III. On the Structure and Development of the Skull in Sturgeons (Acipenser ruthenus and A. sturio).*

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[Plates 12-18.]

INTRODUCTION.

Several years ago the late Mr. William Lloyd procured for me from Hamburg seventeen young Sturgeons (Acipenser sturio); these were from 7 to 8 inches in length. Valuable as these specimens were, they were far too much developed for embryological purposes; and no pains were spared by me to obtain, if possible, newly-hatched embryos and small "fry" of this type.

More lately it was suggested to me by Mr. Balfour that I should write to Professor W. Salensky, of Kasan, who had been working at the development from the egg of Acipenser ruthenus, the small Sturgeon or "Sterlet."† My application to him was promptly and most kindly responded to, and in a short time I received a considerable number of newly-hatched and very small young of that species, ranging from 5½ to 14½ millims. in length. Half these were for Mr. Balfour, and the rest for me. His researches are embodied in that inestimable work, the second volume of his 'Comparative Embryology;' mine are here offered to the Society in the accustomed form.

I purposely refrain at present from working out the structure and development of the trunk and limbs (I have laboured at these regions, and shall be ready to resume that part of my work when this is done); but other workers are from time to time taking up those parts, and when once the cephalic skeleton is mastered what remains will be a comparatively easy task.

I am more anxious to be prepared for my own limited work by acquiring a thoroughly clear conception of the embryology of each type; in this my best helper is Mr. F. M. Balfour. Professor Huxley is, and always has been, my most valued critic and counsellor in all that relates to broad and philosophical views of animal life generally, and of the life of the Vertebrata in particular.

* The skull described in my last paper as that of Discoglossus pictus (Phil. Trans., 1881, Plate 20, figs. 7–11, p. 112) was prepared from a badly-preserved, half-grown Rana esculenta. I am indebted for this correction, and for a genuine Discoglossus, to M. Boulenger.

† This species rarely exceeds the length of 3 feet ( Günther, 'Study of Fishes,' p. 361).
The following is a list of the works and memoirs that have been helpful to me in this present piece of work:—

**Balfour, F. M.**
1. 'Elasmobranch Fishes.' London: 1878.

**Bridge, Professor T. W.**

**Gegenbaur, Dr. Carl.**
1. 'Untersuchungen zur vergleichenden Anatomie der Wirbelthiere.' (Drittes Heft: Das Kopfskelet der Selachier.) Leipzig: 1872.
2. 'Elements of Comparative Anatomy.' Translated by Jeffrey Bell. London: 1878.

**Günther, Dr. Albert.**
2. 'Study of Fishes.' Edinburgh: 1880.

**Hubrecht, Dr. A. A. W.** "Beitrag zur Kenntiss des Kopfskeletes der Holocephalen." Niederländisches Archiv für Zoologie, iii., taf. xvii., pp. 1–22.

**Huxley, T. H.**
2. 'Elements of Comparative Anatomy.' London: 1864.

**Knock, Professor.** "On the Presence of Teeth in Young Sturgeons." Bull. Mosc., 1871, No. 1, p. 281; taf. 6, fig. 7.

**Müller, Joh.** "Vergleichende Anatomie der Myxinoiden, der Cyclostomen, mit durchbohrtem Gaumen." Berlin: 1835.

**Parker, W. K.**
First Stage.—Newly-hatched embryos of Acipenser ruthenus from 5½ millims. to 6½ millims. in length.

The specimens figured by me (Plate 12, figs. 1–3) are rather smaller than the one figured by Mr. Balfour (‘Comp. Embryol.’ vol. ii., p. 88, fig. 53) which measured 7 millims. in total length, but his description may serve for mine, which were nearly as much developed as his slightly larger specimen.

After describing the development of the embryo, Mr. Balfour explains its peculiar outspread form in its unhatched condition (op. cit., p. 86, fig. 52), and says:—“The further changes which take place are, in the main, similar to those in other Ichthyopsida, but in some ways the appearance of the embryo is, as may be gathered from fig. 52, rather strange. This is mainly due to the fact that the embryo does not become folded off from the yolk in the manner usual in the Vertebrates; and as could be shown in the sequel, the relation of the yolk to the embryo is unlike that in any other known Vertebrate. The appearance of the embryo is thus something like that of an ordinary embryo slit open along the ventral side and then flattened out. Organs which properly belong to the ventral side appear in the lateral parts of the dorsal surface. Owing to the great forward extension of the yolk the heart (fig. 52, B) appears to be placed directly in front of the head.” Then, after describing the progress made in the development of the brain and organs of special sense, Mr. Balfour says:—“At the sides of the cephalic plate the visceral arches make their appearance, and in fig. 52, A and B, there are shown the mandibular (Md.), hyoid (Ha.), and first branchial (Br.) arches, with the hyo-mandibular (spiracle) and hyo-branchial clefts between them. They constitute peculiar concentric circles round the cephalic plate, their shape being due to the flattened form of the embryo already alluded to.” And then, further on (p. 88) our author says:—“Before hatching, the embryo has to
a small extent become folded off from the yolk both anteriorly and posteriorly; and has also become to some extent vertically compressed. As a result of these changes, the general form of its body becomes much more like that of an ordinary Teleostean embryo. The general features of the larva after hatching are illustrated by figs. 53, 54, and 55. Fig. 53 represents a larva of about 7 millims., and 54 a lateral and 55 a ventral view of a larva about 11 millims.* There are only a few points which call for special attention in the general form of the body. In the youngest larva figured [fig. 53, 7 millims. long; and see also Plate 12, figs. 1–3 of the present paper of somewhat younger larvae] "the ventral part of the hyomandibular cleft is already closed: the dorsal part of the cleft is destined to form the spiracle (sp.). The arch behind is the hyoid, on its posterior border is a membranous outgrowth, which will develop into the opercular membrane. In the older larvae a very rudimentary gill appears to be developed on the front walls of the spiracular cleft, but I have not succeeded in satisfying myself about its presence; and rows of gill papillae have appeared on the hyoid, and the true branchial arches (figs. 54 and 55, g)." [The mandibular gill, about which Mr. Balfour speaks doubtfully, is according to my observations a thickened mass of hypoblastic cells lining the front wall of the first or "spiracular" cleft. This mass is crescentic (Plate 12, figs. 2, 4, and 7, cl.), and is slightly grooved along its hinder margin; on each side of this groove the low ridges are imperfectly divided into little rounded masses, which appear to me to be, evidently, the rudiments of branchial papillae; at the lowest computation, this soft, tuberculate mass of cells is homologous with the tracts of cells which do develop into branchial papillae in the Elasmo-branchii.] "The biserially-arranged gill papillae of the true branchial arches are of considerable length" [see Plate 12, figs. 4–9], "and are not yet covered by the operculum, but they do not form elongated thread-like external gills like those of the Elasmo-branchii. The oral cavity is placed on the ventral side of the head; it has a more or less rhomboidal form. It soon however (fig. 55) becomes narrowed to a slit with projecting lips, which eventually becomes converted into the suctorial mouth of the adult. The most remarkable feature connected with the mouth is the development of provisional teeth (fig. 55) on both jaws. These teeth were first discovered by Knock (‘Die Beschr. d. Reise z. Wolga Behufs d. Sterlettfbruchtung,’ Bull. Soc. Nat., Moscow, 1871). They do not appear to be calcified, and might be supposed to be of the same nature as the horny teeth of the Lamprey. They are, however, developed like the teeth, as a deposit between a papilla of subepidermic tissue and an epidermic cap. The substance of which they are formed corresponds morphologically to the enamel of ordinary teeth. As they grow they pierce the epidermis and form hollow spine-like structures with a central axis filled with subepidermic mesoblastic cells. They dis-

* These do not correspond precisely to the specimens worked out by me, and of which I also have given figures illustrating the outward form. My first Stage includes larvae from $5\frac{1}{2}$ millims. to $6\frac{1}{4}$ millims. in total length; Stage two, $8\frac{3}{4}$ millims. to $9\frac{1}{2}$ millims.; and Stage three, $13\frac{1}{2}$ millims. to $14\frac{1}{2}$ millims. The largest larva of this species in those sent to me was $14\frac{1}{2}$ millims. ($1\frac{1}{4}$-ths of an inch) in total length.
appear after the third month of larval life. In front of the mouth two pairs of papillae grow out, which appear to be of the same nature as the papillae in the suctorial disc of Lepidosteus (figs. 54, 55, p. 89). They are very short in the embryo, represented in fig. 53. Soon, however, they grow in length (figs. 54 and 55, st.)” [Plate 12, figs. 4, 5, 7, 9], “and it is” [more than] “probable that they become the barbels, since both sets of structures occupy a precisely similar position.”

“The openings of the nasal pits are at first single, but the opening of each becomes gradually divided into two by the growth of a flap on the outer side (fig. 54, ol.)” [Plate 12, figs. 4, 7, 9, ol.]. “It is probable that the two openings of each nasal sack, so established in these and in other Fishes, correspond to the external and internal nares of the higher Vertebrata. At the time of hatching there is a continuous dorso-ventral fin” [Plate 12, figs. 1, 2], “which by atrophy in some parts, and hypertrophy in other parts, gives rise to all the impaired fins of the adult, except the first dorsal and the abdominal. The caudal part of the fin is at first symmetrical, and the heterocereal tail is produced by the special growth of the ventral part of the fin combined with an atrophy of the dorsal part.”

Referring the reader to Mr. Balfour’s work and to my own plates, I shall now simply describe the figures of the general form of the first stage, and then those of the second and third, in which also will be given a detailed account of their skeletal structures.

The fourth, fifth and sixth stages will be of the other species (A. sturio), and that in a thoroughly metamorphosed condition.

The smallest of my specimens (5½ millims. long, Plate 12, fig. 1) is intermediate between figs. 52 and 53 of Mr. Balfour (op. cit., pp. 87, 88); the original of his fig. 52 (A and B), may be found in Professor Salensky’s Russian work (plate 7, figs. 56 and 58), whilst his fig. 53 is only slightly larger than my second specimen (Plate 12, figs. 2 and 3).

In the smallest specimen, scarcely hatched at the time when it was put into the spirits, the large hind-brain (C₃.) and the lesser mid- and fore-brain (C²., C¹.) are seen arranged in an accurate series. The auditory sac (au.) is below and behind the wide, front part of the hind-brain, the eye (e.) below and between the fore- and hind-brain, and the olfactory sac (ol.) on the side of and below the fore-brain, in front of the eye. The mouth (m.) is a considerable rhomboidal space on the ventral aspect of the head, and behind it we see three folds, two clefts, and a general hollow space behind the third fold. These folds are the rudiments of the mandible, hyoid, and first branchial (mn., hy., br¹.), the clefts are the hyomandibular (cl₁.) and the hyo-branchial (cl₂.), and the fossa behind leads to the tissues that are preparing to form the rest of the branchial arches with their intervening clefts. The last third of the spinal region is

* I am glad to be able to give, and the reader will not be sorry to have, an account of these early larvae in Mr. Balfour’s own words. Of course I have been over the same ground, but my work has been made much easier by my friend’s kindness in sending me his proofs as soon as they were in type.
behind the anus (an.); it is the tail, and the intestinal opening is but a small distance behind the huge enlargement caused by the yolk-mass; that mass is three-fifths the length of the embryo. A vertical line drawn through the hind-brain and eye-ball would bisect a special enlargement in front of the yolk-mass. This enlargement, caused by the heart (h.), would be partly in front of that line, and looking at the embryo from the upper end of the line we should see the heart lying in front of the head.

The liver (l.) would be behind the lower end of the line, for most of the yolk-mass which is included in the rudimentary stomach lies in front of the liver; contrary to what takes place in the Lamprey, Frog, Elasmobranch, and the Amniota (Balfour, op. cit., p. 90, fig. 56). According to that excellent observer "the peculiar flattening out of the embryo on the yolk is due to the mode in which the yolk becomes enveloped by the hypoblast" (p. 91).

In an embryo more developed, but slightly smaller (Plate 12, figs. 2, 3, 6½ millims. long) than that figured by Mr. Balfour (his fig. 53 was 7 millims. long), the yolk-mass is only one-third the length of the embryo—in the last it was half as long—and the tail is now also about one-third the length of the whole larva. The head is now fairly free from the yolk-mass, at least as far as to the hyoid fold (hy.), but the heart (h.) is a very short distance behind the mouth (m.), and the end of the intestine (an.) is seen to be three times as far from the yolk-mass (y.). The tail is at present perfectly diphyceral; the notochord running along the middle of the upturned tail, and the azygous fin is equally above and below the axis.

The mouth (fig. 3, m.) is a crescentic slit, with a small anterior bay in the middle of its anterior convex margin, and with a definite labial rim. In front of the oral opening and under the fore-brain (C.), behind a transverse ridge that passes from side to side parallel with the mouth, there are two pairs of pupiform enlargements with their narrow ends behind, and those of each pair approximated; these are the rudiments of the barbels (bh.). There are four visceral folds with their clefts, the two anterior larger folds being the mandibular and the hyoid; from the latter a free edge is growing, the opercular fold (op.); between the two bars the first (or hyomandibular) cleft (cl.1.) is closed ventrally, already, its permanent uppermost part will be the spiracle. The convex front lip of that limited cleft is thickening inside, and tends to produce a mandibular gill. The nasal sac (ol.) is still a shallow pouch with a thickened rim, the outer coats of the eye (e.) are closing over the lens, and the auditory sac (au.) is a smallish oval mass showing no evident involution.

In this larger embryo the basis-cranii and visceral arches are still composed of "embryonic cartilage;" these skeletal structures can be better studied in somewhat more advanced larvae.
Second Stage.—Larva of Acipenser ruthenus, from 8½ to 9½ millims. in length.

The larvae at this stage have a very Selachian appearance (Plate 12, figs. 4-8); altogether they have made a very great advance in development since the last stage: I shall describe first the external form, then a dissection of the visceral arches, and after that a series of transverse sections.

The azygous fins are beginning to be subdivided (fig. 7); now, the axis (notochord) turns downwards behind, but the tail is still diphyercercal; it has become almost as long as the trunk, measuring from the anal aperture (an.), so that the post-anal region is very much longer, relatively, than in the last stage (fig. 2). The azygous fin is more definite along the trunk, almost reaching as a crest to the head, and the pectoral fins (p.f.) that then were at most mere thickenings of the tissue, are now well-developed, free, auriform paddles.

The yolk-mass (st.) makes only half the bulging it did: it is now quite portable; the intestine (in., an.) is now seen as a definite ventral cavity behind the stomach and yolk, and is nearly as long as the wide part in front.

The heart (figs. 5 and 7, h.) is now fairly behind the operculum (op.), but is still seen from the outside as a double swelling.

The mesocephalic flexure is less, and the various parts of the brain (C1., C2., C3.) are very visible through the diaphanous membrano-cranium.* So also the auditory organs show clearly through the skin, and the common tube of the anterior and posterior canals (anu., p.s.c.), and the single lesser tube forming the horizontal canal (h.s.c.), are very apparent without dissection.

The eye-ball (e.) is rapidly finishing and its socket is being formed, and there is a distinct suborbital ledge. The olfactory sac (ol.) is lateral and close to the eye, it has acquired a very definite superficial membranous capsule; this is sending downwards a triangular flap which tends to subdivide the opening.

