IX. *The Early Development of the Skull of the Rabbit.*

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[Plates 35–43.]

Contents.

Introduction.

In the study of the chondrocrania of embryonic mammals, it is probably true to say that no form at the maximum stage of development of the cartilage has been more thoroughly investigated than the rabbit, by Voit. His material, however, consisted of well-developed stages only, of 43, 45, and 70 mm. greatest length; and apart from a few remarks by Noordenbos, the earliest stages of development of the skull of the rabbit remained unknown. This was an unfortunate gap, for while what may be called the morphology of the chondrocranium is now, thanks to the work of Gaupp and Fawcett among others, well understood, the embryology of the chondrocranium is still mysterious.

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In four forms only among the mammals, viz., mole (NOORDENBOS); cat (TERRY); Tatusia (FAWCETT); and man (various authors); can it be said that the earliest appearance of the various cartilaginous structures has been followed. It seemed particularly desirable, therefore, to extend the present excellent knowledge of the late skull of the rabbit back to the earliest stages of its development. The authors owe the incentive to this work to Prof. J. P. HILL, F.R.S., to whom they wish to express their thanks for encouragement and help freely given in many ways. They also desire to acknowledge their debt to Prof. E. S. GOODRICH, F.R.S., whose interest in the work has been of great assistance to the authors.

The observations recorded in this paper fall into two categories. In the first place, in order to obtain as complete a series of early stages of development as possible, some two dozen stages were prepared according to VAN WIJHE's method by G. R. DE BEER. Rabbits were bred specially for this purpose and the embryos were fixed after definite lengths of time. The details concerning this material are given in the next section. These preparations were made and studied in the Department of Zoology and Comparative Anatomy of the University of Oxford.

The other part of these investigations concerns the study of the skull of an embryo, of 22 mm. greatest length, of which a wax model reconstruction was made by J. H. WOODGER, at a magnification of 50 diameters. This model, which was constructed in the Biological Laboratory of the Middlesex Hospital Medical School, serves the useful double purpose of being itself an object for comparison with the chondrocrania of the rabbit at later stages, and of other mammals, and of checking the results of the study of the chondrocrania prepared by VAN WIJHE's method. It may be remarked here that the result of both methods of investigation are entirely concordant.

The figures illustrating the paper are by G. R. DE BEER, assisted in preparation for reproduction by Mrs. G. R. DE BEER. The figures of the VAN WIJHE preparations were drawn under the camera lucida, and it is therefore hoped that the degree of their accuracy is as high as can be obtained. It should be remembered that the figures here given are each seen from one definite point of view, either from the dorsal or from the left side, as the case may be, and that, as the shape of the object is very uneven, some parts appear to be foreshortened. This must be borne in mind when comparing these figures with those prepared freehand by other authors. In any event, the differences are minimal.

Material.

In the estimation of the relative degree of development of different stages, it must be remembered that the period of time measured between pairing, and removal of the embryos from the uterus is not an exact guide. Nor is the length of the embryo (measured as the so-called greatest length from the crown of the head in the region of the midbrain to the curvature of the rump) entirely reliable either, especially as there is considerable difference between measurements of one and the same embryo obtained before and after fixation. Fortunately for students of the rabbit, CHAINE (1911) has tabulated the probable lengths of embryos at different times of development, and with the help of these tables it has been possible to make the following one relating to the material which formed the subject matter of this paper.

TABLE of Stages of Rabbit Embryos.

Number of stage.	Reputed age in days.	Probable age in days.	Greatest length mm.	Head length mm.
1	15	15	12·5	7
2	15	15	13	7
3	15½	15½	13·5	7
4	16	16	14	7·5
5	16	16	16	8·5
6	16	16	16·5	8·5
7	16	16½	18·5	9
8	17	17	19	9
9	16	17	19·5	9
10	16	17	19·5	9·5
11	16	17	20·5	10
12	18	17½	21	10
13	18	17½	21·5	10
14	18	17½	22	10
15	20	21	35	15

DESCRIPTION OF STAGES, 1–14.

Stage 1. 15 days, 12·5 mm. g.l.; 7 mm. h.l. (Plate 35, fig. 1.)

At this stage the anterior cervical vertebræ are chondrified, and take the form of paired rudiments on either side of the notochord. The neural arches of the 1st or atlas vertebra are widely separated from their corresponding centrum, the lateral ends of which are in contact with the lateral ends of the centrum of the 2nd or axis vertebra. There is thus formed a lozenge-shaped structure in the centre of which is a vacuity of similar shape. The earliest appearance of the skull is in the form of a pair of mesenchymatous condensations which stain very faintly with victoria blue, and which represent the rudiments of the occipital arches.

Stage 2. 15 days, 13 mm. g.l.; 7 mm. h.l. (Figs. 2 and 3.)

The centra of the cervical vertebræ are no longer separated by the notochord, but have fused with their fellow of the opposite side across the middle line. The occipital arches are now definitely chondrified, and at the base of each is a foramen through which passes the posterior of the two roots of the hypoglossal nerve. The posterior border of each foramen is of thicker and better developed cartilage than the anterior border, indicating that the main body of the occipital arch is morphologically posterior to the hypoglossal root, which becomes enclosed in a foramen by development of cartilage in an anterior direction.

Median to the occipital arches, and participating in the medio-ventral border of the above-mentioned foramina, are a pair of plates of thin young cartilage: the paired posterior rudiments of the parachordals. Their paired nature is of importance, as is also the fact that they are visibly less well chondrified than the occipital arches, and that although in contact with the occipital arches in front of and behind the hypoglossal foramen, they appear to be distinct from those structures. The importance of this lies in the tendency which is shown by those who advocate an unpaired origin for the parachordal to regard these paired posterior parachordal rudiments as part and parcel of the occipital arches.

Stage 3. $15\frac{1}{2}$ days, 13·5 mm. g.l.; 7 mm. h.l. (Figs. 4 and 5.)

There is little difference as regards the occipital arches and the posterior parachordal rudiments between this stage and the last. Faint staining, however, now reveals the presence of rudiments of two fresh structures. A pair of rudiments which occupy the position of the anterior region of the parachordal has appeared, separate from one another and from the posterior parachordal rudiments. These anterior parachordal rudiments are just about at the lowest degree of histological differentiation of mesenchyme into cartilage which victoria blue staining will reveal.

The other novelty which has appeared at this stage is the auditory capsule, consisting solely of the canalicular portion of that structure, and likewise of very young cartilage. The lateral covering to the semicircular canals is the first part of the capsule to chondrify. This rudiment of the auditory capsule is quite separate from any other part of the skull at this stage.

Stage 4. 16 days, 14 mm. g.l.; 7·5 mm. h.l. (Figs. 6 and 7.)

At this stage the occipital arches have extended further dorsally, and there is a notch in their anterior border, on a level with the hypoglossal foramen. This notch accommodates the anterior root of the hypoglossal nerve. The only other change is that all the parachordal rudiments are now joined together and form a thin elongated plate of young cartilage, continuous, of course, posteriorly with the occipital arches. The centrum of the atlas vertebra is beginning to show that projection which is characteristic of the odontoid peg of the fully formed axis vertebra.

Stage 5. 16 days, 16 mm. g.l.; 8·5 mm. h.l. (Figs. 8 and 9.)

The dorsal extremities of the occipital arches are now beginning to curve in towards one another. The parachordal plate is more fully developed, but it shows curious variations of thickness of cartilage in its different regions. Anteriorly, the parachordal plate shows a transverse ridge which projects upwards. This is the crista transversa, which marks the posterior limit of the future pituitary fossa or sella turcica.

Anterior to the parachordal plate another chondrification has appeared in the form of an unpaired rod in the middle line, representing the rudiment of the trabecula, which FAWCETT calls the pars interorbito-nasalis of the central stem. Anteriorly this trabecular rod grades off into a vertical plate of mesenchyme which extends, forwards between the nasal sacs and represents the procartilaginous rudiment of the nasal septum. Posteriorly, there is mesenchymatous tissue extending between the hinder portion of the trabecula and the front edge of the parachordal plate.

The visceral skeleton has put in its first appearance at this stage, in the form of slender rods representing MECKEL'S cartilages. In one specimen of this stage, the chondrification of MECKEL'S cartilage has not extended to the proximal end of this structure, with the result that the malleus is still absent. In another specimen (reproduced in figs. 8 and 9) the chondrification of MECKEL'S cartilage, although delicate, is complete, and the rudiment of the malleus is present.

Stage 6. 16 days, 16·5 mm. g.l. ; 8·5 mm. h.l. (Plate 36, figs. 10, 11 and 12.)

This stage is of particular interest, for in between the parachordal plate and the trabecular rod there is now an additional cartilaginous element which represents the polar plate of NOORDENBOS and the pars trabecularis of the central stem of FAWCETT. The term hypophysial plate or hypophysial cartilage will be adopted here for this structure. It forms a ring round a foramen, the foramen hypophyseos, through which the hypophysial stalk passes. Anteriorly, the transition is gradual from the cartilage of the hypophysial plate to the procartilage which separates that structure from the trabecular rod. Posteriorly there is likewise a gradual transition into procartilage between the hypophysial plate and the parachordal plate, in such a way as to leave a small zone relatively free from any skeletogenous tissue This zone corresponds to the fenestra basicranialis of other forms. The nasal septum is now chondrified continuously with the trabecula.

The rudiments of the postoptic root of the orbital cartilages (ala orbitalis) have appeared, in the form of paired structures on each side of, though separate from, the hinder end of the trabecular rod. A lateral projection from the base of each occipital arch forms the paracondylar process. In the hyoid arch, the basihyal cartilage has appeared as a dumb-bell-shaped structure, of obviously paired nature, although single at this stage. Delicate bars of cartilage are present representing the stylohyal cartilages in the hyoid arch and the thyrohyal cartilages in the 3rd visceral arch.

The canalicular capsule is becoming more thoroughly chondrified, and the septa semicircularia are visible by transparency.

Stage 7. 16½ days, 18·5 mm. g.l.; 9 mm. h.l. (Figs. 13 and 14.)

The notch in the anterior border of the occipital arch, which in previous stages accommodated the anterior root of the hypoglossal nerve, has now become converted into a foramen. There are, therefore, two hypoglossal foramina on each side. Dorsal to the free upper extremity of each occipital arch is a new cartilaginous element, which has chondrified independently, the supraoccipital cartilage, corresponding to the lateral portion of the tectum interoccipitale of NOORDENBOS' descriptions.

Anteriorly, the ethmoid region is of great interest. The dorsal edge of the nasal septum has extended laterally, right and left, forming the rudiment of the roof of the nasal capsule: the parieto-tectal cartilage. Lateral to the hinder region of the nasal cavity there is on each side the rudiment of the paranasal cartilage, which arises independently. A little distance behind the paranasal rudiments is another pair of rudiments, viz., those of the planum antorbitale, which also arise independently. The nasal capsule is, therefore, at this stage formed of a number of separate elements.

The hypophysial plate is not yet firmly chondrified on to the trabecula or the parachordal plate. In the splanchnocranium the incus has appeared as a small separate cartilage.

Stage 8.—17 days, 19 mm. g. l.; 9 mm. h. l. (Figs. 15, 16, 17, 18.)

This is one of the most interesting and instructive of the younger stages of development in the skull of the rabbit. The supraoccipital cartilages have each fused with the antero-dorsal corner of the upper extremity of their respective occipital arch, and each supraoccipital cartilage is now also connected with its fellow of the opposite side by means of the tectum posterius (tectum interoccipitale). There is now, therefore, for the first time, a completely enclosed foramen magnum.

In front of, and slightly dorsal to, the supraoccipital cartilages another pair of cartilages has appeared and chondrified independently. These cartilages are the parietal plates.

There is now cartilaginous continuity between the hypophysial plate and the parachordal and trabecula, but the original independence of these elements is still betrayed by the greater thickness of the cartilage in those regions and the thinness of the cartilage connecting them. It is now possible, therefore, to refer to a central stem, meaning thereby the floor of the brain-case, extending from the foramen magnum behind to the nasal septum anteriorly. The hypophysial foramen persists, while the basicranial fenestra is obliterated.

The hinder part of the central stem, the parachordal plate, is broad and flat, rising up anteriorly to form the ridge-like crista transversa. It is important to notice that the parachordal plate is of the same width in front as behind; half-way along its length it is slightly narrower, for the lateral borders of the parachordal plate are concave in a graceful curve. The hypophysial region of the central stem is narrower than the parachordal, but wider than the trabecular region, which becomes a thin vertical plate.

Where the crista transversa rises up, the central stem has a certain dorso-ventral thickness which is greater than that of the rest of the parachordal or of the hypophysial region of the central stem. Immediately in front of the crista transversa the dorsal surface of the central stem shows a depression, the pituitary fossa or sella turcica, the floor of which is formed by the hypophysial plate and pierced by the hypophysial foramen. This depression is limited in front by a slight rise in the dorsal surface of the central stem, which is the forerunner of the tuberculum sellæ of later stages, and is situated opposite the postoptic root of the ala orbitalis. In front of this again there is another slight depression which lodges the optic chiasma, and which may be termed the fossa chiasmatica. It is bounded anteriorly by a sudden rise of the dorsal surface of the central stem as the latter becomes a thin vertical plate of considerable depth, which continues forwards as the nasal septum. A portion of this thin vertical plate, however, lies behind the nasal capsule and beneath the brain, and it separates the orbits from one another. To this portion the term interorbital septum must be applied, although it is much smaller than the structure of similar name in lower vertebrates.

The postorbital roots of the ala orbitalis have become attached to the central stem at a point slightly in front of the hypophysial foramen. Further, the paired ala orbitalis itself has now appeared, extending as a plate between the eye and the brain. It has as yet no connexion with the nasal capsule, nor with the central stem in front of the optic nerve, though a process which represents the rudiment of this preoptic root is seen projecting towards the central stem. On each side of the central stem, at the place where the preoptic root of the ala orbitalis will be expected to join on to the central stem, is a little independent cartilage. This paired structure is the ala hypochiasmatica, and it possesses a small process which projects backwards ventral to the optic nerves and chiasma.

As regards the nasal capsule, the planum antorbitale is still isolated, but the paranasal cartilage has established contact with the parieto-tectal cartilage of its own side in such a way as to enclose a hole, the foramen epiphaniale, through which the lateral branch of the ethmoid ramus of the trigeminal nerve emerges to run over the roof of the nasal capsule.

Chondrification of the canalicular capsule has proceeded further than in the previous stages, but it is still isolated. The splanchnocranium shows no new features at this stage.

Stage 9.—17 days, 19·5 mm. g.l.; 9 mm. h.l. (Figs. 19 and 20.)

In the posterior region, the occipital arches, supraoccipital cartilages, and tectum posterius are as in previous stages. The chief interest of the present stage is centred in the auditory and nasal capsules. Now for the first time the canalicular capsule is in connexion with another part of the skull, by means of the basivestibular commissure, which joins the posteroventral corner of the canalicular capsule on to the lateral edge of the parachordal plate, close in front of the base of the occipital arch. This basivestibular commissure forms the anterior border of the future jugular foramen, which is still continuous dorsally with the fissura occipito-capsularis, as the gap between the canalicular capsule and the occipital arch is termed. The basivestibular commissure also forms the median border of the future foramen perilymphaticum. This foramen is already foreshadowed at this stage, for its lateral border is faintly shown by the procartilaginous rudiment of the cochlear capsule, which is beginning to appear. The cochlear capsule arises in connexion with the canalicular capsule, its postero-lateral portion being the earliest to chondrify, which it appears to do as an extension ventrally of the wall of the canalicular capsule. The cochlear capsule has no relation to the parachordal plate.

On each side of the central stem, opposite the place where the hypophysial plate joined on to the parachordal, is a small isolated nodule of cartilage, which represents the ala temporalis and probably that portion of it which becomes the lamina pterygoidea. There is as yet no sign of the processus alaris.

The ala orbitalis shows several advances over previous stages. Its postoptic root is, as before, joined on to the central stem. Its preoptic root has extended towards and fused with the ala hypochiasmatica, but without either of these structures being joined on to the central stem. Anteriorly, the ala orbitalis is attached to the paranasal cartilage of the nasal capsule by means of the sphenethmoid commissure, which forms the anterior boundary to the fissura orbito-nasalis.

In the nasal capsule itself, the paranasal cartilage is now attached to the planum antorbitale of its side, but the latter cartilage is still quite free from the central stem.

Stage 10.—17 days, 19·5 mm. g.l.; 9·5 mm. h.l. (Figs. 21 and 22.)

At this stage, the cochlear capsule has chondrified, and it is most important to notice that while it is developed in close relations to the canalicular capsule, it is wholly independent of the parachordal plate, from which it is separated by the basicochlear fissure. This fissure, which is bounded posteriorly by the basivestibular commissure, is curved between the convex median wall of the cochlear capsule and the concave lateral edge of the parochordal plate.

In the chondrification of the cochlear capsule, three large gaps are left in the walls. One of these is on the median side, facing the cavity of the brain-case; this is the primitive foramen acusticum, which has not yet become divided up into its eventual derivative foramina. The second is in the lateral wall of the cochlear capsule, and in the centre of the aperture is a small isolated disc of cartilage. The aperture is the fenestra ovalis, and the disc of cartilage in its mouth is the stapes, which arises independently of the cochlear capsule although in such close proximity to it. The third gap is in the hinder wall of the cochlear capsule and represents the foramen perilymphaticum.

It is bounded on the median side by the basivestibular commissure and dorsally by the floor of the canalicular capsule. It is impossible to speak of a fenestra rotunda or of an aqueductus cochleæ, at this stage, for they have not yet become differentiated.

In the median wall of the canalicular capsule an aperture is left which gives rise to the foramen endolymphaticum. The processus alaris has appeared, stretching from the lateral border of the central stem in the hinder region of the pituitary fossa towards the ala temporalis on each side, but without as yet touching the latter.

Further forward, a feature of interest at this stage is the fusion of the preoptic root of the ala orbitalis with the central stem. In this way, a foramen opticum is formed on each side of the trabecular region of the central stem, and projecting back into each is an ala hypochiasmatica, which now appears merely as a process of the preoptic root. The planum antorbitale is still free from the central stem, but anteriorly the roof and side-walls of the nasal capsule are fairly well formed, as a result of the further development of the parieto-tectal and paranasal cartilages.

The splanchnocranium at this stage is represented by MECKEL's cartilage with a well-developed malleus, the incus, the stapes, the basihyal, stylohyal, and thyrohyal cartilages, and by the thyroid cartilages, which have now made their appearance. Behind and median to the thyroid cartilages are the rudiments of the cricoid cartilages.

Stage 11.—17 days, 20·5 mm. g.l.; 10 mm. h.l. (Plate 39, fig. 23.)

This stage presents a number of features of considerable interest and importance, most of which are to be seen in a ventral view of the chondrocranium. In the ala temporalis the lamina ascendens has appeared. The processus alaris comes into contact with the ala temporalis, but there is no fusion. The position and relations of the lamina pterygoidea of the ala temporalis might give rise to the suspicion that it represented the pterygoid cartilage, were it not for the fact that at a later stage the pterygoid cartilage is present, separate and distinct from the lamina pterygoidea.

Jutting forward from the front of the cochlear capsule is a process of cartilage which extends towards, but does not reach, the point of contact between ala temporalis and processus alaris, on each side. This process is the rudiment of the alicochlear commissure, which will eventually form a complete lateral boundary to the carotid foramen. This alicochlear commissure is here of particular interest, for it chondrifies from behind forwards, instead of *vice versa*, as in the mole.

In the region of the nose, the paired paraseptal cartilages have appeared as separate and independent strips close to the ventral edge of the nasal septum and to one another. It is to be noticed that the nasal capsule has as yet neither lamina transversalis anterior nor lamina transversalis posterior, to which eventually the front and hind ends, respectively, of the paraseptal cartilages will become attached.

A point of small importance which the specimen illustrated in fig. 23 shows, is that the hind end of each ala hypochiasmatica has become attached to the central stem, thus enclosing a small foramen, which, as a matter of fact, is devoid of significance. This posterior attachment of the ala hypochiasmatica usually forms at a later stage.

It is in the splanchnocranium that the most interesting features of the stage under consideration here are to be found. Two new paired elements have appeared in the hyoid arch. The ceratohyal cartilages are small structures on each side of the basihyal, and they are destined to give rise to the anterior (or small) horns of the hyoid. Dorsally in the hyoid arch, a bar of cartilage has appeared above the stylohyal, separated from the latter by a narrow interval. This small bar is the laterohyal, and both it and the stylohyal are merely independent chondrifications in the blastema of the hyoid arch, which will eventually fuse to give rise to REICHERT'S cartilage, and later form the styloid process.

The thyrohyal cartilages, representing the skeleton of the 3rd visceral arch, are as in the previous stage. The thyroid cartilages, when seen from the ventral side, show that each possesses a pair of processes directed ventrally, one behind the other. The only interpretation of this condition seems to be that the thyroid cartilage represents the skeletal elements of two visceral arches, viz., the 4th and 5th. This will account for the two processes or wings, one corresponding to each arch, and it will also explain the fact that the thyroid cartilage is larger than the skeletal elements of the other visceral arches. In this respect, therefore, the rabbit may be regarded as falling into line with Monotremes and Marsupials, in possessing thyroid cartilages composed of the elements of two visceral arches. Whether in remaining Eutheria, in all of which the thyroid cartilages have been supposed to consist of one visceral arch only, the conditions resemble those of the rabbit can only be decided by further investigation, probable though it may seem.

Another remarkable feature of this stage is the presence of a pair of small spherical cartilages situated immediately median to the ventral extremities of the posterior wings of the thyroid cartilages. These structures, representing, as they must, the ventral skeletal elements of the 5th visceral arch may be termed the hypothyroid cartilages.

The cricoid cartilages have fused with one another in the middle line, dorsally of the trachea.

Stage 12.—17½ days, 21 mm. g.l.; 10 mm. h.l. (Figs. 24, 24A, and 25.)

Each parietal plate has now fused with the anterior corner of the supraoccipital cartilage of its own side, but is still free of the canalicular capsule. The occipito-capsular fissure is, therefore, an extensive curved gap, opening freely above the canalicular capsule, and communicating with the jugular foramen postero-ventrally. The cochlear capsule is still quite free of the parachordal plate.

The nasal capsule has now achieved its definitive form. Seen from the side, the former independence of the constituent elements: the parieto-tectal, paranasal cartilages, and planum antorbitale, is reflected in a couple of grooves, the sulcus lateralis anterior and posterior. Internally, the point of fusion between the parieto-tectal and paranasal cartilages is marked by the crista semicircularis. Similarly, the point of fusion between the paranasal cartilage and the planum antorbitale is marked by the 1st ethmoturbinal. The planum antorbitale has now established contact with the central stem on each side. In this way, the two fenestræ cribrosæ become completely enclosed by cartilage, and a portion of the central stem, between the planum antorbitale and the ala hypochiasmatica, becomes delimited as the interorbital septum. There is still no floor to the nasal capsule, and the paraseptal cartilages remain isolated. Antero-laterally, the nasal capsule shows a vacuity on each side: the fenestra superior.

The splanchnocranium is in precisely the same condition as that of the previous stage. The manubrium of the malleus is well developed, and the incus shows its crus longum and crus breve. The stapes has assumed its characteristic stirrup-shape, with a ring for the passage of the stapedial artery. The laterohyal cartilage comes up to the same level as the stapes, but is a short distance behind it. The anterior and posterior wings of the thryoid cartilage, and the hypothyroid cartilages, are plainly visible. As a new appearance, the arytenoid cartilages are now present.

It should be mentioned that the lateral wall of the canalicular capsule overhangs that of the cochlear capsule, forming a ridge, which is the crista parotica. Beneath this is a depression, lodging the incus and the facial nerve (the fossa incudis and sulcus facialis).

Stage 13.—17½ days, 21·5 mm. g.l.; 10 mm. h.l. (Plate 40, figs. 26, 27, 28.)

The posterolateral corner of each ala orbitalis has extended back and established contact with the canalicular capsule of its own side, but without yet touching the parietal plate. The particular manner in which these structures join on to one another in the rabbit is such that the terms usually given will hardly apply. In other mammals, the posterior extension of the ala orbitalis establishes contact with the parietal plate, so that it deserves its name of orbito-parietal commissure. Then a capsulo-parietal commissure is formed later. While these terms can be used to describe particular regions of cartilage in the fully formed chondrocranium of the rabbit, they do not express the manner of development of the various structures, and cannot be used at the stage now under consideration. Morphologically, the posterior extension of the ala orbitalis should be termed here the orbito-capsular commissure.

The posterodorsal corner of the canalicular capsule has approximated to the occipital arch, with the result that the occipito-capsular fissure has become divided into two portions. The upper portion, or fissura occipito-capsularis superior, is not enclosed anteriorly, for the parietal plate has not yet joined the canalicular capsule. It is synonymous with the foramen jugulare spurium, through which the lateral jugular vein emerges from the cranial cavity. The lower portion, or fissura occipito-capsularis inferior, has been interrupted from the jugular foramen by the development of the lamina alaris from the anterior edge of the occipital arch to the canalicular capsule.

The paracondylar process is really a ventral extension of the above-mentioned lamina alaris, and it is now a well-developed structure projecting across the mouth of the jugular foramen. Morphologically, it must be regarded as a transverse process, and its similarity to the rib and transverse process of the atlas vertebra is obvious.

The basicochlear fissure is now limited in front and separated from the carotid foramen by the development of a commissure connecting the cochlear capsule with the parachordal plate. It seems to correspond to the medial sphenocochlear commissure of NOORDENBOS's description of the mole.

The laterohyal and stylohyal cartilages have become cartilaginously connected on each side, and now form REICHERT'S cartilage, which remains unattached to the crista parotica, and gives rise to a sort of loose styloid process. Secondary cartilage is now present in the mandible, occupying the angular region, and that of the future ascending ramus.

Stage 14. 17½ days, 22 mm. g.l.; 10 mm. h.l. (Plate 41, figs. 29 and 30.)

This stage is the one which was reconstructed in wax, and after mentioning the differences between it and the previous stage, it will be described fairly fully. This description will then serve as a key to the form towards which all previous stages have been tending, and as an object for comparison with VOIT's description of later stages of the rabbit and with other forms.

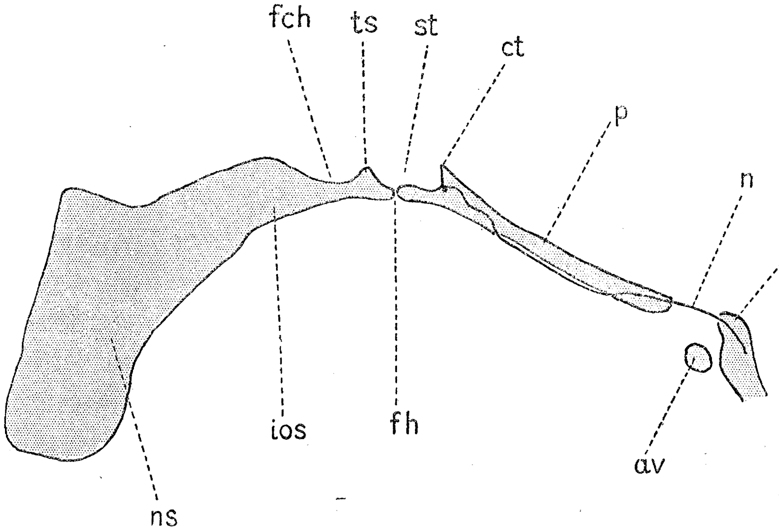
The parietal plate has now fused with the orbito-capsular commissure by means of the orbito-parietal commissure. The superior occipito-capsular fissure (or foramen jugulare spurium) is now therefore completely enclosed.

The alæ hypochiasmaticæ have fused with the central stem, thus forming a small flat plate in the floor of the fossa chiasmatica. This plate is still pierced by a pair of foramina which remain as witnesses of the former independence of the alæ hypochiasmaticæ from the central stem. The ala temporalis is now firmly attached to the processus alaris, on each side.

In the nasal capsule, a process is to be seen projecting downwards from the anterolateral corner of the side wall, on each side. This process is the rudiment of the lamina transversalis anterior, which, when it has fused with the ventral edge of the nasal septum, will form a zona annularis and separate the fenestra narina from the fenestra basalis.

In the splanchnocranium, the ceratohyals have become connected with the basihyal, forming the so-called anterior horns of the hyoid. Parts of the fibrous strands which connect the basihyal with the thyrohyal cartilages have chondrified to form the posterior horns of the hyoid.

Detailed Description of the Chondrocranium at Stage 14. *The Central Stem.*—From the reconstruction of the structures of the median sagittal plane it is seen that the floor of the parachordal plate lies in a plane approximately at right angles to that of the long axis of the nasal septum. The course of the notochord is shown in text-fig. 1. It penetrates the parachordal plate at the dorsal edge of its posterior end, runs a short horizontal course and then sinks gradually down to emerge below the cartilage. It then runs horizontally again beneath the parachordal plate for some distance before it once more penetrates the cartilage, and after an irregular course ends in a small swelling which is separated only by membrane from the sella turcica. The course of the notochord thus conforms to the type which Bolk [1922] has called transbasal.



Text-figure 1.—A median sagittal section through the central stem of the skull at stage 14, showing the course of the notochord through the parachordal plate.

The sella turcica is bounded behind by the well-defined crista transversa, and in front by another elevation—the tuberculum sellæ—which separates it from the fossa chiasmatica. In front of this, the central stem begins to increase in the dorsoventral height of the cartilage until, at the anterior limit of the fossa chiasmatica, there is an abrupt rise to form the interorbital septum. The latter region of the central stem, which is limited dorsally by the ala hypochiasmatica and anteriorly by the planum antorbitale, is directly continuous with the nasal septum, which extends forwards from the place where the planum antorbitale is in contact with it. A hypophysial foramen is still present, perforating the central stem through the floor of the sella turcica.

Seen from the ventral side, the central stem is broad in the occipital region, between the occipital arches. Further forward it narrows slightly, between the auditory capsules, with the cochlear portions of which it is fused, except for a short gap representing all that is left of the extensive basicochlear fissure of previous stages. The position formerly occupied by this fissure in the regions where it has been obliterated by chondrification is indicated by a deep groove, the basicochlear sulcus. The central stem next broadens out again in the region of the crista transversa, and here it bears on each side a boss-like thickening, immediately behind the processus alaris. In front of this, the central stem becomes narrow again, receiving the postoptic and preoptic roots of the ala orbitalis and the alæ hypochiasmaticæ, and then exhibits a median longitudinal ridge on the ventral aspect. This ridge passes without interruption into the interorbital septum and nasal septum, which regions are the narrowest of all the central stem.

The occipital region.—The foramen magnum is surrounded by a complete ring of cartilage, divisible into vault, sides, and floor. The vault is formed by the tectum posterius, a thin curved bar or arch above the brain, and connected on each side with the parietal plate and the occipital arch.

The sides are formed of the occipital arches. Half-way up, these are moderately stout pillars of rectangular cross-section directed forwards and outwards towards the hind border of the auditory capsules, from which they are separated by the short inferior occipito-capsular fissure. More ventrally, the occipital arches are triangular in cross-section. One corner is directed backwards where the articular facet for contact with the atlas vertebra is developed ; one corner is directed forwards and outwards, forming the lamina alaris which is in contact with the auditory capsule (separating the inferior occipito-capsular fissure from the jugular foramen) and is continued downwards into the paracondylar process ; the third corner is directed forwards and inwards, and passes without interruption into the parachordal plate. The median surface of the occipital arches is convex ; the lateral surface is concave.

The floor of the occipital region is the posterior edge of the parachordal plate. Laterally, it forms the articular facets for contact with the atlas vertebra, and it is rather thicker there than in the middle line. Here, a V-shaped notch is scooped out, and into the bay thus formed (the incisura intercondyloidea) the odontoid peg projects. The parachordal plate is rather widely separated from the atlas vertebra in the middle line.

At the place where the roots of the occipital arches are attached to the parachordal plate there are two foramina on each side, which serve for the egress of the two roots of the hypoglossal nerve. The apertures of the two foramina of one side are closer together on the outer than on the inner side.

The auditory capsules.—Each auditory capsule is composed of the usual two portions, the more dorsal canalicular capsule and the more ventral cochlear capsule, the latter being again subdivisible into vestibular and cochlear portions. The canalicular capsule is much the larger of the two parts, and forms a considerable portion of the cartilaginous cranial wall. Seen from the outside, it is very roughly circular in outline, and is surrounded over nearly three-quarters of its circumference by cartilage, the occipital arch posteriorly, the parietal plate and orbito-capsular commissure above. It is fused with the latter cartilage at its anterodorsal corner.

The position of the semicircular canals is faintly indicated by prominences and hollows on the outer aspect, the anterior being the most distinct. At one point in the wall of the anterior semicircular canal the cartilage is perforated, leaving a small deficiency. Further ventrally, the lateral wall of the canalicular capsule overhangs that of the cochlear capsule, forming the crista parotica, which projects over the stapes and incus, and to which the crus breve of the latter is attached. On the inner surface the position of the anterior semicircular canal is indicated by a deep hemispherical excavation of the wall, forming the fossa subarcuata anterior, which then passes without a sharp line of demarcation into the pars cochlearis. The posterior face of the canalicular capsule shows another, but smaller, excavation which outlines the posterior semicircular canal, the fossa subarcuata posterior. Immediately behind the fossa subarcuata anterior is a small foramen endolymphaticum, through which the ductus endolymphaticus emerges from the canalicular capsule into the cranial cavity.

The cochlear capsule consists of a shell-like ventral portion attached along its median side for most of its length to the parachordal plate, and a more dorsal irregular portion, the pars vestibularis. For purposes of description the former portion may be called the pars cochlearis *sensu stricto*, for it lodges the spirally-wound terminal coils of the ductus cochlearis. The pars cochlearis has a smooth convex surface on both its upper (inner) and lower (outer) aspects, interrupted only at one point anteriorly, where it sends out a process towards the ala temporalis, the rudiment of the alicochlear commissure.

