XV. *On the Structure and Development of the Skull in the Urodelous Amphibia.*—Part I.

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[Plates 21–29.]

Introductory Remarks.

Before submitting to the Royal Society a *third* paper on the Skull of the Batrachia, it would seem to be better for me to bring forward the results of my work on one of the simpler kinds of Amphibia, namely the Axolotl, a type belonging to the "Urodela."

Through the kindness of friends* I have been enabled to follow the Axolotl through many stages, and several other types have been worked out both in their larval and adult stages; some of these fill up lacunæ in the series of Axolotls.

That type, however, is here given in *nine* larval stages, besides the *Amblystoma* stage into which certain individuals pass.

Ten or twelve stages are not at all more than are needed for following up and catching every important modification in the skull of a Vertebrate no higher than a Salamander —a type which, practically, stands between the "Pisces Dipnoi" and the true Reptiles. Moreover this leaves a large fore margin to the embryologist proper, whose most important work dovetails into mine where mine begins.

To the morphologist the group of the Urodela is of great interest, first in its relations to the Batrachia, the Cæcilians, and the extinct Labyrinthodonts, and then to the more generalized Fishes below and the Reptiles above.

And not only with the Reptiles, for the more reptilian types of Birds, such as the Dinornis, the Emu, and the Cassowary, have skulls that are easily interpreted by one who is familiar with the Salamandrian skull.

But perhaps the most instructive comparisons are those which may be made of the skull (chondrocranium) of the tailed Amphibia with that of the Elasmobranch Fishes; and, besides my own researches into the development of the skull in *Raia* and *Scyllium* (now being published), I gladly avail myself of the labours of Professors Gegenbaur and Huxley in that and related groups†.

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* In these researches I have been most liberally supplied with materials by the undernamed scientific friends, namely—Messrs. Alex. Agassiz, Flower, Günther, Mivart, Murie, and, above all, Tegetmeier; my specimen of *Proteus anguinus* belonged to the late Henry Christy, Esq., F.R.S., and was given me by his brother, Edmund Christy, Esq.

† The work of the former of these excellent authors here referred to is his 'Untersuchungen zur verglei-

I am also greatly indebted to Professor HUXLEY for his paper on *Menobranchus* (Proc. Zool. Soc. 1874, pp. 184–204, plates 29–31), and his article on the *Amphibia* in the last (ninth) edition of the 'Encyclopædia Britannica.'

But those unspeakably important labours that dovetail into the front margin of my own work are now being carried on by a native worker of the highest ability: I refer to FRANCIS M. BALFOUR, Esq., M.A.*

The reader is referred to the following memoirs, namely:—FRIEDRICH and GEGENBAUR, "Der Schädel des Axolotl (*Siredon pisciformis*)," in the 'Berichte der königlichen zootomischen Anstalt zu Würzburg,' 1849; Dr. ROBERT WIEDERSHEIM on *Salamandrina* [*Seironota*] *perspicillata* (Würzburg, 1875), and his exquisite work, 'Das Kopfskelet der Urodelen' (Leipzig, 1877).

In working out the skull of these forms, then, I have had much more light and help than in beginning the Batrachian skull, besides personal experience considerably enlarged, and new means of research that I have learned from younger labourers†.

In the present paper my endeavour has been to bring into view all the morphological changes or metamorphoses undergone by a tailed Amphibian. But as the Axolotl (*Siredon*), in its occasional metamorphosis into a caducibranchiate Salamandrian, does not even in that give a full measure of the changes undergone by this group, I have added another type, namely *Seironota*.

Moreover the larva of *Seironota* is very instructive, and fills up a lacuna left among my earlier stages of the Axolotl.

Then, as the Perennibranchs are comparable to the larvæ of the Caducibranchs, I have given here the structure of the skull in the lowest type of the former group, namely, that of *Proteus anguinus*—a type in which the form of the Fish is very thinly veiled, and whose relationship to both the Dipnoi and other generalized fishes is evident and unmistakable.

It is in the Amphibia, both tailed and tailless, that the axial elements of the skull are combined with olfactory and auditory capsules that are beginning to show metamorphic modifications, which by plain and evident steps lead us onward and upward, as by a guiding hand, towards the almost untranslatable complexity seen in these organs in the higher types.

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chenden Anatomie der Wirbelthiere' (Leipzig, 1872). Professor HUXLEY's work in this department, here especially referred to, is a paper on the skull of *Ceratodus forsteri* (Proc. Zool. Soc. 1876, pp. 24–59).

* Besides Mr. BALFOUR's part in FOSTER and BALFOUR's 'Elements of Embryology' (London: Macmillan, 1874), I would refer the reader to his following invaluable memoir, 'A Preliminary Account of the Development of the Elasmobranch Fishes' (London: J. C. Adlard, 1874), reprinted from the 'Quarterly Journal of Microscopical Science,' Oct. 1874. Further papers by Mr. BALFOUR on this subject will be found in 'The Journal of Anatomy and Physiology,' vol. x. pp. 517–570 and 672–688. Also by the same "A Comparison of the Early Stages in the Development of Vertebrates," in 'Studies from the Physiological Laboratory in the University of Cambridge,' pp. 1–20 (Cambridge, 1876).

† It is due to my son, Mr. T. J. Parker, to state that in modes of colouring objects, and in making fine sections, his help has been of great value to me.

These things relate to extant and familiar forms; but types like the Urodela, that possess external branchiæ (all for a time, and many persistently) and that never have internal branchiæ, must, it appears to me, be related to groups of extinct forms of low vermiform kinds of Fish, far below any known brain-bearing fishes now existent.

Indeed to me the interest attached to every stage, stage by stage, in these metamorphosing *Ichthyopsida* has been greatly enhanced by the supposition that each of these grades shows me a pattern according to which family after family of the finny tribes was developed—modified, undoubtedly, in these forms by exoskeletal structures that gave the members of each group a perfect fitness for their own conditions of life.

I feel that I need only suggest this view of the matter for it to be accepted by the thinking zoologist and anatomist; the contemplation of such forms as I figured in my last paper, namely, the larvæ of *Dactylethra*, and the larvæ here figured of *Siredon*, unconsciously set the imagination to work in an attempt to pass the great gulf at present fixed between the brainless *Amphioxus* and the lowest brain-bearing Fishes extant, such as the Hag-fish and the Lamprey.

That, however, is not the primary purpose of the work of which the present paper forms a part; the goal aimed at is the interpretation of the skull as part of the Vertebrate skeleton. This, in detail, means to ascertain what relation the cranium bears to the vertebral column, the visceral arches to the ribs, and the subcutaneous cartilages to those superadded arches of the body that sustain the limbs.

The morphological space traversed by a Salamander or Newt in passing from the first fixation of the cartilaginous beams and bars that form its first chondroskeleton, and especially its first chondrocranium, to its adult state is immense; the first grade shows the framework of a fish lower by far than any save the Lancelet, and the last lands us among forms that lie on the border of the true Reptilia.

Here, amongst these types, must the morphologist search for the *alphabet*, and, as the mind learns to arrange the facts, synthetically construct the *grammar*, of his science.

To a great extent the writer has studied the relations of both the nervous and muscular systems as correlated with the skeletal; here, however, he needs much friendly help; that help has already been given in some degree, but most of the work has yet to be done.

On the Skull of the Axolotl.—First Stage. Unhatched Embryos, one fourth of an inch long.

The larva of *Siredon* at this stage is entirely (or almost entirely) composed of cells; but its development is, embryologically, far advanced, for in the head, at least, the greater number of the organs can be made out.

Indeed in the specimen figured, which has been preserved for three or four years in weak chromic-acid solution, very much that is highly instructive could be seen from the exterior; views of these are here given from the side, from above, and from below (Plate 21. figs. 1–3).

A sectional view (fig. 4) throws much further light upon this stage; and altogether we see the condition of the neural axis, the skeletal axis (notochord), the paired sense-capsules, the developing visceral arches and branchiæ, and the opening visceral clefts.

The section (fig. 4) not being exactly in the mid line, only exposes the pharyngeal or branchial region of the alimentary canal, which, however, was developed at a much earlier period; the oral passage is still incomplete.

My work here yokes on to that of the embryologist; the stage which immediately precedes this, as well as earlier stages, can be studied in GÖTTE's magnificent work on *Bombinator igneus*, for the development of the Amphibian embryo, but still more instructively in one of Mr. BALFOUR's papers.

In the paper here referred to ('Studies from the Physiological Laboratory,' pp. 1–20, pl. 1: Cambridge, 1876) the embryo of the Elasmobranch is compared with that of the Amphibian.

The third stage of the Amphibian embryo (fig. 3 C, p. 455) is that which comes in directly before my first morphological stage; this and the other two (A and B) are given by Mr. BALFOUR as "diagrammatic longitudinal sections of *Bombinator igneus*, reproduced with modifications from GÖTTE."

This variously shaded woodcut shows what part the three main layers of the blastoderm take in the formation of the embryo. In the earliest stage (3 A) there was a segmentation cavity, but no alimentary cavity. In the second (3 B) the alimentary cavity is formed, but is closed at both ends, and the segmentation cavity is disappearing. In the third (3 C) the latter has disappeared, and the alimentary canal is open behind; the neural canal opens into it close to this hinder opening, which is the "anus of RUSCONI;" it does not correspond with the proper or permanent anal opening*.

In the third embryological stage the embryo is longer than the diameter of the yolk, which has become elongated and flattened, and is enclosed in a layer of epiblast cells, the future epidermis. Both the head end and the tail end of the embryo, which is like an inverted boat, project beyond the yolk-mass, and, indeed, this mass is now enclosed by a layer of mesoblastic cells inside those of the epiblast. The cephalic and caudal ends of the embryo are curved downwards; and there is a layer of mesoblastic cells both above and below the neural axis, which is swollen where the cerebral vesicles will soon appear. There is no mouth, but at the part below the cephalic end of the embryo the mesoblastic layer is deficient. At this part the closed alimentary cavity is very large; it is roofed throughout by hypoblast, which becomes developed into epithelium.

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* Of the "blastopore" or anus of RUSCONI, Mr. BALFOUR says:—"This is the primitive opening by which the alimentary canal communicates with the exterior, or, in other words, the opening of the alimentary involution. It is a distinctly marked structure in *Amphioxus* and the Batrachians, and is also found in a less well-marked form in the Selachians; in Birds no trace of it is any longer seen. In all those Vertebrates in which it is present, it closes up, and does not become the anus of the adult. The final anus nevertheless corresponds very closely in position with the anus of RUSCONI." ('A Comparison of the Early Stages in the Development of Vertebrates,' pp. 18, 19.)

This must suffice as an introduction to my first morphological stage; but the papers just quoted should be studied before the details here to be given are gone into.

My drawings only reach to the middle of the yolk-mass, a large quantity of which has not yet been used up.

The head is bent down at a right angle by the "mesocephalic flexure." The hind brain (C^3) is long and lanceolate, its direction is straight. The mid brain (C^2) is large and rounded; it is *frontal* in position, forming the actual end of the embryo. The fore brain (C^1) is egg-shaped; it is half the size of the mid brain, and its direction is downwards, with its front margin considerably behind the front of the mid brain. The upper half of the huge hind brain is occupied by the vesicle of the fourth ventricle, and the cranial roof over this part is very thin, showing the cavity in the external views (figs. 1 & 2). These vesicles and their contents are epiblastic products; between them and the epidermis (also epiblastic) there is a stratum of mesoblast which will become differentiated into "cutis vera," cranium, brain-membranes, and vessels.

Rudiments of the chief organs of sense are now visible: the foremost pair are the nasal sacs; they are now circular elevations of the skin, with a shallow, saucer-like depression in the middle; each rimmed rudiment is placed on the hinder part of the lateral depression between the hind and fore brain. Correlated with the budding of the "optic vesicle," right and left, from the fore brain is an elevation of the outer structures; a mass of cells in shape like a kidney, with its notch looking downwards and backwards, is placed in the lower part of the valley which runs between the hind and mid brain. This rough shetch as it were of the outer part of the eyeball shows that the lens is only partially developed.

A very similar mass of cells, but rounder, is seen on the side of the hind brain; at its middle this rounded mass has an imperfect rounded opening above; this is the ear-sac (*au.*), and the opening is the primary involution or "aqueduct."

From the outside, also, we can see the rudimentary, facio-branchial arches, with the commencements, between them, of the visceral clefts, and in front of them, below, that azygous, transverse dehiscence of the facial floor which becomes the "deuterostomatous" mouth.

The mandibular and hyoid arches are marked out externally (figs. 1 & 3, *mn.*, *hy.*); but the arches that follow—the branchials—are largely hidden by the opercular curtain which grows backwards from the hind edge of the hyoid arch (*op.*).

In the side view (fig. 1) the upper part of the mandibular arch is seen as an arched thickening of the facial wall, below and behind the eye, and having a backward bend. In the recess between the thickenings for the eye and the nose there is a small elevation; this is all that is seen at present of the "maxillary rudiment." In the lower view and in the section a band of skin is seen on the front margin of the oral region, *behind* the fore brain; this is the "naso-frontal process"; it becomes the upper lip, but acquires no labial cartilages; ultimately it will have growing into it the fore ends of the trabeculæ in the middle, and laterally their out-turned cornua; these do not exist at present.

Behind the hyoid arch, and partly hidden under its opercular fold, there are, on each side, three dermal vegetations; the first of these is lowest in position, and the last is highest. These are the rudimentary "external branchiæ;" they are decurved, claw-shaped buds, the terminal claw of which is ensheathed in a thick base, which itself gives off two smaller buds externally: thus we have here the first *three* of the branchial filaments.

If we look at the ventral surface of the throat (fig. 3, *cl.* 3–5) we can see three gaping spaces where the skin has undergone dehiscence, and these correspond to the fossæ seen on the inner side of the pharynx (fig. 4, *cl.* 2–5); these clefts are lined on the inside with hypoblast, and on the outside with epiblast, these two laminæ meeting here at these spaces, as in the early "blastopore." The first cleft (figs. 1 & 4, *cl.* 1) is a very small, roundish, thin space, which, as far as I can see, never becomes quite open either in Urodeles or Anura. This cleft is the first to appear in the Shark according to Mr. Balfour (Develop. of Elasmobranch Fishes, p. 539), who shows it in his stage "G." "The alimentary canal in the region of the head exhibits on each side a slight bulging outwards, the rudiment of the first visceral cleft. This is represented in the figure (plate 24. fig. G) by two lines (fig. 1, *v.c.*). The visceral clefts at this stage [a stage corresponding to the one next before my first] consist of a pair of simple diverticula from the alimentary canal, and there is no communication between the throat and the exterior."

The sectional view of the Axolotl embryo shows this diverticulum with three or four behind it; it is a temporary structure in the Urodele, but becomes the tympano-Eustachian cavity in the Batrachia, and is persistently open outside in the Elasmobranchs as the "spiracle;" the "annulus" of the Frog is the counterpart of the spiracular cartilage of an Elasmobranch, which is generally a single "visceral ray," corresponding to the numerous rays on the branchial arches*.

The hyoid and mandibular arches are nearly of a size, and they both project forwards where the two halves meet below; the latter projects most, and in front of this "chin" there is a transverse fossa, somewhat in the form, as to outline, of an hourglass. The section (fig. 4, *m*) shows that dehiscence of the ventral wall has taken place to some degree, and the naso-frontal process forms a "rest" for the mentum. If the lips are parting, the mouth-cavity is still considerably occluded by a mass of cells, that, in this

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* In Gegenbaur's work on the skull of the Elasmobranchs, the "spiracular cartilage" is shown to be single as a rule; in *Scymnus* (plate 11. fig. 1, *kr.*) there are *two*, and in *Centrophorus calceus* (plate 12. fig. 1, *kr.*) there are *three*. Now my own drawings show *four* short external branchial filaments in the spiracle of an embryo of *Scyllium canicula* (which was nearly an inch in length); there can be therefore no difficulty about the homology of the ray or rays growing from that arch as tending to form an operculum to these temporary gills.

In the Batrachia, where the first cleft is much more developed than in the Urodela, although it does not open externally, this mandibular branchial ray, or opercular cartilage, reappears, becoming first crescentic and then circular, and serves for an "annulus tympanicus" in these tribes, whose external auditory apparatus becomes on a sudden, as it were, so highly developed.

bent condition of the head, lie below the apex of the notochord, behind the pituitary floor, and above the cleaving lips*.

The notochord (Plate 21. fig. 4, *nc.*) reaches the pituitary body by its sheath; it is turned downward, and this deflection takes place at both ends (see GÖTTE'S and BALFOUR'S plates). At this stage all obscurity as to the anterior termination of the notochord has vanished, and the solid chromic-acid preparation, whose section is here figured, gave precisely the same results as similar sections of early embryos of the Salmon (see Phil. Trans. 1873, plate iii. figs. 3 & 5, *nc.*). In both these types the watery tissue of the notochord ceases close behind the pituitary body; but its dense sheath passes forwards and upwards beyond the hinder margin of the pituitary body and infundibulum. This Axolotl embryo is at an earlier stage than those of the Salmon, and its notochordal sheath wedges in between the hind and mid brain.

This empty sheath is suddenly folded, as it were, upon itself, and the lower or returning layer develops a cup-shaped process at right angles with the notochord, which forms a well-fitted "rest" for the globular pituitary body (*py.*). This scooped plate, in turn, rests against a loose mass of mesoblastic cells, which are evidently parental to the stroma which afterwards ossifies to form the parasphenoid.

Thus, notwithstanding that the cephalic end of the notochord is, like the caudal end, turned downwards, it seems to seek to grow through the neural region to the upper wall of the head nearly parallel with an ideal line passing through the pituitary and pineal rudiments (*pn.*, *py.*).

The apex of the notochord first straightens, and then acquires more or less of an upward curve. I see this in the embryo of *Scyllium* (11 lines in length), and it is shown in my figured sections (the third, fourth, and fifth) of the embryo Salmon's head. But this is shown very remarkably in the hot-blooded types, as the Fowl and the Pig ("Fowl's Skull," plate lxxxi. fig. 3, *nc.*; and "Pig's Skull," plate xxviii. fig. 6, *nc.*).

I am careful to notice the direction taken by this axial and most fundamental part of the skeleton; around its cranial end cluster most of the difficulties that beset the labourer in this field†.

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* These cells evidently correspond to those described by Mr. BALFOUR as obscuring the view of the notochord in his stage "G" of the Selachian embryo; and as I must now describe the notochord of the Axolotl, it will be profitable to give his observations on that of the Shark. "Another structure which became developed in even a younger embryo than 'C' is now for the first time visible in the living embryo. This is the notochord: it extends from almost the extreme posterior end of the embryo. It lies between the ventral wall of the spinal canal and the dorsal wall of the intestine; and round its posterior end these two walls become continuous with each other (plate 24, G). Anteriorly the termination of the notochord cannot be seen; it can only be traced into a mass of mesoblast at the base of the brain, which there separates the epiblast from the hypoblast." This cell-mass is seen coloured rusty red in the figure of the embryo of *Bombinator igneus* ('Early Stages in the Development of Vertebrates,' plate 1. fig. C 3), and is black in the woodcut in the paper on the Elasmobranchs (p. 545, figs. B, C). With these papers and descriptions before him the reader will much better be able to follow my description and to understand the figure (4).

† The ventral ends of the non-chondrified visceral bars are coloured (fig. 4) to assist the eye; they are becoming quite distinct and solid: below the hinder of these, and in front of the unused yolk-cells, the rudimentary heart (*h*) is seen; it is partly subdivided by a constriction.

The latest observations that I have seen on the origin of the notochord are those made by Mr. BALFOUR (Dev. of Elasm., Journ. of Anat. and Phys. vol. x. p. 682); these quite corroborate his former assertions, namely, that it is developed from the "hypoblast." I must refer the reader to his paper for the proofs of this, and for the views of other anatomists, and proceed to describe the morphology of the Axolotl's skull in the soecnd stage.

Skull of Axolotl.—Second Stage. Embryos unhatched, and measuring from 4 to 4½ lines in length.

In embryos one fourth longer than the last (Plate 21. figs. 5–7) a great change has taken place; the mesocephalic flexure is fast vanishing, and the mouth, now cleft through, is nearer the fore part of the head.

The hind brain (C^3) is now more perfectly roofed in, and is relatively much smaller; the mid brain (C^2) projects but little over the fore brain (C^1).

The mid brain is now symmetrical on its upper surface, being equally divided into two crescentic elevations, placed back to back; these developments in the roof of the mid brain are the optic lobes*.

The azygous rudiment of the cerebral hemispheres now lying near the fore front of the head, the part attached to the hinder margin of the investment of this vesicle is of necessity brought near to the front: this part is the naso-frontal process (*f.n.p.*), and is the rudiment of the upper lip and of the parts within and behind it.

On each side of this naso-frontal selvedge the olfactory rims (*ol.*) are more marked out, but they still retain their place below the head as in Selachians.

The eyeballs (*e*) are almost formed, a fissure existing where there was an open "hilus" before; the distinctly globular ear-sacs (*au.*) still show the primitive opening or involution.

The fore part of the lower lip, and its contained mandibular rudiments, is projected forwards, and being broad makes the mouth to be a transverse cleft, as in the Selachians: but there is a considerable lateral extension of the opening; this is overhung by large labial growths from the so-called "maxillary rudiments;" they resemble the "flews" of a hound.

The elevations caused by the enclosed mandibular and hyoid bars, which did stoop forward above, now lean backward; this direction increases more and more, and then

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* BALFOUR, 'Development of Elasmobranch Fishes,' p. 563. At p. 560 the round fore brain is spoken of as the "impaired rudiment of the cerebral hemispheres;" from these the "optic vesicles," the essential part of the eyeballs, arise. In a note to p. 560, Mr. BALFOUR gives another account of the origin of the "thalamencephalon" to that in Prof. HUXLEY's 'Elements,' where (p. 131) this part, "the vesicle of the third ventricle," is said to arise from the posterior part of the fore brain. The note runs as follows:—"The part of the brain which I have here called mid brain, and which unquestionably corresponds to the part called mid brain in the embryos of higher Vertebrates, becomes in the adult what MIKLUCHO-MACLAY and GEGENBAUR called the vesicle of the third ventricle or thalamencephalon. I shall always speak of it as the mid brain."

lessens; the Urodela, however, go through less of this change of direction than the Batrachia*.

The first two postoral bars, with their enfolding skin, help to make the head very large relatively; and the opercular vallance (*op.*) is now very large, and conceals the lesser or branchial arches to a great degree.

Each of these gill-arches has one gill (one on each side), and these single gills sprout out from the arch higher and higher up.

The opercular fold receives two lesser plaits laterally; for the first gill-arch partly overlaps the second with its gill, and this in turn overlaps the third arch with its gill; the fourth arch is barren.

These three-knobbed, sprouting gills now most resemble the hand of the Aye-Aye (*Cheiromys*), save that they only bear three fingers. This tridigitate condition is not long kept; for the appearance of new buds will result in the production of an elegant branchial feather, of great length; but no new suckers will grow out from the outer edge of the arch, and none appear further in.

The embryos, at this stage, are becoming lively, and soon acquire considerable consistence of their skeletal structure, with their fairly differentiated muscular segments: chondrification has begun.

But the youngest embryo in which it has been possible to dissect and display the nascent skeletal structures was half a line longer than the one whose portrait I have given and described (Plate 21. figs. 5–7). This larger embryo was 4½ lines long (Plate 22. figs. 1, 2). Professor HUXLEY's illustration (Proc. Zool. Soc. 1874, plate xxxi. fig. 1) is from the study of Axolotls one line longer (5½), and corresponds with my next (*third*) stage†.

The results given in the two figures (Plate 22. figs. 1, 2) were obtained from an embryo that had been hardened in absolute alcohol. It was scalped, washed, cleared of all loose tissue, especially brain-cells, stained with carmine, and mounted in glycerine.

The free mandible is given in both figures, but the other arches only in fig. 2, which was drawn as an upper view also, from an object made by slicing away the whole of the lower face. These arches must be conceived of as existing in the object shown in fig. 1, but hidden beneath the basicranial structures.

This is the simplest and most fundamental vertebrate skull I have been able as yet to demonstrate and depict; nor have I seen any thing figured by other labourers that displays so many of the unopened buds, so to speak, that afterwards expand and grow into the complex cranium and face.

Only the inferior arches are chondrified; the corpuscles of the cartilage are

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[*] In that group the mandibular pier has at first its direction downwards and backwards, as in the *first stage* of the Axolotl; it soon becomes nearly *horizontal*, and then, during metamorphosis, swings backwards again, regaining, in the adult, the direction it had during the existence of the mesocephalic flexure.

[†] They were bred by me, and we both worked from the same source. The smallest I supplied my friend with were nearly half an inch long.

large, placed crosswise, and the bars are so small and thin that each cell can be counted.

The only arch that is subdivided is the mandibular, the pier or upper part of which is still granular, indifferent tissue; so also are the trabeculæ (Plate 22. fig. 1, *q*, *tr.*).

There is no cartilage in any of the sense-capsules; the whole cranial cavity is enclosed by a "membrano-cranium," the first morphological stage of this important chamber.

I was not able to work out the cranial nerves; but safe landmarks were found in solid masses of nerve-cells, from which were developing the Gasserian ganglion of the fifth, and, not distinct from it to my view, the geniculate ganglion (5, 7); whilst behind and mesiad of the anditory sac (*au.*) there is the large ganglion of the glossopharyngeal and vagus nerves.

As this specimen was in advance of that whose outward appearance has been just described, the head had become almost straight again; hence the three cerebral regions are now in almost one plane.

Yet the fore brain (C^1) is in front of the mouth (*m.*); the mid brain (C^2) behind both mouth and eyes (*e.*). The floor of the hind brain has all been removed to show the subjacent structures.

The most important of these is the notochord (*nc.*), the dip downward of whose apex is not shown in the figure, nor the ascending process of its sheath (see Plate 21. fig. 4, *nc.*).

Of this massive notochord two thirds belong to the skull and one third to the neck. The two first pairs of muscular segments belong also to the head, but the occipital arch is mere membrane. The investing mass or parachordal cartilages, right and left, will be best seen in my fourth stage; but this notochord is embraced by the trabeculæ, and full half of the cranial notochord will be enveloped by cartilage which is the hinder half of the trabeculæ.

These small, non-cartilaginous trabeculæ are attached, like the horns of an ox, to the fore end of the notochord; they are rounded in front and flat behind. The space whose sides are enclosed by these little rods is not the mere counterpart of the proper "pituitary space;" it is the outline of the vesicle of the third ventricle (or thalamencephalon) which is here marked out. The infundibulum has been cut away from the pituitary body (*py.*), which takes up but little of the room embraced by the trabeculæ. Hence we see that the sudden arrest at this part of the axial structures has arisen from something more than the suspension of the pituitary body; the vesicular mid brain has been a still more important factor.

The morphological meaning of the modified, stunted, non-segmentary axis, and especially of the cartilaginous rods that grow forwards in front of the notochord, is still an unsolved mystery*.

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* The anterior part of the developed trabeculæ for several years seemed to me to be visceral or *pleural*; the base of the septum nasi, the cornua trabeculæ, and the prenasal cartilage, together, appeared to be the foundation of the "intermaxillary arch." (See "Ostrich's Skull," Phil. Trans. 1866, p. 122.)

All that can be done here is to show what parts grow from, and what parts are attached to, these rods. The Axolotl appears to me to be an excellent subject for this purpose.

The fore ends of these bars do not reach quite to the front of the vesicle they embrace, and a space equal to their length divides them in front. Looked at in this view, they do not suggest the idea of serial relationship to the mandibles. A side view (fig. 3, beginning of next stage) lends itself better to such a theory of their nature*.

At present there is nothing that can be satisfactorily determined as to *preoral* visceral arches; but the postoral arches present no difficulty. The first of these, the mandibular, is very large relatively; it is the principal element that goes to form the gates and bars of the face and mouth. The pier of this inverted arch (fig. 1, *q.*) is still mere granular indifferent tissue; it is an incurved, succulent leaf, with its rounded apex or "pedicle" directed upwards and inwards, and the front of its base resting upon its free inferior segment, the cartilaginous Meckelian rod (*mk.*). This stage represents a highly modified vertebrate skull, if the apex of the mandibular pier is the next following attaching point of a "visceral arch" to the apex of the trabecular bar. Now it lies a little outside the fore part of that bar; it grows outwards and downwards, and its free bar (*mk.*) sweeps across the floor of the face, almost at a right angle to the trabeculæ.

The Meckelian rods do not meet by a space equal to a fourth of their length. They are stout, sigmoid cartilages, and fit obliquely to the interior angle of their expanded pier (*q*). Of course they lie in a lower plane than the trabeculæ; this is not so evident as it should be in the figure. A mass of cells (fig. 2, *sp.*) in the inside of each rod is ready to become the "splenial" teeth and bone.

But this free part of the mandible is seen in the next figure (2) to be the first of a series of six pairs of rods. Of these the second pair is a free arch, whose "pier" never develops in this creature, as in many of the Urodela. The last two never segment off a part answering to the lower element of the mandible. This must be made plain afterwards, and the difference between these types (in the development of their pleural arches) and the Selachians fully explained.

The sickle-shaped second pair of rods are the hyoid arch (*hy.*). They are connected at the mid line by indifferent tissue, as are all the rods; no basal piece is chondrified as yet, and the hyoid does not acquire one for itself.

The rest of the bars (*br.* 1–4) are feebler and narrower than the hyoid. They are

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* After Professor HUXLEY had satisfied himself that the whole of the two trabecular rods were pleural, and I had found them in the frog distinct from the investing mass, and also, during the cephalic flexure, dipping so as to be almost parallel with the primary mandibular rods, the question appeared to be settled.

For the last two years or more my doubts have been growing as to the truth of this view; for the trabeculæ do too much work in skull-building to be mere visceral bars. I find also that GÖTTE and BALFOUR doubt or deny their pleural nature. I am inclined to put their "cornua" into that category, and to regard them as undivided representatives of the primary moieties of the vertebral "centra," and as, naturally, developing an undivided neural wall, posterior and anterior, sphenoidal, and ethmoidal.

sigmoid in shape, lessen rapidly in the series, and are so delicate that in some parts they are only composed of a single row of cartilage-cells, arranged crosswise.

The slight shading at the apices of the first three branchial arches shows where the fingered gills arise.

The nasal involution (fig. 1, *ol.*) is becoming differentiated into layers; the eyeball (*e.*) is almost perfect, and the ear-ball (*au.*) shows through its membranous walls seven or eight crystals, the otoconial particles (*ot.*). Behind the ear-sac and ganglion is a gland, evidently the "thymus" (*tm.g.*).

Third Stage. Axolotl "fry" 5 to 5½ lines long.

The process of development takes place rapidly in larvæ that have become free, although they do not increase very fast in size—not above a line in the first week after hatching.

Nevertheless they soon take on the form of the adult perennibranchiate individuals, although the head at first is relatively very large.

The specimen whose skull I now have to describe was only the twenty-fourth of an inch longer than the last; yet its cranial bend was much lessened, and the short lower jaws had grown so as to give the "underhung" form to the face seen in larval *Pipæ* and *Dactylethræ* (Plate 22. fig. 3, *mk.*).

The relationship of the Urodele to the Batrachian is shown in many ways; but the *time* at which any particular morphological stage is attained in either is very different; processes that in one case take weeks, and even months, in the other may be gone through in as many days.

But this is the case to a lesser degree within the margin of each of these groups, so that particular types break the fall from the one to the other.

Here is an instance of the slowness of growth and change of one part and the quickness in another:—In larvæ of the Common Toad (Phil. Trans. 1876) the trabeculæ are as much developed in the first stage as they are in the Axolotl in individuals two thirds of an inch in length, and intermediate between my third and fourth stages (Plate 23. figs. 1, 2, and Plate 22. figs. 4, 5).

But the mandible, its pier, and the relation to it of the hyoid cornu—these are as far forwards in the beginning of my third stage in the Axolotl (Plate 22. fig. 3, *mk.*, *chy.*) as they were in Toads whose metamorphosis was almost complete, the tail having disappeared (Phil. Trans. 1876, part 2, plate 55. fig. 6).

A sphenoidal neural crest has now grown up from the middle of each trabecula; but the hinder end is flat, embracing the notochord, and the fore end rounded (Plate 23. figs. 1, 2, *nc.*, *tr.*).

The mandibular pier inclines very little forward at present. After growing forwards in succeeding stages, it retires somewhat, but in this type never recovers the vertical position. In tadpoles of the Common Frog and Toad at this stage this bar is almost horizontal, but it was vertical in the first stage ("Frog's Skull," plate 3. figs. 2 & 3).

The apex of the pier is thick, its upper part (seen in the figure) is the "ascending process"; the lower spur or "pedicle" is not seen in this view. But from the apex the elbowed part is seen embracing the outer face of the auditory capsule (*au.*). This part is the rudiment of the otic process. It is now, as to this process, quite like a newly metamorphosed Frog or Toad (see "Skull of Batrachia," part 2, plate 55. fig. 6).

The notch on the hinder edge of the quadrate cartilage (mandibular pier) exactly corresponds with the concavity for the condyle of the hyoid cornu of a tadpole; but its position under the ear is attained very late by the Batrachia. In their larva this point is beneath the eye ("Frog's Skull," plate 5. fig. 1, *hy.*).

In an extremely short time the mandible has doubled its relative length (figs. 1 & 3, *mk.*), and from terete it has become flat and steep; it is turned down in front, and the mass of elevated cells seen in fig. 2 have developed into a "splenial" bone and teeth (*sp.*). Moreover the two rami meet at the chin.

The segmentation of the other five rods is now evident, and no other subdivision will appear. The Urodeles divide these arches more than the Batrachia, but far less than fishes (Elasmobranchs especially). There is no segment in any of these answering to the apex of the quadrate or mandibular pier, which in the Skate is distinct, and may be a serial homologue of the "pharyngo-branchials" of fishes; but in some Batrachia, such a segment appears, *sooner or later*, in the hyoid region.

But in this, and in nearly every kind of Urodele, a joint appears near the lower end of the hyoid cornu, the "hypo-hyal." It exists in the Ray (*Raia clavata*), but not in the Dogfish (*Scyllium canicula*), and is present in Osseous Fishes, where it receives two osseous centres. In these, and in the Sturgeon, it is segmented off (M. Micr. Journ. June 1873, plate 20. fig. 1, *h.hy.*), and not indicated merely by a separate bony deposit.

The rest of the hyoid is a flattish bar, gently arcuate, and having now its apex filling in the notch of the quadrate. This apex is the serial homologue of the "angular process" of MECKEL's cartilage (*mk.*). There is no basihyal in these types; but the hypohyal becomes attached to the fore end of the first basibranchial, a part not yet chondrified perfectly.

But the next two arches (1st and 2nd branchials) segment themselves higher up. They have no lower segment or hypo-branchial, so constant in Elasmobranchs, Teleostei, &c., nor does the apex of the arch become detached as a pharyngo-branchial, as in fishes. The longer, upper segment is here the "epibranchial," and the lower, shorter piece the "cerato-branchial"*.

The 3rd and the 4th (or empty arch, *e.br.* 4) are undivided. These are very small rods.

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* As we were working at the same types, Professor HUXLEY and I agreed that this was the proper nomenclature of these segments, which are so named in his invaluable memoir on *Menobranchus* (P. Z. S., Mar. 17, 1874).

The auditory sac (Plate 22. fig. 3, *au.*) shows two masses of otoconial crystals, and its floor is undergoing chondrification.

If the *primordial* trabeculæ have to be eliminated from the pleural category, there is nothing of the kind in front of the mouth at present. But as a long series of more and more imperfect vertebral segments are developed in various types beyond the *secondary* anal opening, so it is no wild search to be looking for rudiments in front of the *secondary* mouth. These will be discussed in the succeeding stages.

In larvæ less than half an inch in length (5½ lines) a still further advance is to be found (Plate 23); but there is no new element*.

The cephalic part of the notochord (Plate 23. figs. 1 & 2, *nc.*) is still large, and full half of it in front is invested by trabecular cartilage. These rods have grown much backward and upward, and but little forward. They are now composed of solid cartilage. They only embrace the sides of the thalamencephalon, and bound it in behind, not quite meeting, being kept apart by the apex of the notochord.

Behind these expansions there is no cartilage, the whole occipital ring being still membranous, and the two muscular segments (*ms.*) being visible from above when the hind brain is removed.

The hind brain is now walled in at the sides by the great trabecular crest (figs. 1, 5, & 6, *tr.*), the height of which is equal to the breadth of the broadest part of the bar whence it arises. The temporal muscle (fig. 6) arises from this crest, and is inserted into the coronoid region of MECKEL'S cartilage.

There is no distinction between alisphenoid and orbito-sphenoid either in Amphibians or Selachians; and there must be some meaning shut up in the fact that the greatest similitude to vertebral segments is seen in the most specialized types of skull. The trabeculæ are oval on section in front (fig. 4, *tr.*), and end opposite the eyeballs on the side, and the junction of the mid and fore brain within. At present, then, the ethmoidal and nasal regions and the lateral "horns" are absent. Only the common, paired rudiments of the posterior and anterior sphenoids are present. There is no "anterior clinoid cartilage," and the "posterior clinoid wall" does not rise behind the small pituitary body (*py.*).

Attached to the under face of the fore half of the free trabecular rod is an oval, bony plate with bristling teeth. This is the palatine bone; and in front of it is a similar toothed plate, the vomer (*p.pg.*, *v.*).

Near the frontal edge of the face, below, a very small pair of bony spicules are set transversely, each bearing two recurved teeth. These are the premaxillaries (*px.*). Between these and the vomer, but further outwards, the nasal sacs (*ol.*) are seen; they are becoming perforated.

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* These minute skulls have received most careful attention, in preparing them for both lateral and bird's-eye views: this has been done by staining some of them with carmine, and by *imbedding* others for sections, and the colouring of such sections with picro-carmine, which gives a rose-pink colour to the cartilage, and makes the bony plates scarlet and the epidermis brown. This latter was my son's work.

The nerve-cells that are becoming the ganglia of the 5th and 7th nerves in front, and the ganglia of the 9th and 10th nerves behind (5, 7, 9, 10, figs. 1 & 2, and 5, fig. 8) are large and conspicuous masses.

The auditory sacs are now chondrified to a great extent below and outside. Prof. HUXLEY'S figure, *op. cit.* plate xxxi. fig. 1, *au.*, shows them as membranous at this stage; but the stained preparations correct this error. A large oval tract above is membranous, and a lesser tract in front of this is granular; the rest is thin cartilage. The base (fig. 2, *au.*) is well chondrified, and the fenestral cleft has not yet appeared. The sections (Plate 21. figs. 8–10) show the structure and condition of these capsules. In fig. 8 the anterior and horizontal canals are shown well in section (*a.s.c.*, *h.s.c.*). Below and in front of the capsule the ganglionic mass of the 5th and 7th nerves is shown (Plate 23. fig. 8), and behind the capsule the ganglion of the 9th and 10th (9, 10, Plate 21. fig. 10).

The large mandibular arch is now well developed, and its pier shows three out of four of its spurs or processes. The pterygoid outgrowth is much later.

As no amount of controversy has sufficed to make Professor HUXLEY'S observations on the mandibular pier quite agree with mine, I shall show what I have seen, stage by stage, gladly naming the regions with his well-chosen terms.

The cartilage of the "pier" closely embraces the front of the ear-capsule; the flattened hinder part, which thins out and is afterwards clamped by the squamosal, is the "otic process" (*st.p.*).

The true apex of the mandible is roughly bifurcate, and the upper knob, which has no counterpart in the Frog, is the "ascending process" (*a.p.*).

The lower knob, which corresponds to the band which in the Frog coalesces with the elbow of the trabecula ("Frog's Skull," plate 5. figs. 1–4, *m.pg.*; see it also *free* in the embryo Salmon, "Salmon's Skull," plate 2. figs. 3 & 7, *mt.pg.*), is the pedicle (*pd.*). It lies *below* the orbito-nasal nerve and the ascending process above it.

Neither of these processes is yet modified by coalescence with the trabecula. The pedicle *never does* coalesce (as in the adult Frog, where it is the only inner process); but the "ascending process" does unite, by cartilage, to the alisphenoidal wall.

Even now the ascending process has come closer to the trabecula than the pedicle; the attachment of the pedicle is now (and always in the Urodeles) to the inner face of the ear-capsule in front. This relationship is secondary in the Frog, whose pedicle wastes above, and then expands further down into a large facet ("Frog's Skull," plate 8, *m.pg.*, and plate 9. figs. 2 & 7, *m.pg.*), whose attachment is to a like cartilaginous surface on the ear-capsule; this surface is a "plaster" derived from the basal plate.

The free mandibular bar (*mk.*) continues to elongate, and it is losing the deflection at the chin. A dentary plate (*d*) is now added to the outside of the rod, besides the dentigerous "splenial."

The series of sections (Plate 23. figs. 3–8 and Plate 21. figs. 8–10) will help to illustrate the present condition of both face and skull.

The *first* (Plate 23. fig. 3) is through the fore brain (C^1) and nasal sacs (*ol.*). Two pairs of bony plates are cut through the vomers (*v.*) inside the nasal capsules and the dentaries (*d.*) near the chin.

The *second* (Plate 23. fig. 4) was made through the front of the mid brain (C^2) and eyeballs. There is no cartilage in the upper lips and cheek, but the terete ends of the trabeculæ (*tr.*) are severed. These have the palatine toothed plate attached.

Below, MECKEL'S cartilages are similarly protected on their inner face by the splenial (*sp.*).

The next section (fig. 5), half of which is shown, is a little behind the last, and shows the orbito-sphenoidal crest of the trabecula (*tr.*).

The *fourth* section (fig. 6) is through the back of the eye and mid brain (*e.*, C^2). In its sensible thickness both the position of the pituitary body (*py.*) and of the apex of the notochord (*nc.*) are shown.

Here the alisphenoidal crest of the trabecula is at its highest. Just in front of the mandibular pier the temporal muscle is seen to pass from this crest to the crested coronoid region of MECKEL'S *cartilage* (wrongly lettered *q*). The transverse floor of the mouth shows *seven* cartilaginous rods in section. Those near the mouth-angle are the hyoid cornua (*c.hy.*), and the cluster in the middle are the first cerato-branchials outside (*c.br.*^{1}); the second cerato-branchials above and within (*c.br.*^{2}), and the second basibranchial below, at the mid line (*b.br.*^{2}). These rods are seen in a full-sized Perennibranch in Plate 25. fig. 5 : that figure will explain the position of these sections.

In the *fifth* section (fig. 7), a little further back, the notochord (*nc.*) is cut through, and we see the descending part of the alisphenoidal crest of the trabecula (*tr.*). Here is seen the great height of the ascending process of the mandibular pier (*a.p.*) and the stunted pedicle. Below these the orbito-nasal nerve is seen cut through.

The pier (*q*) then descends, thick and solid, to the articular region. The free mandible escapes this section, and the flattened upper part of the hyoid (*c.hy.*) is severed.

The second basibranchial (*b.br.*^{2}) is now flattening towards its hind part, and the first two branchials (*c.br.*^{1}, *c.br.*^{2}) are cut through close to their epihyal region.

The *sixth* section (*half*) is through the front of the ear-capsule and hind brain (fig. 8, *au.*, C^3). The trabeculæ and Gasserian ganglion are shown (*tr.*, 5), the otic process of the "pier" (*ot.p.*), the hyoid cornu (*c.hy.*), and an oblique slice is seen of the first epibranchial (*e.br.*^{1}).

The *seventh* (Plate 21. fig. 8) is through the middle of the hind brain and auditory capsule (C^3). Then we have a section of the apices of the trabecular plates at the first third of the notochord (*nc.*, *tr.*). The outer and lower part of the ear-capsule is chondrified, and the anterior and horizontal canals are severed (*a.s.c.*, *h.s.c.*).

An apparently meaningless cavity, lanceolate in section, is seen in this and the next figure, the lower part of which reaches the membranous *inner roof* of the labyrinth. This is evidently the primary involution or "aqueduct."

The mouth-floor shows sections of the same parts as in the last.

The *eighth* section (Plate 21. fig. 9), without the floor, is a front view of a section with some thickness, showing the back of the ear-sac cavity and the thick part of the notochord, behind the trabeculæ (*nc.*, *m.s.*). Here there is only muscle and connective tissue on each side of the notochord. The hyoid (*c.hy.*) has been severed near its apex.

The *ninth* section (Plate 21. fig. 10) is a back view of another section taken between the ear-sacs (*au.*), and showing the ganglia of the 9th and 10th nerves (9, 10).

The front of this section belongs to the back of the eighth. Here the actual apices of the hyoid cornua (*c.hy.*) are caught, but the branchials are not figured. These hind sections explain the two main figures (Plate 23. figs. 1, 2).

Fourth Stage. Young Larvæ ¾ of an inch long.

In this stage the "fry" were nearly twice the length of the last, so that ample time had elapsed for very important structural modifications to appear.

In this stage the pituitary body (Plate 22. figs. 4, 5, *py.*) is halfway between the frontal wall and the occipital condyles; and the cephalic notochord is as long as the prepituitary part of the skull. The front half of the chorda is a long cone with an obtuse apex; the hind half is cylindrical, slightly inclined to the hour-glass shape. There are two equal *parachordal* tracts of cartilage; those which embrace the fore part of the notochord are the slabs of *early* cartilage that form the postpituitary region of the trabeculæ (*tr.*); the *late*, newly-developed cartilages are the moieties of the investing mass, the hinder or Huxleyan "parachordals." These latter are sickle-shaped tracts, whose ends curve outwards away from the notochord. The fore part is sharp, and wedges in between the trabecular plate and the ear-capsule. The hind part is knobbed; it is separated from the ear-sac by the ganglion of the 9th and 10th nerves, and is the rudiment of the occipital condyles. The membranous tract separating these two pairs of cartilage is the primordial boundary-line between the basioccipital and basisphenoidal regions. It is represented in the Mammal, afterwards, when ossification has set in, by the "spheno-occipital synchondrosis."

This primordial landmark, then, separates the occipital from the posterior sphenoidal regions. Its development is very late in the Amphibia. The two tracts appeared to be quite contemporaneous in their chondrification in the Salmon ("Salmon's Skull," plates 1 & 2). They were separate, even in the fifth stage, in that type (plate 4. figs. 2 & 3, *tr.*, *iv.*) in "fry" the second week after hatching; but the ends of the trabeculæ, which overlie the hinder tract (*iv.*), had lost the retiring notochord. In the early stages (plates 1 & 2) they scarcely embraced it at all.

In the Fowl ("Fowl's Skull," plates 81 & 82, *lg.*, *iv.*) the fore end of the investing mass is turned outwards and is truncate, the trabecular apices retire outwards from the notochordal apex, which also retires backwards at the same time.

I do not, then, find these two pairs of basicranial cartilages distinct now for the first time. What is new and suggestive is the immense size of the parachordal region of the trabeculæ, and its earlier birth than that of the hinder plates. Some cause or causes, unknown, have given rise to the anachronism of the vertebræ directly behind the occiput and the trabeculæ on the one hand, and the great occipital ring on the other.

The common sphenoidal wall is chondrified fully a fortnight (perhaps three weeks, even) before the lateral occipital wall. I strongly suspect that the auditory capsules oppress the growth of the occipital ring (or segment), making it to be later in its growth than other parts*.

Whilst the hind brain has only the protection of the implanted ear-capsules, the mid brain has a high wall, the common sphenoidal crest of the trabeculæ; this part is somewhat incurved, but does not form a "tegmen cranii."

The fore brain has merely membranous walls, but it has a cartilaginous floor in front; for the round trabecular rods have become longer and twice as near together in front, and besides this they are conjugated in front by a transverse plate of new cartilage.

This plate has three regions; the middle is the "internasal plate" (*i.n.c*), and the outer pair are the trabecular cornua (*c.tr.*).

These appear first, and lacking a stage, in the Axolotl; to show this I refer to my last Plate (Plate 29. figs. 1, 2), which, happily, shows separate trabeculæ, running to the frontal wall, each giving out a pedate "cornu:" the internasal plate is not yet developed.

These three regions (Plate 22. figs. 4, 5, *i.n.c.*, *c.tr.*) have equal, rounded, front margins; the cornua make a falcate curve; and on their outer edge the nasal sacs (*ol.*) partly rest; the internal nostril (*i.n.*) is seen in this concavity. The primordial pituitary region is now a large oval fontanelle, elegantly regular in form; and this egg-shaped space is about equal in area to the narrower but longer space behind, which is floored on the right and left by cartilage. The roofs of the nasal sacs (*ol.*) are membranous as yet; of the chondrification of the sclerotic I take no note, as it does not graft itself on the basicranial stems; but the ear-capsules seem as closely related to the basilar cartilages as carpels to an axis.

The simple egg-like auditory sac, only partially chondrified in the last stage, has now a complete shell of hyaline cartilage, which has grown big with various swellings that are modelled on the membranous labyrinth, whose three "canals" are now well seen, both in opaque and in transparent preparations of the skull (Plate 22. fig. 4, *a.s.c.*, *h.s.c.*, *p.s.c.*).

Below (fig. 5), the vestibule, with its contained otoliths (*ot.*), swells the general surface; and here the cartilage which was perfectly distributed over the membranous contents has undergone dehiscence.

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* The consideration of *morphological anachronism* is being constantly forced upon me by the study of the Amphibia; this is so great in the common Batrachia, in certain parts, notably the upper parts of the hyoid arch, that Professor HUXLEY himself has not found it easy to harmonize their homologies.

It is as though the cartilaginous coat had been filled to bursting, and giving way, a crescentic cleft, with its convex edge outwards, was formed, a little mesiad of the under surface of the horizontal canal. This space beneath the canal and outside the cleft is the first marking off of the "tegmen tympani."

At the back of this morphological rupture, the fast-increasing otolith is seen, partly floored by cartilage and partly by membrane; the cleft itself is the "fenestra ovalis," opened for the first time in the Vertebrata in this group of the Urodeles.

The thin ragged inner edge of this natural rent, whose lips have been torn by growth and expansion, like the sundering of the leafy rays in the Fan-palm, contains the substance out of which a new morphological element, the stapes, will soon be formed—an individuated leafy bud.

Nor is the mandibular pier of less interest than the metamorphosing ear-capsule; it is "laid out and full of meaning," serving as a key to the modification of this suspensory pier right through the air-breathing *Ovipara.*

This large cartilage, besides grafting its cartilaginous substance on to the alisphenoidal crest of the trabecula, has closely clasped the outer fore edge of the ear-capsule (fig. 4, *a.p.*, *ot.p.*, *au.*). This pedate process ends inwards as a small bud, which, however, grows no further in that direction, but stops against the ampulla of the anterior canal (*a.s.c.*).

The lower part of the apex has grown no nearer to the skull, but it has swollen into an evident condyle in front of the auditory sac (fig. 5, *pd.*).

Thus, the "pedicle" in this case is ready to hinge itself upon the prootic region, below, as it does *after segmentation*, when the apex has been absorbed, in the Frog.

At this stage the otic process exactly corresponds with what is seen in newly curtailed Frogs and Toads: in *Pseudis paradoxa* a like state of things is well seen in individuals with the tail reduced to one third its full *larval* length*.

The lower part or quadrate region is as narrow as the contiguous part of Meckel's cartilage; and this latter meets its fellow at the chin, forming a large, bent bow, united by the raised points of its equal horns.

About four pairs of bony plates have been added to the skull and face, besides the azygous pieces; there are now, in all, nine pairs and two median bones. Some of these subcutaneous bony deposits are brought into more direct union with the chondrocranium than others, but all are drawn to it as by a morphological affinity.

The first of the median bones to be noticed is a deposit which ensheaths the apex of the notochord, like a rudimentary centrum; a narrow bridge of cartilage divides this little bony *cephalostyle* from the pituitary body (*py.*). Under the whole basicranial fontanelle, and also extending back beneath the fore half of the notochord and the trabecular apices, is the thin submucous parasphenoid (*pa.s.*); it is lanceolate in shape.

A film of bone, spatulate above and stalked below, binds down the "heel" of the otic process, and serves as a splint both to the outer face of the auditory sac and the

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* This triple fixation of the mandibular stem, grafted, socketed, and embracing, is in strong contrast with that of the Osseous Fishes, where the simple pedicle is let down to a distance from the skull.

outer edge of the mandibular suspensorium; this is the squamosal (*sq.*), whose name, amongst Fishes, is "præopercular."

On the roof, supplementary to the general deficiency of the cartilaginous "tegmen," there are four nearly equal, thin shells of subcutaneous bone; these are the frontals and parietals (*f.*, *p.*); in this their early deficiency they still leave a lozenge-shaped fontanelle above.

The next five pairs of bones were present in the last (third) stage; the foremost of these, margining the face in front, are the premaxillaries (*px.*); these bones do not yet meet at the mid line, but they have sent upwards a long styloid "nasal process."

The vomers (*v.*) have changed but little; but the palatines are now "pterygo-palatines" (*p.pg.*), for the dentigerous plate in the ethmoid region has sent backwards and outwards a long, sigmoid, ragged, fenestrate plate, without teeth; this is the pterygoid process of the bone; it just reaches the quadrate.