The "barbels" (bb.) are now well formed, and look in the larger specimens of this stage like formidable tusks; they arise from a recess in front of the upper lip, which has over it a fold of the fore face, and in front of it, below the fore brain (Plate 12, fig. 5), there is between the olfactory sacs (ol.) a very remarkable concavity; it is nearly circular, is as large as one of the olfactory sacs, is almost as deep, and has in front of it a crescentic fold, and on each side a lateral lip-like margin. Its somewhat produced hind margin lies between the two inner barbels, and its lateral walls run up to those barbels. In the lesser larvae of this stage (figs. 4, 5, m.) the mouth is still somewhat rhomboidal, but in the larger (fig. 7) its edges come very near together. The lips are now thick and large, the front is emarginate, the hind lip has an apiculate lobe, at the mid-line, looking forward; each is armed with the small, clear, pointed teeth (t.).

* Through want of proper food these larvae soon began to starve. Moreover, the spirit in which they were preserved contracted their tissues; the figures purposely show this contracted appearance.
There are, now, seven cartilaginous arches on each side, the two first are large, the rest smaller; they are all out of sight, more or less, the operculum hiding the two first, and the gills those behind; the clefts also are largely hidden from view by these structures.

In the smaller specimens at this stage (fig. 4) the form of the two first arches can be seen through the skin, the pterygo-quadrate bar running within the upper lip, Meckel's cartilage within the lower jaw, and the hyoid arch (hy.) inside the fore part of the opercular fold (op.). The opercular fold of the mandible is very limited on account of the closing in of the ventral part of the first cleft (cl.), but its serial homology with the large next fold (op.) is manifest. Inside it is thickened by a mass of cells from the first hypoblastic pouch, and this mass, somewhat obscurely, shows on its surface two rows of short mammillate projections—arrested gill papillae.

But the next fold, with its lining, is greatly developed (Plate 12, figs. 4-7, op.), and its inner face is covered with rather long papillae, like those which grow freely from the proper branchial arches (br.). Membranous, at present, this free fold of the hyoid arch is destined to contain three ganoid scutes, the upper of which (the opercular) will be one of the largest of the huge plates developed in this fish.

The rich growth of simple longish papillae on the other arches hides them from view; these gills, however, are much shorter than those seen in the large embryos of Selachians.

When the skin and the gills are removed from the side of the head in one of the larger larvæ at this stage—9½ millims. in length—then the form of the newly chondrified bars is seen (Plate 13, fig. 6).

I have already remarked upon the Selachian appearance of the larvæ at this stage (Plate 12, fig. 7); a dissection, like the one under notice, displays much more than superficial Selachian characters. Even in the adult the Sturgeon has not made much advance towards the Teleostean culmination of the fish-type, but the dermal scutes have been largely dominated, in the head, by the cartilaginous endo-skeleton; and in the face, behind the mandible, we find many of the bars ensheathed in their own "ectostoses."

The hyostylic type of skull, which is not seen in the generalised forms, such as Notidanus and Cestracion, but is common to Skates and ordinary Sharks, is in the "Acipenseridae" carried to its uttermost pitch of perfection, and here, in this minute larva, recently hatched, and scarcely chondrified, the Selachian type of skull is over-passed, and at least two additional segments are seen on each side. These additional joints in the highly subdivided and modified primary hyoid bar are expressly for the purpose of throwing the mouth out far away from the skull; the jaws are suspended on an extremely hypertrophied upper hyoid segment.

This hypertrophy of the "epi-hyal" segment is correlated with the atrophy of the uppermost, or suspensorial part of the pier of the mandible, which pier, even in this early larva, is below the middle of the hyoid arch Plate (13, fig. 6, p.j.q., m.n., h.m., c.hy.).
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This is the more remarkable in a type that might have been expected to show something primitive in its visceral arches, seeing that it is only a *Chondrosteus Ganoid*, with a huge, permanently undivided notochord, and a totally unossified chondrocranium.

Even in the Salmon (Phil. Trans., 1873, Plates 1-3), the embryos of which are much larger and more tractable, I did find, as cartilage, the primitive facial bars; and their metamorphosis into the highly modified hyostylic type could be traced step by step; but this cannot be done in *Acipenser* nor in *Lepidosteus* (my next subject). In *Scyllium* (Zool. Trans., vol. x., plate 34) this was also possible; but in the Skates, *Raia* and *Pristiurus* (ibid., plates 35 and 39) the earliest tracts of true hyaline cartilage were, already, half metamorphosed, for all the uppermost segments (ibid., plate 35, fig. 4) were developed as distinct cartilages, although the remainder of each arch was continuous, and its segmentation could be traced afterwards.*

Here, in *Acipenser*, whilst the cartilage is still very soft, the segments of the highly subdivided hyoid arch are all apparent, although the branchial arches are continuous tracts (Plate 13, fig. 6); but their “pharyngo-branchial” segment—so very distinct in the embryo of the Skate—is already half severed from the main bar (Plate 13, fig. 4, p.br., e.br.).

The pier of the mandibular arch, instead of growing up to the basis cranii, is a falcate cartilage (the pterygo-quadrate, *pg.q.*), which lies half-way down the face, and passes forwards and downwards. It is flat, obliquely-placed, and somewhat uncinate in front; behind, it is thick and rounded, and forms a condyle which lies in the concavity of its own lower segment, the mandible (*mn.*). This segment is thick behind; in front of its condyloid depression it sends upwards a coronoid swelling, whilst, behind, it ends in a rounded angular process. The rest of the bar is rounded; it lessens towards its ventral end, and is curved the opposite way to the pterygo-quadrate.

The rounded quadrate region of the upper bar is attached by ligamentous fibres to the lower end of the hyoid pier; that pier is the hyomandibular (*hm.*), the lower, rounded end of which is being segmented off as the symplectic (*sy.*). The whole bar is a massive phalangiform cartilage, gently bent backwards, altogether running downwards and a little forwards, and articulated above by an oblong condyle, to the “tegmen tympani” of the ear-capsule, under the horizontal canal (*h.s.c.*). It is one-third larger than the pterygo-quadrate, but its own lower piece, the cerato-hyal, is somewhat less than the mandibular pier.

* In Selachians themselves, the best of all Fishes in which to study the development of these parts, it is next to impossible to maintain a consistent nomenclature of the elements of the visceral arches. In the Dog-fish (*Scyllium*, ibid., plates 37, 38) the hyomandibular is evidently the serial homologue of the epi-branchials; in the Skate (*Pristiurus*, ibid., plate 35) the uppermost part of all the arches is developed as a separate nucleus of cartilage, and the metapterygoid and hyomandibular naturally classify themselves with the succeeding pharyngo-branchials. Again, the subdivided hyoid pier of *Acipenser*, which also carries the mandibular apparatus, is not divided into a normal pharyngo- and epi-hyal, but the epi-hyal, apparently, is itself subdivided, and there is no pharyngo-hyal.
The cerato-hyal element is a flattish rod, pinched in the middle, and dilated at both ends; its upper end is articulated to the postero-inferior face of the rudimentary symplectic by means of a small intercalary nucleus of cartilage — the inter-hyal (i.hy.). The lower end of the bar is nearly segmented off as a short semi-oval hypo-hyal (h.hy.). The branchial arches (br.) are about half the size of the hyoid — supposing it to have been in one large bar; there are five of them, and they decrease in size from before, backwards. The top of each is semi-distinct from the rest as a pharyngo-branchial (p.br.); that part is turned inwards, the rest of the arch is curved outwards, and turns inwards and forwards, below, where it joins the basi-branchial bar (Plate 13, fig. 4, b.br.).

Second Stage (continued).—Transversely-vertical and vertical sections of the head of a larva of Acipenser ruthenus, 9½ millims. in length.

The transverse sections (Plate 12, figs. 1–3, and Plate 13, figs. 1–5) will further illustrate the structure of the visceral arches, and also show the state of the basis-cranii at this stage.

Section 1.—The first section (Plate 12, fig. 10) is through the fore-brain (C1.), and the fore part of the mid-brain (C2.), the eye-balls (e.), and the barbels (bb.); here the only cartilaginous tracts are the trabeculae (tr.), which are sub-oval in section, obliquely placed, and separated by a distance equal to their own width; they are sub-concave on their upper surface, where they lie under the thalamencephalon as it narrows to the infundibulum.

Section 2.—The rounded ends of the trabeculae are free for a very short distance in the extremely short head of this larva, which has at present no rudiment of the huge pre-cranial rostrum afterwards to be developed. In this section (Plate 12, fig. 11) the trabeculae are wider, flatter, and are in close contact with each other; they lie here under the infundibulum (C1.) which is covered now directly by the mid-brain (C2.). Here the fore part of the oral cavity is cut through, so that the front row of teeth (t.) are seen, and on each side the outer barbels (bb.) are just in view; this section is behind the eye-ball. Above the mouth two oval masses of cartilage, more solid than the trabeculae, are seen; these are the pterygo-quadrate bars (pg.q.) at their fore end.

Section 3.—The next (Plate 12, fig. 12) is close in front of the auditory capsules, through the widest part of the mid-brain (C2.) where it joins the hind-brain, in the middle of the mouth, and the huge Gasserian ganglia (V.), whose cerebral roots are brought into view. Here the trabeculae (tr.) are in close contact, are wider than in the last section, and they curve well round the base of the hind part of the infundibulum (inf.).

Here the pterygo-quadrate cartilages (pg.q.) are very solid and curved, and have a sharp edge lying over the "adductor mandibulae" muscle (ad.m.), (see also Salensky, op. cit., plate 18, fig. 165, ad.m.); these muscles lie outside the concave face of these oblique cartilages; the front teeth and lip are still seen. Above the front face of the auditory capsules (here, by mistake, lettered e), the auditory involutions (aq.v.) are seen.
Section 4.—The next slice (Plate 13, fig. 1) contains the hinder half of the auditory involution (aq.v.), and below it the auditory capsule (au.) is seen, in the region of the anterior canal; there is some cartilage in the infero-lateral part of the wall of the capsule. This is behind the mid-brain, and the hind-brain (see figs. 1–3, C3.) is very large; large masses of ganglionic cells are seen belonging to the 5th, 7th, and 8th nerves (V., VII., VIII.). Outside, the lip of the spiracle (clv.) is cut through, and below the brain the large notochord (nc.) is shown near its apex. This lies in and between the moieties of the investing mass (iv.), which are nearly square—just a little hollow above, and convex below. Below these parts the oral cavity is laid open; right and left of it the thinner hind part of the pterygo-quadrate (pg.q.) is severed, and, below, the teeth of the lower lip (t., l.l.).

Section 5.—Here the hinder part of the ganglionic mass belonging to the 7th and 8th nerves (Plate 13, fig. 2, VII., VIII.), and some fibres of their cerebral roots are cut through; the spiracle (clv.) is here laid open; above it a cartilaginous tract of the auditory wall is seen. The anterior and horizontal canals, and the vestibule (a.s.c., h.s.c., vb.) are laid open. The notochord (nc.) is enlarging, and is being enclosed in the square moieties of the investing mass (iv.) which lie somewhat under it. Below the mouth the mandibles (mk.) are laid bare throughout their entire length, on account of their almost directly transverse position, and over their articular hollow the articular knob (q.) of the pterygo-quadrate cartilage is shown in situ. The back of the lower lip (l.l.) is seen, whose toothed front face was shown in the last section.

Section 6.—Here, on each side of the narrowing hind-brain (Plate 13, fig. 3, C3.), the auditory capsules are cut through in their widest part, and both the arch and ampulla of the posterior canal (p.s.c.) are cut and laid open, as well as the deep saccular part of the vestibule (vb.). The infero-lateral shell of auditory cartilage is joining itself on to the more thin and outspread part of the investing mass (iv.—line too high); the notochord (nc.) is placed directly above the moieties of cartilage. The pharyngeal cavity is here very large, and in its walls we see the large, massive, arcuate epi-hyal element, undergoing segmentation into a long hyo-mandibular and a short symplectic piece (hm., sy.). Here the directly transverse position of the parts gives, in one section, the whole of the hyoid series, for the symplectic is seen to be followed, lower down, by the little inter-hyal (i.hy.), and that by the long cerato-hyal (c.hy.), which is giving off from its sub-triangular end the short hypo-hyal (h.hy.). This is the front face of the section, and behind and within the hyoid we see the lower half of the first branchial arch and the fore part of the basi-branchial bar (c.br.). The branchial arch, like the hyoid, is becoming subdivided below, to form the hypo-branchial. The front part of the ganglionic mass of cells for the 9th and 10th nerves (IX., X.) is cut across.

Section 7.—These most successful and illustrative sections* display all that is sought for; here (Plate 13, fig. 4), on each side of the narrowing hind-brain (C3.), the

* The sections were made by my son Mr. W. N. Parker.
notochord has become suddenly twice as wide as in the last, and it has now gained a lower position; the investing mass (iv.) is horn-shaped in section, and the base of each "horn" sits on the supero-lateral face of the huge notochord. The back wall of the auditory capsule (au.) is cartilaginous, and at this part is some distance from the basal plate (iv.); in that interspace the ganglion of the vagus (X.) is shown.

Here, happily, another visceral arch, the second branchial (p.br., e.br², e.br°, b.br.) is exposed in one slice; the segments are only indicated by the crowding of cells at the line where segmentation will take place. Within and behind the second branchial arch the third (e.br^3.) is partly seen, and the large, simple gills (g.) are shown fringing the folds of the section, below; they are clavate, because of the loop of the simple capillary vessel within.

Section 8.—Behind the ear-capsules the notochord has a diameter only two-fifths less than that of the hind-brain (Plate 13, fig. 5, nc., C^3.); the investing mass (iv.) embraces it more below, and is rising, right and left, so as to form the lower half of the occipital arch (e.o.). Behind the gills, under the narrowed pharynx, the yolk-mass is now seen.

A vertical section of the head in one of the larger larvae of this stage (9½ millims. long; Plate 14, fig. 1) shows the low position of all the parts of the fore-brain (C^1., C^1°., inf.), the forward position of the mid-brain (C^2.) and the huge size of the hind-brain (C^3.). The cavity of the fold of the mid-brain runs equally forwards and upwards, and the infundibulum (inf.) looks backwards and is quite distinct from the pituitary rudiment (py). The notochord (nc.) nearly reaches the latter, it is very large, arcuate, and bent downwards in front, showing no disposition to enter the fold of the mid-brain in the "post-clinoid" region. Two of the barbels (bb.) are seen to the right of the mid-line, and behind these we see the thick upper lip (u.l.) bounding the mouth (m.), which opens directly below the pituitary rudiment. It is a rather narrow passage, and has in its hinder boundary the thick lower lip (l.l.); in this the mandible (mk.) is seen at its ventral end, and the fore end of the pterygo-quadrate cartilage (pq.q.) is seen in the upper lip; these cartilages lie a little to the right of the section, which is exactly in the middle. In the pharynx, above and behind the oral chink, the first three clefts (c^1−3.) come into view, below these part of the yolk (y.), and in front of the yolk the heart (h.).

Third Stage.—Larvae of Acipenser ruthenus from 13½ millims. to 14½ millims. in total length.

Amongst the more advanced larvae of this Fish only one reached the length of 14½ millims., or 7½ of an inch; the next in size were 1 millim. shorter. One of these latter was made into horizontal sections, and others were dissected; the unique specimen was made into vertically-transverse sections.