The pars vestibularis has three large openings in its walls. The first of these, which is on the outer aspect, is the fenestra ovalis, covered by membrane, and in the mouth of which the stapes is situated. The second is on the inner aspect, and forms the foramen acusticum, giving access to the cavity of the auditory capsule from the cranial cavity for the auditory nerve. The last of these openings, which is on the posterior aspect of the pars vestibularis, is the foramen perilymphaticum, which faces the jugular foramen. The posterior portion of the cartilage which anchors the pars vestibularis on to the parachordal plate is the basivestibular commissure, which forms the anterior border of the jugular foramen. The auditory capsule has at this stage no mastoid process, tegmen tympani, nor suprafacial commissure.

The parietal plate.—The parietal plate is a wall of cartilage which surmounts the canalicular capsule, from which it is separated by the superior occipito-capsular fissure, or foramen jugulare spurium. Posteriorly the parietal plate is continuous with the tectum posterius and the occipital arch; anteriorly it is continuous with the orbito-capsular commissure (and through the latter with the canalicular capsule) by means of what may be termed the orbito-parietal commissure.

The ala temporalis.—The ala temporalis is attached to the central stem by the processus alaris. Each ala temporalis is composed of two portions. One of these, the lamina ascendens, is directed forwards and outwards. It is overlain on its cranial aspect by the Gasserian ganglion, and is situated morphologically posterior to the profundus and maxillary branches of the trigeminal and anterior to the mandibular branch of the trigeminal nerve. The second portion, the lamina pterygoidea, extends downwards and forwards, and is expanded in the horizontal plane. It is crossed on its outer side by the external carotid artery.

The ala orbitalis.—The alæ orbitales consists of a pair of thin irregular sheets of cartilage attached in two places to the central stem (by means of its preoptic and postoptic roots), to the nasal capsule (by means of the sphenethmoid commissure), to the canalicular capsule (by means of the orbito-capsular commissure), and to the parietal plate (by means of the orbito-parietal commissure). In this way three apertures are enclosed in the side wall of the skull on each side, viz., from front to rear: the orbitonasal fissure, the optic foramen, and the sphenoid fontanelle. A little strip of cartilage is attached to the preoptic root and extends back beneath the optic foramen to fuse with the central stem, on each side. This strip is the ala hypochiasmatica, and a small gap is left between it and the central stem.

The Nasal Capsule.—The nasal capsule consists of a median vertical septum along the dorsal edge of which are attached the two scroll-like cartilaginous coverings of the nasal sacs. Each of these coverings exhibits three principal regions. First, an anterior somewhat tubular region which is, however, incomplete ventrally where the nasal sac is not enclosed by any cartilage at all at this stage. The anterior end of the tube is open as the fenestra narina. There is also a perforation of its dorsolateral aspect: the fenestra superior. The ventral margin of the anterior portion of this region of the capsular wall is carried down ventrally as a short pointed process, which forms the rudiment of the lamina transversalis anterior. The anterior region just described is formed from the parietotectal cartilage of younger stages.

The second region is separated from the first by a groove visible on the outside, the sulcus lateralis anterior, and is the product of the paranasal cartilage of younger stages. It is more globular than the anterior region and forms a well-marked prominence. To its posterior upper margin the sphenethmoid commissure is attached, median to the root of which is the foramen epiphaniale. Behind this is the anterior border of the fenestra cribrosa, for the cavity of both the second and the third regions of the nasal capsule is widely open dorsally to the cranial cavity. Through this fenestra cribrosa the olfactory nerves enter the nasal capsule.

The third region extends downwards and backwards from the second, from which it is marked off internally by a ridge of cartilage forming the first ethmoturbinal and externally by a shallow depression, the sulcus lateralis posterior. Its posterior margin is curved inwards in such a way as to form a small posterior wall to the cavity of the nasal capsule, or a cupula posterior. This third region is a derivative of the planum antorbitale of previous stages, and in its posterior region it comes into contact without fusing with the nasal septum.

The dorsal surface of the nasal capsule is marked by a depression running forwards in the middle line from the fenestra cribrosa to the anterior end, the sulcus dorsalis.

Ventrally, the nasal capsule is open through the large fenestra basalis, on each side.

The paraseptal cartilages are independent structures situated on each side of the ventral edge of the nasal septum, being about half as long as the latter. Their anterior end lies at the level of the rudiment of the lamina transversalis anterior. In transverse section they show a crescentic outline with the concavity directed outwards.

The Splanchnocranium (Visceral arch skeleton).—MECKEL'S cartilage consists of a long slender rod of cartilage extending from the auditory region forwards to a point on the same transverse level as the sphenethmoid commissure. Here the two MECKEL'S cartilages meet one another at a rather acute angle. At its proximal end each cartilage passes without interruption into the primordium of the malleus, to form which the cartilage bends inwards and downwards, thus making a sharp angle with the rest of the cartilage. The manubrium of the malleus is expanded in the transverse plane and pushes into the wall of the future tympanic cavity from the outside.

The histological condition is not uniform throughout MECKEL'S cartilage. As far back as the transition to the malleus, MECKEL'S cartilage is composed of shrunken cells, lying in spaces marked out by faint lines stained with eosin, and the cartilage is surrounded by a well-developed compact sheath. In the region of the malleus the cells are not so shrunken and lie closer together, and the surrounding sheath becomes ill-defined. The cells at the tip of the manubrium are still more crowded, the pink-staining lines are absent, and finally the condition of simple condensed mesenchyme is reached.

The body of the incus articulates with the malleus at the bend, which marks off the latter from the main portion of MECKEL'S cartilage. From this body of the incus two arms arise: (1) a short arm (crus breve) extending upwards to end in a mass of mesenchyme in contact with the crista parotica of the capsular wall; (2) a longer arm (crus longum) which runs downwards to end in a mass of mesenchyme in contact with the stapes.

The stapes itself consists of a small disc of cartilage lying in the membrane which covers the fenestra ovalis. From this, two little processes rise up and meet, enclosing the stapedial artery between them, and end in the mass of mesenchyme into which the longer arm of the incus runs. REICHERT'S cartilage is a slender rod, the upper end of which begins in a small mass of mesenchyme lying immediately posterior to the point of articulation between incus and stapes. As this mass is traced downwards it is seen to become cartilaginous and to be accompanied by the facial nerve, which is closely applied to its posterior surface. After a short course in this direction it parts company with the nerve and begins to bend inwards towards the anterior cornu of the hyoid, which rises up as though to meet it. The two cartilages are, however, not confluent, for they are separated by a mass of condensed mesenchyme in which they both end.

The so-called hyoid consists of an oval-shaped mass of cartilage with its long axis disposed transversely, having two pairs of cornua closely connected with it by mesenchyme. Those forming the anterior pair are the shorter, and spring upwards and outwards towards the ventral end of REICHERT'S cartilage, as just described. The posterior cornua are larger, and they extend backwards in the direction of another rod of cartilage (the thyrohyal), from which they are separated by a mass of mesenchyme. The body of the hyoid itself is usually termed the basihyal, and the anterior cornua which are derived from the ceratohyals, are, like the body, part of the skeleton of the hyoid arch. The posterior cornua, on the other hand, are the ventral elements of the skeleton of the third visceral arch, to which arch also belong the thyrohyal cartilages.

The thyrohyal cartilages are a pair of slender rods, the proximal portion of which is expanded and closely connected with alæ of the thyroid cartilages. The distal portion of the thyrohyal cartilages runs towards the posterior cornua of the hyoid, as already mentioned.

The thyroid cartilages are represented by a pair of curved alæ, which are widely separated dorsally, but approximate close to one another ventrally without fusing. Between the ventral margins, at the posterior ends of the thyroid cartilages, lies a pair of small nodules, the hypothyroid cartilages.

Each cricoid cartilage runs an oblique course along the side of the larynx, and is fused dorsally by its anterior end to its fellow of the opposite side. The posterior ends are also fused, but ventrally. The arytenoid cartilages are situated immediately in front of the fused anterior ends of the cricoid cartilages.

Osseous skeleton.—The skull of the rabbit at the stage here considered (stage 14) possesses one pair of bones only, and these are the dermal ossifications which will give rise to the dentary. They form long strips which cover the outer and under surfaces of MECKEL'S cartilages over two-thirds of the length of the latter. Each dentary contains two nodules of secondary cartilage.

Stage 15.—21 days, 35 mm. g.l. ; 15 mm. h.l. (Plate 42, figs. 31 and 32.)

The general form of the skull at this stage is similar to that which is described by VOIT (1909), and consequently there is no necessity for describing it here. One point, however, deserves further consideration, and that is the way in which the fenestra rotunda and the aqueductus cochleæ are substituted for the original foramen perilymphaticum. This matter was briefly described but not figured by VOIT.

Looked at from below, or from the median side through the foramen jugulare, it can be seen that the ventral margin of the foramen perilymphaticum, which is formed by the hind edge of the floor of the cochlear capsule, is drawn out into a process. This process extends upwards across the mouth of the foramen perilymphaticum towards the floor of the canalicular capsule, with which it will eventually fuse, and in so doing it encloses the recessus scalæ tympani from beneath. For this reason, and also for the fact that it lies over and not in the plane of the mouth of the foramen perilymphaticum, this process, which VOIT called the processus intraperilymphaticus, has been termed processus recessus by DE BEER (1929).

At the present stage it is easy to see how the various apertures in this complicated region are disposed.

Relations of the Cartilages to the Neighbouring Structures.

The relations which exist between the cartilages and the neighbouring nerves and blood-vessels are always a matter of interest and importance from the morphological point of view. Most of the important relations are shown in fig. 33 (Plate 43), which is a lateral view of a reconstruction of the conditions which prevail at stage 14. These relations are of considerable interest, for they fill up certain of the gaps in Fuchs' (1905a) account of the development of the arteries of the orbit. Since they are drawn and labelled in detail in fig. 33, it would be superfluous to enter into a minute description of them here. It may, however, be pointed out that at the stage in the rabbit here figured, there are still traces left of the stapedial artery. It is *via* the stapedial artery that primitively blood is supplied to the meningea media, alveolaris inferior, and infraorbitalis arteries, as in the shrew (de Beer, 1929). In the rabbit at stage 14, the stapedial artery has been short-circuited by the external carotid (arteria pterygo-orbitalis); and all that is left of the stapedial artery is the root of the arteria meningea media and the arteria tympanica, in which the original direction of blood-flow is now reversed.

Discussion.

The study of the chondrocranium admits of two lines of discussion. To start with, there is the comparison between the ways in which the various cartilages make their first appearance in different animals, which may be termed the embryology of the chondrocranium. Next, there is the comparison between the cartilages and the relations which they bear to neighbouring blood-vessels and nerves in different animals, regardless of the details as to how the cartilages arose; this may be referred to as the morphology of the chondrocranium, and it may be mentioned that it is usually the stage of maximum development of the cartilage that is taken as the standard for comparison. At such a stage, the various cartilages are fused with one another [in " homocontinuity," to use Gaupp's term], and they often supply no evidence as to the conditions which prevailed during the preceding period [of " heterocontinuity "] when the cartilages were still separate from one another.

It is, of course, impossible, and indeed undesirable, to draw a hard and fast line between these two points of view in the problem of the skull; it is worth noting, however, that the time factor, which is important in the embryology of the chondrocranium, may be neglected in its morphology, so long as corresponding stages are compared.

Embryology of Mammalian Chondrocranium.

For purposes of profitable comparison it is essential that a close and full series of stages in the development of the mammals in question should have been studied. The number of mammalian species which have been subjected to a detailed investigation of this kind is not great, as the following list will show.

Homo .. .. Studied by Hertwig (1898), Levi (1900), Kernan (1916), Fawcett (1918a), Lewis (1920), and Macklin (1921).
Felis .. .. ,, ,, Terry (1917).
Talpa .. .. ,, ,, Noordenbos (1905).
Echidna .. ,, ,, Gaupp (1908).

In addition, there have been studied young and old stages of—

Tatusia .. Studied by Fawcett (1921).

The new observations concerning the manner of origin of the cartilages in Lepus, brought forward in this paper, will now be considered in the light of previous knowledge, in respect of the following points:—The parachordals; polar cartilages; nasal capsule; cochlear capsule; parietal plate; Reichert's cartilage and thyroid cartilage.

The parachordals.—The chief interest of the parachordals from the present point of view is the question as to whether the parachordal plate arises in the mammal as an unpaired median rudiment or as two paired rudiments which subsequently fuse. It may be mentioned that in all other vertebrates it has been established that the paired method of origin of the parachordals is the rule.

Noordenbos claims a single unpaired origin for the parachordal in Talpa, and indeed also in Lepus, Bos, and Sus. In Echidna there seems to be a hypochordal rudiment in contact with the occipital arches from a very early stage. The conditions in Homo would seem to be similar, except that the occipital arches chondrify first, and the hypochordal cartilage develops later.

In the cat, however, Terry has shown that the parachordals arise in the form of paired strips of cartilage on each side of the notochord, only joined together by a hypochordal commissure anteriorly which in no way obscures the paired nature of their origin. These parachordal cartilages are continuous posteriorly with the occipital arches. The conditions in the cat, therefore, agree with those in all lower vertebrates as regards the paired nature of the parachordals, and there can be no question that this method of origin is the primitive one.

In the rabbit, the posterior portion of the parachordal plate appears first in the form of a pair of cartilages in contact with the ventral ends of the occipital arches. Now, it is possible that adherents to the view that the mammalian parachordal plate is by nature unpaired will object that the structures here regarded as paired posterior parachordal cartilages are really the ventral extremities of the occipital arches. This problem turns on the position of the hypoglossal foramina, as to whether they are to be regarded as piercing the occipital arch or as lying between the parachordal and the occipital arch. For the objection outlined above to be valid, it is necessary that the hypoglossal foramina be definitely perforations wholly within the occipital arch. This is a question of morphology cropping up in the embryology of the chondrocranium, and the following points should be considered. FAWCETT (1918A) in his description of the skull of Erinaceus states that the occipital arch " may be taken as extending from an imaginary line drawn through the medial margin of the hypoglossal canal in an antero-posterior direction." It is clear, therefore, that FAWCETT regards cartilage situated median to the hypoglossal canal or foramen as not forming part of the occipital arch.

A similar conclusion can be reached by a consideration of the relations of the hypoglossal roots to the cartilages in lower vertebrates. GOODRICH (1918) has shown that in Scyllium, the last cranial hypoglossal root becomes enclosed, not in a perforation in a single occipital arch, but by the junction above the nerve of the two pillars of which the arch is made up. These pillars rise up from the floor of the parachordal plate on which the hypoglossal nerves rest, and continue to rest even after becoming enclosed in foramina. It can be safely concluded, therefore, that the structures in question in the rabbit, situated median to the hypoglossal foramina, are true paired rudiments of the parachordals and not merely the ventral ends of the occipital arches.

Little importance need be attached to the appearance of anterior parachordal rudiments, for they are almost immediately merged with the general chondrification which results in the formation of the parachordal (= basal) plate.

The Hypophysial Cartilages.—The existence of cartilaginous elements between and separate from the parachordals behind and the interorbito-nasal septum in front has now been established for the following mammals :—

Homo	FAWCETT (1918). " Pars trabecularis."
Felis	TERRY (1917). " Hypophysial cartilage.
Talpa	NOORDENBOS (1905). " Polar plate."
	FAWCETT (1916). " Trabecular part."
Tatusia	FAWCETT (1921). " Pars trabecularis."
Echidna	GAUPP (1908). " Trabecula."

In addition, FAWCETT (1918A) has figured the skull of a 19-mm. embryo of Bos in which a trabeculo-septal fissure and a fenestra basicranialis are present, showing that here also the region of the sella turcica must have had a separate chondrification.

The rabbit agrees with the forms just mentioned in possessing a distinct hypophysial cartilage, and it is worth noticing that this structure has now been found in all the mammals of which full series including young stages of development have been studied. It is very probable therefore that the hypophysial plate or hypophysial cartilages will be found to be universally present in mammals.

The question of the terminology of this structure is bound up with its interpretation, which must be considered first. It has long been a puzzle in the study of the mammalian chondrocranium that the internal carotid arteries appear to enter the cranial cavity on each side of a median central stem, instead of rising up between paired trabeculæ. It is true that the carotid arteries are eventually enclosed laterally by the alicochlear commissures, which are held to be the morphological representatives of the posterior ends of the trabeculæ of lower forms; but the problem remains as to how the manner of origin of this region of the skull in mammals is to be reconciled with that which obtains in all the lower vertebrates.

The hypophysial plate is developed in intimate relation to the hypophysis, round the duct of which it forms a ring, pierced by the hypophysial foramen. This is the condition in the rabbit. In Felis, it forms a transverse bar behind the hypophysial stalk. In other forms (Homo, Echidna), the cartilage in this region is seen to be made up of a pair of structures right and left of the hypophysial stalk. Lastly, in Talpa, NOORDENBOS has shown that there are in this region two pairs of centres of chondrification, sometimes with two unpaired centres in addition.

The next point is to consider the relations of these cartilages to the internal carotid arteries. In Echidna (GAUPP, 1908) the paired cartilages in question are situated *lateral* to the carotid arteries. Later, the two cartilages become joined across the middle line to form the hypophysial plate, and this becomes attached to the parachordal plate lateral and median to the internal carotid arteries, which thus find themselves enclosed in foramina. The same conditions are to be found in Ornithorhynchus (DE BEER, 1926).

Now the cartilages in the hypophysial region of Homo, Felis, Talpa, Lepus, Bos, and Tatusia are situated *median* to the internal carotid arteries, and when they become attached to the parachordal plate this cartilaginous connexion is likewise median to the carotids. The consequence is that the arteries are not enclosed in foramina, but rise up in notches on each side of the central stem. These notches are only converted into foramina later on, when the alicochlear commissures develop forming the lateral border to the carotid foramina.

It used to be thought that the floor of the chondrocranium consisted of two portions only: the parachordals or basal plate behind, and the trabeculæ in front, running into the nasal septum. On the basis of new observations, FAWCETT has subdivided the floor of the mammalian chondrocranium into the following three regions:—pars chordalis behind, pars trabecularis in the middle, and pars interorbito-nasalis in front. The first and last of these terms are quite unexceptionable, but "pars trabecularis" may give rise to confusion. In the first place, it must be remembered that the structure which is often referred to simply as the "trabecula" has now been shown to be composed of an anterior trabecular portion, and a posterior polar element, in a number of forms (Selachians, VAN WIJHE, 1904, 1922; Lepidosteus, VEIT, 1911; Aves, SONIES, 1907). Developed from the polar part of the complete "trabecula" is the basipterygoid or basitrabecular process.

The trabecula *sensu stricto* in lower vertebrates is therefore that anterior portion which participates in the formation of the nasal septum, and of the interorbital septum when such a structure is present. In the mammal, this portion is represented by the pars interorbito-nasalis of FAWCETT's terminology. The polar cartilage in lower vertebrates is precisely similar to the paired cartilages of Echidna. Both are situated lateral to the internal carotid artery, and bear the basitrabecular process which in the mammal is known as the processus alaris. This paired cartilage in Echidna may, therefore, be termed the polar cartilage.

In Echidna and in lower vertebrates, the polar cartilages or hind ends of the "trabeculæ" become connected with one another across the middle line by cartilage, forming what may be termed the hypophysial plate, and situated median to the internal carotid arteries. It is to this cartilage that the hypophysial cartilages of Homo, Felis, Lepus, Talpa, Bos, and Tatusia correspond, and they may appear as one (Lepus, Felis), two (Homo), or more (Talpa) centres of chondrification.

It is clear that these cartilages do not quite correspond to the polar cartilages of lower vertebrates and of Echidna, and it seems necessary, therefore, to apply to them simply the term "hypophysial cartilages" to distinguish them from the polar cartilages. The hypophysial plate formed by these cartilages is the region of the floor of the skull to which FAWCETT has applied the term pars trabecularis, and confusion may arise because this part does not correspond to the trabeculæ *sensu stricto* of lower forms.

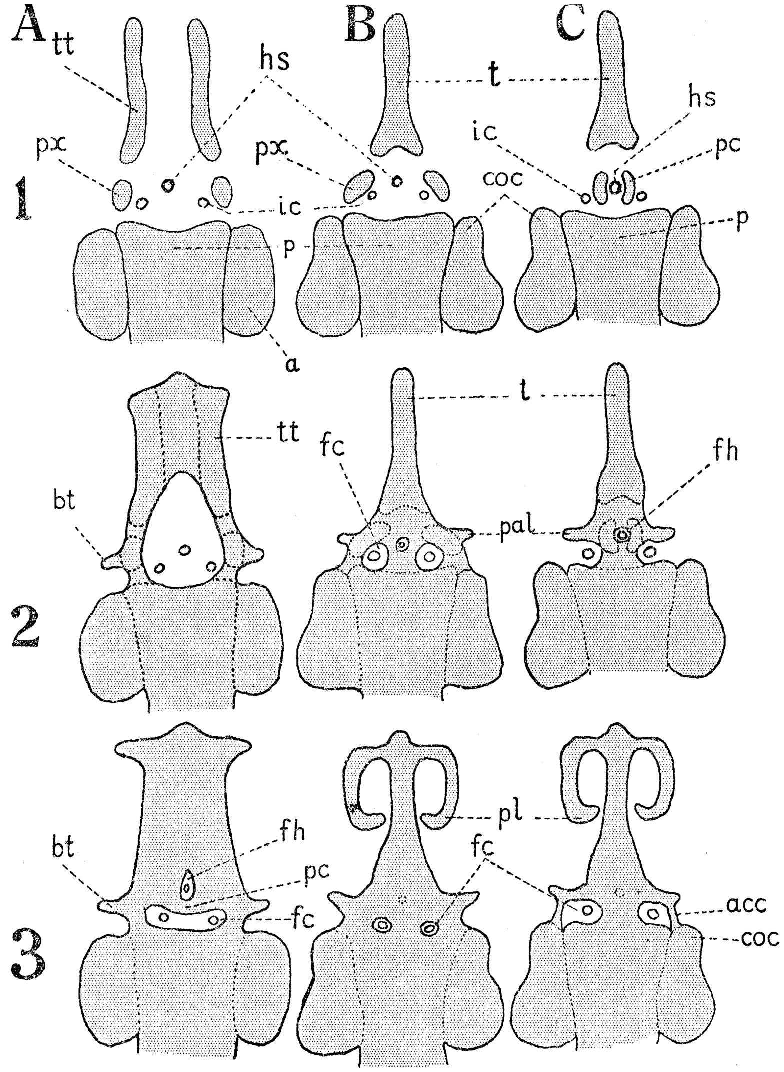
However, it is now possible to trace a series from the lower vertebrate to the mammalian condition, passing through the following stages :—

1. *Selachians and Birds.*—The trabeculæ and polar cartilages form bars which join on to the parachordal plate *lateral* to the internal carotid arteries. The region between these bars eventually becomes chondrified to form the hypophysial plate.

2. *Monotremes.*—The polar cartilages develop lateral to the internal carotid arteries. They become connected with one another in the middle line by cartilage forming the hypophysial plate, and the junction with the parachordal plate takes place *lateral* as well as *median* to the internal carotid arteries.

3. *Placental Mammals.*—The hypophysial plate develops from a varying number of hypophysial cartilages situated median to the internal carotid arteries, and becomes attached to the parachordal plate by cartilage *median* to these arteries. The polar cartilages are delayed in their appearance, and are represented by the alicochlear commissure which eventually closes the carotid foramen on the outer side. Just as in lower vertebrates the polar cartilage bears the basitrabecular process, so in mammals the alicochlear commissure may be said to bear the processus alaris although the latter may chondrify before the former.

The transition from the lower vertebrate to the mammalian condition is thus brought about by a variation in time at which the polar element appears. It must be noted, however, that NOORDENBOS was in error in thinking that the structures in Talpa which he called polar cartilages (here called hypophysial cartilages) were homologous with the true polar cartilages of Selachians, Lepidosteus, and Birds.



TEXT-FIGURE 2.—Diagram showing the relations of the trabeculæ, polar cartilages, and hypophysial cartilages in :—A, Lower Vertebrate ; B, Monotreme, and C, Higher Mammal ; at three successive stages of development. (1, 2, 3.)

In the formation of the alicochlear commissure the rabbit presents a peculiarity. In Talpa this structure develops from in front backwards, as NOORDENBOS showed, giving it the name synchondrosis sphenocochlearis lateralis. Now, in the rabbit the structure which develops in exactly the same position chondrifies in the opposite direction, viz., from behind forwards. The alicochlear commissure in the rabbit starts from the cochlear capsule, and for some time it does not reach the processus alaris. It is difficult to see what significance this variation in the rabbit can possess. The alicochlear commissure arises from a condensation of mesenchyme in which it may be supposed that chondrification can set in anywhere without affecting the morphological significance of the resulting cartilage.

The Nasal Capsule.—There is substantial agreement between the methods by which the nasal capsule arises in Felis (TERRY, 1917), Talpa (NOORDENBOS, 1905), and Lepus (this paper). In all cases the nasal septum chondrifies in continuity with the trabecula and its dorsal edge is produced into the primitive roofing cartilages, the parieto-tectal cartilages. Separate from these arise two isolated pairs of cartilages, the paranasals and the plana antorbitalia. The latter elements have been found in Echidna by GAUPP (1908), together with a pair of isolated cartilages in the roof which seem to correspond to the parieto-tectal cartilages. In this connexion it may be mentioned that TERRY found some evidence of the independent origin of these cartilages in Felis.

From the morphological point of view, the mode of development of the nasal capsule throws important light on the nature of certain structures, viz., the crista semicircularis, the first ethmoturbinal, and the foramen epiphaniale. The results of investigations on the rabbit are in full agreement with the conclusions which TERRY drew from his study of the cat, viz., that where the paranasal cartilage overlaps the parieto-tectal a curved intranasal ridge is formed, which gives rise to the crista semicircularis, while the foramen epiphaniale represents the original fissure between the two cartilages ; and that where the posterior edge of the paranasal cartilage overlaps the planum antorbitale, the latter forms an intranasal ridge, which projects into the fold of epithelium which contains the first ethmoturbinal.

The Cochlear Capsule.—The relations of the cochlear portion of the auditory capsule to the parachordal plate have been treated exhaustively by one of the present authors in a recent publication (DE BEER, 1929), for which reason it will be unnecessary here to go into the matter to any greater length than to say that the conditions in the rabbit agree entirely with the conclusion which was there arrived at, to the effect that NOORDENBOS'S theory was correct and GAUPP'S erroneous. The cochlear portion of the auditory capsule chondrifies with, and is a true part of, the rest of the auditory capsule, and has no relations with, and is in no way derived from, the parachordal plate. One point, perhaps, worth mentioning is that the rabbit furnishes an additional piece of evidence to refute GAUPP'S view, in that the parachordal plate is just as broad in front as behind. It is only in the intermediate region that it is narrower, which narrowing GAUPP attempted to attribute to the appropriation of the lateral part of the parachordal by the auditory capsule to form its cochlear portion, and he based this view on forms in which the front of the parachordal plate happened to be narrower than it was at the back. This was, of course, merely due to the fact that in those forms the cochlear capsules were situated relatively further forward than they are in the rabbit.

The Parietal Plate.—The development of the structures forming the wall of the hinder part of the chondrocranium, above the auditory capsules, agrees in Felis, Talpa, and Lepus, except in regard to the times at which these originally separate cartilages become connected with one another.

In Felis, according to Terry (1917), the so-called parietal plate seems to chondrify in the position of the element which is here called the supraoccipital cartilage, and separately from the occipital arch, auditory capsule, and the orbitoparietal commissure, which latter is also an independent chondrification above and in front of the canalicular capsule, but which seems, nevertheless, to correspond to what is here termed the parietal plate. In Felis the structures which Terry calls the parietal plates form the tectum posterius and establish connexion with the top of the occipital arches. Later, they become connected with the canalicular capsules posteriorly and the structures which Terry calls the orbitoparietal commissures. Lastly, an anterior parietocapsular commissure is formed.

In Talpa, Noordenbos (1905) showed that the tectum posterius arises separate from the parietal plate and occipital arch, and that the parietal plate arises separate from the canalicular capsule. The parietal plate soon joins the canalicular capsule, and the tectum posterius joins the top of the occipital arches. Then the tectum posterius joins the parietal plate, while lastly, the synchondrosis orbitoparietalis joins the ala orbitalis with the parietal plate.

In Lepus, however, as the present results show, the tectum posterius has a paired origin in the form of the supraoccipital cartilages, which chondrify independently of the occipital arches and of the parietal plates. In fact, the conditions agree with the interpretation of the posterior region of the skull of Erinaceus, given by Fawcett (1918a). First, the supraoccipital cartilage joins the occipital arch, and later the parietal plate, which is independent of the canalicular capsule. Next, the ala orbitalis joins the canalicular capsule by the orbitocapsular commissure, and lastly the parietal plate establishes connexion with this orbitocapsular commissure by means of the orbitoparietal commissure.

If the commissures are given the names of the structures between which they establish connexion, then, owing to the relatively different times at which these connexions are made in the various forms, different names would have to be used, with the consequent danger of confusion. The order of their appearance is the following :—

Talpa

1. Occipital arch—supraoccipital (= tectum posterius)
2. Parieto-capsular
3. Parieto-supraoccipital (= tectum posterius)
4. Orbito-parietal.

Felis

1. Occipital arch—supraoccipital (= parietal plate of Terry).
2. Parieto-supraoccipital
3. Parieto-capsular
4. Orbito-parietal.

Lepus

1. Occipital arch—supraoccipital
2. Parieto-supraoccipital
3. Orbito-capsular
4. Orbito-parietal.

It is thus difficult to speak of an orbitocapsular commissure in Talpa or Felis, or of a parietocapsular commissure in Lepus, simply because the relative times at which the joining up of the cartilages takes place differs in the three animals. At the same time, it is obvious that the finished product: a lateral wall to the brain-case above the ears, is equivalent in all three, and it may conveniently be given the term lamina supracapsularis, which GAUPP (1908) applied to the corresponding structure which chondrifies in one piece in Echidna. It may be mentioned that the connexion which TERRY describes in the cat, as joining the "parietal plate" and canalicular capsule posteriorly, is that which separates the superior from the inferior occipitocapsular fissure.

Reichert's cartilage.—REICHERT'S cartilage is the term applied to the dorsal skeletal elements in the hyoid arch, other than the stapes. In BROMAN'S (1898) description of the development of the hyoid arch in man, there is formed a cartilaginous rod situated on the median side of the facial nerve and connected with the stapes by a non-cartilaginous ligament (the interhyal, or hyo-stapedial ligament). This rod may be called the stylohyal. Dorsal to the stylohyal another chondrification appears, on the lateral side of the facial nerve. This is the laterohyal, and when its ventral end joins the dorsal end of the stylohyal, and its dorsal end fuses with the crista parotica of the auditory capsule, the styloid process is formed with its characteristic relations to the facial nerve. The term REICHERT'S cartilage may be applied to the combined stylohyal and laterohyal. In the rabbit, however, REICHERT'S cartilage does not fuse with the crista parotica.

In the mole, NOORDENBOS found that REICHERT'S cartilage chondrified in one piece (1905), but in the rabbit it arose from two centres, as described in this paper. FUCHS (1905B) also found two centres of chondrification in this region in the rabbit. The more ventral one he recognised as REICHERT'S cartilage, while he is inclined to ascribe the more dorsal, to which he gives the name intercalare (following DREYFUSS, 1893), to the auditory capsule. There can, however, be no doubt that the laterohyal (= intercalare) is a part of the splanchnocranium whose relations with the auditory capsule are merely topographical. In stage 14 of the development of the rabbit described in this paper, the stylohyal and laterohyal have joined. The dorsal end of the rod of cartilage which they form is anterior and external to the facial nerve, and so a simple junction with the crista parotica immediately dorsal to its proximal end would produce the characteristic relations of the styloid process.

It may be mentioned in connexion with these considerations on the splanchnocranium that no evidence whatever was found in favour of FUCHS' (1905B) view that the stapes arises in connexion with the auditory capsule, or that the mammalian malleus-incus articulation is not homologous with that between articulare and quadrate in lower vertebrates. On the contrary, the study of the development of the rabbit is entirely consistent with REICHERT'S theory of the homologies of the auditory ossicles, as finally set forth by GAUPP (1912).

The Thyroid Cartilages.—An excellent summary of the state of knowledge regarding the thyroid cartilage is given by EDGEWORTH (1916). While there is universal agreement that in Monotremes and Marsupials the thyroid cartilages are made up of the skeletal elements of the 4th and 5th visceral (= 2nd and 3rd branchial) arches, there is a divergence of opinion concerning the placental mammals. The view that the placental thyroid cartilages contain elements representing the 4th and 5th visceral arches is held by KALLIUS (1897) and GROSSER (1912) from studies on man, whilst the view that they are formed from derivatives of the 4th visceral arch only is held by SOULIÉ and BARDIER (1907) in regard to man, and by EDGEWORTH (1916) working on the pig. The study of the rabbit, described in this paper, is definitely in favour of the former view, since each thyroid cartilage at stages 11 and 12 possesses two wings extending towards the middle line ventral to the trachea. It seems therefore that EDGEWORTH'S explanation of the fact that the recurrent laryngeal nerve enters the larynx ventral to the articulation of the thyroid and cricoid cartilages in Monotremes and Marsupials, and dorsal to it in placental mammals, by supposing the articulations to be not homologous, is deprived of its evidence.