This answers to the "palato-pterygoid" bone of the lower Urodeles, as *Proteus* (see Plate 28. *p.pg.*) and *Menobranchus* (HUXLEY, *op. cit.*); and it is also seen in certain Fishes whose relationship to the Amphibia is most evident and sure, namely the "Dipnoi." In the Batrachia, as in the Sturgeon, there is, from the first, a palatine bone distinct from the pterygoid; and in Osseous Fishes a third primary centre, the mesopterygoid.

The dentary and splenial bones on the mandible (*d.*, *sp.*) have increased in size; and the rod is now ensheathed on its inner side, above, by a rudimentary "articulare."

At this stage we can profitably compare the main nerves with those described by Professor HUXLEY in *Menobranchus* (Proc. Zool. Soc. 1874, p. 191); one description might serve for both.

The olfactory nerves pass to the nasal sacs beneath the nasal processes of the premaxillaries; they are not yet built into a solid wall of cartilage.

The optic nerves pass through the sphenoidal crest of the trabeculæ, and they serve as a landmark to show where the orbital wing begins and where the alisphenoid ends; they are well displayed in the large specimens (Plate 27. figs. 1, 2).

Leaving out of consideration the small 3rd, 4th, and 6th nerves as of minor importance in this research, we find the trigeminal full of interest in this survey.

As in *Menobranchus*, "the orbito-nasal (ophthalmic) division of the trigeminal nerve [fig. 5^1] passes beneath [the ascending process (*a.p.*)], which therefore, morphologically speaking, ascends higher than the eye, inasmuch as the orbito-nasal nerve, as it passes forwards, runs above the optic nerve [Plate 27. figs. 1, 2, 5 ?].

"The orbito-nasal nerve actually leaves the skull by a considerable foramen, common to it and the other divisions of the fifth [fig. 5^2, 5^3], which lies between the trabecula internally and below, the prootic [region] externally and behind, and the parietal bone above. And this foramen is undivided; but, as the ascending process of the suspensorium passes between the orbito-nasal nerve on its inner and anterior side, and the second and third divisions of the fifth on its outer and posterior side, it looks as if the process in question divided the foramen of exit of the trigeminal nerve into two parts.

"The ganglia of the trigeminal and of the seventh nerves are situated, close together, above the trabecula, where it passes into the floor of the auditory capsule—the Gasserian ganglion [Plate 22. fig. 4] lying in front of the anterior wall of the capsule, while the ganglion of the seventh, which is very closely connected with the auditory nerve, is placed rather on the ventral side of the anterior end of the capsule [Plate 22. fig. 5, 7)].

"The posterior division of the seventh nerve (which answers to what is commonly called the facial nerve, and may be termed the *hyomandibular* division of the seventh, runs directly in front of the auditory capsule, and beneath the otic process of the suspensorium [fig. 5, *ot.p.*, 7^2]. The anterior division (palatine or Vidian division) of the seventh [7^1, fig. 5], on the contrary, passes directly forwards, close to the pedicle of the suspensorium, parallel with the orbito-nasal, and below but external to it" (HUXLEY, *op. cit.* pp. 191, 192). The ganglion of the glossopharyngeal and vagus nerve (9, 10) is seen wedged in between the posterior internal face of the auditory capsule and the investing mass (*iv.*). The auditory or eighth nerve cannot be seen in these views; it enters the inner face of the capsule not far behind the Gasserian ganglion.

Before leaving this *4th stage*, I would remark upon the importance of the new *pterygoid* wing that has grown backwards from the dentigerous, primary palatine. In this now enlarged tract we have one bony centre reaching from the quadrate to the vomer. I have already remarked upon the presence of this bone in the "Dipnoi"—a group where we see the dermal plates appearing as *deep layers*, and becoming especially correlated to certain territories of the chondrocranium. We have a similar relation of a few subcutaneous or submucous bones to the cartilaginous endocranium in the low Urodeles and in the larvæ of the higher types.

It is, however, extremely remarkable that in many of the "Sauropsida" one bony bar runs from the quadrate to the vomer—in Snakes and Lizards to the greatest extent, the elongating face necessitating the intercalation of the whole (Snakes) or part (Lizards) of the palatine between the end of this palato-pterygoid bar and the vomer of that side.

In *Anguis fragilis* the palatine intervenes very little, and, contrary to what is general in Reptiles, the fore half of the palato-pterygoid bone is segmented from the hind half to form a "mesopterygoid;" we shall see this state of things higher up.

In *Hatteria* (GÜNTHER, Phil. Trans. 1867, part 2, plate 1, p. 5) there is a long palato-pterygoid bone, undivided, and reaching the whole distance from the quadrate to the vomer of that side. In the Ostrich (*Struthio camelus*) (see my paper on the skull of the Ostrich tribe) the pointed end of the pterygoid scarcely reaches the huge vomer (a double coalesced bone); but in the other types (*Rhea*, *Dromæus*, *Casuarius*, *Tinamus*) these bones meet.

But in the Carinate birds generally (and I have examined and figured these parts in a large number of types) the rule is for the pterygoid bones to grow forwards to the hind part of the vomer (or vomers), and afterwards, as in *Anguis fragilis*, for the pointed anterior part of each to become segmented off as a mesopterygoid. This segment loosed from the pterygoid then coalesces with the upper edge of the inner part of the main palatine bone (" Skull of Ægithognathous Birds," Trans. Zool. Soc. 1875, plates 54–62)*.

Fifth Stage. Young Axolotls $1\frac{1}{4}$ *inch long.*

In this stage (Plate 22. figs. 6, 7) the chondrocranium shows several points in advance of what was seen in the last. The two pairs of basilar cartilages have united with each other and with the auditory capsules, and, leaving out the postmandibular arches, all but the *new parts* are welded together; so that we have now a cartilaginous skull exactly comparable to that of the Elasmobranch (excepting, of course, the lack of the tessellated calcifications).

The occipital condyles (fig. 7, *oc.c.*) are now fashioned, and in front of them the basilar cartilage has sent a lip right and left beneath the notochord (*nc.*). These basilar lips are distinct, and so also are the crests that have grown upwards from the basilar plate to form the *ex-* and *supra-*occipital regions of cartilage (figs. 6, 7, *e.o.*, *s.o.*).

The notochord is not only belted below, it is also capped with the increased and increasing bony *cephalostyle*; a broad selvedge of cartilage also passes between this rudimentary cranial " centrum " and the pituitary body; it is a flat postclinoid conjugation of the trabecular *parachordal* tracts.

The prechordal part of the trabeculæ now exists as a high wall from the auditory to the nasal sacs; and this wall, convex without and concave within, is turned over a little into the roof, and to a greater degree into the floor. But the roof is open from end to end, and the floor is a gaping space for the foremost three fifths of its extent.

But the vicarious exoskeleton keeps up with the requirements of this openwork of cartilage.

The conjugational " internasal plate " (*i.n.c.*) is thickening, especially at the middle, and its hinder margin has become convex; it has retained its relative extent anteroposteriorly; but the lateral leafy growths, the cornua trabeculæ (*c.tr.*), are now large flabelliform outgrowths, having an emargination between them which forms three fourths of a circle. The anterior conjugation of the trabeculæ (internasal plate) may well be the foremost growth of the curiously generalized basilar and neural parts of the skeletal axis; yet, dying out here in the frontal wall, they have sent out a pair of *pleural rudiments*.

But behind the internasal band there is a pair of " pleural rudiments " which are not mere outgrowths. They are separate elements; these are the antorbital cartilages or ethmopalatines (*e.pa.*).

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* We shall soon come to a modification, by segmentation and displacement, of this primary pterygo-palatine bone that will tax our knowledge of these parts and the interpretation of them in a large series of Vertebrate types.

These cartilages are slightly arcuate, and have a forward turn; they have rounded ends, and are broadest above: they are, as far as I have seen, universal in the Urodeles.

Here, again, the Elasmobranchs come in to our help. I have studied their growth in Rays and Dogfish: GEGENBAUR shows, in his invaluable memoir ('Untersuchungen zur vergleichenden Anatomie der Wirbelthiere,' part 3, plates 1–17), that in those types the antorbital is sometimes continuous with the skull and sometimes distinct*.

In Birds also we find an antorbital cartilage, which early coalesces with the antorbital portion of the nasal sac at its lower angle; it chondrifies quite separately from the trabecular (basicranial) bar. In *Corythaix* and *Musophaga* it might easily be taken, in its osseous state, for an "os transversum;" but it runs across the face too far forwards, starting from the ethmoidal and not from the presphenoidal region. In the Passerinæ there is a second pair of *transverse* cartilages, but these are in the middle part of the palate; of these I shall speak in the next stage.

As for the coalescence of the little antorbital bar with the nasal capsule, this does take place even in the Urodela, namely, in *Salmandra maculosa* and *Triton cristatus.*

Another pair of cartilages are to be seen over the nasal sac; these are the foremost of the "paraneural" elements of Professor HUXLEY (*op. cit.* p. 198), who, in discussion with me, spoke of them as upgrowths from the trabeculæ. They soon coalesce with these bars by their lower edge; but I have satisfied myself of their primary distinctness, not only in *Siredon,* but also in *Notophthalmus viridescens* in its larval state.

These crescentic shells of cartilage have their concave edge looking forwards and outwards, and their convex edge looking backwards and inwards (Plate 22. figs. 6, 7, *na.*).

We have all the *essential* elements here, in this stage of the Axolotl, for the morphological development of the nasal labyrinth; superadded parts may come in, as the bony plates which become correlated to or grafted upon the labyrinth; and in many cases there are supplementary cartilages from the "labial" category, but these do not appear in the Urodeles. In the consolidated chondrocranium of the Selachians there is a notable azygous cartilage which grows forwards between the cornua trabeculæ; this is not seen here, but turns up in metamorphosed Salamanders (*S. maculosa*); the bar referred to is large in the embryo bird (the "prenasal rostrum").

Besides general increase of size there is this to be remarked now, in the mandibular pier, that the otic process (fig. 6, *ot.p.*) and the pedicle (fig. 7, *pd.*) are much more solid and massive; the ascending process (*a.p.*) is now of great breadth, especially at its line of union with the skull wall. The articular concavity (fig. 7, *q.*) is now complete.

The chondrocranium is adding fresh bony plates *in the same order* in which they

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* This "lower antorbital" or ethmo-palatine is very common in the Carinate Birds, and I have lately described it in them in papers recently published in the Transactions of the Linnean and Zoological Societies; in these types it is called the "os uncinatum" (Magnus). It is very distinct as a hooked process, both in the "Carinatæ" and in the Emu and Cassowary (see "Ostrich Skull," plate x. fig. 18, *a.i.t.*, and plate xiv. figs. 1 & 7, *a.i.t.*, pp. 151 & 158).

appear in an ascending survey of the Urodeles; the new pair are the maxillaries (*mx.*). These are small dentigerous styles applied to the outer side of the trabecular cornua and nasal roof-plates: in *Menobranchus* there is *sometimes* one of these bones (HUXLEY, *op. cit.* p. 190); in *Proteus* they are absent (Plate 28).

The premaxillaries, frontals, parietals, and squamosals are fast growing into their typical size and shape (figs. 6 & 7, *px.*, *f.*, *p.*, *sq.*), and the parasphenoid (fig. 7, *pa.s.*) is now notched in front and subalate behind; it reaches to the basilar belt of cartilage (*iv.*).

But the pterygo-palatines (*p.pg.*) are most modified; the dentigerous part is now a small territory compared to the long, flat pterygoid wing, which is very narrow in front and gently widens to its oblique end beneath the suspensorium.

This narrow neck between the toothed and toothless regions of the bone is becoming ready for dislocation in the next stage. The only bone that can be as yet called *endoskeletal* is the notochordal "cap."

The free postoral arches need not take our attention for some time to come.

Sixth Stage. Young Axolotls 2¼ inches long.

Every moderate increase of size in these "fry" of the Axolotl is attended with some important and instructive morphological change.

If the metamorphosis of this type was studied for its own sake, irrelatively to the structure and development of the skull in other Vertebrata, it would be fraught with great interest.

But the details of each stage are full of instruction; and when these are compared and commented on, stage by stage, we seem to be acquiring the very grammar of this difficult language, so as to be in a position to decipher these most ancient hieroglyphics.

This stage is perhaps the one which presents us with the greatest number of suggestive conditions in its changed and still changing elements, and nearly every thing one sees here tends to send the mind hither and thither, throughout the length and breadth of the kingdom of the Vertebrata.

The occipital condyles are still more elegantly finished than in the last stage, and the basicranial lips have now united beneath the notochord (Plate 24. fig. 2, *iv.*). The edges of the ascending part of the arch are united now as much, relatively, as they will be (fig. 2, *s.o.*). The trabecular half of the notochord (figs. 2 & 4, *nc.*) is an alate *centrum*, whose jagged bony edges are growing into the substance of the symmetrical cartilages, right and left. This is a "præ-basioccipital" bone; it is not followed by a posterior joint like itself, the rest of the notochord and its investing mass remaining soft. In one important respect this type lies on the level of the "Dipnoi," for it has a pair of small exoccipital bones (figs. 2 & 4, *e.o.*); these are formed as rings round the 9th and 10th nerves (9, 10)*.

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* These bones are very small in *Ceratodus forsteri* (see HUXLEY, Proc. Zool. Soc. Jan. 4, 1876, p. 38) as compared with those of *Lepidosiren*; in the cranium proper these are the only bones that can be called *intrinsic* in those types and in this *larva*.

If we compare this with the foregoing stages it will be seen that the great basal fontanelle has become twice as long (in proportion to its breadth) as it was at first. Its high walls, inbent both above and below, are still unossified; the cross wall (internasal plate) has become a thick mass of cartilage, through the sides of which the olfactory nerves pass obliquely.

The lateral parts now show their morphological meaning clearly; large hollow, cartilaginous crescents cover the inner and posterior regions of the nasal sacs, and the flabelliform trabecular cornua floor the nostrils and form a curved model on which the premaxillaries and maxillaries are grown (Plate 24. figs. 1–3, *px.*, *mx.*, *na.*, *c.tr.*).

In the notch formed by their posterior margin, the internal nostrils appear surrounded by a frame of fibrous tissue and mucous membrane. The primary independence of the curved flap of cartilage behind the simple nasal roof is here well shown (Plate 24. figs. 1, 3, *e.pa.*); it is neither part of the nasal roof nor a mere outgrowth of the trabecular wall: it may *coalesce* with both, as in *Triton cristatus.*

The forward curve of the antorbital is caused by this tendency; it follows the curve of the nasal roof, drawn to it as a tendril is drawn to some stout stem. For in the Selachians it generally runs backwards (GEGENBAUR, *op. cit.*), and it does in *Proteus* (Plate 28); but in the Batrachia it grows both ways, and is like the letter T, the stem running inward and upward.

But the part which I have lately called "ethmo-, pre-, and post-palatine" in *Bufo vulgaris* (Phil. Trans. 1876, part 2, plate 54. figs. 3, 4) in its posterior crus is most probably continuous with another facial cartilage, represented in *Siredon* by a distinct piece or element (Plate 24. figs. 1–3, *pt.pa.*).

This element, which may be called the "postpalatine," is new to me in these low types, this species and this stage having alone yielded it; it is a short flat bar, rounded at both ends, and lying obliquely upon the narrowest part of the pterygo-palatine bone, a little behind the antorbital, and having a similar outward and forward direction. This cartilage is attached by fibrous tissue to the fore part of the pterygoid outgrowth of the suspensorium—the "symplectic" process of the mandibular pier.

A transpalatine cartilage has long been familiar to me in the palate of Passerine Birds (see Monthly Micr. Journ. 1873, plates viii.–x. "Turdidæ," plates xxxiv.–xxxix. "Corvidæ," and plates ii.–xi. "Paridæ;" Trans. Zool. Soc. vol. ix. part 5, Dec. 1875, plate lv. *Corvus* and *Ruticilla*; and Trans. Linn. Soc. ser. 2, Zool. vol. i. plate xxi *Linota* and *Troglodytes*).

This ornithic palatine element, like its counterpart in *Siredon*, belongs to the anterior sphenoidal region, and therefore comes next in front of the mandibular arch, whose suspensory relation is to the posterior sphenoid.

In the Bird this cartilage soon becomes ossified, endosteally, and then rapidly coalesces with a bone (the main palatine) which runs from the front of the pterygoid to the side of the prenasal rostrum. Along *these regions*, then, in *Siredon* it soon coalesces with the *chondropterygoid*, and then, having become the apex of that process, degenerates into fibrous tissue*.

In the fifth stage (Plate 22. figs. 6, 7) the suspensorium gave forth nothing from its front margin, but now there is a long tongue of cartilage (Plate 24. figs. 1, 2, *pg.*), the *chondropterygoid*. This process in its development in the Urodela is curiously like the modifications and stages of the symplectic process of the hyomandibular in Fishes (see GEGENBAUR, 'Selachians,' p. 175, figs. A, B, C, D, E). I have missed that stage in *Siredon* in which the pterygoid was budding, answering to fig. B in M. GEGENBAUR'S woodcut, but I have seen and drawn this stage in larvæ of *Spelerpes* and *Triton*.

The larvæ of Batrachians throw no light upon the interpretation of the pterygo-palatine arcade; for in them it is at first, and indeed for many days, merely a conjugating band between the ethmoidal region of the trabecula and the distal part of the suspensorium†.

So that, equally belonging to both bars, in the larval state, it has to become developed into its adult condition before it teaches any thing. In the Toad (see my last paper) it becomes very instructive, and shows, at least, the independence of the ethmo-palatine.

The huge mandibular pier, which has sucked the life out of the pier of the hyoid arch, now holds to the skull by the broad band of cartilage that has become completely welded to the skull-wall. But below this "ascending process" the "pedicle" (*pd.*) has grown into a ball-shaped bud, which is made to sink into a socket of cartilage just where the trabecula is fused with the ear-capsule; it rests on a bed of fibrous tissue, for there is here (contrary to what we see in the Frog) no joint-cavity (figs. 2, 4).

The otic process (*ot.p.*) is a blunted triangular mass of cartilage, strapped by a fibrous ligament to the ear-sac, and held down by the lathy, splintery squamosal (or preopercular).

The ear-capsule at this stage corroborates the older views of the writer, namely, that the stapes is cut out (or segmented off) from the preformed cartilage of the ear-capsule in the Urodeles. In the last two stages (Plate 22. figs. 4, 5, 6, 7) the inner and anterior part of the fenestral cleft was fringed by ragged cartilage; it is now (Plate 24. figs. 2 & 4, *st. f.o.*) ragged no longer.

There is now a half-severed flap of cartilage, like a *stonecrop*-leaf, which serves as a *stapedial* lid to the vestibular fenestra.

The study of the development of these parts in various Urodeles shows how it is that the pedicle in its stunted condition (*primary* in the Urodeles, but *secondary* in the Anura) articulates with the prootic region of the ear-capsule.

The young of *Triton cristatus* shows clearly that as soon as the parachordal cartilage

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* At present I am not aware of any thing but a *membrane-bone* in this part of the palate in Snakes, Lizards, and Crocodiles—the "os transversum," or osseous transpalatine. The early embryos of Serpents have failed me here; but the development of the skull in the other Reptiles has only very partially been worked out by me.

† Professor HUXLEY will bear me witness that I am not the only morphologist whose mind has oscillated (not once or twice) as to the *independence*, or the *secondary nature*, of the pterygo-palatine arcade.

has become fused with the flat part of the trabecula, the common basal plate so formed plasters, as it were, the antero-internal face of the ear-capsule. In that type the prootic appears early; but when largely spread over the sac, this bone has, covering its fore part, a mass of cartilage derived from the basal plate. The socket for the pedicle is sunk in the lower part of this investing cartilage, and, above, it appears as an outstanding wing over the suspensorium and between the ascending and otic processes*. The seventh nerve (7^2, Plate 24. figs. 2 & 4) escapes from the skull directly beneath this embracing cartilage; the tract in front of that nerve belongs to it, and not to the auditory sac.

In this stage the prootic has not yet made its appearance; nor is it seen in much larger specimens.

The osteocranial elements are just becoming perfect; the squamosals especially (*sq.*) are broadening, and show now that peculiarity of their form in the Axolotl's skull, namely, the fingered splinters at their upper or auditory end.

But the most important thing to be noticed is the segmentation of the small dentigerous palatine from the large pterygoid wing which it had acquired in the fourth stage (Plate 22. figs. 4, 5, *p.pg.*).

Both these newly disparted bones are blunt-pointed where they overlap, having been parted asunder obliquely.

I have long been familiar with the segmentation of the bony bar which in the embryo of *Carinate* birds runs from the quadrate to the vomer. *There*, however, it is the mesopterygoid which is cut off from the front of the pterygoid, to be added to the palatine by ankylosis. *Here* the primary palatine acquires a pterygoid and then moults it again, and the two bones diverge (in the highest or Salamandroid stage) from each other; this will be explained in the *tenth stage*.

The parasphenoid (Plate 24. figs. 2 & 4, *pa.s.*) is now a very elegant and delicate lamina of bone, almost oblong; it has a rounded emargination in front, has basitemporal angular processes, and is rounded behind, where it only ends with the median part of the investing mass; so that it partly underlies the internasal plate in front, and behind reaches the foramen magnum. The rough bony sheath (*o.nc.*) of the fore end of the notochord lies on this bone, and is early more or less united with it. It is seen that both the maxillary and premaxillary form an eave to the adze-shaped trabecular cornu; the former, however, is related also to the nasal capsule and to the outside of the ethmoidal region (figs. 1–3).

Seventh Stage. Young Axolotls 3¼ inches long.

This young Axolotl was 1 inch longer than the last; it shows several things worth notice, and amongst them a curious want of symmetry, right and left, the left auditory

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* Prof. HUXLEY mentions this process in the Siren's skull (Art. "Amphibia," Encycl. Brit. p. 758). It is the "sphenotic" process of the chondrocranium, and is common in Selachian, Ganoid, and Teleostean Fishes. WIEDERSHEIM figures it: see his last work, plate i. figs. 11, 12, *V.F.*

sac being larger than the right, and thrusting the suspensorium further forward (Plate 25. figs. 1, 2, *au.q.*).

In this specimen the notochord showed more on the lower than on the upper side, and the sheath of bone was now unapparent, save perhaps as a slight groove on the parasphenoid; in all the Urodeles this sheath is very evanescent.

The exoccipitals (*eo.*) had doubled in relative size, but I could not detect the prootic centres; this chondrocranium is therefore still the equivalent of that of the "Dipnoi."

A greater approach to the Selachian chondrocranium is evident in the growth inwards of more cartilage in the floor of the skull, making the fontanelle less and less. This is principally in front and at the sides, although, behind, there is more cartilage; this, however, is a very temporary increment; it soon wastes again there. The internasal plate has grown all round, and is very thick and solid at the middle; the nasal roofs are now continuous with it and with the very broad cornua trabeculæ (*c.tr.*). Also we can see a greater distinctness between the fore end of the skull-wall and the precranial growths. Thickening of the cartilage, generally, has caused a greater obscuration of the canals of the ear-capsule as seen from without (fig. 1); below, the *stapes* has become free, and is now a large tongue of cartilage, with its broad end foremost and turned a little inwards. Behind, it does not yet accurately fit to the irregular fenestra ovalis. A bony (intrinsic) centre has appeared in the quadrate region (*q.*); it is spatulate, with the "handle" upwards.

The large size of the left ear-capsule throws that suspensorium further forwards than the other; its ascending process is confluent with the cranial wall; the pedicle is still a knob, and the otic process a large blunt spur below, with a pedate process above.

Now, with the superadded postpalatine cartilages, the chondropterygoid nearly reaches the antorbital (*pg.*, *a.o.*); it is now, relatively, nearly as large as in the Selachian, whose mandibular suspensorium is a swinging quadrate, there being no pedicle or any ascending process, but only a huge chondropterygoid, growing anteromesially.

This bar, in *Siredon*, bears no teeth, and the mouth is armed and surrounded by exoskeletal toothed bones, that have no existence in the Selachian.

The vomers (*v.*) are now longer and more arcuate, and the little, toothed palatine bone is a small distance from the huge "osteopterygoid."

Eighth Stage. Fully grown perennibranchiate Axolotls 8½ *inches long.*

This is a very important stage; it is, indeed, the adult of this species, as a rule; exceptional individuals undergo great metamorphic changes, but mostly this type grows to this large size and retains its gills.

The higher kinds (Caducibranchs) are generally small; and so is the Salamandrian form (*Amblystoma*) which exceptional young Axolotls change into.

As compared with the skull of an *Amblystoma*, this is low and larval; yet it has gained several new things since the last stage, and has become greatly modified in shape.

This chondrosteous skull is a very exact intermedium between the chondrocranium of a Selachian and the osteocranium of a Reptile. Several pairs of bony centres now exist that are intimately blended with, grafted upon, and by ingrowth destructive of, large tracts of cartilage.

But still larger tracts are soft, and only one pair of bones occurs on the inferior arches that have any right to be called endoskeletal, namely the "articular" pieces (Plate 25. fig. 5, and Plate 26. fig. 5, *ar.*).

On the whole this skull agrees well with that of any rather large larva of a Caducibranchiate Urodele.

True to the Amphibian type, there is neither a floor-bone nor a keystone to the occipital arch; the tendency once shown to vertebral segmentation has now vanished, and the notochord, deprived of its bony sheath, has now become a mere thread in the basal cartilage.

On each side of the fontanelle, in front, there is a tract of bony masonry (Plate 26. figs. 3, 4); but for the most part the parachordal and trabecular regions run to the frontal wall as one solid mass of cartilage.

As compared with former stages, the fontanelle is less; but that is due to the huge plate and "horns" in front, for the basal plate (*b.o.*) runs no further forward than the occipital roof; these two territories were extremely unequal (see last stage) (Plate 25. figs. 1 & 2). The upper fontanelle is much larger than the lower, the sides of the latter having grown into the floor considerably; especially in front is the floor cartilaginous, and the two representatives of the many olfactory foramina of a Mammal are conspicuous with their nerve (1) from above.

The exoccipital bones (*e.o.*) are wider apart below than above; but in both cases there is a clear tract of cartilage between them; the cartilage of the condyles (*oc.c.*) looks downwards. Above, these bones run but little in front of a transverse line that might be drawn across the top of the foramen magnum (*f.m.*); but on each side the auditory capsules are largely hardened by them. Also below, shunning the median basal plate, the exoccipitals grow out into a large "opisthotic" shell, which floors most of the vestibular bulb (fig. 4). A little more specialization, and this plate would have become an independent opisthotic centre.

Nearly all the posterior canal and its ampulla is invested by the upper part of the exoccipital bone; therefore that part is an *epiotic region* of the bone.

But the horizontal canal, which burrows the outer edge of the capsule, has its own, evidently independent, periotic centre; this irregular shell of bone, which forms a rough tegmen tympani, is the "pterotic."

The prootic is perhaps the most curious bone of all: it begins as a film on the fore face of the capsule, where the anterior canal and its ampulla is enclosed. During growth it finds its way down to the floor of the front part of the capsule between it and the *plaster of newer cartilage* which was derived from the basal plate, and which persists as a soft socket for the "pedicle" of the suspensorium (*pd.*). But the prootic (which in the Batrachia often vicariously ossifies the alisphenoidal region) here forms a stony coping to the soft hinder half of the skull-wall (fig. 3, *pro.*); it alters but little of the soft wall beneath it, and ends as a spike near the bony ethmo-sphenoidal tract (*e.sp.*). Beneath (fig. 4) there is no such strength added to the foundation of the wall, although the floor, like the roof, has an extraneous source of strength, in the latter derived from the parietals and frontals, and in the former from the parasphenoid (figs. 1 & 2, *pa.s.*, *f.*, *p.*). The stapes (*st.*) will be described with the suspensorium. The ethmo-sphenoid bones (*sp.e.*) are manifestly the lateral rudiments of the Batrachian girdle-bone, without the upper azygous piece (the superethmoid), and left unfinished in their growth. The part formed by the original fore ends of the trabeculæ is here very solid, and is well covered with bone-deposit, which ends abruptly both before and behind, above; but in front on the lower face the bones form sharp wedges, piercing the huge flat underface of the internasal plate (fig. 4). Below, also, they are their own width apart; above, they meet in front of the lower fontanelle and the fore brain, and the olfactory crura rest upon these conjugating processes (1, fig. 3).

At the margin of the upper fontanelle these bones are wide apart; and here the cartilage rises into a crescentic mound, whose concave edge looks backwards on each side; and, in front, the cartilage is bevelled.

In front, the internasal tract ends so as to form a semielliptical notch between the large, flat, trabecular horns (*i.n.c.*, *c.tr.*); on these the reniform nasal capsules are mounted, and with them they are coalesced. The united crura are largest where they have attached to them the small antorbital cartilages (*a.o.*), and the underface of this ethmonasal tract is large, flat, and roughly pentagonal; for below, the "horns," where they become free, are bevelled (fig. 4); they diverge gently, and end in front with a sinuous margin. Above (fig. 3), the naso-trabecular building is very elegant; for these most simple nasal roof-cartilages (first "paraneurals") rest in front on the middle of the cornua, and behind overlap the ethmoidal region; the outer nostril (*e.n.*) is finished behind by a fibrous valve, and not by a cartilaginous labial, as in the Frog.

The inner nostril (*i.n.*) is much further outwards, being external to both the vomer and the dentigerous osseo palatine.

The suspensorium of the mandible is a part of the chondrocranium, and a very large part too, and may be fitly described here.

The quadrato-pterygoid cartilage is now a morphological counterpart of that of the Selachians, with this great difference, namely, that it has three processes attaching it to the cranium that are mostly represented by membrane in them.

These processes, the pedicle and the ascending and otic processes, are, two of them, attached by a strong fibrous web to the basisphenoidal and auditory regions; the ascending process keeps its confluence with the side wall of the skull. That process (figs. 3, 5, *a.p.*) is a thick rod, and it is separated by a shallow groove from the shorter but still stouter pedicle (*pd.*); through the angle of the fork run the Vidian and orbito-nasal nerves. The postero-external or otic process (*ot.p.*), as also the main part of the suspensorium, is convex above and hollowed out below. A large bony spatula now runs upwards and backward from the articular condyle (*q.*) to the top of the front half of the otic process, that is its handle: the broad, lower part takes up much of the cartilage; but higher up it is only a hard wall, with cartilage before and behind it. The otic process ends as a lobe behind, and the lower part of the suspensorium is subalate also.

The condyle is well scooped; its upper edge overlaps the lower. The chondropterygoid is a huge tongue, whose base extends from the hinge, externally, to the pedicle within; it is narrow and terete in front, where it has gained the small postpalatine element, and the blunt point just reaches another cartilage, the antorbital (*a.o.*).

The small osseo palatine (*pa.*) is hatchet-shaped; its blade is on the inside, and its handle behind; this part just touches the "osteo pterygoid" (*pg.*), a large, triangular plate of bone, serving, like the one in front, as a splint to the underface of the quadrato-pterygoid arcade.

The sinuous sides of the bone (figs. 2 & 4) only reveal a little of the cartilage below, which overlaps the bone within and behind; the axes of the two bony plates are coincident.

The suspensorium is tied to the cranium at a fourth place; the stapes (figs. 2, 4, & 5, *st.*) is unusually solid and projecting, its outstanding process looking a little forward. From that process a ligament arises which spreads into a fan-like fascia, which is inserted along the under and outer edges of the suspensorium from the lobe of the otic process to the lobe of the quadrate.

This fascia helps to form the rudimentary tegmen tympani; it lies some height above the portio dura as it passes to the hyoid cornu and the mandible*.

The mandible (Plate 25. figs. 4, 5, and Plate 26. fig. 5) is a large cartilaginous arch, with three bony plates wrapped over it. The dentary (*d.*) is almost entirely external; it reaches nearly to the angle; the splenial (*sp.*) not half so large, but, like the dentary, dentigerous, lies entirely on the inner side; it occupies most of the anterior three fifths in extent. The articulare (*ar.*) forms a trough in which the thicker proximal part of the bar lies; it is principally internal, and reaches nearly to the chin; the thick longitudinal convex condyle rises out of the bone, and appears above it. The quadrate half

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* Professor HUXLEY pointed out this anomaly to me, showing me that this ligament cannot correspond to the "suspensorio-stapedial" ligament of *Menobranchus* (*op. cit.* p. 192). Until quite lately this enigma has remained unsolved; I had found more or less ossified cartilages attached, either directly or by ligament, to the stapes in certain North-American Newts (*Desmognathus fuscus*, *Spelerpes salmonea*, and *S. rubra*); but until I dissected the Menopome they remained uninterpreted.

In the latter type it is impossible to mistake the stem of the stapes (partly ossified where it joins that plate) for any thing else than a "spiracular cartilage," a structure so common in the Selachians (see GEGENBAUR). The spiracular cartilage is an offshoot from the top of the mandibular pier (=the hyoidean and branchial rays of the Selachians), and in the Frog is, during the larval stage, a part of the suspensorium; in that type it becomes separated, and is specialized into the cartilaginous "annulus tympanicus." Professor HUXLEY, in his paper on *Ceratodus* (P. Z. S. 1876, p. 42), rightly compares the spiracular cartilage of *Cestracion* to the "otic process" of the Frog; it does correspond to the permanent process in the metamorphosed Frog (see "Frog's Skull," plates 5–9, where the small mandibular ray, afterwards spiracular cartilage, then tympanic ring, is lettered *s.h.m.*). WIEDERSHEIM ('Das Kopfskelet der Urodelen,' plate 2. fig. 24) represents the facial nerve as passing *over* the stem of the stapes (*op.*); this is an error. I learn from him that the same part occurs in *Cryptobranchus*, *Ellipsoglossa*, and *Ranodon*.

embraces the condyle of the mandible; externally, it seems to lie in it, the hinder part of the articular condyle being somewhat hollowed for the outer lip of the quadrate. The other five arches, notwithstanding their size and solidity, are entirely cartilaginous (Plate 25. fig. 5, and Plate 26. fig. 5); they are for the most part gently arched and oval in section.

In degree of transverse segmentation they are intermediate and between those of the Selachian, where the hyo-branchial series has most superimposed pieces, and those of the larval Batrachian, which has fewest.

In the latter, indeed, the true (inner) branchial arches are distal rudiments of the cerato-branchial pieces, attached to hypobranchial plates; in Selachians (GEGENBAUR, *op. cit.* plates 14–19) there is great subdivision of the bars and permanent separateness.

In these latter types there is so much regularity of these numerous segments, where the hyo-branchial cage is most highly specialized and has its most massive development, that it can be used as an exemplar and rule both for comparison and for nomenclature.

In the Osseous Fishes (see "Salmon's Skull," plate 88. fig. 9) these parts are still more specialized by bony deposit, pharyngeal teeth, &c.; but the segments easily take the same names. The small distal hypohyal (*h.hy.*) of *Siredon* has no representative in its branchial arches, and in the hyoid arch the upper piece or hyo-mandibular is entirely suppressed.

The cerato-hyal (with the small distal segment) corresponds to the free mandible, to which it is attached by the mandibulo-hyal ligament (*m.h.l.*); the hyoid cornu is also strapped to the suspensorium by the hyo-suspensorial ligament (*h.s.l.*).

The next two arches have a suspensorial piece more than twice the size of the lower or free cornu; the next two have no lower segment. In the two large front arches even there is therefore no hypobranchial below nor pharyngo-branchial above. The latter part is represented by a sort of hammer-head to the two middle bars, the first and fourth bowing towards this transverse process (Plate 26. fig. 5, *e.br.*). The two cerato-branchials (*c.br.* 1, 2) are stout, straight styles, the first articulating below to the sides of the basal piece behind, and the next to its end. The three first epibranchials have a long, single, feather-like gill (*e.br.*) attached outside the upper third; these are about the length of the bar from which they arise. The first bar has a snag near where the gill is attached. Tooth-like processes interdigitate between the arch and form the usual gill-colander in this group. The first basibranchial (*b.br.* 1) is a long, oval, thick, high cartilage, rounded in front, and having the hyoid arch attached to it by ligaments. It serves as a conjugational piece for the hyoid and the first two branchial arches. The second basibranchial (*b.br.* 2) has no arch attached to it; it is compressed in front and flat behind, where it becomes spatulate. It is twice as long as the first, and it is the homologue of the so-called "uro-hyal" of the bird*.

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* It should be borne in mind that the suspensorium of the mandible, like the hyo-mandibular (with its symplectic peg), answers to the pharyngo- and epibranchials together. The mandible, the hyoid cornu, and the cerato-branchials also correspond.

Whilst the gills keep their full size and function, this second basal piece keeps its larval condition. Its transformation is a correlate of gill-wasting; when these wither the most remarkable transformations are set up.

Certain investing bones which were appearing in the last stage are now well seen. The prootic and pterotic have been developed *in* the otic capsule, and now the nasals and "osteo-ectoethmoids" (*e.eth.*) have appeared. The nasals (Plate 26. fig. 1, *n.*) are thin shells of bone that form the inner side of the valvular outer nostril (*e.n.*); they are subtriangular, and are wedged in between the nasal processes of the intermaxillaries and the next bone. This bone, the outer ethmoid (*e.eth.*), is here a mere splint; in Osseous Fishes it forms the ossifying plate of the great prefrontal cartilage ("Salmon's Skull," plate 5. fig. 7, *l.e.*). This bone is twice the size of the nasal, is much like the shell of a Mussel or a *Cythere*; it articulates with the ascending plate of the maxillary (*mx.*), and, like the nasal, overlaps the frontal (*f.*). The investing ethmoid and the nasal apply themselves, without ingrafting, to the cartilaginous nasal roof (*na.*). The large semioval frontals (*f.*) creep beneath these bones and the nasal processes of the premaxillaries, and in their turn overlie the parietals (*p.*), which reach the ethmoidal plates. The two great roof-bones on each side are nearly of a size; the parietals have a temporal process and fossa; a notch divides them behind, where they nearly cover the superoccipital plate.

The growing premaxillaries and maxillaries (*px.*, *mx.*) now form a very round fore face; their outline altogether forms half a neat ellipse.

The squamosals are still, like preoperculars, stout and nail-like below, where they bind on the quadrate; they are digitate, with many splintery divisions above, where they thatch the auditory eave.

The vomers and parasphenoid (*v.*, *pa.s.*) are still quite larval; the former are mere arcuate, obliquely placed plates, bearing a rasp of teeth, and the latter is a splintery plank, somewhat scooped above, where it floors the great basicranial fontanelle: almost oblong, it has some little side-growth into the ethmoidal and basitemporal regions.

I have the more carefully gone into the details of this stage because of its morphological interest, as being one good illustration of a perennibranch. When once its very low and primordial gills wither, then a new life crops up in every part of the creature, transforming it both without and within. It is good and profitable for comparison with what is seen in *Proteus*, *Menobranchus*, and *Siren*, but has also many things that are the likeness of what is found in the Selachians and the Dipnoi. It has, indeed, more likeness to them than to its neighbours, the Batrachia.

The next stage takes rank with those Urodeles, such as the great Japanese *Cryptobranchus* and the Menopome, in which the branchiæ almost disappear. These form an intermediate group of great value, which may be called the *Cryptobranchiata*.

Ninth Stage. Large Axolotl ($8\frac{1}{4}$ *inches long*), *with gills reduced to* $\frac{1}{4}$ *inch in length.*

This instructive stage I got from Mr. TEGETMEIR's vivarium. It was about the size of the last, and, metamorphosing late, probably would never have gone beyond the cryptobranch condition.

On the whole, the description just given will serve for this; but there are several points of difference that must be noticed.

The bony deposits and plates are denser, and there is altogether a nearer approach to the Salamandrian type of skull. The hyo-branchial cartilages are as large as in the last, but the second basibranchial has acquired a bony centre (Plate 27. figs. 1 & 5).

The exoccipitals, prootics, pterotics, and spheno-ethmoids (Plate 24. fig. 5, and Plate 27. figs. 1 & 2, *eo.*, *pro.*, *pto*, *sp.e.*) are unaltered. The stapes is now a very solid cone of bone, and its fan-shaped ligament is seen to pass *above* the portio dura to be inserted into the edge of the suspensorium (Plate 24. fig. 5, and Plate 27. fig. 1, *st.* 7). Thus we have here what may may be called a *spiracular fascia*, the counterpart of the spiracular cartilage and bone of the Menopome and others.

There is still a large tract of cartilage in the cranial wall, through the fore part of which the optic nerve (2) passes. The bony tract (*sp.e.*) only reaches to the front margin of the great basal fontanelle, which is margined by a huge tract of internasal cartilage (*i.n.c.*), the outer angles of which have the olfactory crura lying across them.

A great change has taken place in the antorbital cartilage (Plate 27. fig. 3, *e.pa.*). Instead of being a tongue-like flap, projecting outwards and looking forwards, it is now a flat, oval wedge, with its narrow end in front, and closely applied to the articular face of the projection of the ethmoid to which it belongs.

This is a rare condition in the Urodela, for this cartilage generally retains its relative size and coalesces with the back of the nasal roof. In the next stage we shall find the palatine bone assuming a rare condition also, being directed transversely outward, instead of gaining a longitudinal position (Plate 24. fig. 6, *pa.*).

But at present the palatine bones (Plate 24. fig. 5, *pa.*) are more nearly parallel with the axis of the skull than they were. One thing is noteworthy, namely, that there is a definite space between them and the pterygoid bones.

The vomers, premaxillaries, maxillaries, and squamosals all retain their larval condition (Plate 24. fig. 5, and Plate 27. figs. 1 & 2, *v.*, *px.*, *mx.*, *sq.*); but the parasphenoid (*pa.s.*) has become more elegant in form, and is nearer to the state it assumes in the Salamandrian stage (Plate 24. figs. 5 & 6); its ethmoidal region is more outspread, and the basitemporal angles are more definite.

Professor HUXLEY has always contended with the writer for a continuity of both the pedicle and ascending process with the base and side wall of the skull in the Axolotl. This I could never see in the pedicle. I have shown that the ascending process is confluent with the cartilaginous skull-wall; but the pedicle is very short for some time, and never coalesces with the skull. Its relation is to the antero-inferior part of the auditory mass, where that is plastered over with secondary cartilage.

A section through the top of the suspensorium at this stage (Plate 27. fig. 4) shows that the pedicle is quite distinct from the auditory capsule (*pro.*, *a.s.c.*). The section was made *behind* the confluence of the ascending process with the alisphenoidal wall; consequently it also is free in this section.

This section also shows how the squamosal (*sq.*) binds on the outer face of the suspensorium, and the pterygoid bone (*pg.*) on its under face. The substance of the suspensorium is being converted into the quadrate bone (*q.*).

One of the most interesting correlations of structure is that of the second basibranchial with the rudimentary larynx in this group. In the perfect Axolotls (Plate 25. fig. 5) this part is a slightly gapped, broad-edged chisel; it is now a delicate fork (Plate 27. fig. 5, *b.br.* 2). More than the hinder half is ossified—all but the tips of the prongs, and these have the larynx lying behind and between them. They are related to that organ like the single spatulate "urohyal" of a bird*.

This is only a step, however, to complete separation of the second basibranchial from its old attachments (Plate 25. fig. 6, and Plate 27. fig. 7, *b.br.* 2).

These modifications, which have taken place in a full-sized Axolotl, whose gills were only partially absorbed, are but faint indications of what the innate metamorphic energy is capable of performing, when the changes take place timely, so as to convert the Axolotl into a kind of Salamander.

Tenth Stage. Skull of an adult Amblystoma opacum, 3 *inches* 10 *lines long.*

This is a North-American species, closely related to, if not identical with, the form into which the Axolotl changes when its metamorphosis is complete.

The whole appearance of the skull is changed; it is altogether neater, more solid, and its narrowed, more elongate form is much more like that of a Frog.

In fact it has undergone changes quite similar to those which the skull of a metamorphosing Frog undergoes in passing from the short-tailed condition to that of the adult.

Nevertheless the adult skull of the Caducibranchiate Urodeles and that of the Batrachia are very different; the former types belong to a lower and more lateral *fork* than the latter, but both are terminal or culminating. There is no inosculation. Indeed, whilst the Urodeles may be considered as an upgrowth from the Dipnoi, the Batrachia must needs have had ichthyic forefathers, in whom the characters of a Lamprey and a Chimæra were combined ("Frog's Skull," pp. 193, 194).

The process of ossification in the occipito-auditory region has been very intense, and has obliterated all the sutural landmarks.

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* In one of our discussions Prof. HUXLEY controverted my description of the formation of the "thyro-hyals" of the Frog (see "Frog's Skull," p. 172), where they are described as primarily symmetrical and double, because his observations on the Newt showed that its thyro-hyal is formed of a basal azygous piece. They are double, however (as in Mammals), in the Batrachia. That instance, of inferring from the Urodele what would be found in the Batrachian, was parallelled by me when I inferred from the larval Salamander that the stapes of the Frog would be developed by segmentation off of a part of ready-made cartilage taken from the ear-capsule.

But a broad tract of cartilage still divides the two sides of the occipital ring, both above and below (Plate 24. fig. 6, and Plate 27. fig. 6, *s.o.*, *b.o.*).

The ear-masses now stretch outwards as in the Frog and Lizard, and their divergent growths are extended into drooping arms by the addition of the transverse suspensoria, now forming even more than a right angle with the axis of the skull.

The elegant form of the canals of the labyrinth can be well seen in the solid bone that has been fashioned as a mould over them (Plate 27. figs. 6 & 7, *pro.*, *e.o.*). They are, however, partly hidden by the parietals and squamosals (*p.*, *sq.*). The bulging, bony floor of the vestibule forms a widely crescentic bulla, and in the notch the fenestra ovalis contains a small lenticular stapes, the centre only of which is ossified. The spiracular ligament fastens the stapes to the back of the top of the suspensorium (Plate 24. fig. 6, *st.*, *st.l.*).

Further forwards there is an unossified alisphenoidal tract between the fifth and optic nerves (Plate 24. fig. 6, and Plate 27. fig. 7. 5, 2), but the lateral walls are ossified from the optic foramen up to a short distance behind the inner nostrils (*i.n.*). The rest of the endoskeleton is unossified; the cornua trabeculæ lessen considerably after that the vomers have fairly taken their form and pattern; the internasal cartilage (*i.n.c.*) is seen below, with its rounded notch in front of a mimetic notch on the fore margin of the parasphenoid (*pa.s.*). Outside (Plate 27. fig. 7, *e.n.*), the external nostrils are seen to be surrounded by the nasal roof-cartilage.

The roof of the skull is now exquisitely imbricated—all the dense, polished, well-shaped bones overlapping from before backward.

The premaxillary margin, arcuate instead of transverse, passes into the lateral sweep of the long maxillaries (compare Plate 27. figs. 2 & 6, *px.*, *mx.*). The palatal portion of these foremost bones is but little developed, only showing a headland for the close-set teeth. The nasal processes of the premaxillaries (Plate 27. fig. 6, *px.*) are thus visible below (Plate 24. fig. 6). They are well approximated, leaving a chink where the median passage was, and they are large, flat splints, and prefigure, very accurately, those of a bird. The maxillaries (*mx.*) have a narrow palatine edge within the teeth. They have a good face-plate (Plate 27. fig. 7), on which rest the nasal and ecto-ethmoid bones (*n.*, *e.eth.*). As in the Frog, a small rhinal ossification, the septo-maxillary (*s.mx.*), rests upon that part of the maxillary which is articulated to the dentary angle of the premaxillary. The zygomatic process now rivals in height and length that of a high type, such as a Lizard or a Bird; and, exceptionally in this type, it is surmounted at its end by a small seed-like bone, manifestly the jugal (*j.*). There is no quadrato-jugal as in the Frog; but the Urodeles are not of the same stock as the Batrachia. In their ascent, however, they often run almost parallel with them. The nasals (*n.*) are thin shells of bone, with a concave margin towards the nostril, a straight one towards the nasal processes of the premaxillaries, and a ragged, wedge-like hinder margin, which overlaps the frontals, as their outer edge does the ecto-ethmoids (*e.eth.*). These latter bones are now much larger than in the *Siredon* form; they rest upon, and are somewhat overlapped by, the face-plate of the maxillaries. Each bone is twice the size of the nasal. Bending inwards from its fore, broad, overlapped part, it helps to give an orbital margin to the skull in front, and then becomes attenuated where it ends in the middle of the superorbital region, just where the parietal runs under the frontal*.

This very *Varanian* skull has no superorbital or lacrymal on the outside of the dense, large ecto-ethmoid. The frontals and parietals (*f.*, *p.*) are nearly equal in size; they are dense and smooth. The former dip a little towards the median suture, and the latter rise into a very gentle parietal crest. The frontals run under the nose-roofs nearly to the outer nostril; behind they end at a transverse line over the optic foramina.

The parietals (*p.*) form the coping of the skull-wall all along, reaching so far forwards as to underlie the ecto-ethmoidal tiles. A little deficiency appears between the ends of the frontals, precisely where, by more perfect ossification, the Lizard finishes its small pinhole-shaped "parietal fontanelle."

The correlated growth of these now dense and finished parietals to the hind skull and ear-capsules has so completely modelled them over these parts, that it would seem as though they had been applied in a soft state, and then worked on to the subjacent structures.

Although mainly roof-bones, their *parietal* portion is greater than in the Monitor; as in that Lizard there is a supratemporal crest and fossa; and in like manner the edge of the bone is notched gently to fit over the swelling on the prootic caused by the arch and ampulla of the anterior canal.

The junction of the anterior and posterior canals (Plate 27. fig. 6) is just roofed over by the parietals at their posterior angle. They then run transversely across, with dentate edges, overlapping the front part of the occipital roof.

If we would compare the parasphenoid of *Amblystoma* (Plate 24. fig. 6, *pa.s.*) with that of *Monitor*, it should be for contrast. In the latter it is a most delicate style; in the Urodele it is an almost complete floor for the large, flat, barge-shaped skull.

It is roundly notched in front, extended outwards towards the antorbital region, subcarinate in the pituitary region, alate beneath the foramen ovale and Gasserian ganglion, and narrows rapidly towards its transverse hinder end.

The vomers that did but form the back of the narrow arcuate rasp (Plate 24. fig. 5, *v.*) now (fig. 6, *v.*) are leaves of bone, as large as the leafy trabeculæ of the *Siredon*. The row of teeth is arched in the opposite direction, namely, backwards, and occupies only the hind edge of the bone, where it overlaps the parasphenoid.

Each vomer is now roundly notched at its outer margin for the internal nostril.

The oblique outer margin in front fits by a jagged edge against the rudimentary palatal plate of the maxillary.

These vomers are very Batrachian, but they are still larger than in the Frogs and Toads. The relation of the ragged outer edge to the narrow ingrowth of the maxillary

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* If the reader will compare this description and the figures with the skull of a *Monitor* and of a young bird, he will see how nearly this Amphibian skull approaches them.

is quite similar to what are seen in the long-faced Monitor, whose vomers are long, and only moderately broad, planks.

We saw that in the branchial stage the teeth were distributed in two concentric semicircular rows. Those of the premaxillary had the vomerine rows within and behind them, and the maxillary series were similarly imitated by those of the bony palatine (Plate 24. fig. 5). Now all is changed (fig. 6); for not only are the vomerine rasps turned the other way, but the little palatine, with its row, has its gently convex edge looking forwards, and *vice versâ*, the opposite to the row on the vomer, and nearly at right angles to the maxillary series; this type is a "lechriodont."

This little bone, which has turned outwards, like a railway signal, is steep; it helps to surround the inner nostril, and ties the vomer to the maxillary.

This is not a rare condition for the palatine bone of a Urodele; it occurs also in the Batrachia; for instance, in *Ceratophrys*, where it is attached to the under surface of the ethmo-palatine ectostosis.

But as a simple bony plate it may be compared with the palatine of the Monitor Lizard, which has but little longitudinal extent, and, growing directly outwards, forms a second or anterior "os transversum," tying the vomer to the maxillary, as in *Amblystoma*. That process of the pterygoid bone which fastens on to the palatine (nearly reaching the vomer), in the Monitor, is absent in *Amblystoma*; but the apex of its pterygoid runs outwards towards the jugal exactly as in that Lizard. Thus the palatine and pterygoid plates, which were in the larval state one bone, are now far apart, and their axes, which were coincident, are now at a right angle with each other.

Moreover, in the fourth stage, the pterygoid was seen to have arisen as a mere process of the palatine; it is now twenty times the size of the old stock from which it detached itself.

The pterygoid is, like the palatine (or "ethmo-palatine"), composed of a cartilage and a bone; for the palatine dentigerous plate is the bony counterpart (or companion) of the antorbital cartilage; and the pterygoid bone, by using up the substance of the "chondropterygoid," has enucleated, as it were, a distinct epipterygoid cartilage (Plate 27. fig. 7, *e.pg.*) *.

The pterygoid (Plate 24. fig. 6, *pg.*) now binds more completely under the pedicle, which it hides, and the quadrate, or lower part of the suspensorium. The quadrate bony centre has ossified the greater part of the suspensorium, and even the narrowed ascending process is bony (Plate 27. fig. 7).

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* This unossified rod is partly the fixed postpalatine cartilage of a former stage, and partly the anterior end of the tongue of cartilage which grew from the front of the suspensorium.

In the Chelonians and Lizards a similar rod becomes *enucleated* from the indifferent tissue covering the bony pterygoid; this becomes semicartilaginous, and is then invested with a bony sheath. It keeps its half-prostrate posture in the Chelonia, but in Lizards uplifts itself, gradually, to an almost erect position; this "columella" has its base, then, resting on the bony pterygoid, and its capital leaning against the anterior part of the prootic above (*Monitor*), or reaching, *by its upper epiphysis*, to the lower edge of the parietal (*Lœmanctus*).