The external appearance of these, next in size to the last, viz., 13½ millims., is extremely Selachian (Plate 12, fig. 9, and Plate 13, figs. 8, 9). The tail is more than
two-fifths of the whole length, the long arched notochord is ascending towards the upper part of the continuous azygous crest, and three-fifths of the caudal part of the vertical fin, above and below, is being marked off, ready to form the proper heterocercal tail-fin; the narrow crest above develops the "fulcra," and the wider part below the emarginate lobe. The high crest in front of the constriction becomes the backwardly-placed dorsal fin, and the deep crest, below, the anal fin; the ventral fins (v.f.) have a rudiment on each side as a thickening of the mesoblast of the abdominal wall close in front of the vent (an.); the pectoral fins (p.f.) are large and reniform. The region of the stomach still contains enough yolk to give it a swollen appearance; the intestinal region (in.) is narrow. The regions of the brain are still clearly seen from the outside; the eye ball (e.) is nearly perfect; the auditory capsules (au.) are seen as relatively small oval swellings.

The nasal capsules (ol.) have their opening almost subdivided into two by the descending flap. The suborbital fold of the face over the barbels is now large, and they (bb.) are long and finger-like. The lips (u.l., l.l.) are now thick and rounded; the upper is emarginate in the middle, and the lower has a medium lobe; the teeth (t.) are now inside the lips. The spiracle is now a very small triangular hole under the auditory capsule (Plate 12, fig. 9, ol.) ; the operculum (op.) although very large and extensive does not cover the copious growth of young gills.

Dissections of the cranio-facial skeleton of a specimen 13½ millims. long show, already, a well chondrified framework. The basis cranii, as seen from above (Plate 14, fig. 4), shows a structure very similar to that of an embryo of Scyllium canicula 1½ inch long (see Zool. Trans., vol. x., plate 35, fig. 6), or more than twice as long as this embryo Sterlet.

The cartilage investing the notochord (Plate 14, fig. 4, iv., nc.) is continued from the spinal into the cranial region with scarcely any change of form and consistence, a state of things quite like what I have found in the Selachians (op. cit., plate 35, figs. 3, 5). In my preparation four pairs of spinal nerves were seen emerging behind the glosso-pharyngeal and vagus (Plate 14, fig. 4, sp.ni-.x., X., IX.). The bands of cartilage, whose size and form will be further shown in the sections (Plates 14 and 15) are confluent above for a short distance with the auditory capsules (iv., au.) close behind the post-auditory nerves (IX., X.). In front of these conjugations there is a large open space, the "meatus internus" (VIII.), between the cartilage of the capsule and that of the skull floor; the latter widens a little in front of the meatus, then narrows a little to form the inner margin of the foramen ovale; outside this notch we see the huge Gasserian ganglion (V.). The investing mass then widens a little, and ascends a little; this wider ascending part is the "posterior clinoid" wall (p.cl.), and in it the notochord ends as a small rounded knob.

As in Scyllium (op. cit., plate 35, fig. 6) the bands of cartilage then dip considerably, and these prochordal continuations (tr.) of the parachordal tracts, are wider than the roots they spring from. Instead of being wide apart, as in the Salmon, in Lepi-
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doesteus, and in many types, they are really continuous under the pituitary body, as in Scyllium and Raia, forming a complete floor to the skull for some distance in front of the notochord and the post-clinoid wall; but this part has a small fontanelle immediately below the pituitary body (see fig. 1, py.). Opposite the optic nerves they part for a short distance, nearly meet again, and then diverge as two very short out-turned horns, the tips of which are the rudiments of the cornua trabeculae (c.tr.). Between the Gasserian ganglon and the optic nerve (V., e.) the trabeculae grow upwards, forming the rudiment of the alisphenoid (al.s.); the walls and roof, however, will be best studied in the sections.

In front of the eye-balls (e.), between them and the olfactory sacs (ol.), there is a definite antorbital cartilage growing outwards and a little forwards from the trabecula; this is the ethmo-palatine (e.p.a.), a familiar element, which, here, is only semi-segmented from the trabecula. In Skates, as in Urodeles and Teleostei, it is distinct; but in Batrachia and Sharks it is not; it is well seen as a "process" in Notidanus (Heptanchus and Hexanchus, see Gegenbaur's 'Selachians,' plate 1, and also in embryos of Scyllium, T. Z. S., vol. 10, plate 37, fig. 1, a.o.). Here, it helps to form the back wall of the crypt in which the olfactory sac (ol.) is lodged; in these Fishes, as in Lepidosteus and the Teleostei, there is no distinct "paraneural" cartilage for the nasal pouch.

Leaving the walls and roof of the skull, until I come to the sections, I shall now describe the visceral arches, which are greatly developed since the last stage.

In a side view of these parts (Plate 13, fig. 11) I have shown the arches relative to the other cephalic structures, which are left in outline to give prominence to the view of the arches themselves.

In another figure (Plate 13, fig. 12) the arches are shown as seen from above, and in a third (Plate 14, fig. 5) they are shown as seen from below. The hyoid arch is twice as large as the others, and has undergone most segmentation and specialization; the branchial arches decrease in size and in the amount of their segmentation, from before, backwards.

The proper pedicle of the mandibular arch, in this extremely hyostylic type, is not only absent, but the stunted and forwardly projecting "pier" is much further from the normal point of attachment—under the outgoing fifth nerve—than in any of the Selachians. Each of these pterygo-quadrate bars (py.q.) is a curved plate of cartilage, thick and bent forwards in its articular region, where it grows out over the temporal muscle, somewhat, to form the rudiment of the "orbitar process," and flat as it widens out in its pterygoid region.

The right and left plates meet each other for some distance in front, a notch separating their round ends; they are gently convex, above, and gently concave, below. These bars reach as far forwards as the antorbital region, but are embedded in the very loosely attached palatal skin, and are thus only slightly connected with the basis cranii. In the angle formed by their convergence a pyriform wedge of somewhat
newer cartilage (mt.pg') has made its appearance since the last stage; this is, as far as
I know, an unique structure, and but for this stage I should have suspected that this
keystone piece had been formed by the fusion of a right and left nucleus of cartilage.
Others form round it afterwards, but this is the first, as it is also the most important,
morphologically, of the pieces that form the hind palate of the Sturgeon.

It would not have been difficult to have dealt with the paired pieces that appear
afterwards (Plate 16, figs. 5 and 6), as they are manifestly the counterparts of the
single or multiple "metapterygoid" cartilages of the Rays. In Torpedo (Gegenbaur's
'Selachians,' plate 13, fig. 3, and plate 20, fig. 1, Kr., a, b,*) there are four of these
cartilages on each side, but as a rule there is only one in that group, where it is a
true metapterygoid segment of the pier, and not a mere "ray," as in the Shark. In
Carinate Birds, where the skeleton reaches the utmost limits of specialization, remnants
of Ichthyopsidan palatal cartilages reappear—ethmo-palatine, post-palatine, &c.; and
in the Woodpeckers ("Picidae") the palatine membrane bones are joined together under
the basis cranii by an ossified cartilage, the medio-palatine (Trans. Linn. Soc., second
series, "Zoology," vol. i., plates 1–5).*

Muller simply calls the whole compound plate of the adult Acipenser ruthenus
(op. cit., plate 9, fig. 71, A, B) "unpaariger Gaumenknorpel," and the pterygo-
quadrate bars "paariger Gaumenknorpel," so that the interpretation of these parts is
left open. I shall merely, for the present, classify this plate with the free cartilages of
the "Raëdæ," and call the median piece the "azygous metapterygoid" (mt.pg');
the later pieces, right and left, will simply be called "paired metapterygoid segments"
(mt.pg'). In the adult (Plate 18, fig. 4) Mr. Howes finds a row of four more much
smaller segments along the mid line, in front of the main piece.†

The mandibles (mn., mk.) are about as long as the upper bars, but after forming a
shallow articular cavity on their thick upper end they become rounded rods, and their
position is almost transverse, as these dissections, and the transverse sections (Plate 15,
fig. 3, mk.) demonstrate; they do not quite meet in the middle, at present.

The hyoid arch has five segments in it on each side, but, like the mandible, no basal
segment below. The uppermost piece, the hyomandibular (Plate 13, figs. 11, 12, hm.)
is by far the largest element in the whole series of arches; above, it is articulated by
an oval condyle to the under surface of the pterotic ridge, under the horizontal canal
("tegmen tympani"), and below by a cylindroidal condyle to the symplectic (sy.).

* The median cartilage seen in the "Myxinoids" (Muller, "Myxinoids," plate 3, figs. 2–5, U), the
"Gaumenplatte"—which partially unites with the trabecula in the adult Bdellostoma and Myxine, and
early and totally in Petromyzon, is not part of the palate, as Muller's term would suggest, and as I once
thought, but is, as Mr. Balfour showed me, the "intertrabecula"—i.e., its hinder or interorbital part.
† In the scanty living remnants of the "Chondrostean Ganoids," only the "Acipenseridae" show this
peculiar structure; the "Polyodontidae" show no trace of it (see Muller's 'Myxinoids,' plate 5, fig. 7,
there called Planirostra edentula; Traquair, 'Ganoid,Fishes of the British Carboniferous Formations,'
Part I, "Paleoniscidae," Paleont. Soc., 1877, plate 7, fig. 1; and Bridge, "On Polyodon folium," Phil.
Its form is like that of a phalangeal segment, it is curved backwards, gently, and has an enlargement there, above the middle, the rudiment of the "opercular process." Its axis is coincident with that of the symplectic and the mandible (sy., mn., mk.), together they form a crescentic series, passing downwards and gently forwards, and having the convex margin behind; they are bent inwards below (fig. 12). The curve forward, as well as downward, brings the lower end of the symplectic under the pituitary body; this cartilage (sy.) is only one-fourth the length of the upper piece (hm.), but it is as thick as its thickest part; it is scooped above for the hyomandibular, and rounded below, where it is tied, by ligaments, to the two elements of the first arch (pg.q., mn., mk.).

In the Teleostei the inter-hyal is articulated to the inside of the non-segmented cartilage uniting the hyo-mandibular and the symplectic; in the Sturgeon it is articulated to the inside of the distinct symplectic, rather below the middle—at least at this stage (Plate 13, fig. 11, i.hy.). The inter-hyal is a small piece of cartilage, wedge-shaped, with its narrow end upwards; its broad lower end articulates with the top of the cerato-hyal, which is bilobate above, the inter-hyal articulating with the larger upper lobe (fig. 12, i.hy., c.hy.).

The cerato-hyal is a thickish, somewhat sigmoid bar, it passes inwards and forwards and nearly meets its fellow of the opposite side; there is no basi-hyal, but a semi-oval segment is formed out of the ventral end of each cerato-hyal; this is the hypo-hyal (h.hy.).

The branchial arches (Plate 13, figs. 11, 12, and Plate 14, fig. 5) are larger than the lower part of the hyoid at first, but they lessen backwards, so that the last is only one-fourth as solid as the first. The first three develop a hypo-branchial segment (h.br.) exactly like the hypo-hyal, but larger. The inturned dorsal end of all but the last is segmented off as an epi-branchial (e.br.), and its apex becomes distinct as a small pharyngo-branchial (p.br.) in the first four arches.

The basi-branchial (h.hr.) is a thickish rod, rounded in front and compressed behind; it only carries the first three arches; the fourth and fifth meet below.

Bony scutes are now developing in the skin, and in the skin of the mouth and the mucous membrane of the palate and fauces several bony plates have appeared; all these are determinable.

In the upper and lower views (Plate 13, fig. 12, and Plate 14, fig. 5) these plates, most of which are dentigerous, are shown in their relation to the visceral arches and the largest of these bones; the maxillary and dentary—of one side—are shown separately (Plate 14, fig. 6, mx., d.). There is no determinable premaxillary, which like the nasals, and vomers, only exists as one or many of a great number of generalised scutes that are to be found in those respective regions. The maxillary (fig. 5, mx.) runs across and meets its fellow in front of the pterygo-quadrate (pg.q.); it is a long, subarcuate bar, with thickened edges, and carrying five or six sharp, recurved teeth on its anterior third; it is somewhat notched and bent in its hinder third. The dentary (d.) is almost
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exactly like it, but gently bent in the opposite direction; its teeth look a little forwards and fit in between those of the upper jaw.

The palatine (Plate 14, fig. 5, pa.) is a styloid tract of bone binding on the external edge of the broad fore part of the suspensorium (pg.q.); it is edentulous. The pterygoid (fig. 5, pg.) carries teeth; it is a thin plate of bone, which lies inside the hinder convex edge of the cartilage.

Over the rudimentary "orbitar process" of the suspensorium a small scale of bone is visible, just as when the squamosal is formed over the quadrate in the Amphibia;* this is the preopercular (p.op.). In the roof and sides of the pharynx inside the first branchial arch there are three pairs of small, arcuate, dentigerous scales of bone (Plate 13, fig. 12, and Plate 14, fig. 5); these are "upper pharyngeal bones." Clamping the hinder part of the hyomandibular, its rudimentary "opercular process," the opercular bone (op.) is seen; it is a convex shell, with spurs in front and a sharp round margin behind. These bones are evidently all mere parostoses; the "ectosteal" sheaths of the visceral arches have not appeared yet; the cranium never acquires any well-grafted bony plates.

Third Stage (continued).—Horizontal sections of one of the lesser larvae of Acipenser ruthenus, at this stage—13½ millims. long.

Section 1.—The uppermost of these sections (Plate 13, fig. 10) is through the hemispheres and the base of the mid-brain directly over the thalamencephalon (C1v. C1.), the eye-balls (e.), and the front and sides of the mouth (m.). The quadrate and pterygoid regions (q., pg.q.) are severed, being cut through where there is a depression above; moreover, the broad pterygoid plate is obliquely placed, and thus this horizontal section shows its thickness, but not its breadth. Between the hooked fore ends of these cartilages a newer tract, the lozenge-shaped azygous metapterygoid (figs. 10 and 11, mt.pg'), is seen. Behind the transversely oval quadrate region the lower part of the hyomandibular (hm.) is cut across; it is obliquely placed, and between the two sections of cartilage, on the outside, the lower part of the first cleft or spiracle (cl1.) is laid open. Part of the "adductor mandibulae" muscle (ad.m.) is seen outside the pterygo-quadrate bar, and the opercular fold of the first cleft is seen with its rough inner surface.

Section 2.—The next section, below the last, is through the whole length of the pterygo-quadrate bar (Plate 14, fig. 2, pg.q.), which is seen to be of almost uniform thickness, and of a sigmoid shape; the fore end is turned inwards, and the hind part outwards. Behind it the top of the articular region of the transverse mandible (mk.) was sliced off. The basis craniai (tr.) is cut through close in front of the post-pituitary wall and the notochord, where the trabeculae are completely confluent; the large infundibulum (inf.) is severed at its "neck" (see Plate 14, fig. 1, inf.). Here, this process of

* The squamosal of the Amphibia has a large descending preopercular process; but there is no separate preopercular bone, such as Fishes possess.
the brain is above and in front of the distinct pituitary body (fig. 1, \(py\)), and seems to be distinct from the fore-brain (\(C^1\)); this, however, is due to the manner in which it has been cut through on its projecting part. In this section the rudimentary hemispheres (\(C'^1\)) are cut through where they pass forward from the first cerebral vesicle (figs. 1 and 2, \(C^1\), \(C'^1\)). The small olfactory sacs (\(ol\)) are cut across; they lie outside the junction of the hemispheres with the thalamencephalon; the eye-balls (\(e\)) are cut through in the lower part.