A median copula between the ventral ends of the wings of the thyroid cartilages has been found in man by NICHOLAS (1894), KALLIUS (1897), SOULIÉ and BARDIER (1907), and FRAZER (1910); in the pig by EDGEWORTH (1916), who also found it among Marsupials in Dasyurus; and in Monotremes by DUBOIS (1886). It would seem that in the rabbit this copula is represented by the paired cartilages, situated between the posterior wings of the thyroid cartilages, to which the term hypothyroid cartilages has been applied.

Morphology of Mammalian Chondrocranium.

Most of the points concerning the morphology of the mammalian chondrocranium have been dealt with by one of the present authors in connexion with the shrew (DE BEER, 1929), for which reason it will be unnecessary to go into them again here. It will suffice to point out the bearing of the present investigations on the conclusions arrived at in the above-mentioned work, and to consider the morphology of those structures which the shrew does not possess.

The Ala Orbitalis.—The rabbit is to be added to the number of forms in which the ala orbitalis has been observed to chondrify independently.

The Basicranial Fenestra.—The rabbit agrees with the mole in the possession and method of formation of a basicranial fenestra.

The Pterygoid Problem.—The conditions in the rabbit support the view that the mammalian pterygoid cartilage represents the reptilian pterygoid bone and that the reptilian parasphenoid is represented in the mammal by a dermal bone, which FUCHS (1909) observed to arise separate from the pterygoid cartilage (DE BEER, 1929).

The Relations of the Auditory Capsule to the Parachordal Plate.—The conditions in the rabbit lend the strongest support to NOORDENBOS' (1905) view that the cochlear capsule is in no way to be regarded as having been derived from a portion of the parachordal plates of lower vertebrates. In the rabbit the basicochlear fissure extends the whole length of the cochlear capsule until quite late stages, and is then obliterated from behind forwards.

There is a point of some interest concerning the manner in which the basicochlear fissure is obliterated in the mole and the rabbit. In the mole, the auditory capsule is attached to the central stem by four commissures, enclosing three apertures between them. These commissures are :—

1. Synchondrosis spheno-cochlearis lateralis = alicochlear commissure.
2. Synchondrosis spheno-cochlearis medialis.
3. Synchondrosis basicochlearis.
4. Synchondrosis basivestibularis.

In between 1 and 2 is the carotid foramen ; between 2 and 3 the anterior basicochlear fissure ; between 3 and 4 the posterior basicochlear fissure.

Now, in the rabbit, the present observations are in agreement with those of NOORDENBOS in finding only three commissures, of which the first is certainly the alicochlear and the last the basivestibular. But the question arises, is the commissure which joins the cochlear capsule to the central stem median to the carotid artery to be regarded as the medial spheno-cochlear or as the basicochlear ? NOORDENBOS inclines to the latter alternative, and therefore according to him the carotid foramen of the rabbit corresponds to the carotid foramen *plus* the anterior basicochlear fissure of the mole. But it seems simpler to regard the carotid foramina of both animals as equivalent, and to call the commissure in question the medial sphenocochlear. It is known that the basicochlear fissure in the rabbit becomes obliterated from behind forwards, so that, while at early stages the basicochlear fissure is not subdivided into anterior and posterior portions, at later stages the posterior portion is obliterated and the anterior portion remains. The anterior edge of the cartilage which has obliterated the posterior region then corresponds to a basicochlear commissure.

The Foramen Perilymphaticum.—The details of the formation of the processus recessus and of the aqueductus cochleæ and fenestra rotunda in the rabbit, as first described by VOIT and illustrated in this paper, are in agreement with the view that the foramen perilymphaticum has not simply become subdivided to form these two apertures. The transition from the reptilian to the mammalian condition has been associated with the extension of the posterior edge of the floor of the cochlear capsule to form a processus recessus, which encloses the recessus scalæ tympani, in the walls of which the fenestra rotunda and the aquæductus cochleæ are persistent apertures (DE BEER, 1929).

The Interorbital Septum.—The interorbital septum is a portion of the central stem where it takes the form of a thin vertical plate, separating the orbits from one another. It is necessarily posterior to the nasal capsule, but it is directly continuous with the nasal septum. The interorbital septum shows its highest degree of development in

Sauropsida, where, as Gaupp (1900) showed in the lizard, it is an extensive plate between the relatively large eyes. It seems that in these vertebrates the development of the interorbital septum is associated with the large size of the eyes, with the result that the braincase itself is relegated to the more posterior region of the skull. Now, not all mammals possess an interorbital septum, and in those forms in which it is present it appears to be correlated, not with the size of the eye (which is relatively small), but with a reduction in size of the nasal capsule. If the nasal capsule does not extend as far back as it did in previous forms, it follows that a portion of the central stem which had been part of the nasal septum comes to find itself behind the nasal capsule and in the region between the orbits.

Since the mammals must have been derived from a reptilian form, and since the interorbital septum is typical in reptiles, the question arises as to whether the interorbital septum which is found in some mammals can be regarded as a primitive structure directly derived from the reptilian ancestors, or as a secondary structure developed within the evolutionary history of the mammals. In order to deal with this question it will be necessary to consider the distribution of the interorbital septum among the mammals.

The interorbital septum is absent in :—

Cebus	Henckel (1928a)
Mycetes	Frets (1913)
Galeopithecus	Henckel (1929)
Tupaia	Henckel (1928b)
Erinaceus	Fawcett (1918a)
Talpa	Fischer (1901)
Sorex	de Beer (1929)
Miniopterus	Fawcett (1919)
Felis	Terry (1917)
Poikilophoca	Fawcett (1918b)
Equus	Limberger (1926)
Tatusia	Fawcett (1921)
Dasyurus	Fawcett (1918a)
Echidna	Gaupp (1908)

The interorbital septum is feebly represented in :—

Lagenorhynchus	de Burlet (1914b)
Balænoptera	de Burlet (1914a)
Phocæna	de Burlet (1913)
Canis	Olmstead (1911)
Bos	Fawcett (1918a)
Didelphys	Töplitz (1917)

The interorbital septum is well developed in :—

Homo	Macklin (1921)
Semnopithecus	Fischer (1903)
Macacus	Fischer (1903)
Chrysothrix	Henckel (1928a)
Hapale	Henckel (1928a)
Nasalis	Frets (1913)
Ateles	Frets (1913)
Tarsius	Fischer (1905), Henckel (1928a)
Nycticebus	Henckel (1928a)
Lemur	Henckel (1928a)
Lepus	Voit (1909)
Microtus	Fawcett (1917)

It is plain that the only mammals in which the interorbital septum is well developed are the Primates and the Rodents. But before the presence of this structure can be adduced as evidence of particular affinity between these two groups, the conditions of its formation must be considered.

In the first place, it is to be noticed that the evolution of the mammalian chondrocranium has been accompanied by an increase in size of the nasal capsule. This has resulted in a backward extension of the planum antorbitale and a stretching of the floor of the capsule, to such an extent that only in a few forms is the original continuity between the anterior and posterior lamina transversalis preserved (through the paraseptal cartilage). Now this backward extension of the planum antorbitale must have resulted in the inclusion of a considerable portion of the reptilian interorbital septum within the nasal capsule, to form part of the nasal septum, but the Rodents are among those few mammals in which the paraseptal cartilage extends from the anterior to the posterior lamina transversalis (as it does in all reptiles), and so it would seem that in the Rodents the nasal capsule has not encroached so much on the interorbital septum as it has in other mammals. The interorbital septum of the rabbit may therefore be regarded, with some degree of plausibility, as a remnant of the originally extensive septum of the reptilian ancestor.

In the Primates, the case is slightly different, for their evolution has been characterised by a reduction in the size of the nasal capsule. The fact that Mycetes and Cebus lack the interorbital septum might suggest that the higher Primates were descended from forms in which the nasal capsule was larger than it now is and in which the interorbital septum had been incorporated in the nasal septum. The presence of the interorbital septum in the higher Primates would then be a result of the secondary reduction in size of the nasal capsule. But the presence of the interorbital septum in the other Platyrhines as well as in the Lemurs, Tarsius, and the Catarhines, makes it probable that the absence of that structure in Mycetes and Cebus is a secondary feature in these animals. It may be concluded therefore that the interorbital septum is a primitive structure in Primates, and that it is homologous with that of Rodents.

The ala hypochiasmatica.—The rabbit was the first mammal in which the ala hypochiasmatica was found, and it owes its name to Voit (1909), who saw its relation to the cartilago hypochiasmatica of the lizard. The origin of this structure has now been observed in three forms, viz., Homo (Kernan, 1916), Lepus (this paper), and Tatusia (Fawcett, 1921), and in all three it has been found to chondrify as paired independent rudiments. But whereas in Lepus the ala hypochiasmatica becomes joined on to the preoptic root of the ala orbitalis, in Tatusia it is attached to the postoptic root. At all events, the result is the formation of a plate of cartilage which juts out on each side from the central stem and forms the ventral border of the optic foramen. In some forms it has been called the paroptic process. An ala hypochiasmatica of some sort is found in the following :—

Homo	Kernan (1916), Macklin (1921)
Semnopithecus	Fischer (1903)
Macacus	Fischer (1903)
Lepus	Voit (1909)
Microtus	Fawcett (1917)
Erinaceus	Fawcett (1918a)
Canis	Olmstead (1911)
Halicore	Matthes (1921)
Phocæna	de Burlet (1913)
Megaptera	Honigman (1917)
Sus	Mead (1909)
Bos	Fawcett (1918a)
Equus	Arnold (1928)
Tatusia	Fawcett (1921)
Didelphys	Töplitz (1917)

There can be little doubt that the ala hypochiasmatica is a primitive structure derived from the original early mammalian ancestors.

The Paracondylar Process.—The paracondylar process is a ventrolateral extension of the lamina alaris, which itself is the anterior corner of the pillar of the occipital arch. The paracondylar process appears to be widely distributed among mammals, although it is better developed in some forms than in others. Its development seems to be at its highest in the Rodents. With regard to its morphological significance, Voit (1909) has suggested that it represents the transverse process of a vertebra, or vertebræ, which has, or have, been assimilated into the occipital region of the skull, and he regards the rectus capitis lateralis muscle, which is stretched between the paracondylar process and the transverse process of the atlas vertebra, as homodynamous with the intertransversarius muscles which stretch between the transverse processes of adjacent vertebræ. On the other hand, DE BURLET (1916) has objected that it is unlikely that the paracondylar process can represent the transverse process of the hindmost vertebra incorporated in the skull, because it is in position the most anterior structure of the occipital region. It would seem, however, that this objection is not very serious, for there is plentiful evidence of topographical variation in position of the transverse processes, relatively to their respective vertebræ. The vertebral column of the frog, in which some transverse processes are directed forwards and others backwards, is a good example of this.

On the available evidence, then, it is reasonable to regard the paracondylar process as the transverse process of an occipital vertebra, and as such, it must be a primitive feature. Anterolateral processes of the occipital arch more or less corresponding in position to the paracondylar process have been figured, but not labelled, by GAUPP (1900) in Lacerta.

The Hypoglossal Foramina.—The skull of the rabbit is interesting, as showing two hypoglossal foramina on each side, apparently as a constant feature. In other forms, there may be some variation from the more normal number of 1 on each side. MATTHES (1921) has shown that in Halicore the number may vary between one and two foramina on each side, and that it is the anterior one that is variable, sometimes being confluent with the jugular foramen. This process is carried still further in the whales Megaptera (HONIGMAN, 1917) and Balænoptera (DE BURLET, 1916), and in the Monotremes (GAUPP, 1908), in which an independent hypoglossal foramen may be lacking, in which case the hypoglossal nerve effects its exit through the jugular foramen. In another whale, Lagenorhynchus, DE BURLET (1914B) has shown that there may be two hypoglossal foramina on one side, as against one on the other. In view of the greater number of independent hypoglossal foramina in the reptiles, there can be little doubt that the presence of two pairs of foramina in the rabbit is a primitive condition.

The Mastoid Process.—The mastoid process is a ventrolateral projection of the crista parotica of the auditory capsule, and in the rabbit it develops late, for while it is present n the stage studied by VOIT, it has not yet appeared in the oldest stage studied by the present writers. It supplies an attachment for the sternomastoid and cleidomastoid muscles, and appears to be a constant feature in the Rodent skull, for it is present in that of Microtus (FAWCETT, 1917). As regards other mammals, it is present in man (MACKLIN, 1921) and monkeys (HENCKEL, 1928A), and in the horse (LIMBERGER, 1926). Its significance is difficult to interpret, for owing to the function which it fulfils in providing a muscle-attachment it may be a secondary development.

AFFINITIES OF RODENTS AS SUGGESTED BY THE CHONDROCRANIUM.

The chondrocranium of the rabbit is one of the most "interesting" among the mammals, for it possesses almost all the features which an investigator of the mammalian skull might hope to find as points on which to hang a phylogenetic discussion. These points are the following :—

1. Remnants of the original premammalian side-wall of the skull, found by VOIT (1909) as isolated nodules of cartilage ;
2. Cartilaginous continuity between the anterior and posterior lamina transversalis of the nasal capsule by means of the paraseptal cartilages ;
3. An interorbital septum ;
4. Alæ hypochiasmaticæ ;
5. A mastoid process ;
6. A paracondylar process ;
7. Two pairs of hypoglossal foramina.

Of these features, 1, 2, 6 and 7 are certainly to be regarded as primitive, and the same is probably true of 3. The most striking fact when comparing the chondrocranium of the rabbit with those of other mammals is, on the one hand, its dissimilarity to that of the Insectivora (Tupaia, Erinaceus, Talpa, and Sorex), and on the other, its resemblance to that of the Primates.

None of the seven features enumerated above is present in the Insectivores, except the ala hypochiasmatica in Erinaceus and the paracondylar process in Talpa, each of which structures is reduced in these forms. On the other hand, features 3, 4, 5 and 6 are present in the Primates. These facts suggest the following conclusions :—

The possession of the seven features enumerated shows that the Rodents are a primitive type, which diverged at an early date from the main stem of mammalian descent. The absence of these features from the present-day Insectivores shows that they have undergone specialisation and have departed considerably from the conditions which presumably obtained in the primitive Insectivore type. The presence of four of these features in the Primate is evidence of the primitive nature of that group. It is probable, therefore, that the similarities between the chondrocrania of Rodents and Primates are evidence of a general affinity between these groups at an early time in the history of the Mammals, since when the Rodents have become specialised along the line of mastication which is peculiar to them, while the Primates have perfected their nervous system.

SUMMARY.

1. A series comprising 15 stages has been studied in the early development of the skull of the rabbit.

2. The parachordal cartilages arise as paired rudiments.

3. The hypophysial plate chondrifies as a ring surrounding the hypophysial foramen, independently of the parachordals and trabecula, to which it eventually becomes attached. The hypophysial plate corresponds, not to the polar cartilages of lower

vertebrates, but to the cartilage which develops between the polar cartilages in those forms.

4. The supraoccipital cartilages arise independently, and eventually meet one another dorsal to the brain in the tectum posterius. The supraoccipital cartilages fuse with the occipital arch.

5. The parietal plates chondrify independently and become fused with the supraoccipital cartilages.

6. The parieto-tectal cartilages of the nasal capsule arise in connexion with the dorsal edge of the nasal septum.

7. The paranasal cartilages arise independently, and eventually fuse with the parieto-tectal cartilages and the plana antorbitalia.

8. The planum antorbitale chondrifies independently and eventually fuses with the paranasal cartilage laterally, while medially it comes into contact with the nasal septum.

9. The ala orbitalis chondrifies independently, and becomes connected with the central stem by means of the postoptic and preoptic roots, with the nasal capsule by the sphenethmoid commissure, and with the auditory capsule by the orbitocapsular commissure. The latter becomes connected with the parietal plates by means of the orbito-parietal commissure.

10. The ala hypochiasmatica chondrifies independently and becomes joined on to the preoptic root of the ala orbitalis and the central stem.

11. The canalicular part of the auditory capsule chondrifies independently, and eventually becomes attached to the parachordal plate by means of the basivestibular commissure.

12. The cochlear part of the auditory capsule chondrifies in connexion with the canalicular part and independently of the parachordal plate, to which it eventually becomes attached when the basicochlear fissure becomes obliterated.

13. The alicochlear commissure develops from the cochlear capsule towards the ala temporalis.

14. The basihyal cartilage shows evidence of a paired origin.

15. The laterohyal, stylohyal, and ceratohyal cartilages arise independently of one another.

16. The stapes chondrifies in the mouth of the fenestra ovalis but independently of the wall of the auditory capsule.

17. The skeleton of the 3rd visceral arch is represented by the posterior cornua of the hyoid and the thyrohyal cartilages.

18. The thyroid cartilages each possess a pair of wings directed ventrally towards their fellow of the opposite side, and present evidence of their derivation from the skeletal elements of the 4th and 5th visceral arches.

19. A pair of hypothyroid cartilages is present in the 5th visceral arch.

20. The mammalian chondrocranium is discussed in its embryological and in its morphological aspect.

21. The interorbital septum in the rabbit is probably a primitive character.

22. VOIT's view is supported that the paracondylar process represents the transverse process of a vertebra.

23 Attention is called to the dissimilarities between the chondrocrania of Rodents and Insectivores and to the resemblances between those of Rodents and Primates.

24. It is concluded that the chondrocranium of the rabbit is primitive in respect of several features.

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EXPLANATION OF LETTERING ON PLATES.

a., auditory capsule.
a.a.c., arrow passed through aqueductus cochleæ.
a.a.i., arteria alveolaris inferior.
a.b.o., arteria bulbo-orbitalis.
a.c., arytenoid cartilage.
a.c.c., alicochlear commissure.
a.c.n., arteria ciliaris longa nasalis.
a.c.t., arteria ciliaris longa temporalis.
a.c.u., anterior cornu of hyoid.
a.f., arteria frontalis.
a.f.j., arrow passed through foramen jugulare.
a.f.r., arrow passed through fenestra rotunda.
a.h., ala hypochiasmatica.
a.i.o., arteria infraorbitalis.
a.l., arteria lachrymalis.
a.l.i., arteria lingualis.
a.l.n., anterior laryngeal nerve.
a.m.a., arteria meningea anterior.
a.m.e., arteria maxillaris externa.
a.m.m., arteria meningea media.
a.m.o., arteria maxillo-orbitalis.
a.o., ala orbitalis.
a.o.c., arteria occipitalis.
a.o.e., arteria ophthalmica externa.
a.o.i., arteria ophthalmica interna.
a.p.o., arteria pterygo-orbitalis.
a.q.c., aqueductus cochleæ.
a.s.t., arteria stapedialis (remnant).
a.t., arteria tympanica.
a.v., atlas vertebra.
b.c.f., basicochlear fissure.
b.c.s., basicochlear sulcus.
b.h., basihyal cartilage.
b.t., basitrabecular process.
b.v.c., basivestibular commissure.
*c.*1, centrum of 1st vertebra.
*c.*2, centrum of 2nd vertebra.
*c.*3, centrum of 3rd vertebra.
c.c., canalicular capsule.
c.c.a., common carotid artery.
c.h., ceratohyal cartilage.
c.h.t., chorda tympani.
c.i., carotid incisure.
c.o.c., cochlear capsule.
c.o.p., orbitocapsular commissure.
c.p., orbitoparietal commissure.
c.r.c., cricoid cartilage.
c.r.p., crista parotica.
c.s.e., sphenethmoid commissure.
c.t., crista transversa.
d., depressor nerve.
d.p., deep petrosal nerve.
d.s., dorsum sellæ.
e.c., external carotid artery.
*et.*1, 1st ethmoturbinal.
f.a., foramen acusticum.
f.b., fenestra basicranialis.
f.c., foramen caroticum.
f.c.h., fossa chiasmatica.
f.e., foramen epiphaniale.
f.e.n., foramen endolymphaticum.
f.f.h., foramina hypoglossi.
f.h., foramen hypophyeos.
f.j., foramen jugulare.
f.m., foramen magnum.
f.o., foramen opticum.
f.o.c., fissura occipitocapsularis.
f.o.i., fissura occipitocapsularis inferior.
f.o.n., fissura orbitonasalis.
f.o.s., fissura occipitocapsularis superior.
f.o.v., fenestra ovalis.
f.p., foramen perilymphaticum.
f.p.h., foramen hypoglossi posterius.
f.r., fenestra rotunda.
f.s., fenestra superior.
f.s.a., fossa subarcuata.
g.c., ganglion ciliare.
g.g., ganglion geniculatum facialis.
g.j., ganglion jugulare vagi.
g.n., ganglion nodosum vagi.
g.o., ganglion oticum.
g.p., ganglion petrosum glossopharyngei.
g.s., ganglion semilunare trigemini.
g.s.p., greater superficial petrosal nerve.
g.s.s., ganglion sympathicum cervicale superius.
h.s., hypophysial stalk.
h.t., hypothyroid cartilage.
i., incus.
i.c., internal carotid artery.
i.o.s., interorbital septum.

l.a., lamina ascendens alæ temporalis.
l.c.t., ramus lingualis glossopharyngei + chorda tympani.
l.h., laterohyal cartilage.
l.p., lamina pterygoidea alæ temporalis.
l.s.p., lesser superficial petrosal nerve.
m., malleus.
M.c., Meckel's cartilage.
m.o.i., inferior oblique muscle.
m.o.s., superior oblique muscle.
m.p., mastoid process (cut).
m.r.a., internal rectus muscle.
m.r.b., retractor bulbi muscle.
m.r.e., external rectus muscle.
m.r.i., inferior rectus muscle.
m.r.s., superior rectus muscle.
n., notochord.
*n.a.*1, neural arch of 1st vertebra.
*n.a.*2., neural arch of 2nd vertebra.
*n.a.*3., neural arch of 3rd vertebra.
n.a.b., abducens nerve.
n.a.h., notch for anterior hypoglossus root.
n.f., facial nerve.
n.h., hypoglossus nerve.
n.o., oculomotor nerve.
n.s., nasal septum.
n.s.a., spinal accessory nerve.
n.t., trochlear nerve.
o.a., occipital arch.
o.c.c., orbitocapsular commissure.
o.n., optic nerve.
o.p., odontoid peg.
p., parachordal or basal plate.
p.a., anterior parachordal.
p.a.l., processus alaris.
p.c., hypophysial cartilage.
p.c.c., paracondylar process (cut).
p.c.p., paracondylar process.
p.c.u., posterior cornu of hyoid.
p.l., planum antorbitale.
p.n., paranasal cartilage.
p.o., postoptic root of ala orbitalis.
p.p., posterior parachordal.
p.p.l., parietal plate.
p.r., preoptic root of ala orbitalis.
p.r.c., processus recessus.
p.s., paraseptal cartilage.
p.t., pterygoid cartilage.
p.t.c., parietotectal cartilage.
p.x., polar cartilage.
r., rib of atlas vertebra.
r.a.c., rudiment of alicochlear commissure.
r.a.f., ramus auricularis facialis.
r.a.t., ramus auriculotemporalis trigemini.
r.b., ramus buccalis trigemini.
R.c., Reichert's cartilage.
r.c.c., rudiment of canalicular capsule.
r.c.o., rudiment of cochlear capsule.
r.d., ramus descendens hypoglossi.
r.d.i., ramus dentalis inferior trigemini.
r.e., ramus ethmoidalis trigemini.
r.f., ramus frontalis trigemini.
r.l., ramus lingualis glossopharyngei.
r.l.c., radix longa ciliaris.
r.l.n., recurrent laryngeal nerve.
r.l.t., rudiment of lamina transversalis anterior.
r.m., ramus mylohyoideus trigemini.
r.m.d., ramus mandibularis trigemini.
r.m.x., ramus maxillaris trigemini.
r.n.c., ramus nasociliaris trigemini.
r.n.s., rudiment of nasal septum.
r.o.a., rudiment of occipital arch.
r.p.a., rudiment of anterior parachordal.
r.p.c., rudiment of paranasal cartilage.
r.p.g., ramus pharyngeus glossopharyngei.
r.p.l., rudiment of planum antorbitale.
r.p.o., rudiment of postoptic root of ala orbitalis
r.p.p., rudiment of posterior parachordal.
r.p.t., rudiment of parietotectal cartilage.
r.s.a., recessus supra-alaris.
r.t., rudiment of trabecular region of central stem.
s., stapes.
s.c., cervical sympathetic nerve trunk.
s.c.c., spheno-cochlear commissure.
s.d., sulcus dorsalis.
s.f.c., suprafacial commissure.
s.h., stylohyal cartilage.
s.l.a., sulcus lateralis anterior.
s.l.p., sulcus lateralis posterior.
s.o., supraoccipital cartilage.
s.p., styloid process (cut).
s.t., sella turcica.
t., trabecular region of central stem.

t.c., thyroid cartilage.
t.c.a., anterior wing of thyroid cartilage.
t.c.p., posterior wing of thyroid cartilage.
t.h., thyrohyal cartilage.
t.p., tectum posterius.
t.s., tuberculum sellæ.
t.t., trabecula cranii.
V.n., Vidian nerve.

Description of Plates 35-43.

All figures are of *Lepus cuniculus*.

Plate 35.

Fig. 1. Dorsal view of the skull and anterior cervical vertebræ at stage 1. × 17.
Fig. 2. View from the left side of the skull and anterior cervical vertebræ at stage 2. × 17.
Fig. 3. Dorsal view of the skull and anterior cervical vertebræ at stage 2. × 17.
Fig. 4. View from the left side of the skull and anterior cervical vertebræ at stage 3. × 17.
Fig. 5. Dorsal view of the skull and anterior cervical vertebræ at stage 3. × 17.
Fig. 6. View from the left side of the skull and anterior cervical vertebræ at stage 4. × 17.
Fig. 7. Dorsal view of the skull and anterior cervical vertebræ at stage 4. × 17.
Fig. 8. View from the left side of the skull and anterior cervical vertebræ at stage 5. × 17.
Fig. 9. Dorsal view of the skull and anterior cervical vertebræ at stage 5. × 17.

Plate 36.

Fig. 10. View from the left side of the skull at stage 6. × 15.
Fig. 11. Ventral view of the skull at stage 6. × 15.
Fig. 12. Dorsal view of the skull at stage 6. × 15.
Fig. 13. View from the left side of the skull at stage 7. × 15.
Fig. 14. Dorsal view of the skull at stage 7. × 15.
Fig. 15. View from the left side of the skull at stage 8. × 15.
Fig. 16. Oblique view from the left side and behind of the posterior portion of the skull at stage 8. × 15.

Plate 37.

Fig. 17. Dorsal view of the skull at stage 8. × 18.
Fig. 18. Ventral view of the skull at stage 8. × 18.
Fig. 19. View from the left side of the skull at stage 9. × 18.

Plate 38.

Fig. 20. Dorsal view of the skull at stage 9. × 16.
Fig. 21. View from the left side of the skull at stage 10. × 16.
Fig. 22. Dorsal view of the skull at stage 10. × 16.

Plate 39.

Fig. 23. Ventral view of the skull at stage 11. × 15.
Fig. 24. View from the left side of the skull at stage 12. × 15.
Fig. 24a. Oblique view from the left and ventral sides of the splanchnocranium at stage 12. × 15.
Fig. 25. Dorsal view of the skull at stage 12. × 15.

PLATE 40.

FIG. 26. View from the left side of the skull at stage 13. × 12.
FIG. 27. Dorsal view of the skull at stage 13. × 12.
FIG. 28. Ventral view of the skull at stage 13. × 12.

PLATE 41.

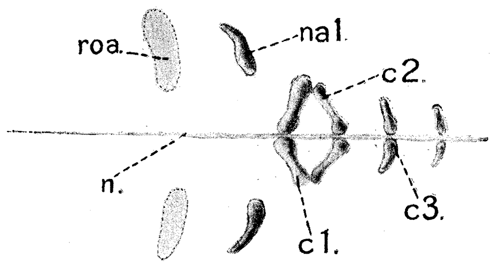
FIG. 29. View from the left side of the model reconstructed from the skull at stage 14. × 14.
FIG. 30. Dorsal view of the model reconstructed from the skull at stage 14. × 17.

PLATE 42.

FIG. 31. Ventral view of the foramen perilymphaticum and associated structures at stage 15. × 17.
FIG. 32. Median view of the auditory capsule and associated structures at stage 15. × 17.

PLATE 43.

FIG. 33. Reconstruction of the relations of the cartilages to the arteries and nerves at stage 14. Cartilage is evenly stippled, arteries ribbed, ventral nerve-roots black, other nerves dotted.



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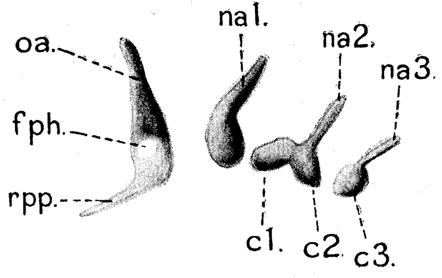

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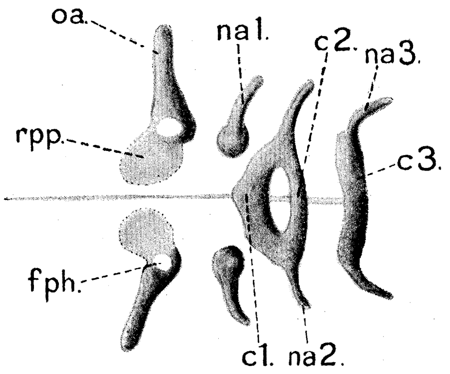

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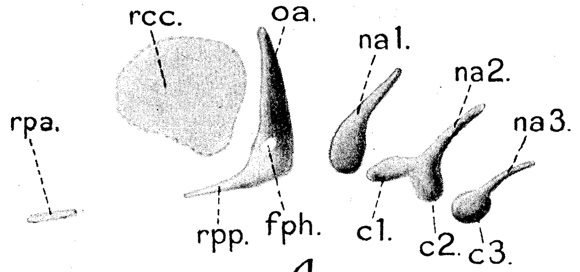

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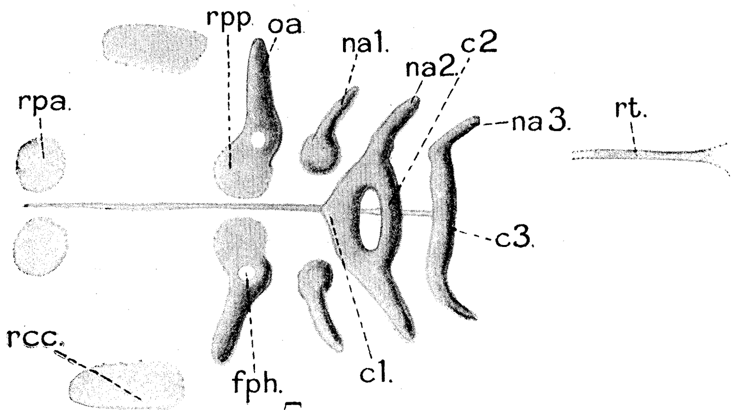

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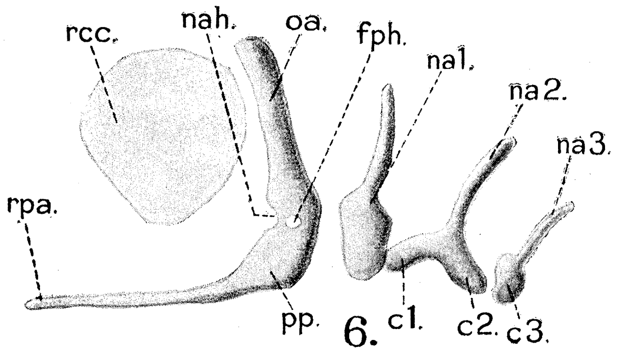

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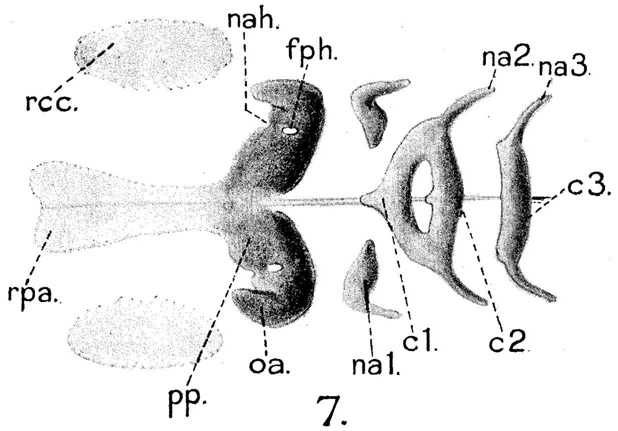

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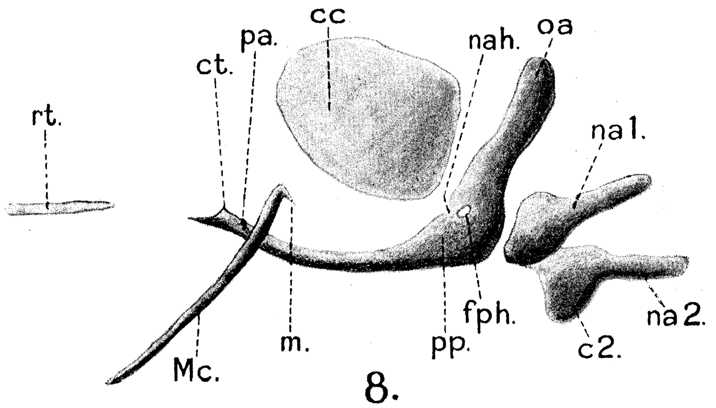