The direction of the squamosal (*sq.*) shows that the angle formed by the suspensorium with the axis of the skull is more than a right angle; this bone is now a very dense strong plate, knobbed and transversely ridged above and below, spiked in front, and lobate behind.

The squamosal of the Amphibia represents the preopercular and the great "supratemporal" lying over and above it in *Clarias capensis*, both in one piece. But in *Polypterus* (TRAQUAIR, *op. cit.* plate 6. fig. 7, *y*) we have the exact counterpart of the Amphibian squamosal. In the figure referred to there are four "post-spiracular" plates lettered *z* (p. 180); one of these appears on the right side only in *Amblystoma* (Plate 27. fig. 6, *s.t.*). I have seen this bone in no other of the group; but it is as valuable a remnant as the spiracular cartilage of *Menopoma*, *Spelerpes*, and *Desmognathus*.

The bone which Professor HUXLEY calls "angulare" now can claim the title I have all along given to it, namely, "articulare" (Plate 27. fig. 7, and Plate 25. fig. 7, *ar.*). It is not now even a deep trough, merely, for the articular part of the mandible, but has ensheathed the cartilage, converting much of it into bone, and rises high, and turns in considerably, in the coronoid region.

The dentary (*d.*) nearly reaches the angle; it has much less affinity for cartilage than the articulare; it is gently angular in the middle, and roundly inturned towards the mentum. The splenial (*sp.*), with its fine saw-like row of teeth, is slender, and occupies most of the fore half of the inner face of the mandible.

The two rami (Plate 25. fig. 6, *d.ar.*) together form half a long and elegant ellipse; their apposed distal ends are enlarged, and tied strongly together by ligamentous substance.

The shrinking and then the absorption of the gills has been attended with very curious changes of the other arches (compare Plate 25. figs. 5 & 6).

The hyoid cornu (*c.hy.*) was oval in section, therefore thick; it is now a flat tape; it is still attached to the mandible by the mandibulo-hyoid, and to the suspensorium by the hyo-suspensorial ligament (*m.h.l.*, *h.s.l.*).

The hypo-hyal (*h.hy.*) was only a gently attenuating fore part of the main rod, just separated by a tract of fibrous tissue; now it is a very slender terete rod turned backwards from the cerato-hyal by a sharp angle, and it has coalesced with the front corner of the first basibranchial (*b.br.* 1).

The first epibranchial is still a stout cartilage, but the distal piece, or first cerato-branchial (*c.br.* 1), has escaped from it, and thus the upper piece has travelled down to the basal piece.

Moreover, the distal piece is now a mere hypo-branchial as to size, and, like the hypohyal, it has turned up, in the manner of a railway signal, becoming nearly parallel with the piece in front.

The second cerato-branchial and both the next arches are absorbed, and the second epibranchial (*e.br.* 2) articulates with the narrow end of the first basibranchial (*b.br.* 1).

That element is flatter in its front part, which is ossified, and longer in its hind part.

The second basibranchial (Plate 27. fig. 7, and Plate 25. fig. 6, *b.br.* 2) has lost its shaft, and only the bony forks, with soft extremities, remain, as the V-shaped thyro-hyal, now part of the laryngeal apparatus.

It is easy to harmonize this hyo-branchial structure with the so-called hyoid of a Bird. The symmetrical cartilages that form the skeleton of its tongue are hypo-hyals that unite and partly ossify; the so-called basihyal of the Bird answers to the first basibranchial of the Newt, and the hinder piece is the second basibranchial. The long cornua of the Bird are the moieties of the first branchial arch—epi- and cerato-branchials (" Fowl's Skull," plate 87. fig. 11).

I think that the stages of this single type will be considered very instructive by all whose pleasure it is to work out the morphology of the skull; to me it seems to be a lamp giving light to all around.

For want of space I am only able to give the lesser part of my researches into the structure and development of the Urodelous skull; but to add to the supposed value of the account of the type above given, I am anxious to describe the *lowest* kind of adult skull, that of *Proteus anguinus*, and that of one of the *highest*, namely, *Seironata* (*Salamandrina*) *perspicillata.*

The larva of the latter has yielded some important conditions of the ground-plan of the skull, and these will be also described.

Skull of the adult Proteus anguinus.

The simple skull of this the lowest known Perennibranchiate Urodele is in a general way comparable to that of small larvæ of *Siredon*; but whilst in some things it is comparable even to the second stage, just described, in others it has to be compared with the largest gill-bearing Axolotls.

It is, however, in some respects unique, and in others only comparable to the most generalized and ichthyic of the group; the difference between its skull and that of the Caducibranch next to be described (compare Plates 28 & 29) is immense.

The half-ossified chondrocranium (Plate 28. figs. 1, 4, 5), simple as it looks, is not in a *primitive* condition; certain tracts of cartilage have been absorbed so as to give it an appearance of bilateral separateness which it did not possess at first, and, on the other hand, bony deposit has in some places bridged over tracts that were always scant of cartilage.

The fewness of the investing bones is very instructive,—just a few more than we find on the chondrocranium of the Lepidosiren; and these are those that appear first in the larvæ of the higher kinds of Urodeles.

Yet this skull-building would have been but half complete if these "shingles" had not been superadded; for here there is no such free growth of cartilage as is seen in those types (the Selachians) whose dermal bones retain their independence, and show no affinity for the skull.

But few as these subcutaneous hard tracts are, they are brought completely under the influence of the chondrocranium, which, itself also, has acquired the power of converting considerable tracts of its own substance into a hardish kind of bone.

This skull, comparable to that of an Eel or a Snake, has its lateral halves only conjugated slightly before and behind; thus the main part is devoid of any intrinsic floor; the basal fontanelle is very large indeed.

If the hind pair of sense-capsules (*pro.*, *ep.*) were not fused with the skull proper, it would indeed be a feeble framework—just a pair of feebly out-bent bars slightly soldered together at either end, and having the facial rods very loosely swung to each side-piece, the main pair, only, confluent at one small point (*pd.*)*.

The superoccipital ring was imperfect in its cartilaginous condition (Plate 28. fig. 4, *s.o.*); but the bony substance has formed a very narrow keystone. Below, the shrunk and retired notochord lies on a narrow ossified bridge of cartilage, and thus the ring is complete. The condyles (*oc.c.*) are large, non-pedunculate, and look inwards; the large notch between them betokens the presence of an odontoid process on the first vertebra, not the homologue of the mammalian spike, but an aborted intercalary vertebra. The occipital floor is inseparable behind from the parasphenoid, which it thickens postero-laterally, the bony matter running thence into the base of the ear-capsules on their inner side. By the analogy of *Menobranchus* I should suppose that the epiotics were at first distinct; they are not now. The ear-capsules are like egg-shaped fruits, and are very large, relatively; unlike those of most of their order, they show scarcely any impress of the arched tubes and swollen bags within. The whole capsule, like the Diatomaceous *Isthmia*, is composed of two hard cases united by a zonular intermedium; *this* is composed of unchanged cartilage; *they* are the prootic and epiotic bones (*pro.*, *ep.*) (the latter includes the opisthotic), and their appearance is as if they were ready to dehisce transversely, like the pyxidium of the Pimpernel (*Anagallis*). These thin divisions are subequal, the prootic being the larger. Infero-laterally there is a long fenestra ovalis, and its adapted stapes (*st.*) is a long oval shell of bone, a little soft at its narrower front end. The epiotic is roughened with bony granules where it projects backwards as the hindermost part of the skull; in front the capsule is lowest, and the granules mark the uplifted epiotic apicular cap.

Instead of the prootic applying a long wall-plate to the side of the skull, as in *Siredon*, it sends forwards a most minute cup, and into this the end of the trabecula fits. That was not the *end*, but the *elbow* of the bar, whose notochordal outspread portion has been absorbed. As in the Snake, the trabeculæ persist as filiform cartilages; they are

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* Professor HUXLEY's paper on the kindred form, *Menobranchus lateralis* (P. Z. S., March 17, 1874) will be incessantly referred to in this description; whilst writing it I have dissected the skull of one $10\frac{1}{2}$ inches long, and probably somewhat younger than his specimen. In mine there is a superoccipital band $\frac{1}{20}$ of an inch across, and an ossified bridge of cartilage below the notochord, just in front of the foramen magnum. The huge epiotics were thoroughly distinct, which is a remarkable character, as they are generally only a tract of the exoccipital. The absence of bony matter in the sphenethmoid region is very remarkable; the want of cartilage, across, behind the pituitary body, is due to absorption of the flat parachordal apices, or hind end of the trabeculæ; it is not a primitive condition.

thicker towards each end than in the middle, and only become bony in the ethmoidal region (*tr.*, *sp.e.*). Thus, in this respect, these bars correspond with their earliest condition in the other types; in a larval *Siredon* less than half an inch in length they have a high crest; and in *Menobranchus*, where they do not ossify, they are high, or crested.

They are almost absolutely parallel from their prootic cup to their ethmoidal shaft-bone; the appearance of inbending, at the middle, is due to attenuation of the bars. A little behind the inner nostrils (*i.n.*) the trabeculæ gently turn inwards, and this inflected part is two fifths the length of the straight or interorbital part.

But the great lower fontanelle is extended forwards to nearly the middle of the inflected tracts; there the rods are ossified; the rest is soft, and to the frontal wall are almost entirely confluent.

This confluent part is a flat internasal cartilage (*i.n.c.*); it is wedge-shaped. Nearly the anterior third is notched, thus forming two short straight horns, the trabecular cornua (*c.tr.*).

Proximally, on the inflected part, there is on each side a free horn of cartilage; it is gently arcuate, looking outwards and a little backwards; this is the antorbital or ethmo-palatine element (*e.pa.*). The internal nostril (*i.n.*) lies in the obtuse angle in front of this bar, and outside the ossified tract of the trabeculæ; its outer margin is a strong fibrous band or fascia. Inside this opening the ethmoidal bony tract of the trabecula is burrowed by the olfactory nerve (1).

As in *Menobranchus*, there is no cartilaginous nasal roof; these types, therefore, correspond to very young Axolotls, and are below *Siren* and *Menopoma*, the former possessing a small distinct nasal roof-cartilage, and the latter a very perfect cartilaginous capsule, with which the large antorbital cartilage coalesces*.

The next cartilaginous element to be considered is the suspensorium, whose free segment is the mandible or, rather, its pith, the articulo-Meckelian rod.

The direction of this arch and its pier is almost directly forward, as in the newly hatched Axolotl (Plate 23. figs. 1, 2, and Plate 22. fig. 3) and as in Batrachian larvæ.

Also, as in Batrachian larvæ, the suspensorium has only one junctional process at its apex, the pedicle (*pd.*), which is fused with the trabecula below where it is ensheathed by the prootic (fig. 7, *tr.*, *pd.*)†.

The "tuberculum" of this bar, the otic process (*ot.p.*), is a remarkably slender, *free*, digitiform outgrowth; it passes obliquely over the front and outer face of the ear-capsule, the portio dura (7^2) emerging beneath its middle.

The only sign of a pterygoid process is in the rather suddenly convex outline of the flat fore margin of the upper, unossified part of the suspensorium. The lower half is a very solid but compressed mass, ossified save at the scooped articular face; its inner side has the styloid end of the osteo-pterygoid process attached to it (*q.*, *pp.g.*).

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* WIEDERSHEIM (*op. cit.* plate 1. fig. 1, N.K.) figures the skull of *Menobranchus* with a fenestrate nasal cartilage.

† In the abstract of my second paper on the Batrachian Skull (Proc. Roy. Soc. No. 165, 1875, p. 141) it is said that the ascending process only is present; this is a mistake.

The free arches will be described after the bony plates of the skull.

The upper surface of the skull is imbricated with four pairs of long, splintery, bony plates, and the lower surface is faced with two pairs and an odd one; these bones are the counterparts of the earliest bones in the larvæ of higher kinds.

Above and in front, the premaxillaries (*px.*) are seen to be almost entirely composed of the nasal process, the dentary part being only one third the length of these roofing spars, whose hind half covers the apices of the long frontals. These latter bones (*f.*) are wedges more than half the length of the skull; their broad interocular part is gently convex above.

The parietals (*p.*) are of the same length, their fore half wedging in under the frontals; they are still more convex than the frontals, for they form much of both the side walls, as well as the roof of the skull (see fig. 8, *f.*, *p.*, *pa.s.*, *tr.*). Near the ear-capsules they send out the normal angular process; they rise very gently towards the mid line, and their outer superauditory margin is almost straight. Behind, they form an arched emargination, parallel with, and slightly in front of, the foramen magnum above. Both sides, behind, and the hind margin also, are raised and thickened at the edge. Running parallel with and a little outside their outer margin, behind, there runs a pair of bones, the squamosals (*sq.*); the fore half of these plates is free of the cranium, and runs along the postero-external edge of the suspensorium, with the "habit" of a preopercular.

The supratemporal and the preopercular halves of the squamosal are both lanceolate, but the upper half is nearly twice as broad as the antero-inferior. The two halves are united by a slender middle portion, and are gently bent on each other, the arched margin being in front. A little below the middle the concave margin gives off a slender process, at an acute angle, half the length of the lower part; it runs backwards, and is bent also a little outwards, and passing over the seventh nerve (7^2) is attached to the fore edge of the stapes (*st.*).

This may be called the "spiracular process" of the squamosal; it exists in rudiment in *Menopoma*, and is above its spiracular cartilage; in *Menobranchus* it is almost as large as in *Proteus* (Huxley, *l. c.*).

The down-bent part has copied the curve of the suspensorium exactly; the elegant, lanceolate supratemporal part protects the broad cartilaginous zone of the ear-capsule, and runs halfway along the epiotic.

The parasphenoid (*pa.s.*) runs but little short of either end of the skull; in front it is wedged between the internasal cartilage and the vomers (*i.n.c.*, *v.*), and behind it has gradually broadened until it forms a huge floor, whose slightly extended basitemporal angles protect the otic zone, nearly to the fenestra ovalis, on each side; and then with a narrowing margin, five times notched, it underlies and coalesces with the feebly developed occipital floor (*eo.*). The trabecular rods can just be seen outside the edges of the parasphenoid (figs. 3 & 8, *pa.s.*, *tr.*).

The vomers (*v.*) are dentigerous, they have a single outer row of teeth; wedging in behind the feeble, facial, dentigerous parts of the premaxillaries, they run back to the antorbital cartilage, and are one third the length of this skull. The inner nostril (*i.n.*) is outside their hinder part, and they there join the pterygo-palatines (*p.pg.*).

The lanceolate vomers diverge considerably behind, and are slightly out-turned; they form the bony margin of the face in front, as there are neither maxillaries, nor nasals, nor ectoethmoids in this type.

The next pair are of the same length as the vomers; these bones, the pterygo-palatines (*p.pg.*), are more developed here than in *Siren lacertina*, where there is no pterygoid process, the plate being arrested at the same stage as in newly hatched Axolotls; in *Proteus* they correspond with the *4th stage* of the Axolotls (Plate 22. figs. 4, 5, *p.pg.*), in which the short dentigerous bony plate has sent a ragged process of bone backwards into the pterygoid region. In *Proteus* the bone is shaped like a "battledoor," but the handle is pointed; a few teeth run along the middle of the broad part; the pointed end binds inside the suspensorium.

The mandible, as in *Siren*, is very strong and steep; its front three fifths is surmounted by a phalanx of high flattened teeth; its hinder part rises high as a rounded boss of cartilage, which lies in the deep trough of the strong articulare (*ar.*), whose angle is tuberculate, like the epiotic.

The steep strong dentary (*d.*) reaches nearly to this angle; the articulare runs far forwards; but the inner face of the mandible shows much of Meckel's cartilage, unprotected. Here, unlike other Urodeles, there is no "splenial," but there is a rough, clubbed bar of bone in front, formed by ossification of the distal part of the cartilage; and although not distinct from the dentary, it corresponds with the "mento-Meckelian" bone of the wide-chinned Frog.

This absence of the splenial, and ossification of the cartilage in front, is a second point in which this low type agrees with the Batrachia*; the other was its having no "ascending process" above the pedicle.

The hyoid arch also is most anomalous, and but for the ossification of the lower piece, would correspond rather with a Shark than with any known Urodele.

Certain kinds, namely, *Siren* and *Menopoma*, have an upper cartilage (hyo-mandibular); but in them it is scarcely one fourth the size of that of *Proteus*, and is partly confluent with the suspensorium.

In the two former types the upper piece is about as much developed as in *Ceratodus* (HUXLEY, *l. c.* p. 35, fig. 6, *H.M.*). In *Proteus* it is larger than in *Cestracion* (*ibid.* p. 42, fig. 8, *H.M.*) and many times the size of that of *Notidanus* (*ibid.* p. 44, fig. 9).

The hyo-mandibular of *Proteus* (*h.m.*) is a large, short ray, thick and solid above, but scooped on its narrowed, lower part, to form an oblique concavity for the condyloid head of the cerato-hyal. The axis of the whole hyoid is parallel with that of the whole mandibular apparatus; the extended top of the hyo-mandibular is attached to the lower

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* WIEDERSHEIM (*op. cit.* plate 2. fig. 16) gives a splenial to the mandible of *Proteus*.

edge of a large fascia which runs along from the upper part of the suspensorium, behind and beneath the stapes (*st.*) and is attached to the infero-lateral face of the epiotic (*ep.*).

The cerato-hyal is a stout rod, not so thick as the upper piece, and it is invested with a strong ectosteal sheath, all but its extremities; the lower end is bent upwards, and has no hypo-hyal segment, another anomaly in this type; for that is a very constant segment in the Urodeles.

Antero-superiorly, the cerato-hyal is attached by a broad hyo-suspensorial ligament to the quadrate, and by a narrow mandibulo-hyoid ligament to the angle of the articulare (*h.s.l.*, *m.h.l.*).

Proteus belongs to a small minority of the Urodeles that have no *fourth* branchial arch; *Menobranchus* also has only three, and certain lechriodont Caducibranchs, namely *Spelerpes*, have only three, as I find in the larvæ of *S. rubra* and *S. salmonea.*

In *Menobranchus* only the second basibranchial is ossified of all the postmandibular structures; in *Proteus* only one small segment in the middle of the second branchial arch, besides the hyo-mandibular, remains soft.

The first branchial arch (*br.* 1) is very stout; it is normal in having a very long epibranchial and a very short cerato-branchial (*e.br.* 1, *c.br.* 1); its pharyngo-branchial, like that of the second and third, is represented by its unossified apex.

The next, much smaller bar is similar, but it has a short, thick, unossified segment wedged in between the upper and lower pieces; to this the third branchial is attached, and has no lower piece unless the intercalary segment belongs to it. This inwedged piece does not occur in *Menobranchus*, nor in the Urodela generally; in that type the second cerato-branchial is very small.

The well-ossified basibranchials are of the same length; but the foremost is the thicker by far; its fore end is strongly tied to the distal parts of the hyoid (*b.br.* 1, *c.hy.*); the hinder piece is not metamorphosed in relation to the larynx.

This most instructive type thus yields a skull well worthy of being placed between the Dipnoi and the higher Urodeles. Of *sixteen* species of its Order, worked out by me, it is the most abnormal.

On the Skull of Seironota perspicillata.—*First Stage. Larvæ* $\frac{1}{2}$ *an inch long.*

This Caducibranch is one of the smallest I have worked out; the adult is only 2 inches long. It is a native of South Europe.

The larva, besides coming in well as an intermediate stage between my third and fourth stages of *Siredon* (Plates 22 & 23), has also some important characters of its own; characters not so clearly shown in the fry of the Axolotl.

The adult, also, carries the *Salamandrian* modification of an Amphibian skull to the highest level, the *finish* of the cranial building being very perfect, and analogous to what is seen in the skull of the higher Batrachia, and even in the Reptiles.

The larval skull (Plate 29. figs. 1, 2) shows what, a year or two since, Professor Huxley considered to be a thing not known, namely, the perfectly distinct chondrification of the parachordals (*iv.*) behind, from the trabeculæ (*tr.*) further forward.

In the third stage of *Siredon* (Plate 23. figs. 1, 2, *tr.*) the trabeculæ were *parachordally related* to the notochord, taking in full half of its cranial part; but in front they still only reached to the vomers, not up, even, to the nasal sacs.

In the next stage (Plate 22. figs. 4, 5) the parachordals are well developed and *quite distinct*; the trabeculæ, also, have grown forward into the frontal wall; not, however, by the direct elongation of the primary rods, which have now grown only to the middle of the nasal sacs; but a large flat transverse "internasal plate," ending in lunate horns, finishes the skull in front.

There is evidently some difference in the method in which the highly modified *axial skeleton* ends, even among the Caducibranchiate Amphibia; for in *Seironota* (Plate 29. figs. 1 & 2, *tr.*, *c.tr.*) the paired rods grow directly forward, only gently lessening in size, right into the frontal wall; there they send out a small *facial lobe*, the trabecular cornu.

At this stage the internasal plate has no existence; it is formed afterwards by a commissural growth bridging over the space between the two rods.

Already the hind part of each trabecula has coalesced with its counterpart of the other side; so that, now, the point of the notochord reaches only halfway to the pituitary space; this state of things corresponds with that of the fifth stage of the Axolotl (Plate 22. figs. 6, 7). The hind part of the trabeculæ is flat; each, being thin, bends outward and then turns forward, thickening at the side, and gently lessening in width.

The arcuation of each bar is not great; and the two are some distance apart, even close to the frontal wall. The hinder half of each has arisen into a sphenoidal crest, which curves inwards, above, fitting itself to the dura mater. There is just a perceptible groove between the rod and its cornu in front; for the process is thick and is hooked outward and backward.

Instead of the proper parachordals, coming up close to the notochordal part of the trabeculæ, as in the fourth stage of *Siredon* (Plate 22. figs. 4, 5), there is an ample space running athwart the floor of the skull obliquely between them, entirely composed of membrane. These spaces are two thirds the size of the parachordals or moieties of the investing mass (*iv.*).

Each moiety is concentric in shape, turning its concavity to the ear-capsule; but the opposite side is scooped, for there is a rudiment now of the ascending part—the occipital wall.

Below (fig. 2), the halves of the basal plate run somewhat under the notochord, and closely embrace it above (fig. 1); thus the axial rod can be fully seen only on this aspect. This rod is composed of two parts, that are more sharply defined than in any other species I have examined as yet.

The foremost part of the notochord is a high, blunt-topped cone; the second is roughly hourglass-shaped, that is to say, it is exactly like the notochordal axis of the succeeding vertebræ, whose arches are formed of a pair of cartilages, manifestly the *serial homologues* of the parachordals that form the occipital ring.

The faintness of this attempt to form *cranial vertebræ* is displayed in a peculiar manner; for the conical segment is enclosed in an ectosteal bony sheath, exactly like that on the first following vertebræ of the spine; this is what may be called a *cephalostyle.*

But the neural laminæ of the cephalostyle are formed by the trabeculæ.

The second occipital segment, so well defined, and so perfect in shape, has *merely calcareous grains* dispersed over its surface, and exactly resembling the semicrystalline points that gather and cluster round ossifying cartilage-cells.

Although a bony cephalostyle occurs very constantly in the larvæ of Caducibranchs, this is yet the most perfect I have seen; in *Salamandra maculosa* it seems to be a tubular process of the parasphenoid, and in all it is *transient*, only continuing for some stages as a groove with lateral ridges on the upper surface of the parasphenoid.

It is as well to say at once that here, in these types, the first segment belongs to the postpituitary region, therefore to the hinder half of the basisphenoid, and the second only to the basioccipital*.

In this species the first *vertebra* is a large joint, as large as its successors; but in several Caducibranchs there is a structure in this part, so curious and instructive, that I must mention it here; although the copious illustrations of these types, prepared by me, must wait for publication at some future period.

The Common Newt (*Triton cristatus*), *Spelerpes salmonea*, *S. rubra*, and *Notophthalmus viridescens* have shown me this structure most clearly in their larval state.

There is a deep notch between the occipital condyles, which, like those of the large vertebra to which they are articulated (its "pro-zygapophyses"), are pedunculated.

Where the notochord lies between the occipital condyles, there the parachordal cartilage is deficient, for a time; but a small oval *posterior parachordal* arises on each side. As the peduncles of the anterior articular facets of the first vertebra are very long, there is a considerable tract of the notochord left uncovered, in front by the parachordals, and behind by that vertebra.

That tract acquires its own bony sheath; the small, intercalary parachordals become separately ossified, like the exoccipitals, and then coalesce with the anterior end of the long notochordal style.

We thus get what at first sight appears to be a mere "odontoid process," but which is a true vertebra, having all the essential elements thereof†.

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* I am now satisfied that in the Vertebrata, generally, the hind part of the trabeculæ, which *lies upon* the front part of the parachordals, is the source from whence the posterior clinoid wall grows.

† See Professor HUXLEY's article "Amphibia," Encycl. Brit. vol. ix. p. 752. After saying that a similar process is seen in the Rays, he goes on to say, "The first spinal nerve which has the distribution of the hypoglossal of the higher *Vertebrata* passes out of the spinal canal either between the first and second vertebræ, or through the foramen in the arch of the first, in the *Amphibia*, which have no proper suboccipital nerve. This is a very curious circumstance, and requires elucidation by the study of development."

I cannot help thinking that both the intercalary vertebra, just described, and also the one through or behind which the hypoglossal or suboccipital nerve passes, are both undifferentiated from the occipital arch in the

In the presence of such curious facts as the skulls of larval Caducibranchs disclose, the mind naturally seeks to know what have been the factors in that marvellous modification of the axis seen in the skull of a Vertebrate animal. I shall reconsider these things in my "Summary."

The auditory capsules of the larval *Seironota* (Plate 29. figs. 1, 2) are thoroughly chondrified, and well show the form of the enclosed membranous labyrinth, with its three canals above (fig. 1, *a.s.c.*, *h.s.c.*, *p.s.c.*), and the crescentic slit, becoming the fenestra ovalis (fig. 2, *f.o.*), below.

Mesiad of this oblique *rent* in the capsule the ragged and imperfect cartilage has not yet formed itself into a stapes.

The suspensorium has all its three upper processes formed; and the ascending (fig. 1, *a.p.*) is grafting its apex on to the alisphenoidal crest. The pedicle (fig. 2, *pd.*) is blunt and rounded; a considerable space separates it from the trabecular convexity.

The otic process (*ot.p.*) is equally well seen in both aspects; but above (fig. 1) it sends forwards and inwards a pedate lobe that cleaves close to the ear-sac against the anterior ampulla, its normal terminus.

The lower surface is gently convex; but the upper is hollowed, relatively, to the ascent of the otic and ascending processes. The direction of the clubbed quadrate region is forwards, and so far outwards, that a line, parallel with the axis of the skull, which should pass through the otic process behind, would cut the inner face of the condyle in front.

Both the articular faces are somewhat convex and then sloping, the movement of the articular end of the MECKEL's cartilage (*mk.*) on the quadrate being loose and free, like a Cow's jaw.

The two cartilaginous mandibles make the face somewhat *underhung*; together they form half an ellipse, and become small, by degrees, to the chin, where they are united by fibrous tissue.

In this early state we miss the pterygoid process of the suspensorium, and the ethmo-palatine visceral rudiment.

Bony laminæ are fast appearing over this simple chondrocranium. Above (fig. 1, *f.*, *p.*, *sq.*, *px.*, *d.*, *sp.*) we see these films, that already have taken on the outline and form of the frontals, parietals, squamosals, premaxillaries, dentaries, and the dentigerous splenials.

The articulars, nasals, ethmoids (outer and inner), the exoccipitals and the prootics, none of these have appeared.

Beneath (fig. 2, *pa.s.*), the large parasphenoid is flooring the unfinished skull with its open rafters (*tr.*); and in the olfactory region there is a triangular tract of teeth on

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higher Vertebrata. I have long ago shown that the notochord of the early chick is *submoniliform* ("Fowl's Skull," plate 82. fig. 3); and it is not an unscientific use of the imagination to suppose that the Sauropsida and the Mammalia have a series of three or four, or even more vertebræ suppressed in the region of the cranial notochord.

each side, adhering to the trabecula, its point in front, and its notched base behind (fig. 2, *v.*, *pa.*). This little crop of teeth is being attached to an undergrowth of bone-cells; the antero-external part is vomerine, and the postero-internal part palatine; they arise, however, as one single upgrowth of pointed, recurved papillæ, that rapidly become denticles.

In such a skull the main nerves are easily seen (figs. 1 & 2; 5, 7, 9, 10); their size, relations, and distribution are precisely like those of *Menobranchus* (Huxley, *op. cit.*) and those I have just described in *Siredon*.

The postmandibular visceral arches are conveniently studied as a separate object in this *micro-morphological* work.

The upper, or hyo-mandibular element never appears in this species; the lower cornu (fig. 3, *c.hy.*, *h.hy.*) is a flattish sigmoid bar, which is blunt-pointed after it has become broad above. Below it is more terete, and a short distal segment, the hypohyal, is evident; each hypohyal is attached by a ligament to the fore end of the first keystone piece of the branchial apparatus.

There are four branchial arches, the last gill-less, and these are conjugated by two azygous pieces (fig. 3, *br.* 1–4, *b.br.*).

These bars rapidly lessen backwards, and the hinder two are unsegmented; the segments in the front two are a short ceratobranchial (*c.br.*) and a long epibranchial (*e.br.*); the last two have no ceratobranchial part or region, and are carried on the third. Both the ceratobranchials articulate with the first basibranchial, which is twice as large as the second or free hind piece (*b.br.* 1, *b.br.* 2).

Last Stage. The Skull of the adult Seironota perspicillata.

The changes through which this larval skull has passed must be conceived of as essentially like what I have described in going through the various stages of *Siredon* to that of *Amblystoma*.

If not in this, yet in several others, I have traced every important change.

The general form of the adult skull is oval as to outline and very flat, and is no larger than a "Ladybird"; it is yet a very finished structure, and represents, very fairly, the culmination of the Caducibranchiate type of skull. Each bone, like the composite cranium, has its own perfectness.

The three capsular regions are almost of equal length (Plate 29. figs. 4, 5, 6); the *optic* is modified, in the Urodele, mainly as a recess; the *nasal* roofs are cartilaginous and almost entirely hidden by outer bones; but the *auditory* sacs are the largest, are densely ossified, and freely exposed.

The occipital arch is strong and largely confluent with the ear-masses; above, its two bony halves meet and unite by an irregular, short, superoccipital suture, which is somewhat overlapped by the parietals (fig. 4, *e.o.*, *p.*).

Below (fig. 5) there is a wider space between the two half-rings; and in this synchondrosis there is no visible trace of the notochord and its evanescent vertebral segments.

The suboval, convexo-concave condyles (*oc.c.*) look mainly downwards and a little inwards; they have a very short neck.

More of the ossified endoskeleton is hidden by the single parasphenoid below than by the paired parietals above.

One large and some lesser teeth of a suture can be seen between the prootic (*pro.*) and the epiotic overgrowth of the exoccipitals. I say *overgrowth*, because in these Caducibranchs I find no separate epiotic or opisthotic, both these regions gathering bone from the edge of the exoccipital.

The prootic ossification (*pro.*) is very large; it occupies all but the hinder fourth of the capsule; and it is remarkable that the only part unossified by it (except that which belongs to the exoccipital) is on its anterior face (figs. 4 & 5), from the front of the anterior ampulla to the facet for the pedicle. The stapes (*st.*) is a little bony lozenge.

The soft tract is due to an ensheathing of the capsule by the basal plate; thus the pedicle articulates with that, and not with the proper capsule.

The chondrocranium is like a little boat with the bottom out, but replaced by an extraneous plank, the parasphenoid (*pa.s.*). The sides of this boat-shaped skull are hardened by ossification, the cartilage ultimately yielding to true bone: this bony tract reaches from the prootic and foramen ovale to near the internal nostril (*i.n.*); it is deficient above, from the optic foramen (2) to the ear-capsule.

I know of no Urodele in which an overlying "supraethmoidal" bone conjugates into one "girdle-bone" these two lateral tracts or "sphenethmoids," although *Siren* has two such superficial plates, and the Menopome one.

The rest of the chondrocranium is cartilaginous; it consists in the Urodele of the nasal roofs, coalescent with the internasal plate, or the remainder of the trabecular cornua in front of the unossified wall of the skull or of the sphenoethmoidal tracts.

Behind the internal nares (*i.n.*) there is a thick lip of cartilage, the antorbital or ethmo-palatine (*e.pa.*); it is confluent in the adult with the nasal capsule. In the larva (figs. 1 & 2) it had not appeared.

Part of the nasal roof can be seen in the outer nostril (*e.n.*)*. Up to the ethmoidal region the skull is very bony; in some, as *Salamandra maculosa*, there is a band of cartilage, across the floor, some distance in front of the parachordal region, which is ossified by the prootics; in *Triton cristatus* this band vanishes in the adult.

In Osseous Fishes this part is large, and is ossified by the prootic, forming the *prootic bridge* ("Salmon's Skull," plates 7 & 8); it is formed by the *trabeculæ*; and thus there is in many types a perfectly clear distinction between those bars and the investing mass throughout life.

The roof of the skull in the adult *Seironota* is a strong piece of masonry.

The parietals (figs. 4 & 6, *p.*) are about the size of the frontals (*f.*); they are

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* In a future communication I shall show the condition of the chondrocranium in the adult *Triton* and *Salamander*, after the outer bones have been removed.

perfectly distinct from each other and from the frontals. Each bone has a raised line, or low crest, outside its middle, the shelving part outside the ridge being part of the temporal fossa.

The coronal suture between the parietals and frontals is sinuous, and projects forwards in the middle. The abrupt coronal junction of the parietals and frontals is a great advance upon the perennibranchiate type of skull, where the parietals run under the frontals up to the prefrontals.

The frontals are quite distinct from each other; they become deficient at the middle, in front, but are very large behind.

Each bone has a median elevation, like that on the parietals; but outside the ridge the bone is grooved and multiperforate; outside this groove there is a strong and well-formed superorbital ridge, which makes a good crescent with the bone in front.

The parietals (fig. 6, *p.*) run into the wall of the cranial cavity, and are not mere roof-bones; the frontals (*f.*) do this still more perfectly; they have a good orbital plate.

Part of the roof and the front part of the orbital edge is formed by the *external* prefrontals. These (*e.eth.*) are strong bony wedges, thrust in between the frontals and nasals (*n.*); they reach the open fontanelle, inwards.

The nasals (figs. 4, 6, *n.*) are irregularly lobate shells of bone; they cover the nasal capsules, which are here as wide apart as in the Selachians; they are fairly fixed on between the prefrontal behind, the maxillaries externally, and the premaxillaries in front.

The latter bones (*px.*) close in the cranio-facial box; in front they remain separate, have very short nasal processes, between which and their body there is a foramen; and they have a large, well-developed palatine plate (fig. 5). Each bone projects so as to leave an emargination in the front of the face; together, they largely help to form the elegant semielliptical *upper jaw*, which is dentigerous up to the commencement of the zygoma.

Each bone, externally, forms the antero-inferior third of the outer narial opening (fig. 6, *e.n.*), to which it gives a thickened rim; this opening has a triradiate series of sutures, the two hinder of which separate the maxillary from the premaxillary below and the nasal above, the other is between the nasal and premaxillary.

The maxillary now (figs. 4–6, *mx.*) is a large, well-grown bone; it has a high, outer facial plate, a considerable palatine plate (fig. 5), and its dentary edge runs for half the extent of the bone, which ends behind in a large, arcuate, zygomatic process.

In this, perhaps the smallest of adult Vertebrate skulls, I can discern no septo-maxillary, although it is very common in the Caducibranchs.

The next bones to be described are the vomers (fig. 5, *v.*); but I must first remark upon the large opening (*m.n.c.*) at the mid line between these bones and the palatine plates of the premaxillaries.

In the Salmon ("Salmon's Skull," plates 7 & 8, *m.n.c*) there is a median nasal canal; and this evidently *Petromyzine* structure is very constant in the Caducibranchs; it is surrounded by bone, and appears in *Spelerpes* as a *well* walled round by the nasal process of the azygous premaxillary.

In *Seironota* (figs. 4 & 5, *m.n.c.*) it is behind the palatal plates of the premaxillaries and between the great vomerine blades (*v.*). Above, it is seen in the middle of the precranial fontanelle. We see that this skull is much like that of a Shark, as to the position of the fontanelle and the separation of the nasal roofs.

As in the larva, so in the adult, the vomers and the palatines are continuous; but, for the same time during the latter part of larval life, they were distinct. The curious behaviour of the dentigerous palatine, after it has once become independent of the vomer, may be traced in all the higher Urodeles.

We have seen that in *Siredon* this bony tooth-bearing plate sent backwards and outwards an edentulous process, and that that untoothed part became the larger bone by far, and was segmented from the part from which it sprung.

The same thing has taken place here; but *Seironota* agrees with most Caducibranchs in having its dentigerous palatine become confluent with the end of the vomer just where it has retained a few teeth, and not turned outwards, as in *Amblystoma*.

All the fore part of each vomer is now a large toothless blade of bone, forming, with its fellow, much of this very strong, *hard palate*, and elegantly notched at its side for the inner nostril.

The sutures on this palate, like the bony plates, are of great extent; the edges of each vomer are denticulated; but on the whole the vomer is just more than right-angled, where it fits between the premaxillary and maxillary palatine plates.

Behind the middle nasal *canal* the left vomer binds strongly on the right; they both then pass insensibly into the long, divaricating, dentigerous palatine.

Thus we have, from the ethmoidal region to the ear-capsule, a bony tract whose outer outline is concave or crescentic; behind the middle there is nothing but a steep ridge of bone bearing teeth.

These bars reach to the *basitemporal angle* of the parasphenoid (*pa.s.*); and if we look at the larval skull (figs. 1 & 2) we shall see that these tooth-tracts run along the trabecular line even then.

Whilst giving off the bony pterygoid plate the palatines turned outwards, and then loosing themselves from their new segment, a separate osseous "stolon," they gradually went back to their old position.

In some Caducibranchs the hinder part of this long rod becomes segmented off, also, forming a postpalatine bone.

The edentulous separated piece, or bony pterygoid (figs. 5 & 6, *pg.*), applies itself as an ectosteal plate to a process of cartilage which grows forwards from the suspensorium.

These diverse parts meet and unite, and now in the adult the bony plate has metamorphosed the cartilaginous process; that process was the quadrato-pterygoid, the homologue of the main part of the "upper jaw" of a Selachian (that bar ends behind in the quadrate).

In the Selachians, however, the process is huge and persistent; in Urodeles it is at best a thin wedge, and becomes largely ossified.

The quadrate (*q.*) is well ossified, and reaches below to the transverse kidney-shaped condyle, which forms the base of the vertical suspensorium.

This *pier* is clamped on the inside by the pterygoid bone (*pg.*), and outside by the squamosal (*sq.*), a strong, triradiate bone, which, like that of the Frog, grows forwards in front of the ear-capsule.

In the Frog it is *free* in front; here it applies its split fore end to the postfrontal process, and thus forms a temporal bridge; below, it resembles the preoperculum of a Fish.

The lower jaw (Plate 29. figs. 6, 7) is strong and gently arched; the dentary (*d.*) nearly reaches to the angle, outside; the dentigerous splenial (*sp.*) runs back two thirds the length of the jaw; and the articular cartilage is well embraced by the large articulare (*ar.*).

The hyo-branchial series has undergone a curious transformation (see figs. 3 & 8).

The ceratohyals (fig. 8, *c.hy.*) are but little altered, except that they are pointed below and have lost their hypohyal segment.

That piece has coalesced with its fellow, and also with the fore end of the first basibranchial (*h.hy.*, *b.br.* 1), giving it an alate and emarginate appearance.

That bar has become very large, crested above, flat below, and ossified for three fourths its extent, that is to say, up to the attachment of the ventral ends of the first and second branchials.

These two bars (*e.br.*) have lost their smaller (distal) piece, the ceratobranchial; the first is a thick rod, and is attached to the bone, behind; the second is small, is attached to the sides of the cartilaginous end of the basal piece, and is partly confluent with the large bar in front.

The second basibranchial has entirely disappeared; I have found the same state of things in an *old* Newt (*Triton cristatus*); in some species there is merely left, here, a moss-like growth of cartilage in front of a similar growth of laryngeal origin.

This loss of independence of the second branchial brings this *hyoid apparatus* very near to that of the Bird, whose so-called "basihyal" is, in truth, the homologue of the first basibranchial of the Ichthyopsida, and its "urohyal" of the second basibranchial: this piece, in the Bird, is often dilated at its end where it lies beneath the larynx; the Cryptobranch *Siredon* (Plate 27. fig. 5, *b.br.* 2) foreshadows, accurately, this avian structure.

Of course the so-called paired thyro-hyals or "cornua majora" of the Bird correspond to the first branchial arch of an Ichthyopsidan; each is composed of an epi- and a ceratobranchial piece.

If the figures of Caducibranchiate skulls given in this paper be compared with figures of the skulls of the various species of *Dinornis**, it will at once be seen how clear a prophecy we get in this low group of that generalized bird's skull.

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* See the invaluable series of papers on these Birds (with their excellent illustrations) by Professor OWEN, in the Transactions of the Zoological Society.

SUMMARY.

As the present paper is but a fraction of the work already done on this particular plot of ground, I must refer, in making general remarks upon the skull in this group, to illustrations only available to the writer, and not to the reader.

I also want to show the likeness and the unlikeness of the Urodelous type of skull to that of the Batrachia; but the work given before, on the latter, will be profitable for that purpose; I refer to my two papers on the Skull of the Batrachia (Phil. Trans. 1871 & 1876).

But these two examples of cranial structure—the Urodelous and the Batrachian—are well fitted for comparison with any skulls that are; for the place of the Amphibia in Nature is in the midst of the Vertebrate tribes; they stand, as it were, at the parting of the way, and you can, in leaving them, go back, at once, to the Fishes, or forwards, immediately, to the Reptilian, Avian, or Mammalian groups.

For in these low creatures the morphological force, like a spirit of change, is rife; and although you begin, in their beginning, with the lowest kind of Fish you can conceive of, yet you end, in their ending, with a creature whose endowments, by metamorphosis, enable it to tread upon the heel of the very noblest forms.

If any of the Vertebrata may be said to be *generalized*, these may, their relations are so radiating and complex; yet they become specialized in structure in many ways, anticipating a great deal of what occurs in groups far above them.

If we compare the Amphibia with any culminating group of a Class, such as the Teleostei among the Fish, the Lacertilia among the Reptiles, or the Carinatæ among the Birds, we shall be struck with the marvellous uniformity of structure in these, and the constant variation of the Amphibia—as though the morphological leaven were, in them, still in full ferment.

To come to particulars: *Rana pipiens*, the Bullfrog, differs in its skull far more from that of *Rana temporaria*, the common kind, than can be seen in the whole Teleostean group, if we except the Siluroids and the Murænoids.

There is no such difference in the skull of any Carinate bird as is seen between the skulls of *Bufo vulgaris* and *Bufo agua*.

To say nothing of the want of uniformity among the low, *quasi-larval* Perennibranchiate Urodeles, there is more difference between the skulls of the various *genera* of the Caducibranchs than can be seen in those of the *families* of the Lacertilia.

The difference between the Urodelous and Batrachian types of skull is of great importance, but difficult to express because of the great variability—a variability in fundamentals and essentials, and not in slight things.

First Stage.—In embryos still coiled up in the jelly there are several differences to be noted.

In the Axolotl there is no appearance of the transverse band which runs across the frontal wall in the Frog*.

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* In the following comparisons the reader is referred to my papers on the Batrachian skull (Parts I. & II.) and to the illustrations in the present paper. The *stages* spoken of now are the same as I have described in these three papers, and I wish not to confuse the text in this part by incessant reference to plates and figures.

In both the notochord is thick and blunt at the apex, and it has a downward curve, but not equal to what Mr. Balfour shows in Selachians at the same stage.

There is no true cartilage at present; but solid rods are formed of dense granular tissue, in which a separation of the cells that will form the perichondrium can be seen as distinct from the pith, within.

These rods in the Axolotl are the visceral arches; in the Frog these with the trabeculæ in front of them.

For in the Axolotl the trabeculæ are very indistinct tracts of the mesoblast beneath the membranous cranium; but in the Frog they are quite as distinct as the visceral rods, and are, indeed, the first pair of the series of rods, and the largest as well.

This parallelism of the trabeculæ with the postoral rods is due to the bend of the head upon itself, whereby the floor of the fore and mid brain becomes vertically placed.

The *clefts* between the arches are already visible as slits, in the Axolotl, all but the first, which never becomes truly open.

In the Frog, also, it scarcely opens on the outside, although it is a deep sulcus within; but in these embryos the second and following clefts are still mere grooves.

In the Axolotl the external branchiæ on the third, fourth, and fifth bar are large and trifoliate; in the Frog there is merely one small rounded papilla on the face of the third and fourth bar (first and second branchial arches).

In the Axolotl the fossa which is opening to form the mouth is large and transverse; in the Frog it is very small and 4-angled, two angles looking outward and the other two fore and aft.

Second Stage.—In embryos that are straightening, and getting free from their glairy envelope, the divarication of the two types goes on increasing.

In both the head is recovering from its bend; the clefts are distinct, and the mouth open. In the Axolotl the three pair of external gills are very long, but only bifid; in the Frog they are shorter, and the two that are visible are palmate with about eight digitiform processes.

The mouth of the Axolotl is now a transverse slit with outturned angles; in the Frog it has passed from the lozenge to a square with rounded angles; and whilst the lips of the Urodele are thin, those of the Batrachian are thick and solid, and contain the rudiments of four cartilages.

In both kinds the first *cleft* is imperfectly open, externally; in both cartilage has begun to form in the facial rods; but whilst in the Frog the trabeculæ still appear to be the first of the series, in the Axolotl they are not yet chondrified, whilst the visceral arches are, all but the suspensorium of the mandible.

That suspensorium in the Axolotl is as long and thrice the breadth of the small trabeculæ, which grow like very minute horns, whose base is attached to the sides of the apex of the immense notochord.

But Meckel's cartilage is already a strong cartilage, sigmoid and transversely placed, just bending forwards to the chin; the suspensorium passes outwards and downwards at right angles to the trabecula, and has its apex near the fore end of that tract.

So that, in the Axolotl, the trabeculæ are wholly incomparable in position to the halves of the first visceral arch, instead of seeming, as in the embryo Frog, to be direct predecessors or "serial homologues."

In the Axolotl the mandible (MECKEL'S cartilage) is chondrified first, before its suspensory part, and before the trabeculæ; whilst in the Frog this rod appears as a small bud, detaching itself from the upper or main part of the arch.

In both the hind ends of the trabeculæ touch the apex of the notochord; but in the Axolotl they lie along it much more, and that part is flattened out more.

Externally the Axolotl has developed a large free operculum from the hyoid region and arch, and this is complete below, as well as at the sides, although of less extent.

In the Frog this part is very small and only covers the proximal part of the first external gill.

Third Stage.—Embryos that have quite recovered from the cephalic flexure, and in which the trabeculæ and visceral arches are well chondrified, show a great difference in their habit of growth—as great a difference as we should find between the development of the embryo of a Bird on the one hand, and of a Mammal on the other.

In the Axolotl the external gills go on growing, and, developing new papillæ, become pinnate; in the Frog they are at their height, and ready to decline, the *internal* gills absorbing them.

In the Axolotl the mouth is widely gaping, the lower jaw underhung, and the form and relative size is like that of the adult Frog; there are no labial cartilages.

In the Frog, at this stage, the mouth is small, round, suctorial, and has horny jaws, and two pairs of labial cartilages in the closely fitting lips; there are no bones or dentigerous patches that acquire bone.

In the mouth and palate of the Axolotl there are, already, *five* pairs of bony, dentigerous plates, namely, the premaxillaries, vomers, palatines, dentaries, and splenials; here, this early appearance of persistent osseous elements is a correlate of the suppression of the "labial cartilages."

In the Tadpole of the Frog, which is a sort of *temporary* Lamprey, the bones spoken of do not appear for two or three weeks to come, when the larva is beginning to abort its *second series* of gills and to acquire lungs, and is therefore just passing out of the larval state.

The Axolotl, however, does not, *in most individuals*, ever cease to be a larva; *now* it is half an inch in length, but becomes eight inches long or more.

The chondrocranium is now composed of a number of cartilaginous bars, and these bars are developing processes and crests.

In both kinds there are two pairs of muscular segments below the hind brain, a pair on each side of the notochord; the *third* pair are cervical; in neither kind are there any "parachordal cartilages" behind the investing hind end of the trabeculæ, and in both kinds these bars are distinct from each other.

In neither is there any roof or floor cartilage, save below, in the trabecular rods themselves; the nasal region is not chondrified; the auditory capsules are cartilaginous below and at their sides, but membranous above.

For the rest the divergence is extreme; in the Axolotl almost half each trabecula is *parachordal*, and the prochordal part does not reach to the nasal sacs, and only encloses the sides of the great pituitary fontanelle; each trabecula is sending up an *alisphenoidal crest*.

In the Frog or Toad the trabeculæ have only a small *parachordal* tract; they are long, grow beyond the pituitary fontanelle as a pair of diverging, but short cornua, but do not quite meet in front of the subcerebral fontanelle.

In the Axolotl the suspensorium is a solid cartilage, growing forwards and outwards; it has three upper processes, all distinct as yet from the trabecula; these are the pedicle and its *ascending* fork, and the otic process; there is no quadrato-pterygoid process for some weeks to come.

The suspensorium is about two fifths the length of the free mandible, which meets its fellow in front of and under the upper part of the face.

In the Batrachian the suspensorium is of the same size, or nearly, as the trabecula; its apex or pedicle is a simple band of cartilage, which has already fused with the elbow of the trabecula behind, and its distal part is continuous with the ethmoidal region in front.

There is no ascending and, for some weeks to come, no otic process; the bar is narrow like the trabecula, runs parallel with it to the nasal region, and the two are, as we have seen, twice conjugated, like the filaments of *Zygæna*.

Instead of being much longer than its pier, the mandible is one fourth the length only; and like the "horns" of the trabeculæ, these two bars are quite in the front of the head; they cross under the fore face, like folded arms, and are evidently, for a long while, non-functional, the labials being, as in the Lamprey, the working jaws.

In both there is no *epihyal* segment, or pier, to the hyoid arch; when it does appear in the Batrachian, after two months or more, it comes with new credentials, and on another mission, than as a support to the arch of the tongue: in the Axolotl, and most of the Urodeles, it is entirely suppressed.

But the *cerato-hyal* or free hyoid cornu is large in both; in *position* and *relation* that of the Axolotl agrees *now* with that of an almost transformed Tadpole, being under the ear-sacs and attached to the back of a short suspensorium, and having a tape-like form.

In the Frog and Toad it is a short, massive, obliquely 4-sided and 4-angled plate, whose attachment to the back of the suspensorium is *in front of the eye*.

In the Axolotl the four *flat* branchial arches are all distinct, and the two foremost are composed of two pieces; there are two basibranchials, and the last arch has no gills. In the Frog and its congeners the four gill-arches are all functional, and are all conjoined together above and below; this series of *pouched* cartilages is conjugated by a single basibranchial.

In the Urodeles they are formed on the same plan as in Selachians, Ganoids, and

Teleostei, but are deficient in segments; in the Batrachian they are manifestly merely a modification of the Marsipobranchiate type, and the *inner* rods are arrested*.

Fourth and two or three following Stages.—Some minor stages may be considered together now, so as to bring the Axolotl up to its Cryptobranchiate stage, and the Frog to the time when its second series of gills are losing their functions; we can then compare the skull of the adult in each type.

In the Axolotl the hind part of the cranial notochord acquires a new pair of cartilages to invest it—the parachordals. I am not certain of their perfect distinctness in the Batrachian; their nasal roof is not so distinct from the trabeculæ in front as in the Urodeles.

Very soon in both cases there is a continuous basal cartilage from the occipital condyles to the frontal wall; for in both cases the trabeculæ become continuous with the basal cartilages behind, grow together between the nasal sacs in front, and send out two free cornua.

In the Axolotl neither a roof nor a floor of cartilage is ever formed in the middle or interorbital region of the skull; in the Tadpole a floor soon forms between the divaricated trabeculæ.

In the Axolotl a slight ethmoidal roof is formed in front and an occipital roof behind; but besides these, which are better developed in the young Frog, there is also in it a band of cartilage (tegmen) over the posterior sphenoidal region.

Whilst the Frog continues *larval* the palato-quadrate band remains as a short, joining tract, and the pedicle remains continuous, behind, with the trabecula.

In the Axolotl after two or three weeks an "ethmo-palatal" cartilage grows from the trabeculæ, behind the nasal sacs, and a process of cartilage grows forwards from the front of the suspensorium; this free cartilage and that process, together, represent the *palato-quadrate* band of the Tadpole.

Of course as long as that band stops in its arrested stage the quadrate hinge runs up to the sides of the nasal region, and the mandibles are transversely placed; this is marvellously unlike the state of things in an Axolotl larva, large or small.

The auditory capsules are now well chondrified in both types, and a crescentic slit, whose convex edge is outwards, appears beneath the capsule.