**Section 3.**—The lowest section (Plate 14, fig. 3) is through the lower part of the curved head, and takes in the whole boundary of the mouth (\(m\); see also fig. 1). The olfactory capsules are removed, and the barbels (\(bb\)) are cut across at their root; each, at present, contains a pith of true cartilage. The fore part of the pterygopalatine and the quadrate region of the same (\(pg\), \(q\)) are shown as severed, and the latter is seen as a transverse process, bulging below to form the hinge of the jaw. Behind the mouth (\(m\)) the lower lip is seen with its teeth (\(l\), \(t\)), and in the substance of this visceral fold the whole length of the mandibles (\(mk\)) is shown, first thick, in the articular region, then slenderer, and again enlarging distally.

**Third Stage (continued).**—*Transversely vertical sections of the head of the largest larva of Acipenser ruthenus; 14\(\frac{1}{2}\) millims. long.*

**Section 1.**—The first section (Plate 14, fig. 7) is through the barbels (\(bb\)) at right angles to the horizontal section just described (fig. 3), and also to the axis of the downbent brain which is here developed into the rudimentary hemispheres (\(C'^2\)). The plane of this section would form an angle of 45° with the plane of a section taken vertically through the hind part of the hind-brain, or through the front of the yolk mass and heart in such a larva as is shown in a longitudinally-vertical section (Plate 14, fig. 1, \(C^3\), \(y\), \(h\)). That, however, was a younger larva, and the head in this had straightened a little.

The hemispheres (fig. 7, \(C'^2\)) are here shown to be, together, sub-oval in section, somewhat grooved above, and slightly protuberant below. The olfactory sacs (\(ol\)) have no roof in front, and their floor is formed by the ethmo-palatine cartilage (\(e.pa\)), which is distinct, in front, from the trabecula. The skin of the fore face, however, is developed into a valvular fold around the opening, and the mucous membrane is applied to the rising and falling of the structures that encompass it; there is no proper "paraneural" cartilage over the nasal capsule; in this, *Acipenser* agrees with *Lepidosteus* and the *Teleostei*, and differs from the Selachians, Cyclostomes, and Amphibia. Here the floor (\(e.pa\)) is flat and distinct, and there is a considerable space between it and the trabecula (\(tr\)) which is thick at its outer edge, and thins out towards its fellow of the opposite side, which it does not quite meet.

**Section 2.**—The next section (Plate 14, fig. 8) is through the widest part of the hemispheres (\(C'^2\)) which are nearly oval in the section, from side to side, the top being convex as well as the bottom; this latter part is, however, narrower than the upper.
Here the roots of the front teeth are cut through in the base of the upper lip (u.l., t.), and here the nasal pouch (ol.) has both roof and floor; the latter is continuous, now, with the trabecula (tr.) and bulges downwards, whilst the roof (s.ob.) is the fore end of a large tract of superorbital cartilage, which grows independently of the floor for some distance backwards—a very common thing in the Ichthyopsida.

This upper band is the lateral rudiment of the tegmen cranii, which in this type so soon covers in the great fontanelle and becomes so very massive; at present it is very similar to the palato-trabecular band (e.pa., tr.) below; here the trabeculae are wider apart than in the last section.

Section 3.—In this third pre-oral section (Plate 14, fig. 9) the projecting fore part of the mid-brain is seen to lie on the fore-brain (C2., C1.). This is through the back part of the olfactory pouch (ol.), which is becoming complicated; its palato-trabecular floor (e.pa., tr.) is, here, at its widest and most solid part, and the superorbital roof over the nasal sac is narrower, and is sharp at its outer edge; the roots of the front teeth are still in view (u.l., t.).

Section 4.—This is through the fore part of the eye-balls (Plate 14, fig. 10, e.); there is, here, a very solid lateral ethmoidal wall uniting the superorbital band and the trabecula (s.ob., tr.); the latter is losing its palatine extension, outwards, and the two plates are still a good distance apart beneath the fore-brain (C1.). Here the antorbital wall is cut through; it is membranous, at present.

Section 5.—In this section (Plate 14, fig. 11) the superorbital band (s.ob.) is simply a moiety of the tegmen cranii, for the projecting part is gone, and each band is creeping towards its fellow over the front of the mid-brain (C3.). So also, below, the trabeculae (tr.) have lost their palatine projection and they are creeping towards each other under the fore-brain (C1.); these latter are the larger plates, and are rather indented below in the middle. Opposite the eye-ball, the front third of which is cut across, there is a small tract of cartilage cut through; it is rounded above and sharp below; this is a tract which runs backwards as far as to the Gasserian ganglion (see Plate 15, figs. 2, 3, al.s., V.); it is orbito-sphenoidal here (o.s.), and alisphenoidal behind.

Section 6.—The lens of the eye (Plate 14, fig. 12, e.) is now reached, and the sclerotic is becoming cartilaginous; this section is very similar to the last, but the superorbital and orbito-sphenoidal bands (s.ob., o.s.) are thinner, and the trabeculae (tr.) are approximating; here the fold of the upper lip (u.l.) is cut through; it is seen to be folded off from the fore face, so that at this point it seems to be attached by a narrow isthmus; the next two figures will explain this (see also Plate 13, fig. 11).

Section 7.—This and the next (Plate 14, figs. 13, 14) are through the highest (or deepest) part of the brain, for here the bulging mid-brain (C3.) lies right over the fore-brain (C1.) in front of the infundibulum, which is cut through behind the second of these (Plate 14, fig. 1, inf.). Here the growing roof and walls of the orbital region of the skull are composed of three bands on each side (s.ob., o.s., o.s'), for over the emerging optic nerve a lower tract of cartilage has appeared, which is thick on its
inner face, growing into the sulcus between the swellings of the brain (C³, C¹). Here
the large optic foramen is a "fenestra," as in Frogs; its upper margin is formed by
this lower orbito-sphenoidal process (o.s.), and its lower edge by the trabecula (tr.);
this plate now touches its fellow of the opposite side. The upper lip (u.l.) is seen in
all its depth here, and the teeth (t.) are in full view; they are looked at from behind.

Section 8.—In this slice (Plate 14, fig. 14) the hinder half of the eye-ball and optic
nerve (e., II.) is seen, and the brain (C¹, C²) is here at its greatest bulk. The trabeculae
(tr.) are confluent, are thicker, and rise more at the sides; this is close in front of the
post-pituitary wall. The thick hind part of the orbito-sphenoid is now ready to
become alisphenoidal; its two parts are molten together, and the upper tract or super­
orbital (s.ob.) is now thickening as it approaches the auditory sac, ready to become the
postfrontal ("sphenotic") wing.

Close behind the upper lip (u.l.) two curved plates of cartilage are cut across;
these are the pterygo-quadrate bars (pg.q.), they are thick outside, and bevelled where
they meet.

Section 9.—In this section (Plate 15, fig. 1) the mid-brain (C²) is at its widest part
and overlies the infundibular end of the fore-brain (inf.), to which the pituitary body
(py.) is becoming attached; this is through the hinder part of the eye-balls (e.), and
close in front of the Gasserian ganglion (see fig. 2, V.).

The superorbital band is now the "sphenotic" (sp.o.); below it there is a large mem­
branous fenestra, and the short oval section of the narrow alisphenoidal band (al.s.).
The trabeculae (tr.) are apart again, where the pituitary body (py.) passes down; they
are altogether narrower here, and are grooved by vessels below. Here the pterygo­
quadrates (pg.q.) are cut through their middle part, and here, in the re-entering angle
behind their upper junction, a considerable wedge of cartilage is seen; this is the
azygous metapterygoid (mt.pg.); it has a pair of smaller pieces (mt.pg'). or lateral
metapterygoids attached to it; underneath this arched palate a number of teeth
(ptyergoid teeth) are seen.

Section 10.—This section (Plate 15, fig. 2) escapes both the eye-balls and ear-sacs, and
is through the body of the Gasserian ganglion (V.) and behind the pituitary body.
Here the trabeculae are confluent again in front of the low post-pituitary wall and the
end of the notochord. The sphenotic cartilage (sp.o.) is now ear-shaped in section,
convex outside, and has two sub-concave inner faces, one applied to the skull-wall and
one hanging down free. The pterygo-quadrates (pg.q.) are cut across a little in front
of the hinge of the lower jaw, they are acuminate-oval in section, with the point down­
wards. The lower lip with its teeth (l.l., t.) is here displayed, and the large "adductor
mandibulae" (ad.m.) is cut across its belly.

Section 11.—This (Plate 15, fig. 3) is the first of the auditory sections; the capsules
(au.) are severed in their antero-superior-angle, to which is attached the upper and
lower processes of the sphenotic (sp.o.). Through the wall of the capsules the
ampulla of the anterior canal (a.s.c.) is seen. The alisphenoid (al.s.) re-appears in this
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section, and is twice as large as in fig. 1; the Gasserian ganglion (V.) is here cut through behind, and lies within its proper boundaries, namely, with the alisphenoid (al.s.) above and the investing mass (iv.) below. This section is near the edge of the low post-clinoid wall (Plate 14, fig. 4, p.cl.) and the apex of the notochord (nc.), which here lies on the gently-scooped plate formed by fusion of the two parachordal bands (iv.). The pterygo-quadrate (pg.q., q.) is cut across close in front of the hinge, above and below, for it appears in two parts on account of its curve downwards to form the hinge. Meckel's cartilages also (mk.) are cut through close to the hinge; they are placed across, behind the mouth, are gently arcuate, and slowly lessen towards the meeting point. Outside the hinge, an angle of the symplectic (sy.) has been cut off.

Section 12.—This section, half of which was drawn (Plate 15, fig. 4) like the last, is a front view; here the cavity of the auditory capsule is laid open, with the ampulla and part of the arch of the anterior semicircular canal (a.s.c.). The sphenotic cartilage is still seen above and below this front part of the capsule; from the capsule to the investing mass is the foramen ovale with the ganglion of the 5th (V.), perhaps also part of the "ganglion geniculatum," which belongs to the facial and auditory nerves (Plate 14, fig. 4. VII., VIII.); the notochord (nc.) still lies on the investing mass (iv.). The hinge of the lower jaw is seen from its front face; the rod of the mandible (mk.) was in the last section, and this shows the articular region. The quadrate end of the pterygo-quadrate (q.c.) is seen in its full size with its orbitar process (or.p.); outside the hinge the symplectic (sy.) is shown, and the hypo-hyal and half the cerato-hyal (h.hy., c.hy.), and some of the teeth of the lower lip (t.), towards the mid line.

Section 13.—In this section (Plate 15, fig. 5) the hind-brain (C³.) is becoming narrower, and each auditory capsule under the arch of the anterior canal (a.s.c.), is cut through so as to expose the ampulla of the horizontal canal (h.s.c.); above, there is a rudimentary tegmen cranii, continuous with the capsule and the hind part of the "sphenotic" tract. At this part the capsule, as is the rule in Fishes, is open towards the hind-brain, and in the fissure, below, the "ganglion geniculatum" (VII., VIII.) is shown. Here the capsules and the basal plates (iv.) are quite confluent, and the notochord (nc.) divides the latter, lying down between the two halves. The front face of this section was figured; here the massive symplectic (sy.) is shown in its front half, and a considerable portion of the cerato-hyal (c.hy.); the hypo-hyals are lost in this section, they were shown in the last (fig. 4); the basi-branchial, the first hypo-branchials, and part of the first cerato-branchials (h.br¹., c.br¹.) are shown here as well as the "protractor hyomandibularis" muscle (pt., hm.). Teeth (t.) are seen as far down, inside the throat, as the first hypo-branchials.

Section 14.—In this section (Plate 15, fig. 6), the hind-brain (C³.) is much smaller, but the auditory capsules are at their widest part; they are continuous with the thickening parachordals, which enclose an enlarging notochord (iv., nc.). Below these parts and their underlying vessels, teeth (t.) are still seen. The super-occipital tegmen (s.o.) is growing inwards from the edge of the capsules, but these margins of the great fontanelle are nowhere closed in (from end to end) at present.
The arch of the anterior and horizontal canals, and the vestibule (a.s.c, h.s.c, vb) are laid open, and below, in the great open "meatus internus," the ganglion of the 7th and 8th nerves is still seen.

The hyomandibular (hm.) is here articulated by its convex head with the concave surface of the auditory capsule, and looks like the proximal segment of a large limb joined to its own limb-girdle. This is correlated with the downgrowth of the mouth, whose own arch has been carried far away from its cranial attachment. Here we see the symplectic, inter-hyal, and proximal part of the cerato-hyal (sy., i.hy., c.hy.); and behind these, near the middle, the lower part of the first and second branchial arches (h.br¹, c.br², h.br², b.br.).

Section 15.—In this section (Plate 15, fig. 7) the posterior canal (p.s.c.) is laid open throughout its whole extent, and here the capsule (au.) is re-acquiring an inner wall. Below, it is joined to a very solid basal plate (iv.), right and left, the moieties of this plate clip the large notochord (nc.), which is only partly embraced by them.

Parts of the first and second branchial arches (p.br¹, c.br¹, c.br², c.br²) and some gill papillae come into view here.

Section 16.—In this view (Plate 15, fig. 8) the back wall of the auditory capsule (au.) behind the posterior canal is shown; here the massive basal plates (iv.) are growing upwards to form the occipital arch (e.o.), and are separated from the auditory capsules by a large chink. Here the 9th and 10th nerves (IX., X.) are seen growing from the hind-brain (C³), forming their ganglia and giving off their trunks. Part of the gill arches (br.) and their gills are shown on each side of the pharynx.

Section 17.—Here we see (Plate 15, fig. 9) that the occipital arch (e.o.) is imperfect above; below, each mass of cartilage (iv.) cleaves closely to the huge notochord (nc.) the arch is produced into the angular processes on each side that project from the auditory capsules (see fig. 13).

Fourth Stage.—Young Sturgeons (Acipenser sturio), 7 1/2 to 8 inches long.

In this stage the Fish is completely metamorphosed, and the only important change which takes place afterwards is immense increase in size, and the addition of certain bony centres, both parosteal and ectosteal.

I have had no intermediate sizes between Sterlets 7 lines long and Sturgeons 7 inches long, but in Lepidosteus, another Ganoid (the subject of my next paper), two instructive stages come in at this point, and make the interpretation of this lower type of skull easy.

In larval Lepidostei the size of my largest larval Sterlets, namely, about 15 millims., the azygous intertrabecula has already filled in the space between the trabeculae, in front; and in specimens already like the adult, and 1 inch long, the trabeculae have developed their cornua, and the intertrabecula has shot forwards as a long pre-cornual rostrum. At that stage the endocranium of Lepidosteus is extremely Acipenserine, and explains, and is explained by, the skull of this stage in the young Sturgeon.
A. Ectocranium of the young Sturgeon (Acipenser sturio).

In this stage there are scarcely any proper "parastoses" and very few "endostoses," but the head is well covered with "dermostoses" that are simply the ordinary Ganoid scutes (Plate 15, figs. 10-12), brought more or less into relation, both in form and in number, with the underlying endo-skeletal structures.

Of course, the homology of these scarcely altered superficial scutes with the special deep laminae of bone that are so completely dominated by the endocranium in higher types, is imperfect and partial. These scutes present us with too much or too little when we are looking for the normal, highly specialised "investing bones" of the higher types; their inner layer, only, can correspond with those bones, and that is but imperfectly related to the parts within. Moreover, it is only in certain regions that any strict comparison can be made: this is in those cases where some unusually large scute has starved out its neighbours and has become the roof or wall of some particular part of the skull or face. Nevertheless, for the sake of uniformity of language, I shall call that scute which more perfectly than any other covers the nasal capsule, the nasal (n'); the large plates over the hemispheres, the frontals (f'); those over the mid-brain, the parietals (p'); and those over the auditory ledge, the squamosals (sq').