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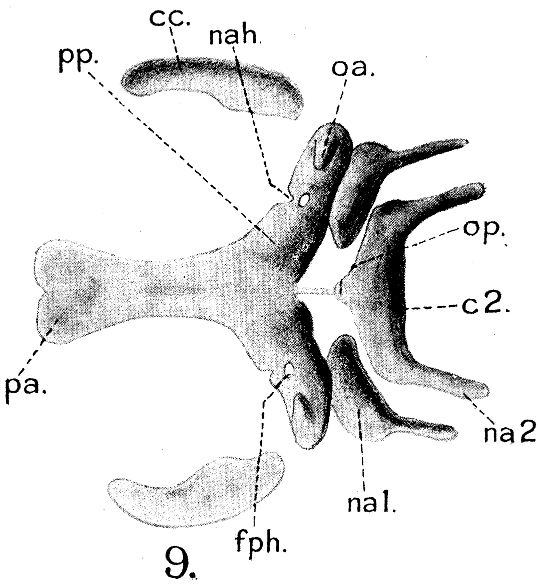

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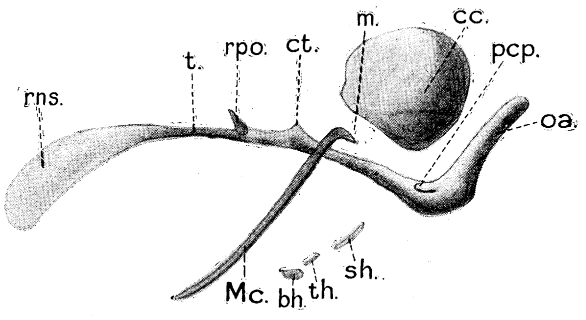

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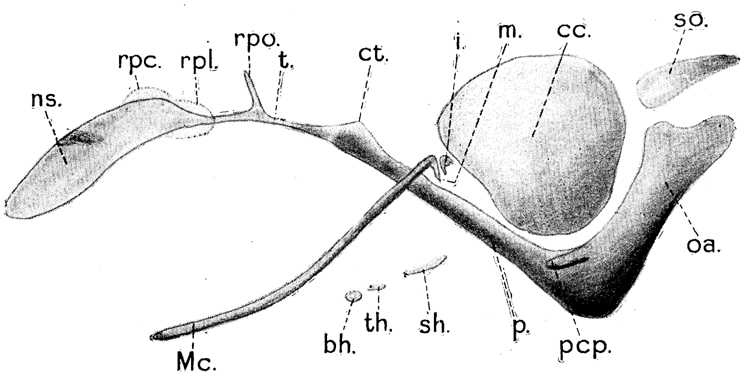

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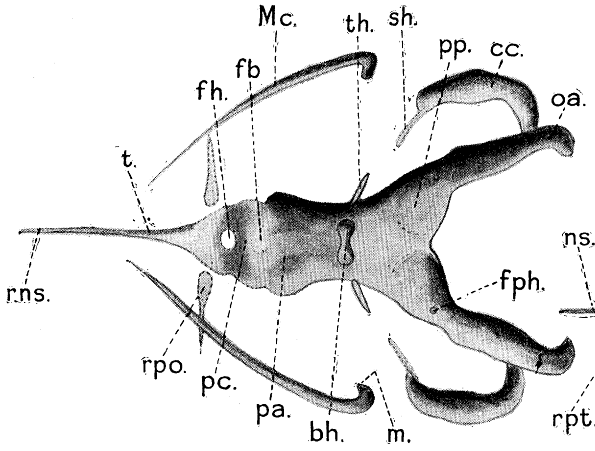

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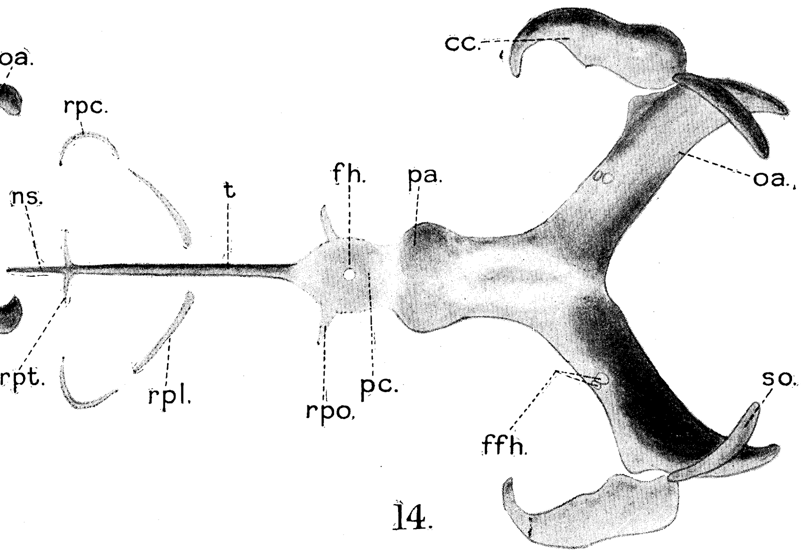

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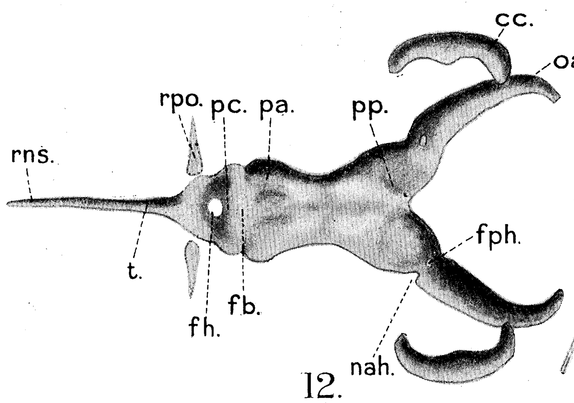

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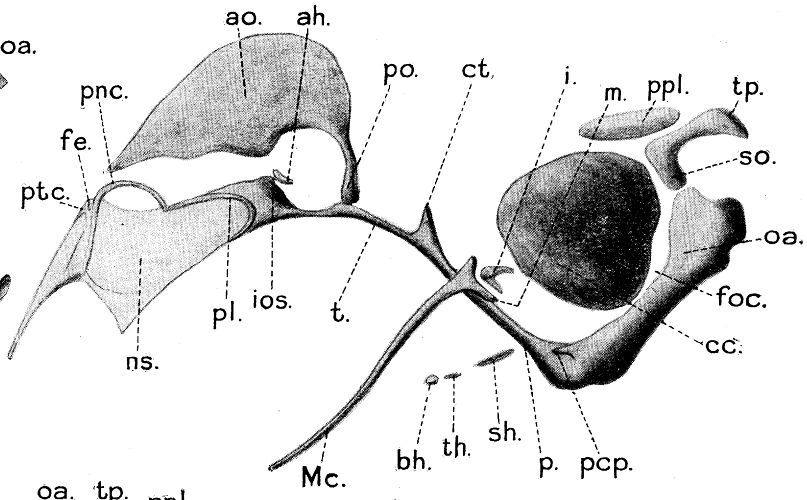

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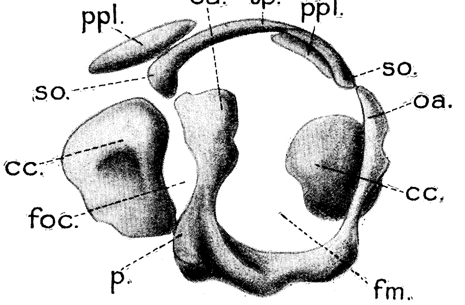

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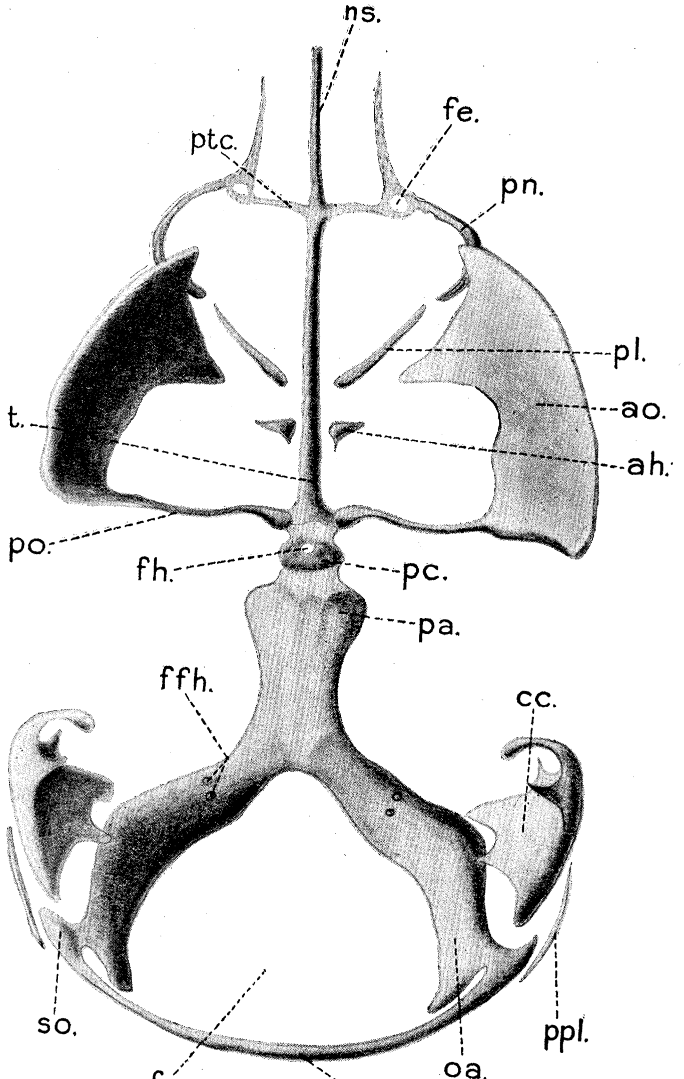

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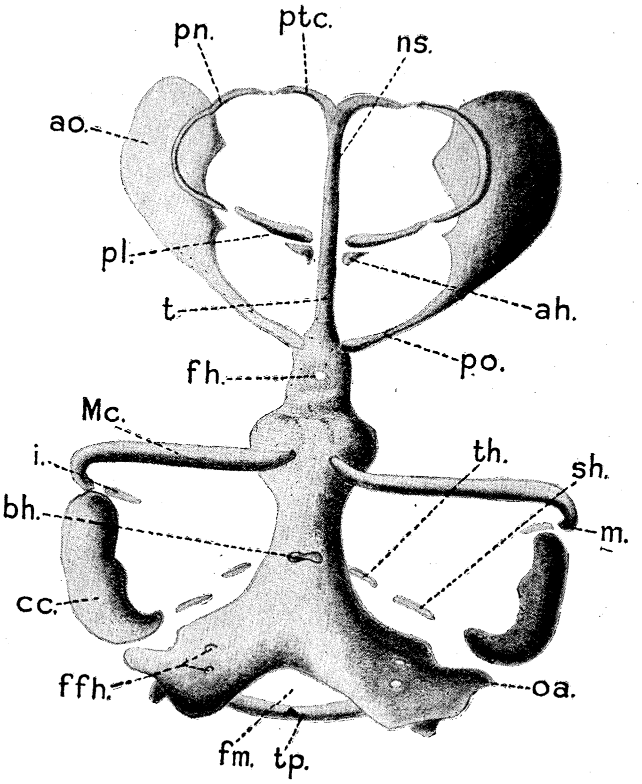

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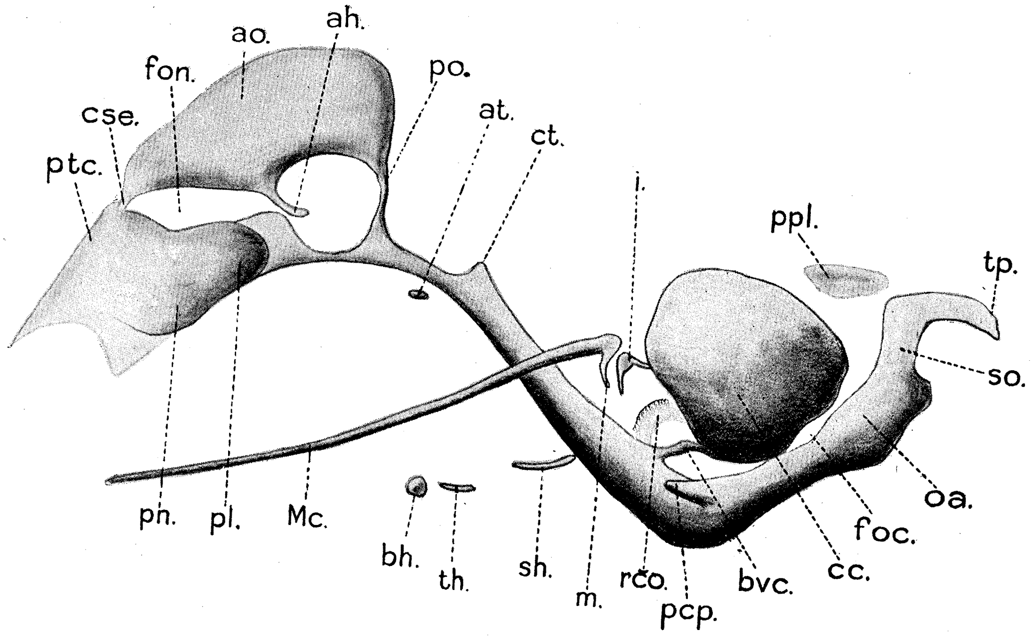

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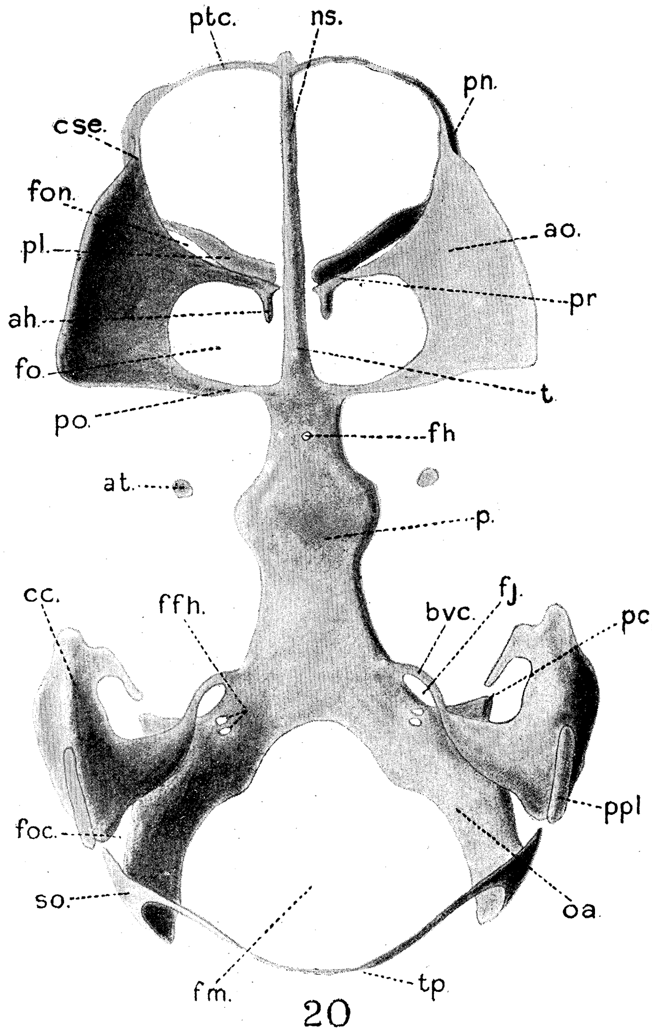

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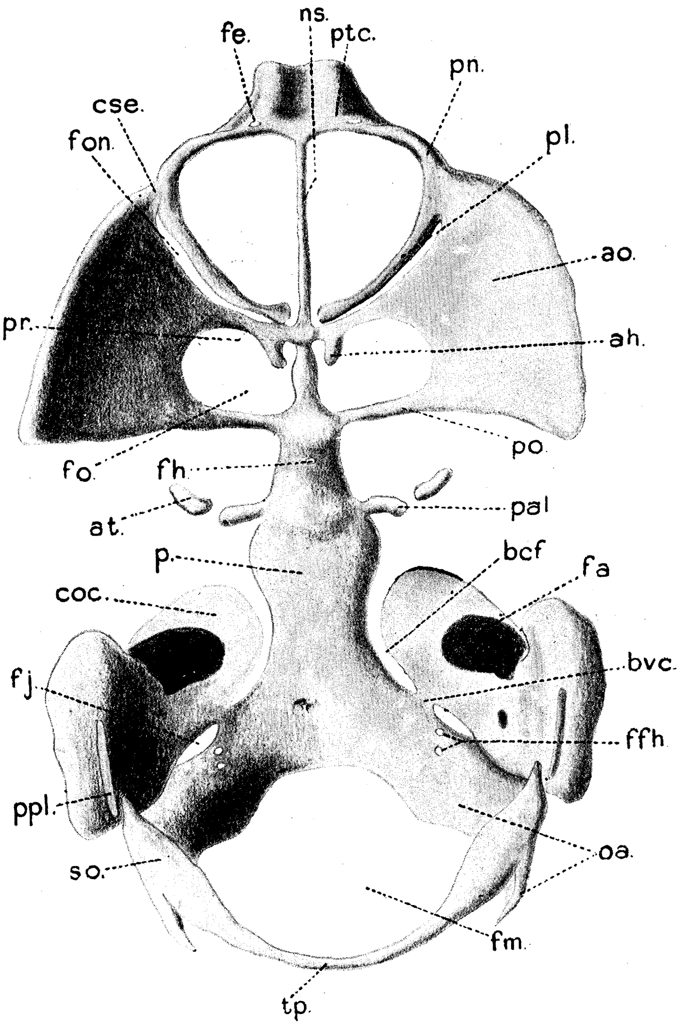

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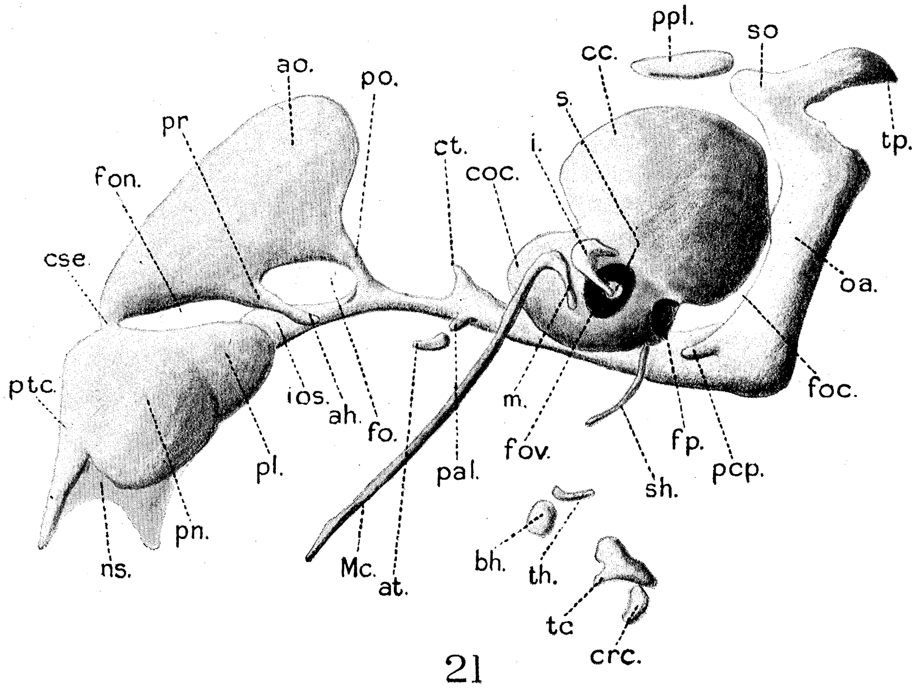

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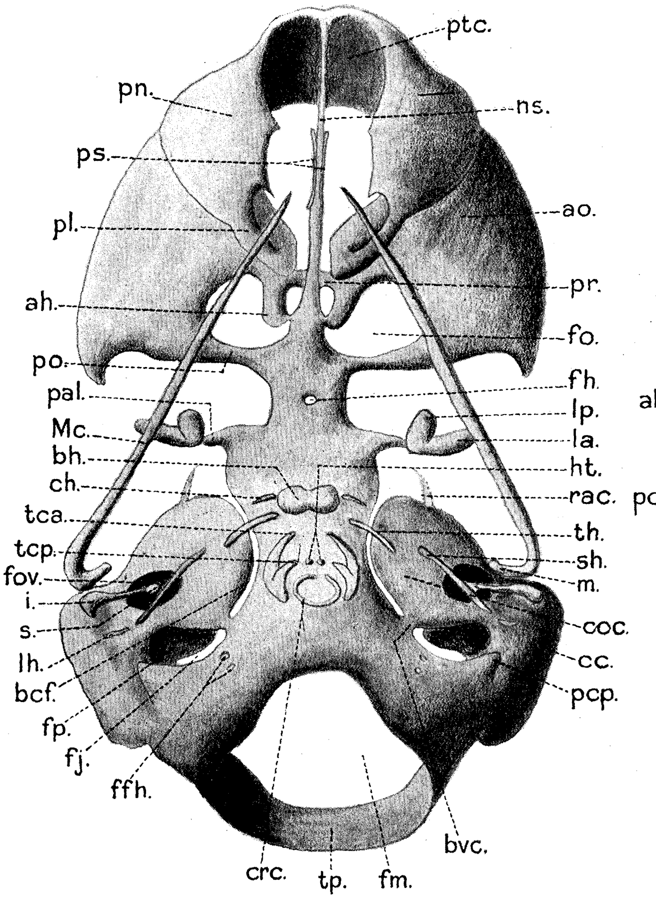

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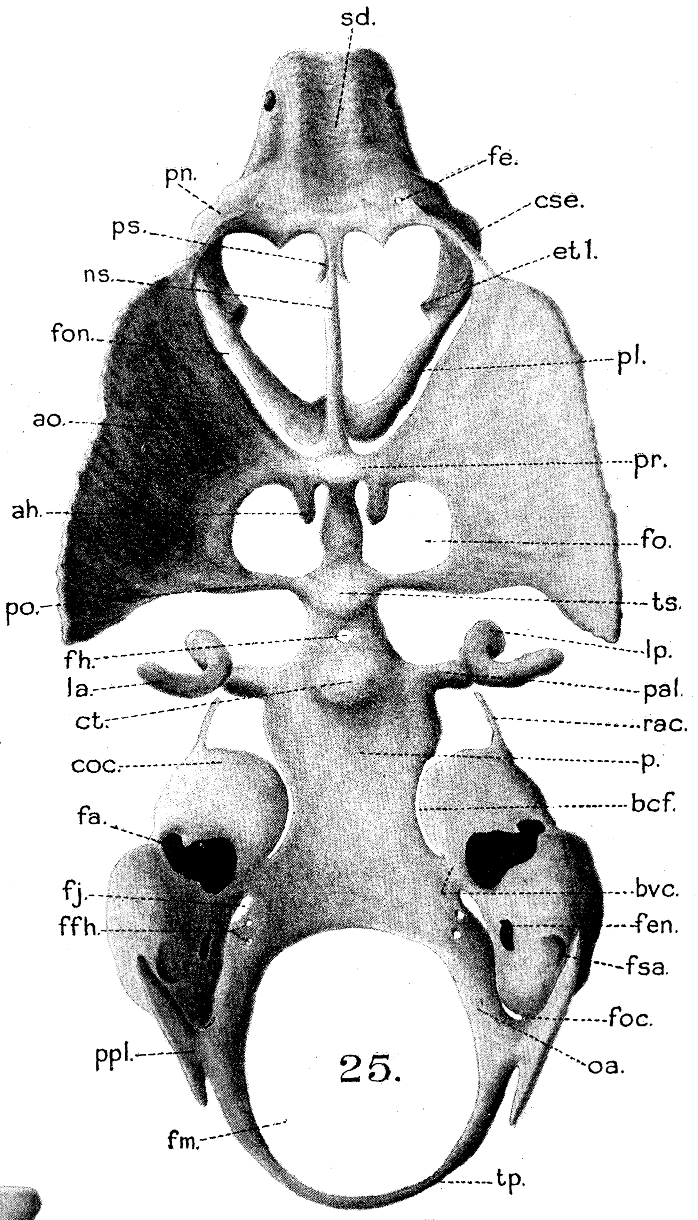

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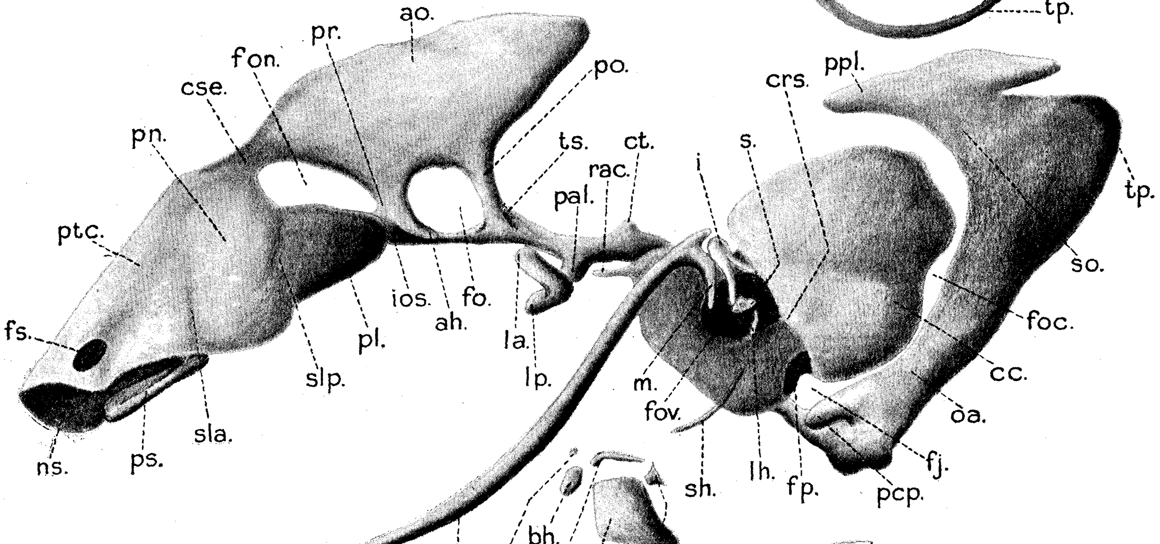

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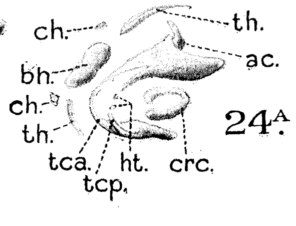

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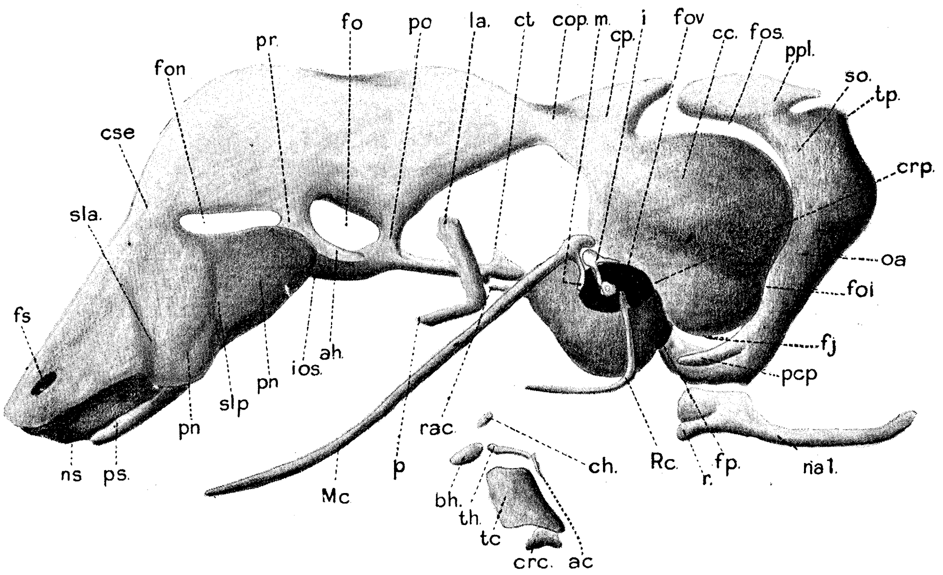

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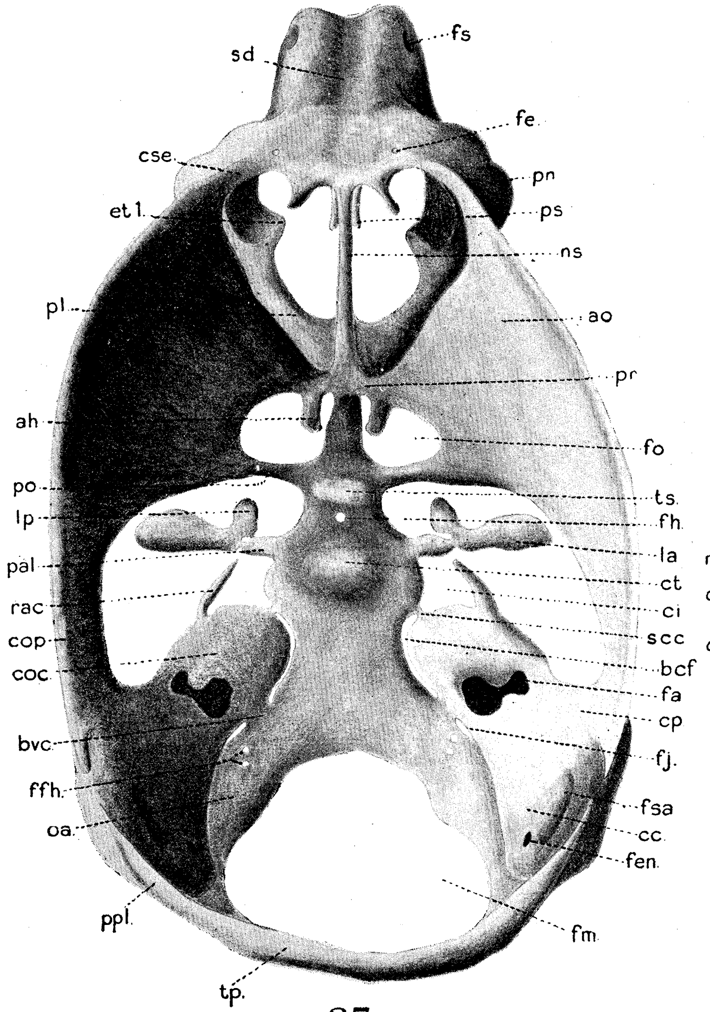

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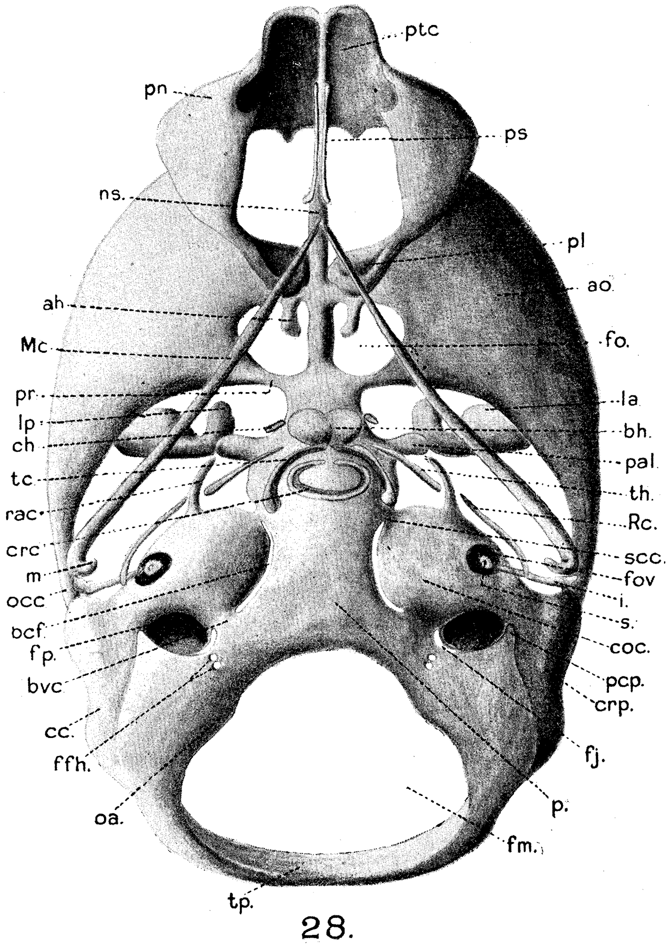

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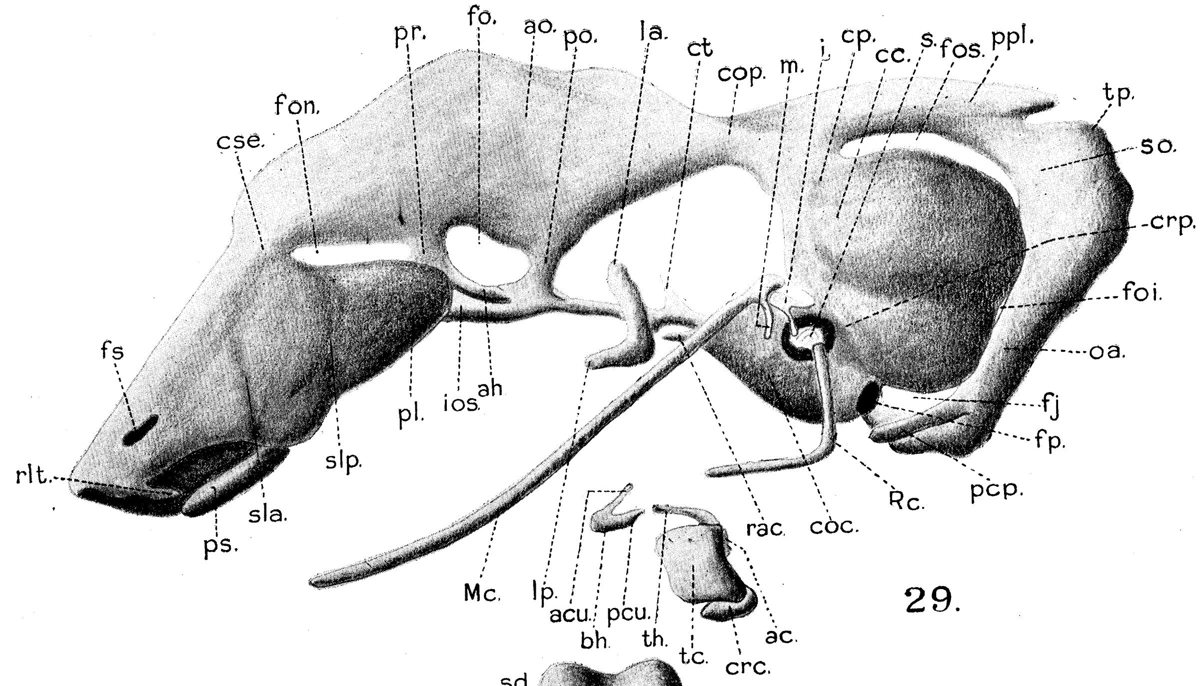

