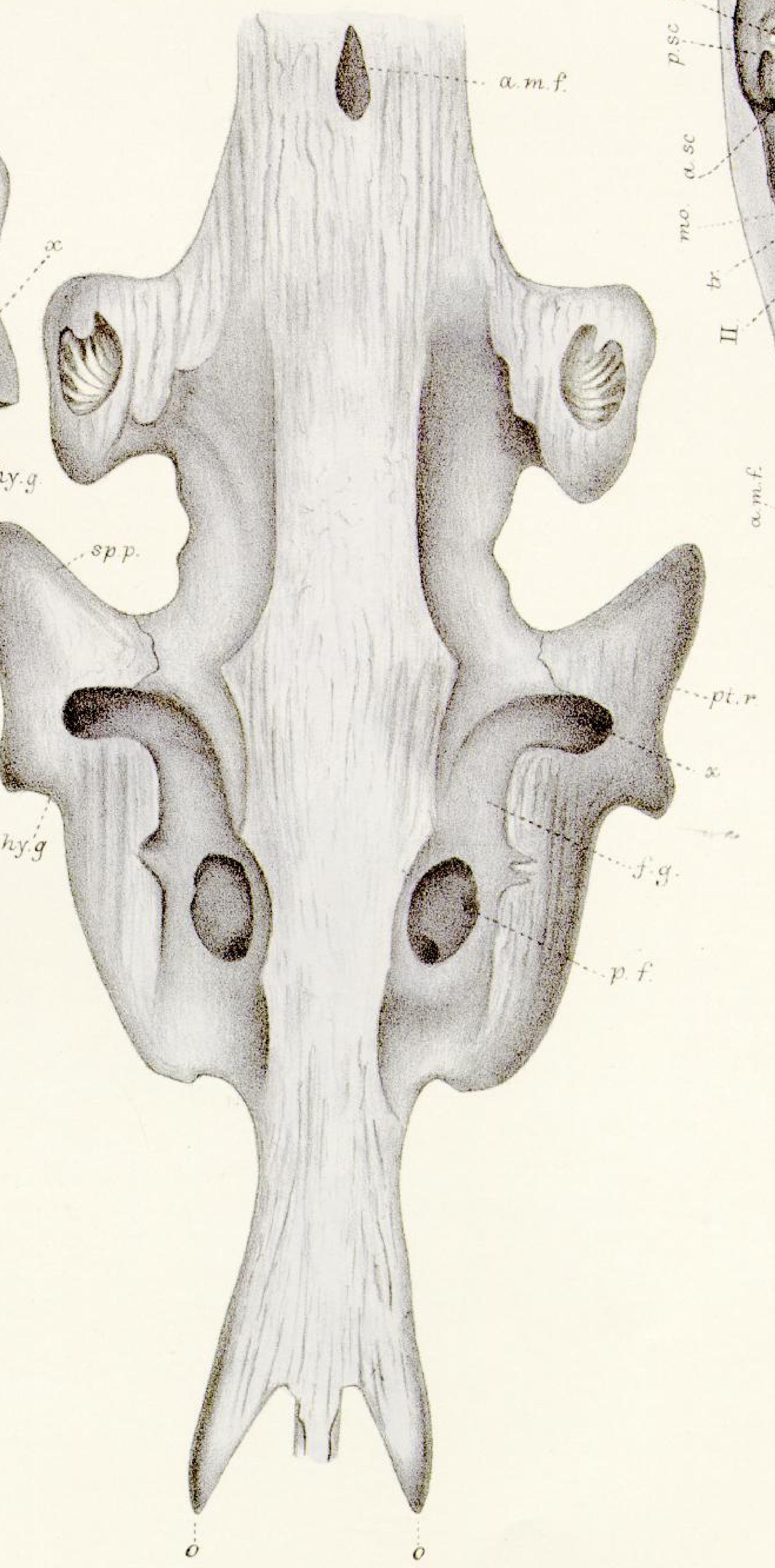

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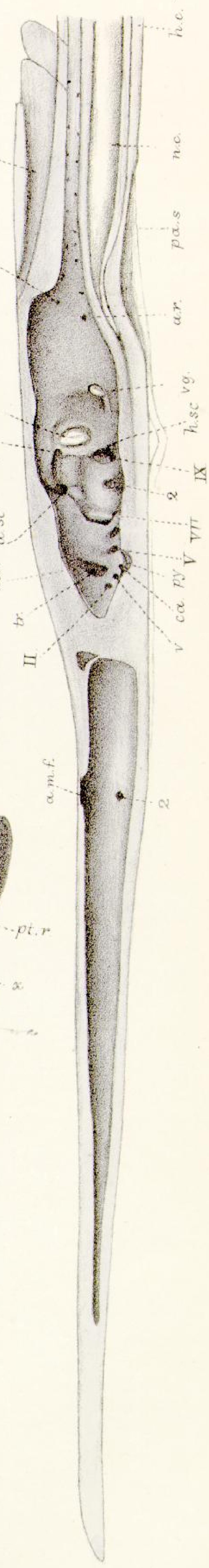

PLATE 56.

Fig. 4. View of ventral surface of cranium. Life size.