In the face it will not be difficult to seize upon the true meaning of certain ichthyic bones, namely, the "operculars;" and the "splints" (parastoses) that are applied to the highly specialised pterygo-quadrate and mandibular apparatus will also, by comparison with like parts in other Ganoids, and in the Teleostei, be interpretable.

The round swollen head of the larva (Plate 12) is now changed into a long wedge-shaped recurved rostral structure (Plate 15, figs. 10-12), and this structure is invested now by solid ganoid plates in great number; but only certain of these can be pitched upon as deserving a special name.* The number of bones covering the snout is very great; none of these can be called "premaxillary," only one can even by courtesy be called "nasal" (figs. 10, 11, n'), whilst below (fig. 12) several bones contend for the name of "vomer." The eye is protected by supra-, post-, and sub-orbitals (s.ob., pt.ob., su.ob.); the post-orbitals run back and become temporal scutes, the chief of which is called the squamosal (sq'). A very fine scute lies over the opercular region and is the true opercular (op.); under it there are two rugged, squarish plates—these are the sub-opercular and inter-opercular (s.op., i.op.); the pre-opercular (Plate 16, fig. 1, p.op.), as in Lepidosteus, is a very small "parastosis," applied to the side of the quadrato region of the suspensorium.

The orbital rim and eye (fig. 10) are small; the nasal pouch has a small upper, and a large lower opening; these openings are obliquely placed, so that the upper is also the foremost space. These capsules keep close to the antorbital region; in Lepidosteus they are carried to the end of the long beak. Behind the main post-orbital, and at

* I must refer my readers to the views of those excellent "experts" whose works are referred to in the Bibliographical List, especially to those of Professors Huxley, Traquair, and Bridge.

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the antero-superior angle of the opercular, the small spiracle (cP.) is seen; inside the opercular the half-gill of the hyoid arch may be seen, transferred from its own arch, now required for suspensory purposes, and attached to the inner face of a specialised ganoid scute. The mouth and lips (fig. 12, m., u.l., l.l.) are now curiously modified, and this structure is extremely protusible; the opening is transverse, and crescentic when closed.

The barbels (figs. 10, 12, bb.) are long and slender, now; they have lost their cartilaginous pith.

I shall describe the oral parostoses with the cartilages to which they are attached.

**B. Endocranium of young Sturgeons from 7\(\frac{1}{4}\) to 8 inches long.**

When the superficial bones have been removed we find an extremely solid chondrocranium underneath (Plate 15, fig. 13, and Plate 16, figs. 1–4). In the last stage there was a continuous membranous fontanelle along the whole top of the head, the orbitosphenoidal region was partly membranous, right and left, a small fontanelle existed under the pituitary body, and an open notch in front between the trabeculae.

Now, the only membranous space is a small trilobate supraoccipital fontanelle (Plate 15, fig. 13, s.o., fo.), not over the proper brain cavity but in an extension of the chondrocranium over the fore part of the spinal region.

Everywhere there is the same intense hypertrophy of the hyaline cartilage, and in no part of the cranium, proper, nor in the auditory capsules, do true "ectosteal" plates graft themselves upon the cartilage—even in very old individuals; moreover there is no calcification of the surface-cartilage, such as is seen in the Selachians. Even now, in these young specimens, the actual size of the brain and brain-cavity is extremely small (Plate 16, fig. 2) in proportion to the size of the skull; which, measured to the end of the rostrum, is three times the length of the cranial cavity. Here we see the permanence of the early "mesocephalic flexure;" for besides the sudden loop formed by the mid-brain, represented now by the post-pituitary chink, which looks forwards, the solid ethmoidal region of the skull is bent gently, but steadily, downwards, before it rises to form the recurved rostrum. The orbits are very large, out of all proportion to the small, thick, cartilaginous sclerotics; the nasal capsules (ol.) are set in the sides of the hind part of the huge rostrum, the ethmo-palatine or antorbital wings of which are thick and twice swollen. The rostrum is composed of three tracts, answering to the three offshoots of cartilage that have grown so rapidly since the last stage from the end of the primary chondrocranial floor-bands—the short prochordal trabeculae. Seen from above (Plate 15, fig. 13) and in section (Plate 16, fig. 2, c.tr., i.tr.) the rostrum is convex at its edges, and gently concave in the middle; but below (Plate 16, figs. 3, 4) it is like a sagittate leaf—thick and succulent—with a very solid convex mid-rib and thickened margins; here the margins are the cornua trabeculae and the mid-rib the intertrabecula (c.tr., i.tr.). The deepest
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part of the skull is in the presphenoidal region, close behind the huge aliethmoidal and ethmo-palatine outgrowths; (compare in Plate 16, figs. 1-4, al.e., e.pa., tr., i.tr.).

Here the deep middle part is formed by the hinder intercalating part of the huge intertrabecula (i.tr.), and the thick suborbital ledges, close beneath the optic nerves (II.), are expansions of the trabeculae (tr.) behind their cornua (c.tr.). In the sectional view (Plate 16, fig. 2) a peninsula of cartilage is almost insulated, below, and the last two of the vomerine series (Plate 16, fig. 3) in front of the fore part of the parasphenoid (p.as.), behind, have crept into the chinks of the cartilaginous mass. A deep, rounded notch, right and left, separates the antorbital from the postorbital (sphenotic) masses of cartilage, which are thick, round, leafy plates turning their convex margin the one to the other (Plate 15, fig. 13; and Plate 16, figs. 1, 3, and 4, al.e., sp.o.).

Here, again, in front of and around the auditory capsules the cartilage has grown freely, yet not, at present, hiding the form of the imbedded labyrinths in the lateral and upper views (Plate 16, fig. 1, and Plate 15, fig. 13, a.s.c., h.s.c., p.s.c.); and here, in the midst of all this profusion of cartilage, there is an open "aqueduct" (a.q.v.) between the anterior and horizontal canals.*

The trilobate fontanelle has a cranio-spinal position (Plate 15, fig. 13, fo.), and behind it the cartilage runs, without division, along the spinal roof as a stout rounded process, whilst on each side there is a longer, arcuate, diverging process, growing from the epiotic and pterotic regions; the paired processes reach almost as far back as the branchial arches; they end over the fourth. Even the segmentation of the skull from the spine is absent, as it was in the larva (Plate 14, fig. 4); and the section (Plate 16, fig. 2, sp.n1-6.) shows the exit of the first six of the spinal nerves.

However we may interpret this continuity of the chondrocranium with the spine, it is a very important thing to note it fairly down. The general form of the chondrocranium as seen from above is like that of two broadly sagittate leaves, set end to end by their broad leaf-stalks—the narrower orbital region; but the hinder half, as we have seen, is trilobate, and not simple at its free end. The arched canals (Plate 15, fig. 13, a.s.c., h.s.c., p.s.c.) are midway between the sphenotic lobes and the roots of the paired cranio-spinal processes (c.s.p.), and the small aqueduct opens in the hollow formed by the arches. They project above the large lateral "eave" (Plate 16, fig. 1); to the front third of this outer projection the hyomandibular (hm.) is articulated by its convex condyle. Looked at laterally, the skull shows the 5th (V.) nerve emerging in front of the hyomandibular, the 7th (VII.) inside it, and the 9th and 10th (IX., X.) further back.

The hind part of the basis cranii is strongly under-floored by the huge parasphenoid (Plate 16, figs. 2 and 3, p.as.), in section (Plate 16, fig. 2) it is only seen as far back as the 2nd spinal nerve, but beneath (Plate 16, fig. 3) its forks are shown to pass far back as to about the 10th; behind the parasphenoid the neuro-central

* This passage, which I find in Siren lacertina, has been described and figured in Polyodon, by Bridge (Phil. Trans., 1878, Part 2, Plate 56, fig. 5, f.g., p.f., p. 699).
cartilages appear right and left of the notochord. That rod (**nc**) is invested with a thick mesoblastic sheath of true cartilage, which, as the sections show, is thoroughly confluent with the parachordals in the basis cranii. In front (Plate 16, fig. 2, **nc**, **p.cl., py.**), it runs up nearly to the pituitary space, but does not ascend into the post-clinoid wall—an arched and almost horizontal plate of cartilage, the **true organic end** of the skeletal axis; all the rest, to the end of the snout, is formed of special outgrowths from the fore end of the basal plates. The relative size and thickness of the various parts of the chondrocranium will be shown afterwards in the description of the sections.

C. **Visceral arches of a young Sturgeon 7 1/4 inches long.**

There is no **distinct** rudiment of any arch in front of the mandibular, with its extended and complex pterygo-quadrate "pier;" the rudiment of the ethmo-palatine cartilage only exists as an extension of the aliethmoidal mass (Plate 16, fig. 1, **a.le.**). The pterygo-quadrate plate (Plate 16, figs. 1, 4, 5, 6, **pg.q.**) lies in an almost horizontal plane, and at a very variable distance from the basis cranii. The right and left plates meet by their extensive straight upper edge; then they curve outwards and backwards; their fore margin is rounded, their inferior edge concave, and their hinder edge is sinuous and notched. Outside the rounded condyle (**q.**) there is a leafy growth, imperfectly adze-shaped, which passes outside the adductor mandibulae; this is the "orbitar process" (Plate 16, figs. 1, 7, **or.p.**). Three-fourths of their inner face is invested by the pterygoid bone (**pg.**), a thickish plate with a deep gap in its blade, in front; the front third of the cartilage is bare, and its hinder margin has suffered absorption—not direct ossification, through the pressure of the pterygoid bone. A sharp style of bone, with its broad end in front, lies along the concave antero-inferior margin; this is the palatine (**pa.**)—a mere parostosis.

A larger bone curves round the front of each plate, where the two sides meet—both bone and cartilage—and then runs backwards, outside the adductor mandibulae, and is attached to the outer face of the orbitar process; this is the maxillary (**mx.**) Mounted on the hind part of the maxillary, and at right angles with it, there is a little triangular bone, with its apex upwards; it binds against the ribbed outer edge of the quadrate region of the cartilage; this is the pre-opercular (**p.op.**), smaller, here, than in *Lepidosteus.*

The mandible (**mk**) is shorter than the forwardly extended pier, it is like that of a Tadpole, having a thick articular region, a hollow for the quadrate, a rounded angular process, and a short terete main rod; a flat dentary bone (**d.**) invests its outer surface, which has a similar outline to the rod.

The most remarkable part of this apparatus, however, is the **common compound** (tesselated) "metapterygoid" region. At first (Plate 13, fig. 10) the main middle piece, only, was present; then a right and left segment appeared (Plate 15, fig. 1); now (Plate 16, figs. 1, 5, 6, **mt.pg', mt.pg"**.) there are fifteen. These have a general
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symmetry, the large median piece being sub-oval and the large lateral pieces wedge-shaped; but the number of the lesser segments varies, and the outermost, on the left side, is only half separated. In front, the edge is turned downwards (Plate 16, fig. 6), and here a second median cartilage appears, with three lesser segments on the right, and two on the left side. The whole of this "unpaariger Gaumenknorpel" (MÜLLER) is a gently convexo-concave, two-winged structure, which finishes the hard roof of this remarkable tubular protractile mouth.

The uppermost segment of the hyoid arch (hm.) is nearly twice the height of the ascending, but arrested, quadrate region; it is the largest of five "internodes" in this double-sized, forked arch, with its double function. The head of the hyomandibular is rounded (Plate 15, fig. 13, and Plate 16, figs. 1, 5, hm.); it curves backwards, and sends from its lower two-thirds a large thick flange, the opercular process; this causes the width of the bar to be more than doubled. Its lower condyle is cylindroidal, and the concavity on the next joint answers to it, so that it is like the humero-ulnar joint of a Mammal. Just the neck of the bar is ringed with an ectosteal deposit. The next segment, or symplectic (sy.), is scarcely half the bulk and length of the last, and its shape is different; it is a phalangiform cartilage, hinged to the hyomandibular, above, tied by ligament to the quadrate and angle of the jaw, antero-inferiorly, and having a little concave facet inside its upper part for the inter-hyal (i.hy.), a very small subquadrate segment.

This small secondary suspensorium carries the lower part of the arch so that it lies inside the upper; it is composed of two segments, for the distal fifth is segmented off; the main piece is the phalangiform cerato-hyal (Plate 16, figs. 1, 4, 5, c.hy.). The middle third is ossified; the distinct piece at the end, the semi-oval hypo-hyal (h.hy.), is soft; they meet by their narrow rounded ends, without the intervention of a basi-hyal.

The rest of the arches—the five branchials (Plate 15, fig. 13, and Plate 16, figs. 1, 4, 5) —are very uniform, very solid, grooved on their outer faces for the branchial vessels, and are quite unossified at present, and at present they have only one common basal bar, the basi-branchial (b.br.), which does not reach the last arch. They form, below (Plate 16, fig. 4), a very regular series with the lower part of the hyoid arch; they are, in their lower part, larger than the cerato-hyal at first, and then lessen, backwards.

Only the first three have hypo-branchial segments (h.br.); these are larger than the hypo-hyal. The upper part of each arch is shorter than the lower; in the first four there is a single small ear-shaped pharyngo-branchial (p.br.); thus the last arch has only one piece on each side, and the last but one, three. The segmentation of the hyoid arch is thus seen to be very different from that of a typical branchial, which has no interbranchial piece, and the upper part of which is directly superimposed on the lower; moreover, I look upon the hyomandibular and symplectic as a divided epi-hyal, with no pharyngo-hyal, above.
D. *Transversely-vertical sections of the head of a young Sturgeon 8 inches in length.*

These sections show much clearer signs of the composition of the great ethmo-nasal tract than can be got from the outside views of dissected skulls; moreover, they display the curiously cancellated and burrowed condition of the very hard hyaline cartilage. There is generally some fatty tissue imbedding the vessels that run in these burrows and spaces.

*Section 1.*—The first of these (Plate 15, fig. 14) is through the end of the beak, and the "prenasal rostrum" or intertrabecula (*i.tr.*) is depressed or spindle-shaped in section; rough dermal bones are seen surrounding it.

*Section 2.*—In the next (Plate 15, fig. 15) the cornua trabeculae (*c.tr.*) are cut through at their fore end; they are depressed at this part, sub-concave above, rounded below, and attached by a narrow isthmus to the top of the intertrabecula (*i.tr.*) which is sub-triangular here, and dilated and convex below. A rounded chink separates these three pre-cranial elements almost to their roots. The dermal bones form a flat upper, a round lower surface, and a lobate side.

*Section 3.*—Here (Plate 15, fig. 16) the three elements have become fused together, but the burrowing vessels and the fatty tissue show the original line of union of the parts. The form of the triple rostrum is, above, concave at the middle, and convex at the sides; below, concave laterally, and convex at the middle.

The dermal covering takes the same form, but the sides are notched; here, as in the last, a sub-marginal groove, right and left, appears, below.

*Section 4.*—Here (Plate 16, fig. 8) the enlarging beak shows a more rounded cartilaginous pith, but is very similar to the last; this is more than half way to the nasal capsule, behind.