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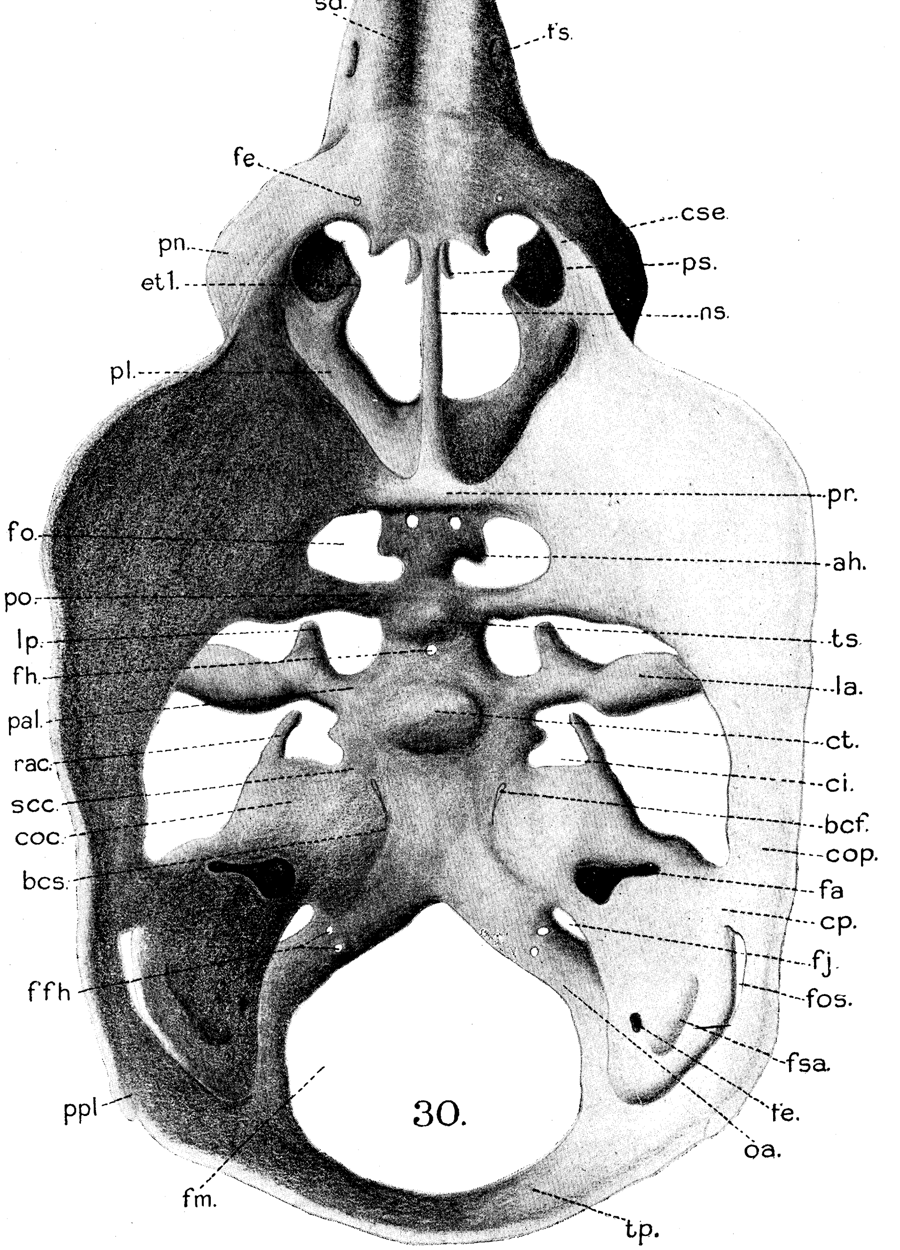

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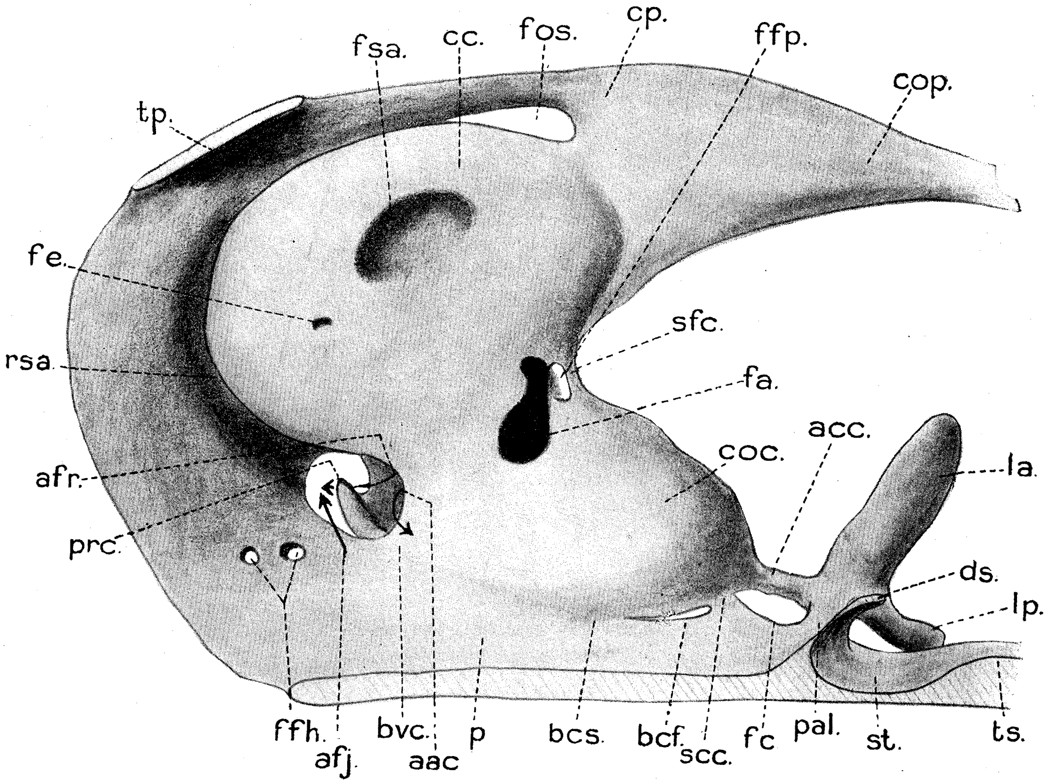

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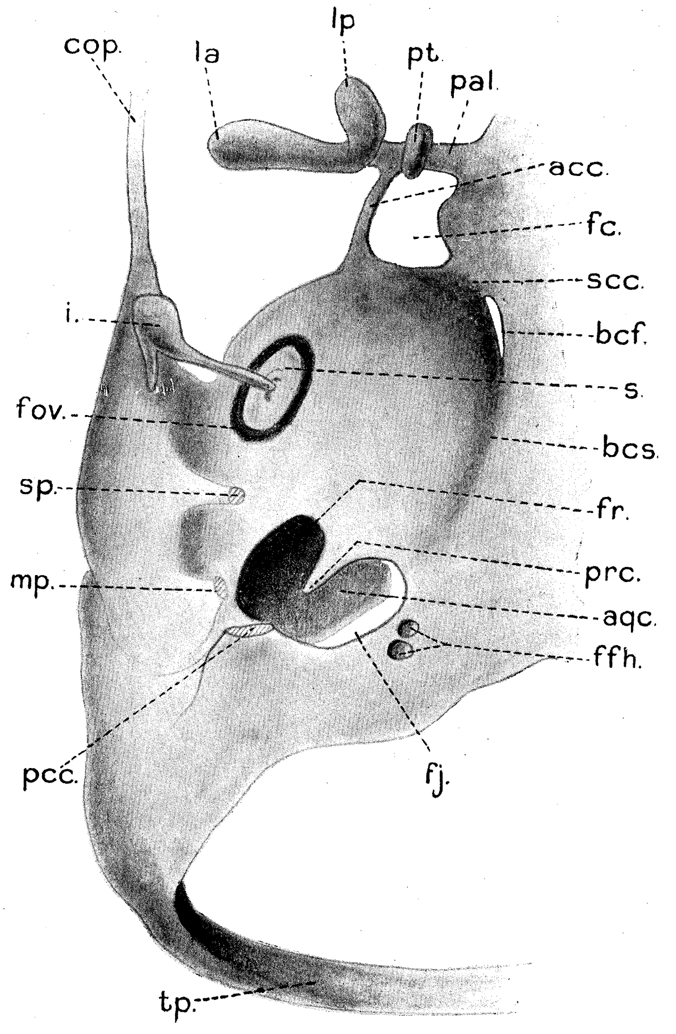

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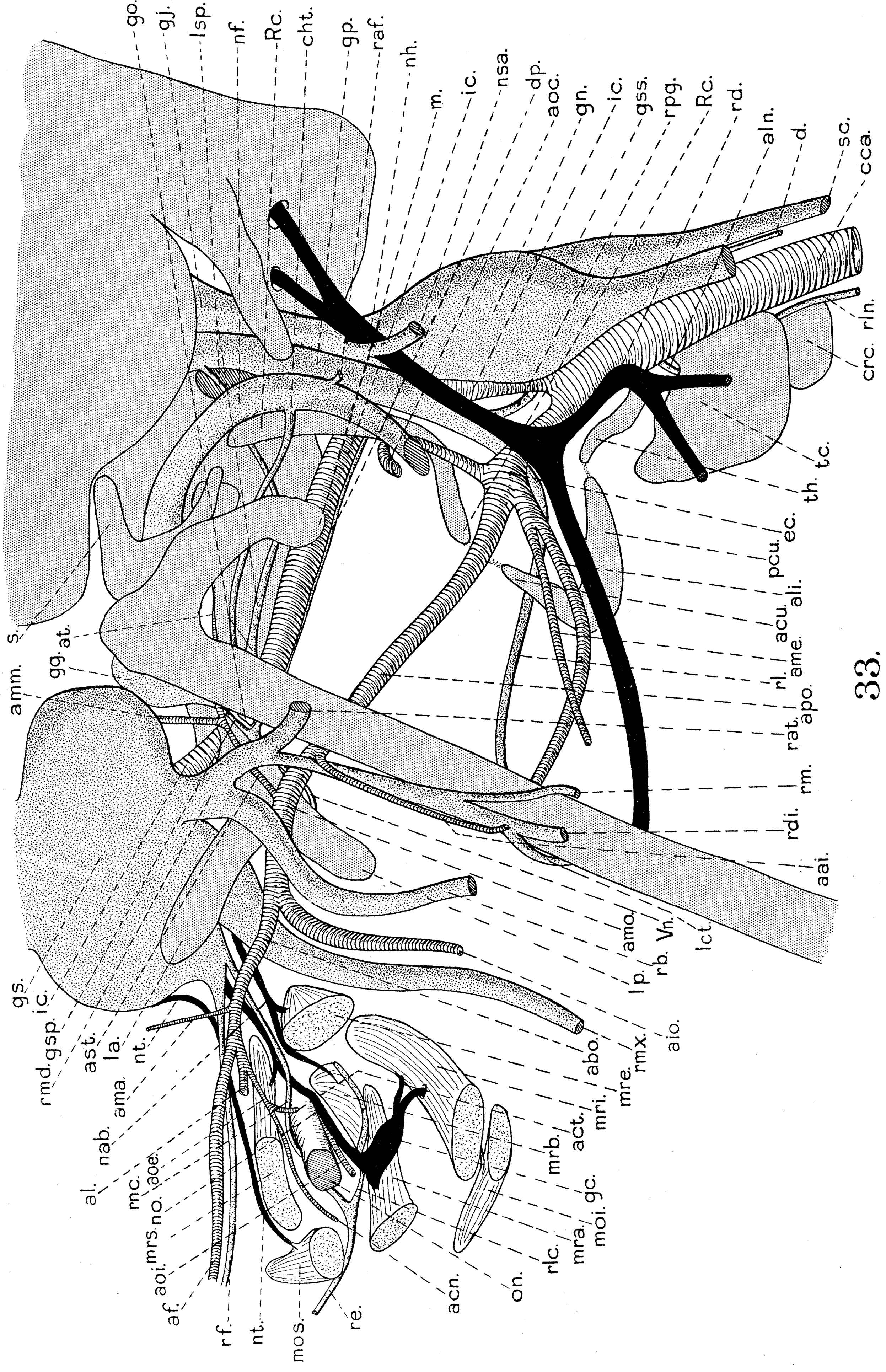

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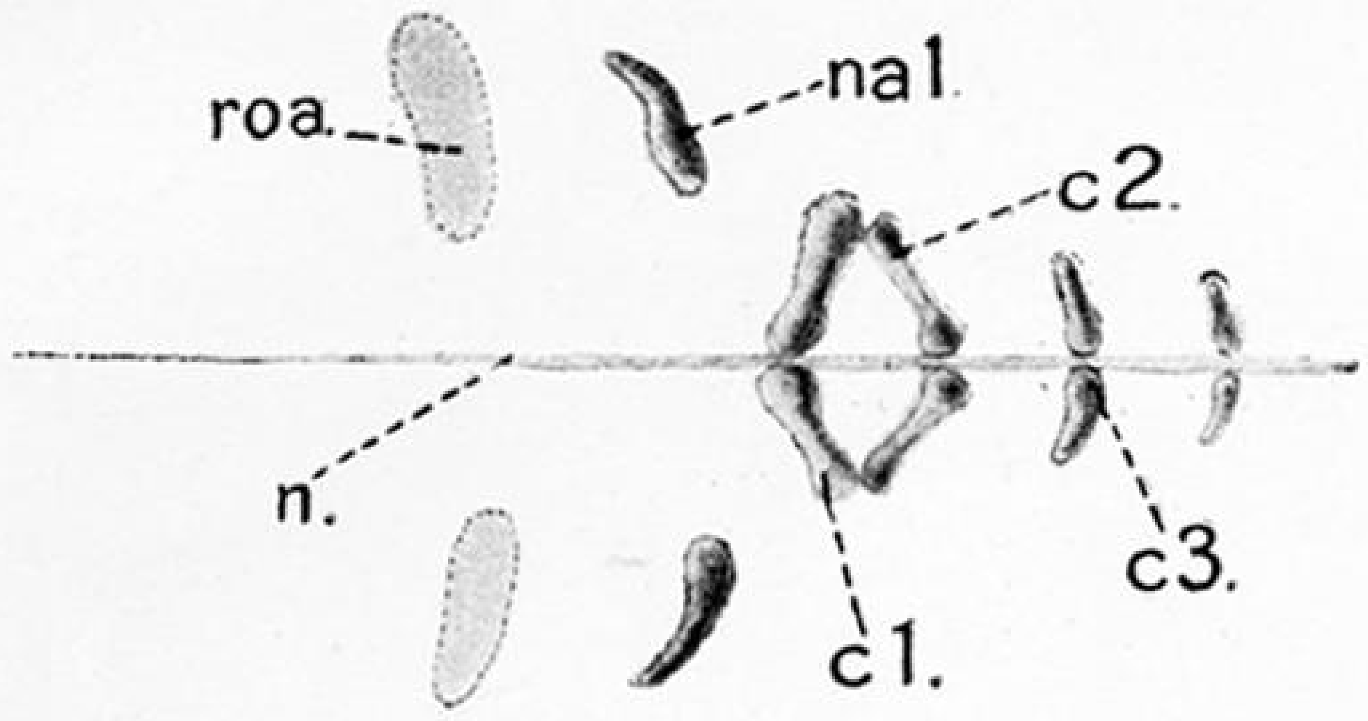
J. H. Woodger & G. R. de Beer del.



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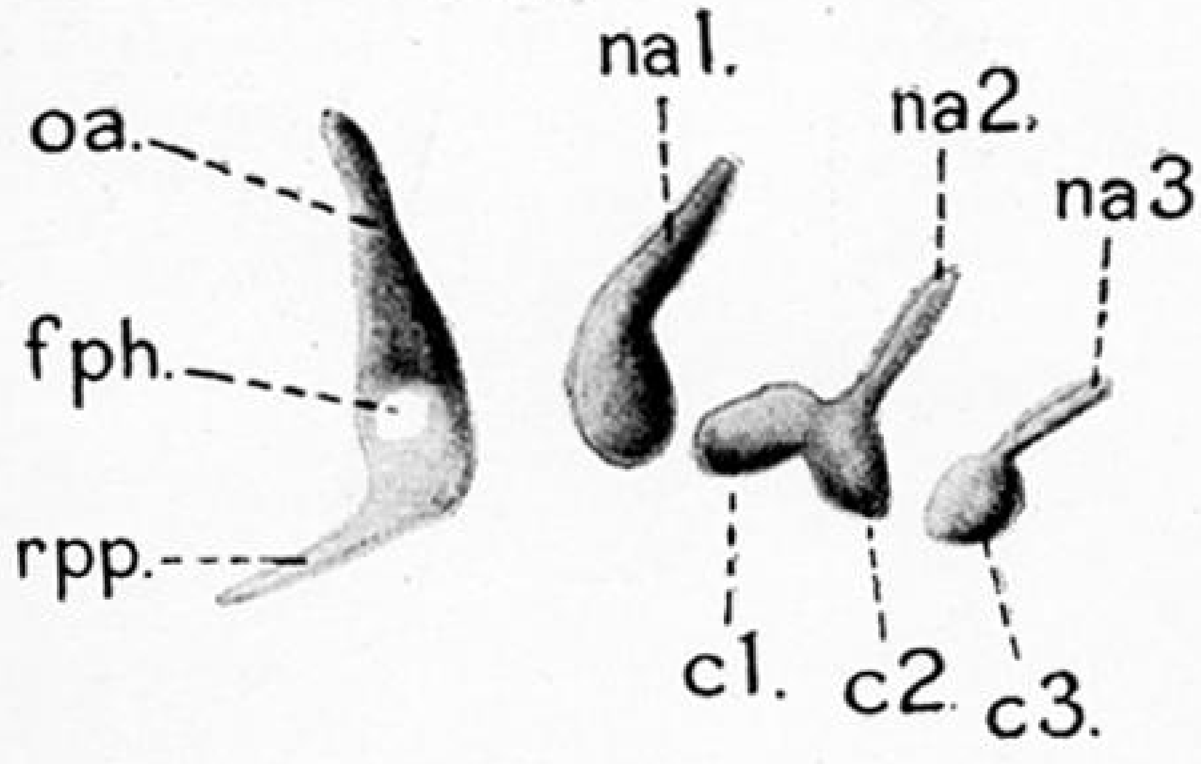

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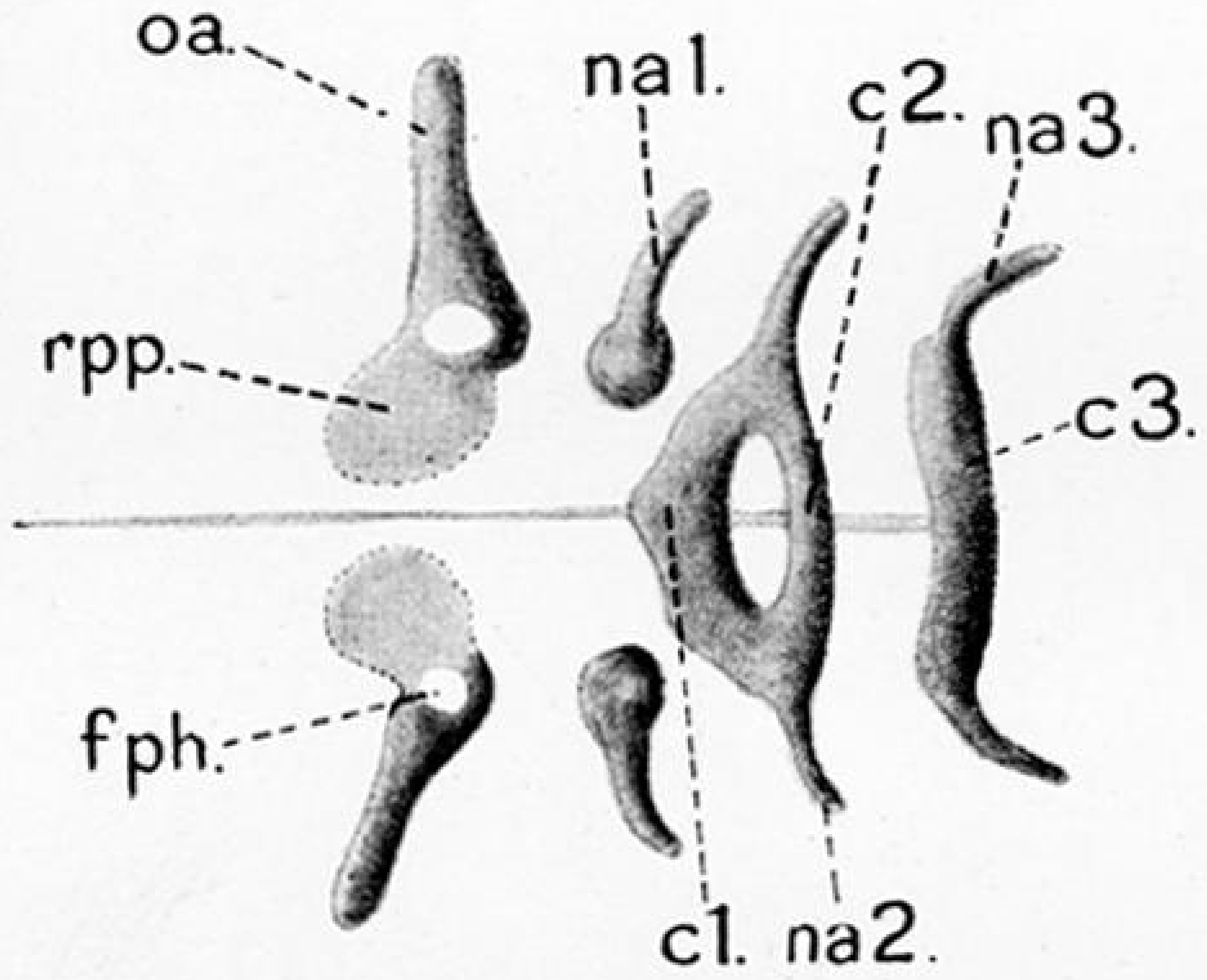

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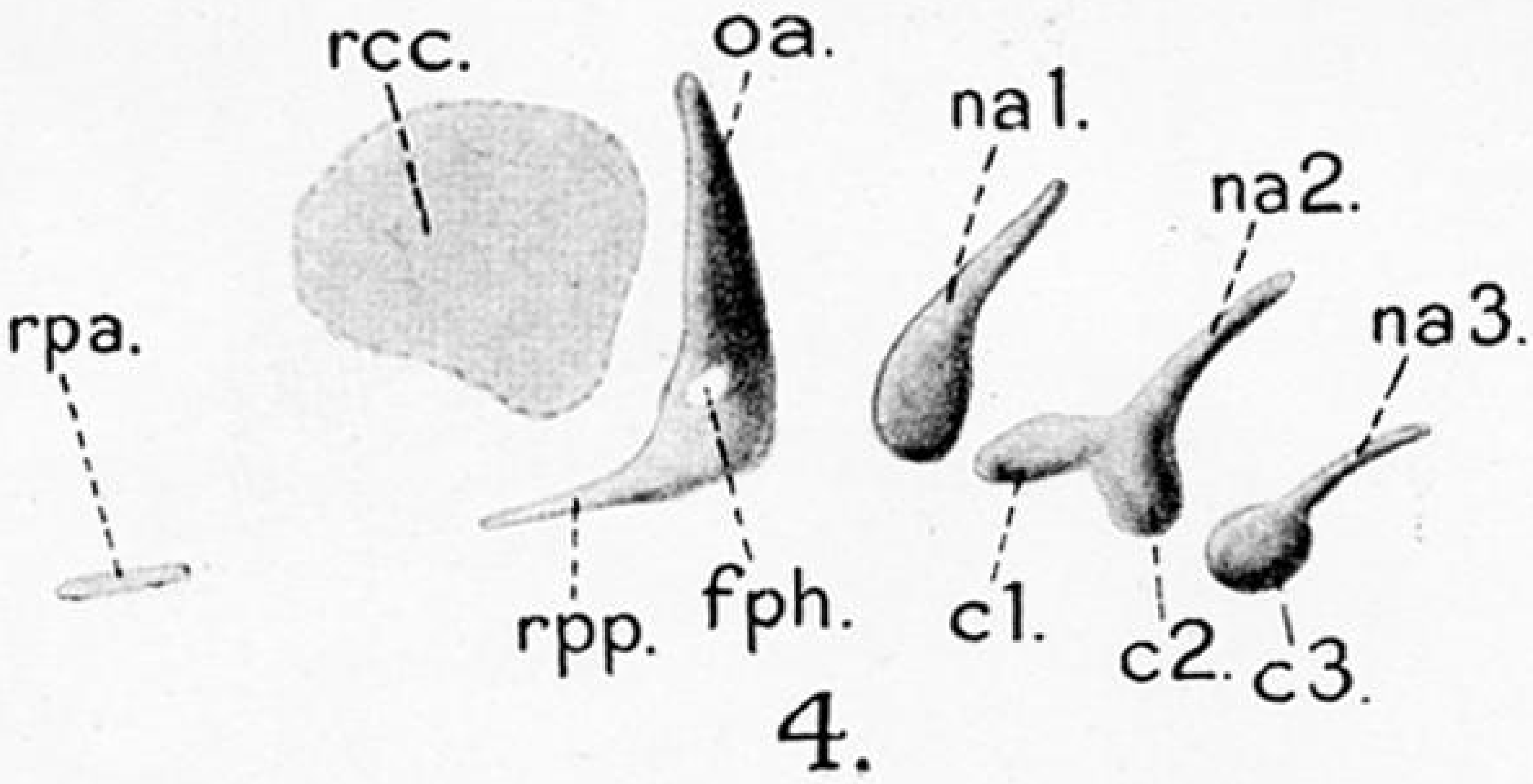

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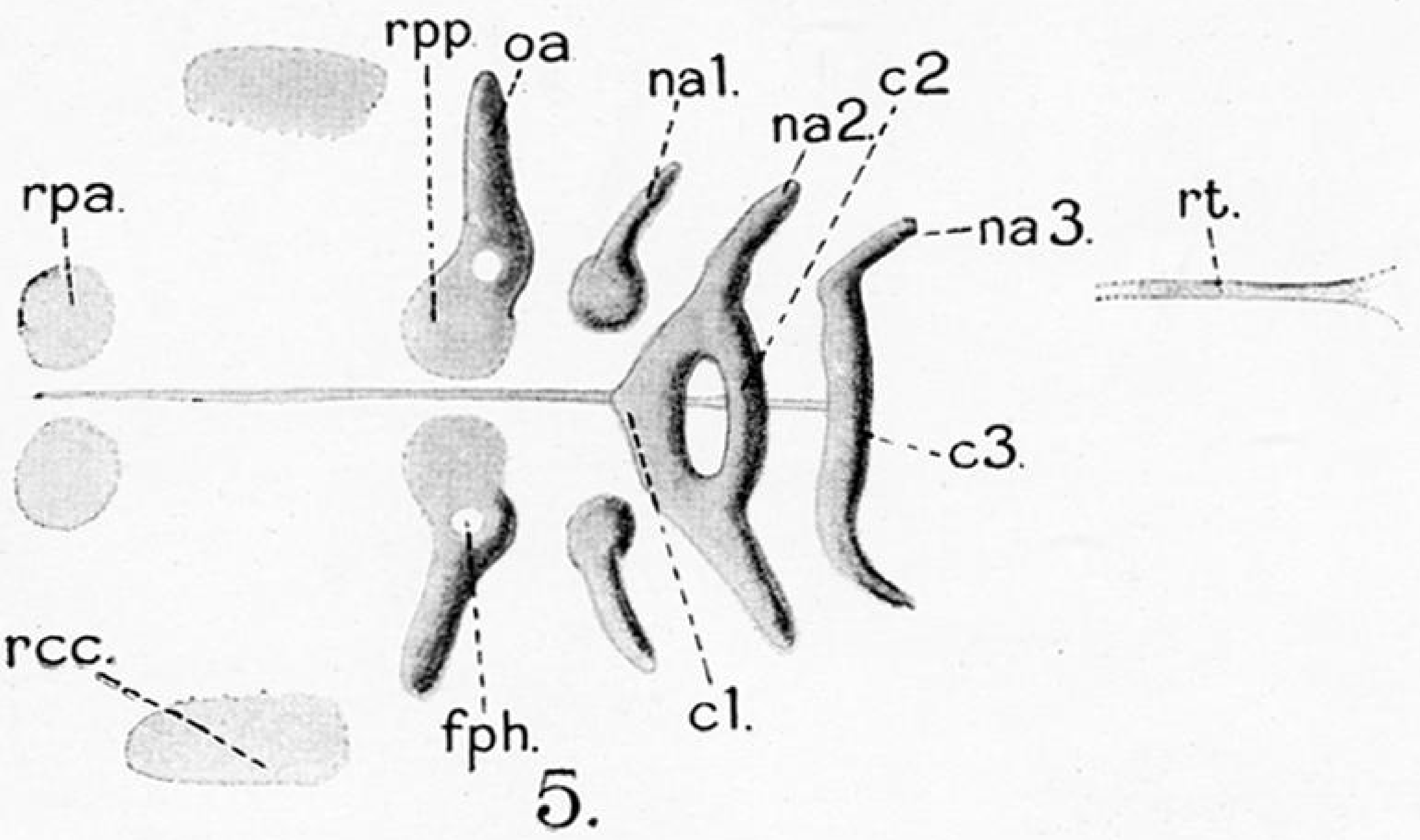

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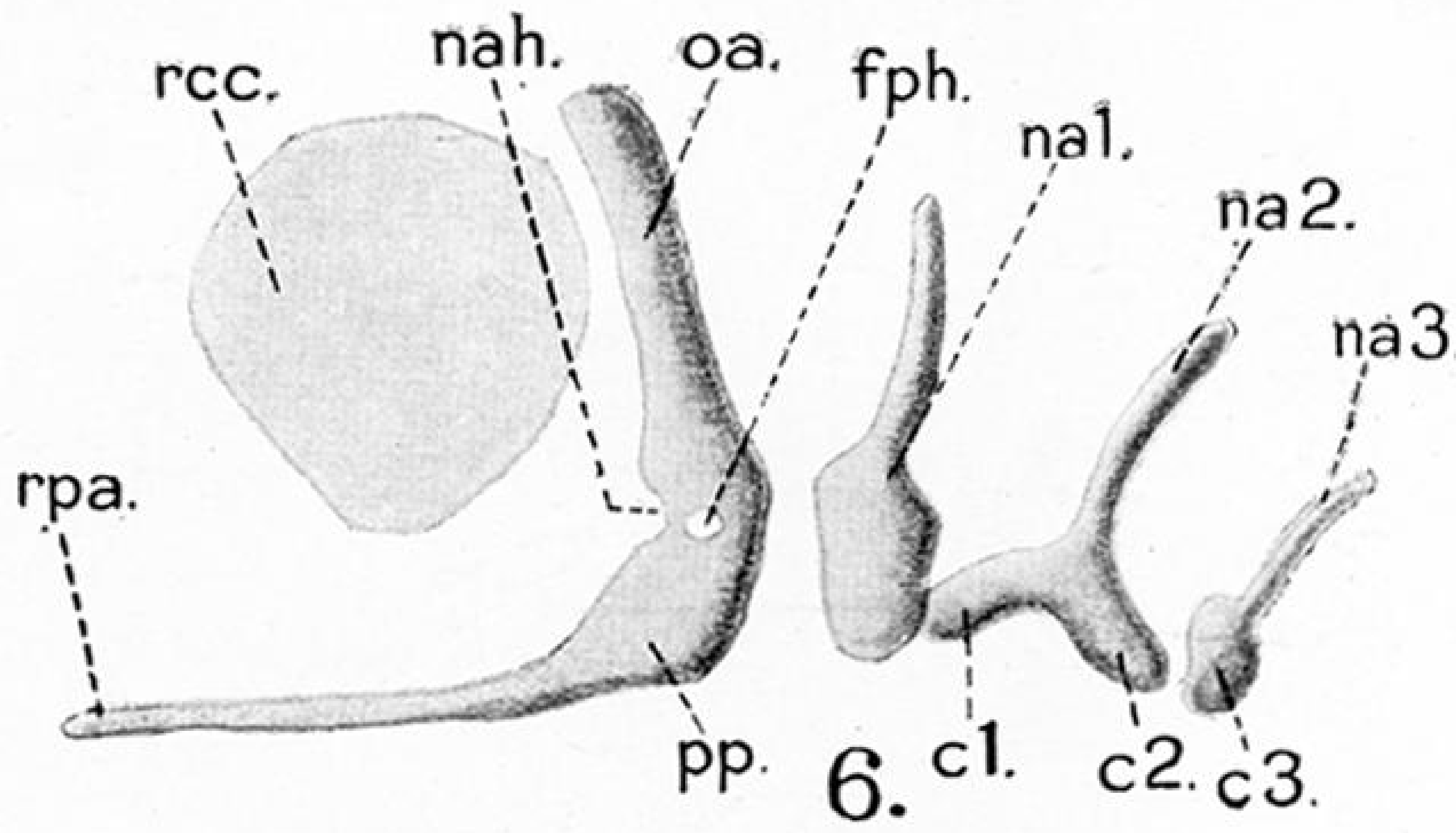