In the Axolotl the thin and ragged edge of the cartilage mesiad of the slit forms itself into a leaf of cartilage which becomes free, and shapes itself into the elliptical stapes.

In the Frog and Toad the soft tissue filling the chink chondrifies separately as the stapes.

In the Axolotl the ascending fork of the pedicle coalesces with the alisphenoidal crest of the trabecula, the lower process becomes bulbous, but remains free; the otic process is pedate above and embraces the capsule.

In the Tadpole the pedicle, without any ascending fork, is fixed, and the "elbow" of the suspensorium is attached to the capsule by a band of cartilage which is pedate behind; this is the *primary*, transitory, otic process—a "spiracular ray," as in the Sharks.

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* In the Shark there are two sets of arches, *outer* and *inner*; the outer are arrested and the inner developed; the contrary takes place in the Tadpole.

The suspensorium of the Tadpole is of a huge size, and in one kind, that of *Pseudis paradoxa*, reaches by its quadrate condyle to the front of the face. A little behind the trabecular band it grows upwards as a large leaf of cartilage that overarches the temporal muscle and "trigeminal" branches, and in the Toad, as in the Lamprey, coalesces with the ethmoid.

I have not yet found a trace of this structure in any Urodele.

In the Axolotl the hyoid cornu alters very little from what it was at first; in the Tadpole it retains its massiveness, breadth, and shortness until the gills begin to shrink; then it soon becomes a long, narrow tape, loosens itself from the suspensorium, and attaches itself to the auditory capsule.

To the end of the tailed and branchial stage the gill-arches are persistent in the Tadpole, but become bands; in the Axolotl they are massive bars that only alter if the *Siredon* turns into an *Amblystoma*.

Up to that time also the pterygoid process of the suspensorium alters but little except that it grows larger and adds a separate piece to its apex, a segment comparable to the autogenous pharyngobranchials of a Skate.

But the osseous plates that apply themselves to the cartilage are very different in their origin in the two types.

In the Axolotl the little dentigerous palatine sends a toothless process backwards and outwards to the suspensorium; this then separates, the toothed piece turns outwards in *Amblystoma*, and inwards and backwards under the skull in Caducibranchs, generally.

In the Batrachian a thin independent toothless bone applies itself to the under surface of the ethmopalatine bar, as its ectosteal plate; and another larger plate applies itself to the inner face of the suspensorium, to its pterygoid process, and in Toads to the pedicle; in Frogs there is a separate mesopterygoid applied to that process, and which in them becomes large and detached from the trabecula.

In *Bufo agua*, under the huge ethmo-palatine ectostosis, a counterpart of the little transverse palatine of *Amblystoma* appears.

Whilst these things are taking place in the Frog the palato-quadrate band keeps lengthening, the gape widening, and consequently the quadrate gets further and further backwards, until at last the suspensorium forms an obtuse angle with the basis cranii. By the time the tail has disappeared in the Frog the primary otic process has become a free trifoliate "spiracular cartilage;" this becomes the cartilaginous "annulus tympanicus:" it is always, at any stage, *above* the portio dura nerve.

In certain Urodeles, namely *Menopoma*, *Spelerpes*, *Desmognathus*, the two latter being Caducibranchs, this cartilage grows to the stapes, and generally fits its narrow posterior end into a cupped process of the stapedial bony centre; in some it is independently ossified and free.

These two specializations of that peculiar *Selachian* cartilage are of great interest, suggesting the possibility of many curious transformations of ichthyic elements in the higher Classes.

These are some of the most important of the modifications in the morphology of the skull of a Urodele as compared with that of a Batrachian; there are several more, but these must suffice for this present summary.

Last Stage. Skull of adult Urodeles and Batrachians.

A reference to the figures in my papers on the Batrachian skull, and to those of *Amblystoma* and *Seironota* in the present communication, will serve to show at once the sharp distinctness between the two types, and yet their general resemblance.

One great difficulty in comparing them arises from the fact that several of the Urodeles are perennibranchiate, and therefore permanently quasi-*larval*; there are no such Batrachians, and one of that group, namely *Pipa*, is nearly abranchiate.

Looking at the skulls of adult (Caducibranchiate) Urodeles and Batrachians from the surface we see the following differences:—

The roof-bones remain distinct in the Urodele; in the Batrachian the frontal and parietal of the same side coalesce.

In the Urodele the nasal is supplemented by *an external* prefrontal bone, and is therefore much smaller.

The premaxillaries are distinct in the lower and about half the higher Urodeles; in the rest there is an azygous bone with two long nasal processes.

These bones are constantly distinct in Batrachia, and the nasal processes are short.

The maxillary grows further backwards along the face in Batrachia than in the Urodeles; in *one* of these, namely *Amblystoma*, there is a small jugal; in none a quadratojugal, a constant bone in the Batrachia, binding the cheek to the quadrate.

There is only one " temporal bone " in both kinds, with the exception, again, of *Amblystoma*; and in the Urodeles this does not so often grow into the postorbital region.

Beneath, the parasphenoid is much smaller and more specialized in the Batrachia than in the Urodeles; it begins much earlier in the latter, in the Batrachia it develops into a dagger with a large basitemporal *guard*.

The vomers are double in both, save in *Dactylethra*; the palatine base is only transverse (as in the Batrachians) in some "Lechriodonts"; in most Urodeles of the higher kinds it lies under the parasphenoid, and is ankylosed to the much enlarged vomer in front; these are called " Mecodonts."

In both we have the double occipital articulation and the absence of basal and keystone pieces in the occiput. Yet in some larval Caducibranchiate Urodeles *two basal vertebræ* are partly developed and then disappear.

In most species of both kinds the prootic is large, and the rest of the ear-capsule is ossified by an overgrowth from the exoccipital.

Except in *Dactylethra* the two wall bones (sphenethmoids) are fused into a girdle by the help of superethmoidal bone; in the Urodeles the later bony tracts run back past the optic foramen, but never, or seldom (for example, in *Siren lacertina*), unite at the mid line.

In a few Urodeles, namely, *Siren lacertina* and *Salamandra maculosa*, there is a short tongue-shaped prenasal in the adult; and these also show a free prorhinal, or lobe of the cornu trabeculæ, on each side.

These paired processes are very constant in the Batrachia, but in them the prenasal is generally a mere bud.

In the Batrachia the nasal capsules, with the conjoined trabecular (subnasal) laminæ, are more developed than in the other group; they also have a larger "appendix alæ nasi," formed of the outer three fourths of the upper labial.

The suspensorium develops a *quadrate bone* in Urodeles, save in *Siren.* This is absent in Batrachia generally, but present in *Dactylethra* and *Bufo agua.*

The "pedicle" is single in *Proteus*, double in the rest of the group. In that type, in *Menobranchus*, *Siren*, and *Menopoma*, it grows up to the trabecula, as in the Batrachia.

In most Urodeles, however, the lower fork, or *pedicle proper*, is attached to a plaster of investing cartilage on the face of the ear-capsules by a mass of fibrous tissue.

In the Frog (*Rana temporaria*) the attached part of the simple pedicle is absorbed, and the lower, swollen part forms a condyle, and there is a joint-cavity, instead of a fibrous bed, where it hinges on the capsule.

In the Toad (*Bufo vulgaris*) the apex of the pedicle merely coalesces with the front of the capsule, and is not absorbed.

In the Urodeles, with the doubtful exception of *Proteus**, there is a dentigerous splenial, besides the dentary and articulare. In the Batrachia there are only the two latter bones.

In the Urodeles the little mento-Meckelian bone, which characterizes the Frog's mandible, only imperfectly appears in *Proteus.*

The epivisceral element of the second arch occurs as a *large* hyo-mandibular in *Proteus*, and as a *smaller* segment in *Siren* and *Menopoma*; but as a rule it is suppressed, and the stapes is merely connected to the suspensorium by a ligament, the "suspensorio-stapedial."

The cerato-visceral is large, but it does not ascend to the ear-capsule. It is connected to the suspensorium by the hyo-suspensorial, and to the angle of the mandible by the mandibulo-hyoid ligament.

Distally it sometimes gives off its hypohyal piece to coalesce with the first basibranchial at its fore end. In some kinds this distal piece becomes very slender and retrally directed. In the Menopome it is subdivided into three pieces; in Osseous Fishes it has two bony centres.

In the Frog the hyoid arch becomes very slender, coalesces with the basihyal, and, above, ascends to attach itself to the auditory sac. This, however, is only the ceratohyal element; it has no hypohyal piece; and this is a common thing, namely, for two hypovisceral elements in one type to be represented by a basivisceral in another.

In *Bufo vulgaris* the top of this piece (the stylohyal region) coalesces with the ear-

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* WIEDERSHEIM figures it in his new work on the Urodeles (plate 2. fig. 16).

capsule as in Mammals. In *Dactylethra* it is suspended by a ligament; in *Bufo agua* it is largely, and in *Pipa* wholly, absorbed.

The epihyal piece is mostly small in the Batrachia; it is developed *early* in *Pipa* and *very late* in *Bufo*, *Rana*, and *Dactylethra*.

This small *hyo-mandibular* element becomes the "columella auris." In Toads it has two bony centres and an orbicular symplectic end. In Frogs it becomes two distinct pieces, and has a spatulate symplectic end (the extrastapedial).

In the Urodeles the two last branchials are absorbed; also the second arch becomes simple. Sometimes the first ceratobranchial is lost. The first basibranchial becomes very large, and the second ossifies behind, and is absorbed in front; this bony remnant becomes a transverse, azygous thyro-hyal; it sometimes is a mere rudiment, and at others is totally absorbed in old age.

In the Batrachia two rudiments of arches remain on the hind part of the side of the hyo-branchial lingual plate.

Their common hypobranchial plates grow further backwards, become terete, ossify, and form symmetrical *thyro-hyals*.

These are some of the more important morphological differences between the two groups. I may mention a *histological* difference, namely, that the *Selachian* incrustation of the cartilage seen in the Batrachia (not in *tesseræ*, but in large, irregular patches) does not occur in the Urodeles.

At the risk of prolixity, I have thus compared these two groups as to their cranial morphology. Much of the work already done has not had time to see the light; and much more will be done, if possible, as no other Vertebrata run through so large and instructive a series of metamorphoses, and no other types have such extensive relationships.

I may remark that the Urodeles seem to approximate most to the "Sauropsida," and the Batrachia to the Mammalia. The *largest* species are invariably the most generalized; and some of the larger Batrachia, such as *Rana pipiens* and *Bufo agua*, have many things in them that remind the observer of the "Labyrinthodonts."

The two *aglossal* Toads, lately described, so extremely unlike in most respects, and yet agreeing in being tongueless, suggest most extensive *lacunæ* in the group. The discrepancies between the larger "Perennibranchs" do the same.

The Amphibia are not studied, however, for their own sakes; but it is sought to gain more and more insight into the meaning of the skull in the Vertebrata generally, and not of the skull only, but of the whole skeleton.

That framework, also, is considered in relation to all the other structures, eminently the nervous system; and thus we seek to have a clear view of a vertebrated creature throughout its adult complexity of structure, and also of all the stages through which it passes.

Of late, the invaluable researches of my friend Mr. BALFOUR have come in to open up more and more the secrets of embryological growth. His memoirs, and the later morphological work done by Professor Huxley, have been giving new life to my own slow research.

I venture to offer now a few remarks on the growth and the architecture of the skull of vertebrated animals generally.

Concluding Remarks on the Formation of the Skull.

The paired mesoblastic plates, that on each side of the azygous notochord support the neural axis, may be considered to be the *first foundation* of the skeleton.

Whether the notochord be developed from the underlying hypoblast, or be a median tract of mesoblast, does not affect the argument.

A vertebrated animal may be imagined which should be equally modified, or as little modified, at either end. It would be *acephalous.*

The least specialization in its sensory nerves, and in the part of the nervous axis from which they spring, by which simple sensibility should develop into the power of appreciating the sapid or odorous qualities of surrounding bodies, or, still further, give to the creature some feeling of sound or light,—such an exaltation of the sensory endowment in the fore end of the animal would be tantamount to the specialization of the *head*, as distinct from the rest of the body.

We can conceive of this taking place with but little change in a vermiform animal. The endoskeleton may be supposed to remain throughout life as a pair of mesoblastic tracts (enclosing the notochord) more solid than the rest of the tissues formed from that embryonic layer. The neural axis would be a simple tube, ending in points, *amphioxine*; and the hypoblastic tube, or digestive canal, might be as simple as the rest of the creature.

Leaving the actual *Amphioxus* out of the question, what we see take place in the embryos of the Vertebrata generally is a rapid departure from the *actual*, and a wide divergence from any *supposed*, simplicity of form.

To get light upon the almost hopeless question of the morphological divergence of the head from the trunk we must, in imagination, remove all the factors of cephalic specialization, and thus, in idea, reduce the head into the mere fore end of the animal, unenlarged, and not transformed, as we actually see it.

What are those factors? If they can be set in array, and their work and influence truly appreciated, we shall be able the better to read the interpretation of this hard chapter in morphology.

The development of nerves of special sense is a correlate of two things:—first, a large regional increase in bulk of the nervous axis; and, secondly, the budding-out of it on each side of special sense-capsules.

But as the mesoblastic beams on which the nervous axis is laid must grow with the growth of that axis, and be modified with its every modification, we have here a great factor in this skull-building.

Moreover, the sense-capsules have to lie in close proximity with their nerve-supply;

they become large and complex; and of the *three* principal pairs the foremost and hindmost form secondary graftings and intimate blendings with the axial skeleton. The middle pair, also the *eyes*, have the surrounding parts cunningly built over and around them; sockets are sunk in the skull for their reception, albeit they are free themselves.

A temporary change in the direction of the axial nervous mass in front, its *mesocephalic flexure*, whereby the straight embryo is formed into a crozier-like body, this, of necessity, is modifying the growth of the axial skeleton as long as the head is thus bent.

Now the beautiful researches of Mr. BALFOUR show that the notochord becomes (in the Selachians) shaped like a sheep-hook* during the period of embryonic growth; and my own researches ("On the Skull of the Shark and Skate," Trans. Zool. Soc. vol. x. plate 35) show that the part of the mesoblastic plates just in front of this bend grow more rapidly than the part behind, from which they have been, as it were, *dislocated*.

Time has now to be considered in the morphology of the skull; and parts that start first and grow quickest generally overshadow the later and slow-growing parts.

We thus get a morphological *anachronism*—some elements of the skeletal structure standing still and waiting, apparently suppressed, until the proper nick of time occurs in the age and growth of the animal.

But for the modifications undergone by the cephalic structures, the vesicular condition of the neural axis, the development of the organs of special sense, &c., the two plates that run along the sides of the notochord might have been chondrified at one and the same time from end to end of the animal, a little slowness being allowed for the extreme ends.

This would not have been materially affected by the *somatomic* subdivision of the tracts; they might have been separated into moieties for each vertebra, or, obliterating the earlier divisions, chondrification may be imagined as running on (as it does in the neck of Selachians) along parallel tracts continuously.

But in the existing Vertebrata chondrification does not take place in the basal mesoblastic tracts of the head at one and the same time; and it would be well if we knew what causes this anachronism.

This is extremely difficult to account for. It is not equally seen in all types; and there are remarkable variations within the limits of an Order, or even Family.

On the whole, the trabeculæ, or interocular tracts, chondrify first; then the interauditory, or parachordals; and, lastly, the internasal, or fore ends of the trabeculæ.

The development of *true* (arrested) vertebræ in the head is possible as far as the *three* essential elements go, namely, the notochord and its pair of investing mesoblastic tracts.

As a fact, such segments, even below the hind brain, are imperfect and transient; under the other two vesicles they are impossible, and in the early embryo only slight traces of somatomic division can be seen, even in the region of the hind brain.

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* Journ. of Anat. and Phys. vol. x. plate 24.

We now come to two causes of modification of the basal plates that are very important, namely, *divarication* of the paired tracts, and *obstruction* of the unpaired axis; the latter is the most important of the two.

The rapid growth of the brain-vesicles, as they turn over the bent skeletal axis, causes the floor of the membranous primordial cranium to bulge, and this bulging affects the hardening bands that are ready to begin to build the "chondrocranium."

The middle tracts (trabeculæ), although starting from the sides of the apex of the notochord, curve round the infero-lateral regions of the brain-sac, and in an early state are merely like two horns, gently curved outwards from their origin, and far apart at their tips (Plate 22. fig. 1, *tr.*).

At their beginning, however, these outbent bars have the notochord between them, so that the posterior trabecular region has in it all the elements that go to form vertebræ.

Now, however, we come to *obstruction.* The posterior part of the oval space, marked out by the divaricating trabeculæ, is occupied by a structure that effectually stops all further forward growth of the notochord.

A process from the postero-inferior region of the fore brain, the infundibulum, here joins on to the *pituitary body*—a tear-shaped sac that passes downwards and backwards from its cerebral attachment, and rests upon the oral mucous membrane.

Here is a perfect barrier; and although the sheath of the notochord may grow upwards between the hind and mid brain, and downwards below the pituitary body, as is seen in the *Axolotl* and *Salmon*, this axial growth is stopped along the basal mid line.

In the *Selachians* it pushes itself against the barrier, and becomes crumpled and beaded; it then smooths out its creases, and presses its fore end against the intrusive body, so as to flatten its point; but it is there arrested.

Therefore it is evident that we can no longer speak of vertebral division of the skull from this point, and this is no further forwards than the "posterior clinoid" region.

From thence we have the highly modified mesoblastic tracts running forwards to the frontal wall, without their proper bond, and subject to conditions that cannot be found in any region of the axis of the body.

I now come to consider another great factor in the specialization of a skull, as such, namely, the sense-capsules, the "paraneurals" of Professor HUXLEY.

Behind the ear-capsules the basal plates are free to grow upwards, and to arch over the neural axis. Between them the basal plate is, as it were, cut away and bevelled; and no upgrowth is possible, as these sacs are built into the sides of the cranium and form much of its side walls.

Moreover, the basal tracts become confluent with these capsules; and afterwards, when ossification sets in, it often works blindly, not keeping to the primary morphological landmarks.

Then, while the neural arch or roof, that should grow up everywhere from the basal plates, is made imperfect by the implantation of these capsules, the arches that should grow ventrad, like the costal arches, miss their point of attachment, and their nervous supply has to find its way round the obstructive masses.

The middle pair of capsules are free; they do not blend themselves with the chondrocranium, but they affect its growth by causing it to harmonize with their size, form, and mobility.

In flat, broad skulls this is the less seen; but in high, compressed skulls the two parallel bands suddenly unite in front of the pituitary body, and grow up into a high wall between the two capsules that mutually become approximated.

In these cases the brain-cavity is lifted up high above this partition, and any *walls* it may acquire grow as wings from the top of this interorbital crest.

Further forwards we have a similar state of things, namely, in the nasal region, these foremost paraneural capsules often approximating very closely.

Here the crest is continuous with that between the eyeballs; but the roof of the nasal labyrinth, right and left, coalesces with the ascending trabecular crest. The capsules here again are blended with the axis.

Only in the lower (ichthyic) types do the basal plates grow up over the brain mass, except behind; so that we have the chondrocranium as a basin or a trough, and not as a finished and roofed structure. This is a great specialization of a neural-arch structure.

The closing in in front of the neural cavity is not necessarily directly over the end of the skeletal axis, and the nasal septum is continued in front of the cranial cavity.

The *ventral* arches of the head are for several reasons very much unlike *costal* arches. They are only perfect behind the mouth, and very independent in their growth.

Costal arches spring, normally, from a vertebral centrum, as directly, indeed, as neural arches do; but the cephalic arches may or may not be attached, even secondarily, to the bands that answer to the distinct vertebral centra.

Where the costal arches grow, there the descending or ventral laminæ are divided into a "splanchnopleure" and a "somatopleure," the pleuro-peritoneal space being between the two, and these arches are formed in the outer layer.

But this division, because of the closing in of that space, does not exist below the head; the old term "visceral arches" still may be used for the bars. They are, to all intents and purposes, *pleural* arches, and they lie close, or near, the outer wall of the throat.

When the visceral arches are attached to the skull-base it is often a secondary attachment, and they, most of them, have a habit of growing over the top of the pharynx, *beneath* the axis.

The intervening clefts, the mode of subdivision of the bars, the structures that are attached to them, and the bony plates that round the mouth are applied to them as *investing* bones; in all these things the *visceral* arches are diverse from the *costal.*

Their *generic* term may be "pleural," but that should not suggest the idea of a true rib or costal arch.

Perchance these two species of arches are but *secular* specializations of one and the same type of ventral arch; but that is a thing hidden from us now.

I can only find two pairs of rudiments of visceral arches in front of the mouth—the ethmo-palatines, which are often separate elements, and the trabecular cornua (with the intervening "rostrum"); but these latter are exogenous processes from the paired basal plates growing into the frontal wall of the embryo.

DESCRIPTION OF PLATES 21–29.

Plate.	Fig.	Stage.		Number of diameters magnified.
21	1	1st	Unhatched embryo of *Siredon*, $\frac{1}{4}$ inch long. Side view of fore part	26
"	2	"	The same. Upper view	26
"	3	"	The same. Under view	26
"	4	"	The same in section (vertical)	26
"	5	2nd	Unhatched embryo of *Siredon*, $\frac{1}{3}$ inch long. Side view of fore part	20
"	6	"	The same. Upper view	20
"	7	"	The same. Under view	20
"	8	3rd	Hatched embryo of Axolotl, $5\frac{1}{2}$ lines long. Transverse section (7th) of skull through middle of auditory region	20
"	9	"	A similar section (8th) further back	20
"	10	"	Another section (9th). Occipital region	20
22	1	2nd	Skull of unhatched embryo of *Siredon*, $4\frac{1}{2}$ lines long. Upper view	25
"	2	"	Visceral arches of same. Upper view	25
"	3	3rd	Skull of hatched embryo of Axolotl (*Siredon*), 5 lines long. Side view	20
"	4	4th	Skull of young Axolotl, $\frac{3}{4}$ inch long. Upper view .	15
"	5	"	The same. Lower view	15
"	6	5th	Skull of young Axolotl, $1\frac{1}{4}$ inch long. Upper view .	10
"	7	"	The same. Lower view	10

Plate.	Fig.	Stage.		Number of diameters magnified.
23	1	3rd	Skull of young (hatched) Axolotl, 5½ lines long. Upper view	20
,,	2	,,	The same. Lower view	20
,,	3	,,	Transversely vertical section (1st) of same skull through nasal sacs	20
,,	4	,,	Same; section (2nd) through front of eyeballs . .	20
,,	5	,,	Same; section (3rd) through middle of eyeballs .	20
,,	6	,,	Same; section (4th) through hind part of eyeballs	20
,,	7	,,	Same; section (5th) through suspensorium . . .	20
,,	8	,,	Same; section (6th) through part of ear-capsule .	20
24	1	6th	Skull of young Axolotl, 2¼ inches long. Upper view	8
,,	2	,,	The same. Lower view	8
,,	3	,,	Part of upper view of same	16
,,	4	,,	Part of lower view of same	16
,,	5	9th	Skull of cryptobranchiate Axolotl, 8¼ inches long. Lower view	3½
,,	6	10th	Skull of *Amblystoma opacum*, 3 inches 10 lines long. Lower view	5
25	1	7th	Skull of young Axolotl, 3¼ inches long. Upper view	5
,,	2	,,	The same. Lower view	5
,,	3	8th	Skull of large Axolotl, full-gilled, 8½ inches long. End view	3½
,,	4	,,	Lower jaw of same. Inner view	3½
,,	5	,,	Visceral arches of same. Lower view	3½
,,	6	10th	Visceral arches of *Amblystoma opacum*. Lower view	5
,,	7	,,	Lower jaw of same. Inner view	5
26	1	8th	Skull of large Axolotl, 8½ inches long. Upper view.	3½
,,	2	,,	The same. Lower view	3½
,,	3	,,	The same, with investing bones removed. Upper view	3½
,,	4	,,	The same. Lower view	3½
,,	5	,,	Skull and visceral arches of same. Side view . .	3½
27	1	9th	Skull and visceral arches of cryptobranchiate Axolotl, 8¼ inches long. Side view	3½

Plate.	Fig.	Stage.		Number of diameters magnified.
27	2	9th	The same skull. Upper view	$3\frac{1}{2}$
,,	3	,,	Part of lower view of same	7
,,	4	,,	Section of suspensorium of same	7
,,	5	,,	Median part of visceral arches of same. Upper view	$3\frac{1}{2}$
,,	6	10th	Skull of *Amblystoma opacum.* Upper view . . .	5
,,	7	,,	The same. Side view	5
28	1	Adult	Skull of *Proteus anguinus.* Side view	$5\frac{1}{2}$
,,	2	,,	The same. Upper view	$5\frac{1}{2}$
,,	3	,,	The same. Lower view	$5\frac{1}{2}$
,,	4	,,	The same, with investing bones removed. Upper view	$5\frac{1}{2}$
,,	5	,,	The same. Side view*	8
,,	6	,,	Lower jaw of same. Inner view	$5\frac{1}{2}$
,,	7	,,	Part of skull showing union of pedicle with trabecula	12
,,	8	,,	Section through the same skull. Orbital region .	$5\frac{1}{2}$
29	1	1st	Skull of larval *Seironota perspicillata*, $\frac{1}{2}$ inch long. Upper view	24
,,	2	,,	The same. Lower view	24
,,	3	,,	Visceral arches of same. Upper view	24
,,	4	Adult	Skull of adult of same species, 2 inches long. Upper view	12
,,	5	,,	The same. Lower view	12
,,	6	,,	The same. Side view	12
,,	7	,,	Lower jaw of same. Inner view	12
,,	8	,,	Visceral arches of same. Upper view	12

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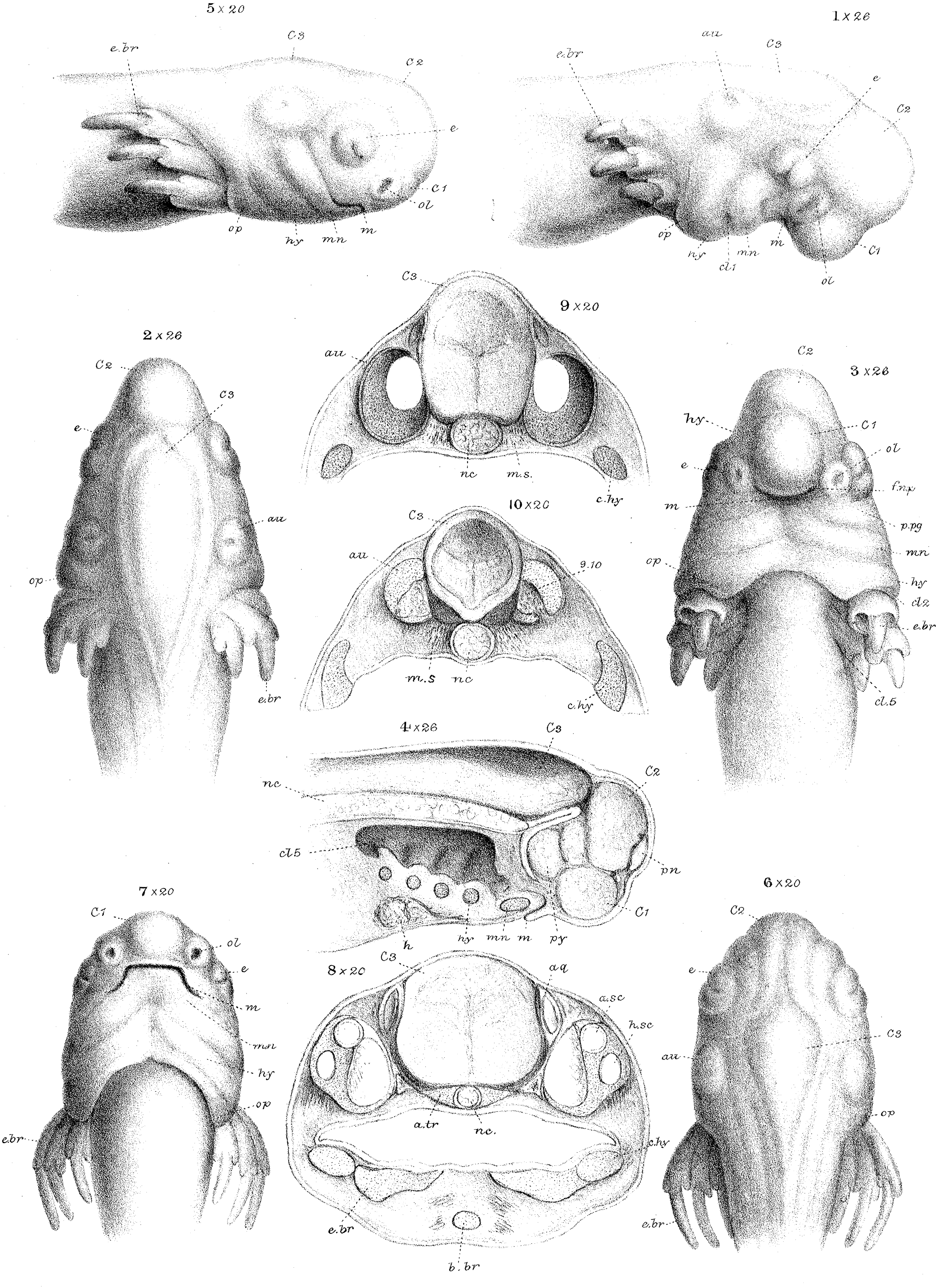
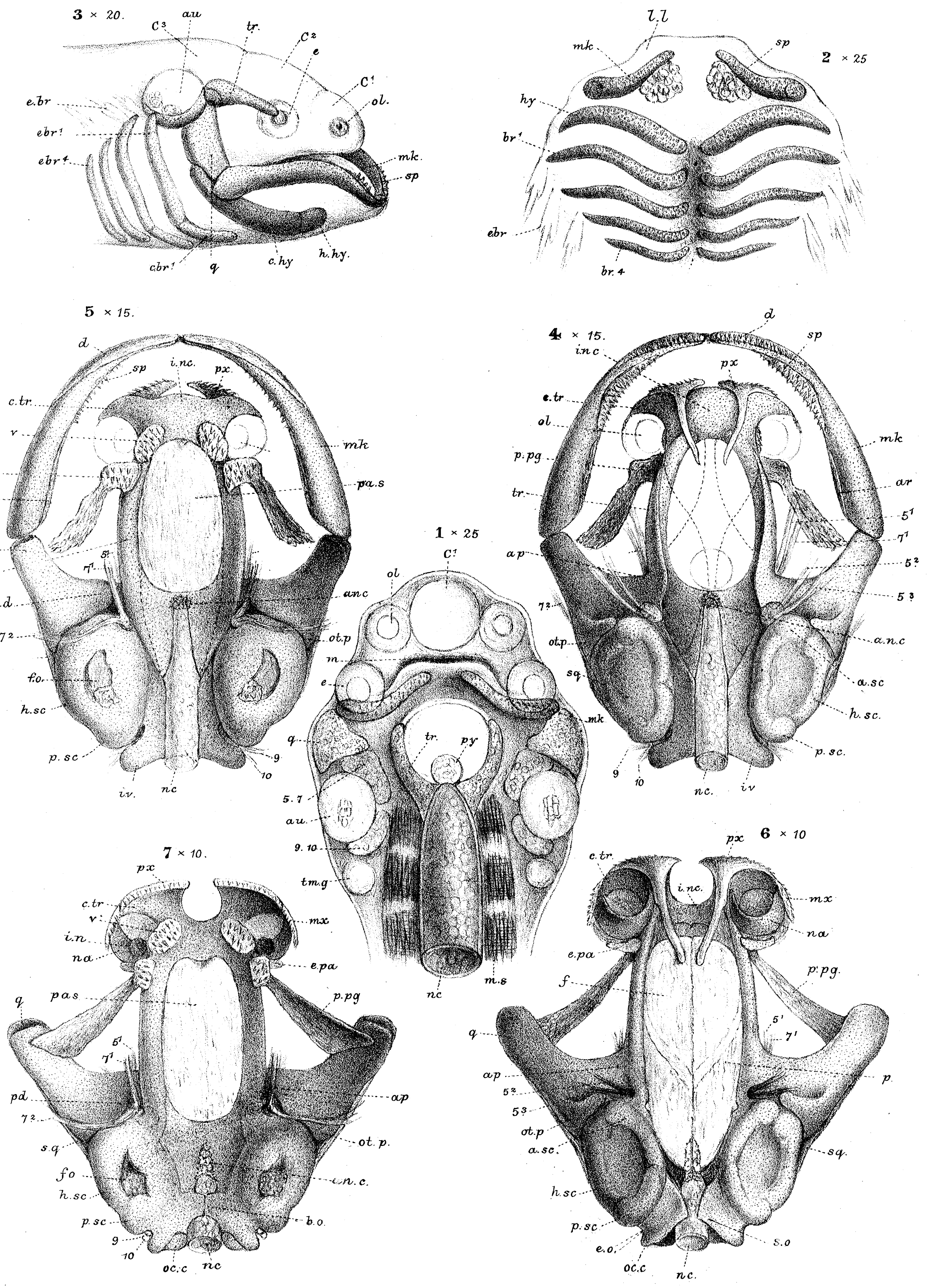
* In the Plate this is lettered " × 11," by mistake.



W.K.P. del. ad nat.
G.West lith.

W.West & Co. imp

Siredon, *Figs.1-4 1st Stage; 5-7 2nd Stage; 8-10 3rd Stage.*



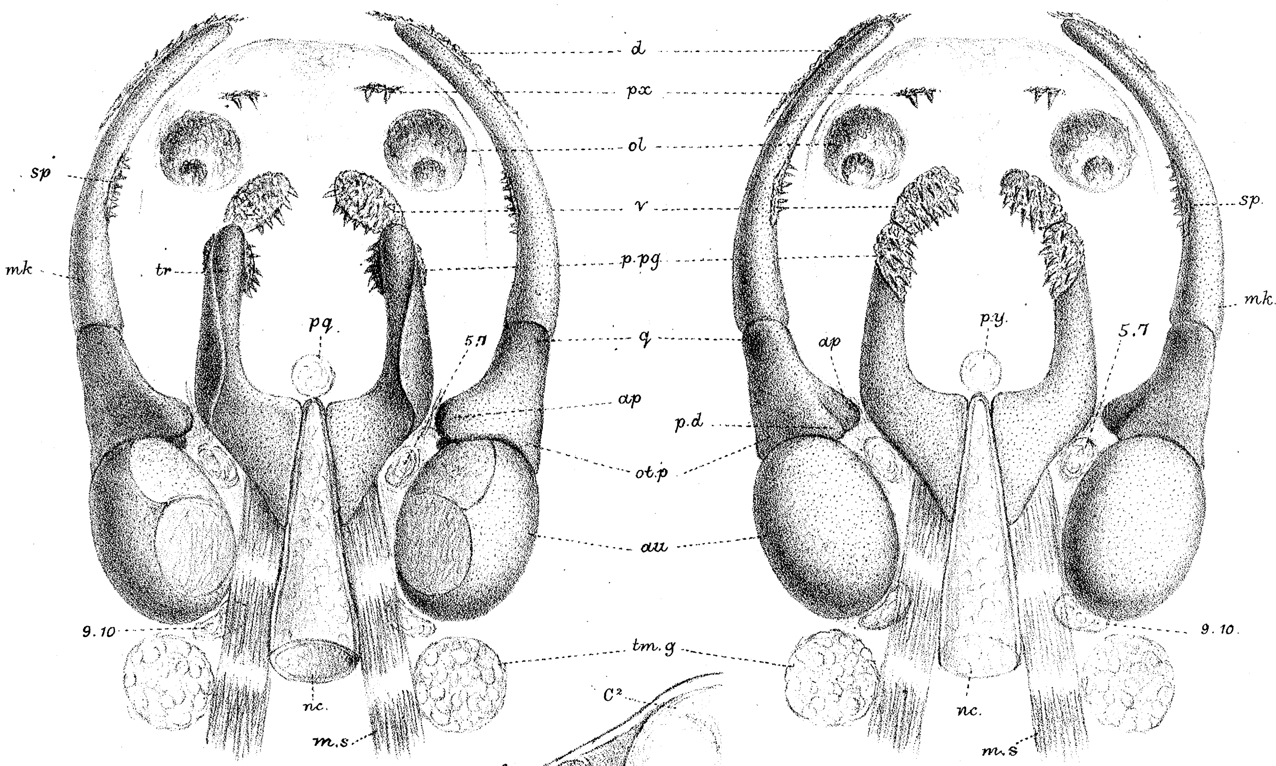
W.K.P. del. ad nat.
G. West lith.

W.West & Co. imp.

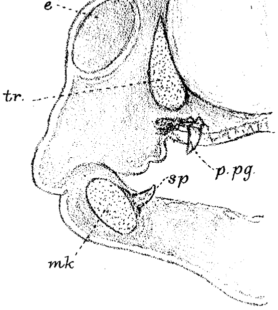
Siredon, Figs. 1, 2, 2nd Stage. 3, 3rd Stage. 4, 5, 4th Stage. 6, 7, 5th Stage.

1. ×20.

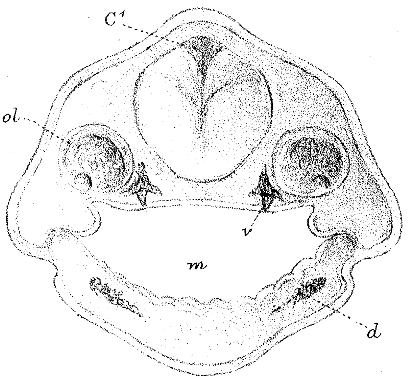
2. ×20.



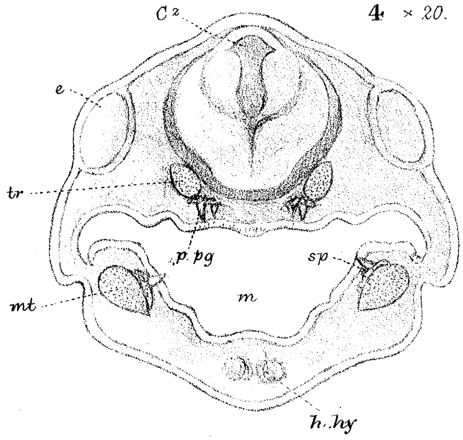
5. × 20.



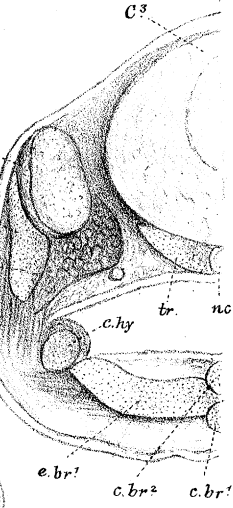
3 × 20.



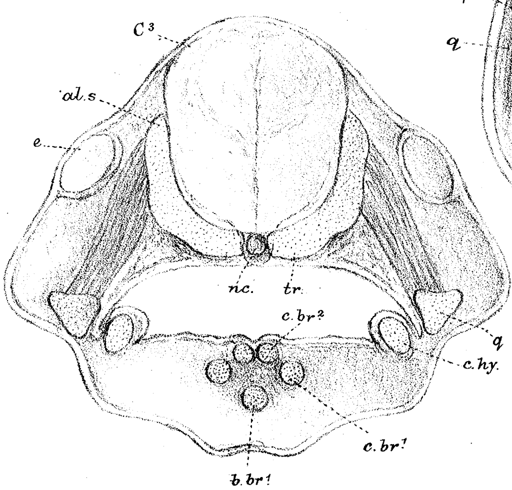
4 × 20.



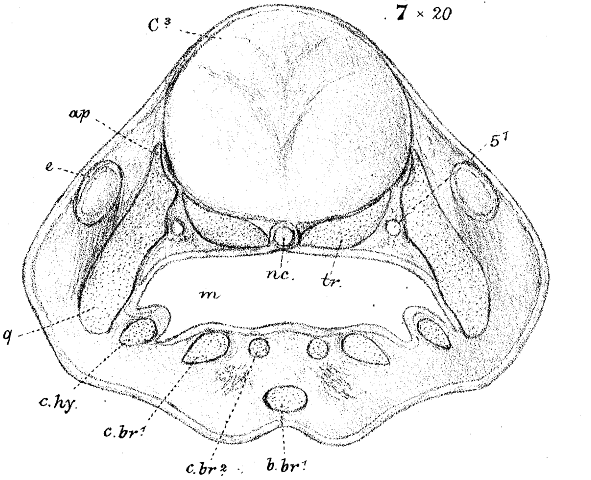
8 × 20.



6 × 20



7 × 20

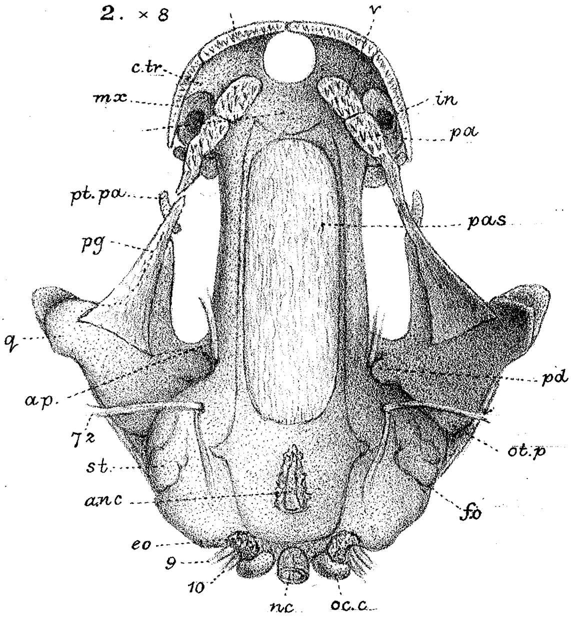


W.K.P. del. at nat.
G. West lith.

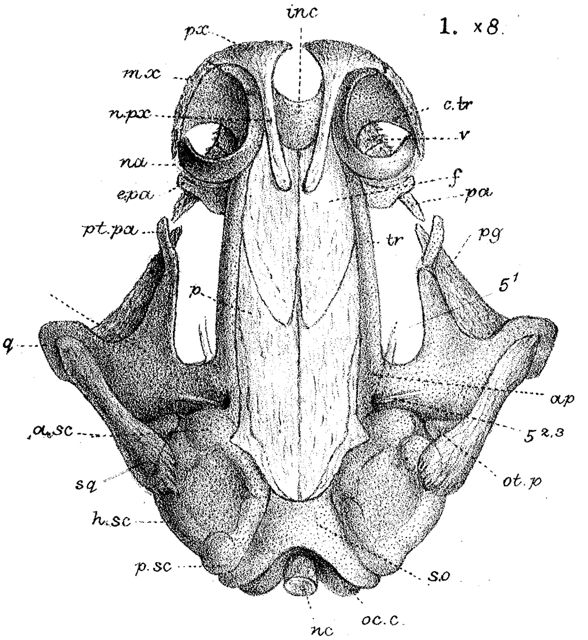
W. West & Co. imp.

Siredon. 3rd Stage.

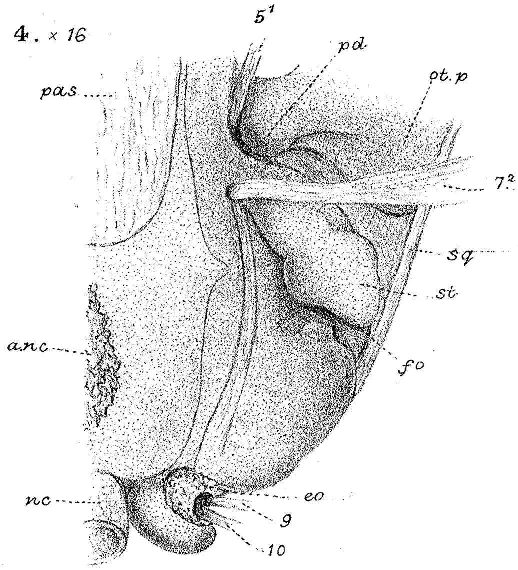
2. × 8



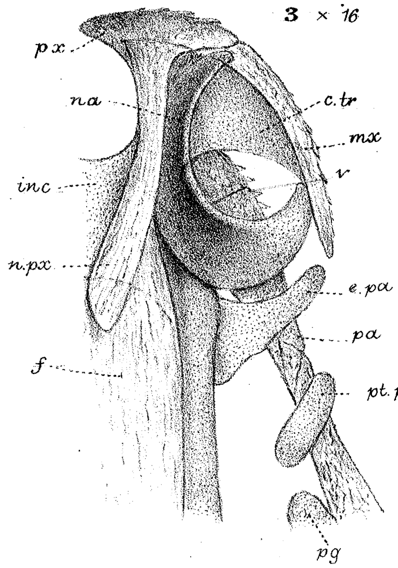
1. × 8.



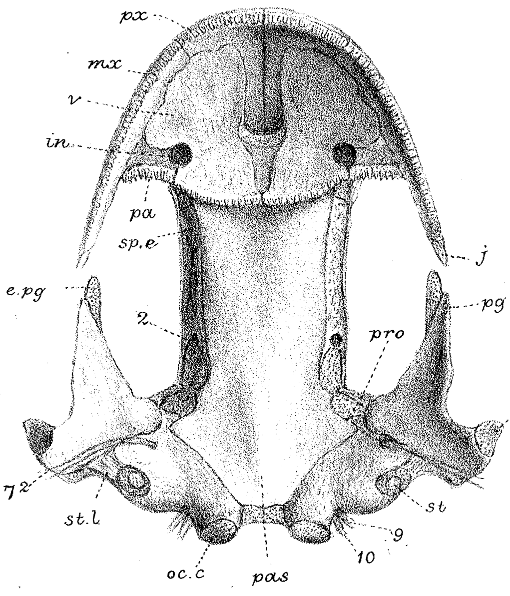
4. × 16



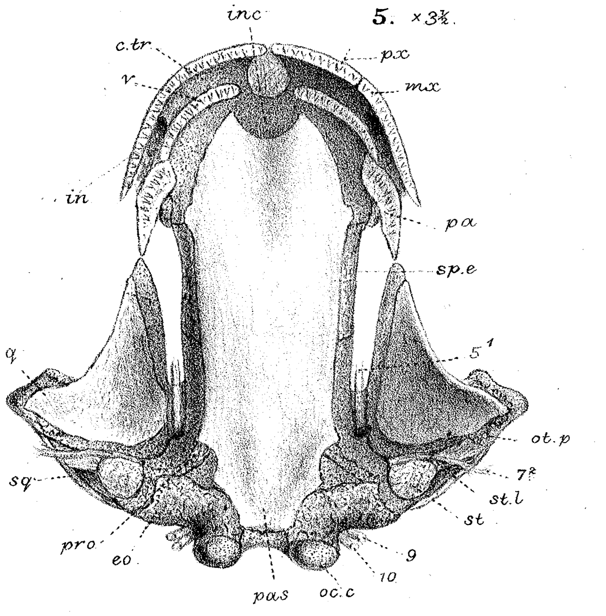
3 × 16



6. × 5.



5. × 3½.

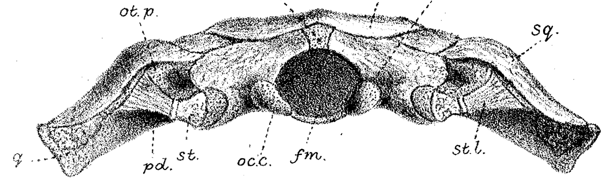


W.K.P. del. at nat.
G. West lith.

W. West & Co. imp

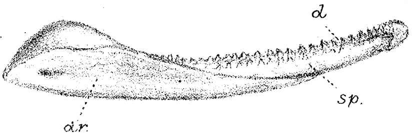
Siredon. Figs, 1–4 6th Stage. 5, 9th Stage. Amblystoma, Fig. 6.

3. × 3½.

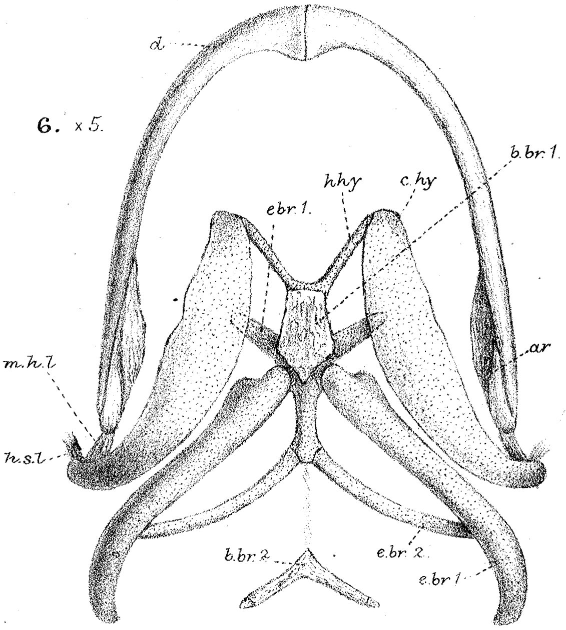


7. × 6.

4. × 3½.



6. × 5.



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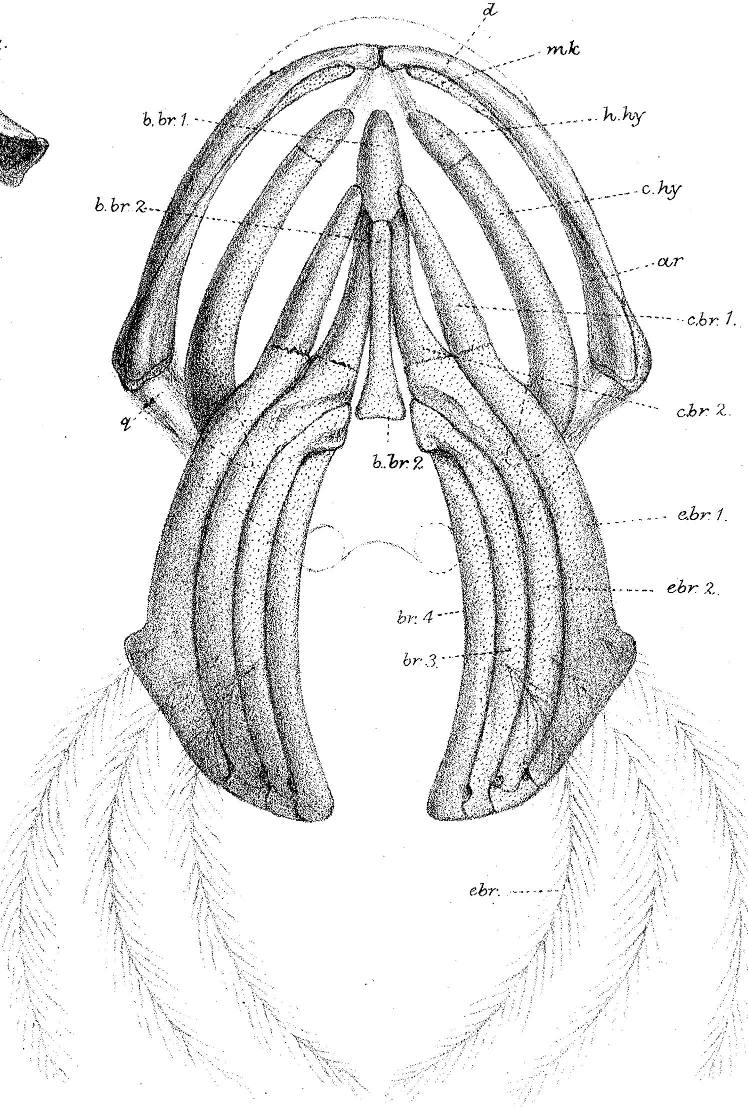
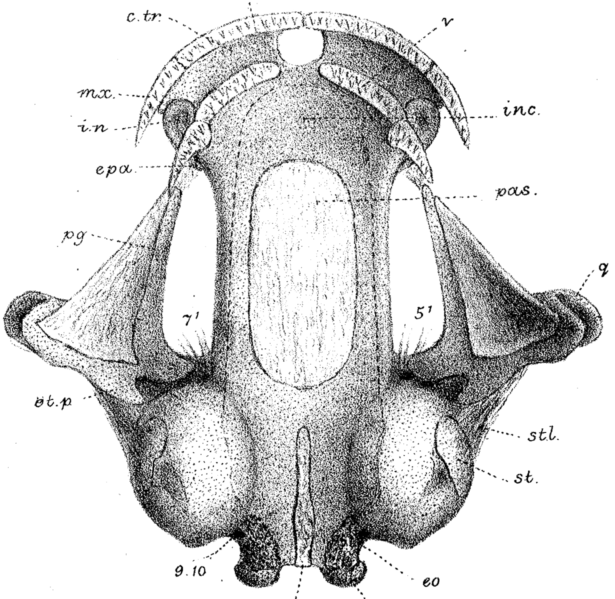
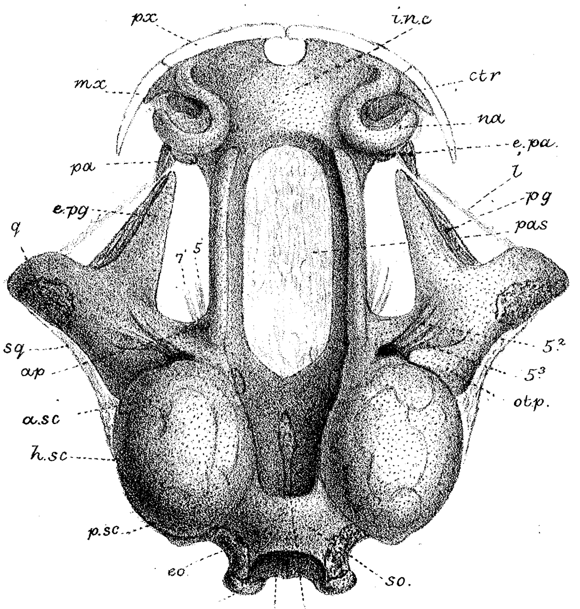


2. × 5.