*Section 5.*—In this (Plate 16, fig. 9) the rostrum, close in front of the nasal capsules, has become multiangular; the cornua trabeculae (*c.tr.*) are again united merely by an isthmus to the intertrabecula mass; they are thick, almost bilobate, and descend obliquely; they are separated by a semicircular notch, laterally, from the middle part (*i.tr.*); below, also, a similar concavity is seen, right and left, but twice as large as those on the sides. Between the latter the intertrabecula is a rounded beam; above, it is concave, and on each side has a lateral angle which bounds the lateral notch. The bones outside carry out this ridged form; below, a thick squarish mass of bone is seen, which is one of the vomerine series (*v.*).

*Section 6.*—Here (Plate 16, fig. 10) the olfactory sacs (*ol.*) are cut through their middle, and here the angulation of the parts is intensified; the cornua trabeculae (*c.tr.*) are now large wings, pedate at their free ends, and are separated laterally from the intertrabecular mass (*i.tr.*) by a very large semi-circular notch, in which the nasal capsule lies. Here the intertrabecula forms a roof over the sac, right and left, and it is very hollow above; below it is burrowed by a vomerine scute (*v.*), and is becoming
narrower, and more like a distinct beam; here also the outer bones do but fringe and enlarge the section.

Section 7.—In this (Plate 16, fig. 11) section the antorbital wall is exposed, behind the nasal sacs; that wall is composed of the aliethmoids (al.e.) and the ethmo-palatines (e.pa.). Here the paired cartilages are the trabeculæ (tr.) for this section is behind the cornua; but the intertrabecula (i.tr.) is very large from top to bottom. The middle region of the intertrabecula is the perpendicular ethmoid (p.e.), on each side of which the olfactory nerves (I.) are escaping; its also above are becoming the superorbital bands (s.ob.), whilst below, its huge beam is burrowed by a vomerine bone (v).

Section 8.—In this section (Plate 16, fig. 12) the eye-ball (e.) is just caught, and the cranial cavity laid open at the olfactory foramina, with their nerves (I.); the rest is very similar to the last section; in both, dermal bones defend the sides of the face, and above, the frontal scute is cut through.

Section 9.—This (Plate 17, fig. 1) is through the middle of the orbit, where the superorbital band (s.ob.) narrows in; here the supercranial valley is very large and deep, and the section of the skull has the shape of an Ox's face. In this young specimen the chondrocranium is very massive, and the pyriform cavity for the hemispheres (C1a.) is only one-fourth as large as the section itself, which is widest below, and rather pinched in the middle. The skull, below the cranial cavity, is as deep as the cavity, and is burrowed, below, by the splintery fore end of the huge parasphenoid (pa.s.); the swelling cartilage on each side belongs to the trabeculae (tr.) the middle part to the intertrabecula (i.tr.). The orbital muscles (or.m.) are planted in chinks of the basal mass.

This section is in front of the mouth and through the front of the upper lip (u.l.); there is, here, a crescentic cavity, with the horns below.

Section 10.—In the next section (Plate 17, fig. 2) the small eye-ball is just missed, but the optic nerves (II.) are seen emerging from the brain (C1a.). Here the cavity is something like an hour-glass, being as wide below as above; the tegmen cranii (t.cr.) is twice as thick as in the last, and the basal mass (tr., i.tr.) only half as thick, for this is behind the lobes that envelop the parasphenoid (see Plate 16, figs. 1-4).

Here the superorbital bands are wider and more solid, and externally, a new plate of cartilage has come in, on each side from the coves of the hind skull; this is the sphenotic (post-frontal) lamina (sp.o.). The solid basal plate is grooved sub-laterally and in the middle, and the parasphenoid (pa.s.) fitting to these sinuosities is, in section, like a stretched bow.

Below the base of the skull there is a quantity of very lax tissue, permitting the greatest freedom to the movements of the protrusible oral apparatus, and below this we see the large arched mass of the "adductor mandibulae" muscle (ad.m.) on each side. Below the muscles, the fore part of the pterygo-quadrate cartilages (pq.q.) are cut through, and they are flanked by the maxillary and palatine bones (mx., pa.) the former outside, and the latter beneath.
The mouth is nearly closed, the upper and lower lips, as in the next section (u.l., l.l.), are seen with their rugae, but without their teeth, and in the lower lip the mandibles (mk.) are just brought into view.

The parietal scutes were cut through above, and post- and sub-orbitals were seen, at the sides, and below, but not figured.

Section 11.—In this section (Plate 17, fig. 3) the sphenotic lamina (sp.o.) is thicker, but is still separated by a notch from the tegmen cranii (t.c.r.); that part is thinner in the middle, and deeply concave. Here the cranial cavity has widened, for the section is close in front of the mid-brain. The section, now, is that of an Ox face with drooping horns, and the muzzle is now narrower around and under the infundibulum (inf.). On account of the very small size of the eye-ball (Plate 17, fig. 1, e.), four of these sections are between the eye and the ear; in this the orbital wall (o.s.), which is extremely thick, is twice scooped for the orbital muscles and the fatty masses that occupy the orbit—much too large for the eye-ball. Here the intertrabecula has died out, and the trabecule (tr.) have united directly with each other, and the plate thus formed has lost half the thickness seen in the last section (Plate 17, fig. 2, tr., i.tr.).

The primary form of the trabecule is still seen at the sides, below, and the whole of the basal plate is crenate, making the parasphenoid (pa.s.) assume an undulated form as it follows the risings and fallings of the cartilage. In this section the oral apparatus is cut through the middle, and the opening itself is crescentic below, with a notched upper outline; this is due to the projection right and left of the pterygoquadrate (pq.q.) and their investing bones, the palatines (pa., pg.).

Here, the cartilages covered by the large adductor muscles (ad.m.) are sigmoid in section, and besides the outer bones, the pterygoids (pg.) now show themselves, both as an inner and an outer section, being through their forks. The quadrato region, with its orbitar process (q., or.p.) is separate, now, and over it is the maxillary (mx.); to the quadrate the mandible (mk.) is articulated, it then passes almost directly inwards towards its fellow, which it does not quite meet; the dentary (d.) is seen flanking the Meckelian rod.

Section 12.—In this section (Plate 17, fig. 4) the cranial cavity is Y-shaped, and contains the front of the mid-brain above the fore-brain (C1.), with the infundibulum passing into the pituitary body (py.). Here, in front of the post-clinoid wall, the alisphenoidal region (al.s.) is extremely thick—twice as thick as the tegmen (t.c.r.) and the continuous sphenotic wings (sp.o.).

In this section the parts round the mouth are like those of the last, but the foremost azygous metapterygoid (mt.pg') comes into view, and the mandibles (mk.) are cut away, distally.

Section 13.—This (Plate 17, fig. 5) is through the middle of the mid-brain (C2.), and the back of the pituitary body (py.). The post-clinoid wall, which is an oblique shelf running forwards and a little upwards (Plate 16, fig. 2, p.cl.), is here cut through obliquely so as to appear thicker than it is actually. This section seems to show
the pituitary body as lying in a separate and very solid box, for the rest of the skull is quite distinct from it, above. This arises from the fact that the foramina ovalia are here, with the trigeminal nerves (V.); the alisphenoidal wall, the roof, and the thickened sphenotics are seen in the upper part of the section. The parasphenoid (pa.s.) curls round the flatter base, the parietal (pg. by mistake for p'.) and post-orbital scutes were cut through. Below, the adductor mandibulae muscles (ad.m.), the pterygoid cartilages and bones (pg.q., pg. q., read pg.) are severed, and the latter are in one piece, for this is behind their great notch. The smaller azygous metapterygoid (mt.pg'.) is seen; the extreme angle of the quadrate (q.c.) ; and the hinge and part of the shaft of the mandible (mk.) through the dentary and the pre-opercular bones.

**Section 14.**—Here (Plate 16, fig. 6) the breach in the lower part of the walls is repaired, for this is behind the foramina ovalia, and through the fore part of the auditory capsules (au.); the ampulla and front part of the arch of the anterior canal (a.s.c.) are laid open. The roof is thicker and flatter; the sphenotic wings (sp.o.) are still large and thick; the cavity of the skull is single, narrower, and is half a long ellipse in shape, the angles of the broad upper end being rounded. Here the notochord is not seen, it has retreated too far backwards, but the parachordal mass (iv.) is hugely thick, and is wider; it is close behind the post-clinoid wall. The fore part of the hind-brain (C3.) is cut across, where it is giving off the facial nerves (VII.), close behind the roots of the trigeminals (fig. 5, V.). The last section was cut through the interspace between the pterygoid band and the orbitar process (fig. 5, pg.q., q.c.; and see also Plate 16, figs. 1 and 7); here the back of the suspensorium (q.c.) is cut through, at the hind part of the maxillary bone and the orbitar process (mx., or.p.). A notch seen in the hind margin of the pterygo-quadrate cartilage (Plate 16, fig. 5, pg.q.c.) is cut across here, and the median part of the cartilage crops up, again, right and left; between these the main azygous metapterygoid (mt.pg'.) is seen. The angle of the mandible (mk.) and the end of the dentary (d.) are also cut across.

**Section 15.**—In this section (Plate 17, fig. 7) the chondrocranium attains its greatest solidity, and here the small cranial notochord (nc.) has its point cut through. The sphenotic has given place to the "pterotic" region, the arch of the anterior and the ampulla of the horizontal canals (a.s.c., h.s.c.) are exposed, and so also is the auditory nerve (VIII.), as it arises in the hind-brain (C3.) and runs through the meatus internus into the vestibule (vb.). Here the tegmen cranii is thick and concave, and the pterotic expansions (pt.o.) are very rough and lobulate. Under the bulging sinuous parachordal mass the parasphenoid (pa.s.) has become very wide, and now sends down its free edges. Under the capsules the "protractor hyomandibularis" muscles (pt.hm.) are seen as huge triangular masses, and the "adductor mandibulae" muscles (ad.m.) are cut through in their hinder part. A little of the pterygoid region (pg.q.) and the hind angle of the quadrate (q.c.) come into view, and between the former the median and main lateral metapterygoids (mt.pg', mt.pg".). The deepest part of the pterygoid bone (pg.) is seen flanking the inner face of the suspensorium. Under the quadrate
a new and thick cartilage appears; this is the symplectic (sy.), it is crescentic in this, its front edge (lower end), and between it and the quadrate there is a small nucleus of cartilage which will be described in the next stage—it is a "suspensorial ray" (sp.r.). The chief scutes seen are the parietals; the squamosal, the opercular, and the sub-opercular, also, may be traced at this point, but are not figured.

Section 16.—In this slice (Plate 17, fig. 8) we see several new parts come into view below; above, the skull is altogether flatter, and the supercranial valley narrower. The auditory nerve (VIII.) is still shown, also the arch of the anterior and horizontal canals (see also fig. 7, a.s.c., h.s.c). The basal plate (i.v., nc.) is very irregular, as it passes into the auditory capsules, right and left; the parasphenoid (pa.s.) partakes of this irregularity, and here its decurved wings are larger. The compound metapterygoid plate is composed at this hind part of a large middle, two large lateral, and two lesser intervening plates (int.pg',, mt.pg''). The top of the hyomandibular is just seen and most of its great protractor muscle (pr.hm.); below, the symplectic is cut through from top to bottom. Below the wide oral cavity the cerato-hyal (c.hy.) with a thin ectosteal coating, the hypo-hyals (h.hy.), the fore part of the basibranchial (b.br.), and the fore end of the first hypo-branchials (h.br¹.) are also seen. The scutes are very similar to those of the last.

Section 17.—In this (Plate 17, fig. 9), the cranial valley is seen to be wider again; the auditory sacs are cut through where the posterior canal (p.s.c.) is descending, and the whole structure is lessened laterally; a thin pterotic cave (sp.o., read pt.o.) grows down on each side. Here the hind-brain (C³.) is less, and it is giving off the roots of the large vagus nerve (X.) whose ganglion root and stem are laid bare. Here we still see that the auditory sacs are open to the skull (or only closed by membrane), and here the sacculus (s.) is seen hanging from the rest of the vestibule (vb.). The notochord (nc.) is becoming larger, and the thick curved basal plate (i.v.) is here separate from the auditory capsules; below it the parasphenoid (pa.s.) is thick, and at its notched sides we see a pharyngo-branchial (p.br.) and outside this part of the gills (g.). The lower part of the hyomandibular, part of the symplectic, interhyal, and cerato-hyal (hm., sy., i.hy., c.hy.) are cut across; and near the mid line the basibranchial, the first cerato- and hypo-branchials, and the second hypo-branchials (b.br., c.br¹., h.br¹., h.br².).

Section 18.—In this section (Plate 17, fig. 10) the post-auditory fontanelle is just missed, and we see that it must answer to the interspace between the supra-occipital and first vertebral arch; for the chondrocranium (see Plate 15, fig. 13) sends its copious growths over the proper spinal region. The cavity here is very large, this being, indeed, the "foramen magnum," and the ex-occipital walls are very thick, and almost vertical. The hinder part of the vagus nerve (X.) is still seen in the chink which separates—up to this point the sides form the base, which is increasingly massive, but has not a very large notochordal section (nc.) in it. The parasphenoid (pa.s.) is beginning to break up at the middle; outside it a pharyngo-branchial is
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seen (p.br.), and outside that the most backwardly projecting part of the massive hyomandibular (hm.).

Section 19.—The last of this series (Plate 17, fig. 11) is post-cranial; the ganglion of a spinal nerve (sp.n.) is cut across; the medulla spinalis (my.) is seen to be very small in proportion to the spinal cavity, and the notochord (nc.) is twice as large as in the skull, and reaches the theca vertebralis. The parasphenoid (pa.s.) is in two parts (see Plate 16, fig. 3); the hind and transverse processes of the undivided vertebral tract are very large, and are covered with large scutes. This section is behind the operculum (Plate 15, fig. 10, op.), and through one of the hinder branchial arches; in the general branchial recess, the pharyngo-, epi-, and part of the cerato-branchials (p.br., c.br., e.br.) of a middle gill arch, and some of the gills, are shown.

Behind this part the notochord becomes thicker, and its chondrified sheath more distinct; the forked parasphenoid dies out, and the neuro-central cartilages appear (Plate 16, fig. 3).

Fifth Stage.—Adult Sturgeon (Acipenser sturio).*

The Sturgeons dissected for this stage were about 4 or 5 feet long, such as are most commonly seen in the markets; my last stage is from a much larger specimen, but not from the largest. Dr. Günther ('The Study of Fishes,' p. 362) says that this species attains a length of 18 feet.

The swelling of the fore part of the trabeculae and intertrabecula in the orbital region becomes very remarkable, and the cartilage becomes subdivided into an upper and a lower stratum; between these the parasphenoid (Plate 18, fig. 3, tr., i.tr., pa.s.) grows as a thin dentate lamina, with one very long median spike. The clavate swellings of the trabeculae bind on the sides of the exposed part of the parasphenoid, and the second floor of cartilage in the middle (i.tr.) runs up to the base of the huge rostrum, appearing below as a rounded elevation, separated from the lateral lobes by a deep sulcus, which is filled with fatty tissue. In the fatty tissue outside the paired lobes of cartilage there is a series of four thin cartilaginous plates (e.pa.); they are outside the trabeculae, and behind the ethmo-palatine boundary of the nasal sac, and probably represent, partly, as Mr. Howes suggests, the free ethmo-palatines of other kinds; in Siredon I have shown that there are two of those cartilages on each side (Phil. Trans., 1877, Plate 24, figs.1–3, e.pa., pt.pa.) an "ethmo-palatine" and a "post-palatine."†

* The dissections, figures, and notes for this stage were made for me by my friend Mr. George Howes, Professor Huxley’s talented Demonstrator.
† I wish to put all these pre-oral growths together for comparison, in hope of obtaining a clue to their real nature. Mr. Balfour’s writings have made me very doubtful of the view that, at one time, seemed to me to be almost demonstrable—viz., that these antorbital cartilages were in reality the rudimentary upper part of a pre-mandibular visceral arch, but their position, in front of the hypoblast, makes their determination as difficult as that of the pro-chordal part of the basis cranii.
The most important further modifications to be seen in these large individuals, are in the visceral arches.