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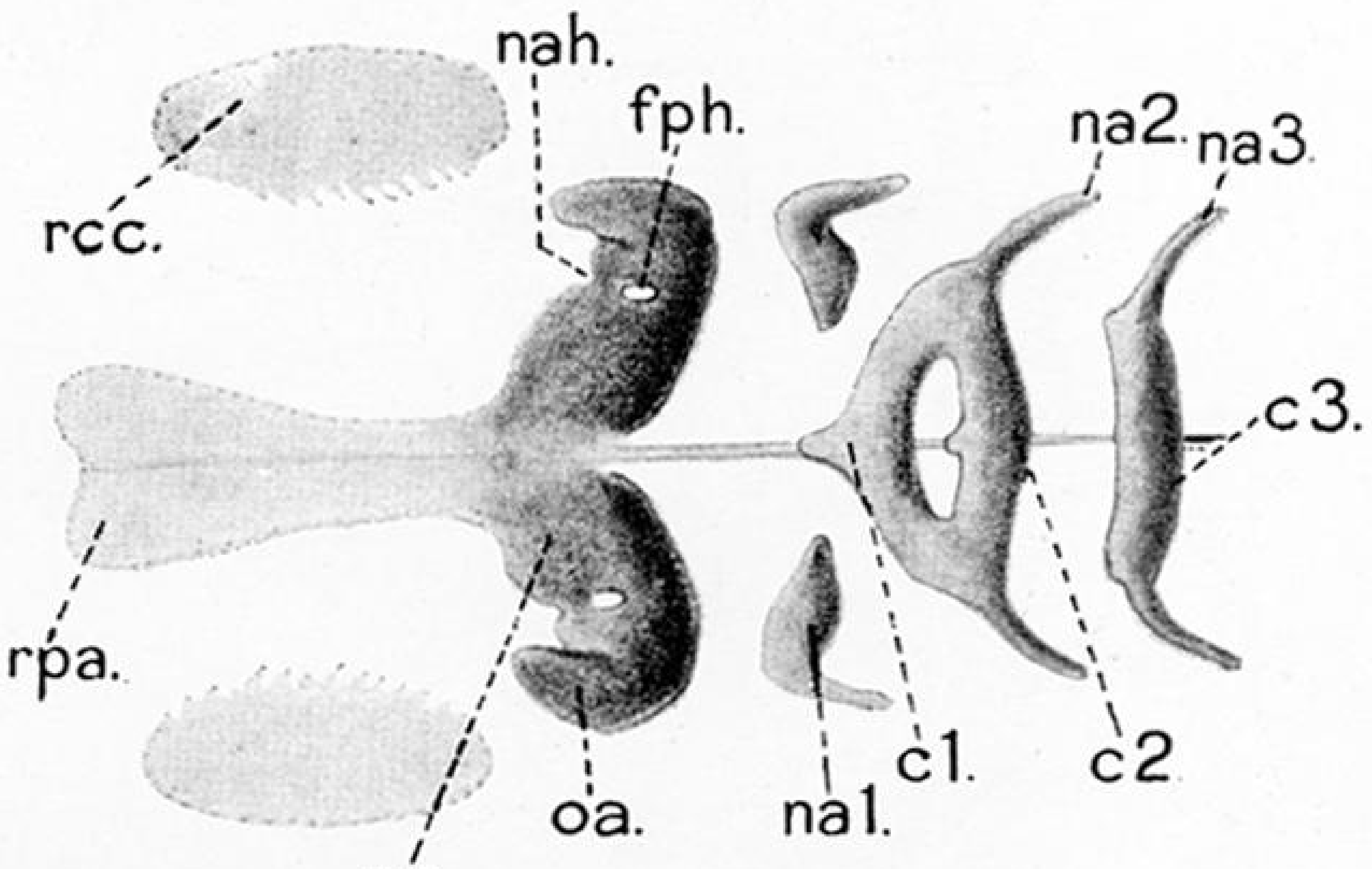

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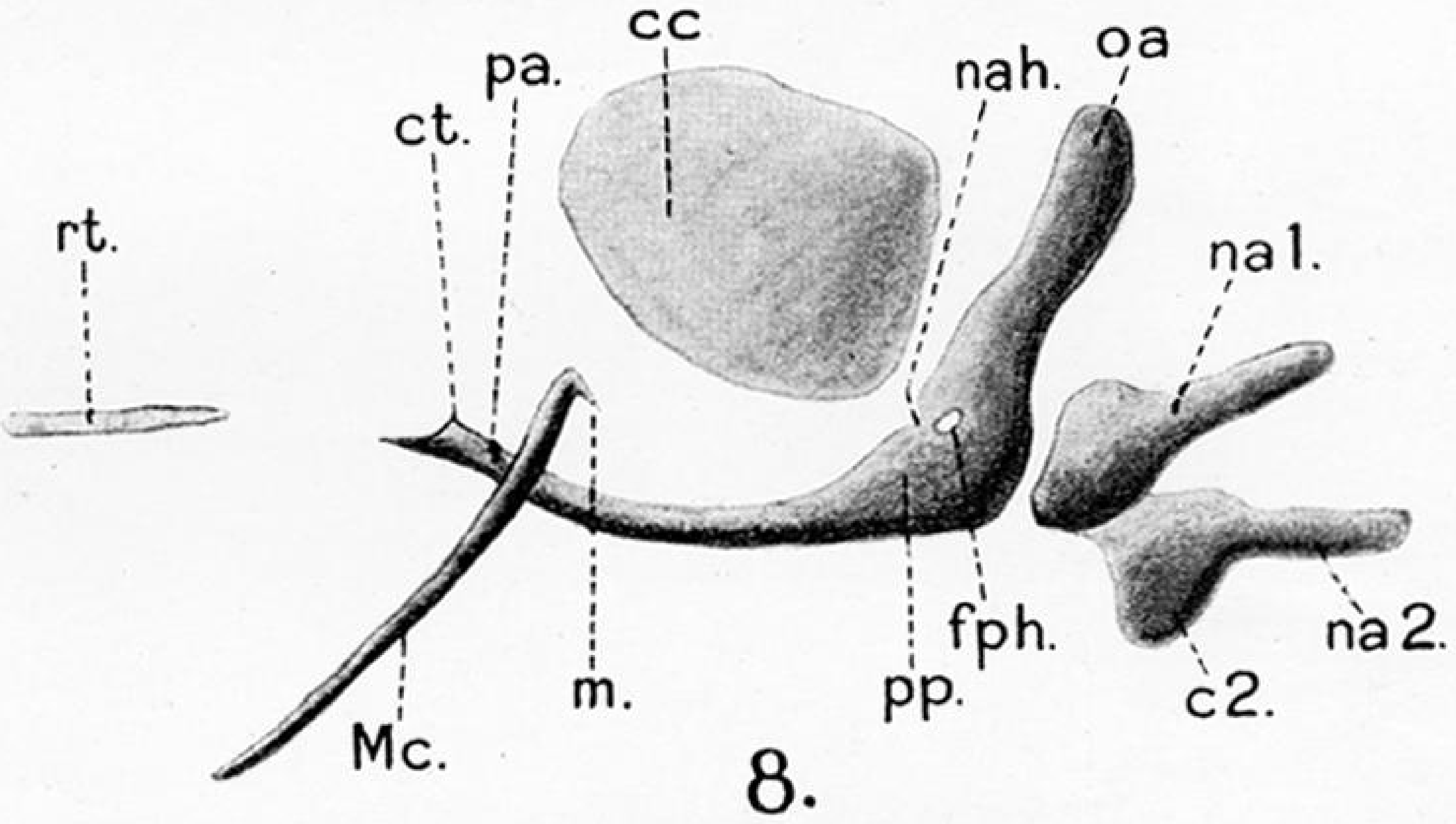

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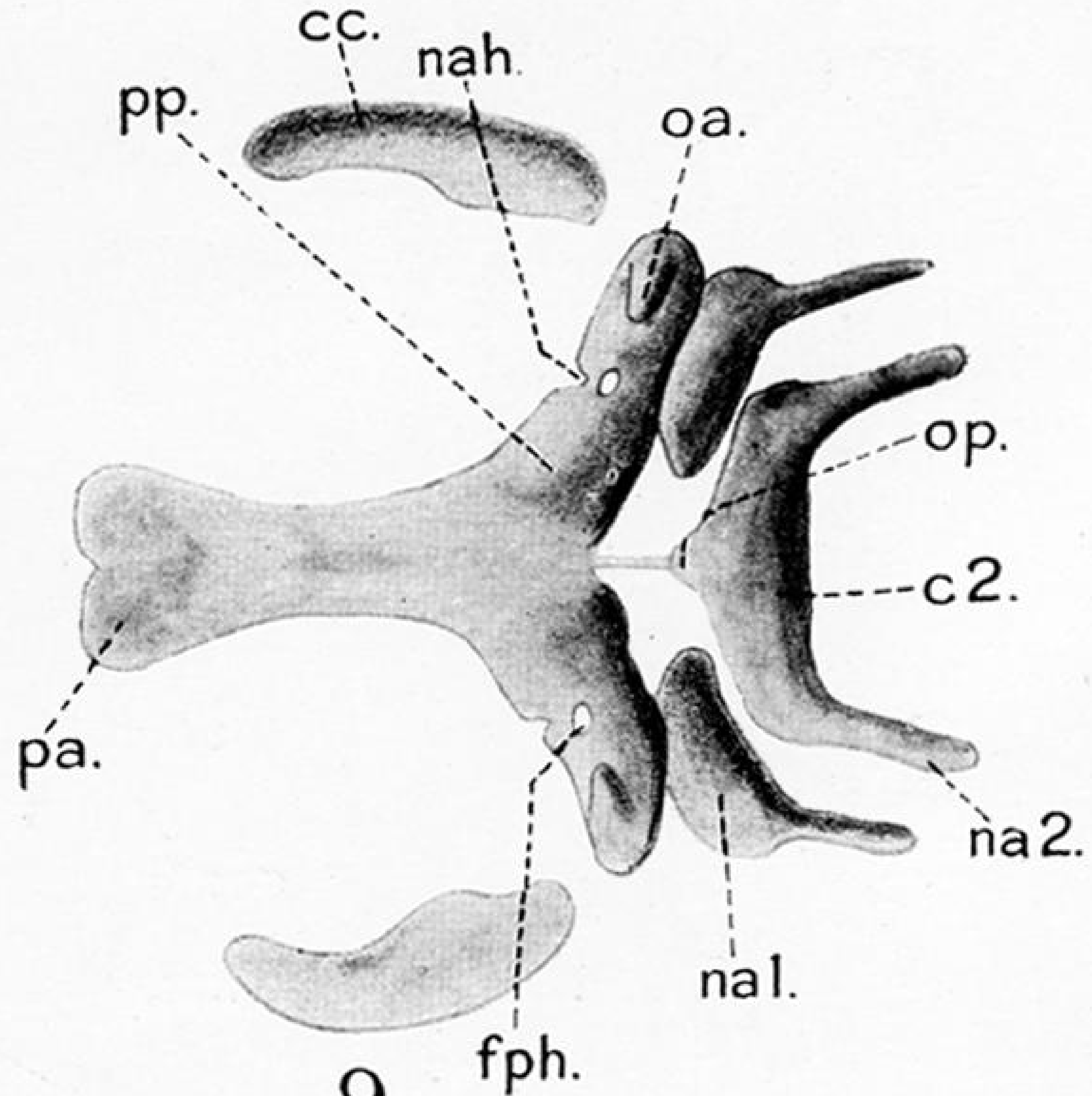


9.

PLATE 35.

FIG. 1. Dorsal view of the skull and anterior cervical vertebræ at stage 1. × 17.

FIG. 2. View from the left side of the skull and anterior cervical vertebræ at stage 2. × 17.

FIG. 3. Dorsal view of the skull and anterior cervical vertebræ at stage 2. × 17.

FIG. 4. View from the left side of the skull and anterior cervical vertebræ at stage 3. × 17.

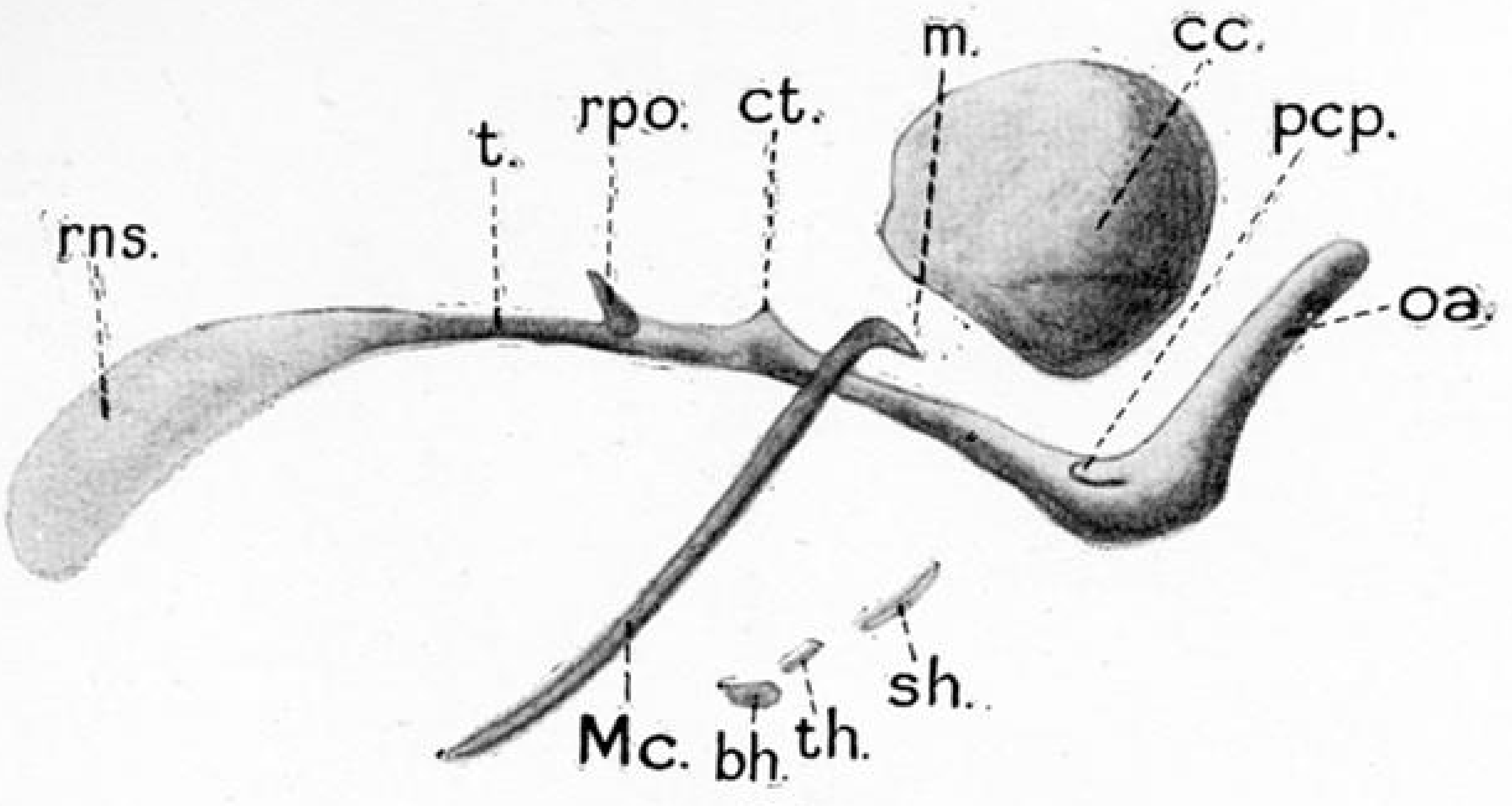
FIG. 5. Dorsal view of the skull and anterior cervical vertebræ at stage 3. × 17.

FIG. 6. View from the left side of the skull and anterior cervical vertebræ at stage 4. × 17.

FIG. 7. Dorsal view of the skull and anterior cervical vertebræ at stage 4. × 17.

FIG. 8. View from the left side of the skull and anterior cervical vertebræ at stage 5. × 17.

FIG. 9. Dorsal view of the skull and anterior cervical vertebræ at stage 5. × 17.



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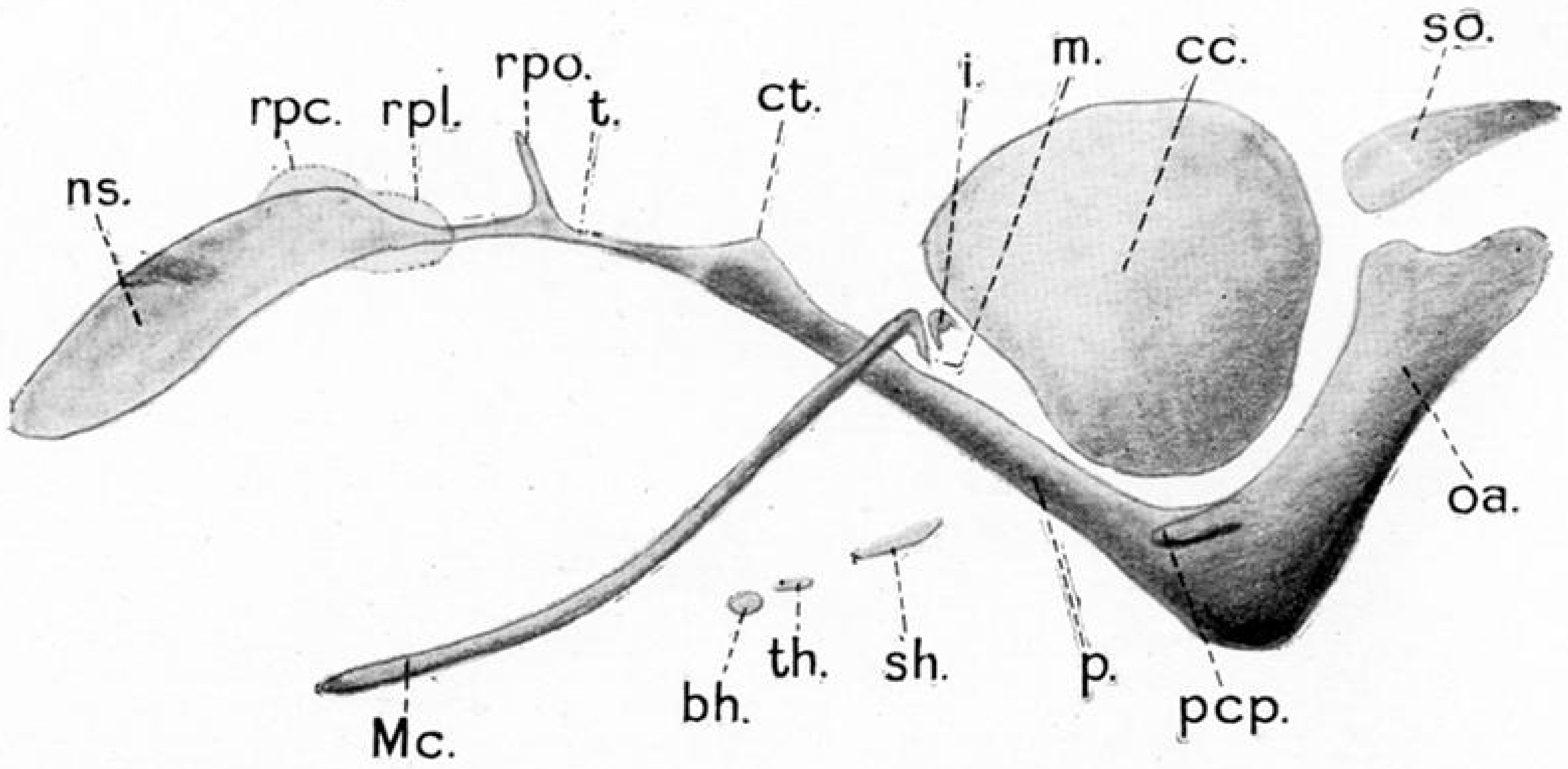

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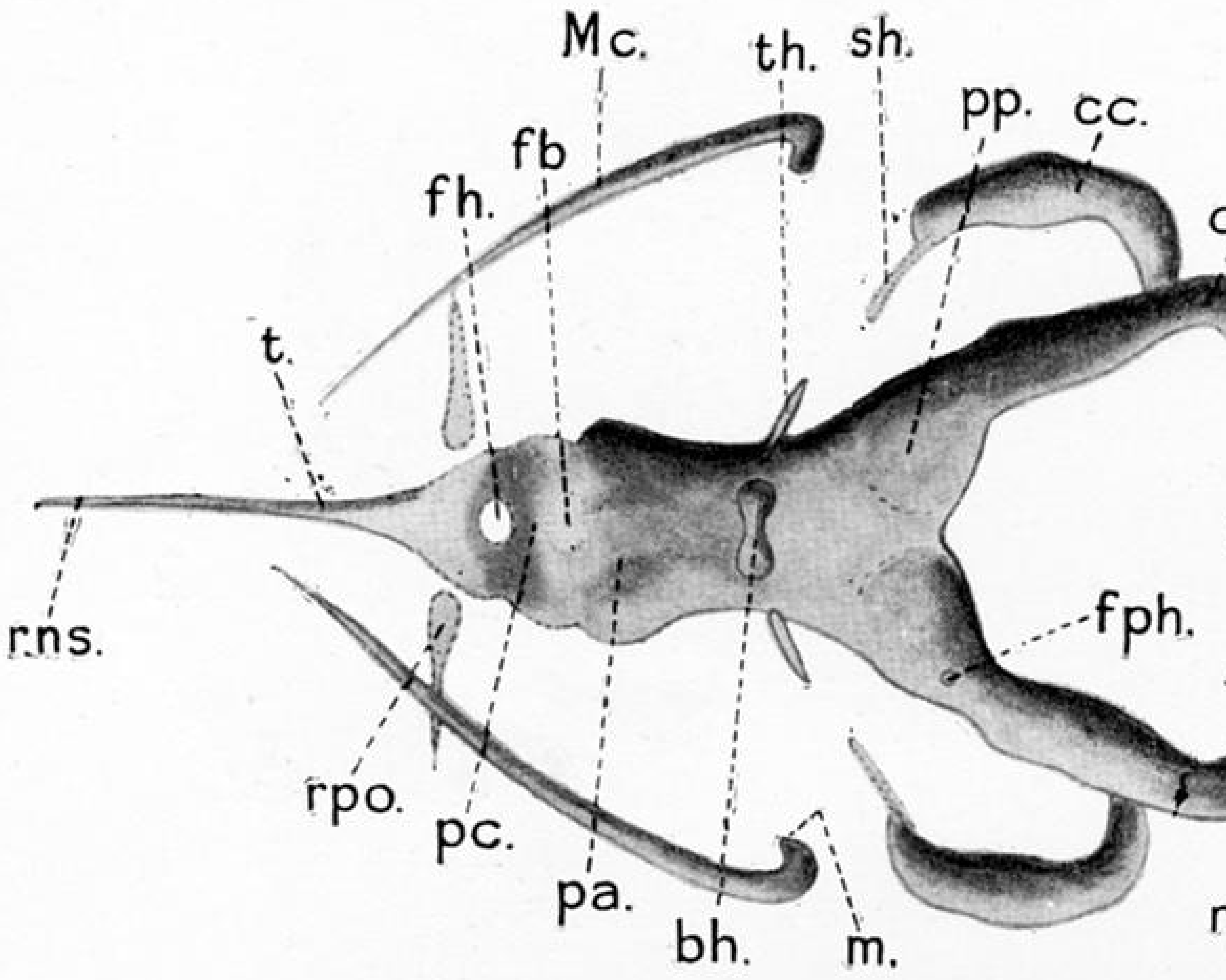

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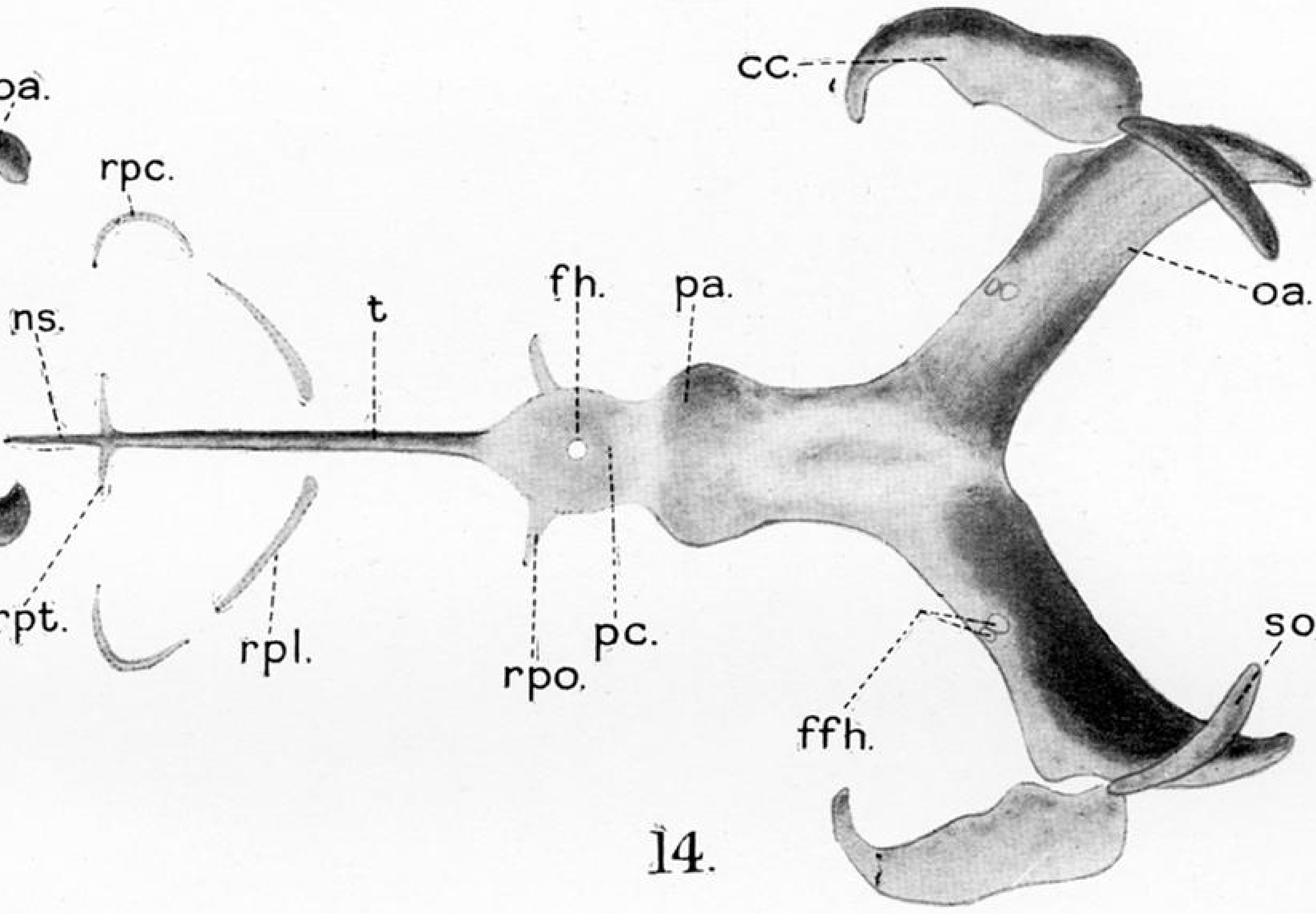

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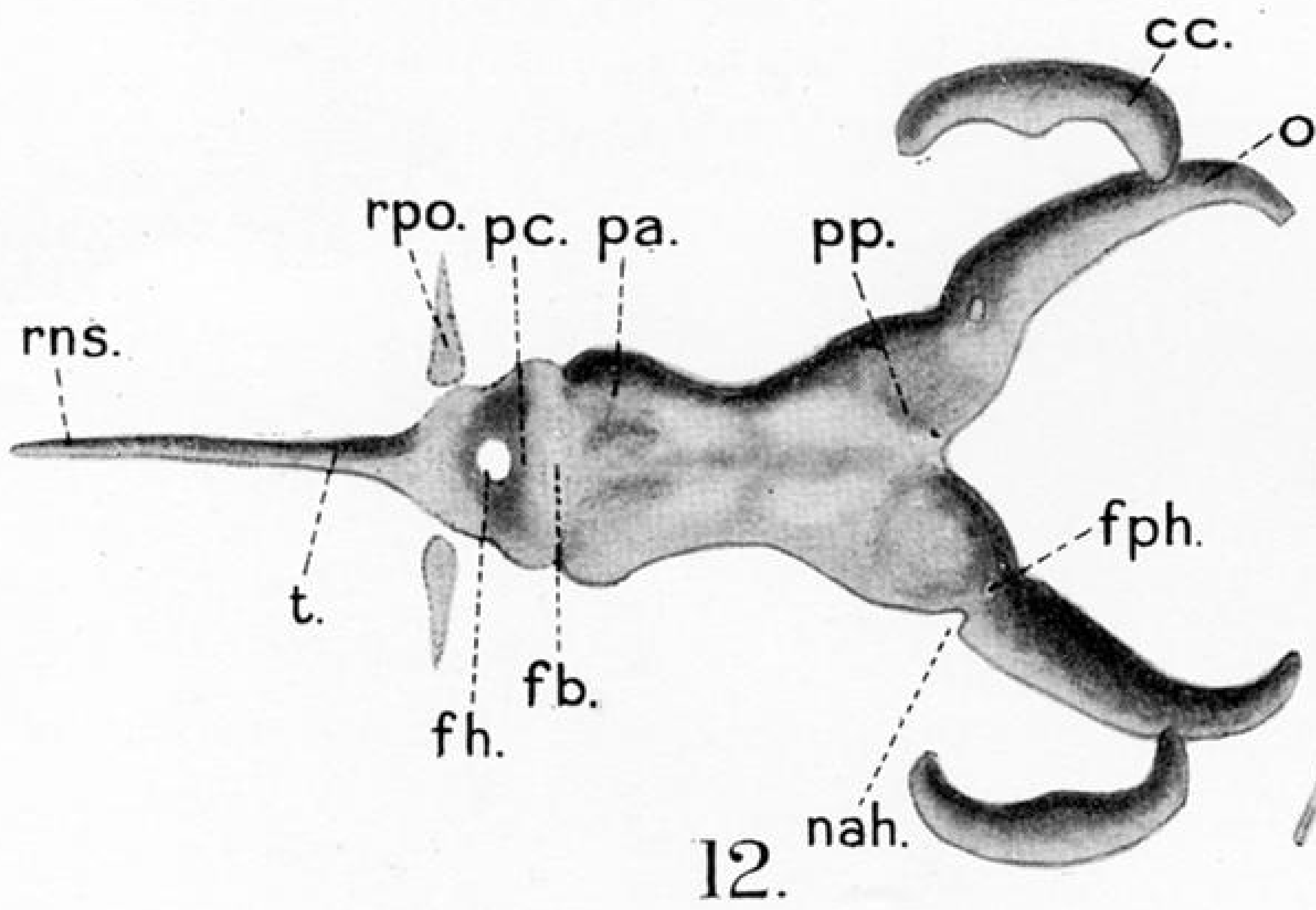