1. × 5.

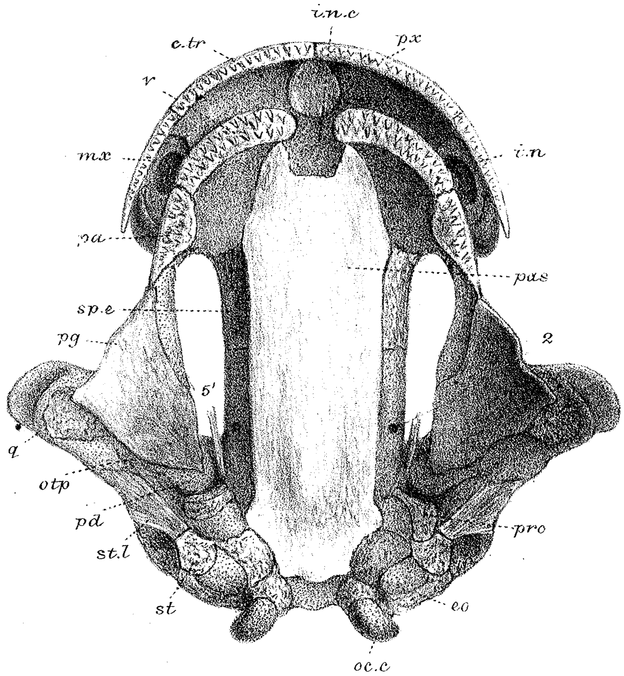


W.K.P. del. ad nat.
G. West lith.

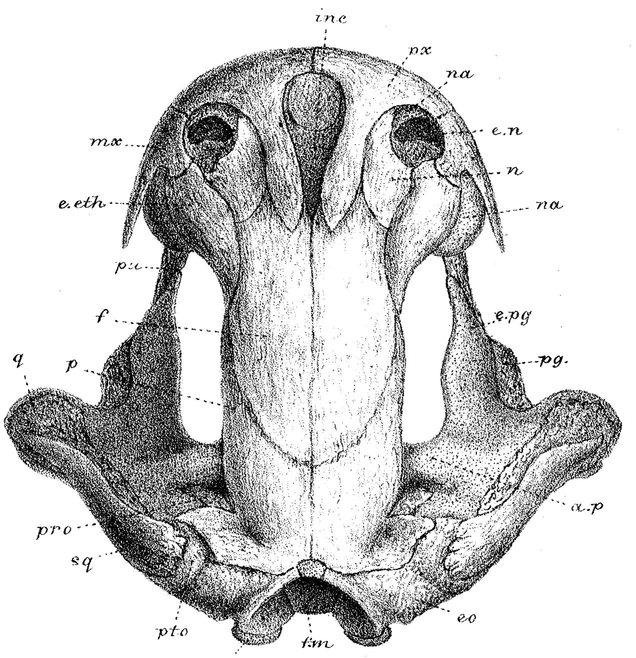
W. West & Co imp.

Siredon. Figs, 1, 2, 7th Stage. 3–5. 8th Stage. Amblystoma Figs. 6–7.

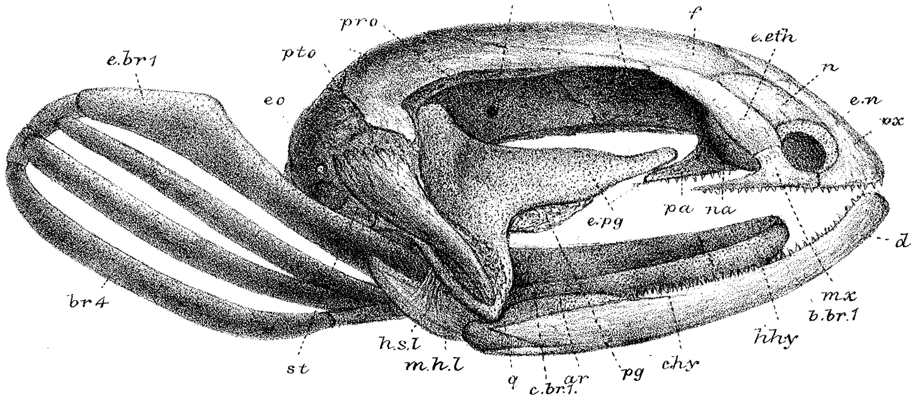
2 x 3½



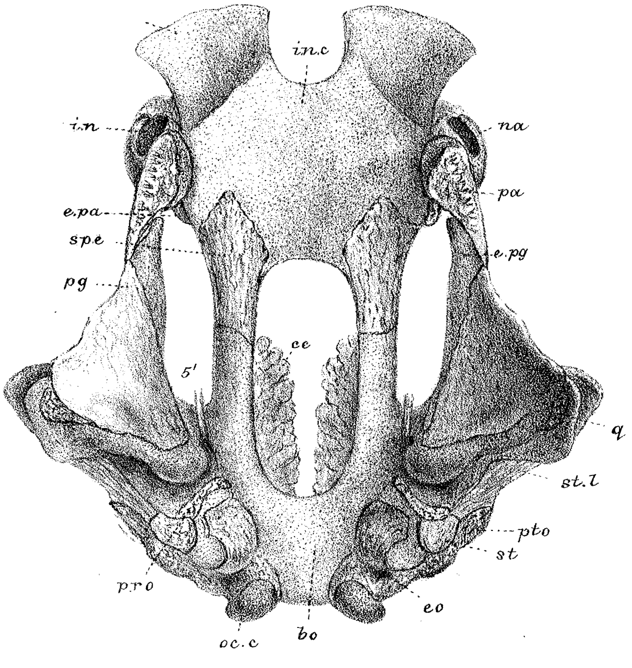
1 x 3½



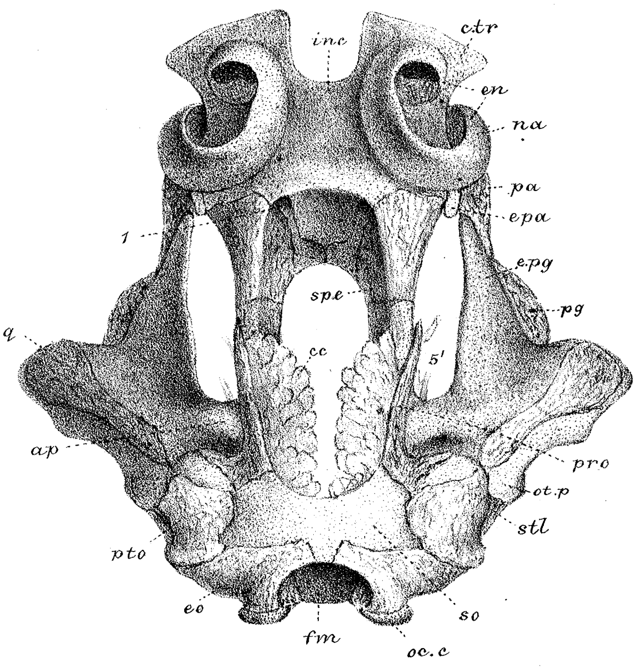
5 x 3½



4 x 3½



3 x 3½

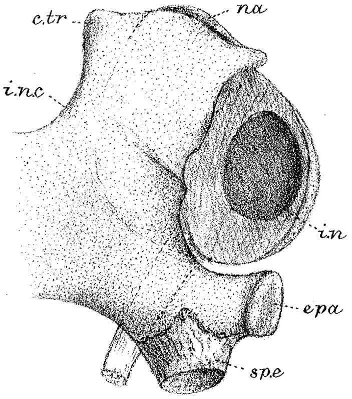


W.K.P. del. ad nat. G. West lith.

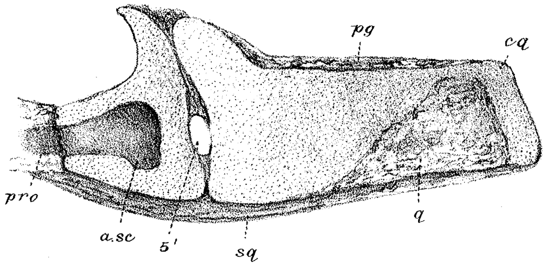
W. West & Co. imp.

Siredon 8th Stage.

3 x 7



4 x 7



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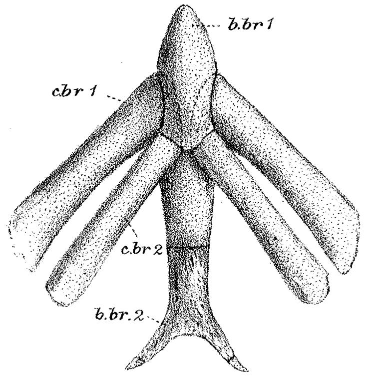
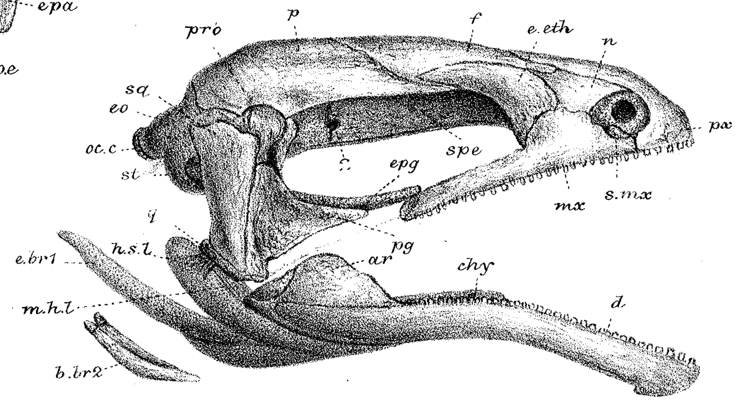
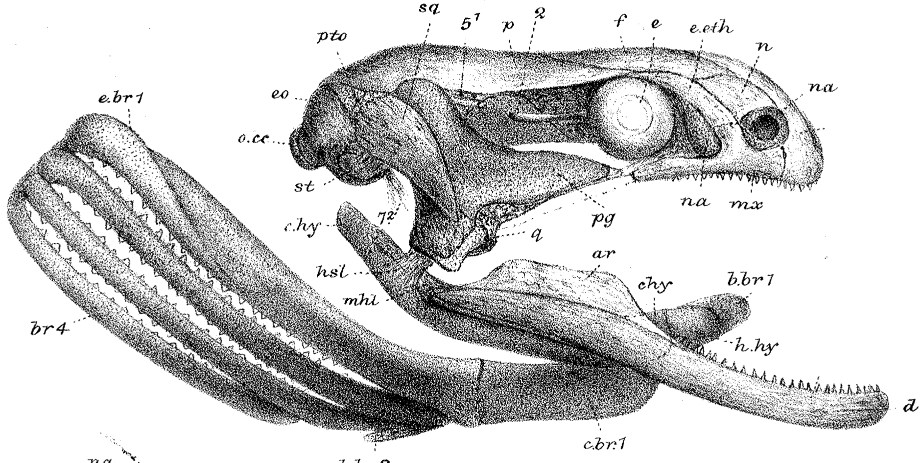


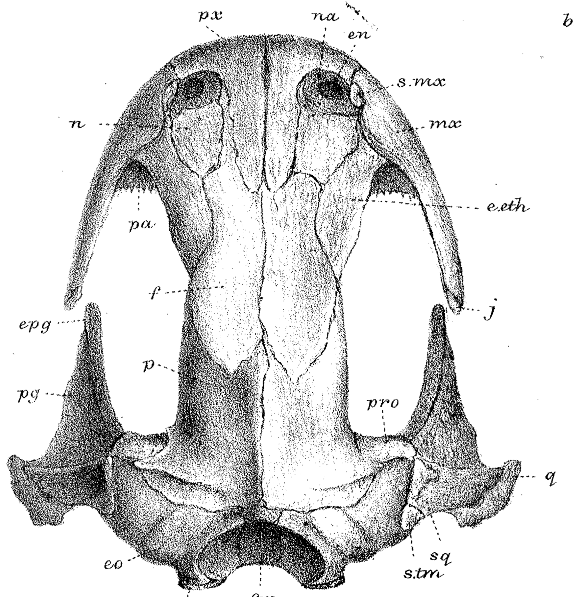


7 x 5

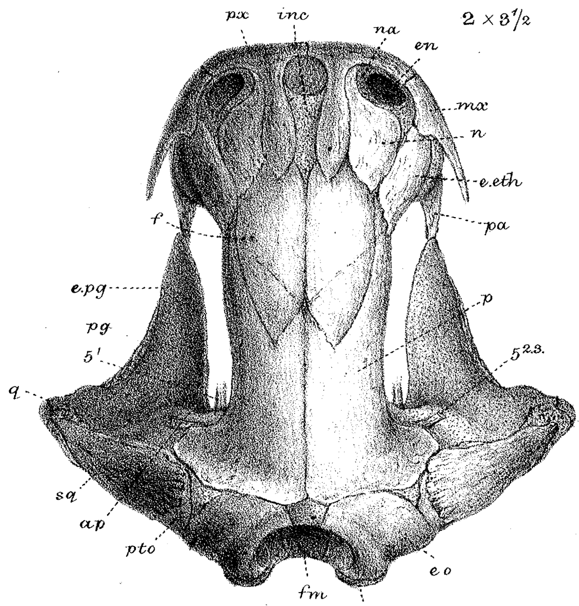
1 x 3½



6 x 5



2 x 3½

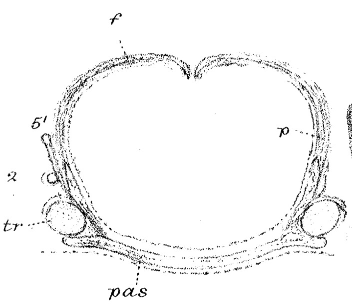


W.K.P. ad nat. del. G. West lith.

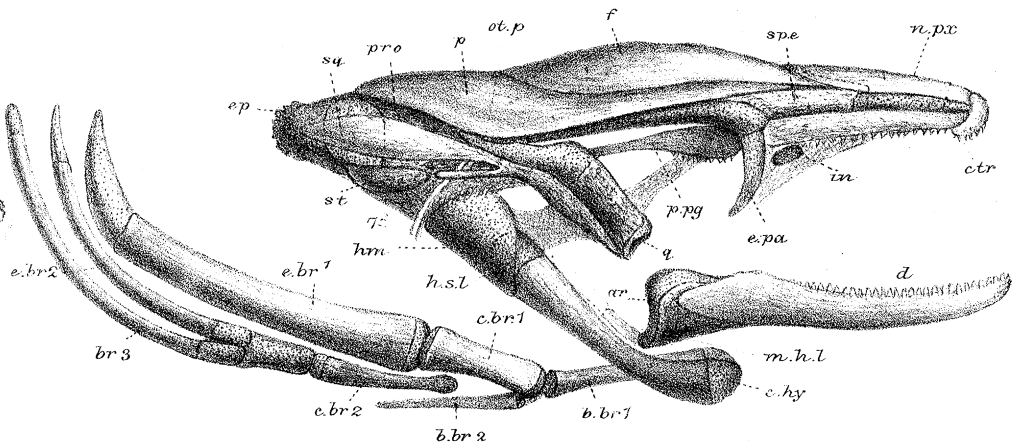
W. West & Co. imp.

Siredon *Figs.* 1–5 9th *Stage*; Amblystoma *Figs.* 6, 7.

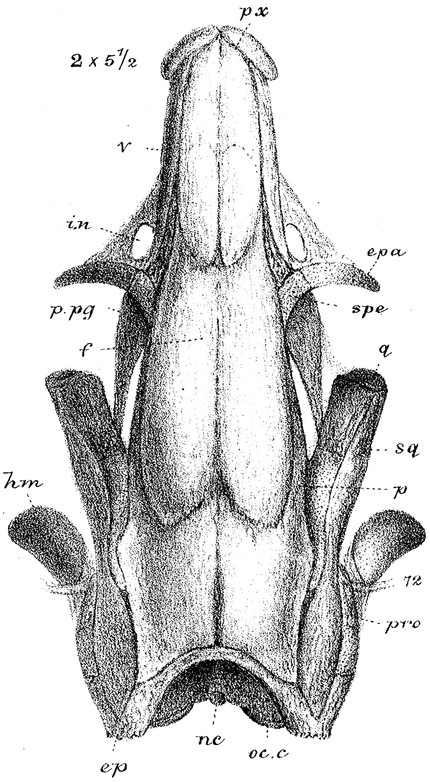
8 x 5½



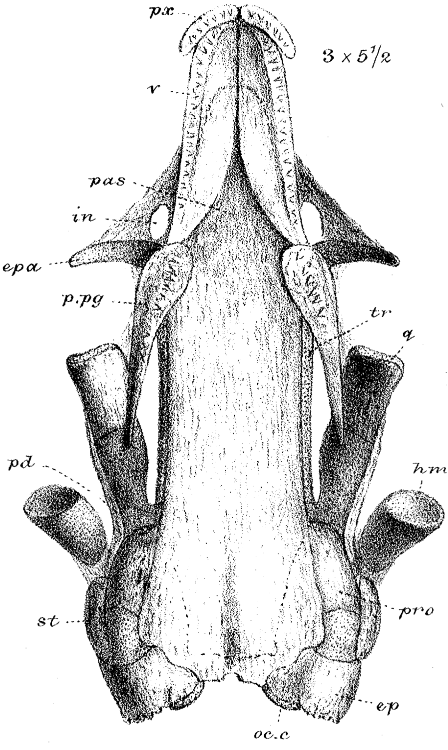
1 x 5½



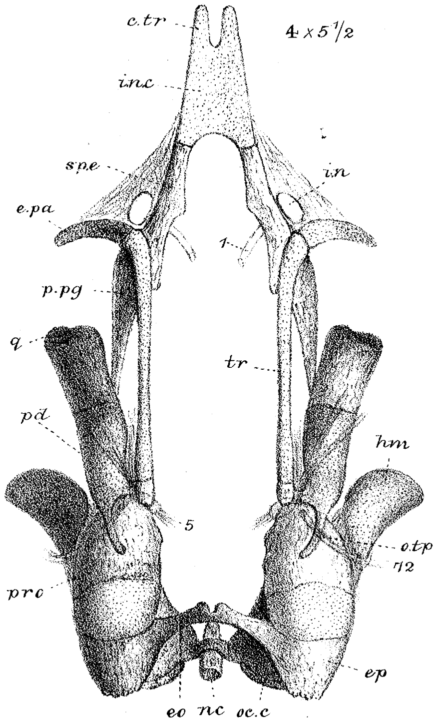
2 x 5½



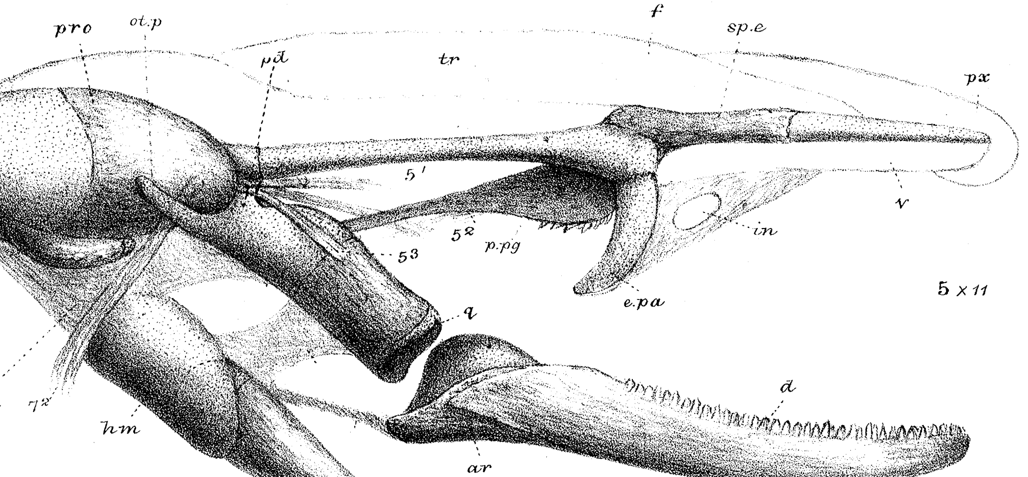
3 x 5½



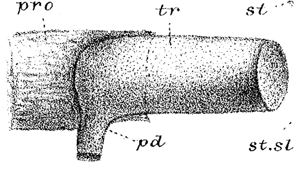
4 x 5½



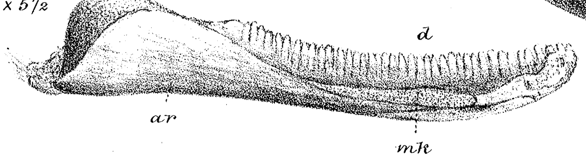
5 x 11



7 x 12



6 x 5½

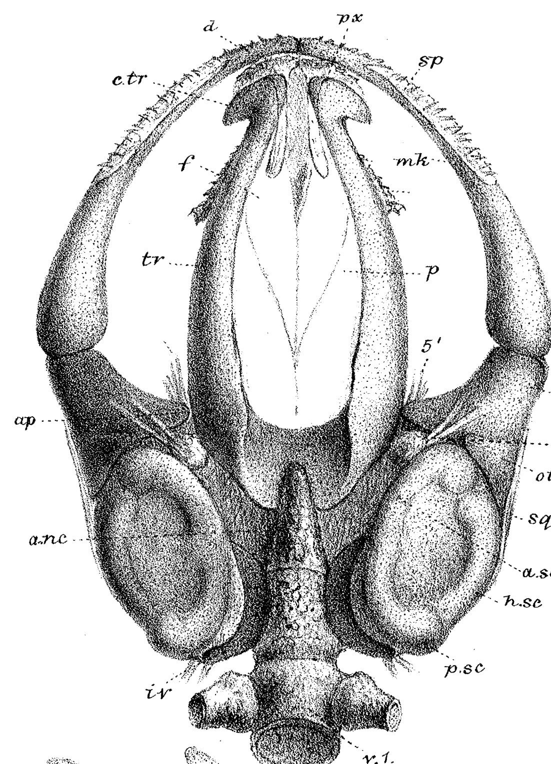


W. K. P. del. ad nat. G. West lith.

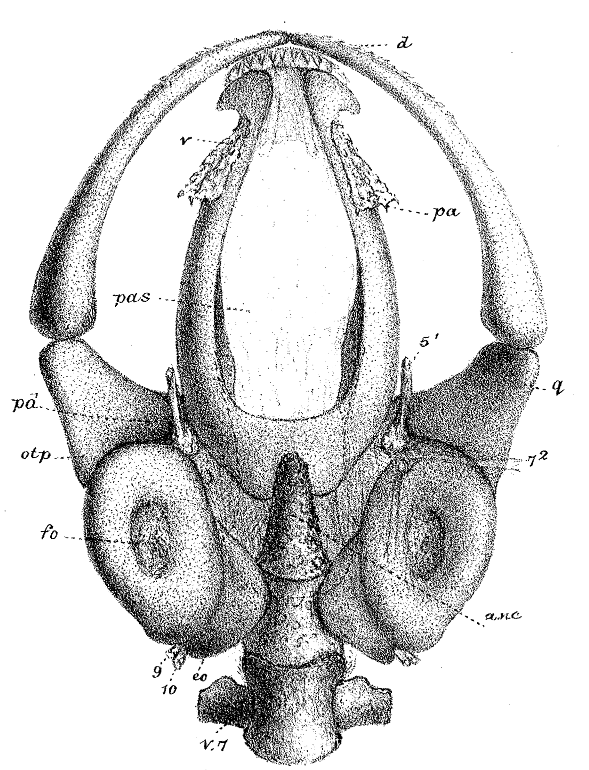
W. West & Co. imp.

Proteus anguinus:

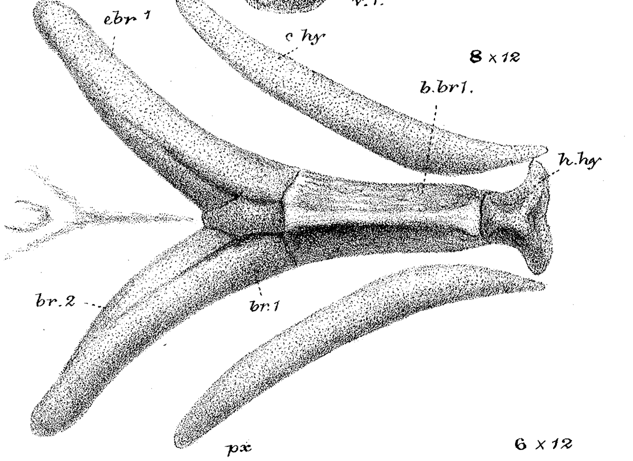
1 × 24



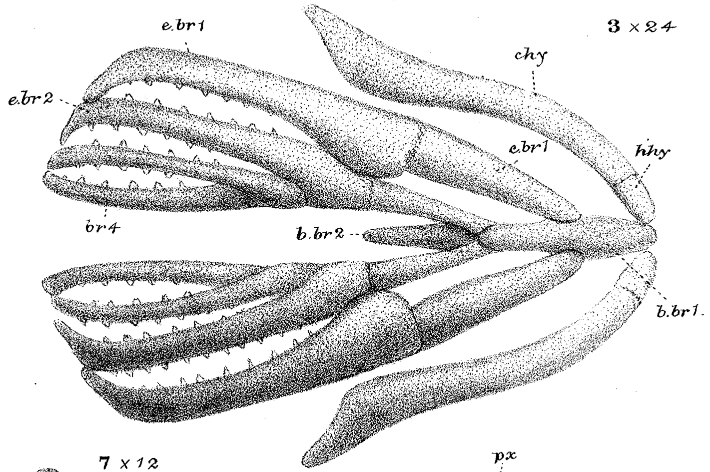
2 × 24



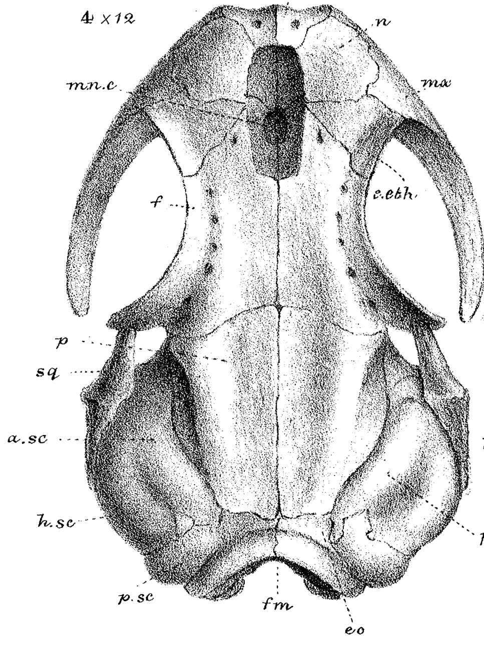
8 × 12



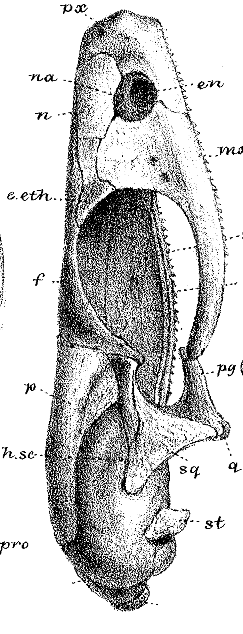
3 × 24



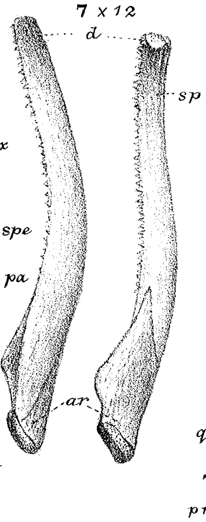
4 × 12



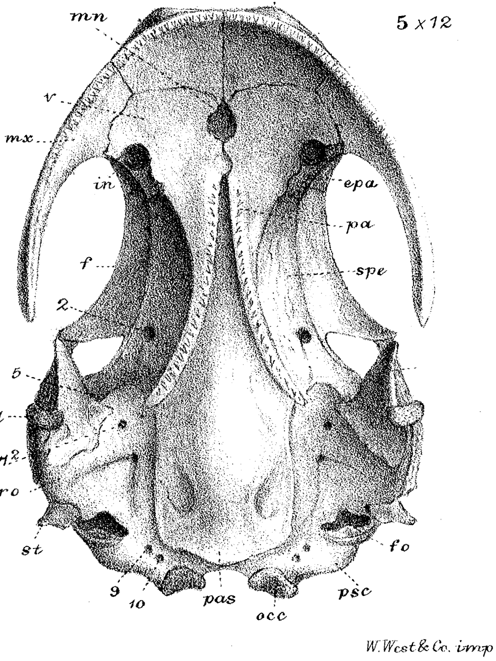
6 × 12



7 × 12



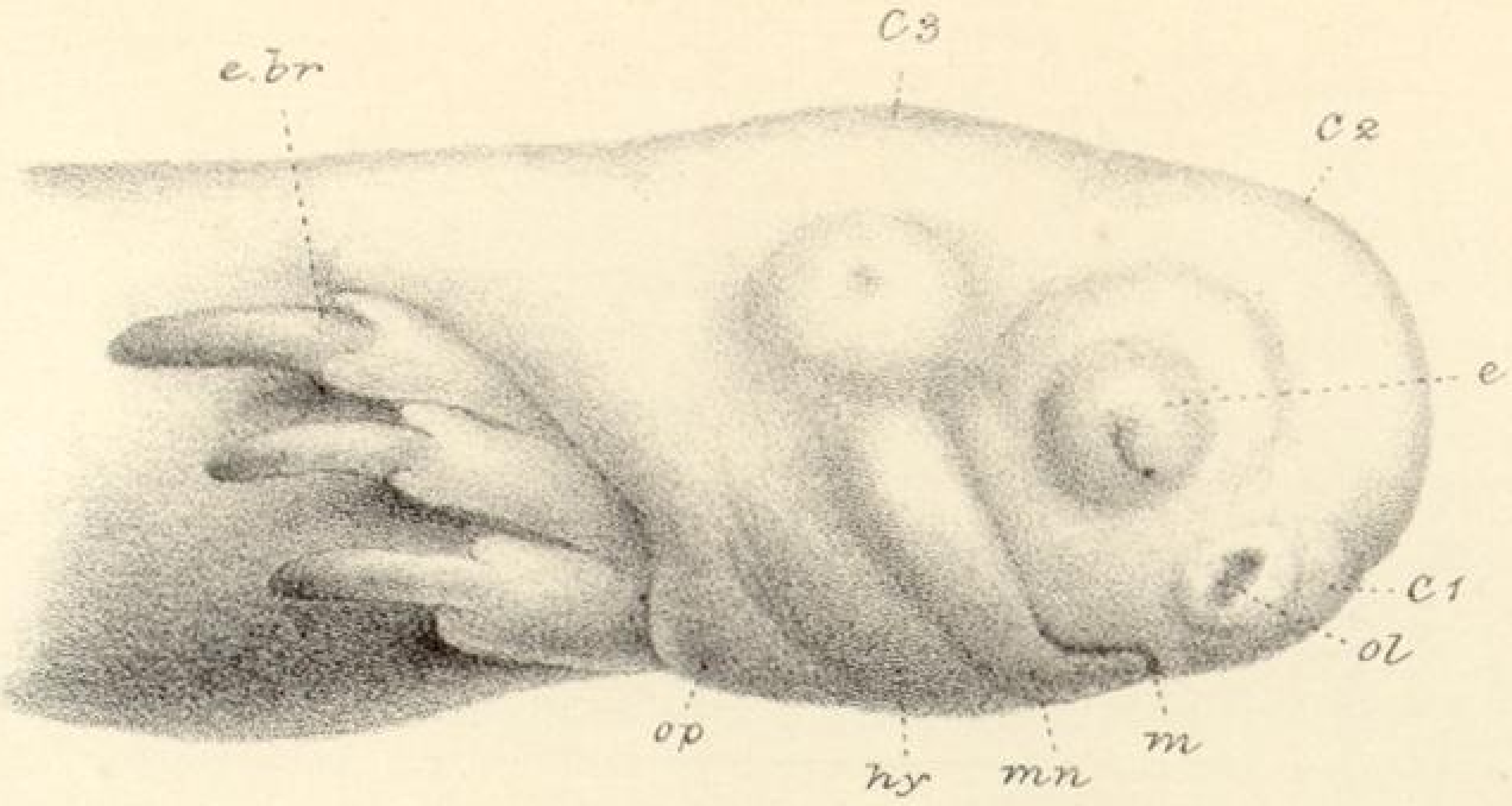
5 × 12



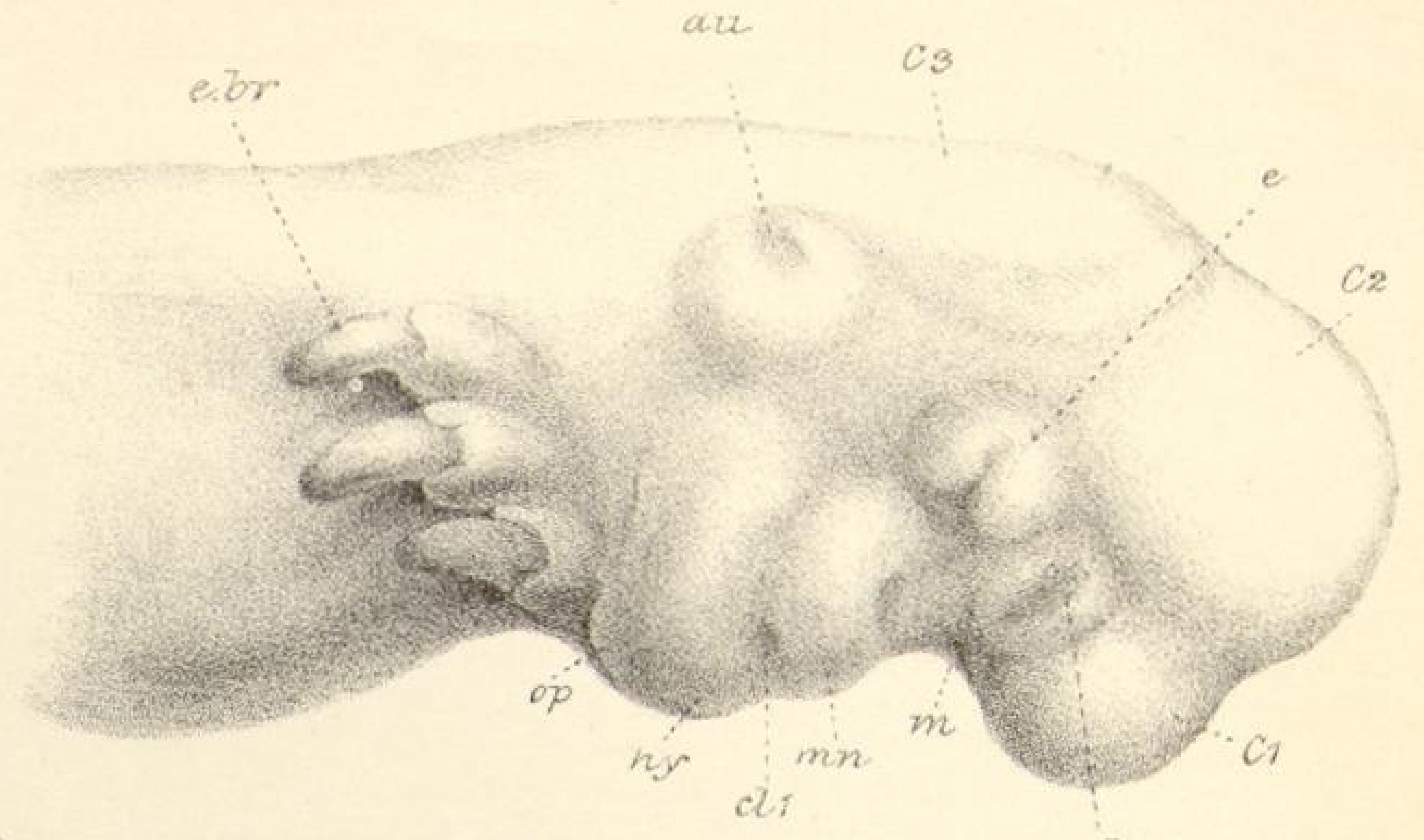
W.K.P. del. ad nat. G. West lith.
W. West & Co. imp.