Fig. 5. View of upper surface of chondrocranium when the insisting parostoses have been removed. Life size.

a.m.f. Anterior median fontanelle.
f.g. *f*-shaped groove.
hy.g. Groove for head of hyomandibular.
p.f. Parietal foramen.
γ. Superior opening of first visceral cleft.
ϕ. Upper and posterior extremity of the oblique ridge.

Fig. 6. Vertical and longitudinal section. Reduced one-half.

B. Canal lying above spinal canal.
ar′. and *pr′.* Anterior and posterior root of first spinal nerve.
p.sc., *a.sc.*, *h.sc.* Foramina by which the anterior and posterior vertical and the horizontal semicircular canals leave the recess in which the membranous vestibular sac lies.
Ca. Carotid foramen.
Py. Pituitary fossa.
Fa. Foramen by which the facial nerve leaves the cranium.
h.c. Hæmal canal.
n.c. Notochord.

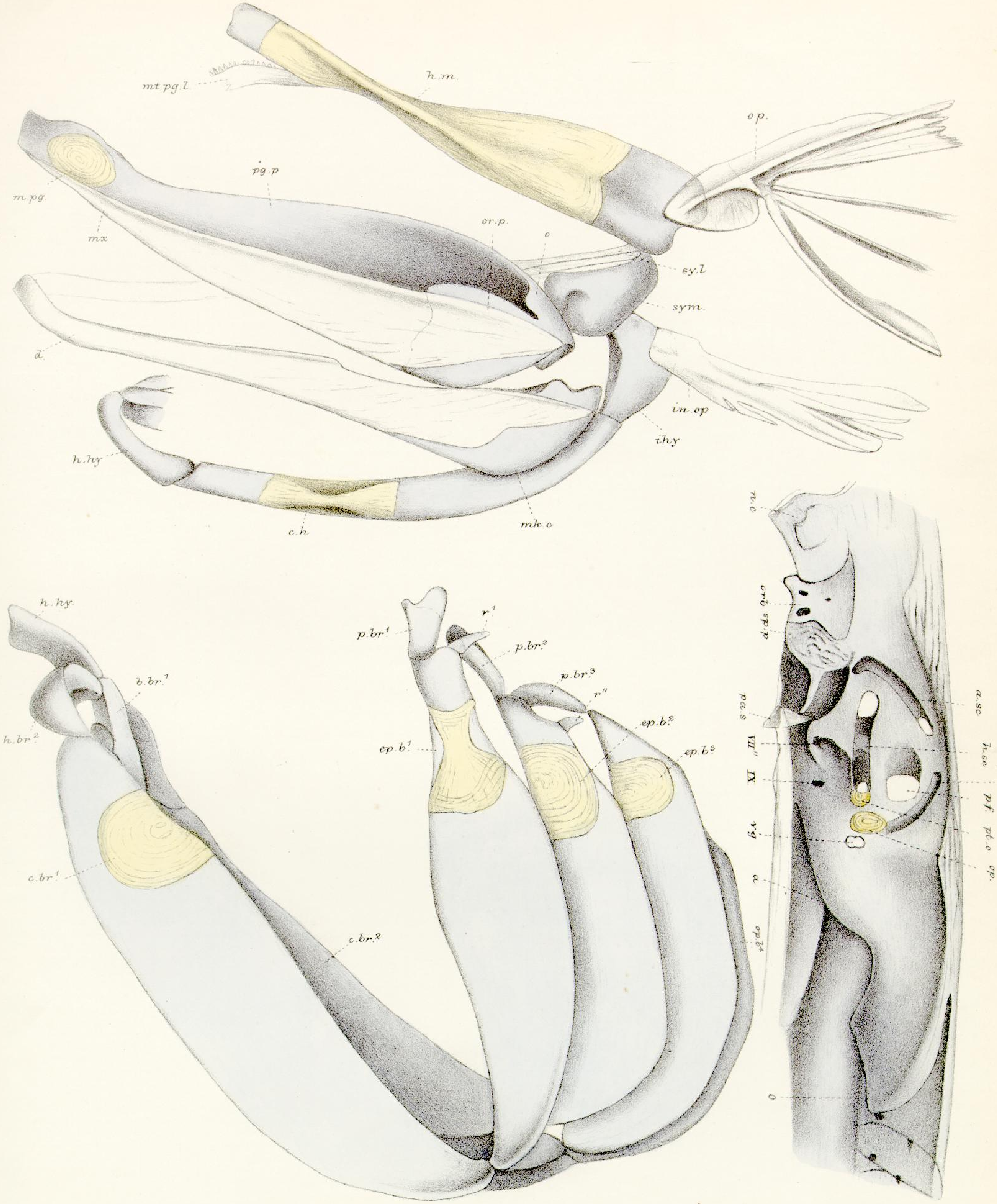

PLATE 57.

Fig. 7. Side view of the otic capsule, which has been dissected to show the semicircular canals and their relations to the parietal foramen, and pterotic and opisthotic bones. Natural size.

a. Oblique ridge, terminating above and behind in the decurrent flap of cartilage ϕ.

Fig. 8. Mandibular and hyoid arches, and opercular bones. Life size.

mt.pg.l. Metapterygoid ligament.

Fig. 9. Branchial arches.

r.r'. Rays attached to first and second epibranchials.