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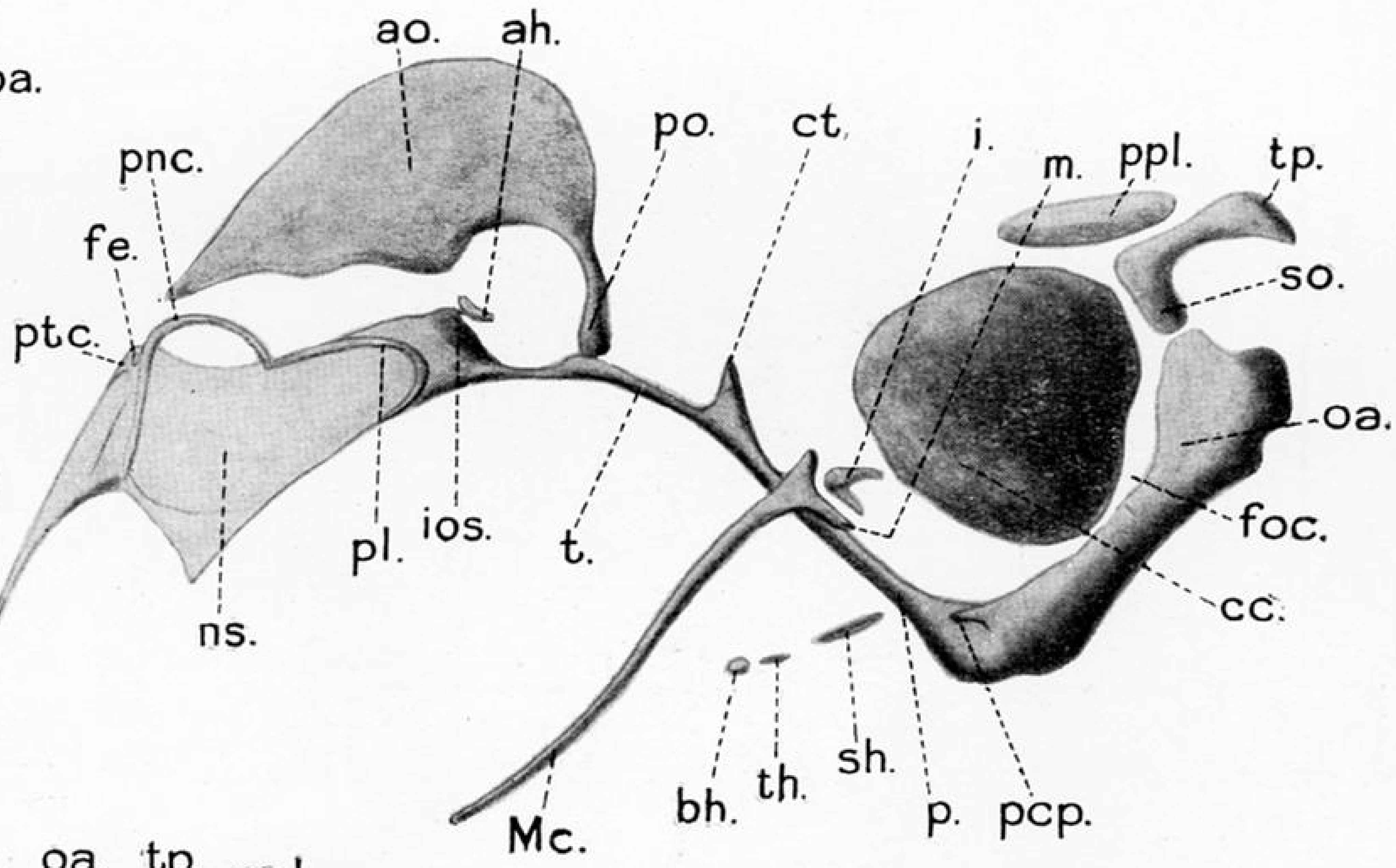

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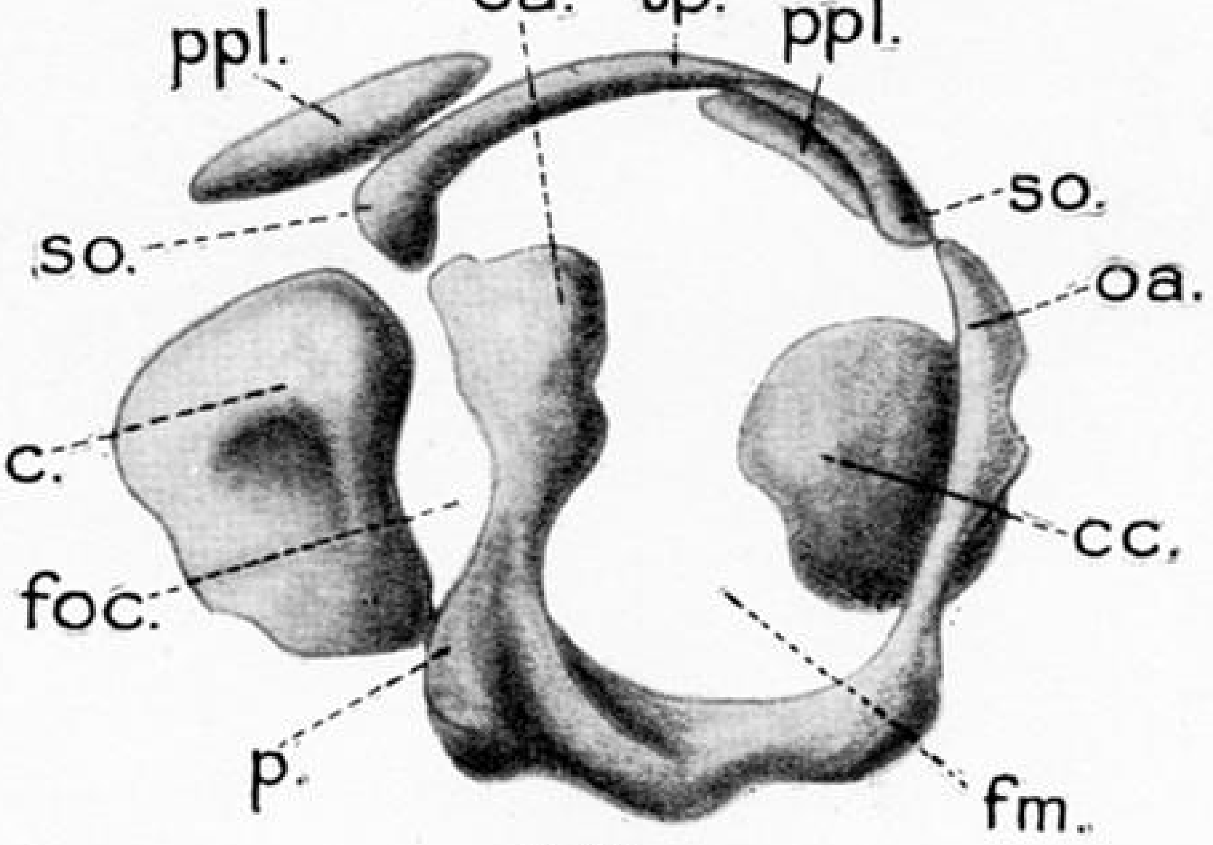


16.

PLATE 36.

FIG. 10. View from the left side of the skull at stage 6. × 15.

FIG. 11. Ventral view of the skull at stage 6. × 15.

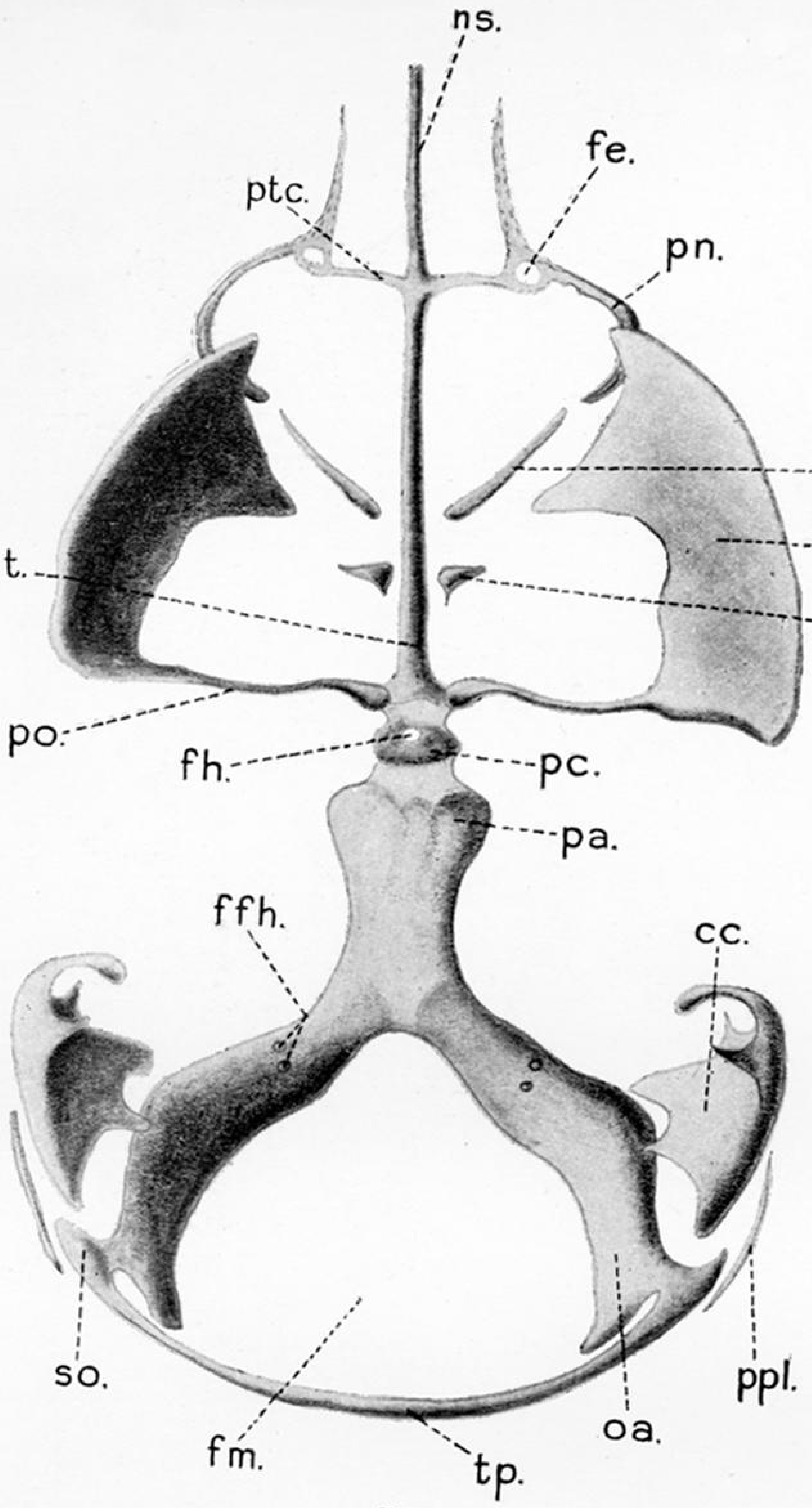
FIG. 12. Dorsal view of the skull at stage 6. × 15.

FIG. 13. View from the left side of the skull at stage 7. × 15.

FIG. 14. Dorsal view of the skull at stage 7. × 15.

FIG. 15. View from the left side of the skull at stage 8. × 15.

FIG. 16. Oblique view from the left side and behind of the posterior portion of the skull at stage 8. × 15.



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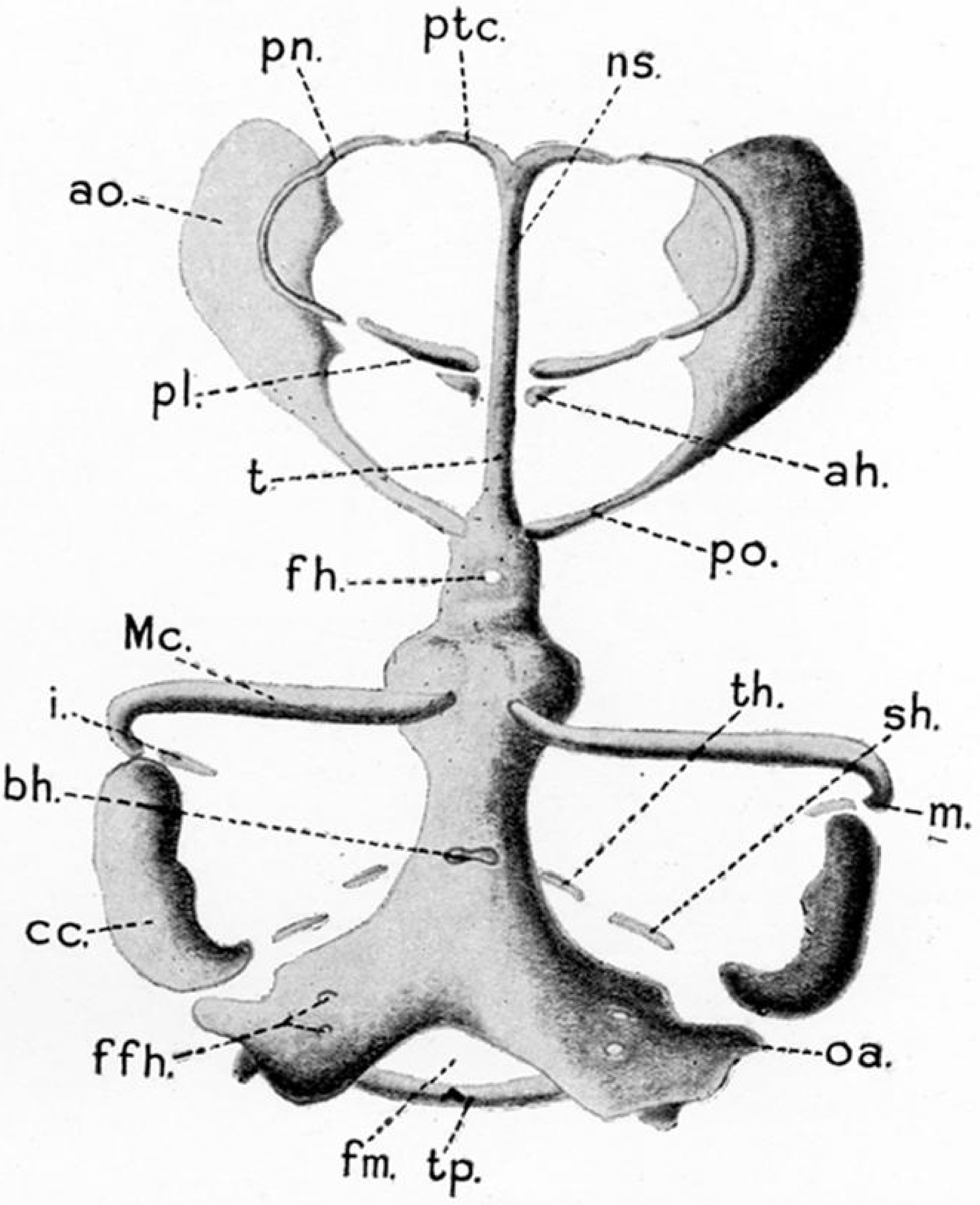

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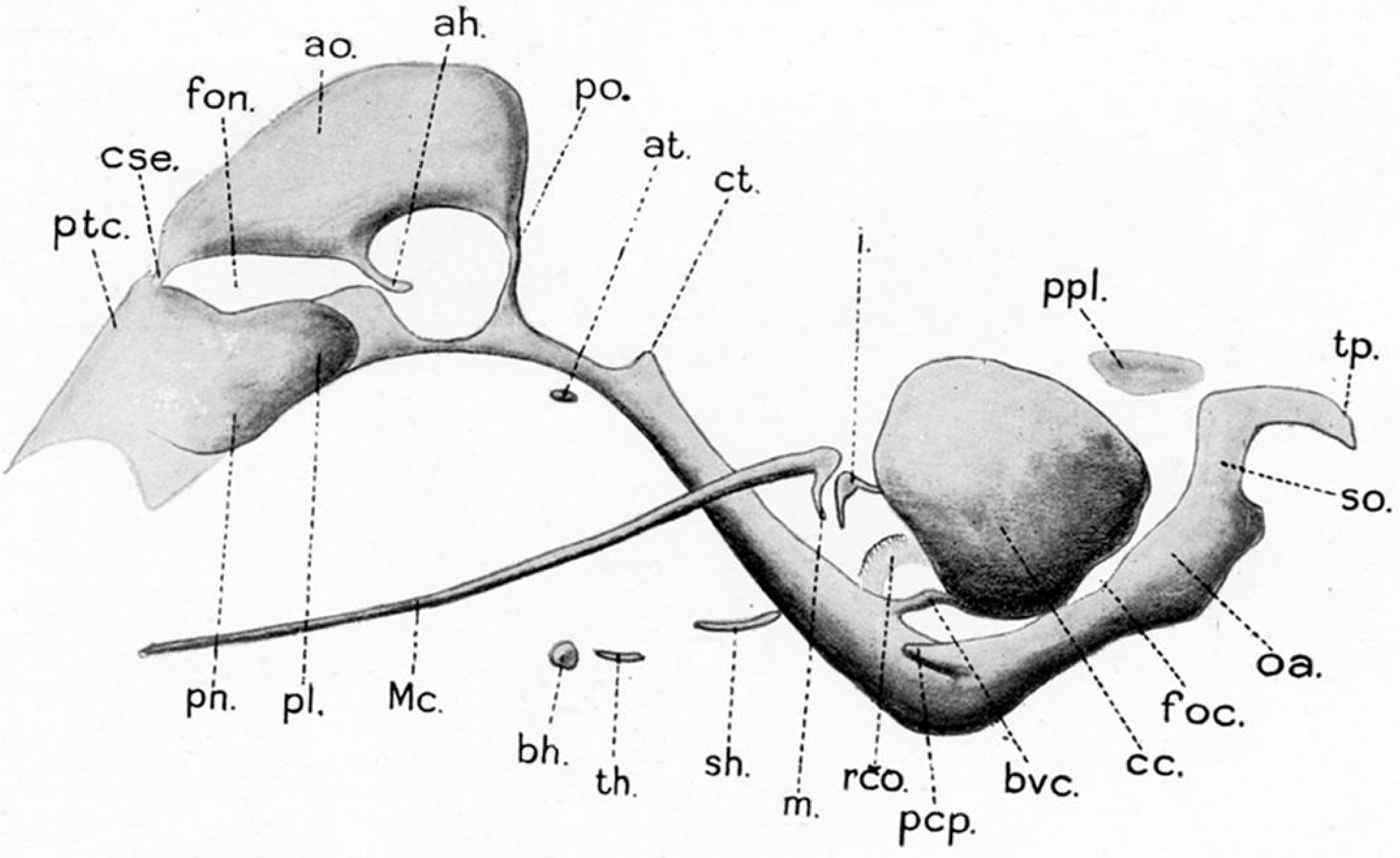


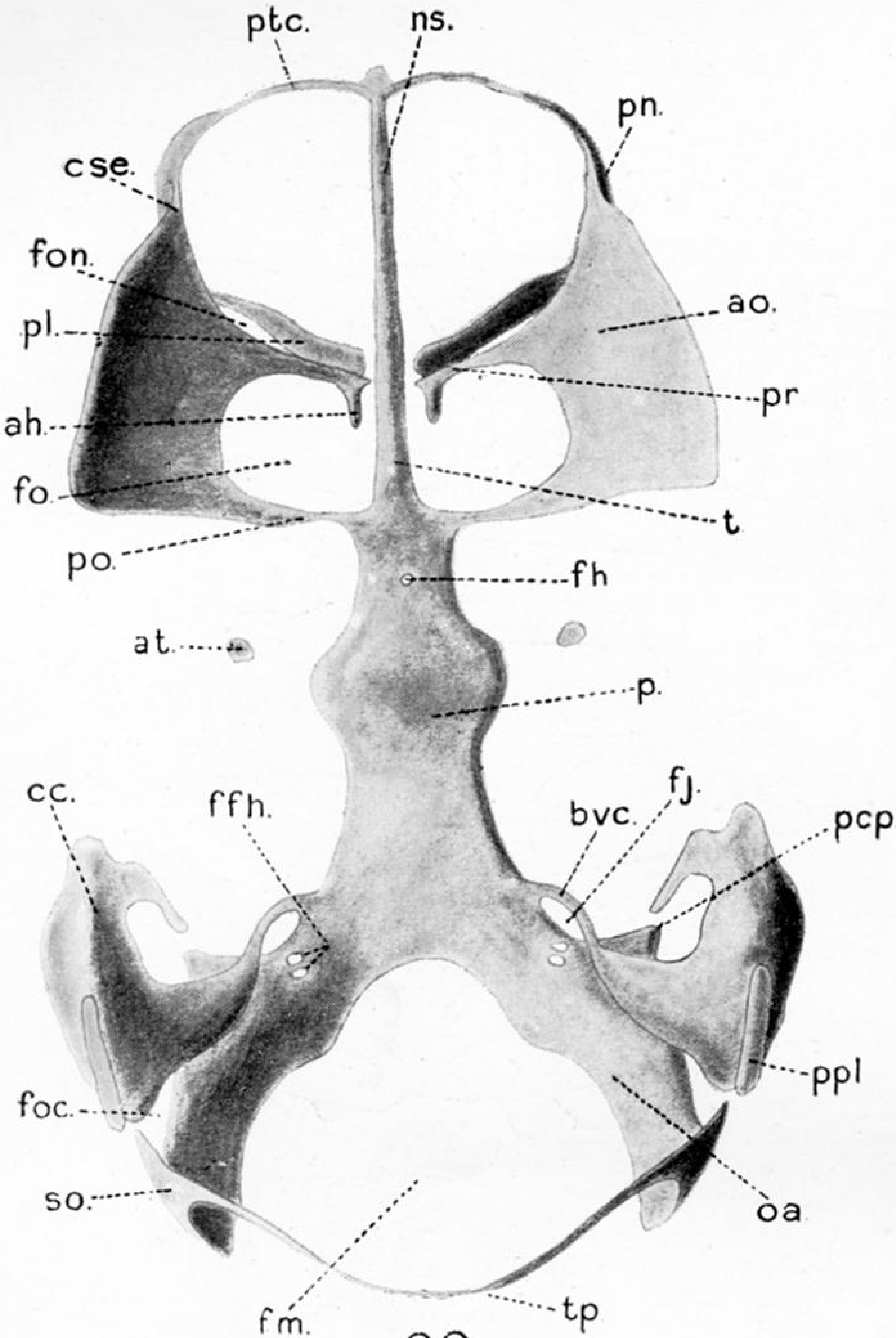
19.

PLATE 37.

FIG. 17. Dorsal view of the skull at stage 8. × 18.

FIG. 18. Ventral view of the skull at stage 8. × 18.

FIG. 19. View from the left side of the skull at stage 9. × 18.



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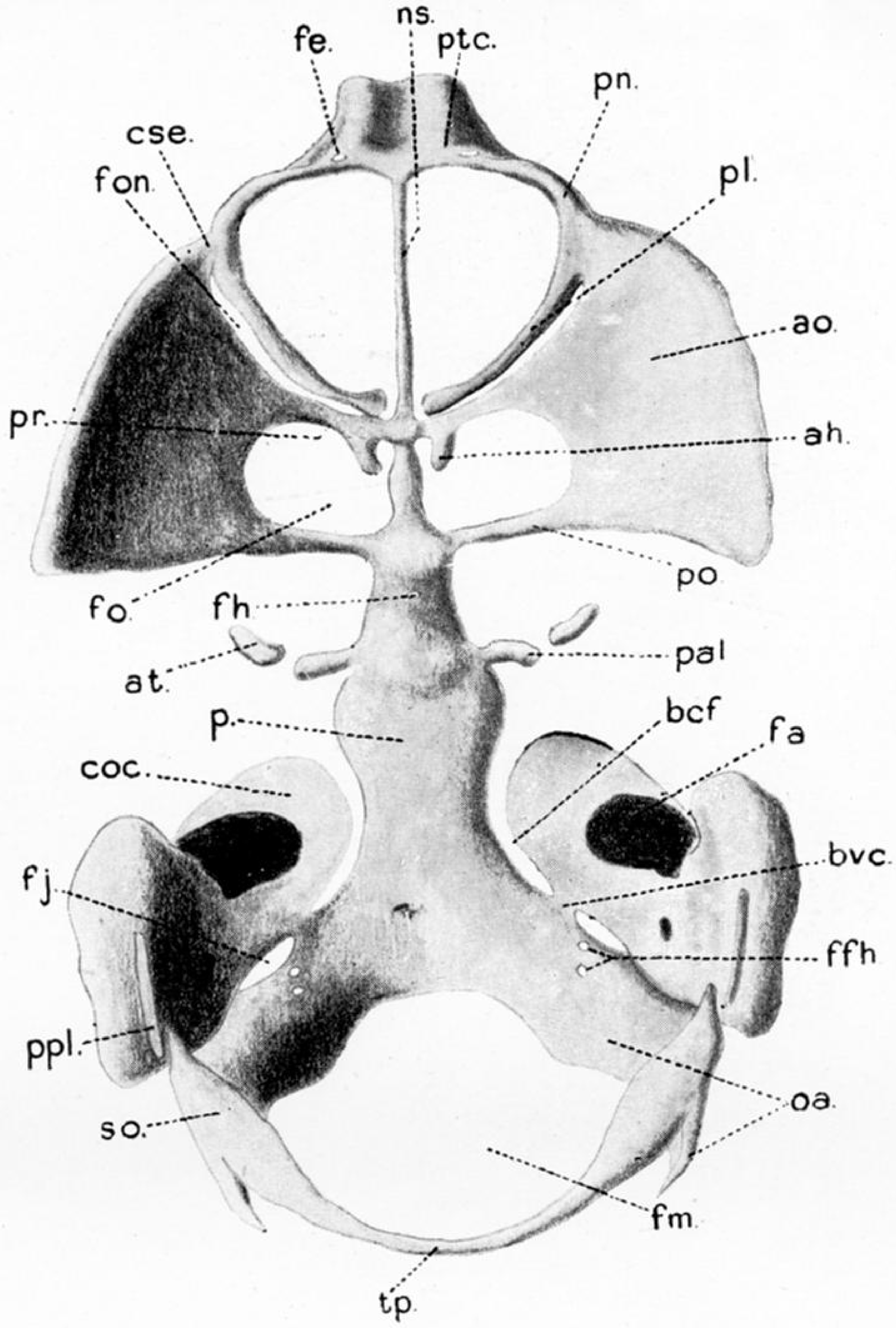

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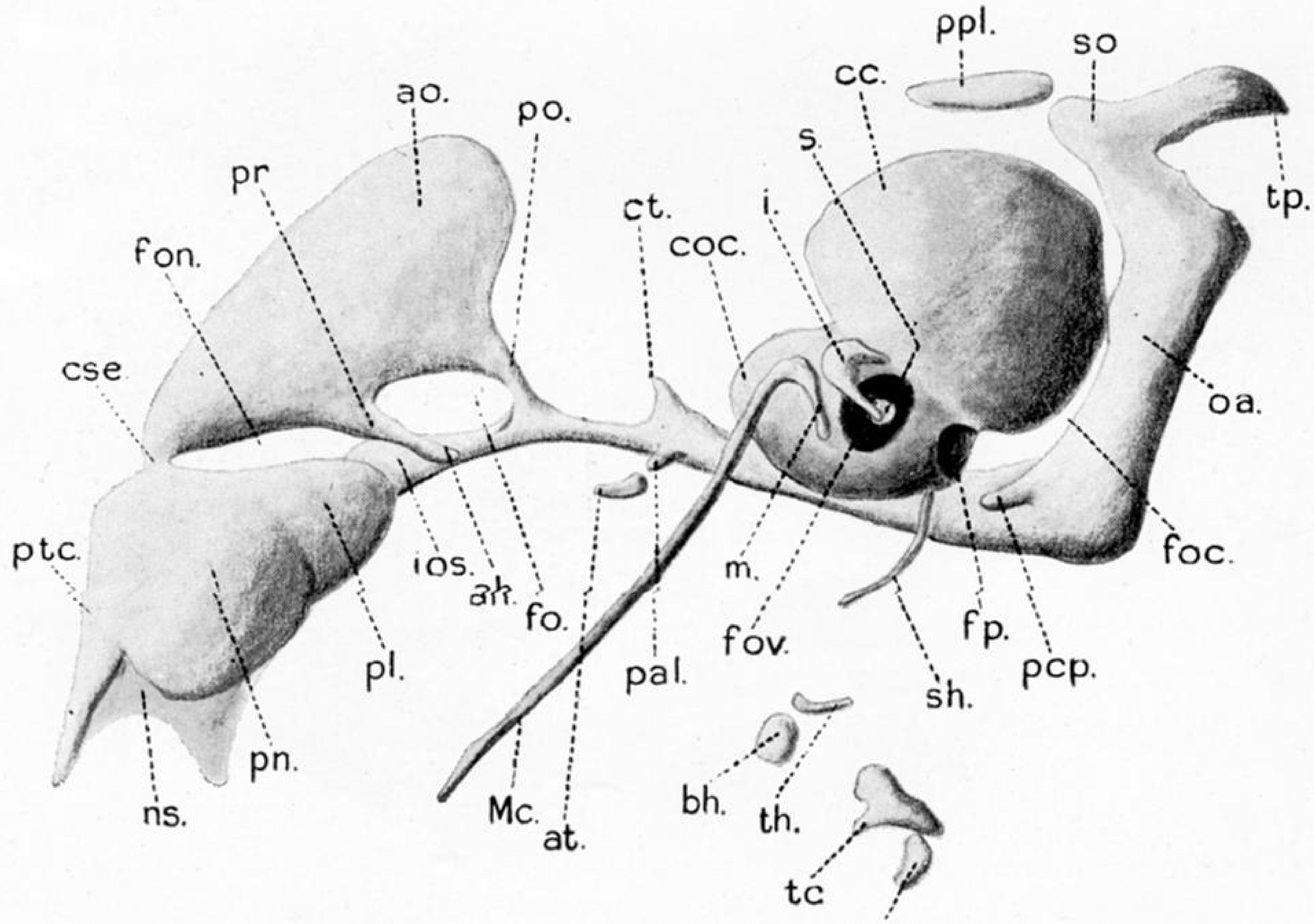

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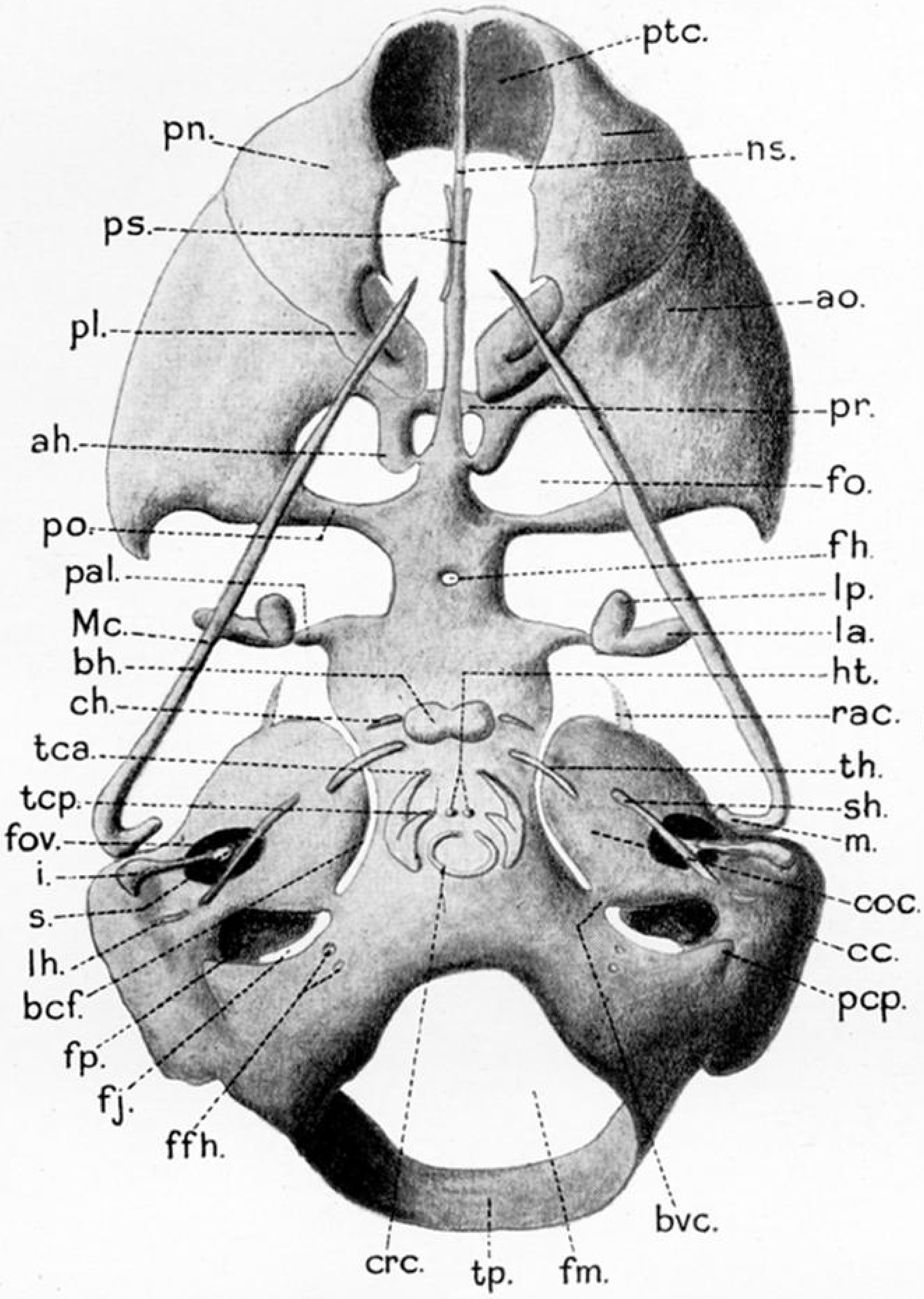
PLATE 38.

FIG. 20. Dorsal view of the skull at stage 9. × 16.

FIG. 21. View from the left side of the skull at stage 10. × 16.

FIG. 22. Dorsal view of the skull at stage 10. × 16.