Seironota perspicillata; *Figs.* 1–3 *larva* 4 — 8 *adult*

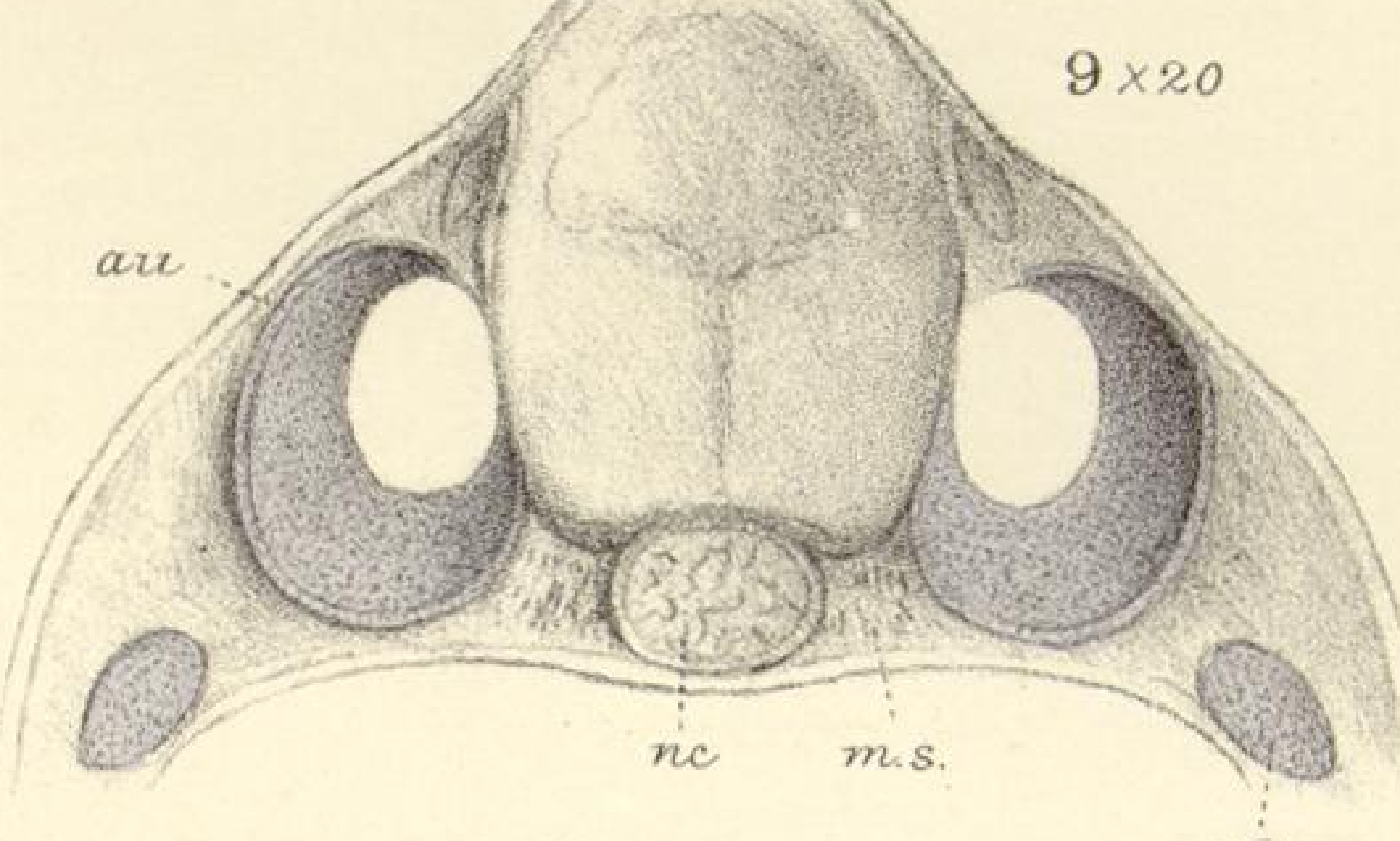
5 x 20



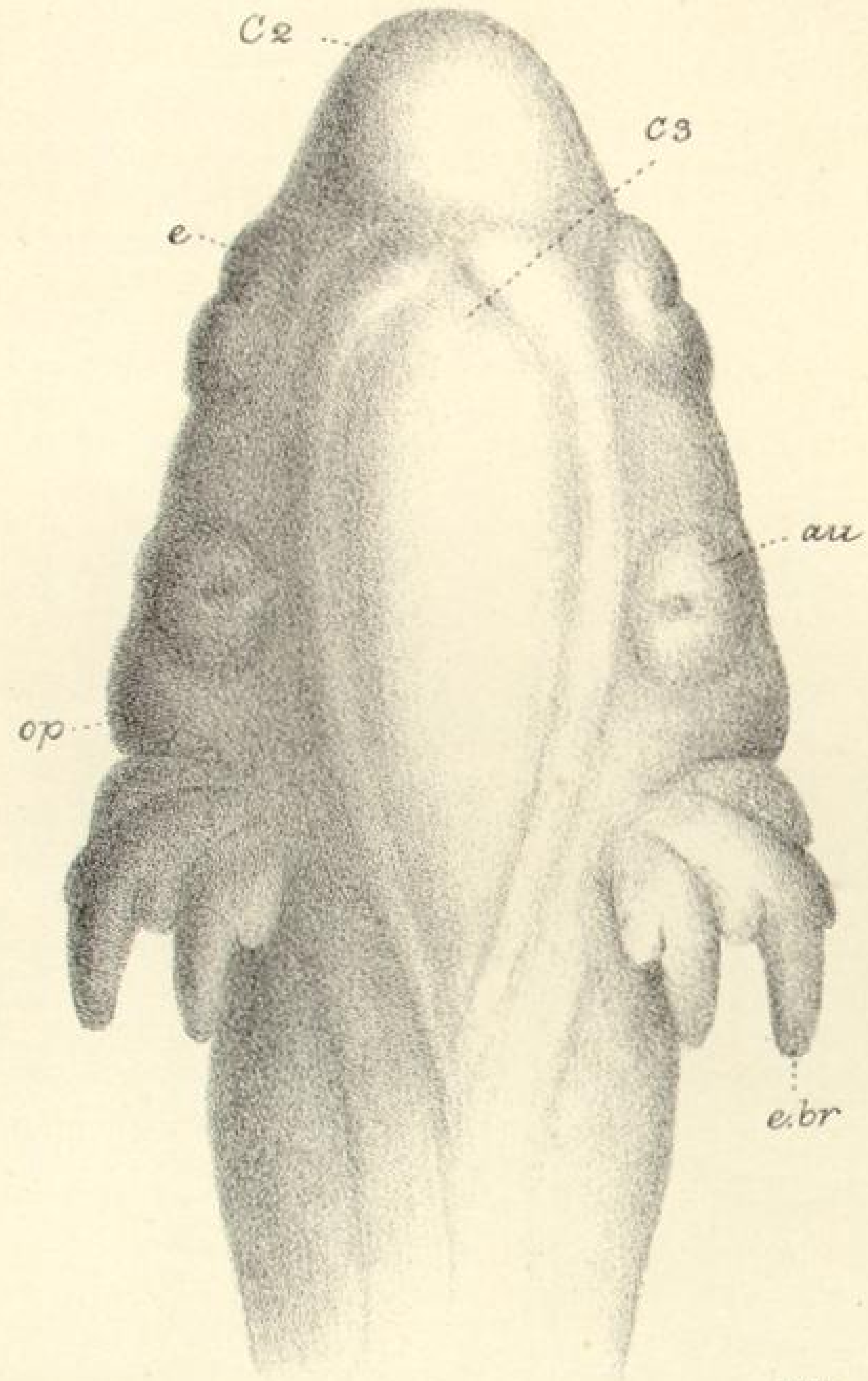
1 x 26



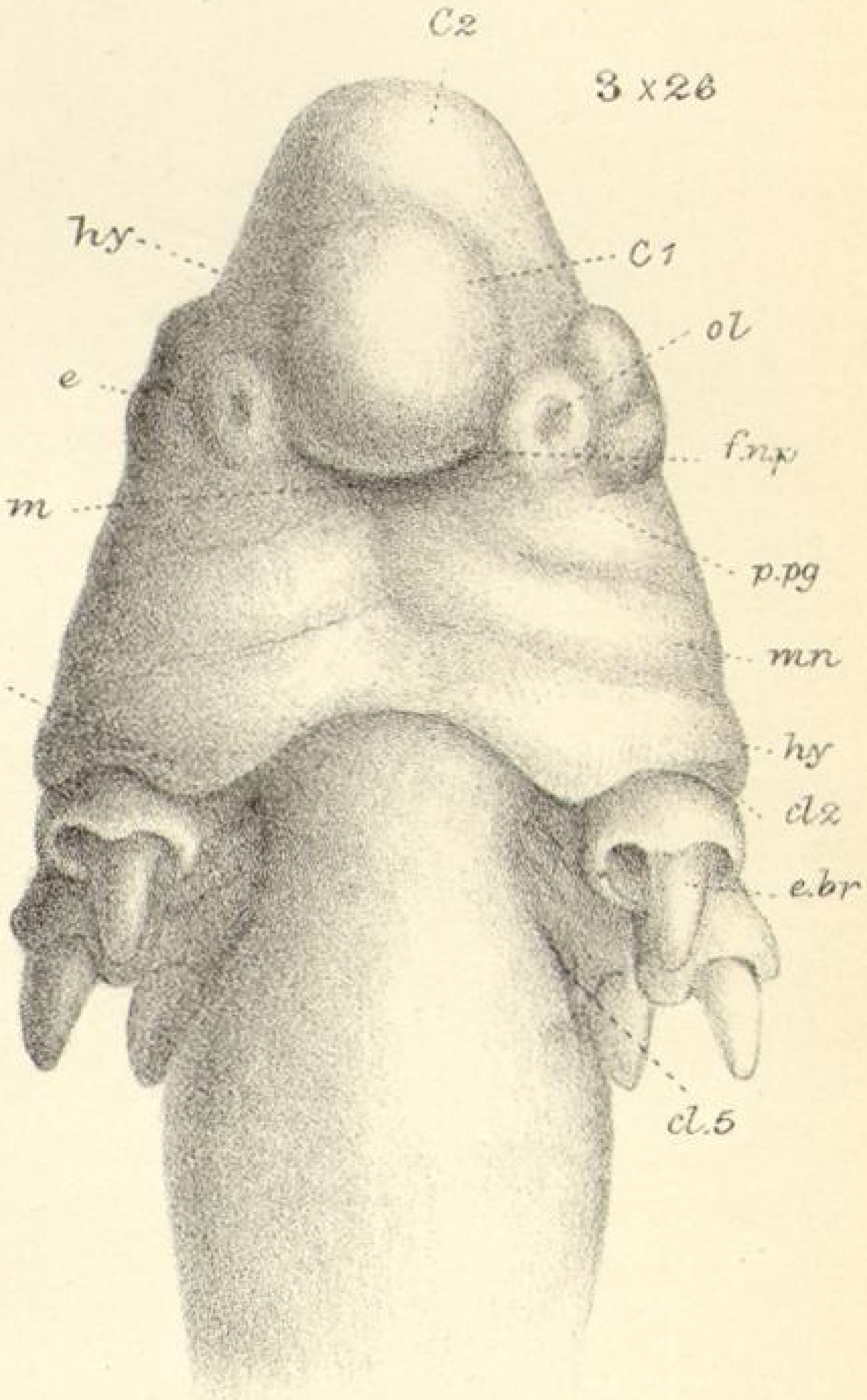
9 x 20



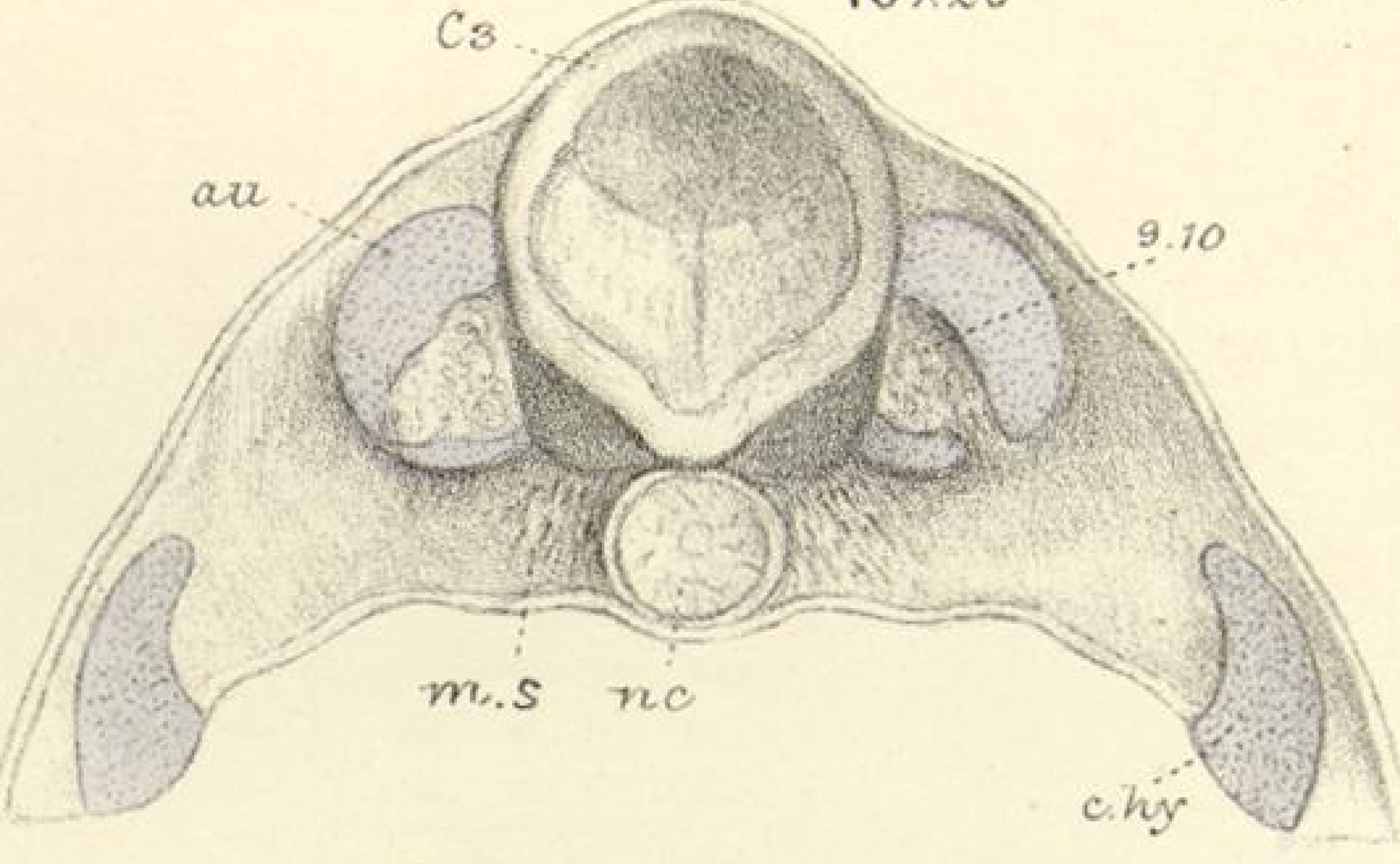
2 x 26



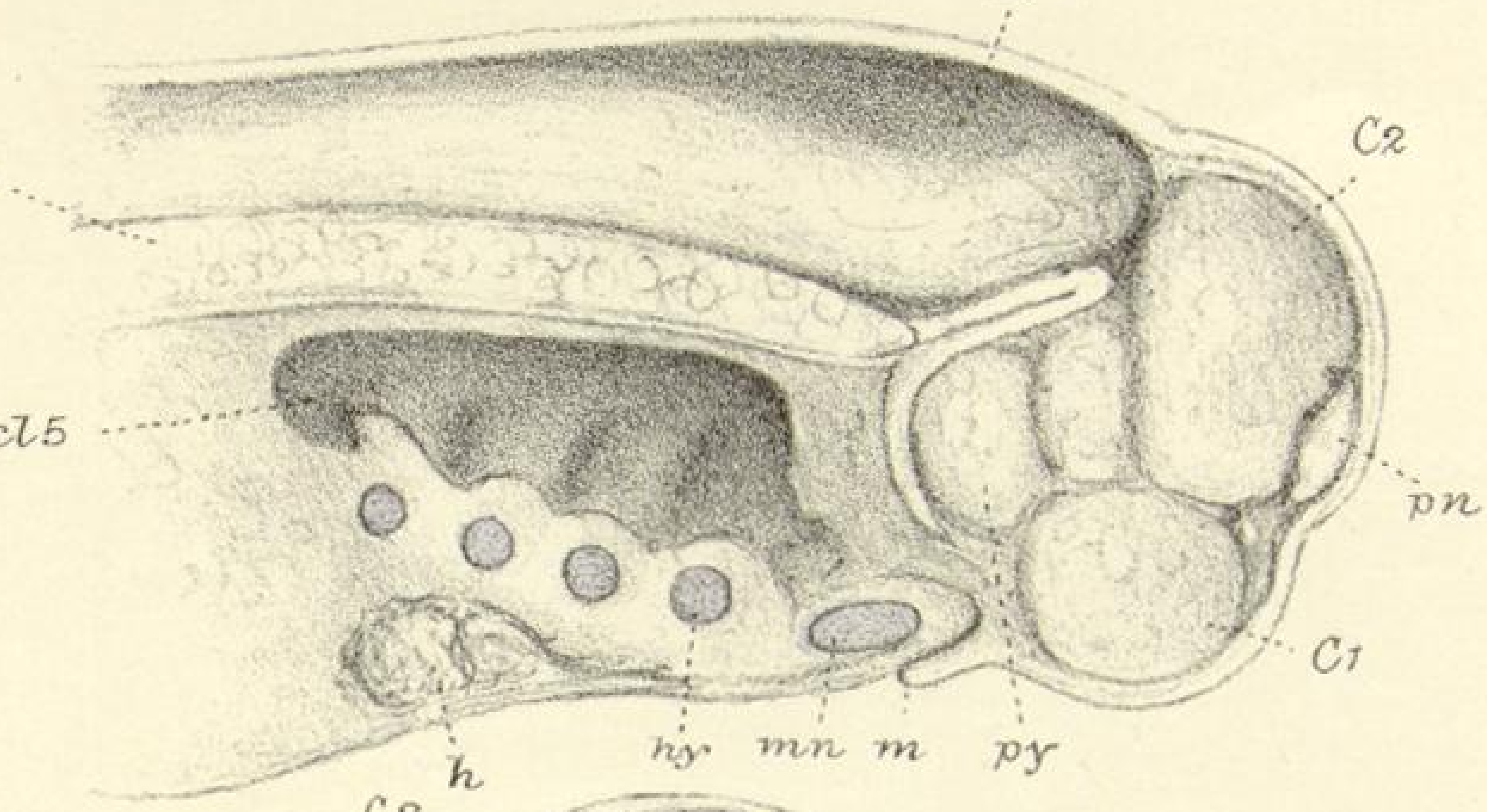
3 x 26



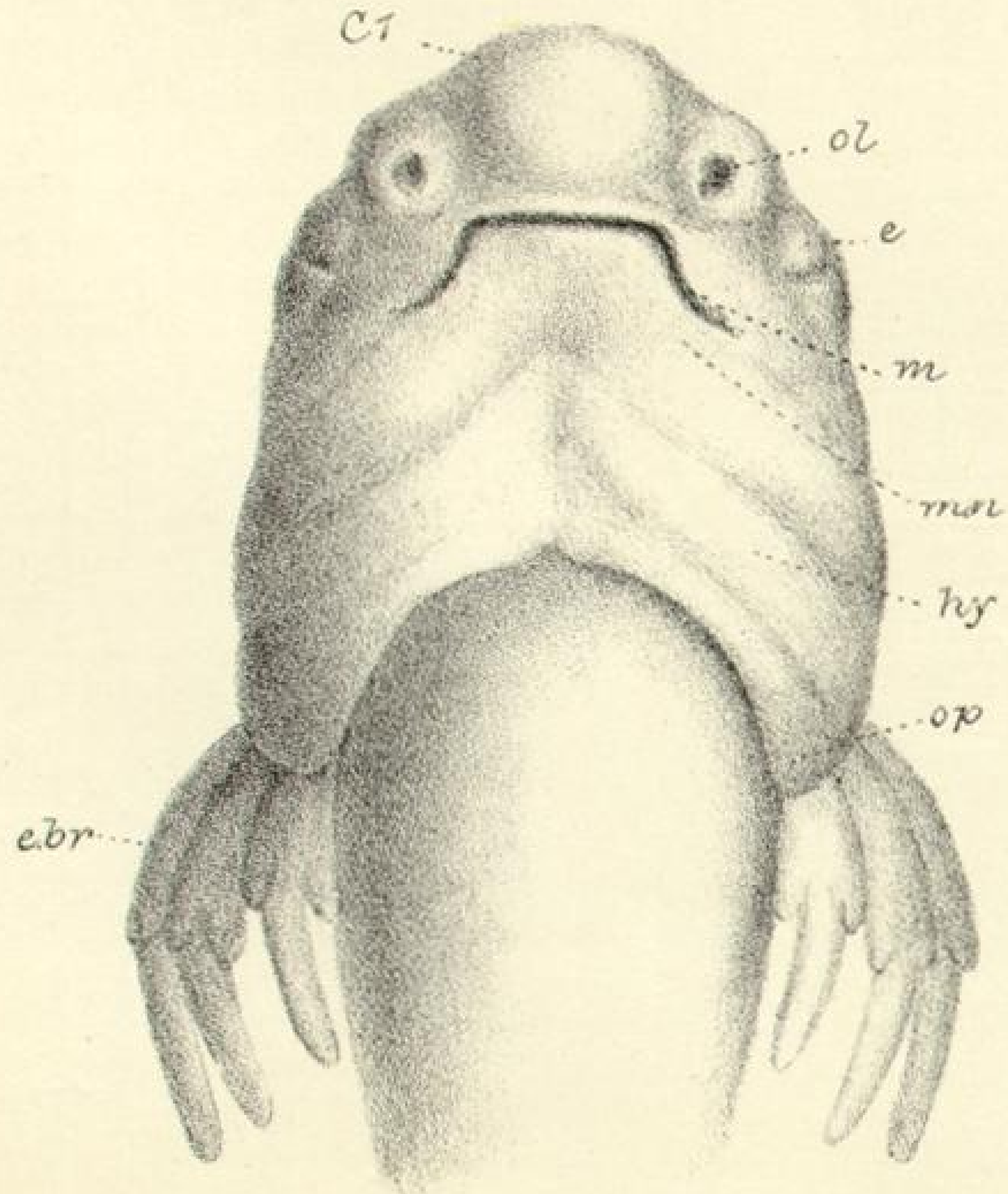
10 x 20



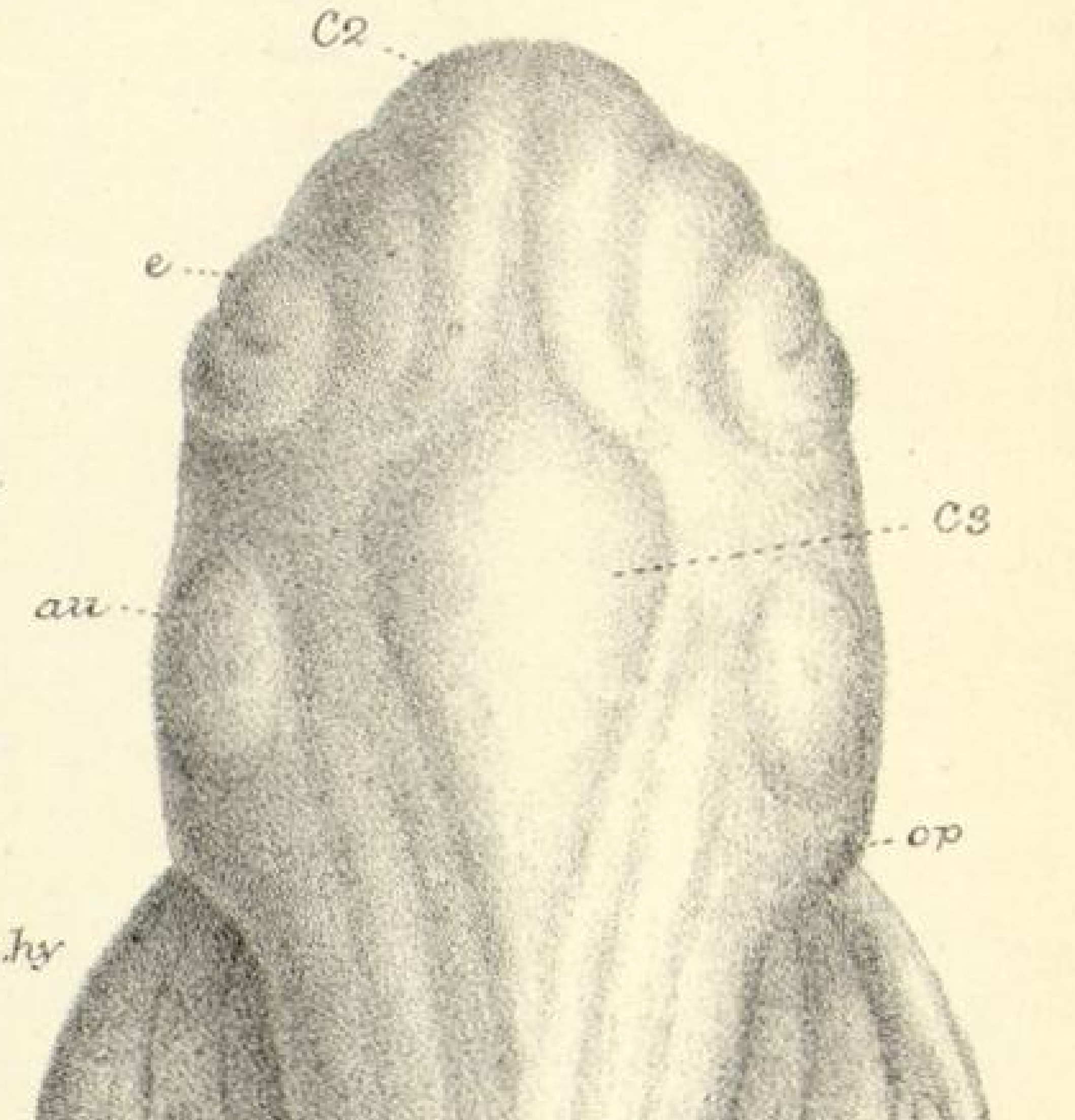
4 x 26



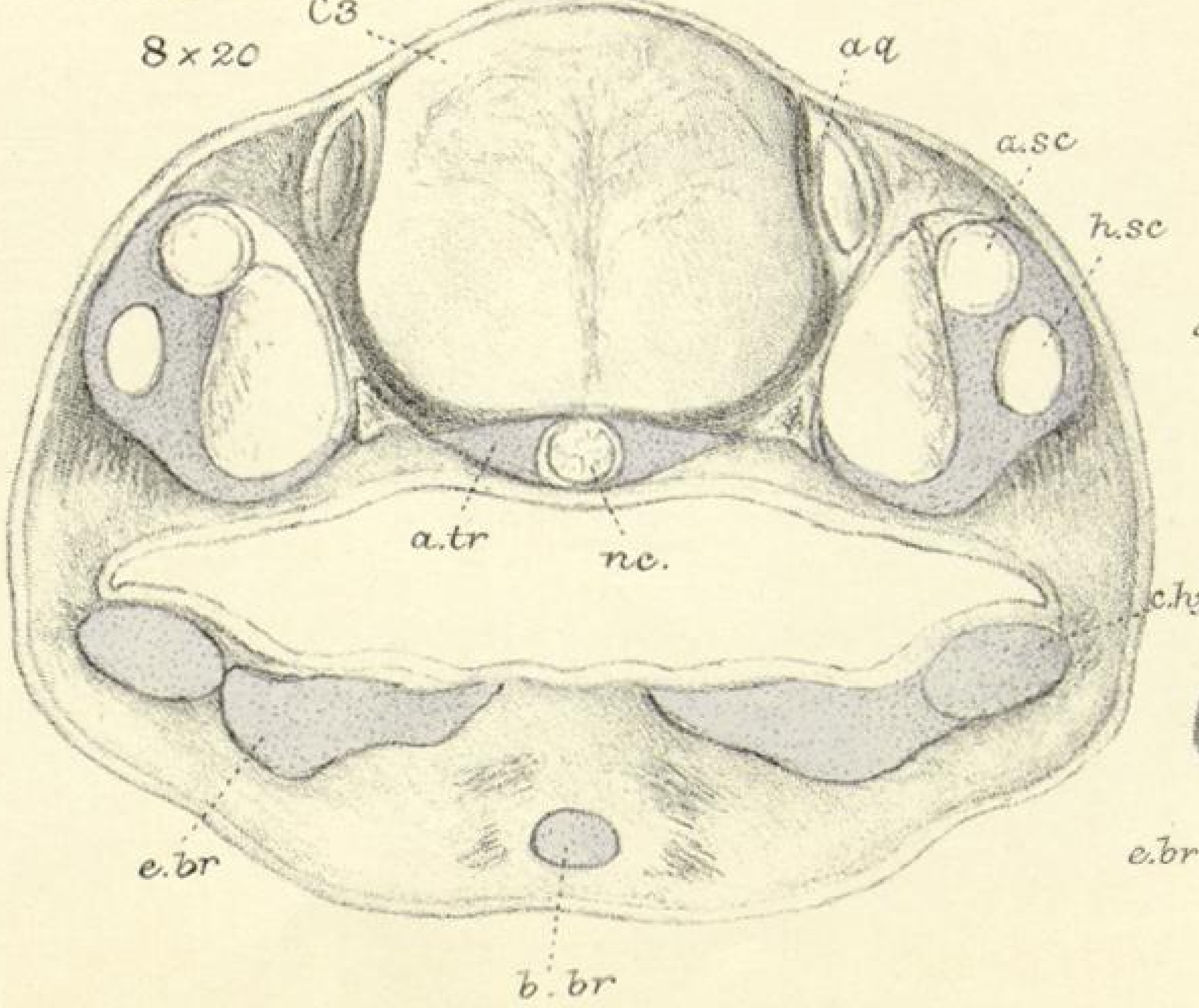
7 x 20



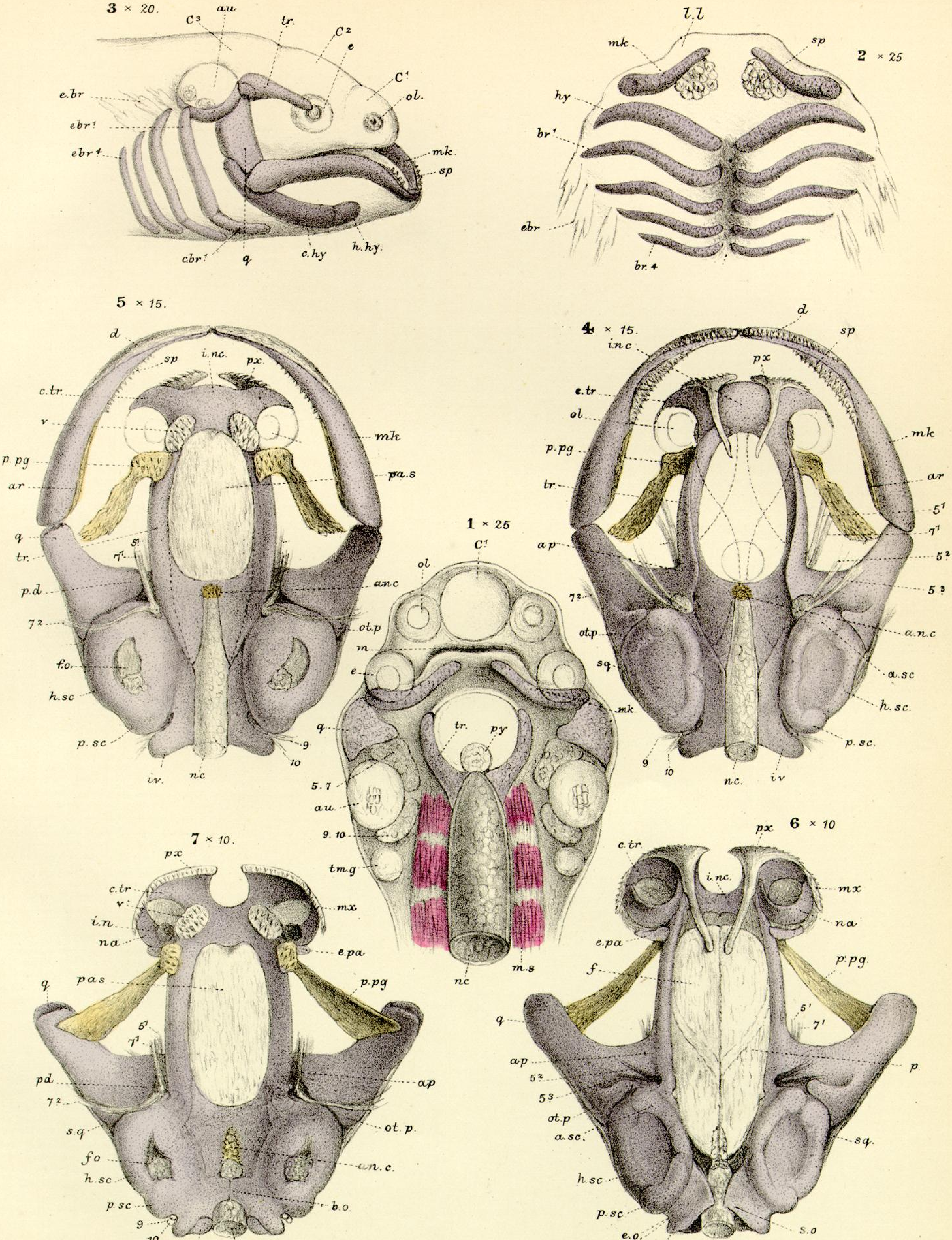
6 x 20



8 x 20

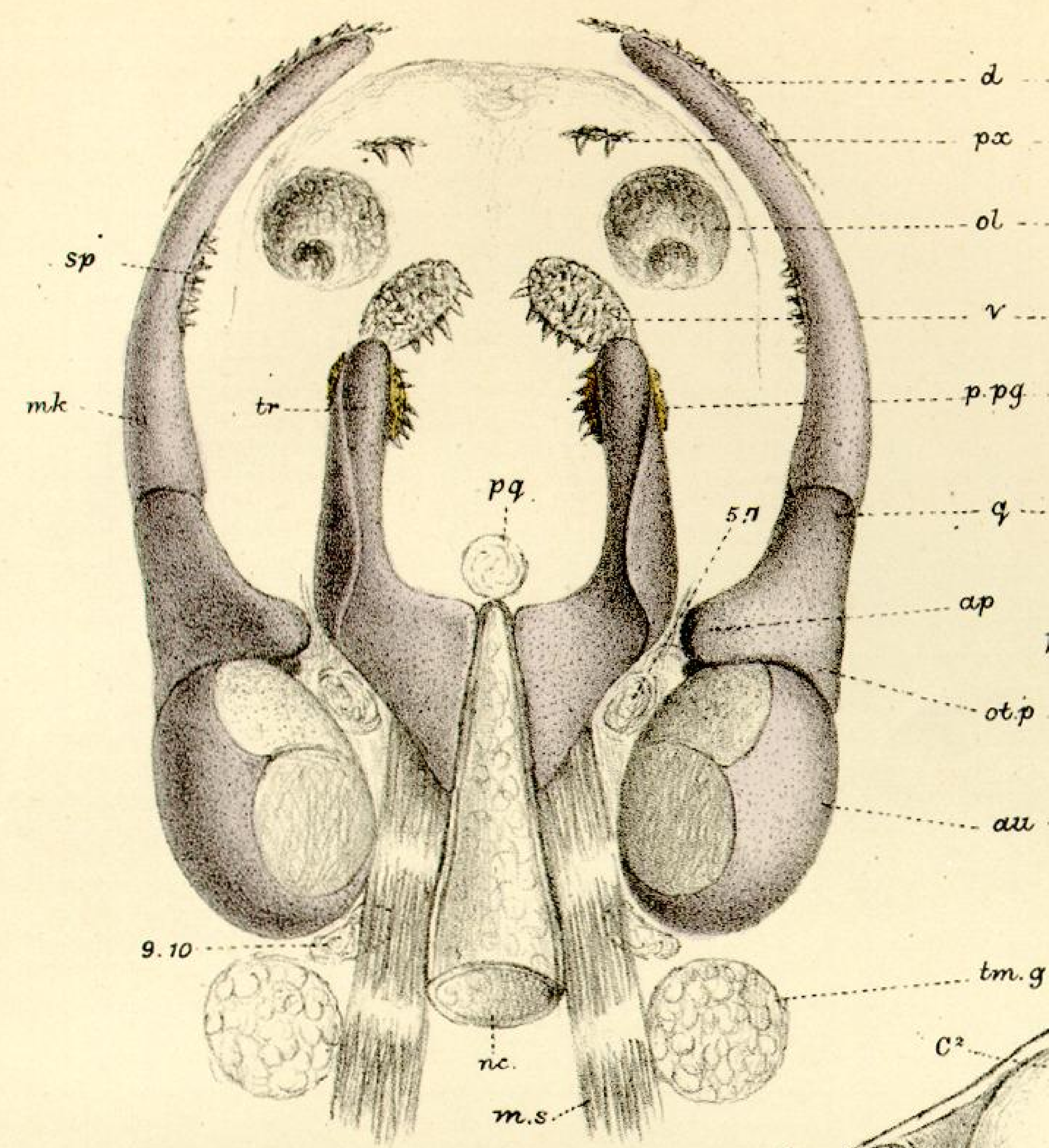


Siredon · Figs. 1–4 1st. Stage; 5–7 2nd. Stage; 8–10 3rd. Stage.

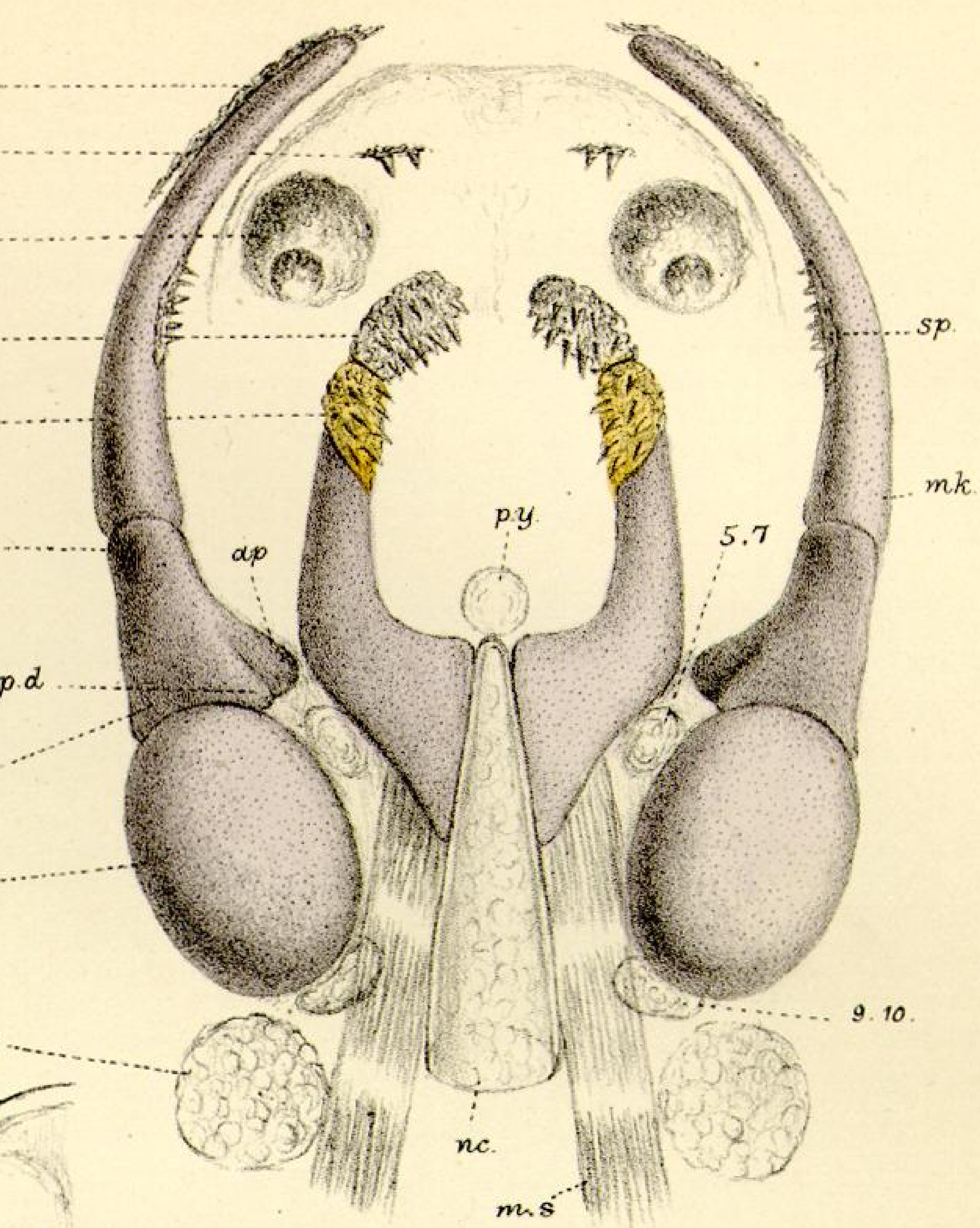


Siredon, Figs. 1, 2, 2nd Stage. 3, 3rd Stage. 4, 5, 4th Stage. 6, 7, 5th Stage.

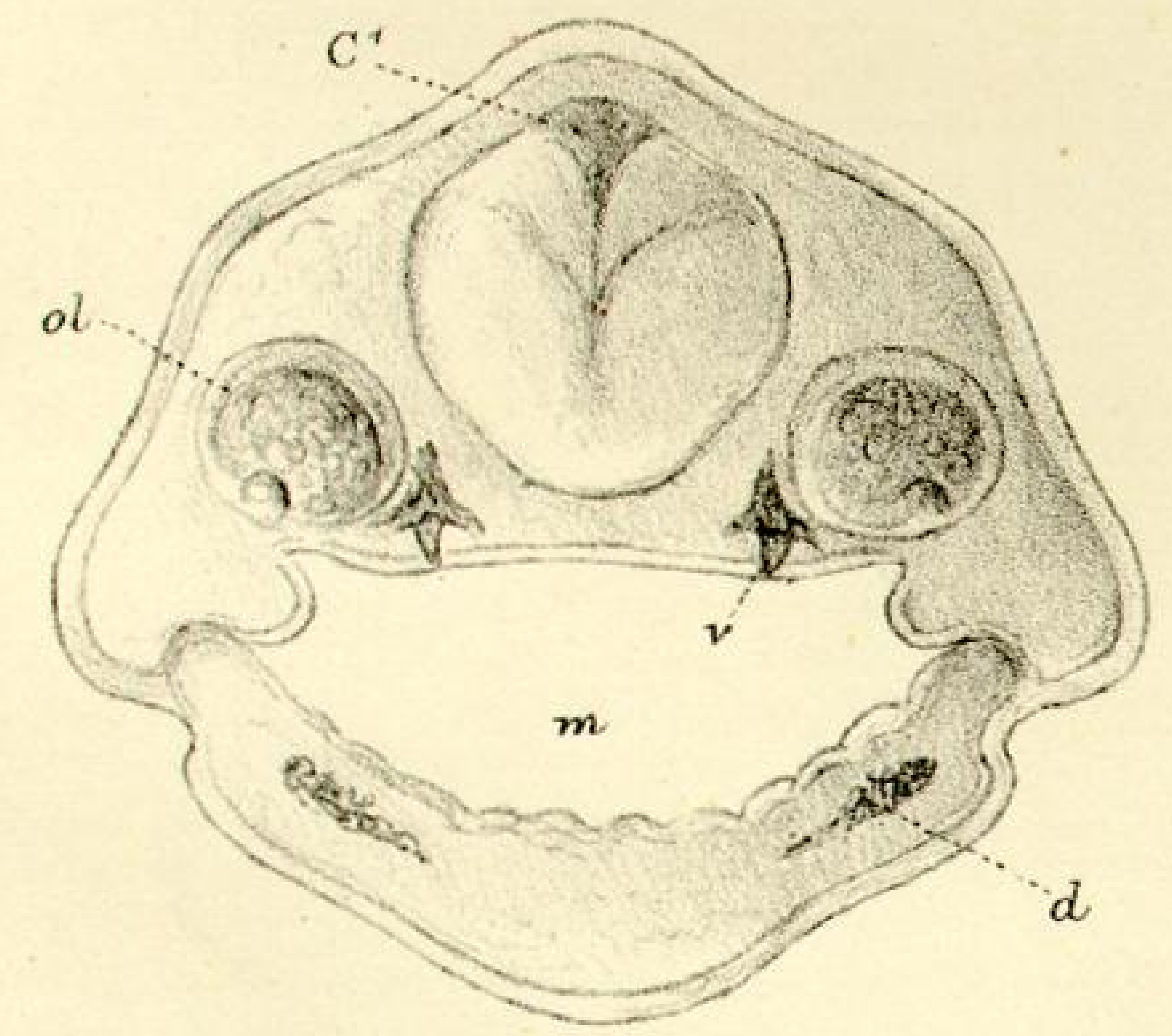
1. × 20.



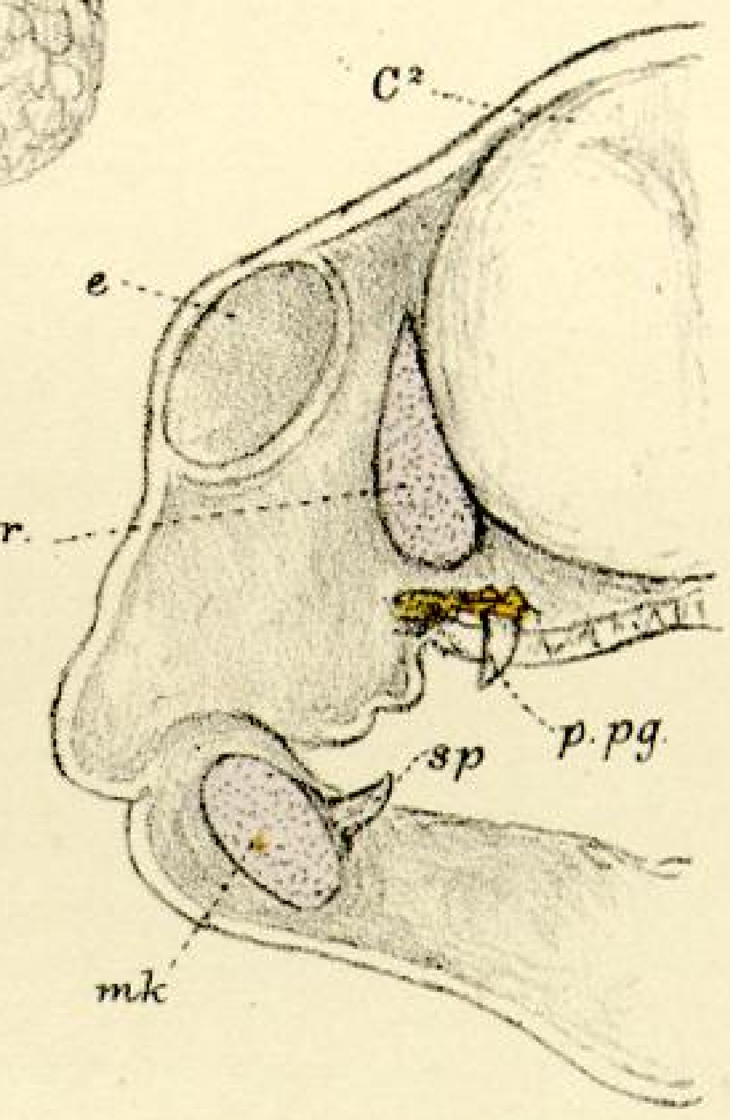
2. × 20.



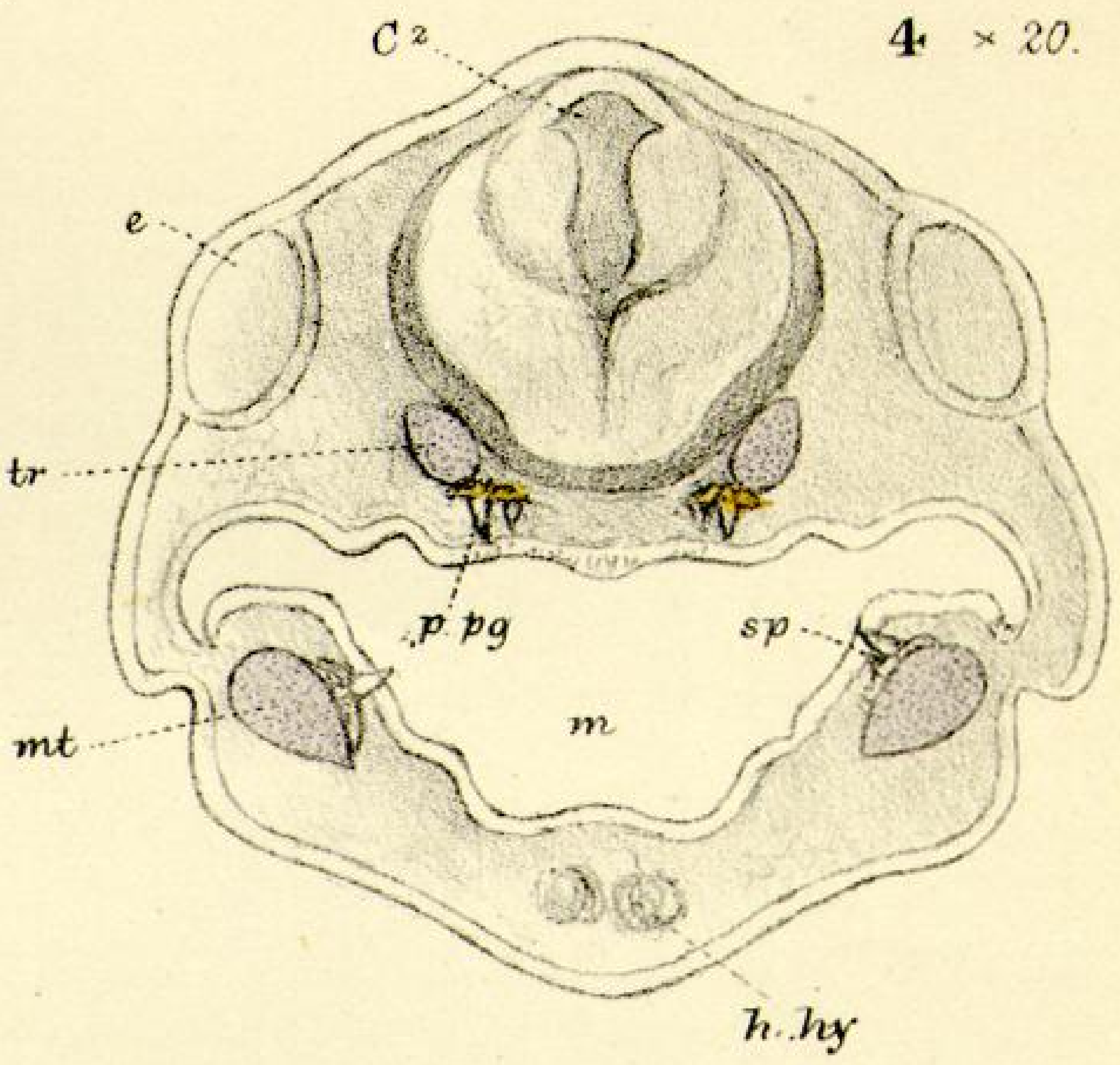
3 × 20.



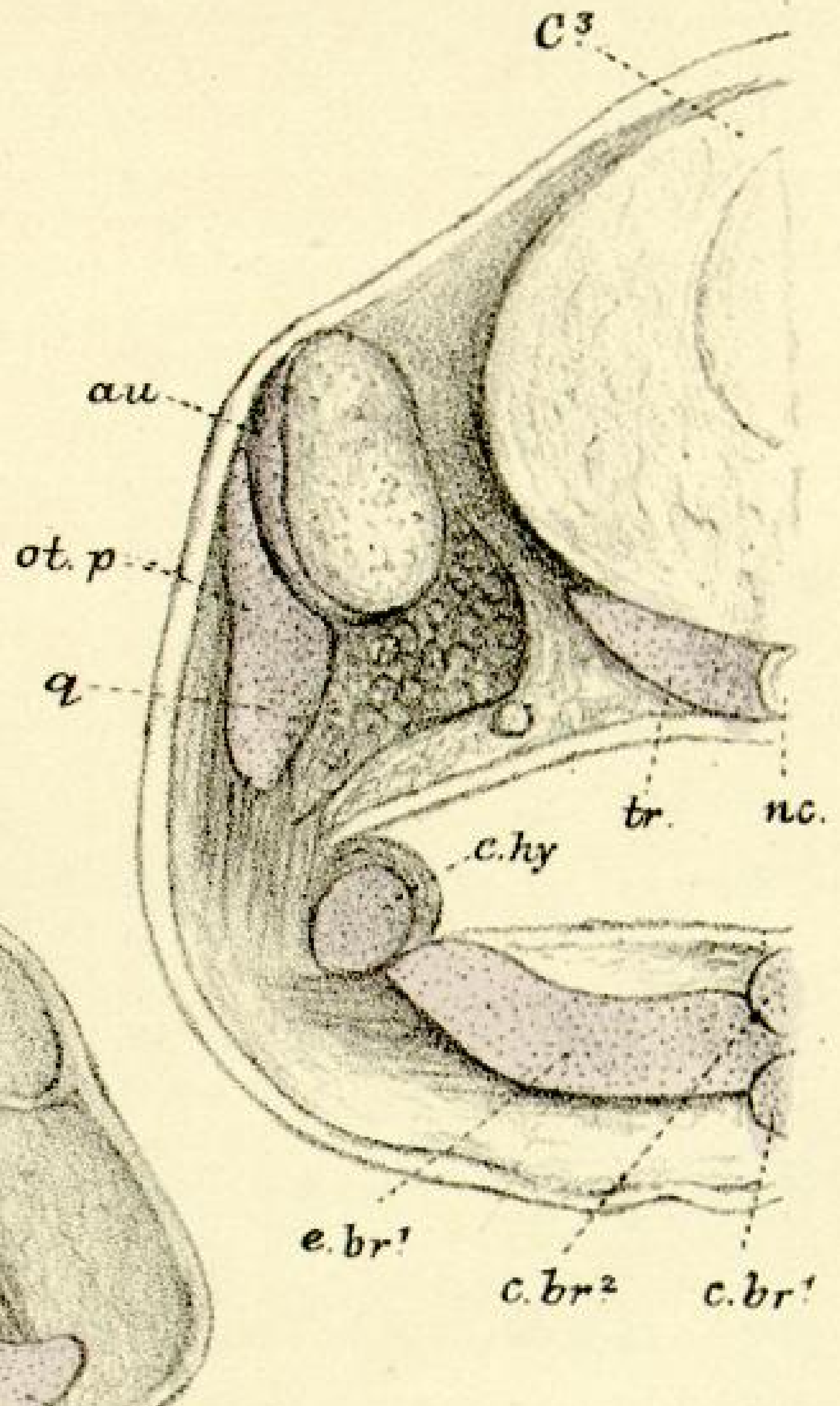
5. × 20.



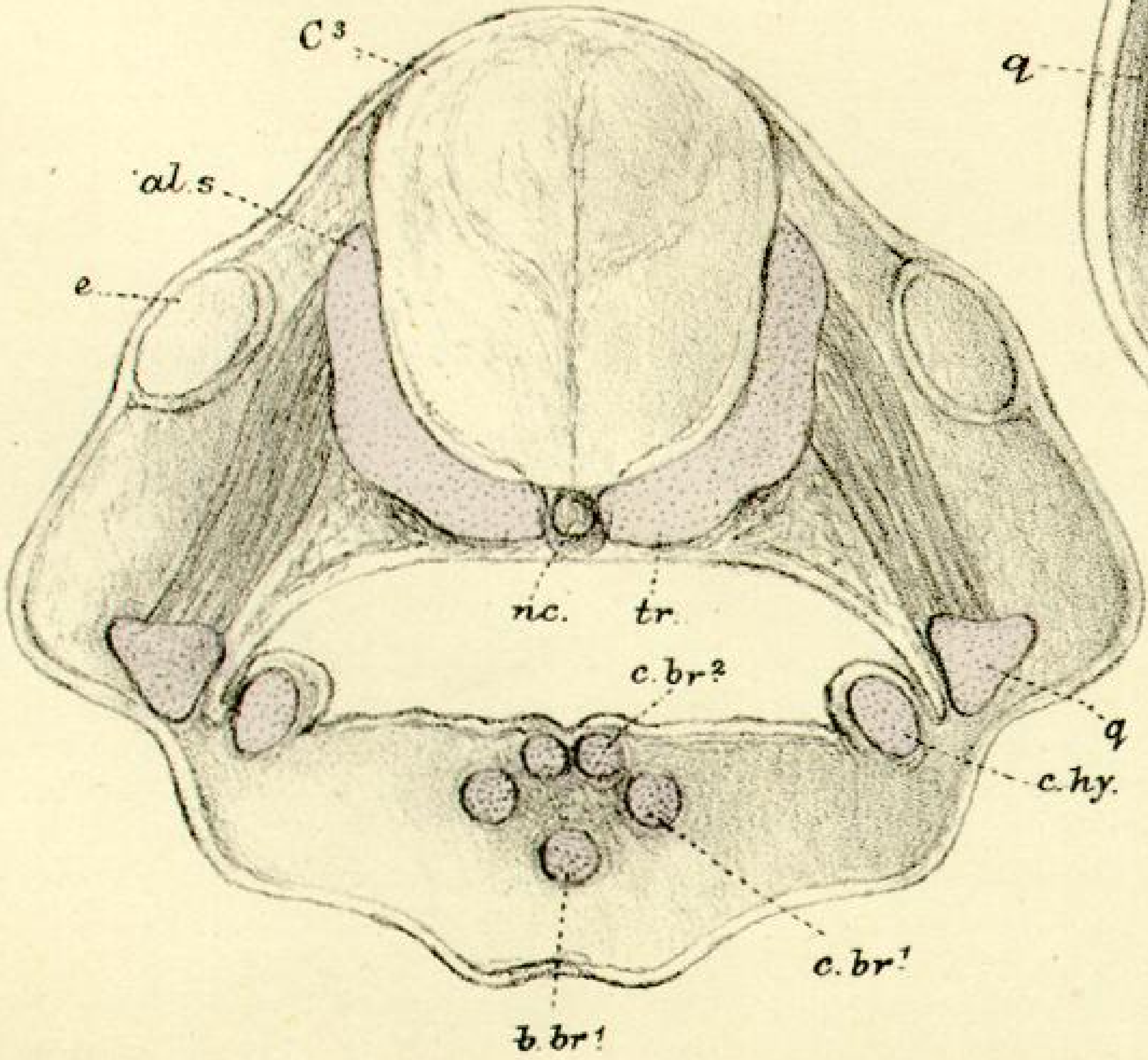
4 × 20.



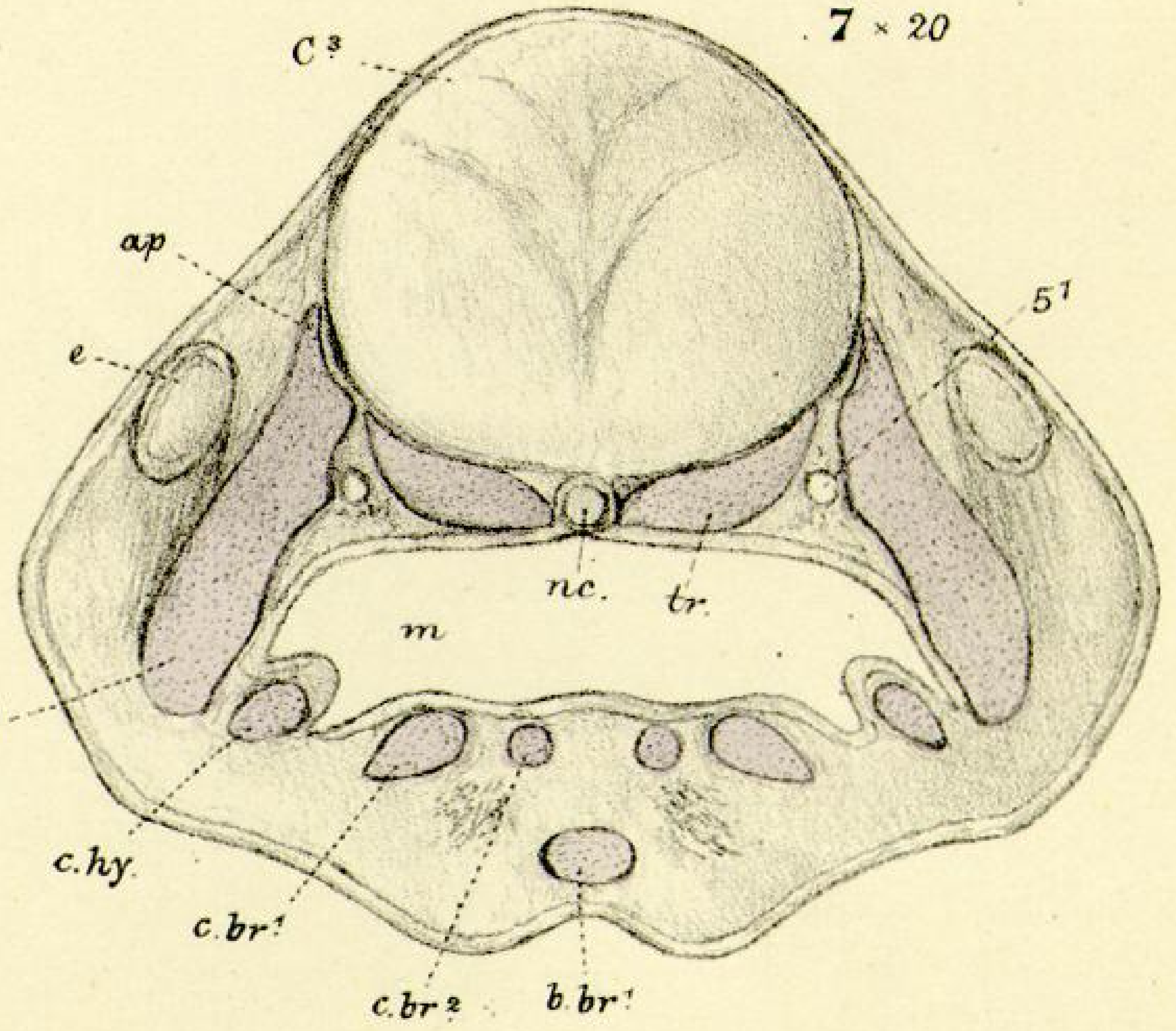
8 × 20.



6 × 20

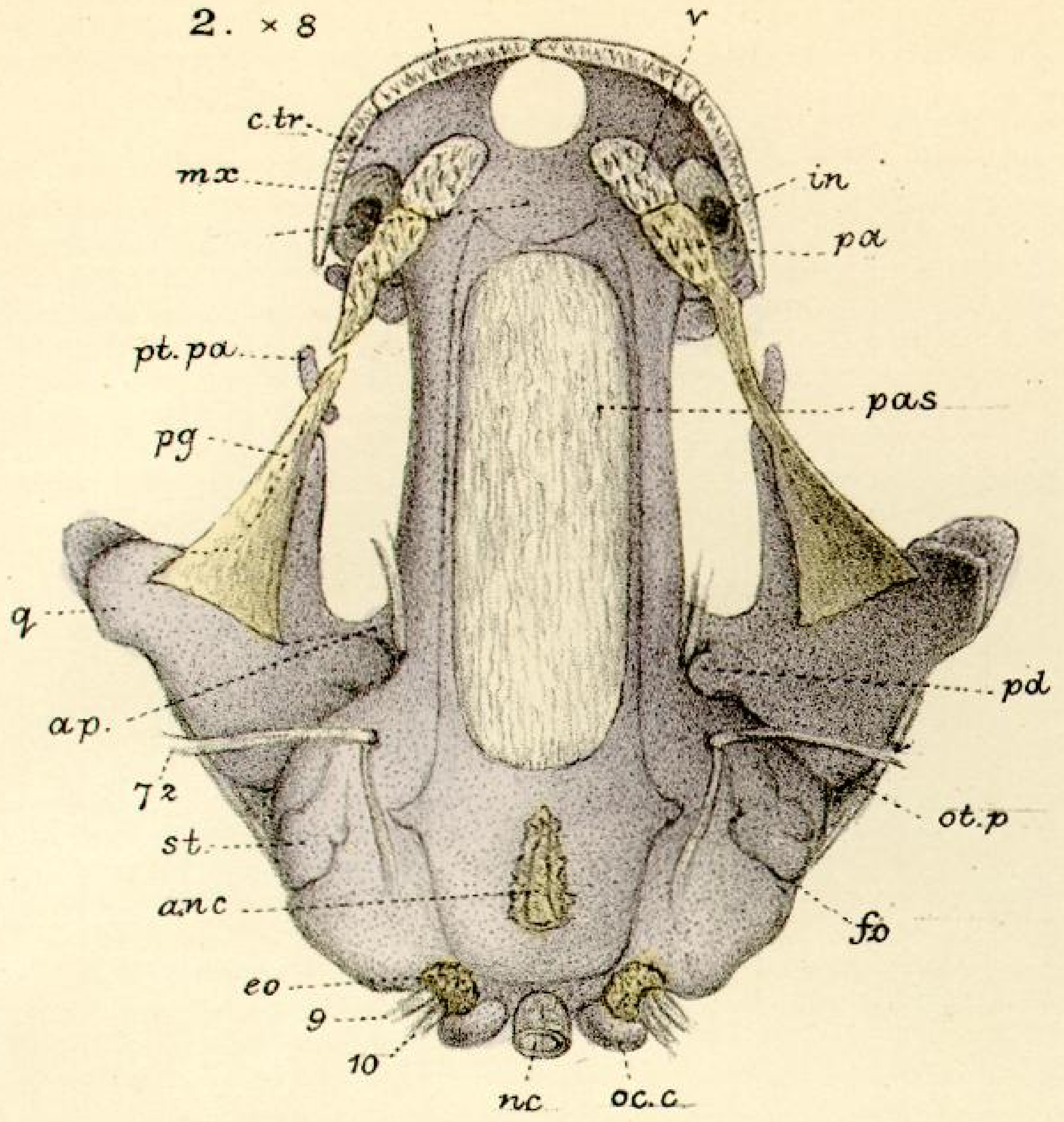


7 × 20

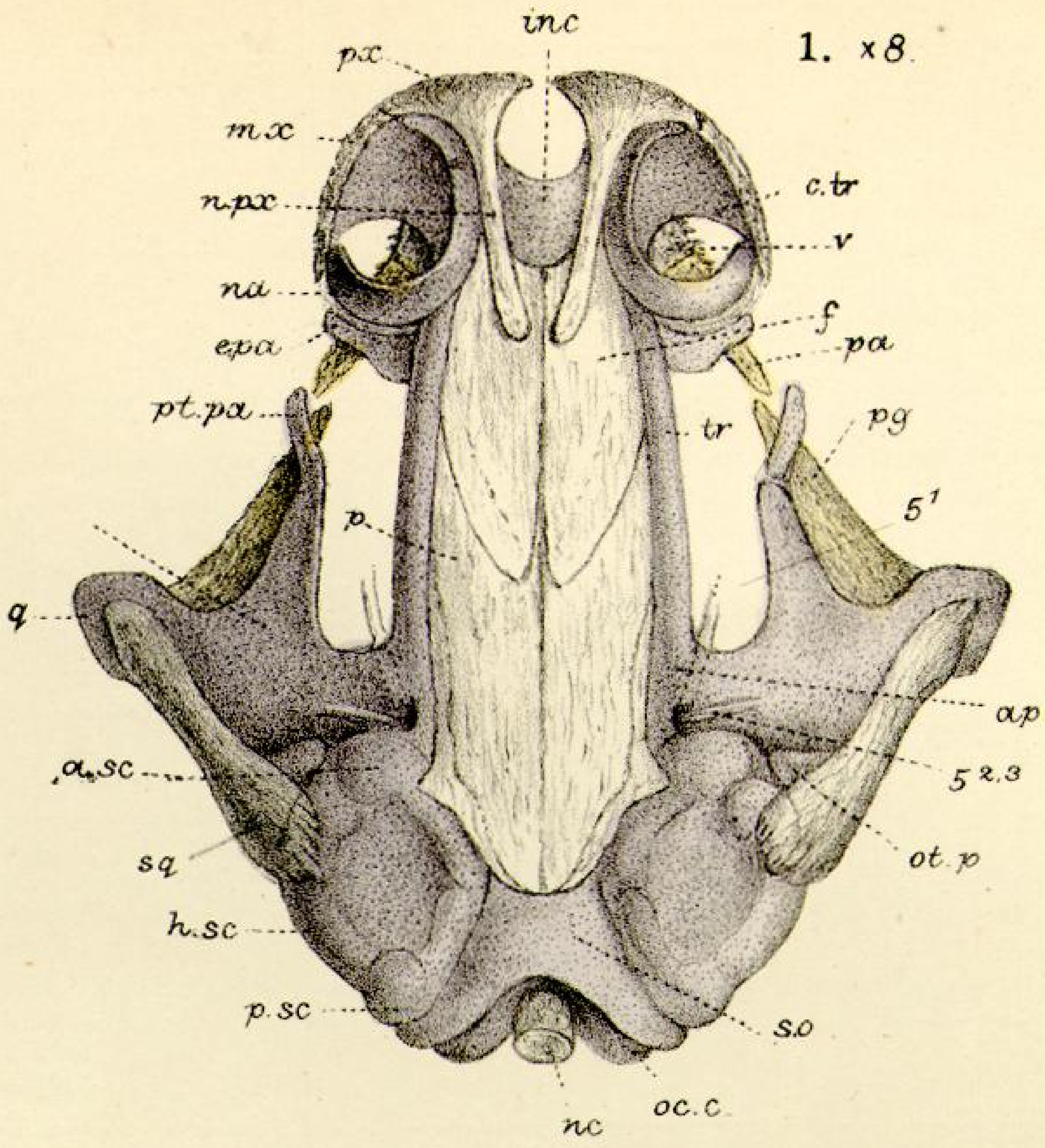


Siredon. 3rd Stage.