There are seven arches, and the whole series is displayed in a side view (Plate 18, fig. 5) so as to show their relative size, and their varied modification; in that figure the inferior part of the hyoid arch is shown as drawn backwards towards the first basi-branchial (c. hy., b. hy., b. br‘); in reality it runs across to meet its fellow in the floor of the mouth (fig. 10, c. hy., b. hy.).

The two first arches, the mandibular and hyoid, are intensely specialised; the other five are very similar to those of the Elasmobranchs, save that they have some of the larger bars partly ossified; and are still more like the branchial arches of Holostean Ganoids and Teleosteans. The upper elements of the mandibular arch, the right and left “suspensoria,” are transformed into the oblique convex roof of the very mobile protrusible mouth, and the free mandibles are made to be antagonistic to the antero-inferior part of this complex structure. Each cartilaginous suspensorium is a broadly falcate plate, whose arched upper border comes in contact with that of its fellow in front and above; below and behind, it suddenly bends forwards and becomes very solid, to form the quadrato condyle (figs. 4, 5, q. c.). The whole plate is gently and sinuously convex above and concave below; behind, over the hinge, it thickens into a rib-like enlargement, and grows outwards and forwards as a superficial “orbitar process” (or. p.).

The upper margin is arched regularly until near the hinge, and then is hollowed a little; the lower margin is twice-notched and concave. The bones applied to these pterygo-quadrate plates have not caused the absorption of the cartilage in this stage, which is relatively more extensive than in the last stage, in which the hind margin was notched. The outermost bones are the largest; they are the maxillaries (m. x.), they are strongly bowed, dilated most where they meet in front of the cartilaginous plates, and to a lesser degree where they bind upon the orbitar processes behind. A large space for each “adductor mandibulae” muscle exists between the maxillaries and the pterygo-quadrate cartilages. Another superficial bone stands upright on the hind end of the maxillary; it is a high triangle, and its base is below. It binds on the thick, ribbed, outer edge of the suspensorium in its quadrate region; this is the small “pre-opercular” (p. op.), whose almost equally small counterpart exists in Lepidosteus. Along the lower edge of the cartilage, in front, a very jagged little bony scale is seen, overlapped by the fore end of the maxillary. This is the mesopterygoid (m. s. pg.); it was not a separate bone in the last stage. Behind it there is a small style, with its sharp end behind, reaching to the end of the foremost and larger notch; this is the palatine (p. a.). Inside the plate (pg. q.) there is a large parostosis, the pterygoid; it lines all the cartilage except a falcate tract in front and above; this causes it to be sharply notched in front; this form is well shown by the shading of the cartilage (Plate 18, fig. 4).

The mandible or Meckelian rod (Plate 18, figs. 5 and 8, m. k.) is a very short stout cartilage like that of a Tadpole; the condyle is convexo-concave, and the angular
process is large and projecting. That is the only part not covered, on the outside, by the flattish but thick dentary bone (d.). On the inside (Plate 18, fig. 8, d.) it shows a large crescent of bone, where the rod becomes slenderer in the middle. Behind that part, on an apophysis of the cartilage, a small oblong second bone appears. This is the coronoid (cr.); its direction is backwards and a little downwards. The distal end of the rod is thick and massive, and is united to its fellow by ligamentous fibres.

A small squarish suspensorial ray is seen behind the angle of the mandible (Plate 18, fig. 5, sp.r.); it is far below the usual place for the spiracular cartilage of a Shark. The other half of the general roof of the mouth is fan-shaped (Plate 18, figs. 4 and 5, mt.pg'., mt.pg''). the narrow handle running in between the two pterygo-quadrates, and the outspread part growing round their convex hind margin. Thus this complex plate has two convex edges behind and two concave edges in front; then it runs to a sharp point between the symmetrical plates. The earliest pieces of this patchwork are still the largest; they are the main azygous plate and the main symmetrical plates (mt.pg'., mt.pg''); the single piece is like the bowl of a spoon, but longer; the other two are roughly three-cornered. Outside, between the latter and the quadrate region of the paired plate (q.c.) there is a much smaller but tolerably constant piece on each side. Behind, between the three main patches, there are three or four on each side, inconstant in number and form; and in front, in the interspace between the three main patches and the pterygo-quadrates, there is a patch or two on each side, and then a single row of four or five, lessening forwards. These patches are all set in one common web of fibrous tissue, so as to look, in a rough dissection, like one unpaired hard-palate plate.

Half this complex palate of pterygo-quadrates and metapterygoids is nearly equal in length and width, but far inferior in thickness, to a single hyomandibular (Plate 18, fig. 5, hm.). That segment has no "serial homologue" either before or behind it, for the subdivision of the upper part of the visceral arches is different in the mandibular, hyoid, and branchial arches. The hyomandibular is not the uppermost segment of a normal visceral (branchial) arch, for there is no pharyngo-hyal in this type. Nor does it correspond to more than the upper two-thirds of an epi-branchial; the lower third is the separate symplectic (sy.). Neither does it harmonise with the pier of the arch in front, which is segmented quite after another fashion; there, the part answering to the symplectic is the pterygoid foregrowth of the suspensorium, whilst the part which should correspond to the head of the hyomandibular is partly continuous with the head of the pier of the opposite side, and largely broken up into a tesselated pavement of irregular segments. The upper "epi-hyal" (hm.) is, above, a normal phalangiform segment, but below and behind it expands into a huge pedate plate; the "toe" below, is tied to the next segment, the "heel" behind, carrying the "opercular," and answering to the opercular process in Teleostei; this convex pedate slab is almost entirely unossified.
The neck and shoulders of the hyomandibular are ossified, so as to leave the round convex head and expanded lower part unchanged. The osseous shaft is hour-glass-shaped, very thick, and leaving only a small core of cartilage unossified (Plate 18, figs. 5-7, *hm.*); this bony tract is very angular, in section, and somewhat four-cornered. On the outside of the bony sheath, embedded in the periosteum, there are simple and forked cartilages (Plate 18, figs. 5, 6, 7, *hm.r.*), evidently rudimentary "branchial-rays;" as seen in the sections (figs. 6, 7) they are very solid, "and usually exist upon (a) the anterior, and (b) the outer face only; in one specimen, however, (fig. 7) they also occurred upon the anterior and inner" (Howes); they are very variable as these sections show.

The "toe" of the hyomandibular (*hm.*) rests upon the upper face of the upper end of the next segment, the symplectic or lower epi-hyal (Plate 18, fig. 5, *sy.*); the two are attached together by a strong fibrous joint. This distal segment of the hyoid "pier" is half the length and half the medium width of the upper piece; it is phalangiform, straight, and thick. Distally it is attached by a strong fibrous joint to the quadrate region (*q.c.*), which it carries; proximally, at its proper upper end it is articulated to the inter-hyal (*i.hy.*); it is wholly unossified.

The intercalary segment, or "inter-hyal" (*i.hy.*) is a sub-cubical, lobulated mass of cartilage, interposed between the symplectic and the lower element of the hyoid arch, the cerato-hyal (*c.hy.*). This latter segment in the undisturbed condition of the parts runs across and a little forwards under the throat; it is about the size of the symplectic, but more slender and has a narrow waisted ectosteal tract a little below its middle. This bone is nearly half the height of the bar, is pinched and angular, has an unossified pith and extra-hyal cartilages (Plate 18, fig. 9, *c.hy.*, *c.hy.r.*), like the hyomandibular.

There is a thick wedge of cartilage segmented off from the cerato-hyal, the hypohyal (*h.hy.*); it is attached by fibrous tissue to its fellow, the related ends being narrow, and also to the fore end of the first basi-branchial (Plate 18, figs. 5 and 10, *h.hy.*, *b.br*).

The thick, solid, strongly bent branchial arches (Plate 18, figs. 5 and 10) lessen and become simpler from before backwards. The joint between the main upper and lower segments (*e.br.*, *c.br.*) is a well formed "elbow," the upper part is a little less than the lower. Only the first and second branchial arches are perfect, and they have acquired an additional pharyngo-branchial (fig. 5), and these small segments rest on short forks of the epi-branchial (*e.br.*). There is only one pharyngo-branchial on the third arch (*p.br*), and that on the fourth has (evidently) become fused with the epi-branchial (*e.br*). The fifth arch is in one piece, it is a cerato-branchial (fig. 10, *c.br*), and like the four cerato-branchials in front of it, has a bony tract in its middle part. Only the first and second epi-branchials (*e.br*, *e.br*) have ectosteal tracts. On the first of these there are at least two imperfect "rays" (*br.r.*), as on the arches in front. The lower part of each arch is bowed outwards, the upper is sigmoid, and they are very
angular, especially where the ectosteal tract exists. Only the first three have hypo-
branchials (Plate 18, figs. 5 and 10, \( b.br^1-3 \)); these begin much larger than the hypo-
hyal and then lessen backwards; they are flat, finger-shaped, and not ossified.

Another addition of cartilaginous segments has taken place below; in the young
Sturgeons (Plate 14, fig. 5, and Plate 16, fig. 5) there was only one basi-branchial
carrying the three first arches. Now, *three* new smaller segments have appeared
\( b.br^4-6 \), the last of these is wedge-shaped, and belongs to a suppressed arch, for it passes
behind the pedate end of the arrested fifth arch; the foremost piece belongs to three
arches.

These piers are compressed, and the first, which belongs to *three* arches \( b.br^1-3 \), is
nodose.

**Sixth Stage.**—Skull of an unusually large* Sturgeon (*Acipenser sturio*) (*in the
[Hunterian Museum]*).

This very valuable specimen of a much older individual, shows some very important
modifications, which have, as it were, an upward look towards the Holostean Ganoids
and the Teleostei.

In the last stage the pterygo-quadrate cartilages were even more perfect than in
the young of 7 or 8 inches in length. In this specimen, however, the “parostoses”
have caused a considerable amount of absorption of the hyaline cartilage, just as the
dentary, normally, causes Meckel’s cartilage to shrink and even become absorbed;
but I cannot find any evidence of a direct ectostean relation of the bone to the
cartilage. The pterygoid bone (Plate 17, figs. 12, 13, \( pg \)) gets over to the outer
side over the convex inner margin, and causes the absorption of the cartilage in that
region. Moreover, the jagged bony tract which represents the mesopterygoid, and
which in the last was at the antero-inferior edge of the cartilage, is now (Plate 17,
figs. 12 and 13, \( ms.pg \)) a sharp wedge of bone filling up the space between the forks
of the pterygoid on the inner side (fig. 13), and is seen as an oval plate of bone nearer
the top than the bottom, on the outer side (fig. 12, \( ms.pg \)). These differences are not
all due to age; there is a considerable amount of variation in individuals of the same
age in these types, where the sub-cutaneous and sub-mucous bony tracts are but
deeper scutes, and where the chondro-skeletal regions are so generalised and, as it were,
*hypertrophied.*

With regard to the buried scutes, we see a right and left variation in this same
specimen (Plate 18, figs. 1 and 2, the right and left orbital region in this large skull).
Here there are no proper ectosteal prefrontals (ecto-ethmoids), orbito-sphenoids, ali-
sphenoids, or prootics; but, since the last stage, parosteal tracts have appeared in
all those places; they are deep “scutes,” not shallow endo-skeletal elements, and are
the prophecy, so to speak, of the special “ectostoses” seen in the Holostean Ganoids
and the Teleostei, and in all the types above them. Round the thick antorbital

* Even this specimen was not half the size this species sometimes attains to.
(ecto-ethmoidal) mass of cartilage I find a thin but rough irregular layer of bone, just where the Teleostei have their proper ecto-ethmoid (Plate 18, figs. 1 and 2, e.eth'.). Also over the optic foramen (II.) there is a very large splint (os'.) applied to the orbital cartilage; it runs upwards and forwards. On the right side only (fig. 1, al.s.) there is a much smaller plate in the alisphenoidal region, and behind and partly round the foramen ovale (V.) a thin semi-annular plate (pro'.) representing the prootic of the higher types. But no direct grafting of bone on the cartilage can be seen, and the affinity of the bone for the cartilage or, vice versa, of the cartilage for the bone, is here extremely feeble; there is no material interaction; the co-ordinating force, however, has produced a plate of the proper form, and put it ready for use in the proper place.

Summary and comparison with other types.

It is evident that we have in the Sturgeon a form which is practically intermediate between the Selachians and the Osseous Ganoids (Holostei); the form of the larvae (Plate 12) suggests this view at once. I must again refer the reader to the researches of Salensky and Balfour on the embryology of this type; my own recapitulation and comparison must be confined to the cephalic skeleton.

A. The primordial skull.

We saw that in the larvae of Acipenser ruthenus only about a third of an inch in length (9\(\frac{1}{2}\) millims.) the "embryonic cartilage" had largely become "hyaline;" that the foundations of the cranium were laid, and the visceral arches were differentiated and becoming quite solid. Here, it would seem, that in so small a larva of so large a Fish—and that Fish lying at the base of the great archaic group of the Ganoids—we have a good chance of seeing the primordial vertebrate skull in its utmost simplicity. The fact is, that we have a confusingly simple state of things.

In the fore part of the spine, as well as in the whole basi-cranial region, the paired skeletal tracts that lie right and left of the mesoblastic sheath of the notochord, the hardening cartilage shows no signs of segmentation or intercalary vertebral subdivision; this is just like what occurs in the Selachians (Trans. Zool. Soc., vol. x., plate 35). Moreover, this Chondrosteous Ganoid remains in this condition, as far as I can find, throughout life, and does not acquire the occipito-cervical articulation, so well known in the Selachians, but which in them is a secondary modification of the parts. By careful comparison of all the facts I have been able to gather by observation of many types and at many stages, I cannot help coming to the conclusion that the normal intercalary vertebral segmentation with which we are so familiar in the post-cephalic region of the Vertebrata, generally, is a comparatively late and secondary specialization in the evolution of this, the highest, group of animals.

If Mr. Balfour's suggestion ("Comp. Embryol.," vol. ii., p. 366) be true, viz.: that the fore-brain with its special optic and olfactory outgrowths is a sort of outgrowth or
addition, itself, to the neural axis, then we have to reconsider the meaning of any and every part of the cranial skeleton which may be formed in front of the notochord and of the overlying and overfolded mid-brain.

Thus all the prochordal cranial, and all the pre-mandibular facial growths of the skeletal cartilage have to be subjected, again, to the severest morphological inquisition under that light—the light of Embryology—which alone can make manifest their true meaning.

If the notochord be the true organic axis of the skeleton of the animal, and if the visceral (or branchial) arches were only developed in relation to the hypoblastic branchial outgrowths of the dilated respiratory pharynx, then it seems to be necessary that we should consider all the skeletal parts in front of those structures as superadded specializations of, or "outgrowths" from, the front end of the proper Vertebrate form.*

In certain types, namely, the Lamprey, the Selachians, the Urodela, and the Anura, the trabeculae are chondrified before the hinder or parachordal tracts. Nevertheless, the posterior part of the trabeculae in them is parachordal; the rest, up to the "atlantal" region, may afterwards chondrify separately, as in the Urodela, or continuously, as in the others.