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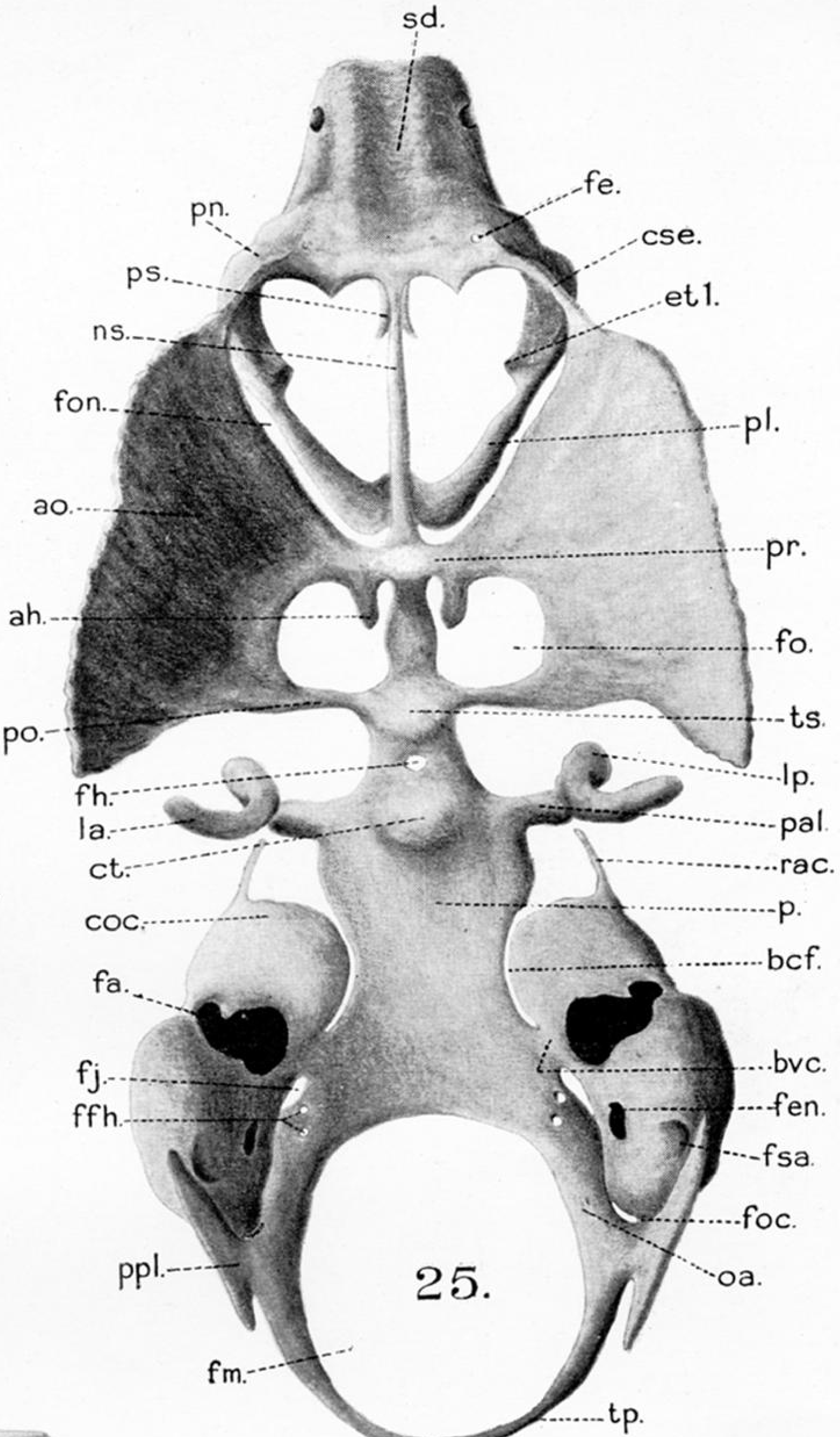
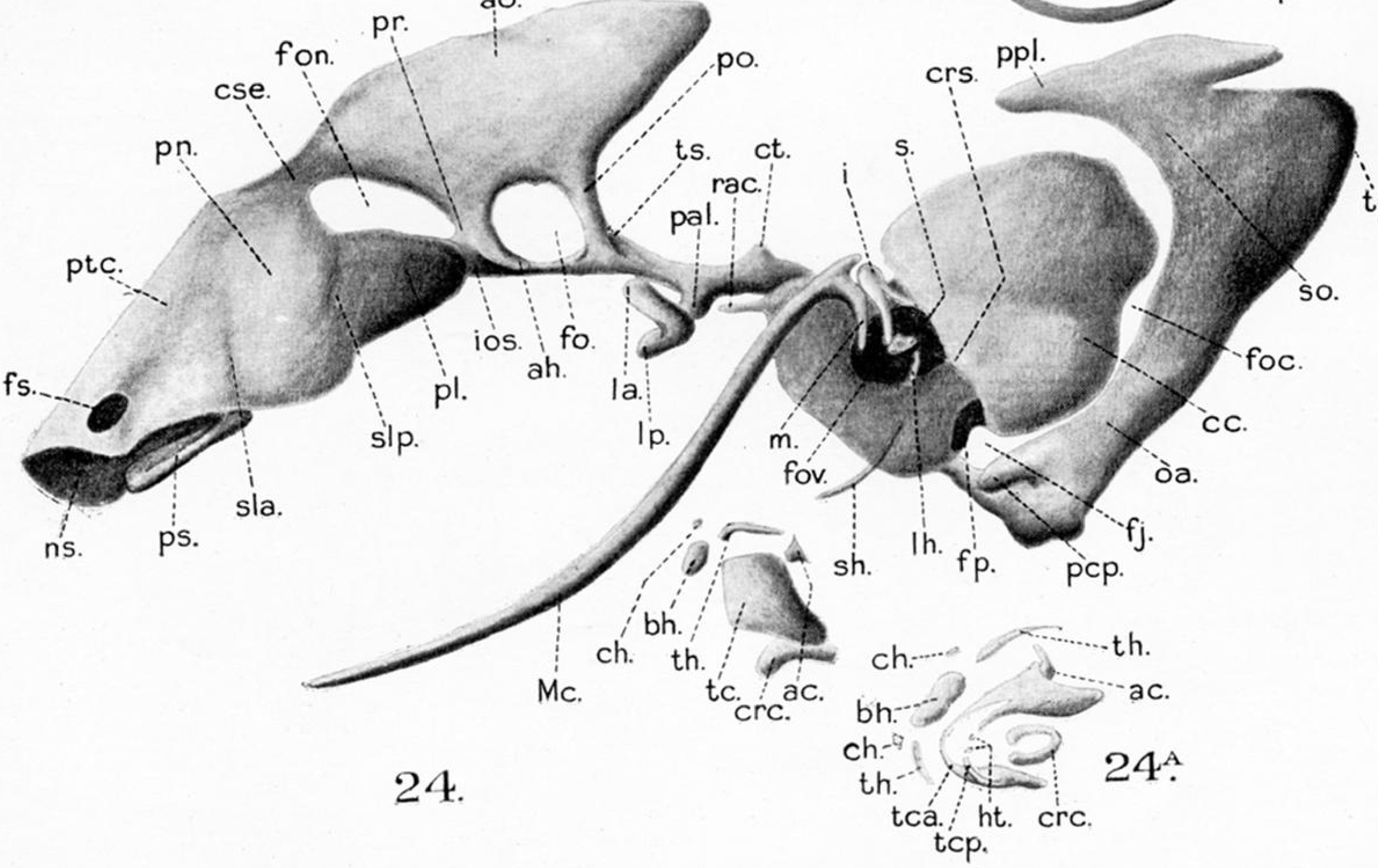




24.

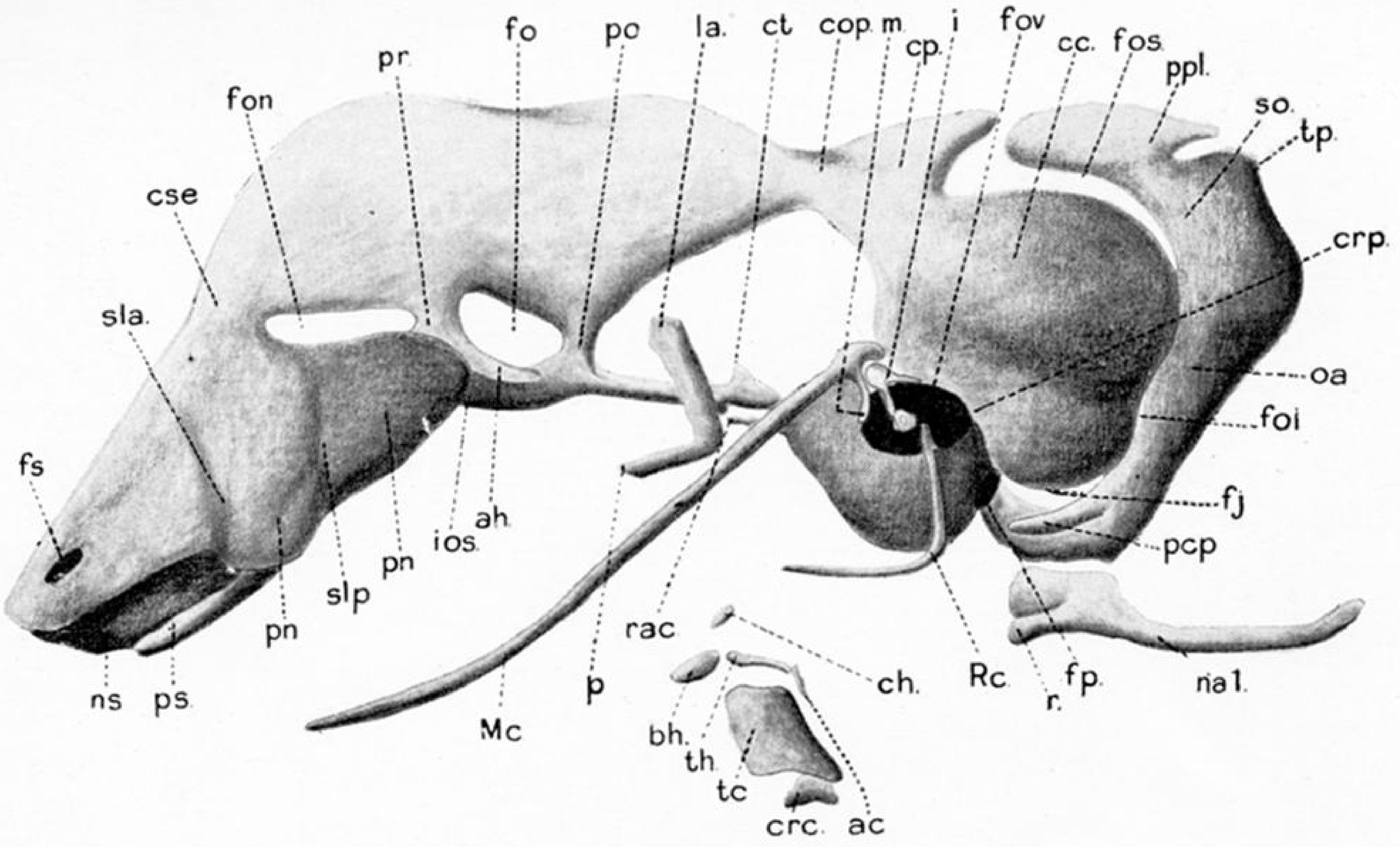
PLATE 39.

FIG. 23. Ventral view of the skull at stage 11. × 15.

FIG. 24. View from the left side of the skull at stage 12. × 15.

FIG. 24A. Oblique view from the left and ventral sides of the splanchnocranium at stage 12. × 15.

FIG. 25. Dorsal view of the skull at stage 12. × 15.



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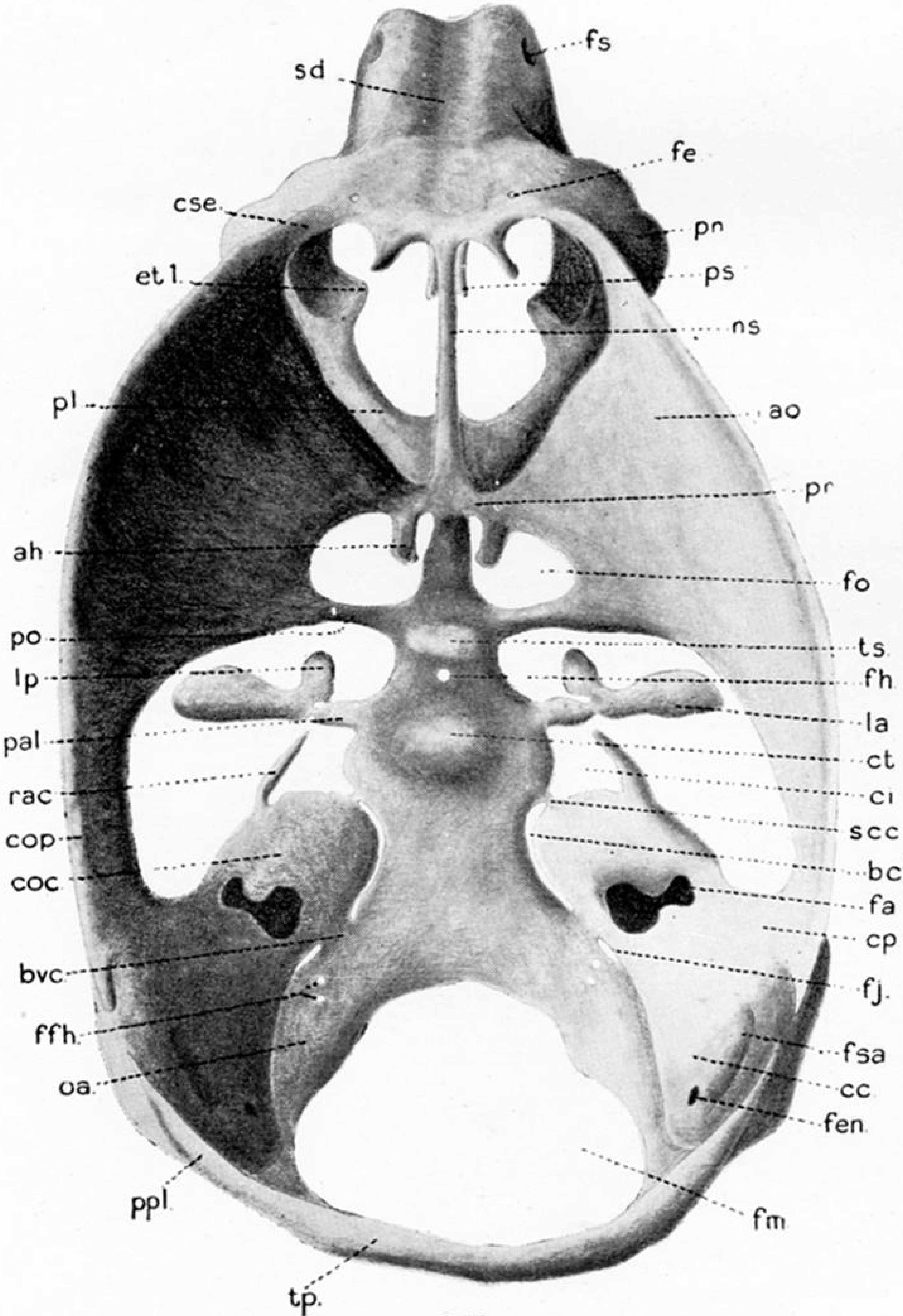

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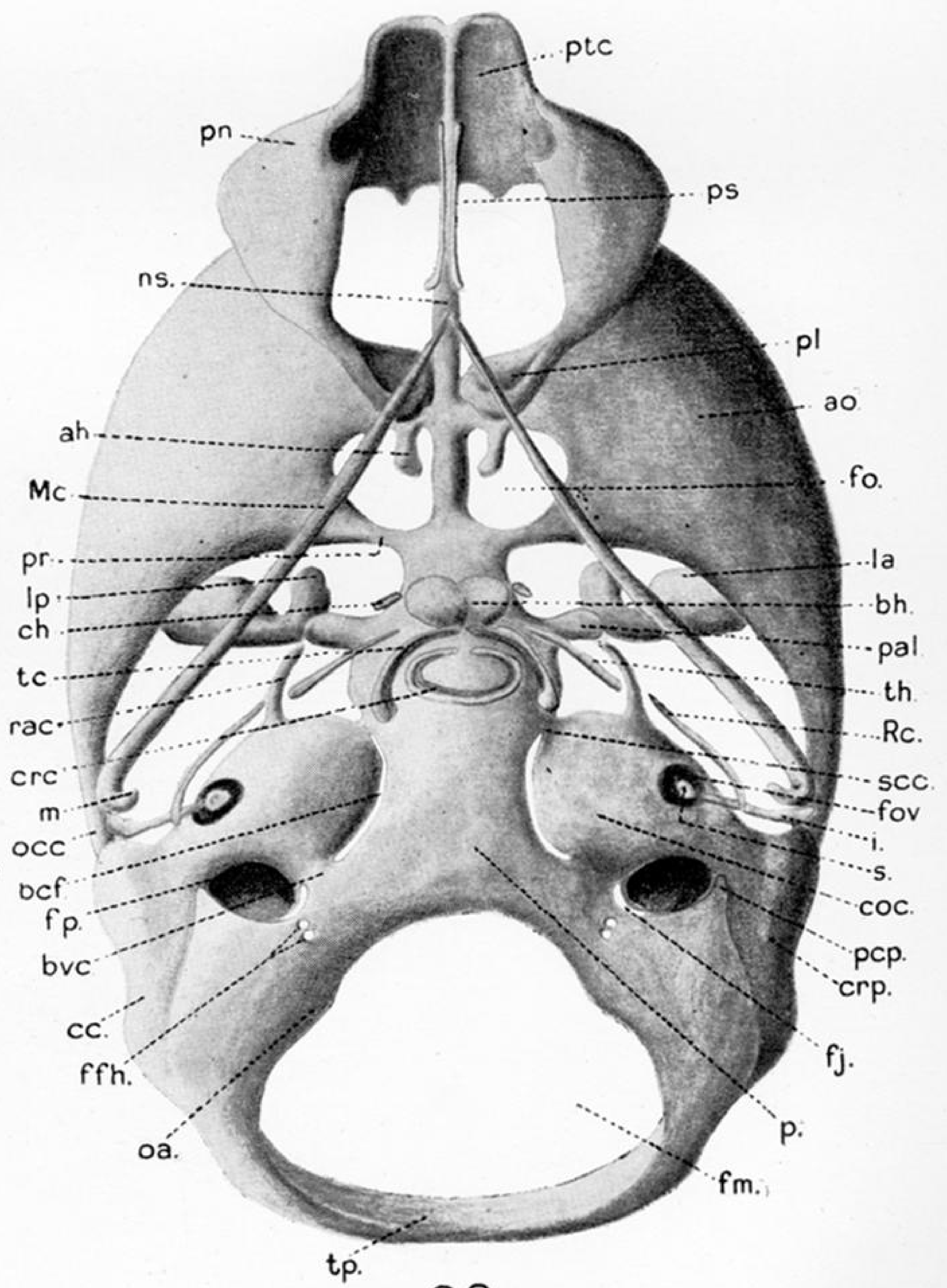


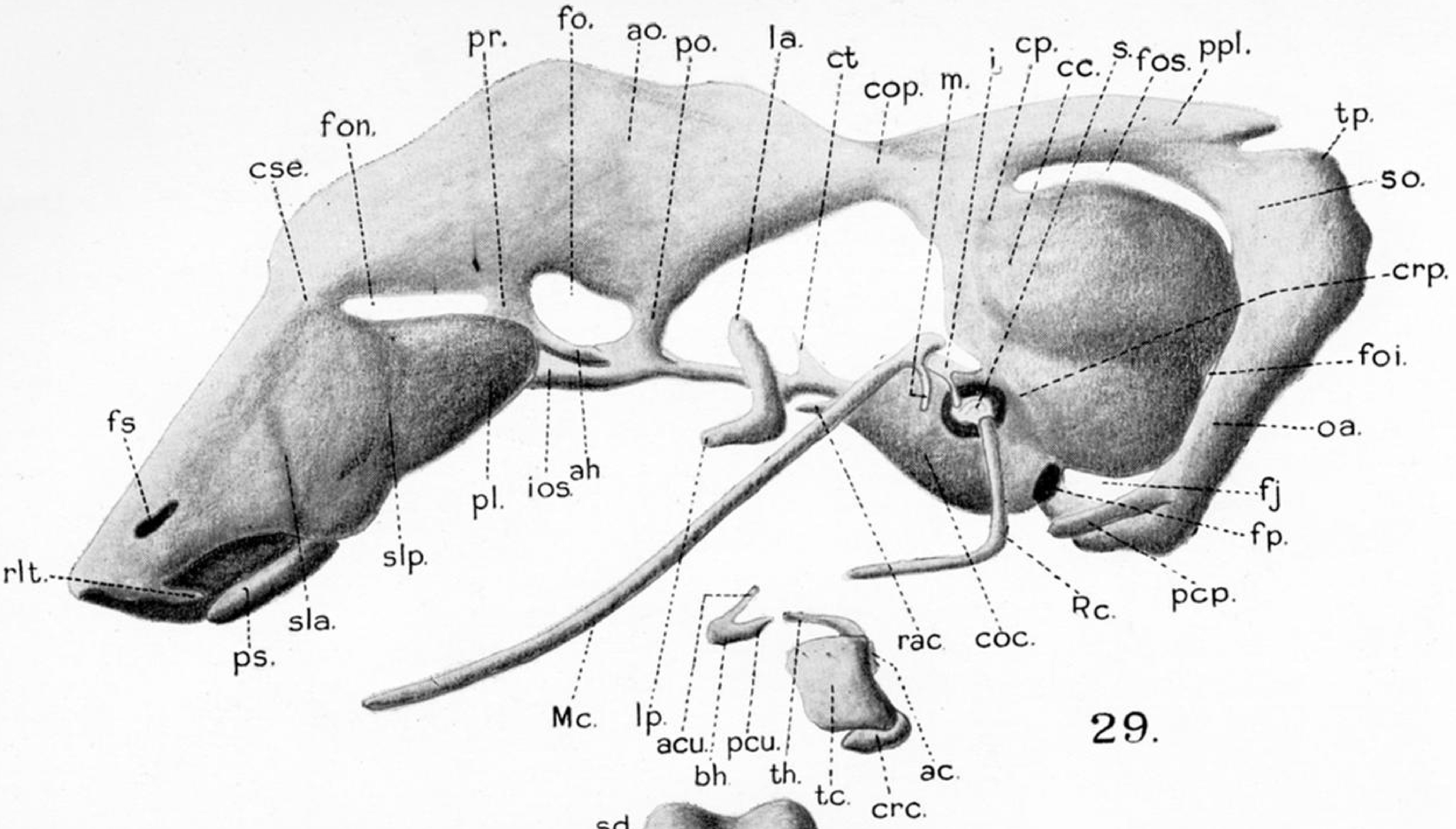
28.

PLATE 40.

FIG. 26. View from the left side of the skull at stage 13. × 12.

FIG. 27. Dorsal view of the skull at stage 13. × 12.

FIG. 28. Ventral view of the skull at stage 13. × 12.



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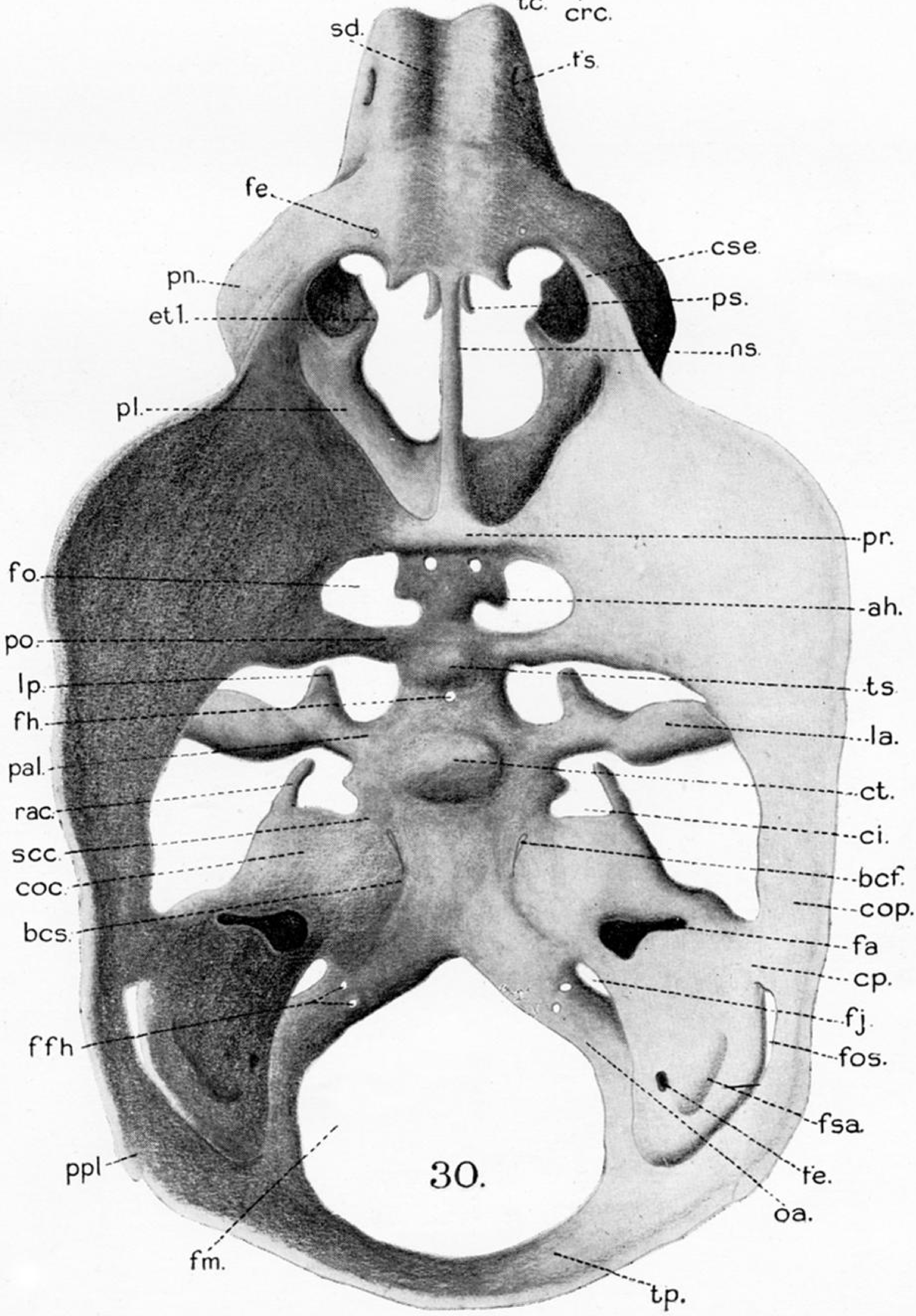
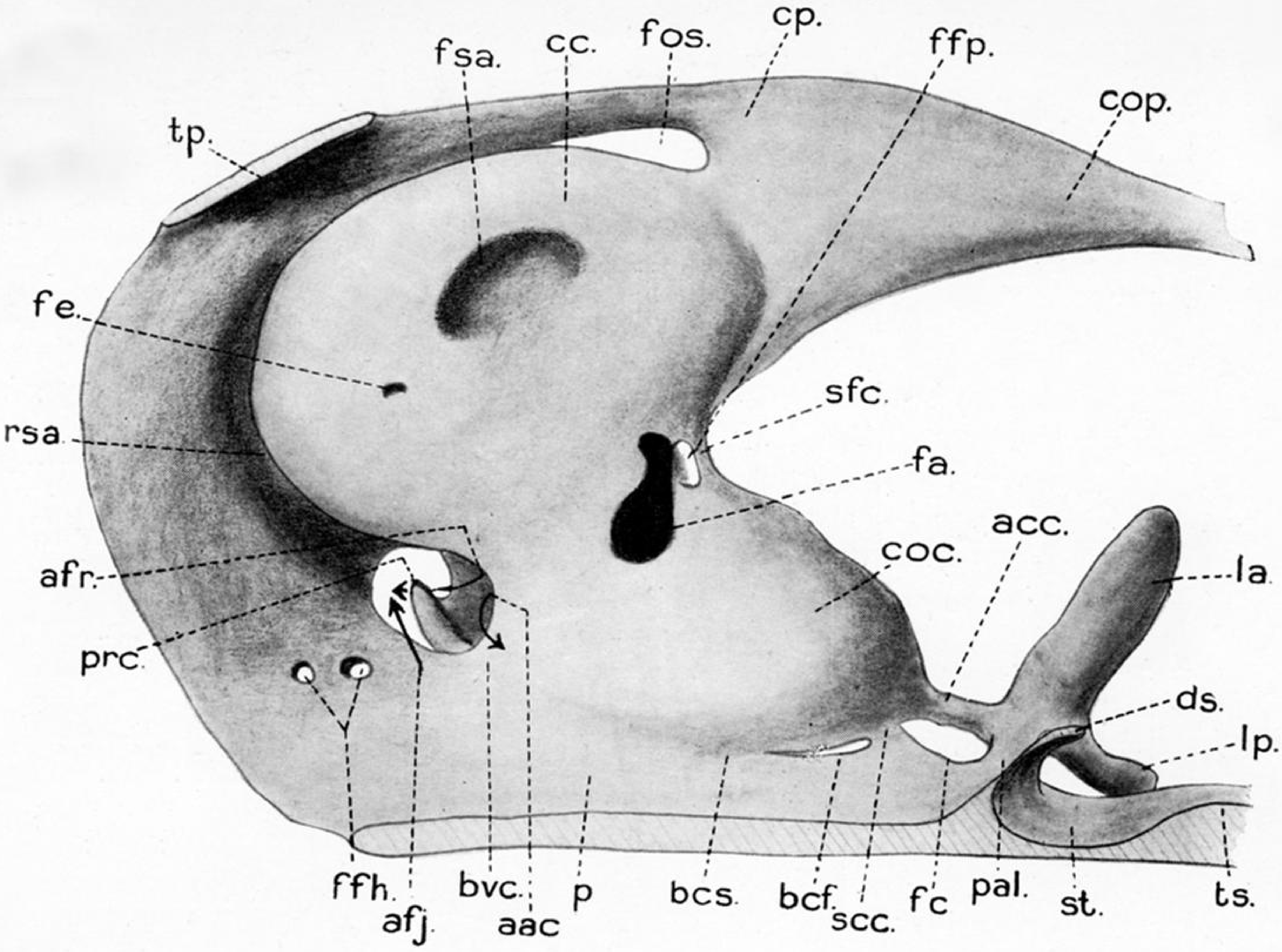


30.

PLATE 41.

FIG. 29. View from the left side of the model reconstructed from the skull at stage 14. × 14.

FIG. 30. Dorsal view of the model reconstructed from the skull at stage 14. × 17.



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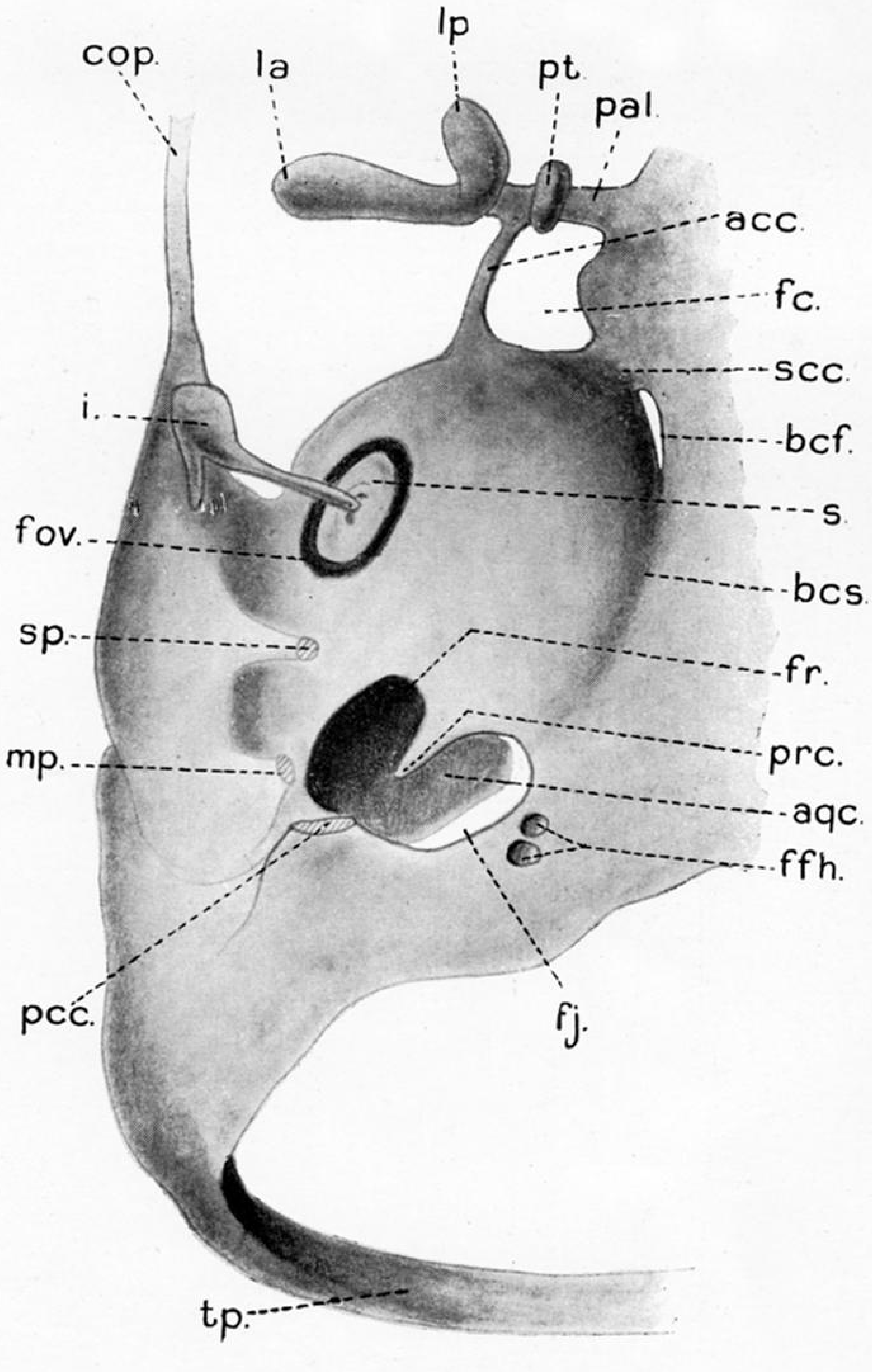

32.

PLATE 42.

FIG. 31. Ventral view of the foramen perilymphaticum and associated structures at stage 15. × 17.

FIG. 32. Median view of the auditory capsule and associated structures at stage 15. × 17.