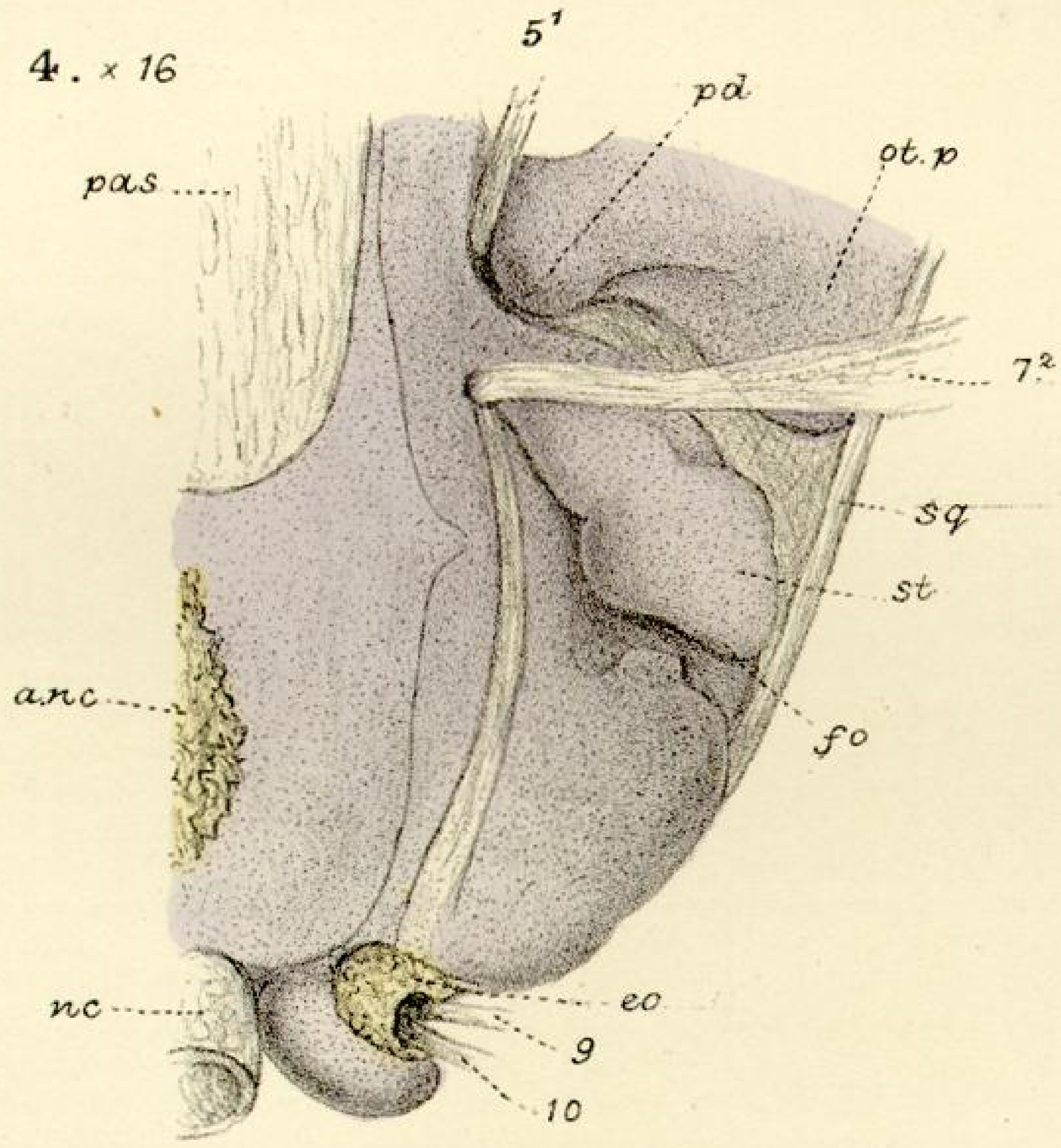
2. × 8



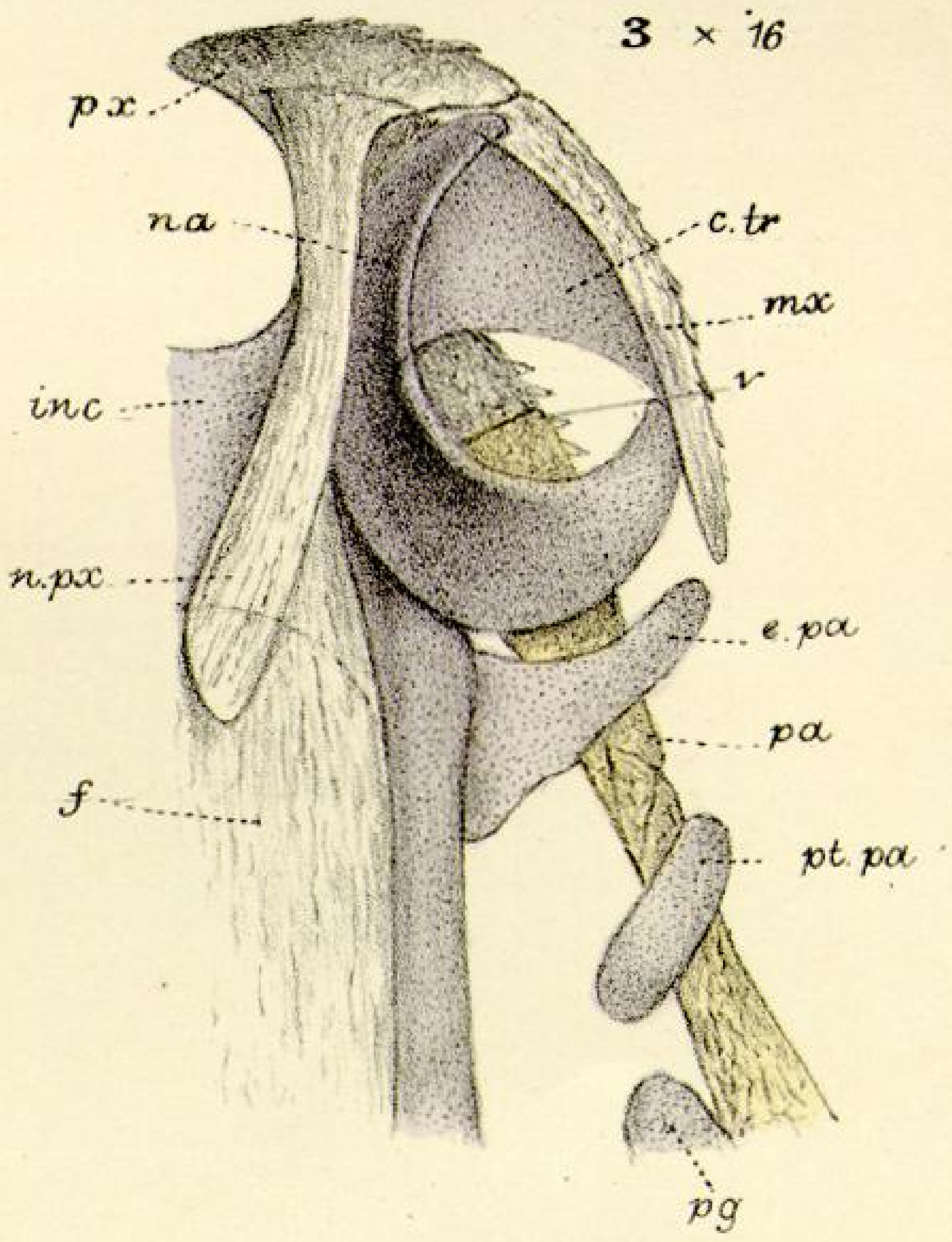
1. × 8



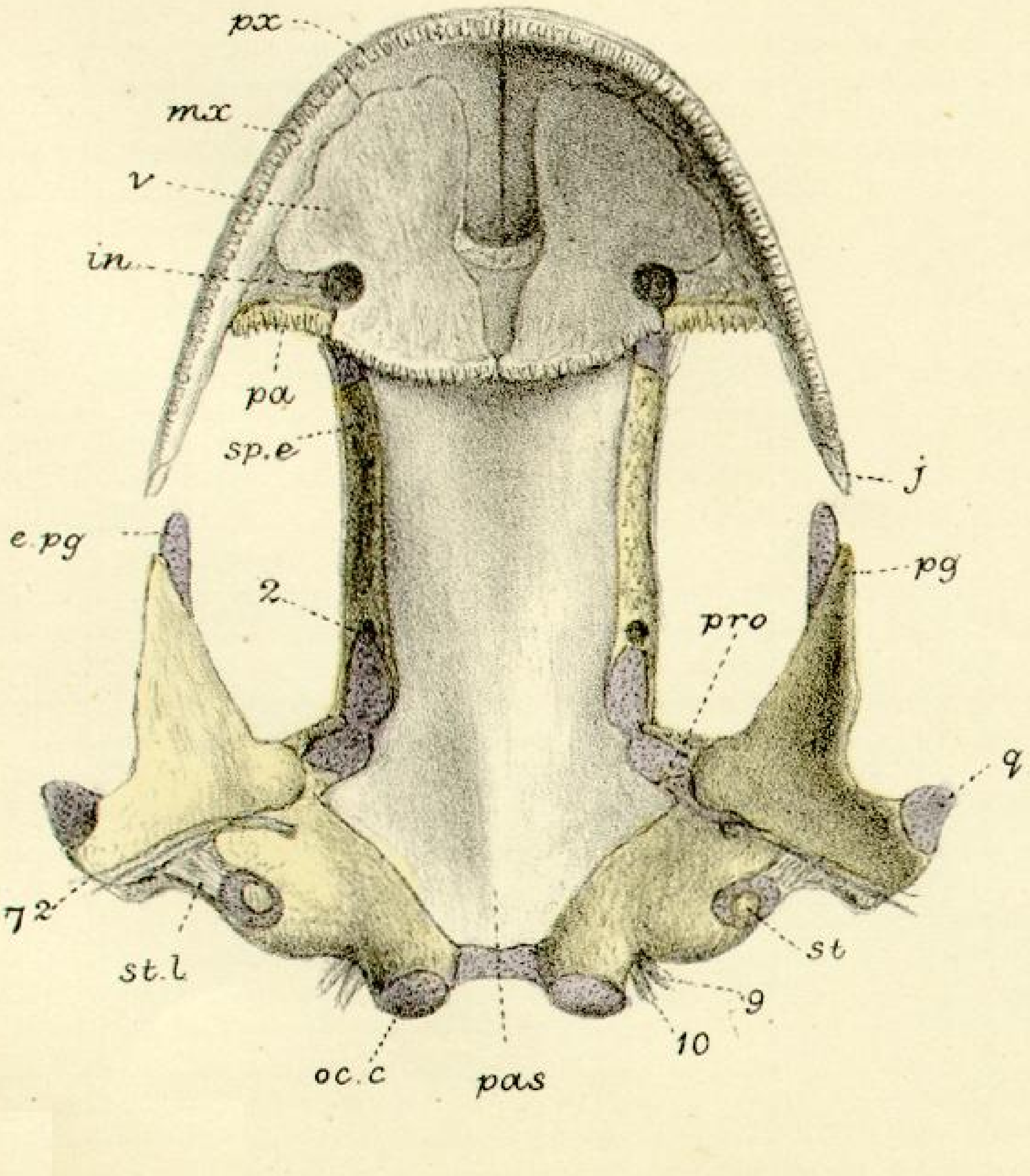
4. × 16



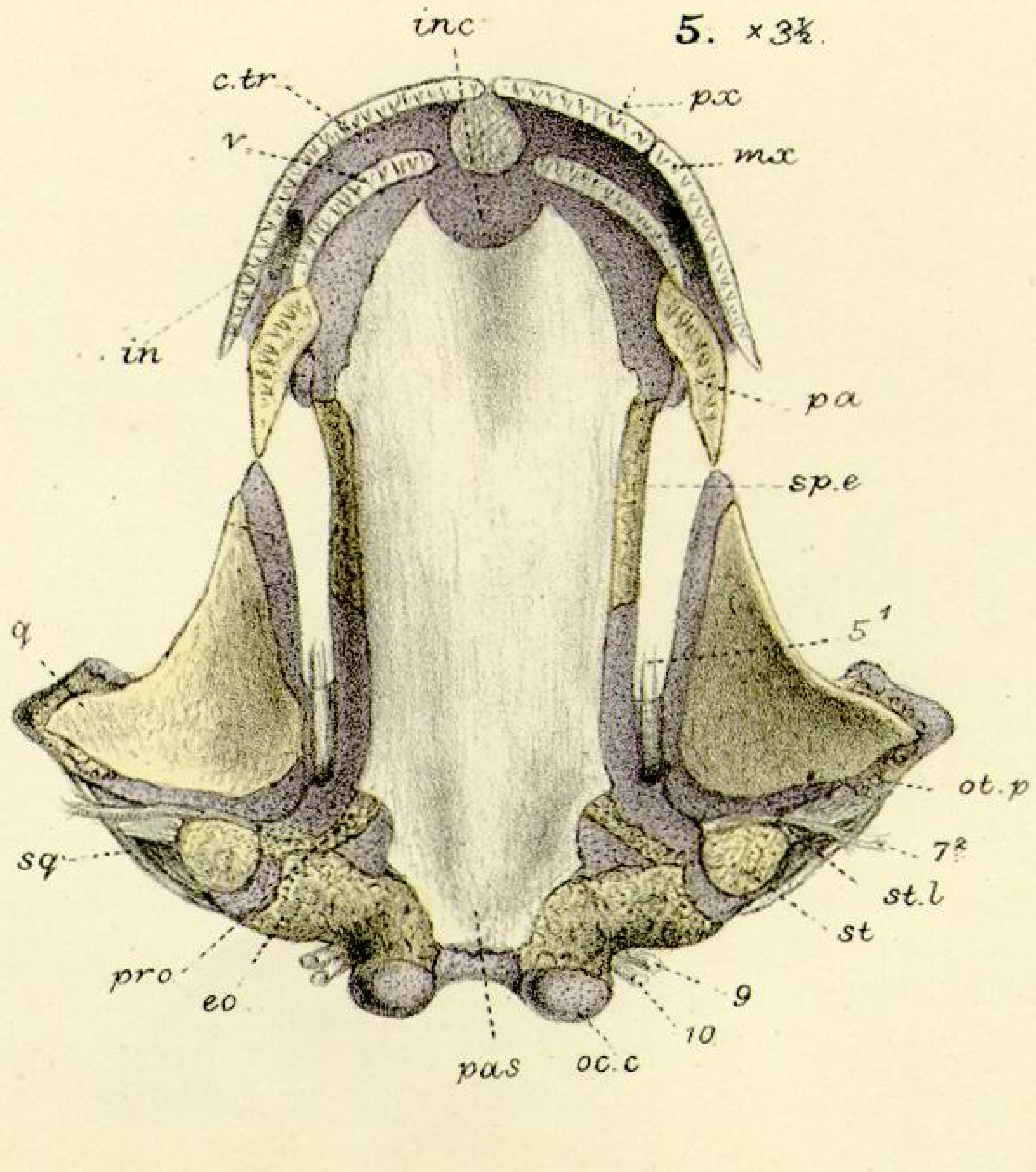
3 × 16



6. × 5

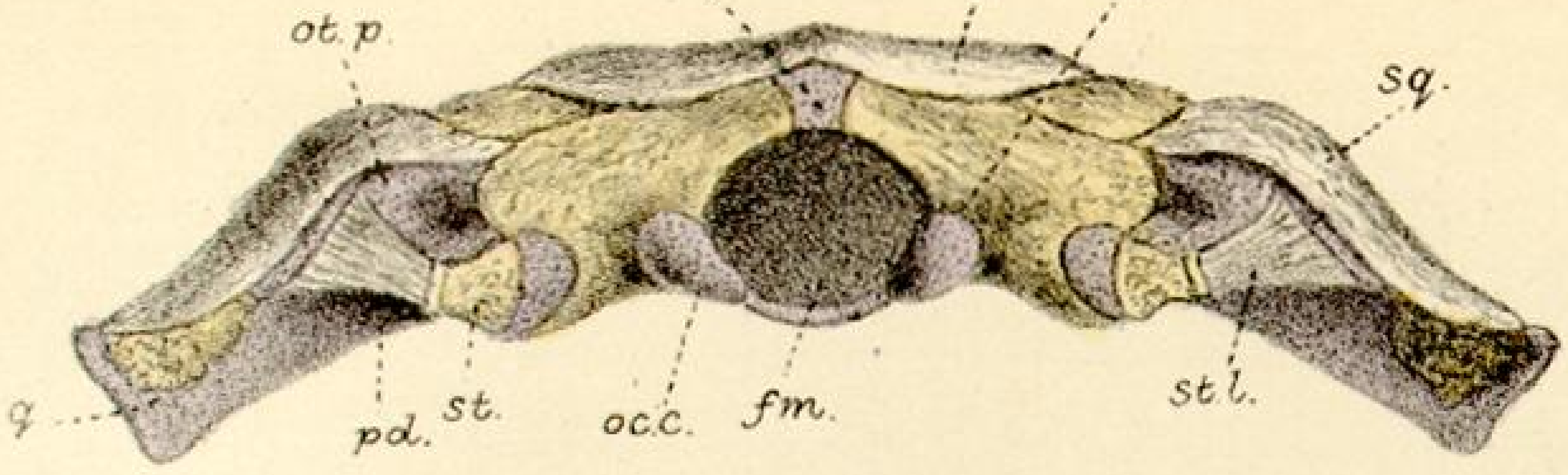


5. × 3½

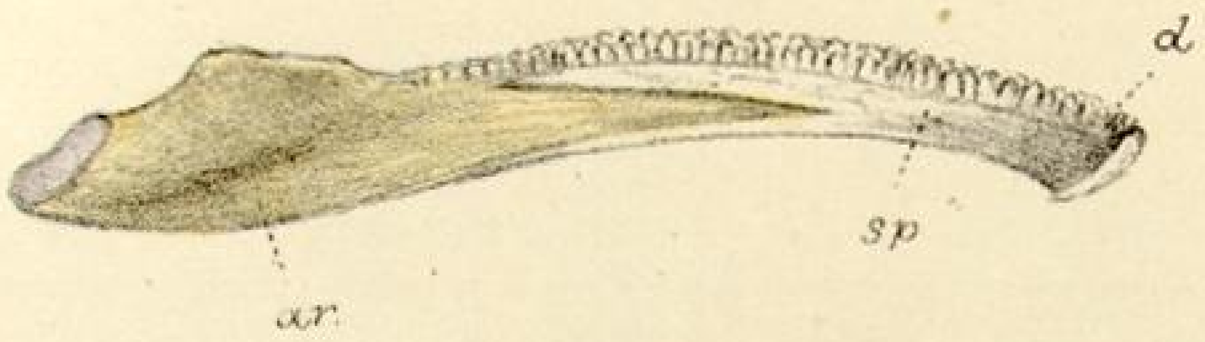


Siredon. Figs, 1–4 6th Stage. 5, 9th Stage. Amblystoma, Fig. 6.

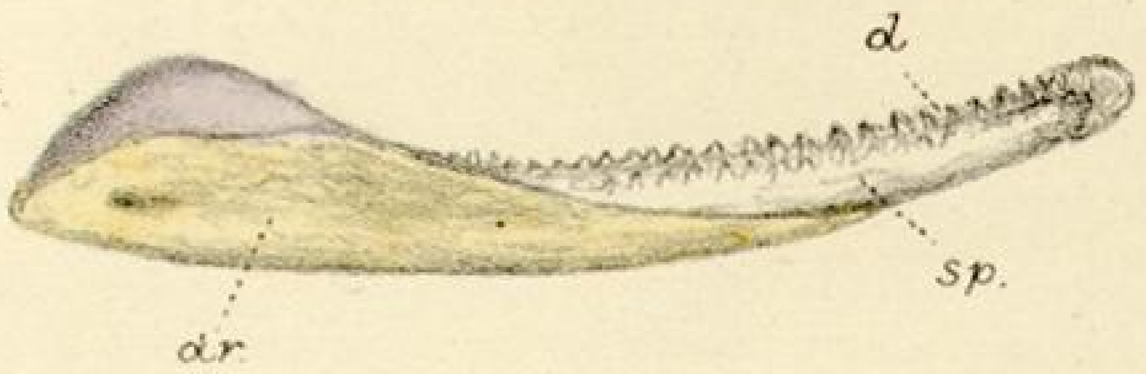
3. × 3½.



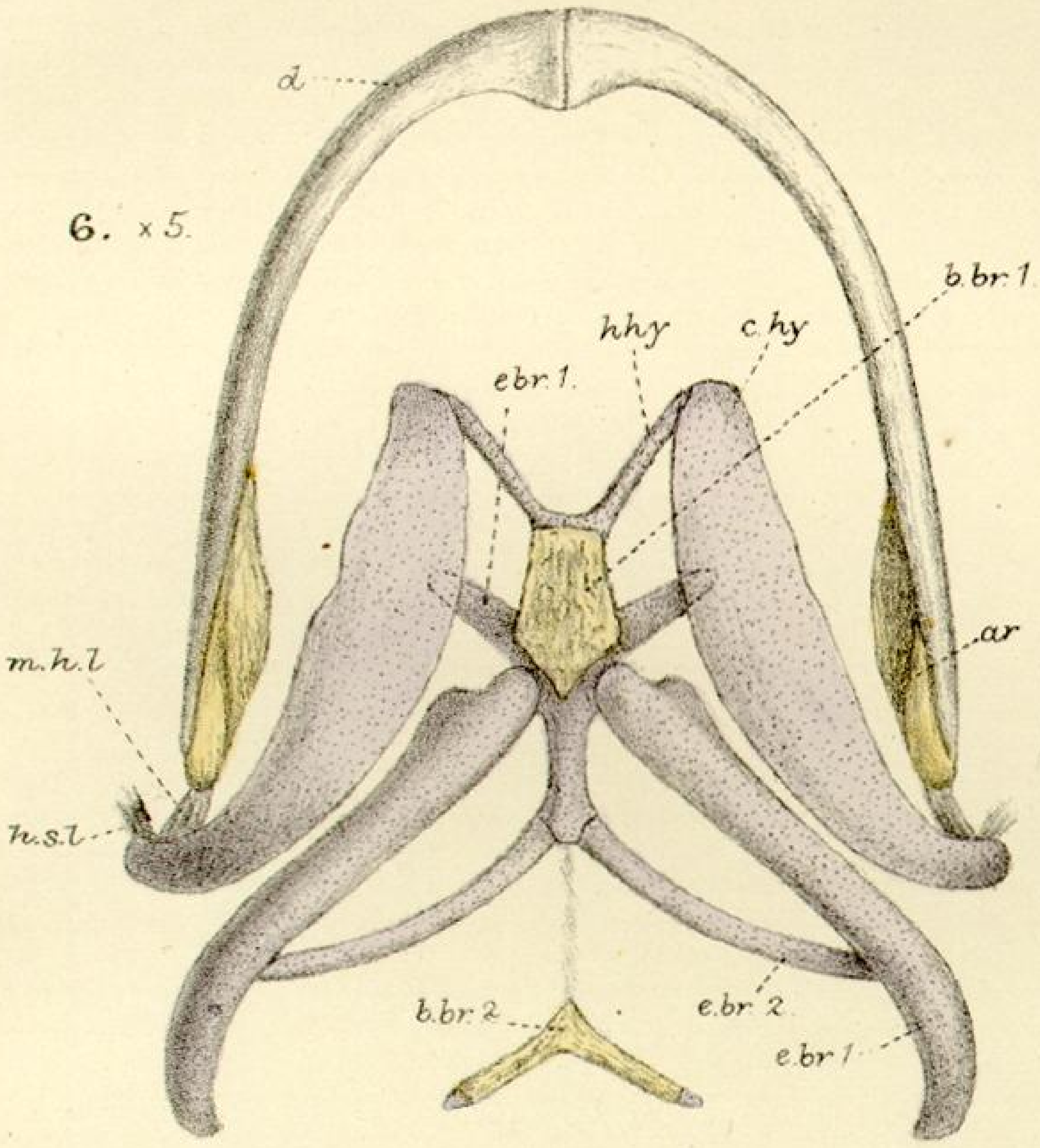
7. × 6.



4. × 3½.



6. × 5.



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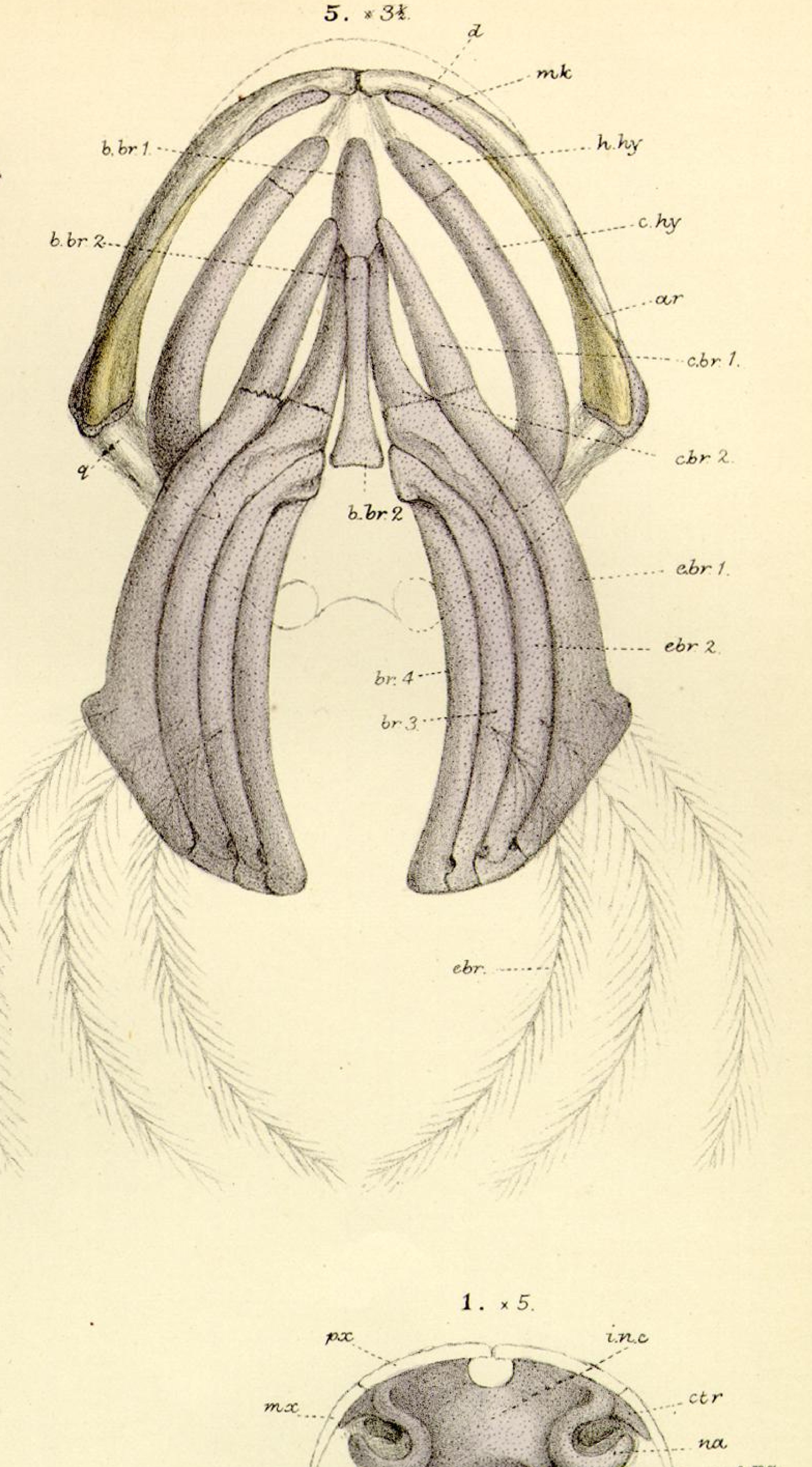
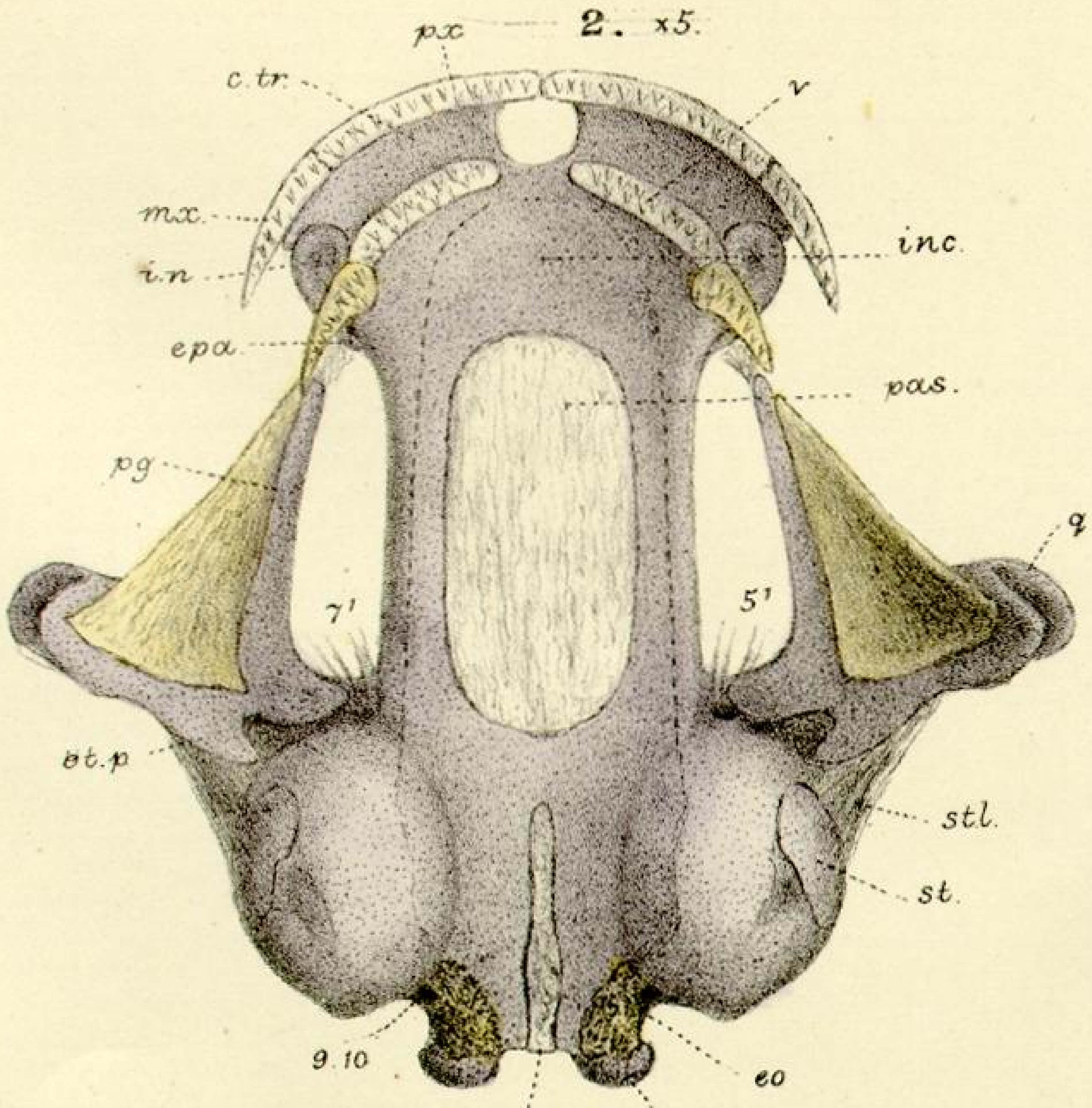
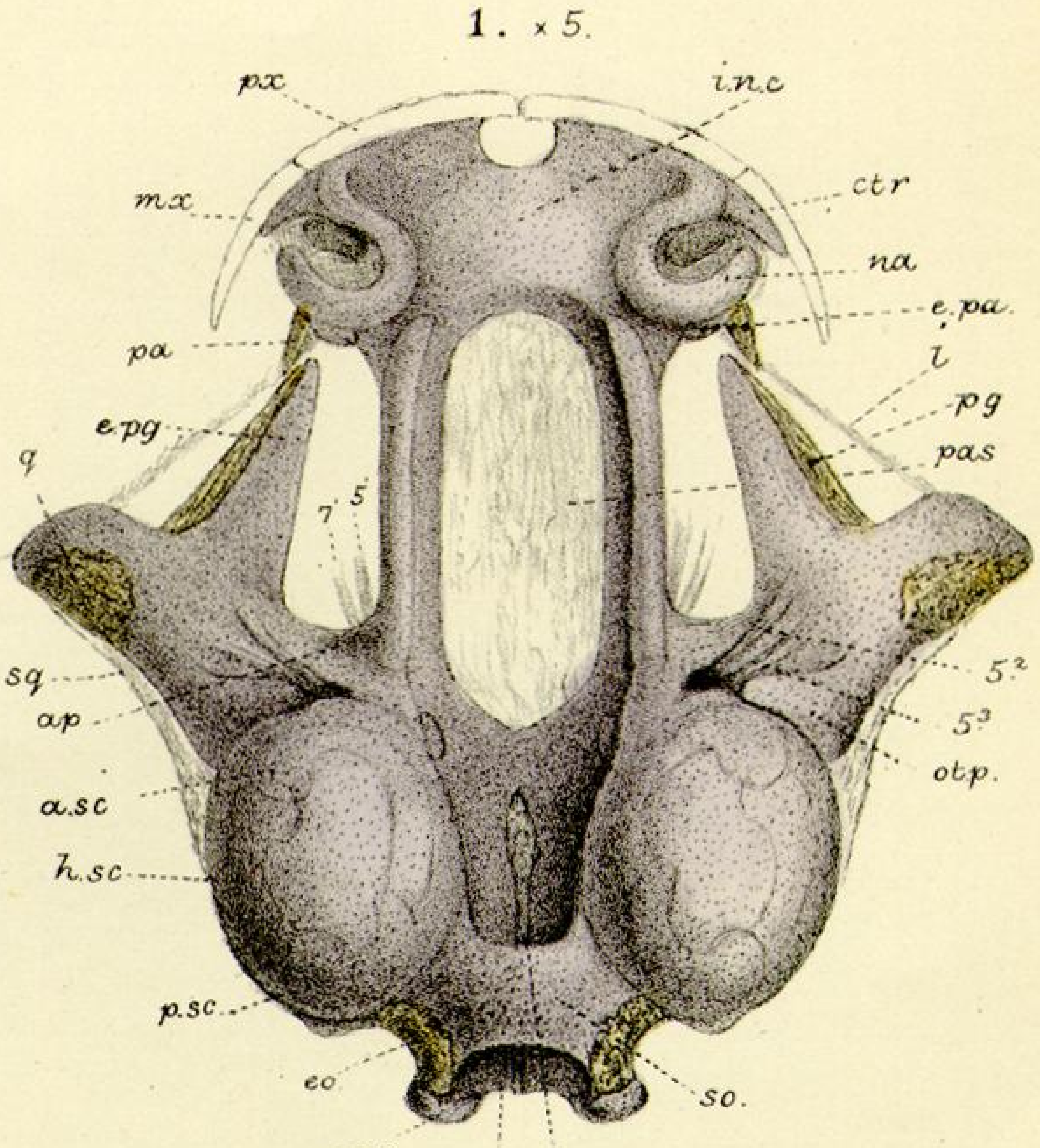


2. × 5.

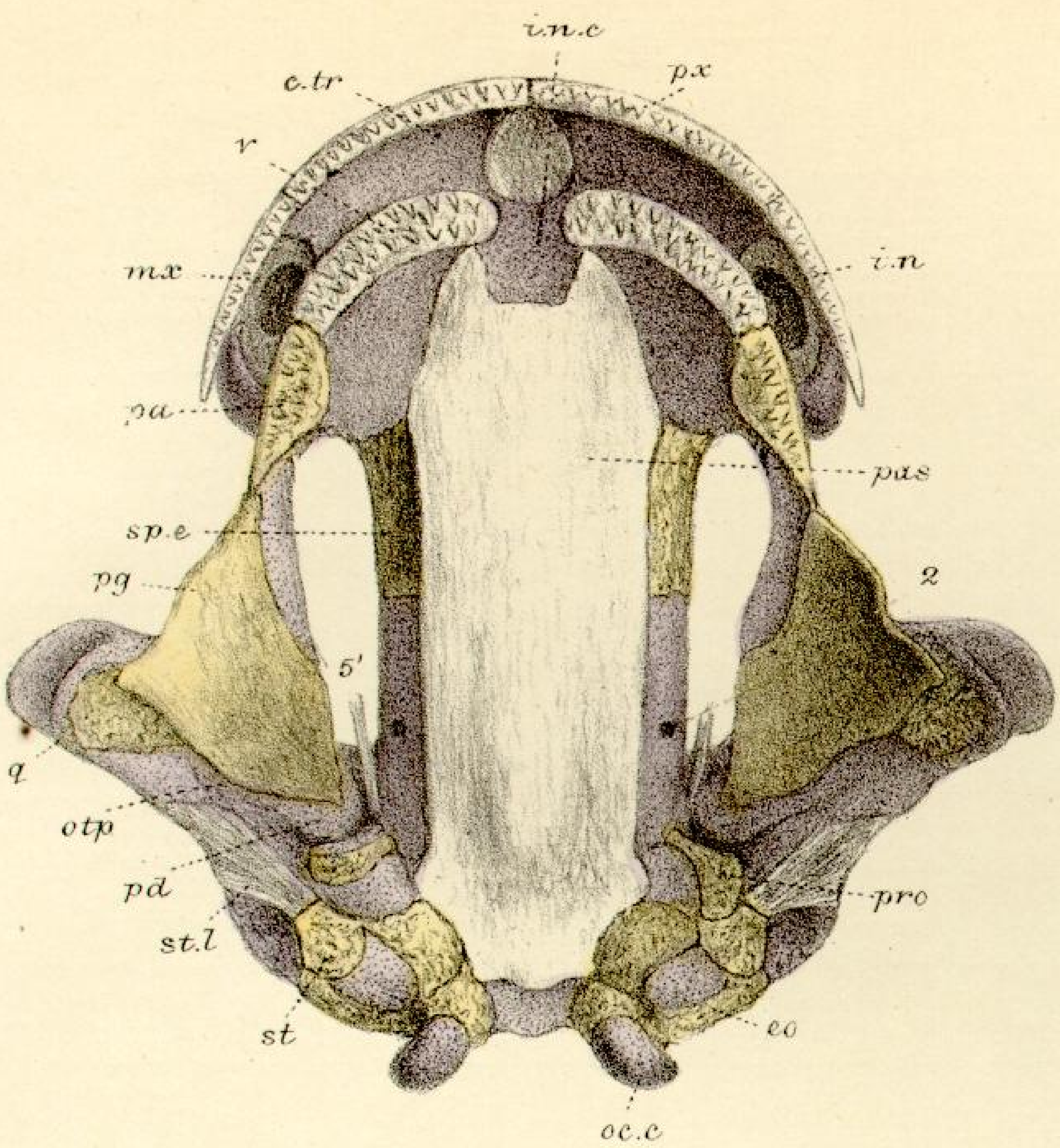


1. × 5.

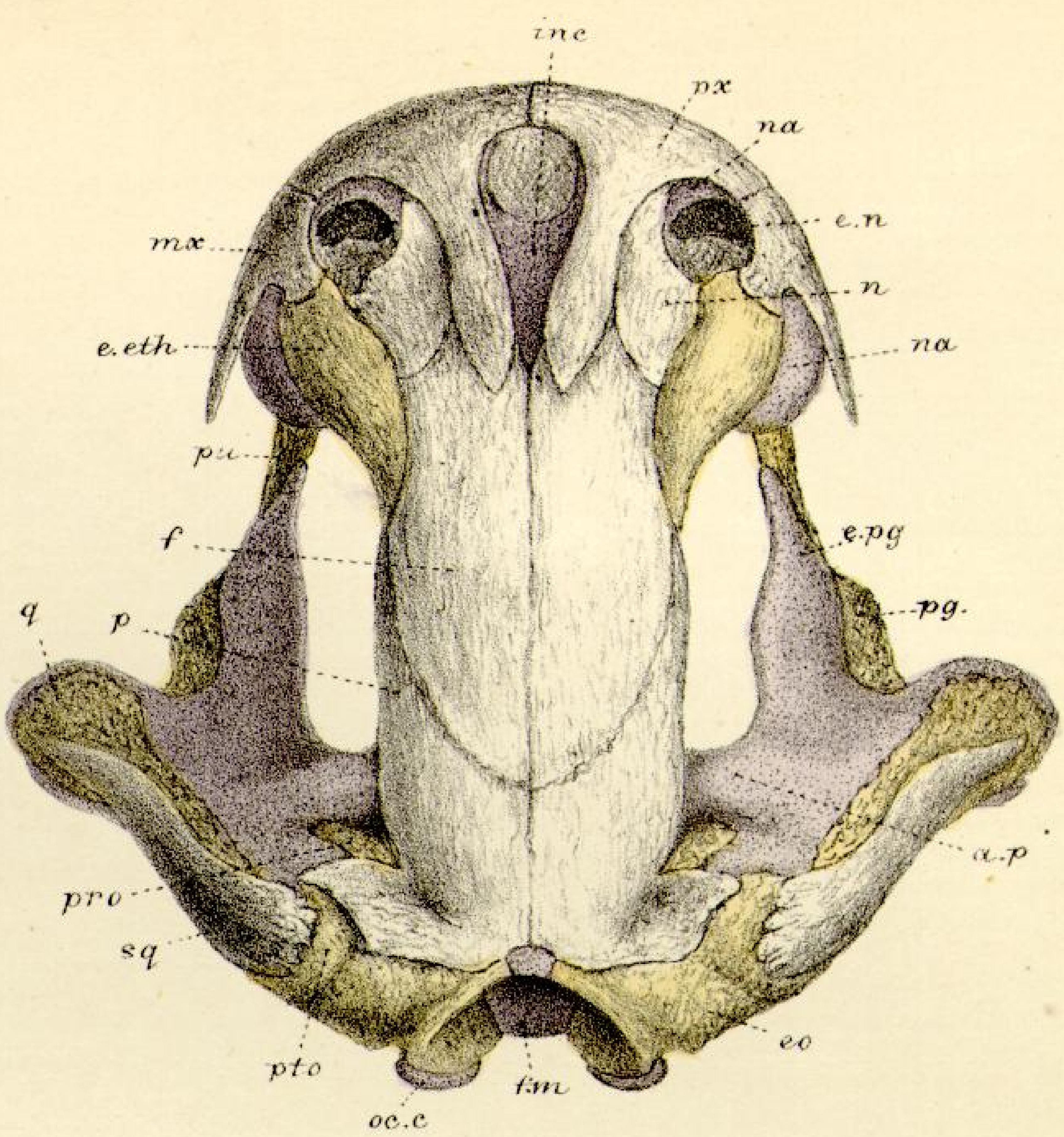


Siredon. Figs, 1, 2, 7th *Stage*. 3–5. 8th *Stage*. Amblystoma Figs. 6–7.