In Acipenser, Lepidosteus, and Salmo I find no difference of time in this matter, and should therefore be inclined to look upon the earlier growth of the trabeculae as due to the special weight and pressure of the fore-brain in those cases, and as a non-essential modification, just as I consider the later segmentation of the trabeculae from the investing mass in Salmo and Chelone, and to a less extent in Crocodiles and Birds, as a non-essential specialization.

Yet the trabeculae are as truly part of the proper mesoblastic axial skeleton as the fore-brain is part of the proper epiblastic neural axis.

The whole of the pre-cerebral tracts of the skull, namely, the cornua trabeculae and the greater part of the intertrabecula—all of it that lies in front of the exit of the olfactory nerves—I should consider to be mere outgrowths or "apophyses" of the cranial skeleton.

The axial skeleton is more aborted in front than the axial nervous system, even if the fore-brain is reckoned as an additional part, for the mid-brain bends completely over upon itself, and the notochord only partially. Yet, as I have shown in Chelone viridis, its cartilaginous mesoblastic sheath is continued downwards as solid cartilage below and in front of the end of the notochord. I am inclined to think that the intertrabecula is a breaking out again of that mesoblastic tract (a sort of cranial "spadix") but with its continuity, for a short space, interrupted.

The ventral part of the primordial skull presents as many difficulties as the dorsal; the post-oral visceral (or branchial) arches, which may be both superficial and deep,

* For my own part, I am quite content that this should be so, albeit my own descriptive language will have to undergo a considerable amount of evolulutional modification, and many things that seemed to me, once, to be clear and certain, made dark and uncertain.

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have to be compared with such facial growths as may exist in front of the mouth, and these, if possible, have their relation to the post-cephalic arches determined.

Long ago, to those who knew nothing of Embryology, all this seemed to be easy enough; now, with all the new, increased light from that source, the problem has become extremely difficult, and is certainly not solved, as yet.

I do not see that the superficial cartilages that surround the mouth have any right to be compared, serially, to the arches of the pharynx or of the chest; they appear to me to be the most archaic structures in the skeleton—"barbels," "labial cartilages," "nasal valves"—all these appear to me to be lineally descended from the inner supporting tracts of tissue of oral palpi, such as are met with in so many of the aquatic Invertebrata. The investing bones of the face may be grafted on such cartilages, but the two things are quite different in their nature. The condition of the visceral arches in this type, both in the larva and in the adult, has led me to reconsider the whole question of the nature of these arches.

There are several things to be considered at the outset, before a comparison is made of the skeleton of the throat, the branchial skeleton, and the skeleton of the chest. The post-auditory part of the cranium has manifestly undergone secular shortening, so that the pharyngeal or ventral region belonging to it often extends under the twice-segmented spine, whose fore part is, so to speak, intercalary or superadded, and does not correspond with the arches beneath it, which often extend backwards for some distance.

At one time this appeared to me to be an explanation of the fact that the inner (or proper) branchial arches of Fishes are developed beneath the fore part of the spine and the hind part of the basis cranii, whilst the mandibular and hyoid arches, the first and second of the branchial category, often fix themselves to the basal plates of the cranium.

I now strongly suspect this view of the matter to have been a mistaken one; and that it is the abnormal size and special modification of the mandibular and hyoid arches that make it necessary for those arches to seize hold of swinging points above their normal dorsal region or apex.

I think that the figures I have given of the visceral arches in the larval Sterlet (Plate 13, figs. 6 and 11) will make my meaning plain. Here only one arch is attached to the edge of so much of the parachordal plate as may creep under the auditory capsule; all the other arches are fairly under the head and forepart of the neck.

This normally inferior position of the visceral arches is best seen however in the early embryo of the Skate (see in "Pristiurus," Trans. Zool. Soc., vol. x., plate 35, fig. 4), where the metapterygoid, hyomandibular, and all the pharyngo-branchials, are shown in situ, after the whole cranium had been removed from above.

The sub-division of the pleuro-peritoneal cavity by the hypoblastic branchial pouches in the early embryo, the rapid closure of those cavities (the "head-cavities"), and the relation of the skeletal bars of the pharynx and mouth, whether deep or superficial—all
Development of the Skull in Sturgeons.

These things have to be carefully reflected upon before any classification of these ventral arches can be made.

It seems to me that a cartilaginous arch developed inside a recently-closed "head-cavity" must be a part of the "splanchno-pleure," and that a cartilage developed outside such a recently-closed cavity must belong to the "somato-pleure." *

The ribs belong to the outer lamina of the body-wall of the embryo, so also, it appears to me, do the "extra-branchials" of the Lamprey, the Tadpole, and the Shark.

If all this be true, the normal "intra-branchial" arches have no counterparts whatever in the skeleton of the trunk; they culminate in the class of Fishes, and are imperfectly developed, not only in the Abranchiata, but also in the degenerate Marsipobranchii, and the metabolic Amphibia Anura.

The extra-branchials of some of these latter types, and of the Sharks, have some right and title to be classified as a sort of cephalic ribs, but perhaps that claim had better not be pressed for the present; it is safer for the Morphologist to keep certain things in solution, when any doubt remains, than to crystallize them into what may turn out to be obstructive error.

In the metamorphosis of the larval Sturgeon the additional parts are easily explained, and are, for the most part, due to mere increase of certain tracts of tissue, and super-additions of secondary nuclei of cartilage, and of various centres of ossification.

Moreover, the fact that the dermal scutes are largely dominated by the cartilaginous endoskeletal structures of the cranium and pharynx, however interesting from one point of view, is not of any great fundamental importance.

With regard to the great "shoots" of cartilage that grow out, forwards, from the primary basis-cranii, these are parts that undergo a most extraordinary amount of modification in various types; they are specialised superadditions to the essential skull, of great importance in Taxonomy, but of little account in that which is fundamental in Morphology.

Comparison with Polyodon.

The skull of the other principal existing Chondrosteous Ganoid type comes singularly near to that of the Acipenserine skull, and in some things is curiously unlike it. Near as Polyodon approaches in the structure of its skull to Acipenser, it differs in having no complex metapterygoid plate, in the feebler ossification of its visceral arches, and in the presence of three pairs of "endosteal" centres not to be found in the Sturgeon. The anterior palatine ectostosis placed just where both the mesopterygoid and palatine plates meet in the Sturgeon, is probably the true homologue of the palatine bones of the Holostean Ganoids; the presence of a small prootic and opisthotic brings us nearer in this case to those higher types. The much larger and more perfect "orbitar

* The branchial artery lies inside the head cavity, and afterwards, when the branchial arch is developed, runs up a groove on the outside of it (see Balfour's 'Elasmobranchs,' plate 14, fig. 13, a, p. 208; and 'Comp. Embryol.,' vol. ii., p. 472, fig. 328).
process" shows in Polyodon a nearer relationship to the larval Frog; the absence of a metapterygoid plate brings it nearer to the Sharks, and the three pairs of *ectosteal* centres to the Holostean Ganoids. (See Bridge, Phil. Trans., 1878, Plates 55-57.)

**Comparison with the Selachians.**

The development of the basis-cranii and cranial walls in *Acipenser* is very similar to what is seen in the Selachians; and the after modifications are essentially alike, except that in the Sturgeon the cartilage is very massive, and the occipito-cervical articulation is not formed. The separation of a large symplectic, and a lesser interhyal segment, the complex metapterygoid plate, and the partial ossification of the visceral arches, are all modifications that separate this from the Selachian types.

**Comparison with the Holostean Ganoids.**

Most of the peculiarities which distinguish the skull in that group from that of a Sturgeon are so many steps in the direction of the Teleostean skull. To say nothing of the lighter build of the chondrocranium, the numerous ectosteal patches in the skull wall, the intenser ossification of the visceral arches, and the absence of a distinct symplectic cartilage (it may exist as a separate bony centre, as in the Teleostes), all these things show how far the Holostei have become specialized beyond the chondrosteous *Acipenser*. An important modification occurs early in *Lepidosteus*, namely, that the palato-quadrate is continuous, at first, with the trabecula; the intertrabecula also appears earlier. I shall compare the skull of the Ganoids, generally, with that of the Teleostei, in my next paper, which will treat of the skull of *Lepidosteus*. 
# EXPLANATION OF THE PLATES.

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<td>Side view of dissected head of another larva, 9\frac{1}{2} millims. long</td>
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<td>Horizontal section of head of a larva of the same, 13\frac{1}{2} millims. long</td>
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<td>Larva of <em>Acipenser ruthenus</em>, 13\frac{1}{2} millims. long; side view of dissected head</td>
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<td>The same; upper view</td>
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<td>Plate</td>
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<td>Dissection of head of same; upper view</td>
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<td>The same; and same view, with visceral arches attached</td>
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<td>Visceral arches of same; upper view</td>
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<td>Fore part of same object; lower view</td>
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<td>The same; inner view</td>
<td>$\frac{1}{3}$ natural size</td>
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<td>Right orbital region of old specimen</td>
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<td>Left orbital region of old specimen</td>
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<td>Basis cranii, orbital region, in adult <em>Acipenser sturio</em></td>
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<td>4</td>
<td>5</td>
<td>Palato-quadrate apparatus of same, from above</td>
<td>Slightly enlarged</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>5</td>
<td>Visceral arches of same, side view</td>
<td>$\frac{3}{4}$ natural size</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>5</td>
<td>The same; section of hyomandibular</td>
<td>Slightly enlarged</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>5</td>
<td>The same; section in another specimen</td>
<td>Slightly enlarged</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>5</td>
<td>Mandible of same; inner view</td>
<td>Slightly enlarged</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>5</td>
<td>Section of cerato-hyal of same</td>
<td>Slightly enlarged</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>5</td>
<td>Visceral arches of same, from below</td>
<td>Slightly enlarged</td>
</tr>
</tbody>
</table>
Phil. Trans. 1882. Plate 14.

ACIPENSER.
### List of Abbreviations

The Roman figures indicate nerves or their foramina.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>ad.m.</td>
<td>Adductor mandibulae.</td>
</tr>
<tr>
<td>al.s.</td>
<td>Alisphenoidal region.</td>
</tr>
<tr>
<td>al.s'</td>
<td>Alisphenoidal bony plate.</td>
</tr>
<tr>
<td>an.</td>
<td>Anus.</td>
</tr>
<tr>
<td>aq.v.</td>
<td>Aqueduct of vestibule.</td>
</tr>
<tr>
<td>a.s.c.</td>
<td>Anterior semicircular canal.</td>
</tr>
<tr>
<td>au.</td>
<td>Auditory capsule.</td>
</tr>
<tr>
<td>bb.</td>
<td>Barbel.</td>
</tr>
<tr>
<td>b.br.</td>
<td>Basi-branchial.</td>
</tr>
<tr>
<td>C1</td>
<td>Fore-brain.</td>
</tr>
<tr>
<td>C2</td>
<td>Mid-brain.</td>
</tr>
<tr>
<td>C3</td>
<td>Hind-brain.</td>
</tr>
<tr>
<td>d.</td>
<td>Dentary.</td>
</tr>
<tr>
<td>e.</td>
<td>Eye-ball.</td>
</tr>
<tr>
<td>e.br.</td>
<td>Epi-branchial.</td>
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<tr>
<td>e.eth’</td>
<td>Ethmoidal bony plate.</td>
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<tr>
<td>e.o.</td>
<td>Ex-occipital region.</td>
</tr>
<tr>
<td>e.pa.</td>
<td>Ethmo-palatine.</td>
</tr>
<tr>
<td>e.pa’</td>
<td>Extra ethmo-palatine.</td>
</tr>
<tr>
<td>f’</td>
<td>Frontal bony scute.</td>
</tr>
<tr>
<td>f0</td>
<td>Fontanelle.</td>
</tr>
<tr>
<td>g.</td>
<td>Gills.</td>
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<tr>
<td>h.</td>
<td>Heart.</td>
</tr>
<tr>
<td>h.br.</td>
<td>Hypo-branchial.</td>
</tr>
<tr>
<td>h.hy.</td>
<td>Hypo-hyal.</td>
</tr>
<tr>
<td>hm.</td>
<td>Hyomandibular.</td>
</tr>
<tr>
<td>hm.r.</td>
<td>Hyomandibular ray.</td>
</tr>
<tr>
<td>h.s.c.</td>
<td>Horizontal semicircular canal.</td>
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<tr>
<td>hy.</td>
<td>Hyoid fold.</td>
</tr>
<tr>
<td>i.hy.</td>
<td>Inter-hyal.</td>
</tr>
<tr>
<td>i.tr.</td>
<td>Intertrabecula.</td>
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<tr>
<td>iv.</td>
<td>Investing mass.</td>
</tr>
<tr>
<td>l.</td>
<td>Liver.</td>
</tr>
<tr>
<td>l.l.</td>
<td>Lower lip.</td>
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<tr>
<td>m.</td>
<td>Mouth.</td>
</tr>
<tr>
<td>mk.</td>
<td>Meckel's cartilage.</td>
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<tr>
<td>mn.</td>
<td>Mandibular fold or bar.</td>
</tr>
<tr>
<td>ms.pg.</td>
<td>Mesopterygoid.</td>
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<tr>
<td>mt.pg’</td>
<td>Median metapterygoids.</td>
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<tr>
<td>mt.pg”</td>
<td>Lateral metapterygoids.</td>
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<tr>
<td>mx.</td>
<td>Maxillary.</td>
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<tr>
<td>nc.</td>
<td>Notochord.</td>
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<td>ol.</td>
<td>Olfactory capsule.</td>
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<td>op.</td>
<td>Opercular scute.</td>
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<td>o.s’</td>
<td>Orbito-sphenoidal bony plate.</td>
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<td>Parietal scute.</td>
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<td>pa.</td>
<td>Palatine bone.</td>
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<td>Parasphenoid.</td>
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<td>p.br.</td>
<td>Pharyngo-branchial.</td>
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<td>p.f.</td>
<td>Pectoral fin.</td>
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<td>pg.</td>
<td>Pterygoid bone.</td>
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<td>pg.q.</td>
<td>Pterygo-quadrate.</td>
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<td>px.</td>
<td>Pharynx.</td>
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<td>p.op.</td>
<td>Pre-opercular bone.</td>
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<td>pr.o’</td>
<td>Prootic bony plate.</td>
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<tr>
<td>p.s.c.</td>
<td>Posterior semicircular canal.</td>
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<tr>
<td>pt.hm.</td>
<td>Protractor hyomandibularis.</td>
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<td>pt.ob.</td>
<td>Postorbital scute.</td>
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<td>q.c.</td>
<td>Quadrate condyle.</td>
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<td>s.ob.</td>
<td>Superorbital scute.</td>
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<td>Spiracle.</td>
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<td>Spiracular ray.</td>
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<td>sq’</td>
<td>Squamosal scute.</td>
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<td>su.ob.</td>
<td>Suborbital scute.</td>
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<td>sy.</td>
<td>Symplectic.</td>
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<td>Teeth.</td>
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<td>t.cr.</td>
<td>Tegmen cranii.</td>
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<td>tr.</td>
<td>Trabeculae.</td>
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<td>u.l.</td>
<td>Upper lip.</td>
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<td>v.</td>
<td>Vomerine bone.</td>
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<td>vb.</td>
<td>Vestibule.</td>
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<td>v.f.</td>
<td>Ventral fin.</td>
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<tr>
<td>y.st.</td>
<td>Yolk-mass and stomach.</td>
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