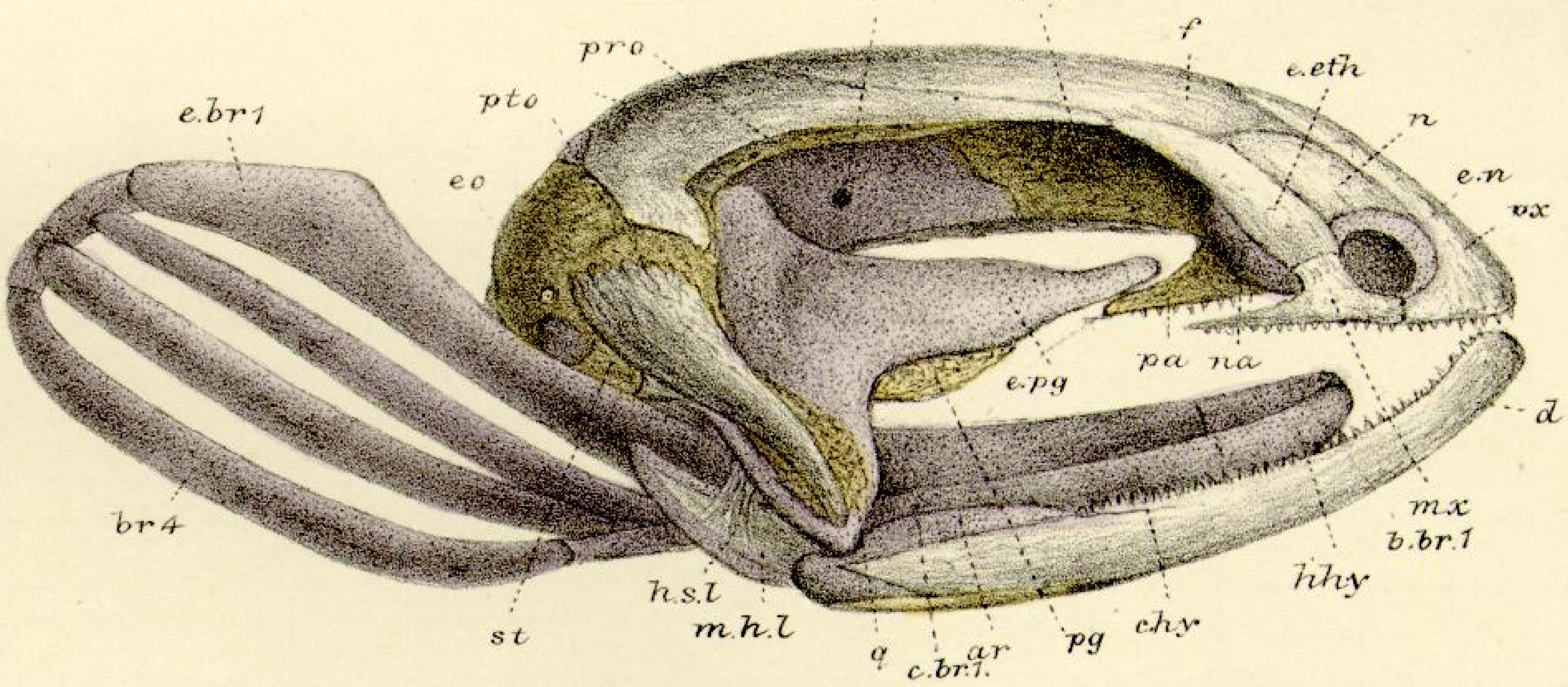
2 × 3½



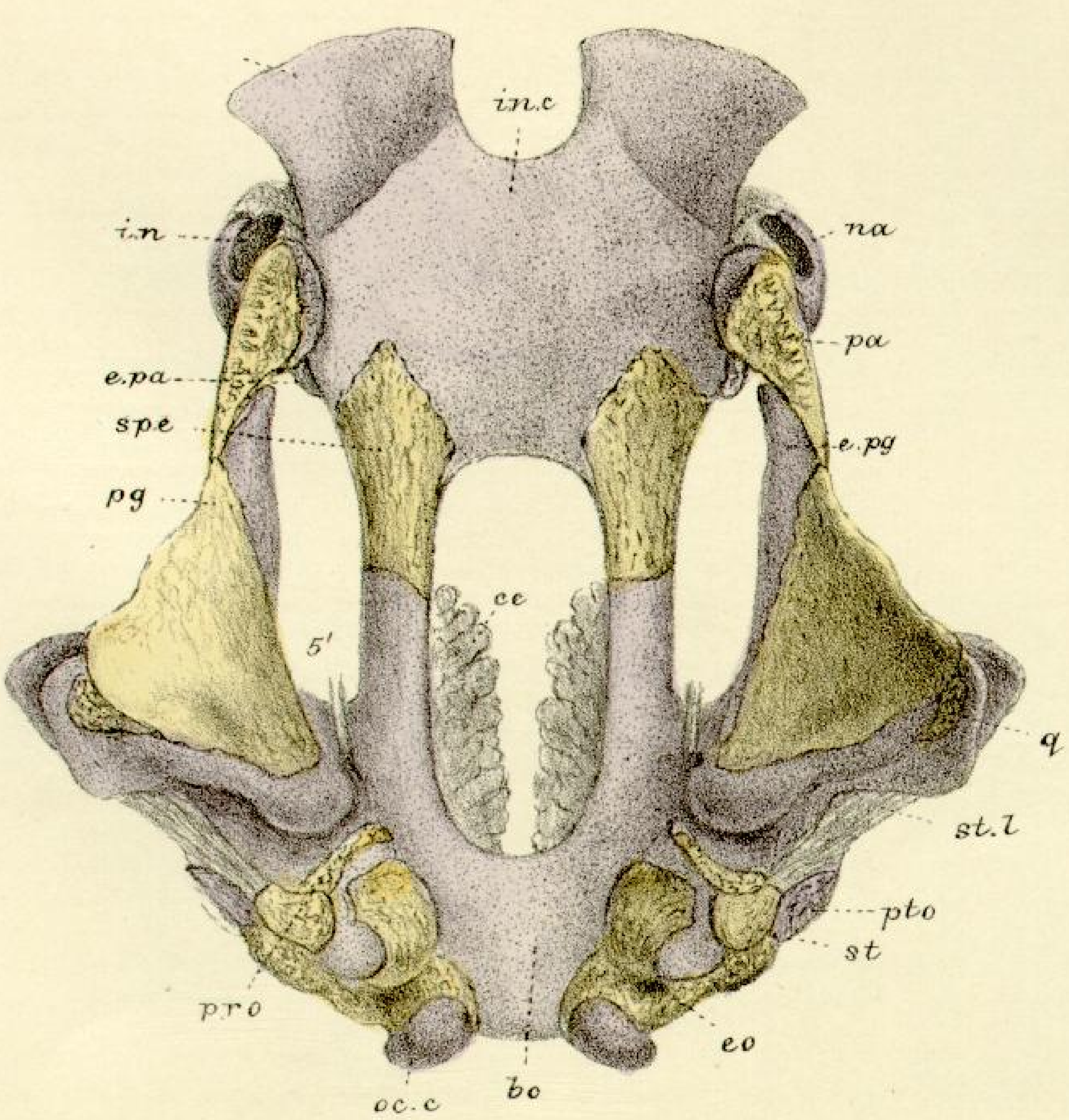
1 × 3½



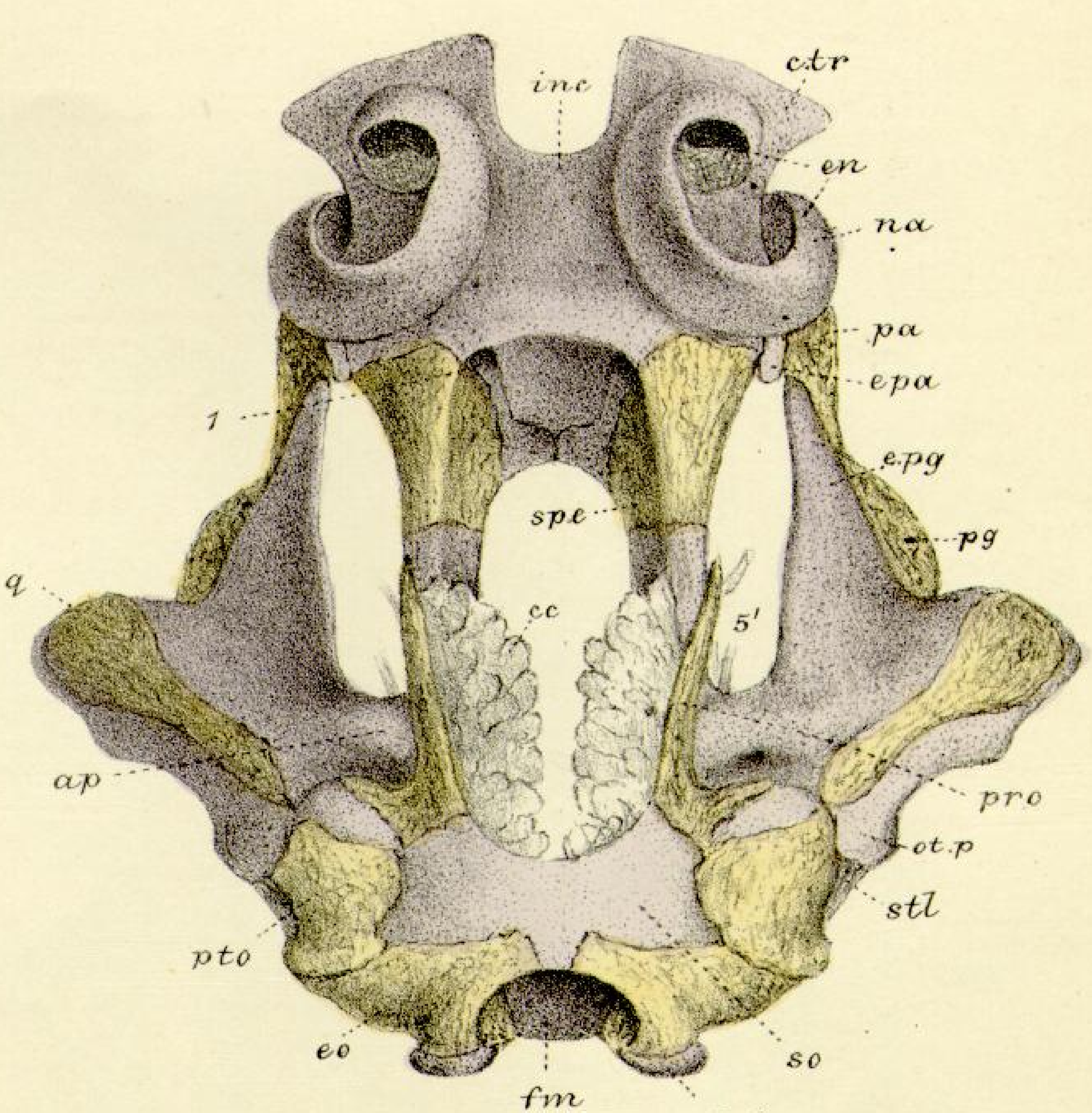
5 × 3½



4 × 3½

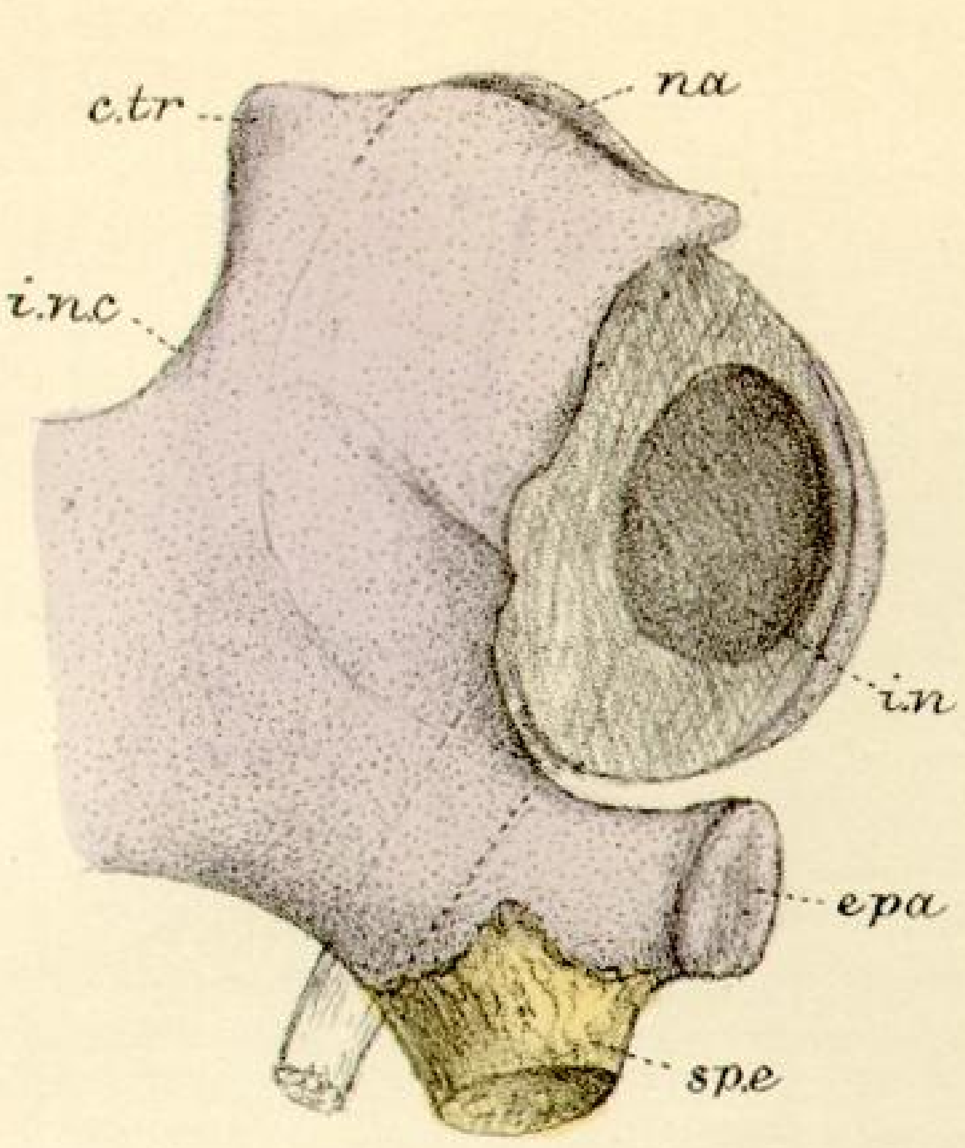


3 × 3½

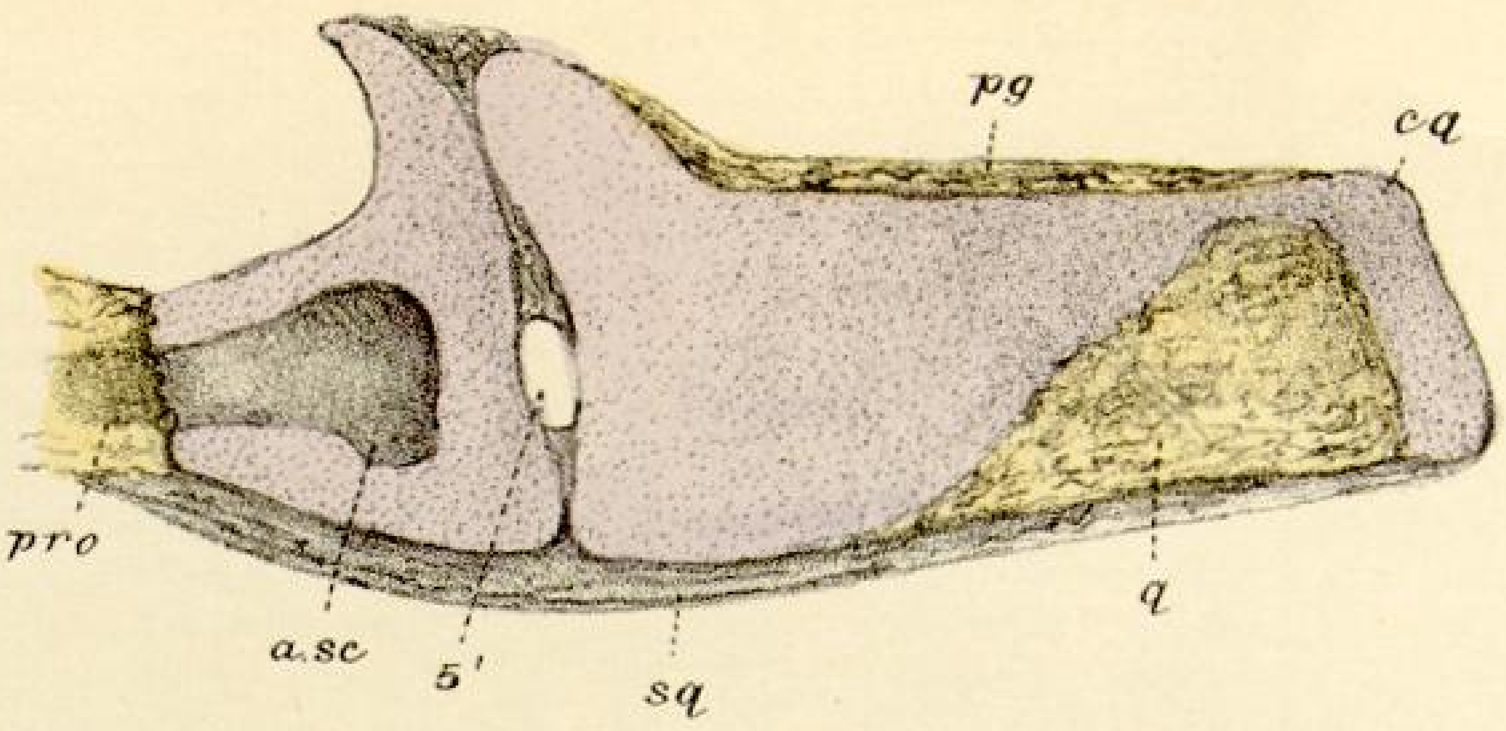


Siredon 8th Stage.

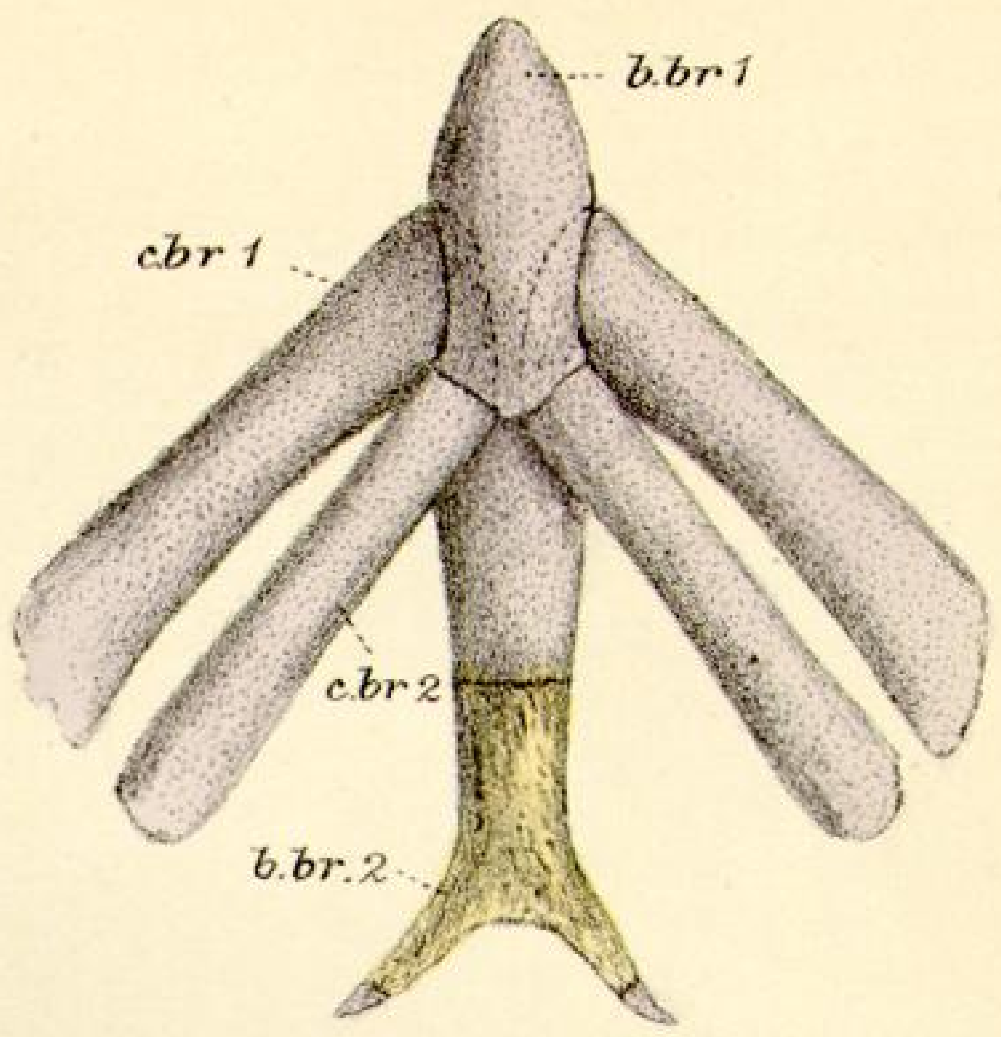
3 × 7



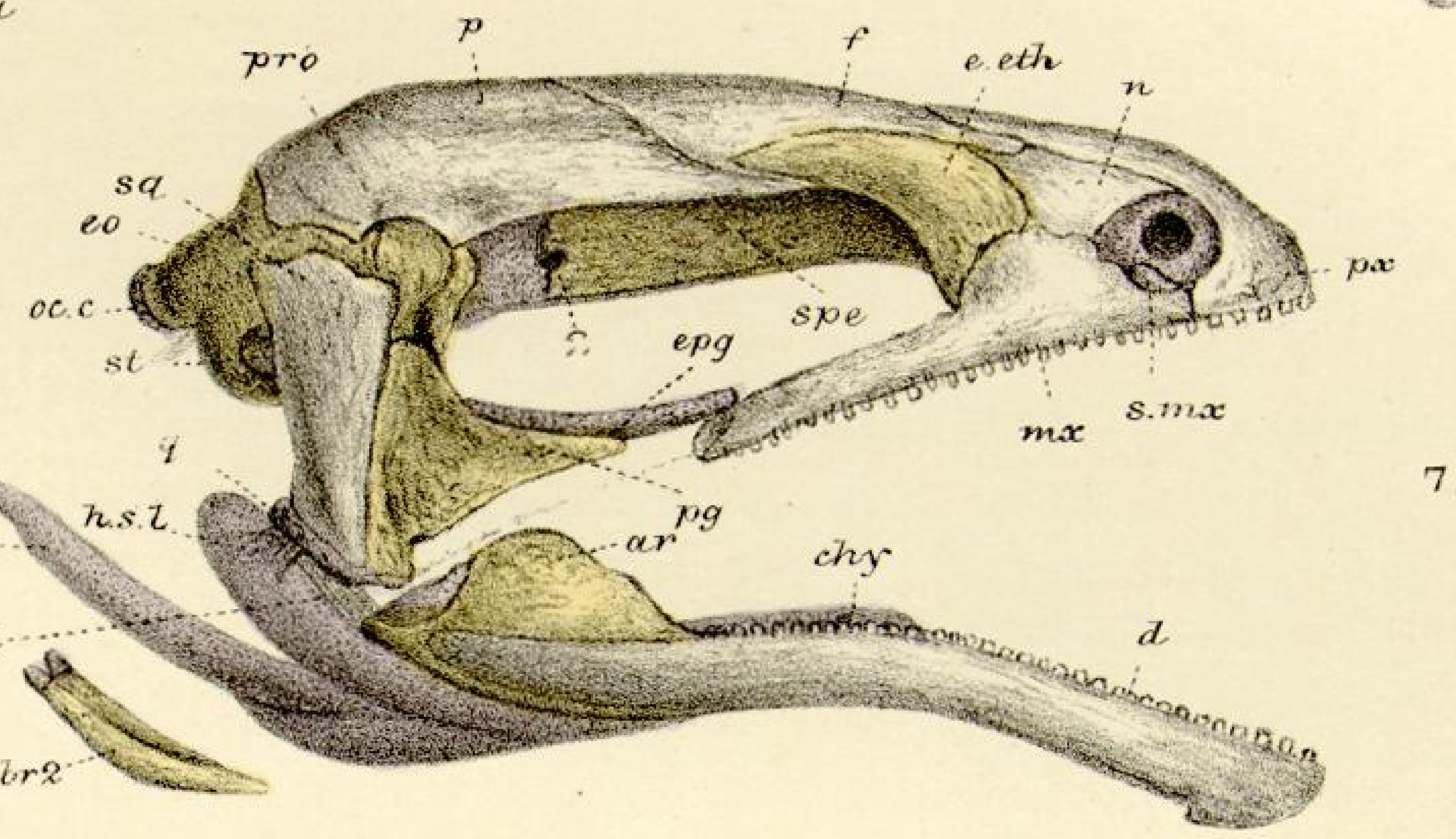
4 × 7



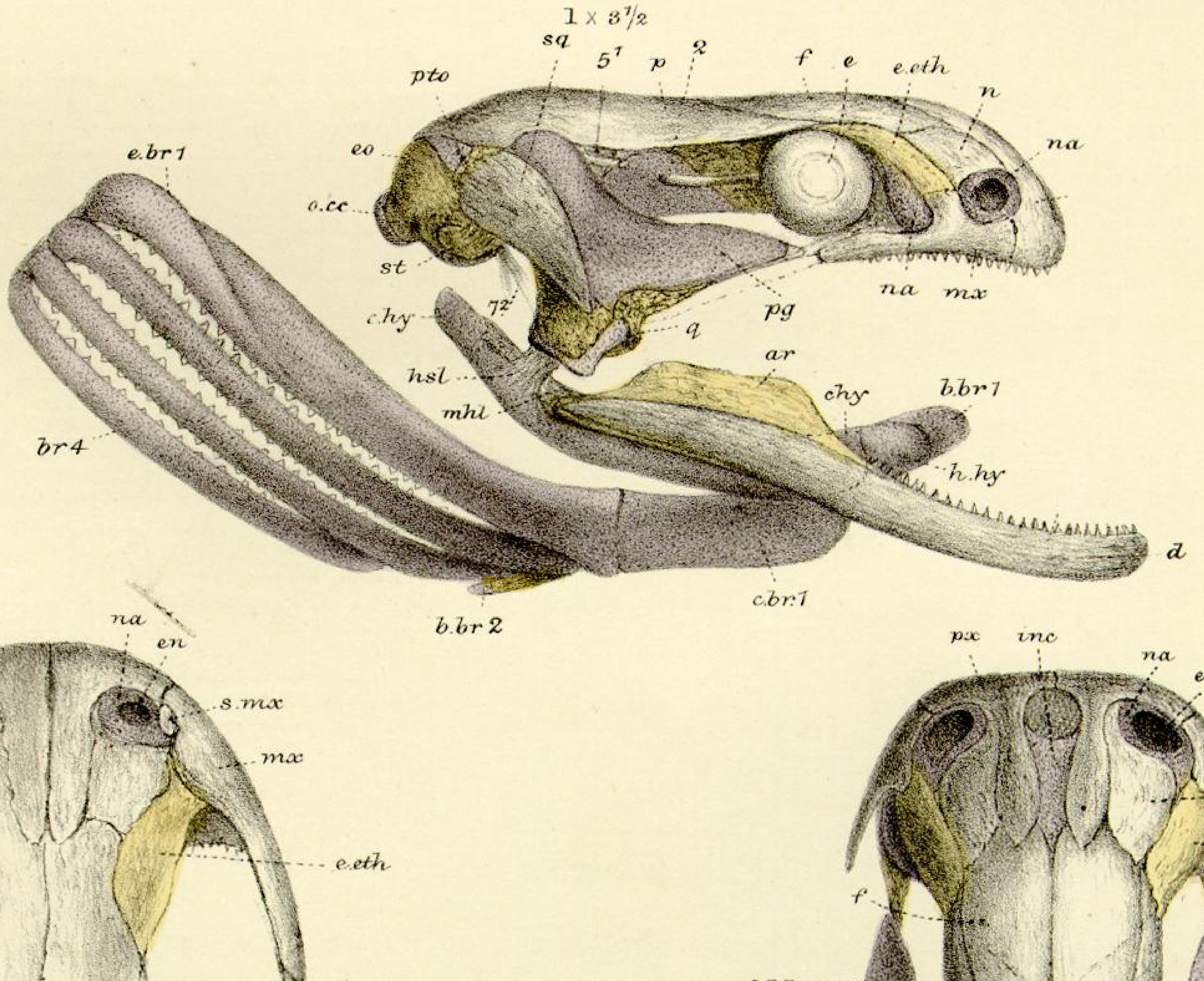
5 × 3½



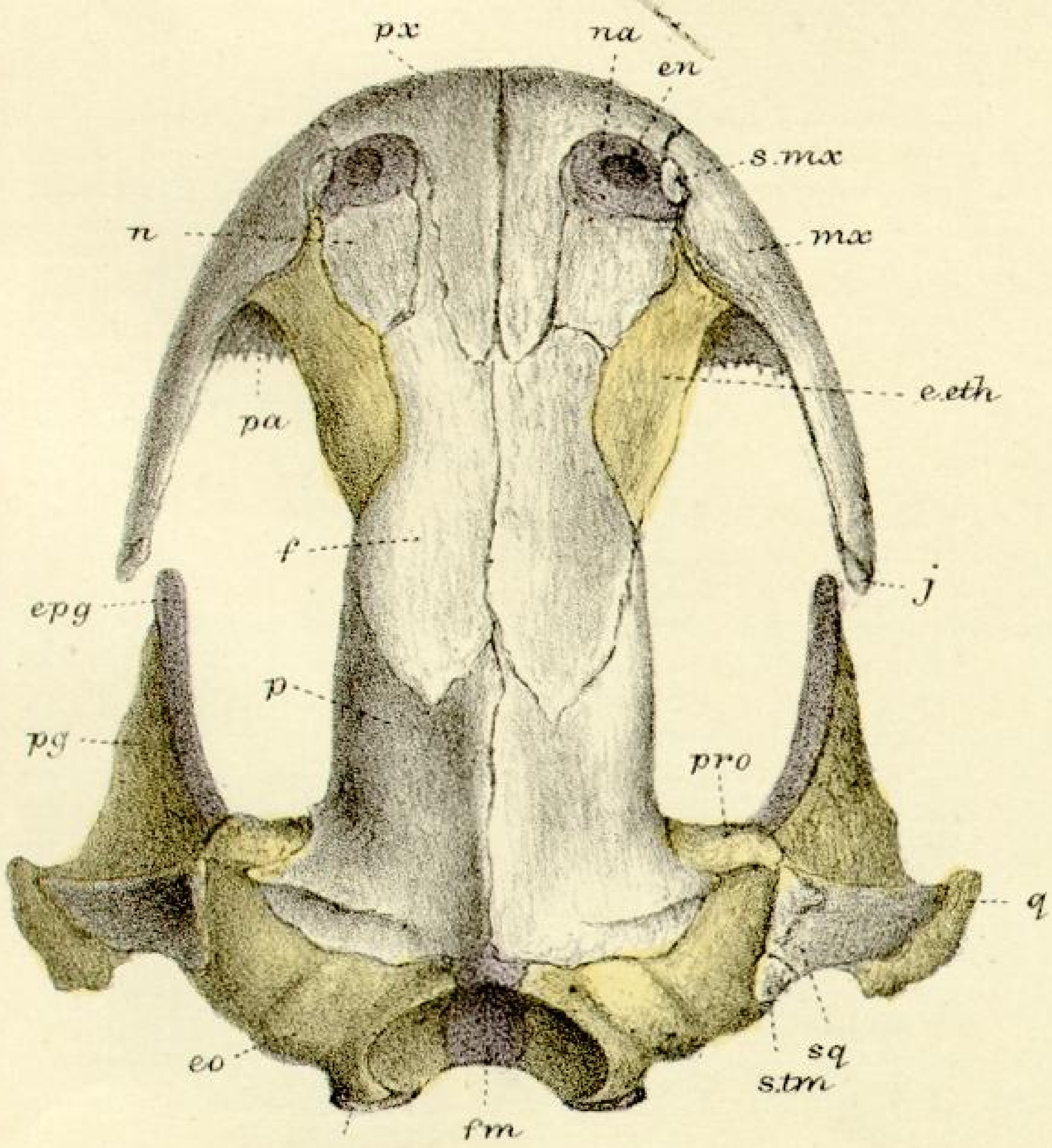
7 × 5



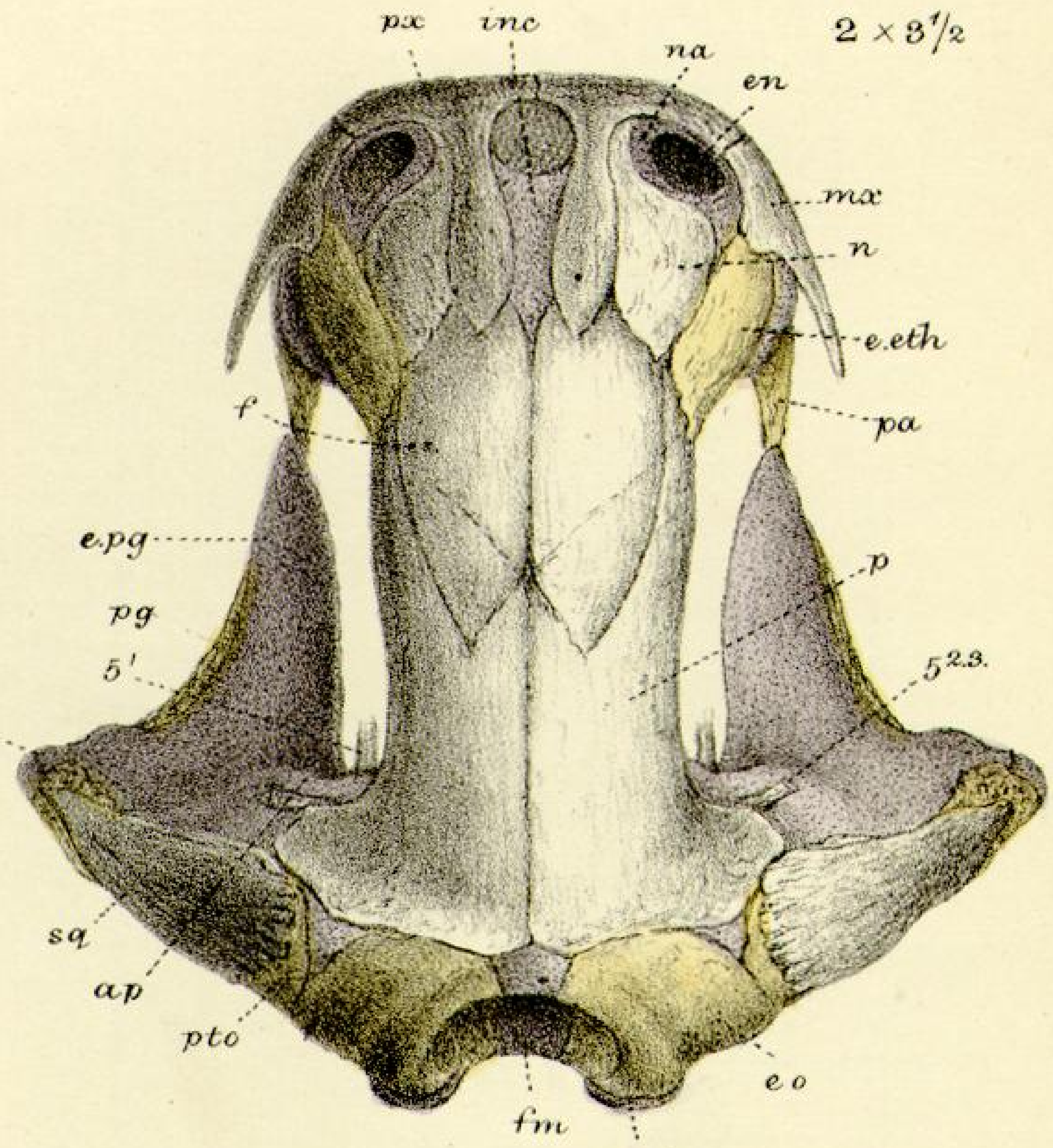
1 × 3½



6 × 5



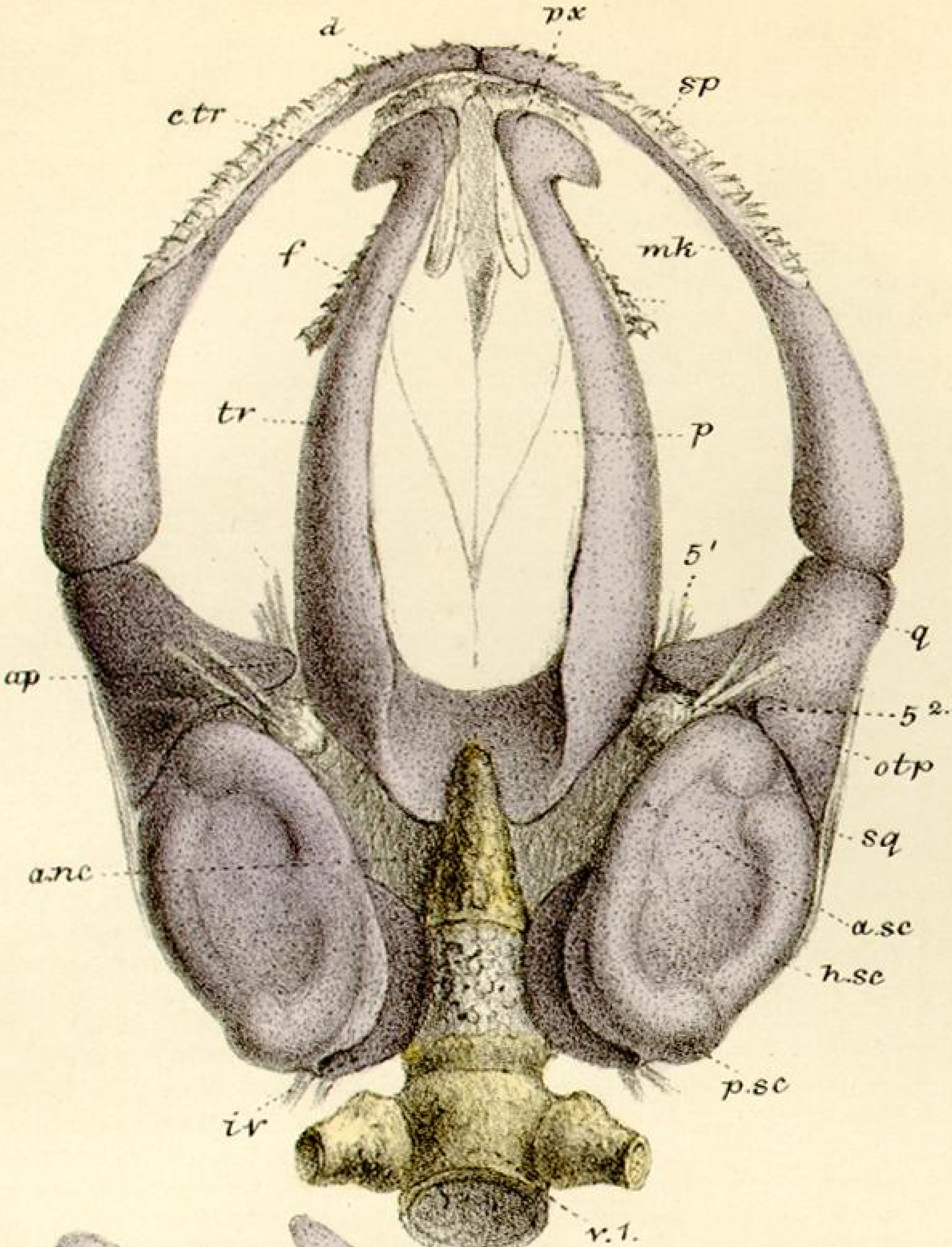
2 × 3½



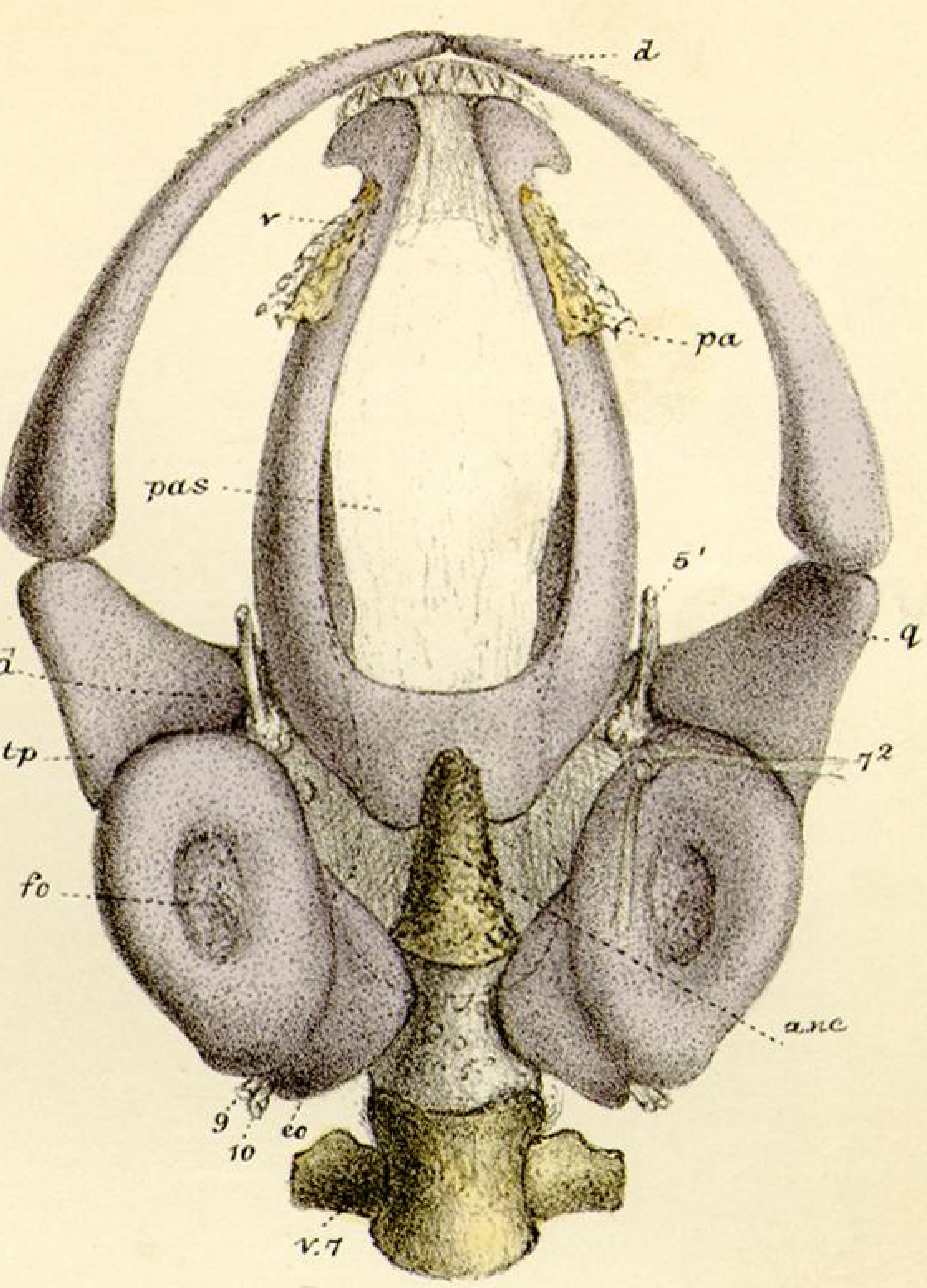
Siredon *Figs.* 1–5 9th *Stage*; Amblystoma *Figs.* 6, 7.

Proteus anguinus:

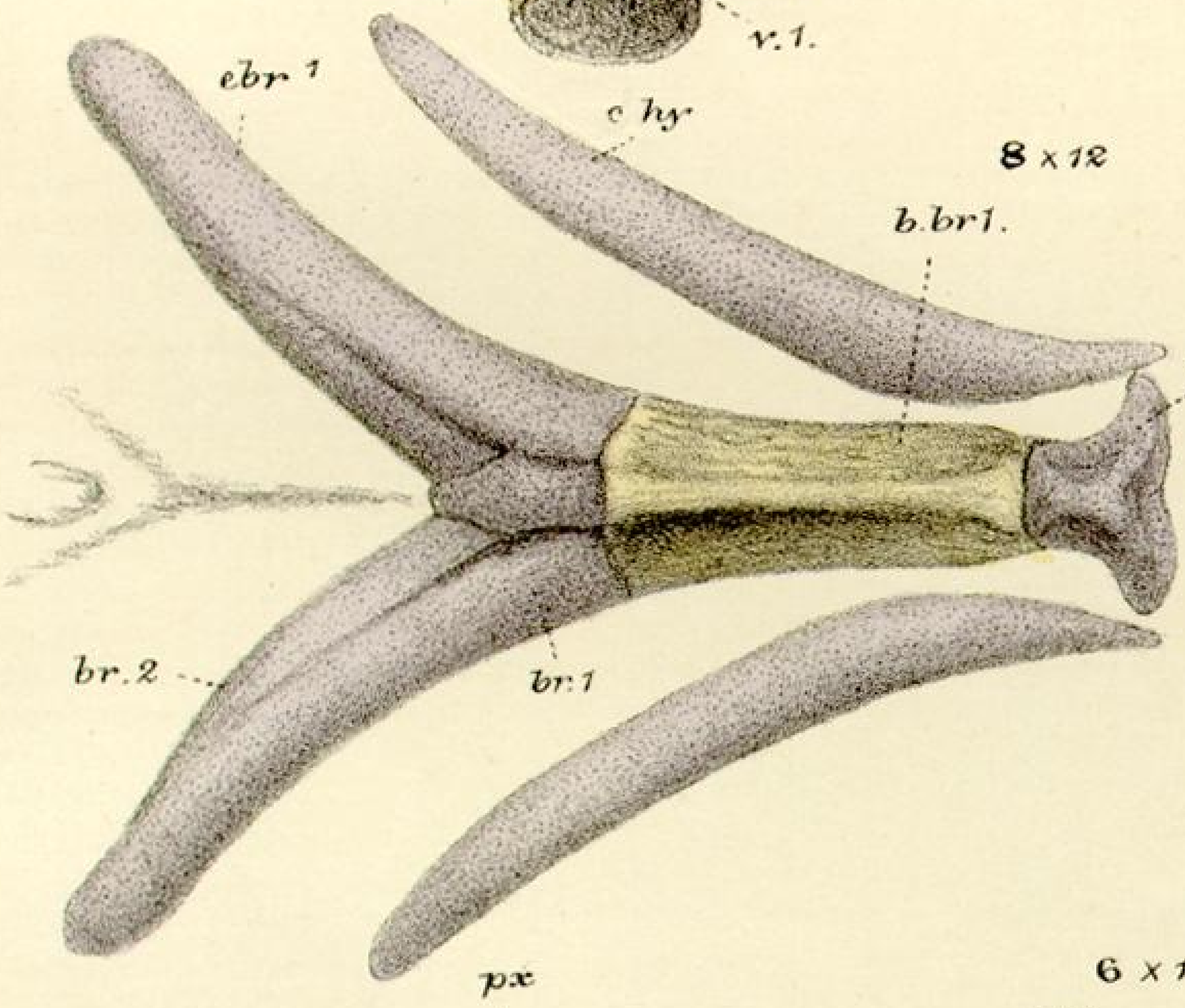
1 × 24



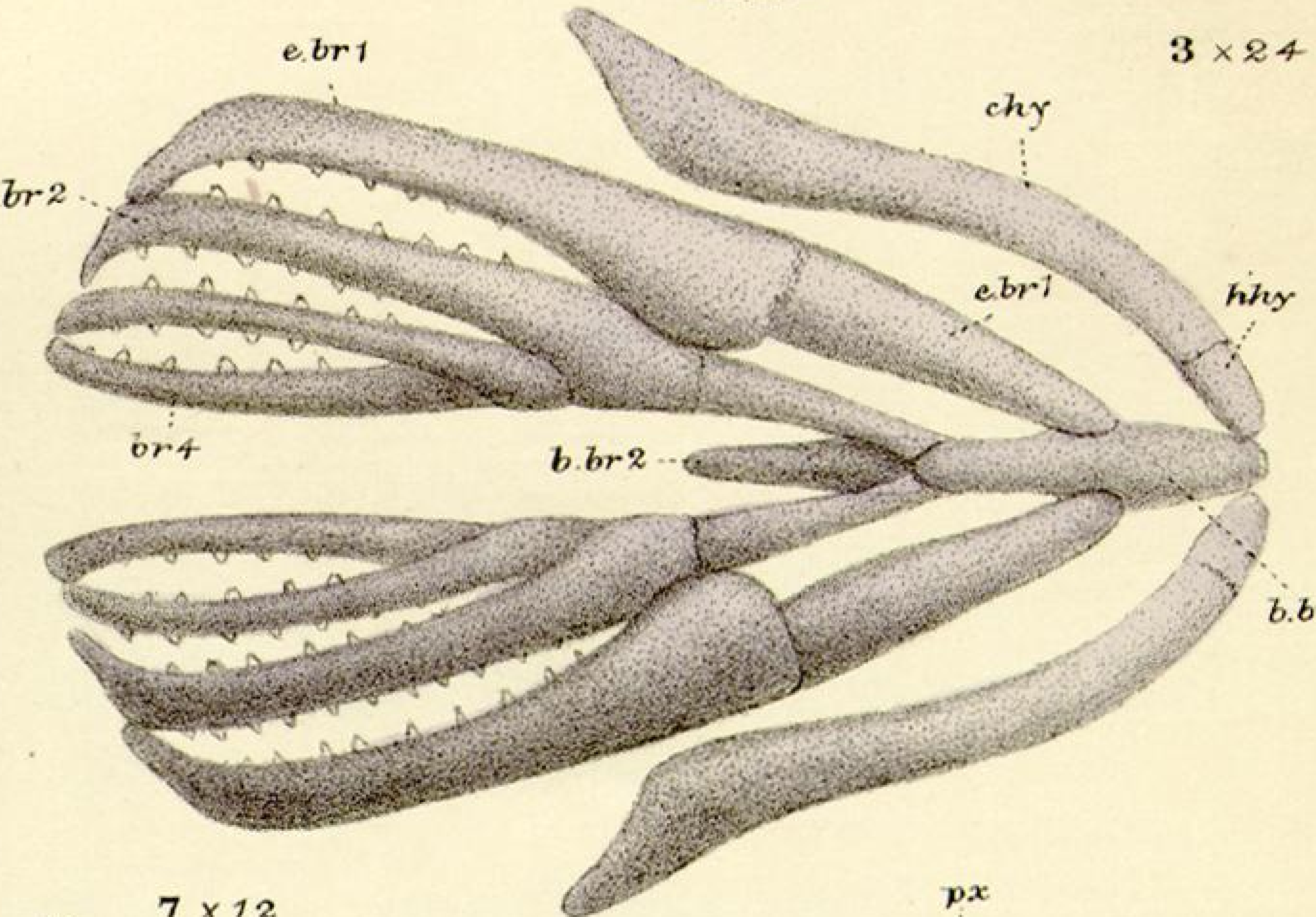
2 × 24



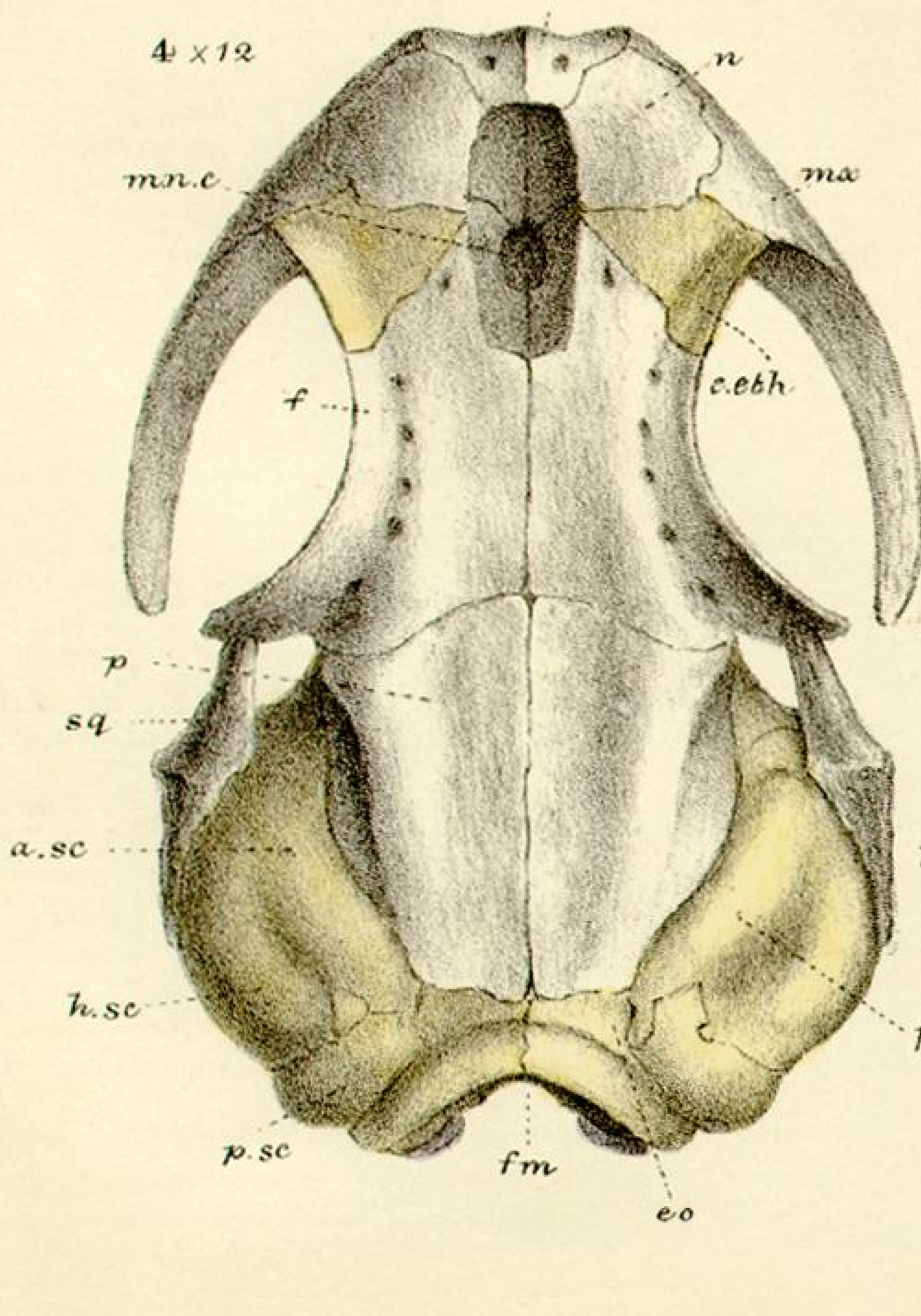
8 × 12



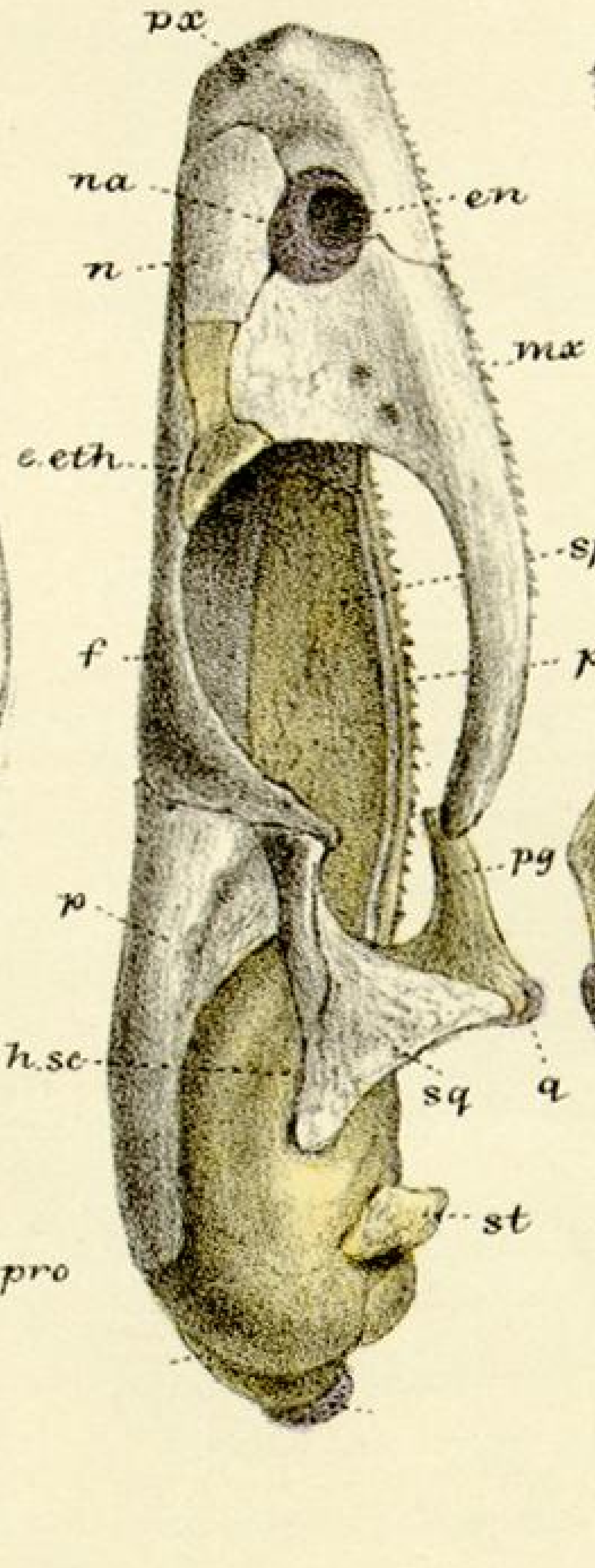
3 × 24



4 × 12

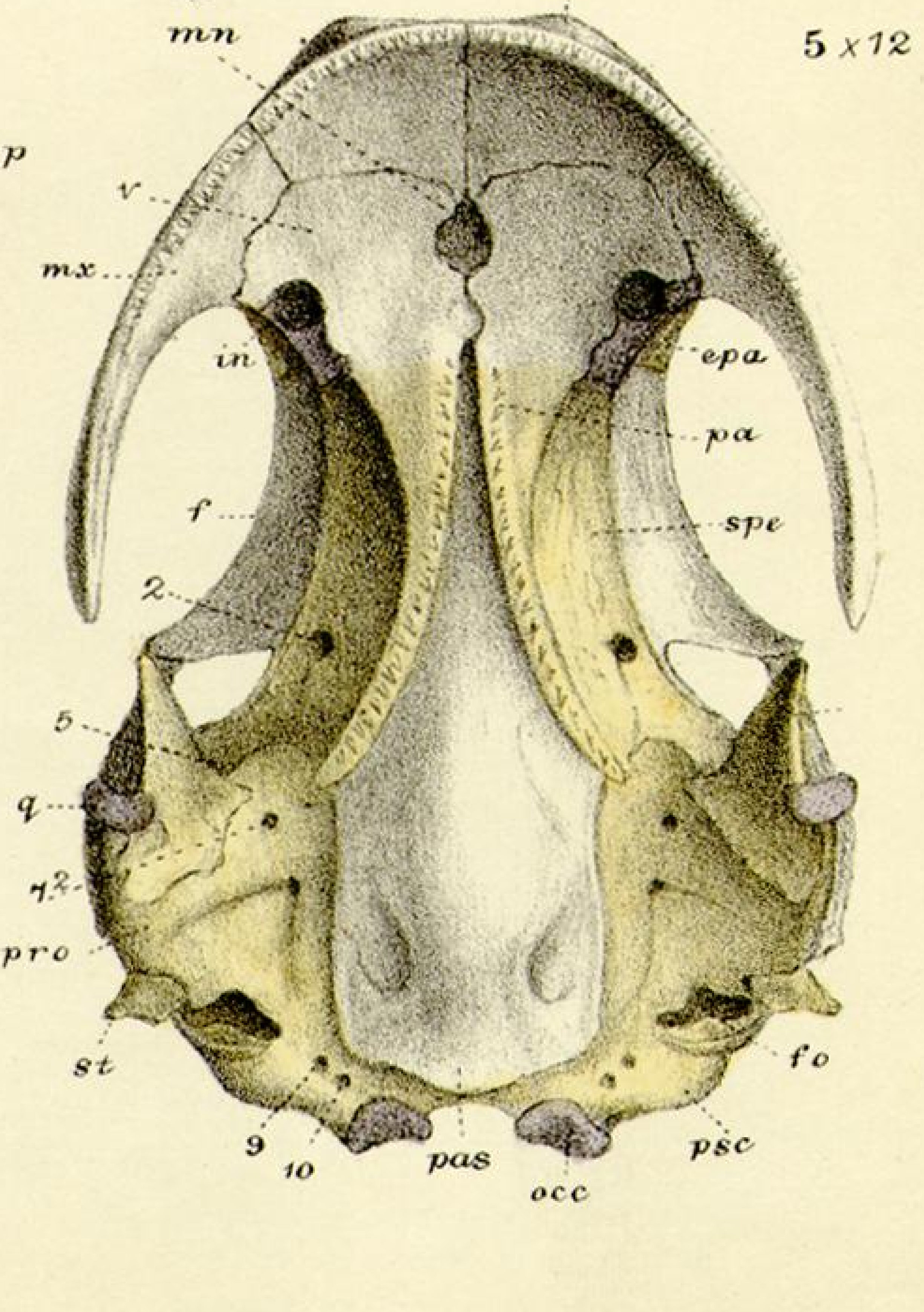


6 × 12



7 × 12

5 × 12



Seironota perspicillata; *Figs.* 1–3 *larva* 4 — 8 *adult*